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The importance to fish species of the various habitats in nearshore marine waters of south-western Australia

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2000/159 The importance to fish species of the various habitats in nearshore marine waters of south-western Australia.

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OBJECTIVES

1. Develop a quantitative scheme that can be used to readily identify the different habitat types found in nearshore marine waters along the lower west coast of Australia.
2. Determine the compositions of the fish faunas in representative examples of the different habitat types, and thereby determine which habitat types are used most extensively by main commercial and recreational fish species.
3. Establish the suite of environmental characteristics that can be readily used to determine the habitat type of any site in this nearshore region and thus predict the fish species that are likely to be found at that site.
4. Determine the compositions of the benthic macroinvertebrate faunas at the same sites at which fish are sampled to ascertain whether the extent of the relationship between a less mobile assemblage of fauna and the characteristics of the different habitat types differs from that with the highly-mobile fish fauna.
5. Determine, for a subset of the different habitat types present along the lower west coast of Australia, the compositions of the diets of selected fish species and the assemblages of their potential invertebrate prey in the benthos and water column, *i.e.* benthic macroinvertebrates, zooplankton, meiofauna, and hyperbenthic invertebrates. Such data will be used to examine predator/prey inter-relationships between these faunal assemblages.
6. Collate the key components of this study in a form that will enable fisheries and environmental managers to ensure that those areas along the lower west coast of Australia that provide crucial habitats for important fish species are protected from deleterious anthropogenic activities.
7. Note that some of the specific objectives have been amended from those in the original application (see Chapter 1 for rationale).

OUTCOMES ACHIEVED TO DATE

1. The outcomes of this project are that environmental and fisheries managers and/or scientists working in nearshore waters on the lower west coast of Australia are now able to undertake the following.
2. Use readily accessible data for enduring environmental variables to identify the habitat type of any site along that coastline.
3. To be able to readily predict the compositions of the fish and invertebrate faunas that are likely to be associated with any site along that coastline.
4. To develop more appropriate plans for ensuring that habitats, which contain the most diverse faunas and/or are important for key commercial or recreational fish species, are conserved.
5. To develop scientific hypotheses regarding spatial differences in the distribution of nearshore fauna and their biotic inter-relationships, *e.g.* predator-prey relationships.

Non-technical summary

This study has developed an approach that will enable fisheries and environmental managers to predict which fish species, and particularly those of recreational and commercial importance, are likely to be found at any site along the lower west coast of Australia. The first step thus involved developing a method whereby the main types of habitat in these waters could be readily and reliably identified. This method used rigorous multivariate statistical techniques to select the suite of quantitative and enduring environmental criteria that were most important for distinguishing among habitat types. Once this had been achieved, we were then able to sample regularly the fish faunas, and also their main invertebrate prey, at sites that had been selected to represent each of those habitat types. This then enabled us to determine the ways in which the densities, diversity and species composition of those faunas are related to habitat type. The predictive approach we have developed is crucial for enabling fisheries and environmental managers to develop appropriate plans for protecting those types of habitat that are most important for key fish species and/or for maintaining biodiversity.

Six main habitat types were identified on the lower west coast of Australia on the basis of differences in the values for seven enduring environmental characteristics, namely direct fetch, north-westerly fetch, the minimum distance from the shoreline to the 2 m depth contour, the distance from the shoreline to the first offshore reef chain along a south-westerly transect, and the area of nearshore substrate covered by bare sand, subtidal reef and seagrass. Values for each of these characteristics were obtained from sources such as bathymetric charts and thus did not require measurements to be made in the field. Data for these characteristics were used to develop a quantitative method for enabling any site along this coastline to be assigned to its appropriate habitat type.

Fish at two representatives of each of the six habitat types (1-6) were sampled seasonally for two years using two different seine nets. The 21.5 m seine nets was used during both the day and night, while the 60.5 m net was used only during the day and, due to the presence of reefs and/or high wave activity, at neither habitat types 5 or 6. The density, number of species, taxonomic diversity and species composition of samples collected at the various habitat types using both net types differed significantly overall, and these differences were maintained throughout the year and during the day and night. Furthermore, the extent of the differences in the compositions of the ichthyofaunas among the various habitat types matched statistically those among the suite of seven enduring environmental criteria that were used to distinguish those habitat types. This thus enabled us to use the values for those enduring environmental characteristics to predict with confidence the fish species that are likely to occupy those habitat types.

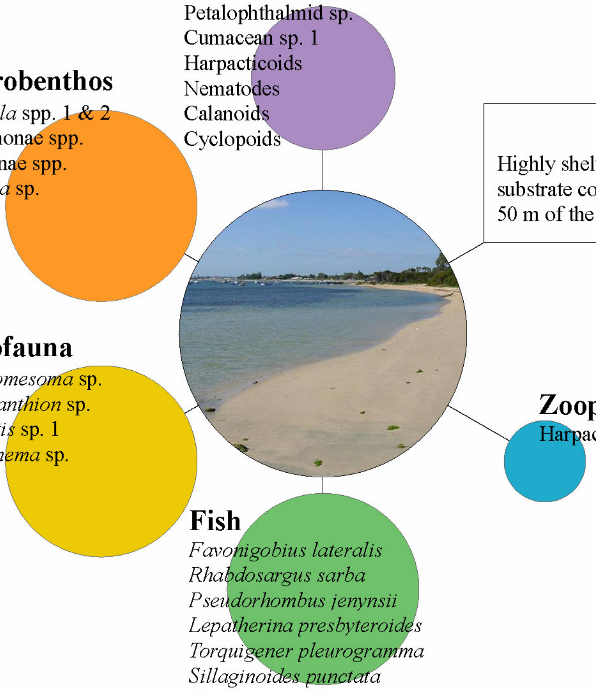
Some species characterised the ichthyofauna of only one habitat type. For example, *Sillaginodes punctata* and *Pseudorhombus jenynsii* in the highly sheltered habitat type 1, *Arripis georgiana* and *Enoplosus armatus* in the moderately sheltered habitat type 2, *Pelsartia humeralis* and *Schuettea woodwardi* in the moderately exposed habitat type 4. Although several other species characterised more than one habitat type, they still exhibited a marked affinity for a particular habitat type. For example, while *Spratelloides robustus* characterised the faunas at habitat types 2-5, it occurred most consistently and was most abundant by far at habitat type 2, and *Sillago bassensis*, which characterised the faunas at habitat types 2-6, was far more prevalent at habitat type 4 than any of those other habitat types.

The samples collected with the small net showed that the characteristics of the nearshore fish fauna in several of the habitat types differed significantly among seasons and between day and night. The seasonal differences were largely attributable to differences in the time when the new 0+ recruits of species such as *Sillago bassensis, Sillago vittata* and *Aldrichetta forsteri* first appeared in nearshore waters. Diel differences were due mainly to the nocturnal offshore emigrations of the juveniles of several small pelagic species and the concurrent onshore migration of several larger piscivorous fish species. In contrast, the compositions of the fish faunas did not differ significantly between years, reflecting the fact that the same suites of species recurred consistently in each year in the various habitat types.

As with the fish fauna, the characteristics of the assemblages of benthic macroinvertebrates, zooplankton, epibenthic invertebrates and meiofauna (and particularly of the Nematoda) differed significantly among the various habitat types, and that these differences were usually greater than those detected between day and night, seasons and years. This emphasises that the habitat types identified in this study can be used to predict the ways in which a wide range of biota are spatially distributed in nearshore waters.

Comparisons of the dietary composition of eight abundant fish species demonstrated that they utilised a wide range of invertebrate prey, with S. *robustus* and *Atherinomorus ogilbyi* feeding to a large extent on zooplankton, while three sillaginid species (*S. bassensis, Sillago schomburgkii* and *S. vittata*) fed on benthic macroinvertebrate, hyperbenthic and zooplankton communities. The small pleuronectid *Ammotretis elongatus* fed on small hyperbenthic crustaceans, while the closely-related bothid *Pseudorhombus jenynsii* fed largely on crabs, mysids and teleosts. *Lesueurina platycephala*, which reached only a small size, also fed to a large extent on fish. The diets of each fish species could be related to their location in the water column, head and mouth morphology. The extent of size-related changes varied amongst the species, but typically reflected a tendency for small crustacean prey to be consumed by small representatives, and for larger prey, such as teleosts, bivalves and/or polychaetes, to be consumed by larger fish. The diets of each species, and particularly those of the sillaginids, were shown to be opportunistic, with dietary compositions often reflecting differing densities between habitat types and seasons.

Summary of the broad environmetal characteristics at



Habitat type 1

Highly sheltered from wave activity, with the substrate containing areas of dense seagrass within 50 m of the shoreline and also further offshore.

Hyperbenthos

Exoediceroides sp. 1
Petalophthalmid sp.
Cumacean sp. 1
Harpacticoids
Nematodes
Calanoids
Cyclopoids

Macrobenthos

Capitella spp. 1 & 2
Exogononae spp.
Eusyllinae spp.
Aricidea sp.

Meiofauna

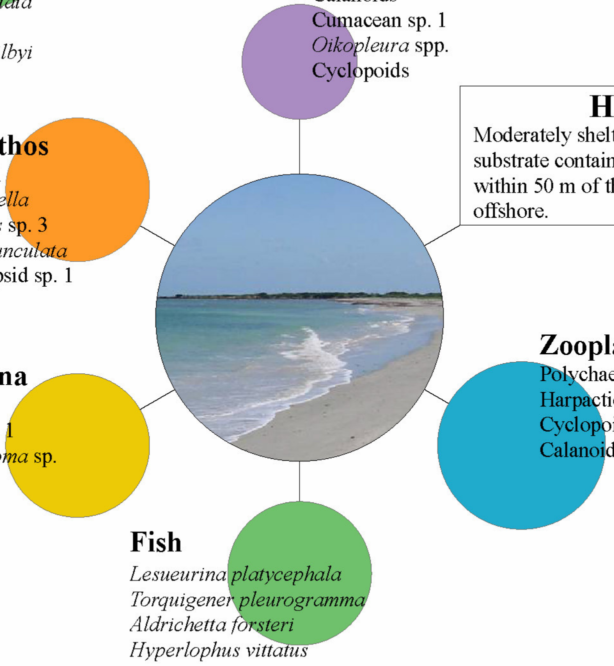
Paracomesoma sp.
Mesacanthion sp.
Theristis sp. 1
Daptonema sp.

Zooplankton

Harpacticoids.

Fish

Favonigobius lateralis
Rhabdosargus sarba
Pseudorhombus jenynsii
Lepatherina presbyteroides
Torquigener pleurogramma
Sillaginoides punctata
Apogon ruepellii
Atherinomorus ogilbyi
Sillago burrus



Habitat type 2

Moderately sheltered from wave activity, with the substrate containing patches of sparse seagrass within 50 m of the shoreline and also further offshore.

Hyperbenthos

Exoediceroides sp. 1
Petalophthalmid sp. 1
Penelia avirostris
Calanoids
Cumacean sp. 1
Oikopleura spp.
Cyclopoids

Macrobenthos

Donacilla sp. 1
Donax columbella
Exoediceroides sp. 3
Scolelepis carunculata
Phoxocephalopsid sp. 1

Meiofauna

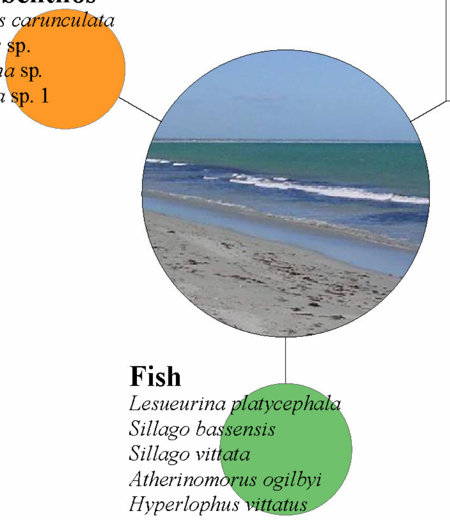
Enoplus sp.
Theristis sp. 1
Paracomesoma sp.

Zooplankton

Polychaete (1.s.1.) spp.
Harpacticoids
Cyclopoids
Calanoids

Fish

Lesueurina platycephala
Torquigener pleurogramma
Aldrichetta forsteri
Hyperlophus vittatus



Habitat type 3

Moderately exposed to wave energy, with no seagrass in the vicinity.

Macrobenthos

Scolelepis carunculata
Isocladus sp.
Leptocuma sp.
Donacilla sp. 1

Fish

Lesueurina platycephala
Sillago bassensis
Sillago vittata
Atherinomorus ogilbyi
Hyperlophus vittatus

Summary of the broad environmental characteristics and fauna at each of the six habitat types along the lower west coast of Australia. For each type of fauna, differences in the relative sizes of the coloured circles reflect differences in the relative densities of that fauna in the various habitat types.

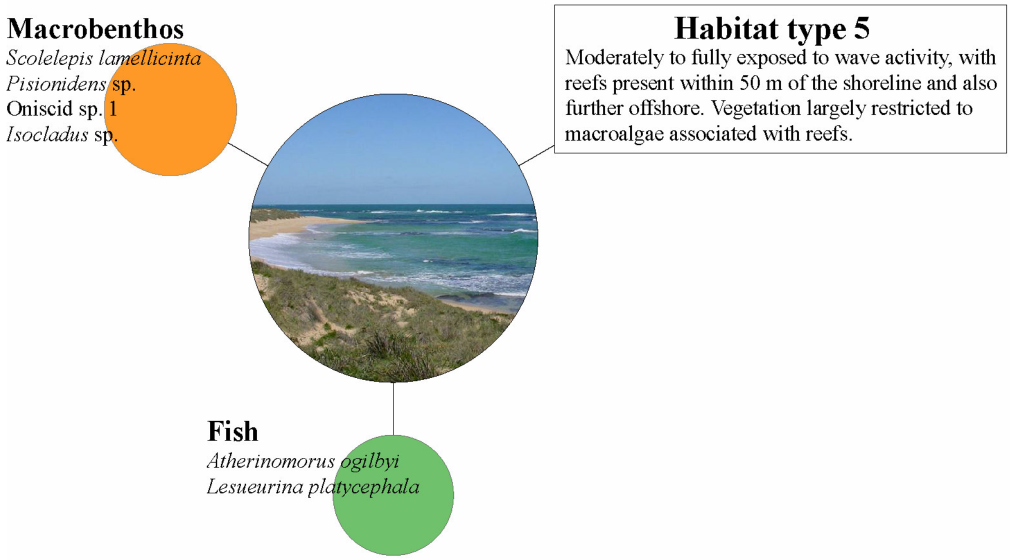
habitat types 1-6 and their associated faunal assemblages

Habitat type 4

Moderately exposed to wave energy, with dense seagrass beds located more than 50 m from the shoreline.

Macrobenthos
Scolelepis lamellicinta
Scolelepis carunculata
Hippa australis
Donacilla sp. 1
Atheta sp.

Fish
Lesueurina platycephala
Hyperlophus vittatus
Sillago bassensis
Spratelloides robustus

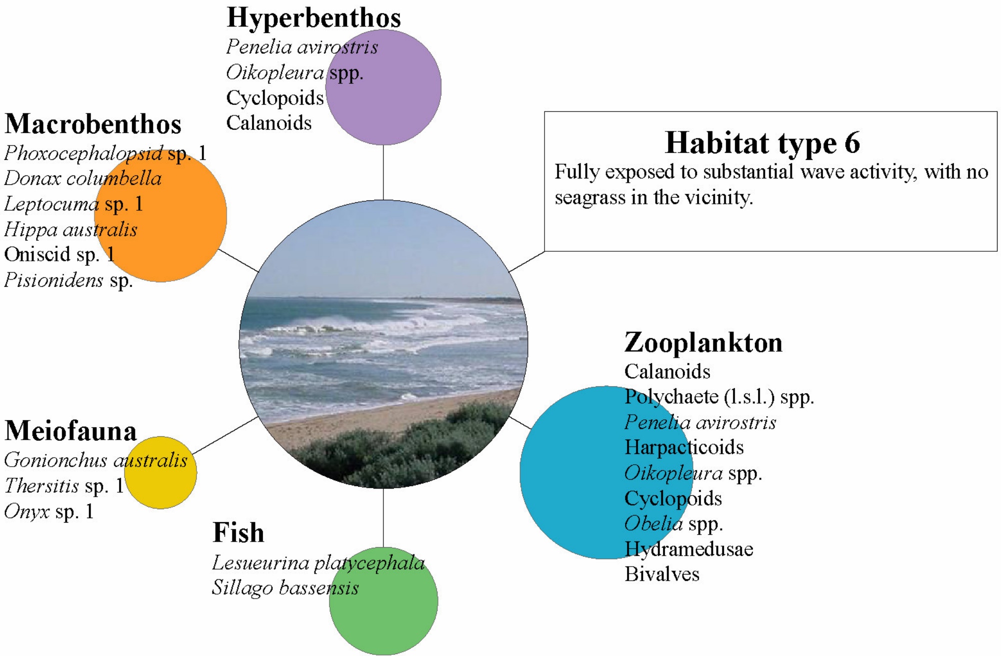


Habitat type 5

Moderately to fully exposed to wave activity, with reefs present within 50 m of the shoreline and also further offshore. Vegetation largely restricted to macroalgae associated with reefs.

Macrobenthos
Scolelepis lamellicinta
Pisionidens sp.
Oniscid sp. 1
Isocladus sp.

Fish
Atherinomorus ogilbyi
Lesueurina platycephala



Habitat type 6

Fully exposed to substantial wave activity, with no seagrass in the vicinity.

Hyperbenthos
Penelia avirostris
Oikopleura spp.
Cyclopoids
Calanoids

Macrobenthos
Phoxocephalopsid sp. 1
Donax columbella
Leptocuma sp. 1
Hippa australis
Oniscid sp. 1
Pisionidens sp.

Meiofauna
Gonionchus australis
Thersitis sp. 1
Onyx sp. 1

Fish
Lesueurina platycephala
Sillago bassensis

Zooplankton
Calanoids
Polychaete (l.s.l.) spp.
Penelia avirostris
Harpacticoids
Oikopleura spp.
Cyclopoids
Obelia spp.
Hydramedusae
Bivalves

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Gratitude is also expressed to the professional fishers Ray Butler and Dick Winter who helped add an extra dimension to our knowedge of the local fish fauna

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The following papers have resulted from this FRDC project:

Valesini, F. J., Potter, I. C. and Clarke, K. R. (in press), To what extent are the fish faunas along a heterogeneous coast related to habitat type? *Estuarine, Coastal and Shelf Science.*

Valesini, F. J., Clarke, K. R., Eliot, I. and Potter, I. C. (2003). A user friendly quantitative approach to classifying nearshore marine habitats along a heterogeneous coast. *Journal of Experimental Marine Biology and Ecology* **56**, 1-15.

Hourston, M., Platell, M. E., Valesini, F. J. and Potter, I. C. (in press). Factors influencing the diets of four morphologically divergent fish species in nearshore marine waters. *Journal of the Marine Biological Association of the United Kingdom.*

Schafer, L. N., Platell, M. E., Valesini, F. J. and Potter, I. C. (2002). Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *Journal of Experimental Marine Biology and Ecology* **278**, 67-92.

Chapter 1. General Introduction

1.1 Background

Nearshore marine waters comprise the area between the point at which incoming waves begin to interact with the substrate and the upper limit of wave swash on the beach face. These waters are among the most physically dynamic of all environments and are subject to various types of physical energy forces, each of which change continually in either predictable or highly variable ways (*e.g.* Pearse *et al.* 1942, King 1972, McLachlan 1983, Short and Wright 1983, Carter 1988, Short 1999). They contain many different types of habitats, reflecting differences in their physical energy regimes, geomorphology and inputs from surrounding areas, and thus support diverse assemblages of biota (*e.g.* Pearse *et al.* 1942, McLachlan 1983, Brown and McLachlan 1990, Suchanek 1994, Day and Roff 2000).

Nearshore marine waters along temperate coastlines provide crucial environments for fish, which are generally the most obvious and commercially and/or recreationally important component of the nearshore fauna. Many fish species spend the whole of their life cycle in these coastal waters and, in Australia, include both small species, such as several belonging to the Atherinidae, Clupeidae, Apogonidae, Leptoscopidae, Pleuronectidae, Gobiidae, Syngnathidae and Blenniidae, and also some larger species, such as certain sillaginids, plotsids and sparids (*e.g.* Lenanton 1982, Ayvazian and Hyndes 1995, Blaber *et al.* 1995, Hyndes and Potter 1997, Vanderklift and Jacoby 2003). Numerous other species, such as some mugilids, sillaginids, pomatomids and arripids, use nearshore marine waters only during the juvenile phase of their life (*e.g.* Blaber and Blaber 1980, Lenanton 1982, Blaber *et al.* 1995, Hyndes *et al.* 1996a, Jenkins *et al.* 1997a, Fairclough *et al.* 2000). For such species, nearshore environments thus represent important alternative nursery areas to those found in estuaries and, in some cases, constitute their sole nursery environment (*e.g.* Bennett 1989, Blaber *et al.* 1995, Harris and Cyrus 1996, Hyndes *et al.* 1996b, Hyndes *et al.* 1998).

The value of nearshore waters as environments for fish resides in the rich supply of food and the shelter and protection from predators they provide (*e.g.* Lasiak 1981, Lenanton 1982, Lasiak 1986, Bennett 1989, Du Preez *et al.* 1990, Shaw and Jenkins 1992, Nash *et al.* 1994, Gibson *et al.* 1998, Harvey 1998, Layman 2000, Beyst *et al.* 2001a). The new recruits of fish that spawn in offshore waters have developed sufficiently by the time they reach these shallow waters to be able to maintain their position in these productive and protective areas and thus grow rapidly (Lasiak 1986). The diverse benthic and planktonic food sources for fish that are available in nearshore waters include benthic macroinvertebrates (*e.g.* McLachlan *et al.* 1984, Fleischack and Freitas 1989, Leber 1992, Jamarillo and McLachlan 1993, Dexter 1994, Haynes and Quinn 1995, Archambault and Bourget 1999), meiofauna (Gee 1989, Ellis and Coull 1989, Coull *et al.* 1995), epibenthic invertebrates (*e.g.* Young and Wadley 1979, Morin *et al.* 1985, Pihl 1986, San Vicente and Sorbe 1999, Beyst *et al.* 2001a) and zooplankton (Alldredge and King 1980, Jacoby and Greenwood 1989, Mullin and Onbé 1991, Noda *et al.* 1998), and the densities of such prey are often much greater in these environments than in adjacent offshore waters (Wooldridge 1983, Brown and McLachlan 1990, Batchelder *et al.* 2002). Furthermore, the shallowness of nearshore waters limits the numbers of many large piscivorous predators, and small and juvenile fish are thus able to avoid such piscivores by shoaling in the shallowest zones of these coastal environments (*e.g.* Lasiak 1986, Wright 1988, Gibson *et al.* 1998, Harvey 1998, Layman 2000).

The food supply, shelter and protection from predators provided for fish in nearshore waters are enhanced by the presence of more structurally-complex features in those environments (Heck *et al.* 2003), such as seagrass beds (*e.g.* Orth and Heck 1980, Robertson 1980, Scott 1981, Robblee and Zieman 1984, Shaw and Jenkins 1992, Gotceitas *et al.* 1997, Jenkins *et al.* 1997b, Ornellas and Coutinho 1998), reef and rocky substrata (*e.g.* Robblee and Zieman 1984, Howard 1989, Clark *et al.* 1996a, Guidetti 2000) and drifting accumulations of detached macrophytes (*e.g.* Lenanton *et al.* 1982, Robertson and Lenanton 1984, Lenanton and Caputi 1989, Kingsford 1992). Along more energetic and sandy coastlines, increased shelter from predators may also be provided by depressions in an undulating substrate (*e.g.* Lenanton 1982, McLachlan and Hesp 1984, Harvey 1998, Layman 2000) and a reduction in water clarity due to water turbulence and suspended sediment (*e.g.* Lasiak 1981, Ross *et al.* 1987, Blaber *et al.* 1995, Beyst *et al.* 2002). Moreover, the type and extent of the food resources and shelter in nearshore waters vary temporally, both over short time scales, *e.g.* between day and night (Modde and Ross 1981, Burrows *et al.* 1994, Gibson *et al.* 1998, Layman 2000), and/or for longer periods, *i.e.* seasons or years (Allen and Horn 1975, Lenanton *et al.* 1991, Gibson *et al.* 1993, Clark *et al.* 1996a, Friedlander and Parrish 1998, Kokita and Nakazono 2000).

The nearshore marine waters within any particular coastal region almost invariably contain several types of habitat, which are usually able to be distinguished by differences in their (1) hydrodynamic regime, *i.e.* the type and extent of wave and current activity, (2) substrate type and (3) the extent to which they contain other features associated with the substrate, *e.g.* seagrass, macroalgae and/or reefs (Dethier 1992, Allee *et al.* 2000). Spatial heterogeneity in these environmental characteristics result primarily from differences in the physical setting of sites in relation to surrounding enduring geomorphological structures, such as headlands, offshore reef chains or proximity to estuaries (Sanderson *et al.* 2000, Short 1999, Roff and

Taylor 2000, Jackson *et al.* 2002). For example, the relative heights of oceanic swell waves arriving at different sites along a coast will depend largely on any variation in the extent to which those sites are protected by offshore structures such as reefs and islands, their orientation with respect to the direction from which swell waves approach the shore, and the configuration of the local bathymetry. Furthermore, the composition of the substrate at a nearshore site, *i.e.* mineralogy and grain size, is influenced by such hydrodynamic forces through the role they play in the weathering and alongshore/onshore transport of sediment, and also by the proximity of that site to sediment sources such as bedrock, seagrass beds and estuaries (*e.g.* Pyökäri and Lehtovaara 1993, Shih and Komar 1994, Carranza-Edwards and Rosales-Hoz 1995, Shaghude and Wannäs 1998). Along heterogeneous coastlines, such as the lower west coast of Australia, marked and predictable geomorphological differences can occur over very short distances (*i.e.* less than 10 km), and lead to pronounced variability in the environmental conditions among nearshore sites. Ray (1991) refers to such geomorphological differences as “shore-perpendicular boundaries”, and considers that they lead to the formation of various types of habitats.

The compositions of the faunal assemblages at any particular nearshore marine location are the product of complex interactions among the physical, chemical and biological characteristics of that location (Menge and Sutherland 1987, Menge and Farrell 1989, Ray 1991, Roff and Taylor 2000). It thus follows that a similar suite of species will be expected to recur consistently in locations with similar environmental attributes, *i.e.* habitat types (Erwin 1983, Ray 1991, Roff and Evans 2002). Although biological interactions, such as competition and predation, invariably play a role in structuring the composition of faunal assemblages in nearshore marine waters, many of the spatial differences in the characteristics of such assemblages are related to spatial differences in enduring geomorphological characters and recurrent oceanographic processes (Erwin 1983, Ray 1991, Dethier 1992, Schoch and Dethier 1996, Roff and Taylor 2000, Zacharias and Roff 2001b). Moreover, unlike biological interactions, the geophysical characteristics of a nearshore location are often easy to measure. Indeed, several workers consider that the latter characteristics have the greatest influence on the composition of faunal assemblages in marine environments, particularly at higher trophic levels and in more physically-dynamic areas such as nearshore waters (Sanders 1968, Menge and Farrell 1989, Zacharias *et al.* 1998a).

The physical aspects of nearshore marine waters influence the spatial distribution of fish in those areas by testing the limits of their physiological tolerance, either directly by determining the characteristics of the water column, or indirectly by determining the boundaries within which biotic interactions occur, *e.g.* by influencing food type and availability or reproduction success (*e.g.* Lasiak 1984, Abou-Seedo *et al.* 1990, MacKenzie *et al.* 1994, Friedlander and Parrish 1998, Hakala *et al.* 2003). Differences in these types of characteristics have therefore been widely used as acceptable surrogates for discriminating among different types of marine habitats and thus assemblages of biota (*e.g.* Ray 1991, Dethier 1992, Schoch and Dethier 1996, Zacharias *et al.* 1998, Ward *et al.* 1999, Allee *et al.* 2000, Roff and Taylor 2000, Zacharias and Roff 2001a, Banks and Skilleter 2002).

The nearshore marine waters of a region frequently contain a wider range of habitat types than have been recognised in many of the studies that have related spatial differences in the composition of fish assemblages to differences in the physical characteristics of these environments. Thus, numerous studies have focused specifically on determining the extent to which the nearshore fish species are partitioned amongst extremes in habitat type that can be easily distinguished by a single environmental characteristic, such as unvegetated substrata *vs* vegetated areas, (*e.g.* Orth and Heck 1980, Gotceitas *et al.* 1997, Jenkins *et al.* 1997b, Ornellas and Coutinho 1998, Arrivillaga and Baltz 1999, Lazzari and Tupper 2002), reef or rock *vs* sand substrata (*e.g.* Howard 1989, Pihl and Wennhage 2002) and sheltered from *vs* exposed to strong wave activity (*e.g.* Shaw and Jenkins 1992, Hyndes *et al.* 1996a). However, obvious differences in a single characteristic neither encapsulate the environmental complexity that is present in temperate coastal waters, nor take into account the fact that several inter-connected environmental factors are usually required to characterise adequately the different nearshore habitat types (Roff and Taylor 2000, Skilleter and Loneragan, in press).

Although other workers have examined how the spatial variation in the composition of nearshore fish assemblages might be explained by differences in several physico-chemical characteristics (*e.g.* Gilligan 1980, Ayvazian and Hyndes 1995, Clark *et al.* 1996, Mueter and Norcross 1999, Dean *et al.* 2000, Beyst *et al.* 2002), these workers made no attempt to elucidate how the collective differences among a suite of such environmental variables might reflect differences among the various types of habitat and thus of their ichthyofauna. Moreover, the environmental differences examined in some of these studies were investigated at a largely qualitative level (*i.e.* Gilligan 1980, Ayvazian and Hyndes 1995, Dean *et al.* 2000).

The nearshore marine waters along the lower west coast of Australia, as elsewhere in the world, are often focal areas for recreation and for residential and industrial development (Department of Environmental Protection 1996, Australian Bureau of Statistics 2001). These coastal areas and are thus becoming increasingly subjected to the effects of anthropogenic changes, such as those brought about by the construction of marinas, harbours and groynes (*e.g.* Chamberlain and Barnhart 1993, Nordstrom 1994, Klein and Zviely 2001), dredging and mining activities (Cambridge *et al.* 1986, Lindeman and Snyder 1999, Blomgren and Hanson 2000, Chesney *et al.* 2000) and nutrient enrichment (*e.g.* Cambridge and McComb 1984, Tolosa *et al.* 1996, Cloern 2001, Connelly *et al.* 2001, Gaus *et al.* 2001, Kendrick *et al.* 2002). The importance of these waters for fish, either as a nursery area or sole habitat (*e.g.* Lasiak 1981, Lenanton 1982, Bennett 1989, Gibson *et al.* 1993, Ayvazian and Hyndes 1995, Clark *et al.* 1996a, Layman 2000), means that such environmental changes have the potential to exert a deleterious impact on the diversity of the ichthyofauna and health of the commercial and/or recreational fisheries in a region (Brazner and Beals 1997, Chesney *et al.* 2000, Rose 2000, Vanderklift and Jacoby 2003). However, the implications for fish of changes to the physico-chemical nature of the nearshore waters in a particular region will differ among the various types of habitats in those waters, since each of these habitat types are likely to contain a relatively distinct ichthyofaunal assemblage.

It thus follows that, in order to develop effective plans for reducing or preventing the adverse effects of anthropogenic activities on the ecological health of nearshore marine areas, environmental and fisheries managers initially require a systematic and readily-usable method for identifying the different types of habitat present within a region, *i.e.* a habitat classification scheme. Such schemes facilitate an inventory of habitat types, provide a framework for ascertaining the relationships between biotic assemblages and the environmental attributes of those habitat types, and provide a benchmark for detecting any significant changes in the environmental and biotic characteristics of a particular site of interest (Suchanek 1994, Robinson and Levings 1995, Mumby and Harborne 1999, Allee *et al.* 2000, Day and Roff 2000, Roff and Taylor 2000, Banks and Skilleter 2002, Roff *et al.* 2003). Such information will enable managers to conserve those habitat types that are particularly biodiverse and/or crucial for certain recreationally or commercially important fish species. To reliably achieve these objectives, the classification scheme must be quantitative to ensure that it can be used consistently, and also applicable at regional to local scales (10s-1000s km) to maximise it’s usefulness as a decision-making tool to environmental managers who usually require information at these spatial scales.

This broad ecosystem-based approach to managing the fish fauna of a nearshore region contrasts with the traditional methods that have often been adopted by managers of marine waters in many parts of the world, where conservation efforts have been directed largely towards (1) particular species of interest, *i.e.* those that are rare, endangered or commercially important (*e.g.* Kerr and Ryder 1989, Suchanek 1994, Zacharias and Roff 2000, 2001a) or (2) protecting unique types of habitat (*e.g.* Ward *et al.* 1999, Zacharias *et al.* 1998, Day and Roff 2000, Roff and Evans 2002). However, while focal species and unique habitats clearly warrant appropriate protection (Day and Roff 2000, Roff and Evans 2002), inadequate knowledge of the broader associations between faunal assemblages and environmental structures and processes in marine waters has led to predictions of large-scale biotic collapse in these environments (*e.g.* Suchanek 1994, Zacharias *et al.* 1998, Andrew and O'Neill 2000, Chesney *et al.* 2000, Roff and Taylor 2000, Rose 2000). This is due mainly to the inability of environmental managers to identify and protect representative examples of the range of habitat types in a region (*e.g.* Edyvane 1999, Ward *et al.* 1999, Day and Roff 2000, Department of Primary Industries, Water and Environment, Tasmania 2000, Roff and Taylor 2000, Banks and Skilleter 2002, Roff and Evans 2002).

Several workers, mainly in North America and Europe, have recognized the value for both managers and ecologists of being able to distinguish consistently among the different types of habitat in marine waters, and have thus developed schemes for classifying those habitat types on the basis of a suite of environmental criteria (*e.g.* Dethier 1992, Schoch and Dethier 1996, Zacharias *et al.* 1998, Mumby and Harborne 1999, Allee *et al.* 2000, Roff and Taylor 2000). While their general conceptual framework may be applied to other nearshore waters, such as those along the lower west coast of Australia, many of the schemes that have been devised for use at regional spatial scales are based on environmental criteria that are either objective or semi-quantitative (*e.g.* Dethier 1992, Zacharias *et al.* 1998, Allee *et al.* 2000, Roff and Taylor 2000). Thus, as such schemes are not based on precise quantitative criteria, they are limited in the extent to which the resultant habitat types can be statistically related to their biota (Zacharias *et al.* 1999) and thus be used to accurately predict the type of fauna that are likely to characterise a particular nearshore site.

1.2 Need

The final FRDC report produced by Cappo *et al.* (95/055), entitled "A Review and Synthesis of Australian Habitat Research", highlighted several main areas in which there was a lack of knowledge of the habitats used by commercial and recreational fish species. These included (1) the characteristics and locations of important fisheries habitats at scales useful for research and management, (2) life-history information for fish species, related to the types of habitats occupied throughout their life-cycles, and data on the densities and/or biomass of those other components of fish habitats, which provide food and/or protection for fish, such as invertebrates and aquatic vegetation, (3) habitat dynamics and ecosystem processes, including food webs, habitat use and fisheries production in soft sediment substrata, such as beaches and (4) fisheries-habitat links, including the influences of hydrodynamic and other processes on the recruitment of commercial and recreational fish species.

Moreover, the proceedings of the Marine Classification Scheme Workshop held in September 2002 by the National Oceans Office (NOO) and the Australian Fisheries Research Development Corporation (FRDC) regarding the proposed need by researchers and government agencies for a consistent and common framework to classify marine habitats in Australia (NOO and FRDC 2002), highlighted the requirement for any such classification scheme to (1) be robust, adaptive and able to operate at multiple spatial scales and (2) include a predictive element, and thus be able to identify associations between groups of flora and fauna and a particular set of environmental characteristics. Discussions held during this workshop also identified the need for more information on fish and invertebrates in different habitats, and the validation that physical data are an acceptable surrogate for biota.

Managers and ecologists working in nearshore marine waters along the lower west coast of Australia thus have the following specific requirements.

1) A readily-usable, quantitative and adaptive scheme for identifying the various types of habitats in nearshore marine waters over local to regional spatial scales.
2) A procedure for predicting the species and life-history stages of fish that are likely to occupy any particular site within this nearshore region.
3) An ability to predict how physical changes to any particular nearshore site are likely to affect the composition of the fish assemblages in those waters and/or fisheries in the region.
4) A basis for constructing and testing hypotheses regarding the inter-relationships between fish fauna and their invertebrate prey.

1.3 Objectives

The main objectives of the study are provided below. The more specific aims of each component of the study are provided in the subsequent chapters.

1) Develop a quantitative scheme that can be used to readily identify the different habitat types found in nearshore marine waters along the lower west coast of Australia.
2) Determine the compositions of the fish faunas in representative examples of the different habitat types, and thereby determine which habitat types are used most extensively by main commercial and recreational fish species.
3) Establish the suite of environmental characteristics that can be readily used to determine the habitat type of any site in this nearshore region and thus predict the fish species that are likely to be found at that site.
4) Determine the compositions of the benthic macroinvertebrate faunas at the same sites at which fish are sampled to ascertain whether the extent of the relationship between a less mobile assemblage of fauna and the characteristics of the different habitat types differs from that with the highly-mobile fish fauna.
5) Determine, for a subset of the different habitat types present along the lower west coast of Australia, the compositions of the diets of selected fish species and the assemblages of their potential invertebrate prey in the benthos and water column, *i.e.* benthic

macroinvertebrates, zooplankton, meiofauna, and hyperbenthic invertebrates. Such data will be used to examine predator/prey inter-relationships between these faunal assemblages.

6) Collate the key components of this study in a form that will enable fisheries and environmental managers to ensure that those areas along the lower west coast of Australia that provide crucial habitats for important fish species are protected from deleterious anthropogenic activities.

Some of the above objectives have been modified since the original application for this research project was submitted in June 2000. Thus, while it was initially proposed that work would be carried out in both estuarine as well as nearshore marine waters along the lower west coast of Australia, it was subsequently decided that it would be better to focus the study specifically on nearshore marine habitat types and their fish and invertebrate faunas. This decision was discussed with Dr Patrick Hone and documented in the Milestone Progress Report submitted in June 2001. Secondly, hyperbenthic invertebrates were also sampled at the habitat types referred to in Objective (5) above, in addition to the benthic macroinvertebrates, zooplankton and meiofauna that were originally proposed. This additional sampling was undertaken in view of the importance of hyperbenthic fauna to the diets of fish in nearshore waters, and commencement of the sampling for these invertebrates was documented in the Milestone Progress Report submitted in December 2001. Moreover, the contributions of the various prey items to the diets of the fish species selected for analysis was determined satisfactorily using the volumetric contribution and frequency occurrence of the different taxa to the fish gut contents. Thus, inclusion of biomass data for these prey items, as stated in the original Objectives, was considered unnecessary.

Chapter 2. Study Area

2.1 Location and surrounding land use

The stretch of coastline selected for study, which is located along the temperate lower west coast of Australia between 31°41'S and 32°32'S (Fig. 2.1), is used for recreational, residential, commercial, fishing and industrial purposes. The management of these nearshore waters and their resources is the responsibility of various agencies that range in their jurisdiction from international levels, *e.g.* Convention on Wetlands of International Importance Especially as Waterfowl Habitat (Ramsar Convention), to local levels, *e.g.* Conservation and Land Management Act 1984 for Perth Coastal Waters and the Fremantle Port Authority Act 1902 (Department of Environmental Protection 1996, K. Ryan, pers. comm.). Two marine conservation reserves, namely the Shoalwater Islands Marine Park and the Marmion Marine Park, have been established under State legislative Acts in the nearshore marine waters along this coastline (Fig. 2.1).

The population of Perth, the main city in the study area, and its surrounding suburbs, is estimated to be 1.3 million, more than 70% of which live within 20 km of the coast (Australian Bureau of Statistics 2001). The nearshore waters in this region are thus the focus of many recreational activities, such as swimming, boating and fishing (Pearce 1991a). Industrial activity is focused largely around Fremantle Port, which is located at the entrance of the Swan Estuary and is the main shipping facility in this area, and Cockburn Sound (Fig. 2.1), which contains ship-building and maintenance facilities and subtidal sand mining, industrial waste, mineral processing, fertilizer, petroleum refining, grain handling/storage, gas and chemical companies (Department of Environmental Protection 1996).

Several commercial baitfish and finfish fisheries are based in the inshore (*i.e.* <20 m depth) and coastal waters of this region, including those for *Hyperlophus vittatus, Spratelloides robustus, Sardinops sagax, Mugil cephalus, Aldrichetta forsteri, Sillago schomburgkii, Hyporhamphus melanochir, Sardinella lemuru* and *Engraulis australis.* The stock size of many of these fisheries is small, and most are considered to be fully exploited by the commercial fishing sector (Penn 2002). Species which are recreationally sought after in this region include *Arripis georgiana, Sillaginodes punctata, Pseudocaranx dentex, Pomatomus saltatrix, Hyporhamphus melanochir* and *Pagrus auratus* (Penn 2002).

Some areas of the coastline and nearshore waters in the study region have been modified substantially as a result of residential, commercial and industrial activities, including dredging of the substrate and the construction of harbours, waste outfalls, marinas and jetties. For example, the discharge of waste into the waters of Cockburn Sound from the 1950s to 1970s

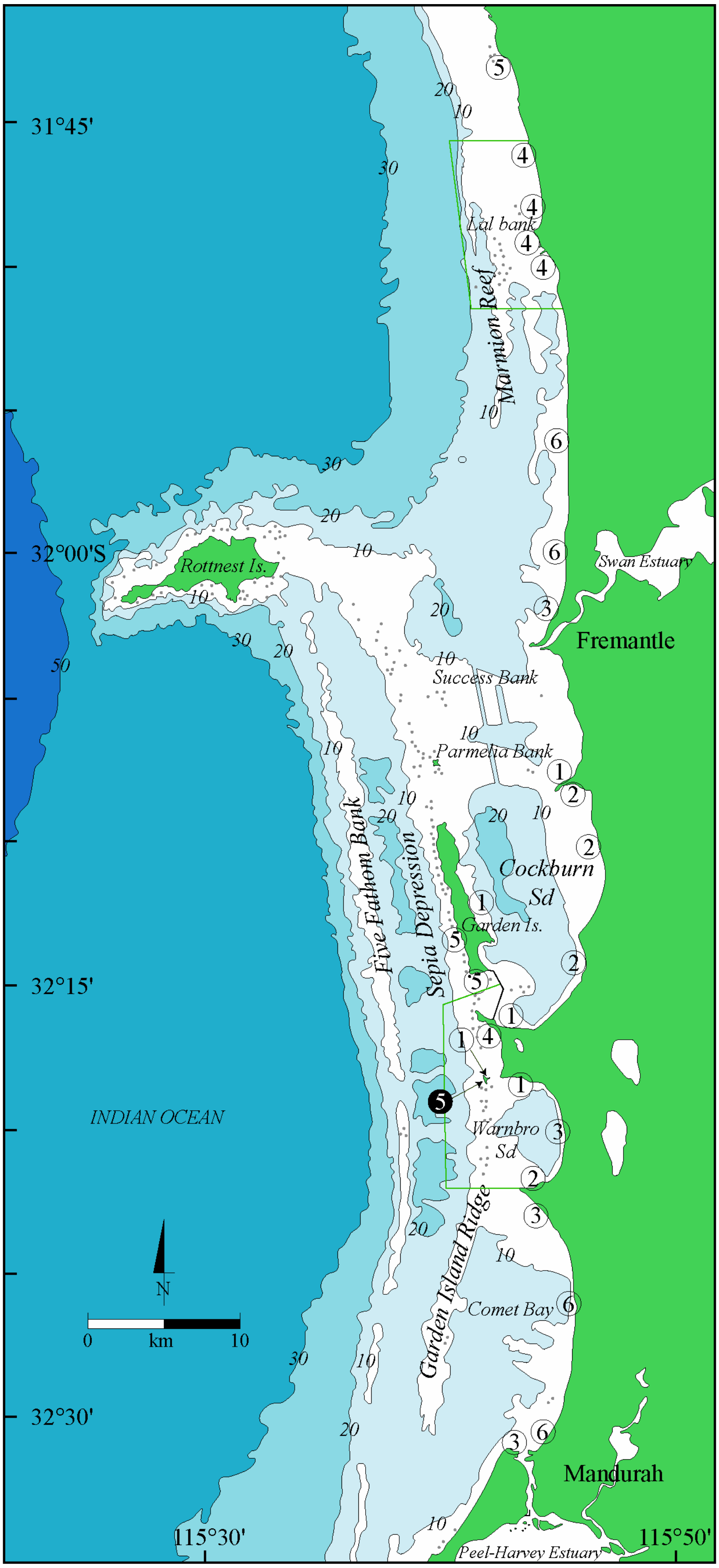


Figure 2.1: Map showing the 25 study sites, coded for habitat type, on the lower west coast of Australia. The site within the filled circle is the additional site chosen to demonstrate the use of the habitat classification procedure (see Chapter 3). Grey dots indicate shallow reefs. Areas enclosed within green lines represent the Marmion Marine Park (northern-most) and the Shoalwater Islands Marine Park (southern-most).

resulted in the accumulation of unacceptable levels of contaminants and nutrients and the subsequent loss of seagrass beds in that area (Cambridge and McComb 1984, Cambridge *et al.* 1986, Silberstein *et al.* 1986, Kendrick *et al.* 2002). While improved management practices have reportedly reduced the levels of a range of toxic contaminants so that they are now largely below ecological and human health standards, nitrogen enrichment of these waters is still a widespread problem (Department of Environmental Protection 1996). Furthermore, it is predicted that the population in this coastal area will increase by about 65% within the next 50 years (Australian Bureau of Statistics 2001), which will invariably place increasing pressure on the ecological health of these nearshore waters (Pearce 1991a).

2.2 Geomorphology

The geomorphology of the lower west coast of Australia comprises a succession of ancient shorelines and dune systems on the submerged Rottnest Shelf and adjoining terrestrial Swan Coastal Plain, which were formed during global changes in sea-level from the early Pleistocene to Holocene (Searle and Semenuik 1985, 1988). These ancient shorelines form a series of parallel ridges that lie seaward and landward of the present coastline, and are comprised of Tamala limestone overlaid with accumulations of Holocene sediment (Searle and Semenuik 1985). To the south of Perth, the most seaward of the submerged ridges is the Five-Fathom Bank Ridge, which extends northwards from just south of Mandurah to Rottnest Island and is located at depths of *ca* 2 to 30 m (Searle 1984). The Garden Island Ridge lies approximately 10 km to the east of this ridge, and also commences south of Mandurah and extends northwards, before curving in a north-westerly direction and merging with the Five-Fathom Bank Ridge just south of Rottnest Island (Fig. 2.1). Parts of the Garden Island Ridge are expressed as islands (*e.g.* Garden Island) and rocky outcrops, while other parts are submerged to depths of up to *ca* 20 m (Searle 1984). The Spearwood Ridge, which is connected to the Garden Island Ridge at its southern tip and forms the basis of the present coastline, is expressed as rocky outcrops along the shore in some places, but is largely overlain by accumulations of sand (Searle 1984, Searle and Semeniuk 1985). The most seaward ridges, in particular, are eroded continuously by approaching oceanic swell waves and have collapsed in parts (Searle and Semenuik 1985, Sanderson 2000).

Some of the inshore waters to the north of Perth do not contain submerged limestone ridges, and the bathymetry along this relatively straight section of the shoreline is relatively simple. The substrate in these waters slopes to depths of *ca* 20-30 m, and is comprised of Holocene sediment. Shore-parallel limestone ridges recur to the north of these waters, and from west to east, are Marmion Reef and the Spearwood Ridge, which are located *ca* 4 and 2 km, respectively, from the current shoreline (Searle and Semenuik 1985; Fig. 2.1). The majority of

Marmion Reef is submerged to depths of only *ca* 5 m and occasionally forms rocky outcrops. The Spearwood Ridge forms discontinuous submerged rocky platforms and emergent reefs in the shallows close to shore along this section of the coast, and is expressed in some areas as limestone headlands and low fringing cliffs (Searle and Semenuik 1985).

Depressions are interspersed between each of the submerged limestone ridges present along the length of the Perth metropolitan coastline. South of Perth, these are the Sepia Depression and Warnbro-Cockburn Depression, moving from west to east. While the water depths in the former depression are generally 10–20 m, those in the latter are frequently less than 10 m, except in the middle of some embayments where they reach *ca* 20 m. The depressions between the two most seaward limestone ridges to the north of Perth reach depths of *ca* 15 m (Searle and Semenuik 1985; Fig. 2.1).

The refraction of approaching swell waves by the reefs and islands along this coastline has resulted in the formation of several submerged sandy cuspate forelands, predominantly between the Garden Island and Spearwood ridges (*i.e.* the adjoining Success and Parmelia banks that lie to the north of Cockburn Sound) and the Marmion Reef and Spearwood ridges (*i.e.* Lal Bank; Fig. 2.1). Many of these sandy banks have been colonized extensively by seagrass beds (see subsection 2.4), which, in turn, increase the extent of wave shoaling and thus sedimentation in those areas (Kirkman 1985, Searle and Semenuik 1985, Semenuik and Searle 1986, Kirkman and Walker 1989, Sanderson and Eliot 1996). These cuspate forelands have partitioned the coastline south of Perth into a series of embayments, including Cockburn Sound, Warnbro Sound and Comet Bay (Searle 1984, Searle and Semenuik 1985; Fig. 2.1). Furthermore, some of these submerged accretions extend to the shoreline and have formed sandy headlands between the various embayments (Semenuik and Searle 1986, Sanderson and Eliot 1996). The formation of these sedimentary deposits along the shoreline is influenced by spatial differences in the wave refraction and shoaling patterns, which are complex due to variability in the continuity of the reef chains and seagrass beds, and by the interactions between these wave patterns and the predominantly northward alongshore currents in this region (see below; Sanderson and Eliot 1996).

The sediment along the lower west coast of Australia is derived mainly from erosion of the submerged limestone ridges and from the skeletons of marine organisms inhabiting the seagrass beds. Some sediment is also supplied from other regions along the coast by alongshore currents. While the mineralogy of the submerged forelands is comprised mainly of carbonate material, the surface layers of the shoreline are dominated by quartz. However, the precise mineralogy in this region varies spatially in relation to the extent and location of seagrass beds and exposed rocky shores (Searle and Semenuik 1988).

Two estuaries are located in the study region, namely the Swan-Canning (32˚03’S) and the Peel-Harvey (32˚31/’S32˚36’S) estuaries, the mouths of which remain permanently open to the sea (Fig. 2.1).

2.3 Climate and Oceanography

2.3.1 Winds

The lower west coast of Australia has a temperate, Mediterranean climate, which is characterised by warm, dry summers (December to February) and cool, wet winters (June to August; Gentilli 1971). The large-scale weather patterns of this region are controlled largely by the latitudinal shift of a belt of anticyclonic high-pressure systems between summer and winter. Thus, from October to April, this belt of anticyclones is located to the south of the continent (37-38°S), and the Trade Winds produce predominantly easterly winds (Gentilli 1971). However, the anticyclones are displaced northwards during May to September by the strong low pressure mid-latitude cyclones that occur just to the south of Australia at this time, and become located over the southern part of the continent (29-32°S). The mid-latitude cyclones produce strong winds that approach the lower west coast of Australia largely from the west, south-west and north-west, and generally reach maximum velocities (*ca* 15 m s^{-1}) and frequency in mid-winter (Gentilli 1971, M.P. Rogers and Associates 1995).

The winds produced by these large-scale weather systems are modified locally by other wind systems, the most prominent of which is the diurnal land/sea-breeze cycle that occurs along the study region in summer. Thus, during this season, the local winds switch between the easterly land-breezes that occur in the evening and morning, to the south to south-westerly winds that occur during the early afternoon. The sea-breeze system along the lower west coast of Australia is one of the most consistent and energetic in the world, occurring on *ca* 60% of summer days and frequently exceeding wind speeds of 15 m s^{-1} (Pattiaratchi *et al.* 1997, Masselink and Pattiaratchi 2001a). Local onshore winds are more variable in winter, and occur for roughly equal amounts of time from the south, west and north quadrants. However, the strongest winds are derived from the southwest, west, north-west and north in that season, and are usually associated with winter storms (M.P. Rogers and Associates 1995).

2.3.2 Waves

The total wave climate along the lower west coast of Australia comprises both distantly-generated swell and locally-generated seas. However, the significant wave height of each of these wave types and their relative contribution to the total wave climate exhibits pronounced seasonal differences.

The offshore swell waves that advance towards the coast in the study region are generated mainly by the low-pressure mid-latitude cyclones in the Indian and Southern oceans.

However, the difference between the location and intensity of these cyclones in summer and winter (see section 2.3.1) leads to seasonal variations in the characteristics of the resulting swell. Thus, these offshore waves approach the coastline from a southerly to south-westerly direction in summer and their significant wave heights range between 1 and 2 m, while swell arrives from a westerly to south-westerly direction in winter and typically has a significant wave height of 1-3 m (M.P. Rogers and Associates 1995, Lemm *et al.* 1999). Local seas in summer, which are generated mainly by the energetic sea-breeze system, approach the coast mainly from the south-west and are of a similar height to the swell at that time. The variable local wind climate in winter produces equally variable seas, which range in their approach from the northwest to southwest and in height from *ca* 0.5 to 2 m (M.P. Rogers and Associates 1995). However, during winter storms, the mean significant wave height reaches 6.7 m (Lemm *et al.* 1999). The total offshore wave climate along the lower west coast of Australia is thus characterised by waves with mean significant wave heights of 1.8 m in summer and 2.8 m in winter (Masselink and Pattiaratchi 2001b).

The offshore reef chains, islands and shallow sandy banks in the study region attenuate a substantial amount of offshore wave energy through the effects of wave shoaling, refraction and breaking. Consequently, waves that arrive at the shore are *ca* 60% of the height of those offshore (Masselink and Pattiaratchi 2001b). However, due to spatial differences in both the level of sheltering provided by these offshore barriers and the configuration of the complex nearshore bathymetry, the extent of wave attenuation varies markedly along the coastline. Thus, the height of the nearshore waves at some locations on the coast is as small as 5% of those offshore (Department of Environmental Protection 1996).

2.3.3 Changes in sea-level

The mean spring tidal range along the lower west coast of Australia is less than 0.5 m (Department of Defence 1998), and this region is thus classified as microtidal (Davies 1964). The frequency of high and low tidal states is mixed, but they are predominantly diurnal (Department of Defence 1998). The changes in sea-level produced by these small tides are often exceeded by those brought about by other influences, such as wind stress, storm surge and changes in barometric pressure (Hodgkin and di Lollo 1958, Clarke and Eliot 1983, Eliot and Clarke 1986, Hegge *et al.* 1996). Thus, variations in atmospheric pressure regularly alter sea-level in these nearshore waters by *ca* 0.2 m (Pattiaratchi and Buchan 1991), and by up to 0.4 m on some occasions (Sanderson 1997). Surges associated with offshore storm activity also produce local rises in sea-level of up to 0.5 m (Allison and Grassia 1979).

2.3.4 Currents

The Leeuwin Current is the main oceanic current that operates in the vicinity of the lower west coast of Australia, and is generated by the Trade Winds that occur near the equator in the western Pacific and northern Indian oceans. This current occurs at relatively shallow depths, *i.e.* <300 m deep, and is narrow, *i.e.* <100 km wide, and flows southwards along the margin of the continental slope of the west coast of Australia before rotating eastwards at the south-western tip of the continent and flowing along the south coast of Western Australia (Cresswell and Golding 1980, Pattiaratchi and Buchan 1991). It is unique in that it is the only oceanic current in the southern hemisphere which flows south along a western coast (Pearce 1991b).

Due to its tropical origins, the waters of the Leeuwin Current are warm, *i.e. ca* 22 ºC, and relatively low in salinity, *i.e. ca* 35.2 ‰ (Cresswell and Golding 1980). Flow is generally strongest in autumn, winter and early spring, and reaches speeds of 1.5 m s^{-1} (Pearce 1991b). The strength of this current also exhibits considerable interannual variability, which is related to differences in the extent of El Niño-Southern Oscillation events in the Pacific Ocean that influence the extent of the Trade Winds (Pattiaratchi and Buchan 1991). The Leeuwin current plays an important role in the reproductive and recruitment success of many marine biota (*e.g.* Hatcher 1991, Hutchins 1991, Hutchins and Pearce 1994), and in extending the spatial distribution of those with planktonic phases in their life cycle, many of which would normally only occur in more tropical waters (Maxwell and Cresswell 1981, Hutchins 1991, Ayvazian and Hyndes 1995).

The waters shoreward of the limestone reef chains along the lower west coast of Australia are also subject to complex alongshore currents that are driven mainly by local winds. Thus, the strong and persistent southerly winds that occur along this coastline in summer generate northward flowing currents, while those in winter are more variable but are mainly southward-flowing. The characteristics of these wind-driven currents are influenced heavily by the heterogeneity of the coastal bathymetry in this region. Thus, the presence of the various islands, shallow banks and headlands along the coastline restricts, to varying extents, the degree of water exchange between embayments and can lead to localised water circulation patterns (Department of Environmental Protection 1996).

2.4 Submerged aquatic vegetation and detached macrophytes

Seagrass occurs predominantly in those waters along the lower west coast of Australia that are relatively shallow and protected from wave activity, such as on sandy forelands in the lee of reefs and islands and within sheltered embayments. While 18 species of seagrass have been recorded in this coastal region, the majority of the seagrass beds comprise monospecific or mixed stands of *Posidonia australis*, *Posidonia sinuosa*, *Amphibolis antartica* and *Amphibolis griffithii* (Department of Environmental Protection 1996). However, the extent and location of these beds varies considerably within this region.

Some of the largest and most dense beds of seagrass occur at depths of 4-5 m on the sandy forelands in the lee of the Garden Island Ridge (*i.e.* Success and Parmelia banks) and Marmion Reef Ridge (*i.e.* Lal Bank). The dominant species in these areas is *P. sinuosa*, which is interspersed occasionally with *P. australis* and *Posidonia angustifolia* in the most sheltered areas, and with *Posidonia coriacea* and *Posidonia denhartogii* in areas that are relatively more exposed to wave action (Kirkman and Walker 1989). Some shallow nearshore areas in Cockburn Sound also contain relatively dense beds of seagrass dominated by *P. sinuosa*, but include some patches of *P. australis*, *P. coriacea*, *A. antartica, A. griffithii, Halophila ovalis, Syringodium isoetifolium* and *Heterozostera tasmanica* (Kendrick *et al.* 2002). However, the extent of seagrass cover in this embayment has declined substantially since the 1940s as a result of nutrient–rich discharge from surrounding industries and, in some areas, increases in sea urchin populations (*e.g.* Cambridge and McComb 1984, Department of Environmental Protection 1996, Kendrick *et al.* 2000, 2002). Thus, Kendrick *et al.* (2002) determined that only 23% of the 2929 ha of seagrass that was present in Cockburn Sound in the late 1960s was still present in 1999. Conversely, the seagrass cover on Success and Parmelia Banks to the north of this embayment doubled over a similar time period in the case of the former sandy foreland and decreased only slightly on the latter (Kendrick *et al.* 2000).

Warnbro Sound contains *ca* 930 ha of seagrass, which is mainly distributed on the shallow sandy headlands adjoining the shore at the northern and southern ends of the bay. These fringing beds consist mainly of monospecific stands of *P. australis*, *P. sinuosa*, *A. antartica* and *A. griffithii*. However, the beds in this embayment, particularly those at the southern end, are relatively less continuous and dense than those in Cockburn Sound due to a greater level of exposure to wave activity (Kirkman and Walker 1989).

The seagrass meadows that occur in the lee of Marmion Reef to the north of Perth are extensive and diverse. While this area contains large continuous meadows of *P. sinuosa*, these beds are often interspersed with patches of nine other species, namely *H. ovalis, A. antartica, A. griffithii, S. isoetifolium, Thalassodendron pachyrhizum, P. angustifolia, P. australis, Posidonia ostenfeldii* and *H. tasmanica* (Kirkman 1985). Unlike the embayments south of Perth, virtually none of these beds of seagrass occurs in the immediate vicinity of the shore, which is due to the more energetic nearshore wave conditions at those northern beaches.

The subtidal and intertidal limestone reefs along the lower west Australian coastline also provide a substrate for diverse and extensive growths of macroalgae. For example, 82 macroalgae taxa were recorded by Phillips *et al.* (1997) on Marmion Reefs. The kelp *Ecklonia* *radiata* is the most abundant macroalgae by far and, together with other brown algae such as *Sargassum* spp*.,* often form a canopy over these reefs. Various types of red, green and brown algae comprise the understorey, and some taxa exhibit seasonal changes in abundance, *e.g.* the green foliose algae *Ulva lactuca,* which is considerably more abundant in winter (Department of Environmental Protection 1996).

Large amounts of these seagrasses and macroalgae become detached during periods of increased wave activity and frequently accumulate in the shallow waters and on the beaches along the coast (Hansen 1984). While the temporal and spatial occurrence of these detached macrophytes is often variable, the greatest accumulations usually occur during winter when the level of wave activity is generally the greatest, and in those areas in the vicinity of sandy forelands where refracted waves converge, *e.g.* the southern and northern ends of Warnbro Sound, northern Cockburn Sound and at beaches adjacent to Marmion Lagoon (Hansen 1984). However, local winds and alongshore currents can also distribute these accumulations to other locations along the coast.

Chapter 3. Classification of nearshore marine habitats on the lower west coast of Australia

3.1 Introduction

As in many other regions of the world, the nearshore waters along the lower west coast of Australia are becoming increasingly subjected to the effects of anthropogenic changes, such as those brought about through the construction of marinas and harbours (*e.g.* Coogee Coastal Action Coalition 2002), residential and commercial developments (*e.g.* Environmental Protection Authority 2000, The Planning Group 2002), dredging and mining activities (*e.g.* Cambridge *et al.* 1986) and eutrophication (*e.g.* Cambridge and McComb 1984, Kendrick *et al.* 2002). These nearshore marine waters provide nursery areas for a diverse range of fish species and constitute the sole habitat for many others (*e.g.* Lenanton 1982, Ayvazian and Hyndes 1995, Gaughan *et al.* 1996, Hyndes *et al.* 1996a, Vanderklift 1996). Moreover, many of these species are commercially and/or recreationally important (Penn 2002). Thus, detrimental changes to the environmental quality of the waters along this coastline have the potential to exert a deleterious impact on the diversity of the fish assemblages and the health and value of the fisheries in this region (Vanderklift and Jacoby 2003). However, the type and extent of the impacts of such environmental changes on the nearshore fish fauna will vary among the different types of habitat found in these waters.

In order to develop effective plans for reducing or preventing the adverse effects of anthropogenic activities on the ecological health of nearshore marine areas, environmental managers firstly require a systematic and readily-applicable method for identifying the types of habitat within a coastal region, *i.e.* a habitat classification scheme. Such schemes represent “a set of rules or procedures that are used to identify, delimit and describe the habitats of naturally occurring biota” (Robinson and Levings 1995), and thus provide a basis for (1) carrying out an inventory of the range of habitat types in a nearshore region, including those that are representative and those that are unique, (2) ascertaining the relationships between faunal assemblages and the environmental characteristics of each habitat type and thereby predicting the type of fauna that is likely to occur at particular nearshore locations, (3) detecting change in the environmental, and thus biotic, characteristics of a particular nearshore site and (4) interpreting the underlying processes that influence the composition of fish assemblages (Suchanek 1994, Robinson and Levings 1995, Mumby and Harborne 1999, Allee *et al.* 2000, Day and Roff 2000, Roff and Taylor 2000, Banks and Skilleter 2002, Roff *et al.* 2003).

The usefulness of nearshore habitat classification schemes for environmental management depends on the extent to which they satisfy several criteria. Firstly, the scheme should be able to be used reliably at local to regional scales, *i.e.* 10s-1000s of km, thereby facilitating sufficiently detailed measurement of environmental variables to enable different habitat types to be identified accurately (Zacharias *et al.* 1999, Banks and Skilleter 2002), and yet ensuring that the scheme encompasses an area that is large enough to include several examples of each habitat type and can be reliably extrapolated to other coastal areas. Furthermore, it is at these spatial scales that environmental managers are most frequently required to implement plans for managing and conserving nearshore resources (Zacharias and Roff 2001a, Roff *et al.* 2003). Several schemes have been devised throughout the world for classifying nearshore habitats at these spatial scales (*e.g.* Dethier 1992, Zacharias *et al.* 1999, Allee *et al.* 2000, Roff and Taylor 2000).

Secondly, the scheme should be based ideally on relevant criteria that are relatively easy to determine, and which do not require measurement in the field. Thus, the use of enduring geophysical and submerged aquatic vegetation criteria, both of which have been widely accepted as a reliable basis for explaining differences in the spatial distribution of marine fauna (*e.g.* Ray 1991, Dethier 1992, Schoch and Dethier 1996, Zacharias *et al.* 1998, Ward *et al.* 1999, Allee *et al.* 2000, Roff and Taylor 2000, Zacharias and Roff 2001a), ensures that measurements can be made from remote sources, such as bathymetric charts, and can be mapped easily over large spatial scales (Roff and Taylor 2000). This contrasts with those schemes that initially use data for assemblages of co-occurring biota as the basis for classifying nearshore habitat types (*e.g.* Connor *et al.* 1997, Zacharias *et al.* 1999), and which thus necessitate the prior collection of extensive biotic samples in the field. It also contrasts with the traditional schemes that have been adopted for classifying beach morphotypes in many parts of the world, most of which require the detailed measurement of *in situ* geomorphological and hydrodynamic characteristics (*e.g.* Wright and Short 1983, 1984, Lippmann and Holman 1990, Masselink and Short 1993, Hegge *et al.* 1996, Doucette 2000). Furthermore, most of these morphodynamic models have been developed along coasts that are exposed to moderate to high wave energy, and more recent research has indicated that their usefulness for categorising beaches along relatively sheltered coastlines is, at best, limited (Hegge *et al.* 1996, Masselink and Pattiaratchi 2001b).

Thirdly, a habitat classification scheme should also be based on quantitative criteria to ensure that it can be used reliably by other workers. Moreover, the use of quantitative criteria also enables the relationships between the environmental characteristics of each habitat type and their associated biota to be explored in a statistically rigorous manner. The use of objective or partially-quantified environmental criteria in several existing nearshore habitat classification schemes thereby restricts the extent to which they can be used for predicting the composition of biotic assemblages at other locations in a region (*e.g.* Dethier 1992, Allee *et al.* 2000, Roff and Taylor 2000, European Environment Agency 2002).

Several different approaches to identifying habitats in marine coastal waters have been undertaken previously in Australia. Many of these approaches have been based primarily on producing a map for a particular area containing "habitat units" which have been delineated on the basis of one or more physical, and in some cases, biotic, characteristic(s). Some of these mapping approaches have been carried over large spatial scales and contain broad classifications of habitats, such as the Interim Marine and Coastal Regionalisation of Australia (IMCRA; IMCRA Technical Group 1998), which is a nested scheme devised for use at a national scale. However, even at its finest level, this scheme provides only a coarse segregation of the Australian coast into broad "bioregions", which rarely provide sufficient detail to be useful for local environmental managers. Moreover, since these bioregions were delineated for each state by employing a Delphic approach and were thus based on varying combinations of qualitative physical and biological information, only limited comparisons can be drawn between different bioregions. Numerous other marine habitat maps have been devised for particular coastal regions in Australia, including those by Edyvane (1999) for South Australia, Ferns *et al.* (1999) and Ferns and Hough (2002) for Victoria and Barrett *et al.* (2001) for south-eastern Tasmania. However, the habitats in some of these studies have been delineated mainly on the basis of descriptions of their geophysical features and/or data for substrate type, including any associated vegetation. In those studies where data for more than one type of physical parameter was employed, such information was not combined to provide a suite of features that could be used collectively to define a "habitat type". Thus, as the approaches adopted in the above studies do not provide a systematic classification framework or set of criteria that can be used to allocate sites outside the mapped area to a habitat type, they are not predictive. In contrast, Banks and Skilleter (2002) recently employed a hierarchical classification scheme to identify the range of habitat types in intertidal waters along a regional stretch of coastline in Queensland, which was based on that developed in North America by Howes *et al.* (1994) and Dethier (1992), and which used mainly descriptive physical criteria.

The aim of this component of the study was thus to develop a readily usable and quantitative approach for classifying the different types of habitats in the nearshore marine waters along the lower west coast of Australia to be classified. This approach involved a novel use of the BVSTEP routine in the PRIMER v5.2 multivariate statistical package (Clarke and Gorley 2001, Clarke and Warwick 2001a) to select the subset of easily-recordable and enduring environmental characteristics that would most readily discriminate among the range of habitat types in this region, which had initially been categorised on the basis of broad criteria considered likely to influence the distribution of nearshore fish. It was envisaged that this classification scheme, when allied with information on the composition of fish assemblages in the different habitat types, would enable managers and ecologists to predict which fish species are likely to occur at any location along this coastline on the basis of values for a selected suite of enduring environmental criteria.

3.2 Materials and Methods

3.2.1 Designation of nearshore habitat types

After obtaining a thorough knowledge of the geophysical and submerged aquatic vegetation characteristics of the waters along the lower west coast of Australia from both existing scientific literature and field-based observations, 25 nearshore sites were selected for study that were considered to represent examples of the range of physical variability in this coastal region (Fig. 2.1). A subjective visual assessment of the overall level of wave activity, and the extent to which seagrass and reefs are present in nearshore waters at the 25 study sites, suggested that it was appropriate to separate those sites into the following six broad *a priori* habitat types. Each habitat type was represented by at least three sites (Fig. 2.1).

1) Highly sheltered from wave activity, with the substrate containing areas of dense seagrass within 50 m of the shoreline and also further offshore (Plate 3.1).
2) Moderately sheltered from wave activity, with the substrate containing patches of sparse seagrass within 50 m of the shoreline and also further offshore (Plate 3.2).
3) Moderately exposed to wave activity, with no seagrass in the vicinity (Plate 3.3).
4) Moderately exposed to wave activity, with dense seagrass beds located more than 50 m from the shoreline (Plate 3.4).
5) Moderately to fully exposed to wave activity, with reefs present within 50 m of the shoreline and also further offshore. Vegetation largely restricted to macroalgae associated with reefs (Plate 3.5).
6) Fully exposed to substantial wave activity, with no seagrass in the vicinity (Plate 3.6).

Although habitat types 3–5 are each described as moderately exposed, the level of wave activity increases progressively between those habitat types. Note that the above levels of wave activity reflected the following categories of typical modal wave heights (*i.e.* the most frequently occurring wave height in a series of observations), which have been based on local expert knowledge (I. Eliot, pers. comm.). Highly sheltered ≤ *ca* 15 cm; moderately sheltered = *ca* 15 24 cm; moderately exposed = *ca* 25-44 cm; moderately to fully exposed = *ca* 45-54 cm and fully exposed ≥ *ca* 55 cm.

Plate 3.1 Example of habitat type 1 along the lower west coast of Australia, *i.e.* highly sheltered from wave activity, with the substrate containing areas of dense seagrass within 50 m of the shoreline and also further offshore.

Plate 3.2 Example of habitat type 2 along the lower west coast of Australia, *i.e.* moderately sheltered from wave activity, with the substrate containing patches of sparse seagrass within 50 m of the shoreline and also further offshore.

Plate 3.3 Example of habitat type 3 along the lower west coast of Australia, *i.e.* moderately exposed to wave activity, with no seagrass in the vicinity.

Plate 3.4 Example of habitat type 4 along the lower west coast of Australia, *i.e.* moderately exposed to wave activity, with dense seagrass beds located more than 50 m from the shoreline.

Plate 3.5 Example of habitat type 5 along the lower west coast of Australia, *i.e.* moderately to fully exposed to wave activity, with reefs present within 50 m of the shoreline and also further offshore. Vegetation largely restricted to macroalgae associated with reefs.

Plate 3.6 Example of habitat type 6 along the lower west coast of Australia, *i.e.* fully exposed to substantial wave activity, with no seagrass in the vicinity.

A range of enduring environmental variables, *i.e.* which exhibit either no or minimal variation throughout the year, were then quantified for each of the 25 sites. These 27 variables, which are presented in Table 3.1, generally reflected the following two attributes.

The physical setting of each site, and hence its predisposition to exposure to wave activity generated either by large wind systems in offshore waters, *i.e.* oceanic swell, or locally by prevailing winds, *i.e.* seas. The compass directions along which both ocean swell and local wind variables were measured reflects the prevailing oceanographic climate and onshore wind conditions in both summer and winter on the lower west Australian coastline (see subsection 2.3 in Chapter 2). Variables in this group also include those that are important for determining how the height and behaviour of waves may be modified as they approach the shoreline. Data for the wave refraction coefficients were derived from wave refraction charts for this coastal region (P.W.D., W.A.; 52609-1-4; 52609-1-9; 52609-1-15; 53072-1-0; 53072-1-2; and 53072-1-5). Quantitative data for the remaining physical setting variables were derived from readily available bathymetric charts (Aus 112; Aus 11; Aus 755; DMH 277; DMH 449; P.W.D., W.A. 51346; P.W.D., W.A. 51347).

The type of nearshore substrate and the location and extent of any seagrass and/or nearshore reefs. The percentage contributions made by bare sand, bare silt, intertidal and subtidal reefs and seagrass beds to the waters within a 500 m radius from the central point on the shoreline at each site were determined from digitally-mapped habitat data (Bowman Bishaw Gorham 1994, Department of Environmental Protection 1996). The information for these variables could also be obtained from aerial photos of this nearshore region.

3.2.2 Statistical Methods

3.2.2.1 Data transformation and Multidimensional Scaling Ordination

Data for each of the 27 quantified environmental variables at the 25 sites were examined for both their conformity to the ideal of exhibiting continuous, univariate normal behaviour and the extent of their correlation with each of the other variables by the use of pairwise "Draftsman plots" as described in the PRIMER v5.2 statistical package (Clarke and Gorley 2001). Normality would be reflected by both a linear relationship and an even distribution of samples between the variables in these scatter plots. However, for many of the environmental variables, such assumptions were, at best, only approximate, as several are highly discrete with few categories, while others are heavily skewed. This problem was ameliorated through an appropriate transformation (see Table 3.1). The correlation coefficients that were calculated between each pair of the 27 environmental variables were not particularly high in any case and thus all data were retained for further analysis.

Table 3.1 Quantitative environmental variables, representing both the physical characteristics that influence the extent of nearshore wave activity and the relative contribution of different substrate types (including any vegetated or reef areas), recorded at each of the 25 sites along the lower west coast of Australia. The units in which each variable was measured and the type of transformation to which they were subjected prior to data analysis is also provided.

Variable	Unit of measurement	Type of transformation	Physical setting (extent of wave activity)			Substrate
			seas	swell	wave behaviour	
Aspect	degrees	deviation from 100°	•	•		
[a] Direct fetch	km	square-root	•			
[a] S fetch	km	square-root	•			
[a] NW fetch	km	square-root	•			
[a] W fetch	km	square-root	•			
[a] SW fetch	km	square-root	•			
[a] WNW fetch	km	square-root	•			
[a] WSW fetch	km	square-root	•			
[a] SSW fetch	km	square-root	•			
[b] Min. distance from shore to 2 m depth contour	km	square-root			•	
[b] Max. distance from shore to 2 m depth contour	km	square-root			•	
Number of offshore reef chains	number	none		•		
[c] Continuity of reef chain 1	score	none		•		
[c] Continuity of reef chain 2	score	none		•		
[d] % of island in W-SW arc	%	square-root		•		
[d] % of 1st reef chain at 0-5m depth in W-SW arc	%	square-root		•		
Distance from shore to 1st reef chain along W transect	km	none		•		
Distance from shore to 1st reef chain along SW transect	km	none		•		
Mean of water depths recorded at 500 m intervals from shore to 1st reef chain along W transect	m	none			•	
Mean of water depths recorded at 500 m intervals from shore to 1st reef chain along SW transect	m	none			•	
[e] Refraction coefficient for swell waves with W approach	unitless	none			•	
[e] Refraction coefficient for swell waves with SW approach	unitless	none			•	
[f] sand	%	fourth-root				•
[f] silt	%	fourth-root				•
[f] intertidal reef	%	fourth-root				•
[f] subtidal reef	%	fourth-root				•
[f] seagrass	%	fourth-root				•

[a] fetch exceeding 100 km was recorded as that maximum value.

[b] represents water depth at which waves approaching the lower west coast of Australia are likely to begin shoaling (I. Eliot, pers. comm.).

[c] based on a visual assessment of bathymetric charts. Scored 1 if discontinuous or 2 if relatively continuous. Two major reef chains, *i.e.* Garden Island Ridge (reef chain 1) and Five Fathom Bank (reef chain 2) were located offshore of those sites located between 31°55'S and 32°32'S, while only one major reef system, *i.e.* Marmion Reef, was located offshore of those sites between 31°41'S and 31°52'S (see Fig. 2.1).

[d] the "W-SW arc" was based on transects drawn from the shoreline at each nearshore site to reef chain 1 (which sometimes encompassed islands as landward expressions of this reef chain) in both W and SW directions, and quantifying the contribution of each reef depth category in the stretch that lay between those two transects.

[e] refraction coefficient $(K_r)=(b_0/b_1)^{0.5}$, where b_0=wave ray spacing in deeper water; b_1=wave ray spacing in shallower water (Carter 1988).

[f] based on the percentage contribution of each type of substrate, reef or extent of seagrass to the waters within a 500 m radius from the central point on the shoreline at each site.

Since the environmental variables were measured in different units and the distances calculated between each of the points in a high-dimensional space were thus meaningless, it was essential to normalise the data for each variable (*i.e.* by subtracting the mean of a variable from each measurement and dividing that value by the standard deviation), after the appropriate transformation, where necessary, had been carried out. After normalisation, each environmental variable is set to have a mean of zero and a variance of unity across each of the sites, so that the values for each of those variables range from approximately –2 to +2 (dimensionless units). Each variable therefore had the propensity to contribute equally to the subsequent distance matrix, which is sometimes undesirable, but is largely unavoidable with mixed units.

The distance matrix containing each pair of the 25 sites, calculated from normalised Euclidean distances and using all 27 environmental variables, was displayed as a two dimensional multidimensional scaling (MDS) ordination, from which the tendency for the sites to be distributed into the same groups as those of the *a priori* habitat classification could be informally assessed. Since this ordination technique was based on Euclidean distance as its dissimilarity measure, the same normalised distance matrix, similarly transformed, could be subjected to a Principal Component Analysis (PCA).

The formal demonstration that the quantitative information and the *a priori* habitat classification were related was achieved by the ANOSIM test (Clarke 1993). This test, which operates directly on the Euclidean distances rather than on the ordination plot, was thus used to test the null hypothesis that, based on the full set of 27 environmental variables, the *a priori* habitat classification was unrelated to the among-site distances. The null hypothesis was rejected if the significance level (p) was <5%. The extent of any significant differences yielded by this test were determined using the R-statistic value, the values for which can range from +1, *i.e.* all samples within each of the groups are more similar to each other than to any of the samples from other groups, down to approximately zero, when average similarities between and within groups are the same (the null hypothesis). Small negative values for R are possible by chance under the null hypothesis, but are not generally interpretable since they correspond to similarities being smaller between groups than within groups, and the ANOSIM test for R is thus one-sided (Clarke 1993).

Given that the above null hypothesis was decisively rejected, it was then valid to ask whether the full set of 27 variables was essential to delineate the habitat groups, or whether a smaller subset would be more convenient for future recording and classification purposes. Indeed, a reduced set of variables might enhance the habitat distinctions by removing ‘noise’ variables and thus allowing the ‘signal’ to be more readily perceived. This proposition was tested by using, in the following novel way, the BVSTEP routine in the PRIMER v5.2 software

(Clarke and Gorley 2001). It should be noted that, since BVSTEP is a relatively new statistical routine and that its application in this component of the study was unique, a detailed account of the properties and use of this procedure is provided in the following subsection. This account was prepared with the assistance of K.R. Clarke.

3.2.2.2 The use of BVSTEP

A model matrix of "distances" between each pair of the six habitat types in the original and subjective *a priori* classification was first constructed, solely on the basis of scored data that reflected the perceived and relative level of difference between them. This triangular matrix contained, for each pair of habitat types, the sum of their scores from both a simple wave exposure gradient and a substrate type gradient (including seagrass and reef areas). The magnitude of the scores in each of these gradients reflected a subjective assessment of the extent of differences between the respective characteristics of each of the habitat types. The exposure and substrate gradients ranged from 0 to 2 and 0 to 1.5, respectively, with intervals of 0.5 (Tables 3.2a and b, respectively). Thus, for any pair of habitat types, the exposure score was determined by taking the absolute difference between the individual scores for each of the habitat types, and the substrate score was obtained from a scored triangular matrix containing each of the substrate categories. The sum of the distance scores from the two gradients for any pair of habitat types ranged from 1 to 3.5, with greater scores representing greater environmental differences between habitat types. For example, habitat type 1, defined as highly sheltered from wave activity with dense seagrass beds near the shoreline, was placed at 2.0 units distance from habitat type 2 (moderately sheltered with a largely unvegetated substrate), by summing the absolute difference of the respective scores from the exposure gradient, *i.e.* $|0\text{-}0.5| = 0.5$ (see Table 3.2a), and the substrate gradient, *i.e.* 1.5 (see Table 3.2b). Similarly, habitat type 1 was placed at 2.5 units from habitat 3 (moderately exposed and with an unvegetated substrate) and 3.5 units from habitat 6 (fully exposed and with an unvegetated substrate). This scored distance matrix was then expanded to include each of the 25 sites, which were scored according to the habitat type to which they had originally been assigned. Pairwise combinations of sites from the same habitat type were scored 0.

The next step involved taking subsets of the 27 quantitative environmental variables, appropriately transformed (see subsection 3.2.2.1 and Table 3.1), and linking them to the scored model matrix in order to determine how well that particular subset of variables captured the broad distinctions among the groups of *a priori* habitat types in the model matrix. This was accomplished in the BVSTEP procedure by calculating a triangular matrix of normalised Euclidean distances between each pair of the 25 sites, as described in subsection 3.2.2.1, but using only the particular subset of quantitative environmental variables under consideration. This distance matrix was then compared with the model matrix by unpeeling the elements of both matrices in a consistent order (*i.e.* by rows) into single columns, which were then correlated using Spearman's rank correlation (ρ). This coefficient is appropriate for two reasons. Firstly, this ranking correlation overcomes the potential problem of the two matrices being expressed in different units, *i.e.* one is a simple 8-point scale of equal steps, whereas the other is a continuous distance measure, and consequently there would be no reason to expect their elements to scale linearly in relation to each other. Secondly, by using Spearman's rank correlation, only the rank orders of the elements of the two distance matrices are exploited. This is precisely the same information that is used in a (low-stress) non-metric MDS based on quantitative data, and represents a convenient way of approximating the overall site inter-relationships in a low-dimensional plot. Thus, a subset of variables giving a high value of ρ will also generate a large ANOSIM R-statistic (*i.e.* high separation of the groups), relative to other subsets. The calculation of the ρ statistic for the model matrix can be regarded as an extension of the ANOSIM R-statistic to cases where, under the alternative hypothesis, there is some partial ordering structure on the various groups.

Table 3.2a Scores representing a subjective assessment of the level of wave activity at the six *a priori* habitat types along the lower west coast of Australia.

0	**0.5**	**1**	**1.5**	**2**
Highly sheltered	Moderately sheltered	Moderately exposed	Moderately exposed to fully exposed	Fully exposed

Table 3.2b Scores representing a subjective assessment of the level of difference between each of the main substrate types (including seagrass and reef) at the six *a priori* habitat types along the lower west coast of Australia.

	Unvegetated	Nearshore seagrass	Offshore seagrass	Reef
Unvegetated	**0**			
Nearshore seagrass	**1.5**	**0**		
Offshore seagrass	**0.5**	**1**	**0**	
Reef	**1**	**1.5**	**1**	**0**

Ideally, the procedure would then examine all possible subsets of the quantitative environmental variables and compute the Spearman ρ statistic between the resulting among-site distances and the scored model matrix. The subset which maximises the value of ρ is the one with collective properties that best capture, in quantitative terms, the subjective *a priori* habitat distinctions as represented by the model matrix. However, since there are a vast number of possible subsets with 27 variables (*i.e.* 2^{27}-1), an alternative procedure is adopted in BVSTEP to avoid having to search for all of those subsets. This procedure involves a forward and backward-searching stepwise algorithm of a type that is common in stepwise multiple regression. Firstly, the single environmental variable, *e.g.* (a) with a distance matrix that best matches the model matrix is selected, after which each of the remaining variables is scanned sequentially to find the one (b) which, when combined with the first selected variable, optimises the value of ρ. A further variable (c), which accounts for the greatest increase in ρ, is then added. At this point, the backward-stepping part of the algorithm is invoked to check that the combination b+c, which has not been considered up to this point, does not provide a better match to the model matrix, *i.e.* results in a higher ρ value. If this is the case, the forward-stepping part of the algorithm then searches for the next best third component (d), which, by definition, must improve on the combination a+b+c, and then moves on to the fourth added variable (e). Potentially, there are now up to two backward-stepping moves before forward selection again continues (*e.g.* b might now be dropped and then c, the combination d+e never having been considered at an earlier stage). The algorithm proceeds in this way until the addition of no single variable to the already retained set results in an increase in the value of ρ. At this point, the search terminates. The BVTSEP routine was restarted several times (*i.e.* using all, none or a randomly chosen set of variables, and thus involving either sequential addition or deletion of variables during the stepwise search), to ensure that the subset of variables selected by the procedure was the best solution attainable.

The above procedure thus selects the subset of quantitative environmental variables that maximise the differences between each of the six habitat types. These variables were used to construct a Euclidean distance matrix, computed between sites, which was then subjected to non-metric MDS ordination. The resultant plot thus displayed the sites representing each of the six habitat types at relative distances from each other in a manner that best reflects the distances in the *a priori* model matrix. The quantitative values for each of the selected environmental variables at each of the sites were also displayed as circles of proportional sizes over the corresponding points for those sites on the ordination plot. This allowed an immediate visual interpretation of the relative contributions made by each of the selected variables to the optimal configuration, based on the subset as a whole.

3.2.2.3 Nearest-replicate classification

The ready allocation of a further nearshore site (*i.e.* outside those used in the present study) to one of the six habitat types, required a classification of the existing 25 sites in a low-dimensional space which can be easily visualised. The use of formal discriminant analysis was impossible here, partly because the standard multivariate normality and constant variance-covariance matrix assumptions were difficult to justify. However, even more importantly, such an approach would lead to non-identifiability, *i.e.* the presence of an insufficient number of observations to be able to estimate the various parameters. Thus, a more *ad hoc* procedure was required, and a simple but effective possibility was provided by the use of "nearest-replicate" classification in the two-dimensional principal component space derived from the subset of environmental variables selected by the BVSTEP routine. The procedure involved the following steps.

(a) Perform a 2-d PCA using the normalised Eucliudean distance matrix created from the appropriately-transformed subset of environmental variables for the 25 sites, *i.e.* the same distance matrix that was subjected to MDS in subsection 3.2.2.1. This provided the first two principal component axes, PC1 and PC2, as simple linear functions of those environmental variables.

(b) Graph the resulting 2-d configuration of the 25 sites, *i.e.* as replicate points coded according to habitat type (1-6), plotted on the first two PC axes.

(c) Construct the Voronoi tessellation for the 25 replicate points in this 2-d PC space, *i.e.* surround each replicate by an area consisting of all points which are closer to that replicate than to any other replicate. These areas are convex polygons dividing the whole 2-d plane.

(d) Join up all polygons that represent a replicate from the same habitat type, thus creating a division of the total 2-d space into six regions representing each of the six habitat types.

(e) A useful refinement is to define a seventh region which was considered to be "outside previous experience" of the six habitat types. This was achieved by surrounding each of the 25 replicate points by a circle of threshold diameter, the threshold being taken as the maximum distance between any two replicates from the same habitat type. Any points that fell outside all such circles were considered to be outside previous experience.

The measurements for the subset of environmental variables selected by the BVSTEP routine for any future nearshore site can then be converted into their 2-d PC co-ordinates, using the linear functions referred to in (a) and plotted as a point in the PCA space. Its allocation to a habitat type is simply dictated by the region of that space into which it falls.

3.2.2.4 Misclassification rates

A measure of how successful the classification scheme was likely to be when allocating future nearshore sites to one of the seven types (*i.e.* habitat types 1-6 and the one outside previous experience), was gauged by a "leave one out" approach, usually referred to as "jack-knifing". Thus the first replicate was omitted and the regions redrawn, as described above in steps (c) to (f), based on the remaining 24 points alone (the PCA construction itself was not recomputed). The omitted replicate was then regarded as the future point in step (f), and allocated to one of the seven categories. The whole procedure was then repeated, omitting replicate two rather than one, then replicate three, four *etc*. The effect of categorising each of the 25 jack-knifed points is presented in a misclassification Table , describing the number of occasions a point is correctly or incorrectly classified and, if the latter, to which group(s) it was assigned (Table 3.3). Although this is a useful way of approximating the misclassification rates, it is generally conservative, especially for small numbers of replicates per group (as is the case in this study). It is thus likely to overestimate substantially the true error rate, as can be seen by considering what happens when the original classification uses only one replicate per group, *i.e.* the jack-knife procedure must then misclassify all points! On the other hand, for larger numbers of replicates, it will converge to a realistic assessment of the true misclassification rate.

Table 3.3 Classification table for allocating each of the 25 nearshore sites along the lower west coast of Australia to one of the six habitat types under jack-knifing.

		Allocated habitat type					
		1	**2**	**3**	**4**	**5**	**6**
True habitat type	**1**	4	1	0	0	0	0
	2	0	3	1	0	0	0
	3	0	1	0	2	0	1
	4	0	0	0	5	0	0
	5	0	0	0	0	2	1
	6	0	0	1	0	0	3

3.3 Results

3.3.1 MDS ordination and BVSTEP

The use of Draftsman's plots showed that some of the environmental variables, such as the distance from the shoreline to the first offshore reef chain along a westerly transect and the refraction coefficient for swell waves with a westerly approach, did not require transformation. Others, such as the values for fetch in various compass directions, required a square-root transformation, and yet others, such as the percentage contributions made to the substrate surface by sand and silt required a fourth-root transformation (Table 3.1). Each of the values recorded for beach aspect, which were measured as a compass bearing, were "linearised" by expressing them as the number of degrees by which they deviated from an arbitrary value of 100º.

When the data for each of the 27 environmental variables had been appropriately transformed (where necessary), normalised and subjected to MDS ordination, the points for sites representing habitat types 2, 4 and 6 formed tight and relatively discrete groups (Fig. 3.1a). The points for four of the five sites representing habitat type 1 lay to the right of those for habitat type 2, while those for sites representing habitat types 3 and 6 lay immediately to the left of those for habitat type 2 and almost invariably below those for habitat type 4. The relatively dispersed points for the three sites representing habitat type 5 lay either immediately above or to the left of those for habitat type 4 (Fig. 3.1a). There is thus a pronounced tendency for the groups representing habitat types 1, 2, 3, 4 and 5 to form a curve that moves from right to left and then upwards on the plot.

ANOSIM demonstrated that there were significant differences overall among the groups of sites representing the six habitat types (p=0.1%; Global R=0.639) and that, in each of the 15 possible pairwise comparisons, each habitat type was significantly different from all others (p=0.8-3.6%; R=0.969-0.61), except for habitat types 1 *vs* 2 (p=6.3%), 2 *vs* 3 (p=14.3%) and 3 *vs* 6 (p=51.4%). The lack of a significant difference between the sites representing the latter pair of habitat types was hardly surprising, given the extent to which their representative points intermingled on the ordination plot (Fig. 3.1a). In view of the significant differences in the quantitative environmental characteristics of the groups of sites representing the various *a priori* habitat types (*i.e.* both overall and in the majority of pairwise comparisons), focus was thus placed on determining whether a subset of the original 27 environmental variables would reduce the amount of "noise" in the multivariate analysis and thereby provide a clearer quantitative distinction among the *a priori* habitat types.

The model matrix containing scored data for the characteristics of each *a priori* habitat type (*i.e.* extent of exposure to wave activity and whether the nearshore substrate was largely unvegetated or contained areas of seagrass or reef), was subjected to MDS ordination. The points for the sites assigned to habitat types 1 and 5 lay towards the lower right-hand and upper left-hand corners of the plot, respectively, while those for habitat types 2, 3, 4 and 6 lay some distance away in the bottom left-hand corner of the plot (Fig. 3.1b). The BVSTEP routine was then used to match quantitative variables from the full suite of 27 environmental characteristics recorded at each of the 25 sites (*i.e.* that used to produce the ordination plot shown in Fig. 3.1a), with the model matrix formed using the scored data for the same 25 sites that represented the six *a priori* habitat types (*i.e.* those used to produce the ordination plot shown in Fig. 3.1b). The results of this procedure showed that the following subset of seven quantitative environmental

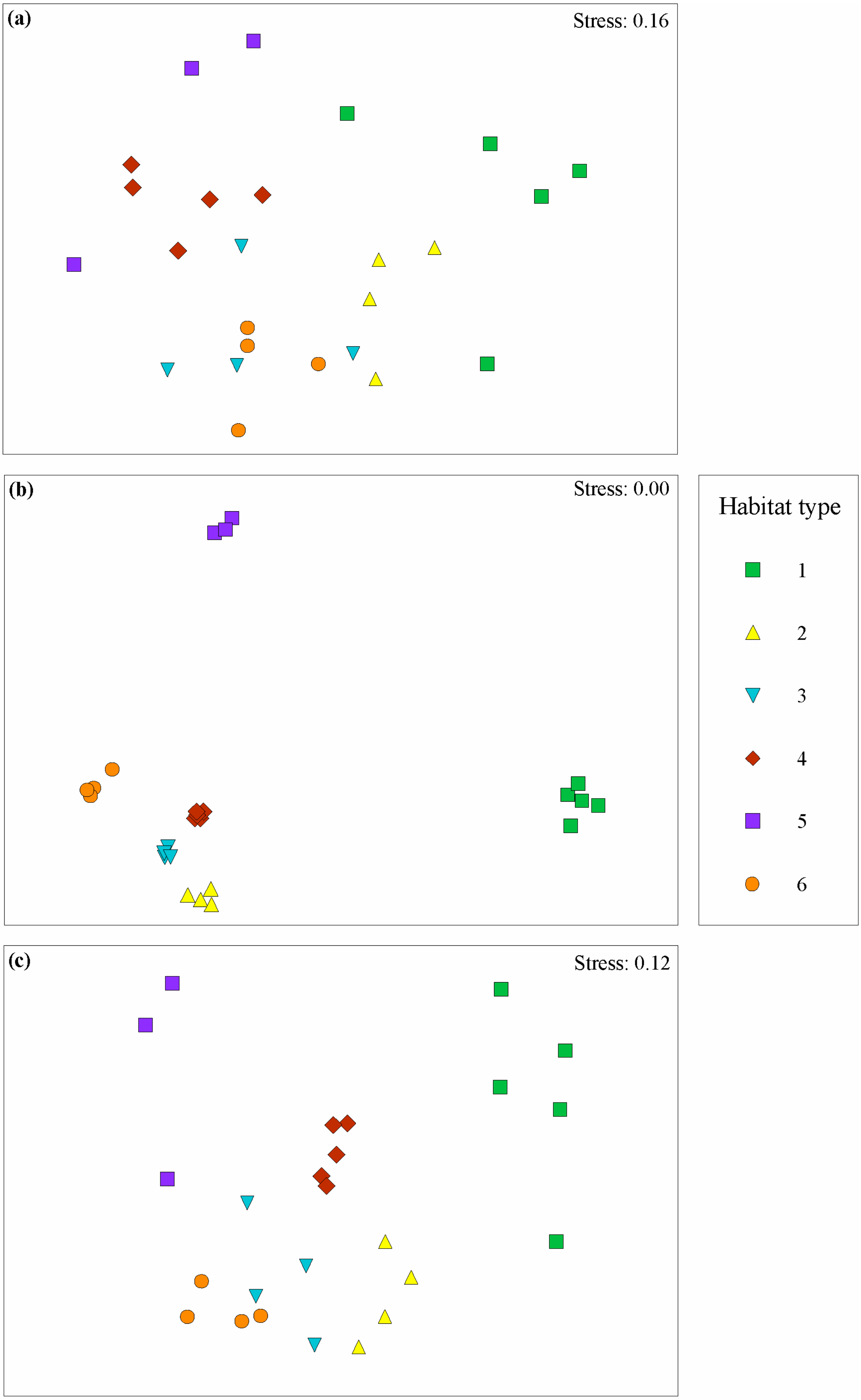


Figure 3.1: Two-dimensional MDS ordination of the values for (a) the full suite of 27 enduring environmental variables, (b) the scores reflecting the *a priori* criteria of the six habitat types and (c) the seven enduring environmental variables selected by the BVSTEP routine from the original full suite, recorded at the 25 nearshore sites along the lower west coast of Australia. Each site is coded for the *a priori* habitat type to which it was assigned.

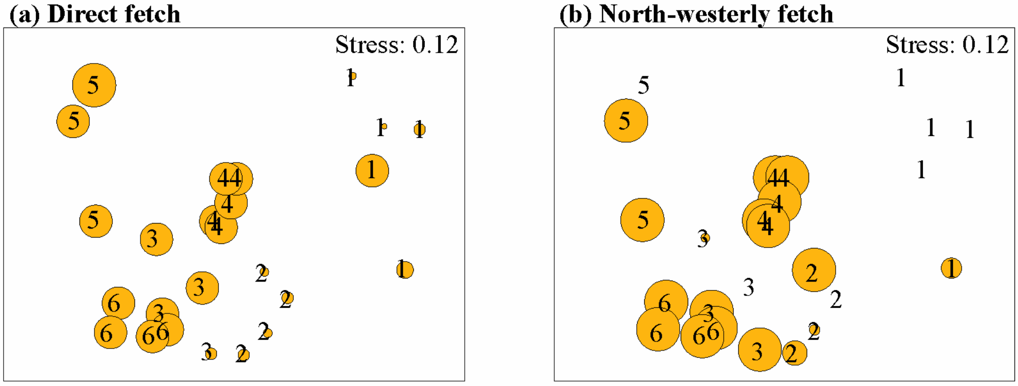
variables produced the best correlation (ρ=0.823) between the two matrices: direct fetch, north-westerly fetch, the minimum distance from the shoreline to the 2 m depth contour, the distance from the shoreline to the first offshore reef chain along a south-westerly transect, and the area of nearshore substrate covered by bare sand, subtidal reef and seagrass. Moreover, when these seven variables were removed from the suite of environmental data and the BVSTEP routine restarted with the remaining 20 quantitative variables, the maximum correlation that could be obtained was markedly lower, *i.e.* ρ=0.558. These results indicate that the seven quantitative variables listed above are clearly the most important for distinguishing among the six *a priori* habitat types.

The latter three of the seven variables selected by BVSTEP are each expressed as percentage contributions to a given nearshore area and are thereby related to some extent. However, it should be noted that, since five substrate categories (including seagrass and reef areas) were recorded in the study region overall and that the number and combination of these categories differed among the 25 sites, the extent of this relationship is not particularly strong. This contrasts with a hypothetical situation in which the substrate could only possibly be designated to one of two opposing categories, *e.g.* sand or not sand, in which case, the contribution made by each of the substrate variables to the nearshore area at each site would be inversely proportional, and no additional information would be provided by retaining both variables in the data matrix. In addition, the draftsman's plots that were constructed prior to data analysis (see subsection 3.2.2.1) demonstrated that the extent of the correlations between each pair of the five substrate variables were not particularly high. Moreover, the BVSTEP procedure does not require each of the variables used in the analysis to be completely independent (K.R. Clarke, pers. comm.).

When the data for the selected subset of seven environmental variables for each of the 25 sites were subjected to MDS ordination, the points for the sites representing each of the six habitat types formed distinct groups on the ordination plot, with those for habitat types 1 and 5 being particularly discrete and lying on the right and left-hand sides of the plot, respectively (Fig. 3.1c). The extent to which the relative magnitudes of each of the seven environmental variables varied amongst the 25 sites was reflected by the differences in the relative size of the circles superimposed on the corresponding points for those sites on this ordination plot (Figs 3.2a-g). Thus, direct fetch was almost invariably far less at the sites in the highly and moderately sheltered habitat types 1 and 2, respectively, than at those in the moderately to fully exposed habitat types 3–6 (Fig. 3.2a). Although the trends exhibited by north-westerly fetch were similar in most cases to those for direct fetch, marked variation in the extent of this variable was apparent among sites in habitat type 3 (Fig. 3.2b). The minimum distance from the shoreline

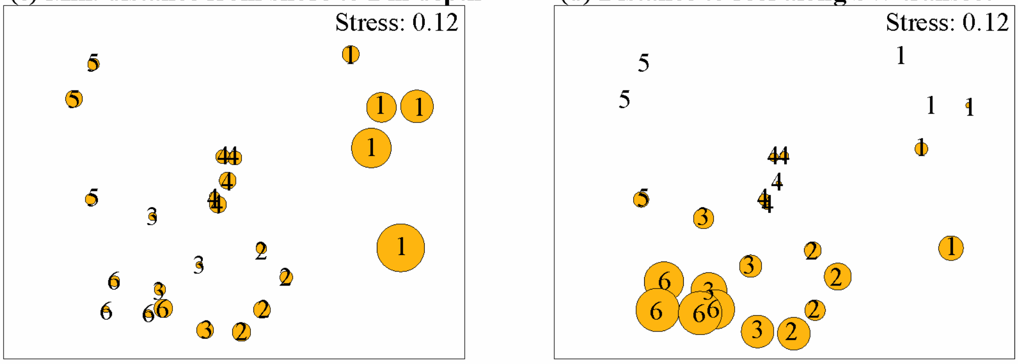
(a) Direct fetch

(b) North-westerly fetch



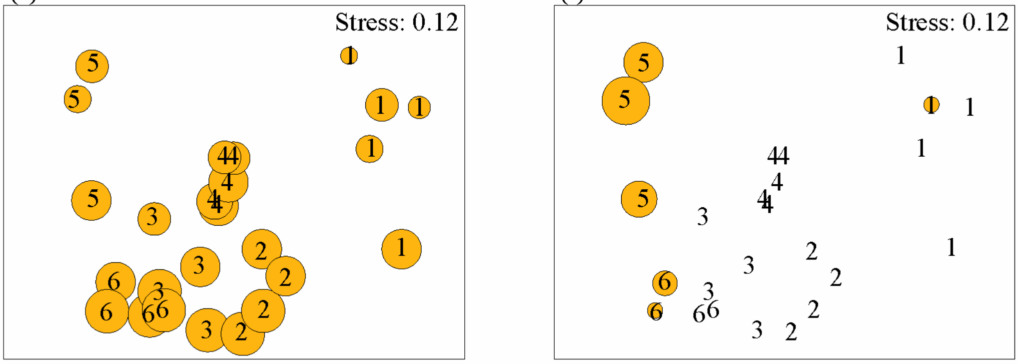
(c) Min. distance from shore to 2 m depth

(d) Distance to reef along SW transect



(e) % sand

(f) % Subtidal reef



(g) Seagrass

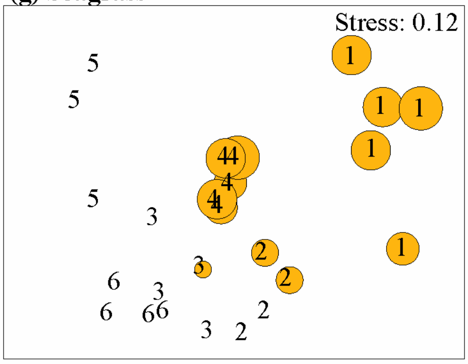


Figure 3.2: Two-dimensional MDS ordination of the values for the seven enduring environmental variables selected by the BVSTEP routine from the original full suite of 27. The values for each of the selected variables, namely (a) direct fetch, (b) north-westerly fetch, (c) minimum distance from the shoreline to the 2 m depth contour, (d) distance from the shoreline to the first offshore reef chain along a south-westerly transect and the relative areas of (e) bare sand, (f) subtidal reef and (g) seagrass covering the substrate, are superimposed as circles of proportional sizes over each of the 25 sites (coded 1-6 for habitat type).

to the 2 m depth contour was typically far greater at sites representing the highly sheltered habitat type 1 than at any of the sites in the other five habitat types (Fig. 3.2c). The distance from the shoreline to the first offshore reef chain along a south-westerly transect was consistently high at sites in the highly exposed habitat type 6 and low at sites representing the moderately exposed habitat types 4 and 5 (Fig. 3.2d). It was also usually low at the highly sheltered habitat type 1, and tended to be intermediate at sites in habitat types 2 and 3. The *a priori* categorisation of habitat type 1 as highly sheltered and of habitat type 5 as moderately to fully exposed, even though both are evidently in close proximity to offshore reefs, is explained by the fact that the sites in the latter habitat type lay within areas of exposed subtidal reef, rather than being located just on the landward side of a reef chain, as was the case with sites in the former habitat type. The extent of bare sand showed a marked tendency to be greater at sites in habitat types 2, 3, and 6 than at sites in habitat types 1 and 5 (Fig. 3.2e). Substantial areas of subtidal reef were found only at sites in habitat type 5 (Fig. 3.2f). Although seagrass was abundant at sites in habitat types 1 and 4 (Fig. 3.2g), it was located further from the shore in the latter, which accounts for the appreciable areas of bare sand found at sites in that habitat type (Fig. 3.2e).

3.3.2 Nearest-replicate classification

When the distance matrix that was used to produce the ordination plot shown in Fig. 3.1c was subjected to PCA, the relative distribution of the points for the 25 sites on the resultant two-dimensional plot was very similar to that produced by MDS ordination (*cf* Figs 3.3 and 3.1c). The PCA of the seven environmental variables (*i.e.* x_1 = direct fetch; x_2 = north-westerly fetch; x_3 = the minimum distance from the shoreline to the 2 m depth contour; x_4 = the distance from the shoreline to the first offshore reef chain along a south-westerly transect; x_5 = relative area of bare sand covering the nearshore substrate; x_6 = relative area of subtidal reef covering the nearshore substrate; x_7 = relative area of seagrass covering the nearshore substrate), after appropriate transformation, as previously described, gave the first two axes:

$$\mathbf{PC1} = 3.065 - 0.0732.x_1 - 0.0800.x_2 + 1.909.x_3 - 0.0887.x_4 - 0.932.x_5 - 0.0798.x_6 + 0.350.x_7$$

$$\mathbf{PC2} = 1.343 + 0.137.x_1 + 0.0142.x_2 - 1.015.x_3 - 0.0782.x_4 - 0.657.x_5 + 0.680.x_6 - 0.0994.x_7$$

Note that the (x_i) variables are on transformed scales but back-normalised, *i.e.* the (x_i) are not in normalised form in the above equations. The first two principal component axes accounted for 64.4% of the variability in the full matrix.

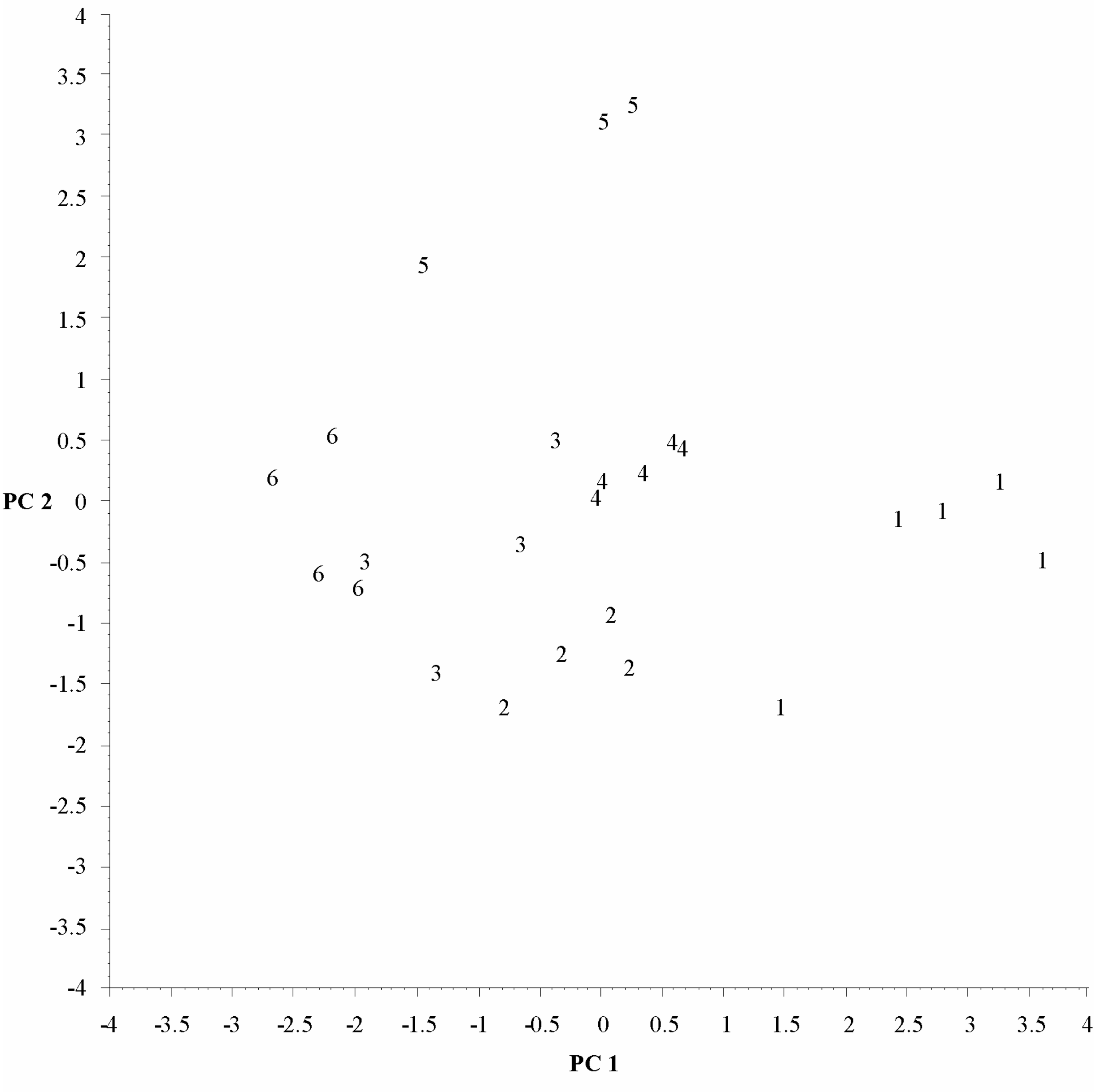


Figure 3.3: Two-dimensional PCA ordination of the values for the seven enduring environmental variables that were selected by the BVSTEP routine from the original suite of 27 variables, at each of the 25 nearshore sites. Each site is coded for the *a priori* habitat type to which was assigned (1-6).

The grid subsequently produced by the nearest-replicate classification procedure, using the location of sites on the PCA plot as a basis (see subsection 3.2.2.3), defined the extent of the area occupied by each of the six habitat types in two-dimensional space (Fig. 3.4). It also showed the area that could not be allocated to any of the existing habitat types, *i.e.* that area that was beyond the limits of any of the sites representing one of six habitat types identified in this study (coloured grey in Fig. 3.4). The habitat type of any other site along the lower west coast of Australia can thus be identified by (1) measuring, for that site, each of the seven environmental variables selected by the BVSTEP routine (see subsection 3.3.1), (2) inserting this suite of values into the above simple linear equations that define each of the PC axes and (3) plotting the resulting co-ordinates on the grid.

Table 3.3 shows the misclassification from jack-knifing the original 25 sites. These classifications were far from perfect, *i.e.* a success rate of 17 from 25 sites, and it was apparent that the group with the greatest propensity for misclassification was habitat type 3. This was also reflected in Fig. 3.4, where the area representing this habitat type lay between those for habitat types 2, 4 and 6, and the distance between replicates in habitat type 3 and those in other habitat types was sometimes less than within that group itself. However, as stated in subsection 3.2.2.4, the jack-knifing technique tends to be conservative and overestimate the true misclassification rate in cases such as this where the number of replicate points in each group is relatively small.

3.3.3 Removing the PCA step

Nearest-replicate classification can be performed in the full 7-d space of the seven selected environmental variables, without first needing to reduce these to a two-dimensional summary of the first two principal components. Steps (c) to (f), as described in the subsection 3.2.2.3 remain essentially unchanged in this case. To determine the habitat type of any other nearshore site along the lower west coast of Australia, one needs to compute how close its 7-d point is to those for each of the 25 sites in the existing classification. The new site is thus allocated to the habitat type of its nearest neighbour, or to the group outside previous experience if these distances all exceed the threshold determined by the maximum distance apart of replicates within a single habitat type. However, despite the removal of the approximation step implicit in working in 2-d principal component space, the jack-knife error rate did not improve in 7-d space, *i.e.* 8 from 25 sites. The loss of simplicity in no longer being able to view the areas representing each of the habitat types in 2-d space thus has no compensating gains in habitat classification success, and the simpler PCA-based approach was therefore preferred.

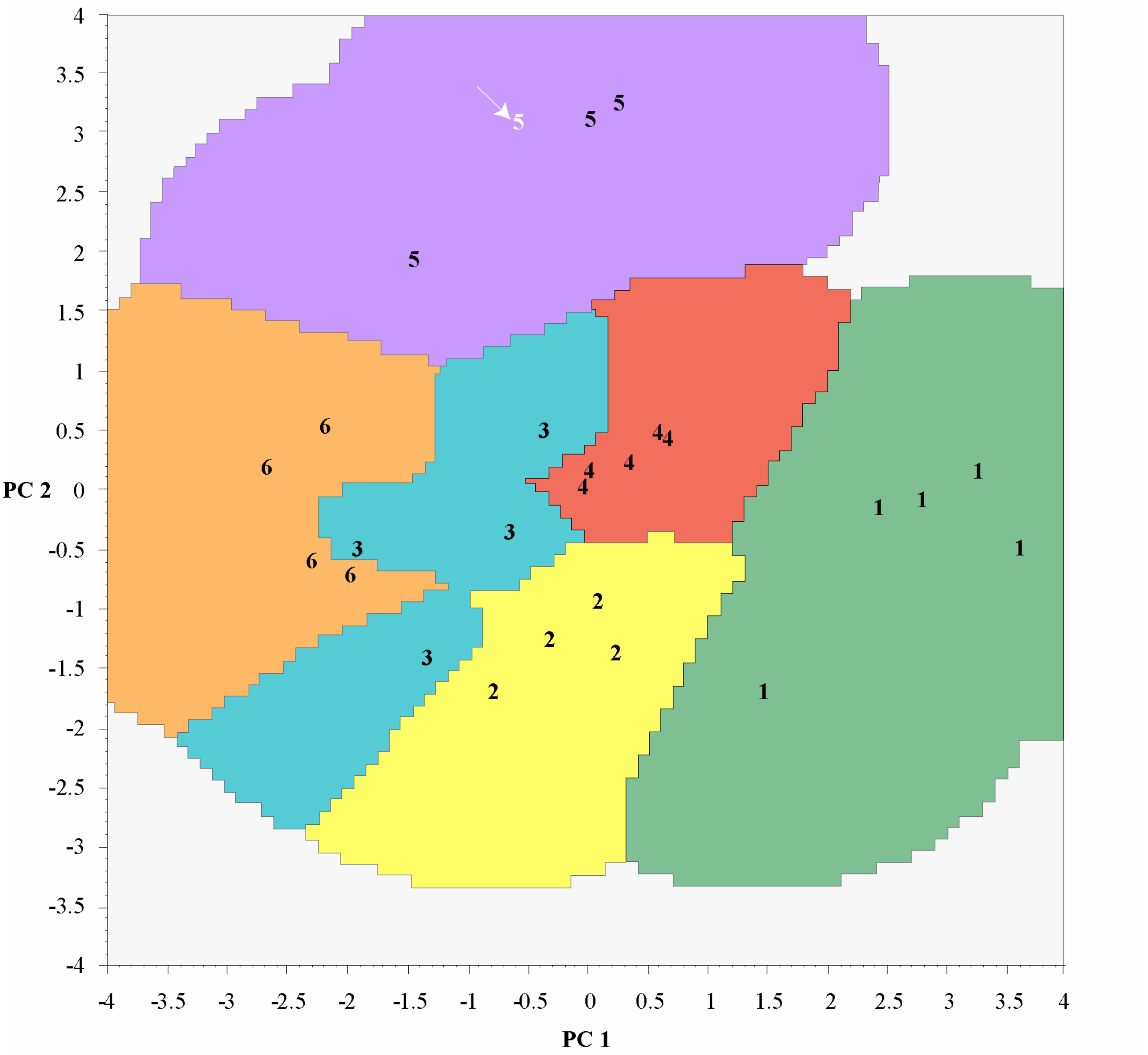


Figure 3.4: Grid of the area occupied by each of the six habitat types in 2-d space that was produced from both the PCA ordination of the selected set of seven environmental variables at the 25 nearshore sites and by the use of the nearest-replicate classification procedure. The example of a new site allocated to its habitat type is indicated by the white arrow. The grey area denotes that which could not be assigned to one of the six habitat types along the lower west coast of Australia.

3.4 Discussion

The statistical approaches adopted in this study verified that the initial and largely subjective separation of nearshore marine habitats along the lower west coast of Australia into six main types was appropriate, and that the classification scheme thus had a sound and quantitative basis. The use of a rigorous statistical approach was important because the initial habitat designations were made largely on the basis of visual criteria and, in the case of the degree of exposure to wave activity, were relative and subjective. Thus, if these broad descriptions were the only means by which any other site along this coastline could be assigned to a habitat type, the result would depend, to some extent, on personal interpretation of the precise meaning of those criteria and experience with the coastline. Furthermore, the use of quantitative criteria in a habitat classification scheme is essential if that scheme is to provide a sound basis for predicting which faunal species are likely to be found at particular nearshore sites in a region.

The measurement of a range of enduring environmental characteristics that would be likely to distinguish among the nearshore habitat types along the lower west coast of Australia was thus imperative to address the above criteria. However, for two reasons, the full suite of 27 variables did not prove entirely satisfactory. Firstly, this number of environmental variables is unwieldy and thus not readily usable by environmental managers. Secondly, ANOSIM did not detect significant environmental differences between three of the pairwise combinations of *a priori* habitat types. Yet, it is still important to note that the significant and relatively large environmental differences detected by ANOSIM among the six *a priori* habitat types, both overall and between 12 of the 15 possible pairwise comparisons, demonstrated that there was a valid and quantitative basis to the *a priori* classification that warranted further interpretation.

The above two problems were overcome by the use of the BVSTEP routine to remove “noise variables” and tease out a more manageable subset of environmental characteristics that provided a good quantitative basis for the largely subjective criteria employed in the *a priori* classification scheme and a clearer separation of the habitat type groups. The fact that the correlation between the distance matrix produced from the quantitative data for the seven selected environmental variables and the model matrix produced from the scored data for the *a priori* criteria was as high as 0.823, and that the former matrix produced distinct groups following MDS ordination, validated this approach.

It is important to recognise that the seven environmental variables selected by the use of the BVSTEP routine (and indeed all of the environmental variables used in this component of the study), were enduring and could thus be readily quantified over regional scales from easily obtainable sources, such as bathymetric charts or digitally-mapped benthic habitat data, the latter of which could have been obtained from aerial photographs. In other words, since the environmental variables quantified in this study were chosen to reflect both the physical setting of each site with respect to the surrounding geomorphology of the region and the type of nearshore substrate (including the extent of any seagrass or reef areas), the measurement of those variables did not require work to be undertaken in the field.

This contrasts with other schemes for classifying nearshore marine habitats. For example, the complex series of environmental characters developed by Hegge *et al.* (1996) for identifying beach morphotypes along the coast of south-western Australia necessitated the use of sophisticated field equipment and subsequent detailed analysis. Furthermore, unlike the criteria used in this approach, those employed by Hegge *et al.* (1996) were not intended to focus specifically on environmental characters considered likely to influence the distribution of fish or other nearshore fauna. The scheme devised by Schoch and Dethier (1996) for classifying intertidal habitats along the west coast of San Juan Island in Washington also requires the collection of a range of detailed environmental data from the field. Moreover, the scheme developed by these workers was devised using a stretch of coastline that was only 5 km in length, which would have probably been too short to facilitate a reliable extrapolation of their results to a regional spatial scale, *i.e.* at which it would be of greater use for environmental managers. The stretch of coastline selected for the present study, which was *ca* 130 km long, was selected specifically to accommodate the requirements of managers for a region that is highly populated, industrial in places and widely used for recreational purposes. However, the results of this study would almost certainly be valid for a certain distance to the north and south of this area.

The simplicity of the output of our approach to habitat classification is illustrated by the following example. A nearshore site requiring classification along the lower west coast of Australia is “western Penguin Island” (see Fig. 2.1), which, on the basis of the broad criteria outlined in subsection 3.2.1, would be assigned to habitat type 5, *i.e.* “moderately to fully exposed to wave activity with reefs present within 50 m of the shoreline and further offshore”. The values at this site for the seven environmental variables selected by the BVSTEP routine were as follows. Direct fetch = 100 km; north-westerly fetch = 100 km; minimum distance from the shoreline to the 2 m depth contour = 0.025 km; distance from the shoreline to the first offshore reef chain along a south-westerly transect = 0.125 km; and the relative areas of bare sand, subtidal reef and seagrass covering the nearshore substrate = 30, 69 and 0%, respectively.

Each of the values for these variables were then transformed appropriately (see Table 3.1), and the transformed values were inserted into the linear equations for the two PC axes (see subsection 3.3.2). Thus,

$$\mathbf{PC1} = 3.065 - 0.0732.(10.00) - 0.0800.(10.00) + 1.909.(0.16) - 0.0887.(0.12) - 0.932.(2.34) - 0.0798.(2.88) + 0.350.(0.00) = \mathbf{-0.58}$$

$$\mathbf{PC2} = 1.343 + 0.137.(10.00) + 0.0142.(10.00) - 1.015.(0.16) - 0.0782.(0.12) - 0.657.(2.34) + 0.680.(2.88) - 0.0994.(0.00) = \mathbf{3.10}$$

By plotting these coordinates onto the habitat type grid provided in Fig. 3.4, the site is readily, and quantitatively, allocated to habitat type 5.

It is important to note that, while the characteristics that were selected for distinguishing among the nearshore habitat types along the lower west coast of Australia would not necessarily be amongst the most relevant for separating nearshore habitats in other regions, the underlying approach developed during this study could be readily adopted for classifying habitats in nearshore marine waters elsewhere. Thus, the flexibility of this approach to habitat classification allows the physical data employed in the scheme to be easily changed to accommodate the particular environmental characteristics of nearshore waters in different geographical regions, *e.g.* presence of mangroves or coral reefs. Moreover, as the current scheme has been devised for use at a spatial scale that is sufficiently fine to incorporate local to regional variability in the physical characteristics of the nearshore environment, *i.e.* and thus at a level that is relevant for managers of this coastline, it can easily be incorporated into the lower level(s) of any common, hierarchical marine habitat classification framework that may be developed for Australia in the future (NOO and FRDC 2002).

The following chapters focus on elucidating the extent to which differences among the various nearshore habitat types along the lower west coast of Australia, as reflected by the statistically selected suite of seven enduring environmental criteria, were correlated with differences in the composition of the fish and invertebrate assemblages in examples of those habitat types.

Chapter 4. Non-enduring environmental characteristics of nearshore marine habitat types along the lower west coast of Australia

4.1 Introduction

Differences among nearshore marine habitats, and thus also their faunas, are the result of a combination of differences in hydrodynamic regime (*i.e.* the relative extent of wave, tidal, current and surge activity), substrate type and the extent to which the substrate contains associated physical features such as seagrass, macroalgae and/or reefs (Dethier 1992, Allee *et al.* 2000). Spatial variability in these environmental characteristics are fundamentally attributable to differences in the surrounding enduring geophysical structures, *e.g.* headlands, offshore reef chains or proximity to estuaries (*e.g.* Pyökäri and Lehtovaara 1993, Shih and Komar 1994, Carranza-Edwards and Rosales-Hoz 1995, Hegge *et al.* 1996, Shaghude and Wannäs 1998, Short 1999, Roff and Taylor 2000, Sanderson *et al.* 2000, Jackson *et al.* 2002). These can vary markedly over local spatial scales along heterogeneous coastlines such as the lower west coast of Australia (Hegge *et al.* 1996).

At any particular nearshore location, the hydrological and benthic components of the environment (*i.e.* substrate and any associated structural features) continuously interact, with the result that a change in one of those components produces a reciprocal change in the other. Thus, hydrodynamic forces provide the driving physical energy for eroding bedrock and transporting sediment, which is subsequently deposited at the limit of those forces. The type and extent of the water motion at any nearshore site thus determine the characteristics of the sediment (*e.g.* mineralogy and grain-size, particulate organic matter content and sediment penetrability) through the degree of physical weathering and the extent to which unconsolidated components of the substrate are kept suspended in the water column (*e.g.* King 1972, Calliari 1994, Carranza-Edwards *et al.* 1998, Bird 2000). In turn, the sedimentary deposits, and any seagrass beds or reefs, modify the extent and behaviour of hydrological processes in the nearshore environment through influencing wave shoaling, refraction and breaking and the circulation patterns of local currents (*e.g.* Fonseca and Cahalan 1992, Sanderson and Eliot 1996, Möller *et al.* 1999, Short 1999, Bird 2000, Doucette 2000). The interactions between the hydrological and benthic components of nearshore areas thus determine the morphology of any particular site along a coast (King 1972, Short and Wright 1983, Wright and Short 1984, Hegge 1994, Short 1999, Bird 2000).

Unlike surrounding enduring geophysical characteristics, the *in situ* hydrodynamic, sedimentological and morphological attributes at any given nearshore location are highly susceptible to temporal changes as a result of the large extent to which they depend on climatic conditions, *e.g.* wind conditions, rainfall and atmospheric pressure. Pronounced diel, seasonal and/or inter-annual differences in the morphology and hydrology of nearshore sites along the lower west coast of Australia have been reported by several workers, particularly during the strong and frequent local sea-breezes that occur along this coastline during the day in summer, (*e.g.* Masselink 1996, Masselink and Pattiaratchi 2001a, b), and by the strong low pressure mid-latitude cyclones which produce markedly higher swell waves and storm seas in winter (*e.g.* Kempin 1952, Eliot and Clarke 1986). Seasonal differences that have also been detected in the characteristics of nearshore sediments have been attributed to temporal differences in the extent of sediment weathering, shoreward drift from the seafloor and alongshore drift from adjacent coastal areas (*e.g.* Bird 2000).

Several other non-enduring environmental attributes of nearshore marine environments are likely to vary spatially along a stretch of coastline due to differences in their surrounding enduring environmental characteristics and to differ temporally due to changes in climatic conditions, *e.g.* the extent to which wracks of detached macrophytes accumulate on the beach face (*e.g.* Hansen 1984, Clark *et al.* 1996a, Ochieng and Erftemeijer 1999), water temperature and salinity (Clark *et al.* 1996a, Beyst *et al.* 2001a).

During this component of the study, a suite of non-enduring environmental parameters, which have been shown to influence the spatial and temporal distribution of nearshore fish and/or invertebrate faunas elsewhere (see earlier), were measured regularly at representatives of each of the six nearshore habitat types that had been identified along the lower west coast of Australia on the basis of quantitative differences in their enduring environmental characteristics (see Chapter 3, Valesini *et al.* 2003). These non-enduring variables were, topographic profile of the beach and nearshore zone, sediment parameters (*i.e.* grain-size, particulate organic matter content, penetrability and depth of the redox discontinuity layer), the volume of detached macrophyte accumulations on the beach face, water temperature and salinity. Collection of such data enabled us to test whether each of the non-enduring environmental variables differed significantly among habitat types (accounting for any confounding differences among zones and/or seasons). This facilitated an examination of whether such non-endiring data could be used as a reliable basis for identifying spatial differences anong the divergent habitat types present along this coastline. In the following chapters, the question will be addressed as to whether any such differences can further account for differences in the characteristics of fauna in those habitat types that have been identified along the lower west coast of Australia (see Chapter 3, Valesini *et al.* 2003).

4.2 Materials and Methods

4.2.1 Measurement of non-enduring environmental characteristics

A range of non-enduring environmental characteristics were measured at two representative sites of each of the six nearshore marine habitat types that were identified along the lower west coast of Australia (see Chapter 3, Valesini *et al.* 2003). These characteristics included the following.

(i) Topographic profile of the beach and nearshore area.

(ii) Sediment grain-size.

(iii) Particulate organic matter content of the sediment.

(iv) Penetrability of the sediment.

(v) Depth of the redox discontinuity layer, *i.e.* the point at which the interstitial spaces in the sediment become depleted of oxygen.

(vi) Collective volume of any accumulations of detached seagrass and macroalgae on the beach face.

(vii) Water temperature.

(viii) Salinity.

All of these *in situ* environmental variables were measured in each season between summer 2000 and spring 2001, except for the four sediment parameters (*i.e.* ii-v), which were measured seasonally only during 2000. Water temperature and salinity were measured during the day and night at each of the 12 sites on each sampling occasion, while the other environmental characteristics were measured only during the day, due either to the difficulty of measuring these variables at night (*e.g.* surveying beach profile or detecting all detached macrophyte accumulations), or to minimal diel variation in that characteristic, *e.g.* depth of the redox layer. Replicate measurements for all environmental variables, except topographic profile, were collected over *ca* 1-2 weeks in the middle of each season to reduce the chance of encountering atypical circumstances on any particular day that would unduly influence the resultant data.

The topographic profile of the beach and nearshore area at each site was surveyed along a transect that lay perpendicular to the shoreline. The transect extended from a fixed benchmark that was located landward of any dune vegetation, to water depths of *ca* 1.5 m, *i.e.* which usually included the first wave breaking zone, if present. On each sampling occasion, aluminium rods were inserted at all significant inflection points along the transect to mark those locations at which survey measurements should be recorded. These survey points typically included the following.

(i) Major features of any dune formations located immediately adjacent to the beach, *i.e.* dune crest, mid-point on the dune scarp and the base of the dune.

(ii) Seaward edge of any dune vegetation.

(iii) Crest(s) of any berm(s), *i.e.* the intersection between the flat, upper (landward) accreted portion of the beach face and the point at which the beach slopes seaward.

(iv) Location of the high water mark left on the beach face by the last high tide.

(v) Upper and lower extents of wave swash, *i.e.* the swash zone.

(vi) Location of the effluent line, *i.e.* the point at which groundwater intercepts the beach face, thus separating those areas on the beach face that contain sediment with unsaturated (landward) and saturated (seaward) interstitial spaces.

(vii) Landward and seaward extent of any accumulations of detached macrophytes on the beach face.

(viii) Crest, mid-scarp and base of any subtidal beach step or ridge and runnel formations.

(ix) Location at which incoming waves were breaking (where possible).

(x) The edge of any seagrass beds or areas of reef.

The typical morphology and location of many of the above morphological features on hypothetical beach profiles are documented in Hegge *et al.* (1996), Short (1999) and Bird (2000).

Survey points were also interspersed between some or all of the above features if they were separated by a distance of more than 5 m to ensure that the topography of the beach and nearshore area was measured in sufficient detail. Surveying was carried out using an automatic leveller (Sokkisha B-2), mounted on a tripod (Sokkisha), and a 5 m staff (Survey Chief, model AT). The tripod and level were deployed at an appropriate point along the transect and used to record height and distance (m) measurements from the staff. The staff was initially placed level with the fixed benchmark, then on the sand at the base of that benchmark and at all other marked survey points thereafter. All height and distance information that were recorded at each survey point was thus relative to the height at and distance from the fixed benchmark.

Samples were collected from three zones at each site for determining sediment grain-size and organic content. These zones differed in the extent to which they were covered with water during a tidal cycle, and were demarcated as follows. Zone A comprised the area between the most recent high tide mark and the effluent line, and thus represented that area on the beach face that is covered by at least wave swash during high tide, but where the interstitial spaces in the sediment are not fully saturated. Parts of this zone are thus exposed to the air during falling and low tides. Zone B was located between the effluent line and the lower (seaward) extent of wave swash zone. This zone was thus always subjected to swash activity and contained sediment that was fully saturated. Zone C was located in waters that were *ca* 1 m in depth, and was thus always fully submerged. The locations of these zones were based loosely on the zonation schemes for sandy beaches that were devised by Dahl (1952) and Salvat (1964). Three randomly-located sediment cores were taken from each of the three zones at each of the sites on each sampling occasion using a hand-held corer that was 3 cm diameter and sampled to a depth of 10 cm. The contents of each core were wet sieved through nested meshes of 2000, 1000, 500, 250 and 63 µm. A base pan was also placed at the bottom of these nested sieves to collect any sediment grains that were smaller than 63 µm. The sediment retained on each sieve was dried at 80°C for 12 h and then weighed in order to determine the percentage contributions of each grain-size fraction to each sample. Each of the sieve fractions were then ashed at 500°C for 2 h and reweighed to determine the amount of particulate organic material in each fraction.

The penetrability of the sediment was recorded by dropping a graduated iron rod from a fixed height through a polyvinyl chloride tube that was placed vertically on the substrate surface, and recording the depth (cm) to which the rod was driven into the sediment. Three replicate measurements were recorded in zones A, B and C at each site on each sampling occasion. The depth of the redox discontinuity layer, *i.e.* marked by a distinct change in sediment color that is easily detectable, was also recorded if it was within the first 15 cm of the substrate surface.

The volume of detached macrophytes that had accumulated on the beach face (*i.e.* between the base of the sand dunes and the seaward limit of the wave-swash zone), was measured along a 50 m transect running parallel to the shoreline at each site on each sampling occasion. The volumes of these macrophyte accumulations were estimated from the number of times containers of a known volume had to be filled to account for all of those accumulations. These measurements, which were considered proportional to the amount of detached plant material likely to accumulate in the nearshore waters at each site, were carried out on the beach face rather than in the nearshore waters to overcome the difficultly of measuring weed accumulations moving within the wave-breaking zone.

Three replicate measurements of water temperature (ºC) and salinity (‰) were recorded in the middle of the water column at each site on each sampling occasion using a Yellow Springs International Model 30 conductivity meter.

4.2.2 Statistical Analyses

4.2.2.1 Univariate analyses

The relationships between the means and associated standard deviations for percentage contribution of sedimentary particulate organic matter, penetrometer depth, volume of any detached macrophyte accumulations, water temperature and salinity were examined in order to ascertain the type of data transformation (if any) that would be required to satisfy the assumptions of constant variance and normality for ANOVA. The results of this procedure showed that, while no transformation was required for water temperature and salinity, the volume of detached macrophytes required $\log_{10}$ (n+1) transformation, particulate organic matter content a fourth-root transformation and the penetrometer depth and depth of the redox discontinuity layer a square-root transformation.

The replicate values for each of the environmental variables were then subjected to either three or four-way ANOVA to ascertain whether they differed significantly among habitat types, seasons and/or zones, years or day *vs* night. All replicate samples in each ANOVA were considered to be independent of each other, and all independent factors were regarded as fixed. The null hypothesis that the values for a dependent variable did not differ significantly among any of the independent variables was rejected when the significance level (p) was <0.05. When ANOVA detected a significant difference for an interaction term or a main effect that was not involved in any significant interaction, plots containing the marginal means and 95% confidence intervals of each level of the relevant factor(s) were used to ascertain the source of those differences. The data in these plots were back-transformed, where necessary, to allow them to be interpreted more easily. When ANOVA showed that there were significant differences in the values for a dependent variable among the levels of a main effect that was not involved in any significant interaction, Scheffé's *a posteriori* test was used to determine where those differences occurred.

4.2.2.2 Multivariate analyses

All of the following multivariate analyses were carried out using the PRIMER 5.2 statistical package (Clarke and Gorley 2001). The mean percentage contributions of each sediment grain-size fraction derived from the five replicate samples collected at each site on each sampling occasion were square-root transformed and used to construct a Bray-Curtis similarity matrix, which was then subjected to non-metric Multidimensional Scaling ordination (MDS). One way and two-way crossed Analysis of Similarities (ANOSIM; Clarke 1993) tests were used to identify whether there were any significant differences in the grain-size compositions of the various samples among habitat types, zones and/or seasons. The particular factors that were employed in each of these tests are provided in detail in subsection 4.3.2. When ANOSIM detected a significant difference on the basis of one of those factors, Similarity Percentages (SIMPER; Clarke 1993) was used to identify which grain-size fractions made the greatest contributions to those differences.

4.3 Results

4.3.1 Topographic profile in each habitat type, season and year

The topographic profiles of the beach and nearshore area recorded at each of the sites representing the six habitat types were plotted separately for each season in 2000 and 2001 to investigate the extent of any spatial and temporal differences in their morphology (Figs 4.1, 4.2). It should be noted that, while the height and distance of each survey point on those profiles is relative to the fixed benchmark at each of those sites, the profiles include only those data that were recorded at the seaward edge of any dune vegetation or the base of the dune formation.

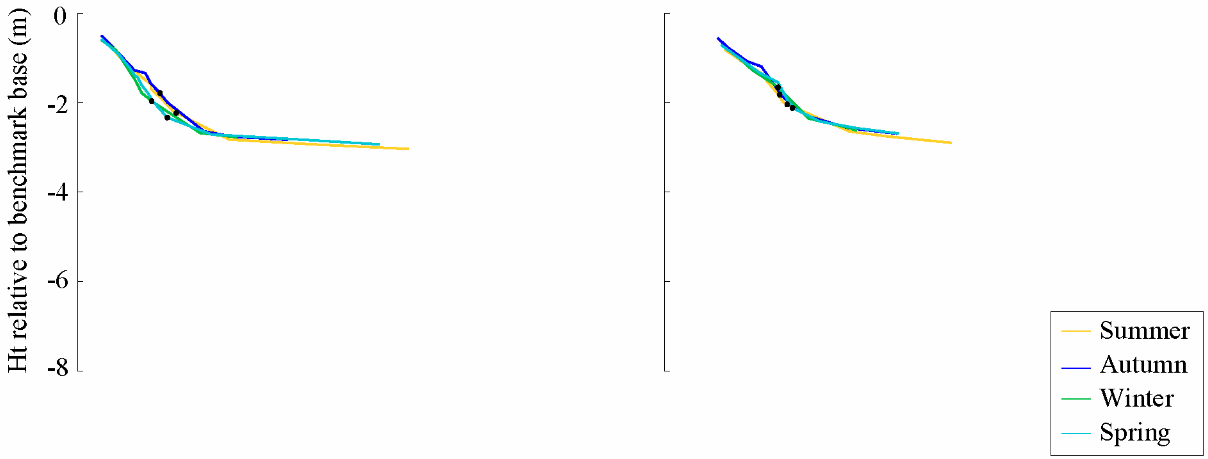
These plots showed that the overall profiles of the moderately exposed-exposed habitat types 4 and 5 were particularly steep, especially in the case of the second of these habitat types, and the widths of the beaches at those habitat types were thus particularly narrow (Figs 4.1e, d , 4.2e, d). The profiles recorded at the exposed habitat type 6, and at the moderately sheltered habitat type 2 were also relatively steep in certain seasons (*e.g.* Figs 4.1c, b, respectively). In contrast, the overall slopes of the topographic profiles at the highly sheltered habitat type 1 were particularly shallow (Figs 4.1a, 4.2a), and this was also true, but to a lesser extent, for the moderately exposed habitat type 3 in several seasons (Figs 4.1c, 4.2d).

The extent to which the topographic profiles of the beach and nearshore area contained obvious morphological features also varied among the six habitat types. Thus, while the profiles at habitat types 3, 4 and 6 often contained prominent berm crest formations on the beach and beach steps at the lower extent of the wave swash zone (Figs 4.1c, d, f and 4.2c, d and f), those at habitat type 5 rarely contained noticeable berms and any beach steps that did occur were usually very narrow (*e.g.* Fig. 4.1e). Berm formations at the highly sheltered habitat type 1 were often present, but their heights and widths were usually far smaller than those at habitat types 3, 4 and 6 (*e.g. cf* Figs 4.1a, c). Moreover, there was a pronounced change in slope between the beach and nearshore areas at habitat type 1, with the slope of the nearshore area being markedly flatter than that recorded for the beach (Figs 4.1a and 4.2a).

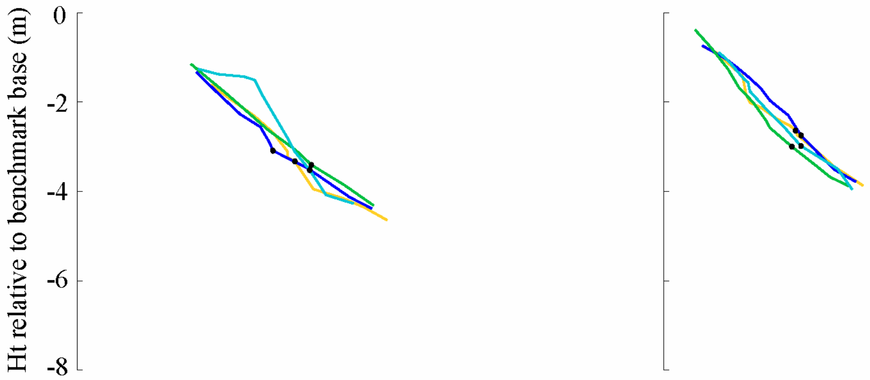
Seasonal differences in the morphology of the beach and nearshore areas were clearly evident at habitat types 3, 4 and 6, whereas those at habitat type 1 exhibited very little intraannual variation. In those cases in which seasonal differences in the beach profiles were

2000

(a) Habitat type 1



(b) Habitat type 2



(c) Habitat type 3

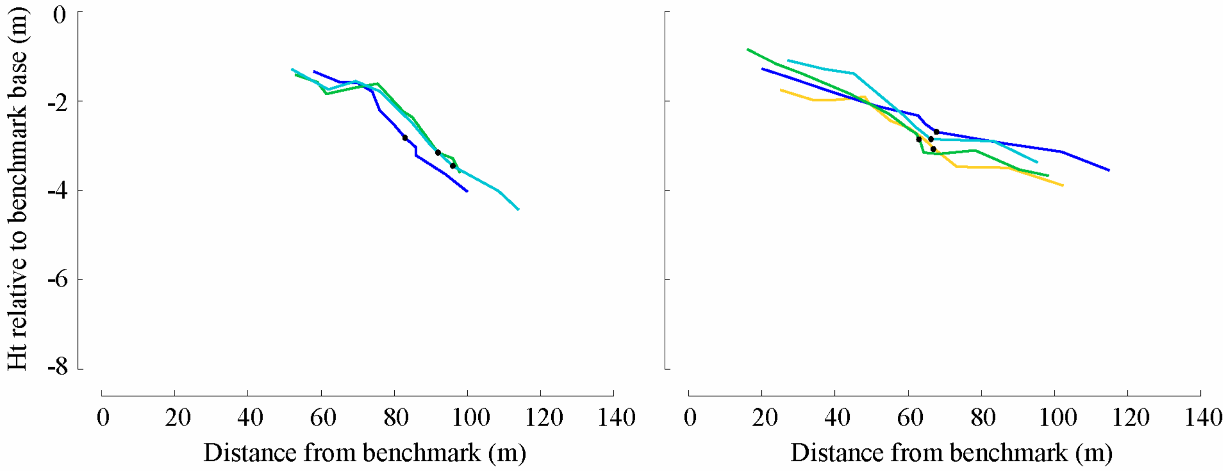
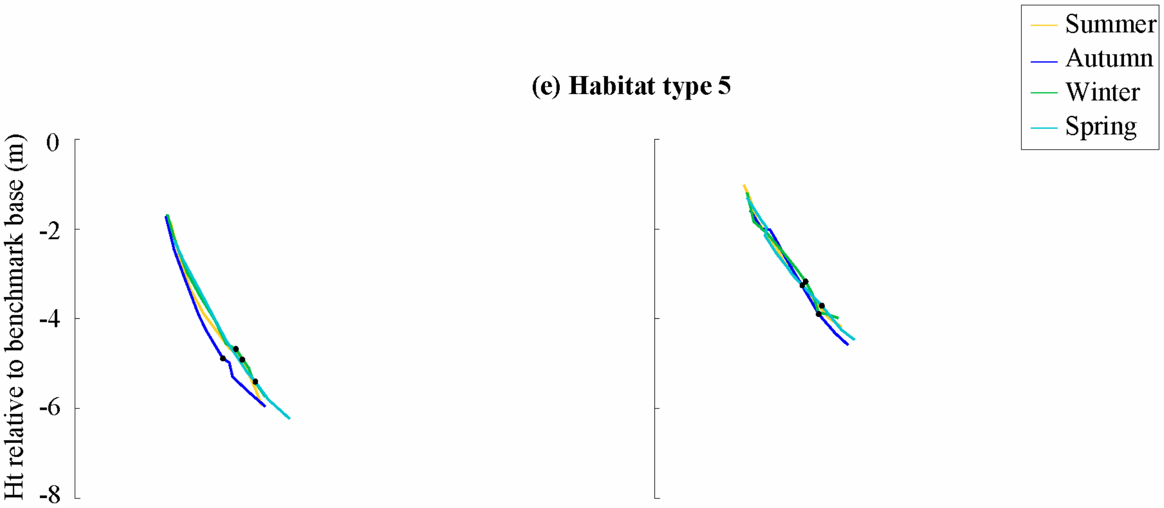


Figure 4.1: Topographical profiles of the beach and nearshore area at sites representing habitat types 1-6 in each season during 2000. Each profile includes only those measurements recorded between the edge of any dune vegetation or the base of dune formations, and water depths of *ca* 1.5m. The location of the lower limit of the wave swash zone is also provided on each profile (denoted by black symbols).

2000

(d) Habitat type 4

(e) Habitat type 5



(f) Habitat type 6

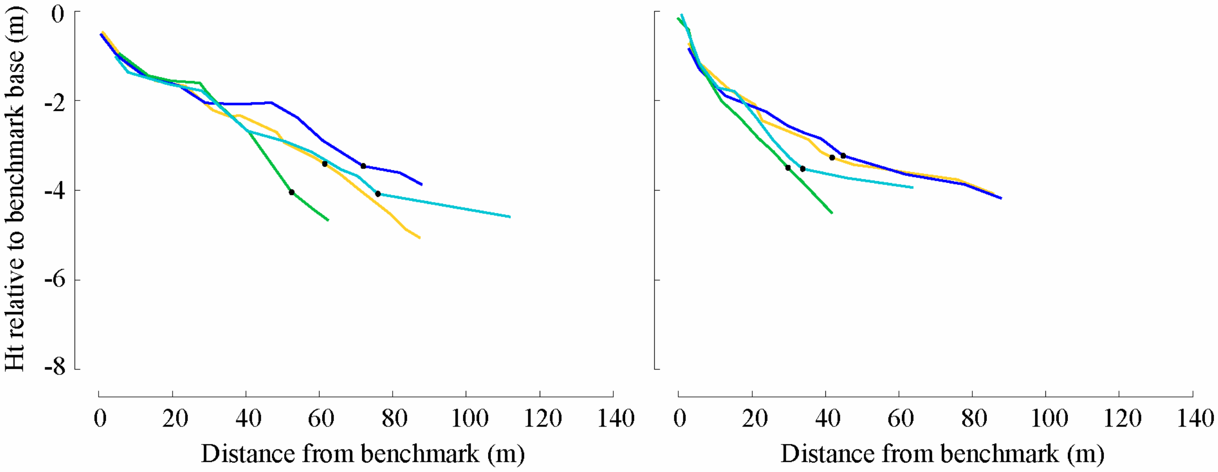
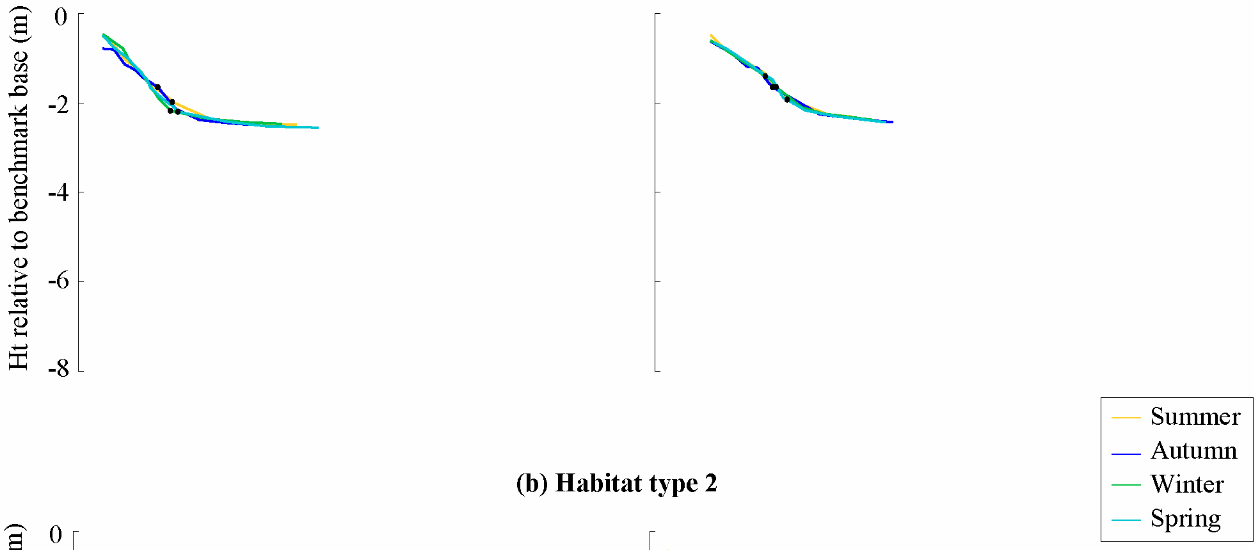


Figure 4.1: Continued.

2001

(a) Habitat type 1



(b) Habitat type 2

(c) Habitat type 3

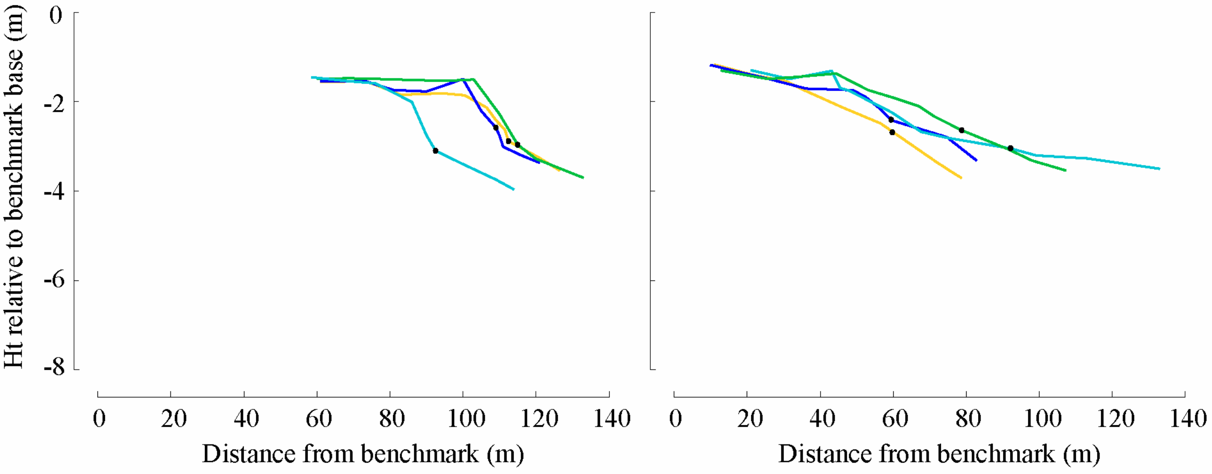
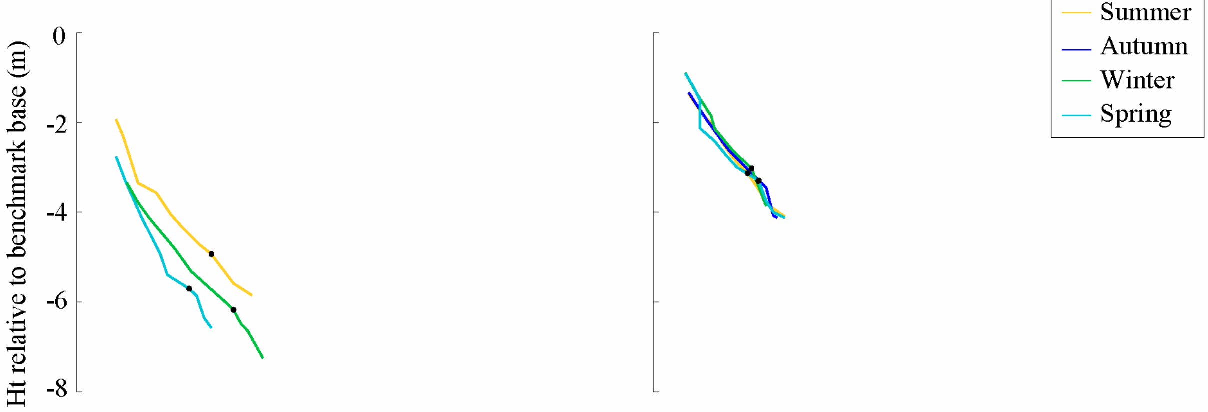


Figure 4.2: Topographical profiles of the beach and nearshore area at sites representing habitat types 1-6 in each season during 2001. Each profile includes only those measurements recorded between the edge of any dune vegetation or the base of dune formations, and water depths of *ca* 1.5m. The location of the lower limit of the wave swash zone is also provided on each profile (denoted by black symbols).

2001

(d) Habitat type 4

(e) Habitat type 5



(f) Habitat type 6

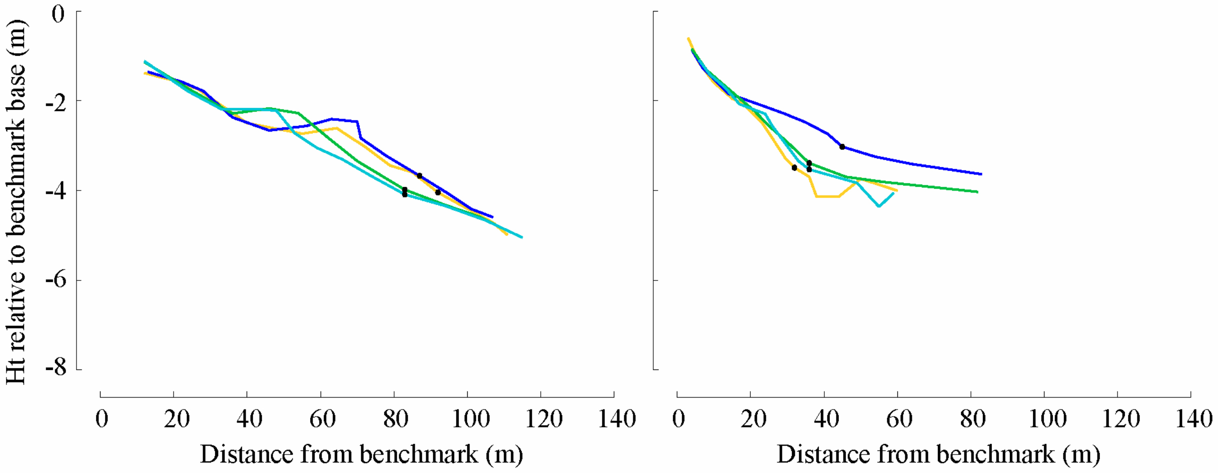


Figure 4.2: Continued.

particularly marked, *e.g.* habitat types 4 and 6 in 2000 and habitat types 3 and 6 in 2001, the overall height of the beach and nearshore area was usually greater in summer and/or autumn than in winter and/or spring, thereby indicating an accretion of sediment in the former season(s) and erosion during the latter season(s) (*e.g.* Figs 4.1d, f, 4.2f). Moreover, the berm crest at representatives of those habitat types in summer/autumn was often located seaward of that recorded at the same habitat types in winter/spring and, in some of those cases, no crest could be discerned during those latter seasons. However, the reverse of these seasonal trends was also true in some cases, *e.g.* one of the sites representing habitat type 3 in 2001 (Fig. 4.2c). While some interannual differences were evident in beach and nearshore profiles measured at the various habitat types, these differences were small compared with the seasonal differences in their morphology (*cf* Figs 4.1 and 4.2).

4.3.2 Sediment parameters, detached macrophytes, water temperature and salinity among habitat types, seasons and/or zones, years or day vs night

Three-way ANOVA showed that the contribution of particulate organic matter to the sediment differed significantly among habitat types (p <0.001), but not among zones or seasons (Table 4.1a). Scheffé's *a posteriori* test demonstrated that the mean organic content of the sediment was significantly greater at habitat type 1 than that at habitat types 2, 4, 5 and 6, and was significantly greater at habitat type 3 than that recorded at habitat type 5. The extent of the differences in this dependent variable among habitat types is illustrated in Fig. 4.3a.

Table 4.1a Mean squares and their significance levels for three-way ANOVA of sedimentary particulate organic matter, penetrometer depth and redox discontinuity layer depth recorded in zones A, B and C in the six nearshore habitat types along the lower west coast of Australia during the day in each season in 2000. "df"=degrees of freedom. ***p <0.001; ** p <0.01.

	df	Organic matter	Penetrometer depth	Redox depth
Main Effects				
Habitat type (H)	5	1.52***	6.19***	134.61***
Zone (Z)	2	0.26	44.16***	178.47***
Season (S)	3	0.21	3.26***	16.38
Two-way Interactions				
H x Z	10	0.80	1.31**	42.22***
H x S	15	0.79	1.66***	7.01
Z x S	6	0.77	3.83***	9.92
Three-way Interactions				
H x Z x S	30	0.21	1.21***	4.81
Error	70	0.17	0.45	10.25

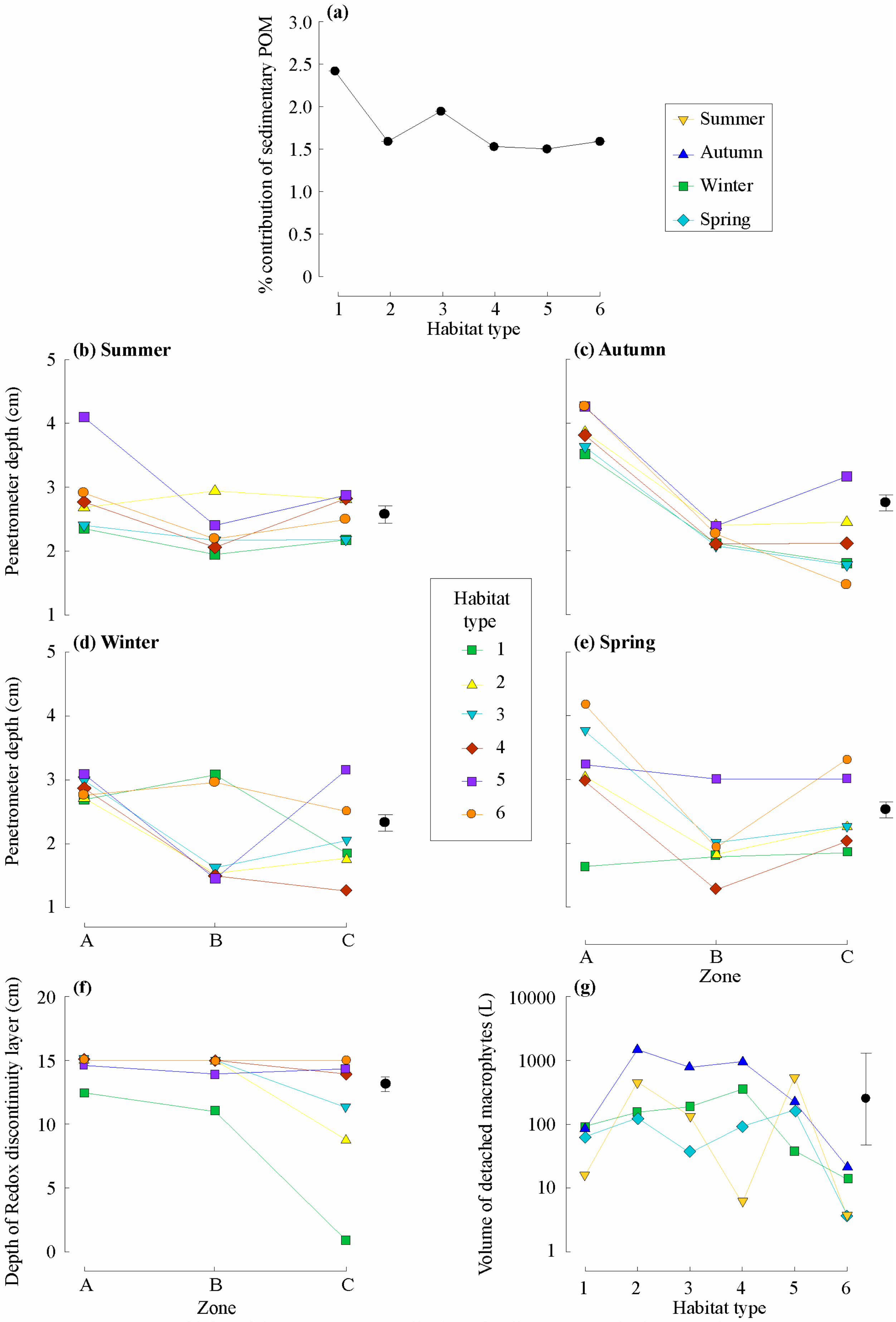


Figure 4.3: Mean (± 95% CI) of the percentage contribution of sedimentary particulate organic matter (POM) at habitat types 1-6, the penetrometer depth in zones A, B and C in (b) summer, (c) autumn, (d) winter and (e) spring at habitat types 1-6 and the volume of detached macrophytes in each season at each habitat type. For the sake of clarity, the overall mean (± 95% CI) is provided on plots b-g on this figure and all plots on Fig. 4.4 (denoted by black symbols and lines).

Mean penetrometer depth differed significantly among zones, habitat types and seasons, and all two-way interactions between these independent variables, and the three-way interaction, were significantly different ($p < 0.001$-0.01; Table 4.1a). However, the mean square was far greater for zone than that for any other main effect or interaction. Thus, the values for this dependent variable in any particular habitat type and season were frequently greatest in zone A and least in zone B (Figs 4.3b-e). Some exceptions to this trend occurred in certain habitat types and seasons, *e.g.* habitat types 5 and 6 in winter where mean penetrometer depth was greatest in zone B (Fig. 4.3d), thus contributing to the significant interactions detected by ANOVA. Furthermore, the mean penetrometer depth recorded for most zones at the relatively exposed habitat types 5 and 6 were often greater than those in the other four habitat types during most seasons (Figs 4.3b-e).

Three-way ANOVA showed that the depth of the redox discontinuity layer differed significantly among habitat types and zones ($p < 0.001$), and that the interaction between these main effects was significant ($p < 0.001$; Table 4.1a). The mean square was slightly greater for zone than for habitat type, which, in turn, was far greater than for the interaction. Plots of the mean redox depth in each zone and habitat type showed that, while the value for this dependent variable was least in the submerged zone C at habitat types 1, 2, 3 and 4 (and particularly in the case of the first of these habitat types), the redox depth varied little among zones at the relatively exposed habitat types 5 and 6 (Fig. 4.3f). Moreover, the mean redox depth was lower in each zone at habitat type 1 than in the corresponding zones at all of the other habitat types, while those recorded at habitat type 6 were either greater than those of all other habitat types or equal greatest (Fig. 4.3f).

When the mean volume of detached macrophytes present on the beach face during the day at each of the six habitat types in each season and year were subjected to three-way ANOVA, significant differences were detected among both habitat types and seasons ($p < 0.001$) and the interaction between these two factors was also significant ($p < 0.05$; Table 4.1b). A plot of the mean volume of macrophytes in each habitat type and season showed the lowest overall volumes of detached macrophytes were generally recorded at habitat type 6, followed by that at habitat type 1. Moreover, the greatest volumes of detached macrophytes were usually recorded in autumn at the various habitat types, followed by those recorded in winter and spring. The weak habitat type x season interaction was caused mainly by large variations in the volume of macrophytes among the six habitat types during summer (Fig. 4.3g). Thus, while the smallest volumes of detached macrophytes were recorded in summer at habitat types 1, 4 and 6, the greatest quantity was recorded in this season at habitat type 5. Furthermore, the extent of the seasonal differences in this environmental characteristic was especially high at habitat type 4, and particularly low at habitat types 1 and 6 (Fig. 4.3g).

Table 4.1b Mean squares and significance levels for three-way ANOVA of the volume of detached macrophytes recorded at the six nearshore habitat types along the lower west coast of Australia during the day in each season in 2000 and 2001. "df"=degrees of freedom. ***p <0.001; *p <0.05.

	df	Volume of detached macrophytes
Main effects		
Habitat type (H)	5	9.67***
Season (S)	3	5.67***
Year (Y)	1	0.16
Two-way interactions		
H x S	15	1.85*
H x Y	5	0.37
S x Y	3	0.32
Three-way interactions		
H x S x Y	15	0.83
Error	143	1.03

Mean water temperature was shown by four-way ANOVA to differ significantly among seasons (p <0.001), between day and night (p <0.001) and among habitat types (p <0.01; Table 4.1c). Significant differences were also present for all two-way interactions involving season (p <0.001) and that between habitat type and year (p <0.01), and the three-way interactions among habitat type, season and year and diel period, season and year were also significant (p <0.001 and <0.05, respectively). However, the mean square for season was far greater than that for any other significant main effect or interaction. Diel changes also accounted for a considerable amount of variation among mean temperatures, and the mean square for this term was also markedly greater than those for habitat type and the significant interactions (Table 4.1c).

The interactions involving habitat type, season and/or year were explored by plotting the mean temperature in each habitat type and season separately for 2000 and 2001 (Figs 4.4a and b, respectively). These plots showed that, in both years, the mean water temperatures at each habitat type were greatest in summer (*ca* 24-25 ºC) and least in winter (*ca* 16-17.5 ºC; Figs 4.1a, b). The means for autumn and spring were very similar in all habitat types in both years (18.6-20.8 ºC), except in habitat type 4 in 2000 when it was far greater in spring than autumn, *i.e.* 23.1 *vs* 18.6 ºC (Fig. 4.4a). The significant interactions involving diel period, season and/or year were likewise examined by plotting the mean water temperature in each season and during the day and night separately for 2000 and 2001 (Figs 4.4c and d, respectively). Thus, in both years, the mean water temperatures in each season were greater during the day than night and greatest in summer and least in winter. However, while the day and night-time temperatures in summer, autumn and spring were similar in the corresponding seasons in the two years, they were lower in the winter of 2000 than 2001 (Figs 4.4c, d).

Table 4.1c Mean squares and their significance levels for four-way ANOVA of water temperature and salinity recorded at the six nearshore habitat types along the lower west coast of Australia during the day and night in each season in 2000 and 2001. "df"=degrees of freedom; * p <0.05, ** p <0.01, *** p <0.001.

	df	Water temperature	Salinity
Main Effects			
Habitat type (H)	5	4.62**	1.67**
Year (Y)	1	2.12	72.14***
Season (S)	3	1416.12***	62.36***
Diel (D)	1	294.42***	0.01
Two-way Interactions			
H x Y	5	4.96**	3.53***
H x S	15	5.50***	0.87**
Y x S	3	14.91***	39.32***
H x D	5	1.41	0.12
Y x D	1	0.95	0.09
S x D	3	10.96***	0.25
Three-way Interactions			
H x Y x S	15	6.78***	2.64***
H x S x D	15	0.63	0.19
H x Y x D	5	1.12	0.31
Y x S x D	3	4.59*	0.32
Four-way Interactions			
H x Y x S x D	15	0.88	0.14
Error	454	1.26	0.03

Four-way ANOVA showed that the mean salinity differed significantly between years, seasons (p <0.001) and habitat types (p <0.01), and that the year x season, habitat type x year and habitat type x season two-way interactions were significant (p <0.001-0.01; Table 4.1c). Moreover, the three-way interaction between habitat type, year and season was also significant (p <0.001). The mean squares were greatest for year, followed closely by that for season. The mean square the two-way interaction between these independent variables was also far higher than that for any of the remaining significant main effects or interactions (Table 4.1c). Plots of the mean salinity in each habitat type and season in both 2000 and 2001 showed that the values for this dependent variable at all habitat types in summer, winter and spring 2000 were lower than those in the corresponding habitat types and seasons in 2001, except for that recorded in habitat type 4 during winter (Figs 4.4 e and f). In contrast, the mean salinities in each of the six habitat types during autumn 2000 were markedly greater than those recorded in this season in 2001. Moreover, while the mean salinity at each habitat type was greatest during autumn in 2000, it was greatest in summer in 2001 (Figs 4.4 e, f).

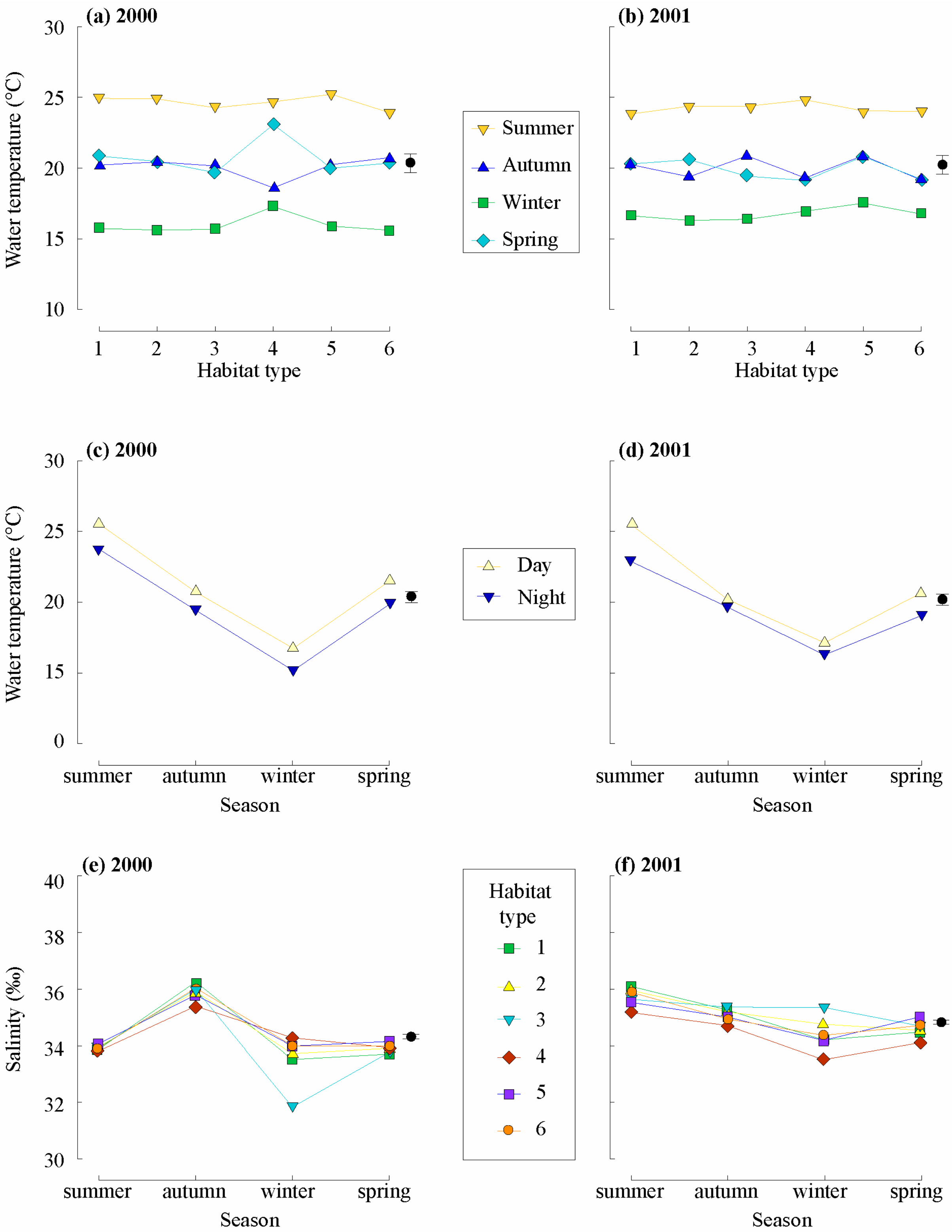


Figure 4.4: Mean (± 95% CI) water temperature in each season and habitat types in (a) 2000 and (b) 2001, and during the day and night in each season during (c) 2000 and (d) 2001.
Mean (± 95% CI) salinity at each habitat type and season in (e) 2000 and (f) 2001.

4.3.3 Sediment grain-size composition among habitat types, zones and seasons

When the percentage contributions of each of the sediment grain-size fractions to samples collected in zones A, B and C of each of the six habitats in all seasons during 2000 were subjected to MDS ordination and the points on the resultant plot coded for habitat type, only those from the relatively exposed habitat type 5, which also contains areas of subtidal reef, exhibited any tendency to form a separate group (Fig. 4.5a). Moreover, when the samples on the same plot were coded separately for zone and season, they showed little tendency to separate on the basis of either of those factors (data not shown). While one-way ANOSIM showed that the grain-size compositions of the sediment samples differed significantly on the basis of each of these factors (p=0.1-4.8%), the extent of those overall differences were relatively low in each case, *i.e.* Global R ranged from 0.181 for habitat type to 0.021 for season.

In order to ascertain whether more distinct differences in sediment grain-size composition among habitat types could be detected when the influence of the other two confounding factors was removed, the data were separated on the basis of zone (*i.e.* since the extent of the overall differences in grain-size composition were next greatest for this factor) and used to construct separate Bray-Curtis similarity matrices (see Figs 4.5b-d for MDS ordination plots of these matrices). Two-way crossed ANOSIM tests, employing habitat type and season as factors, were then carried out using each of those matrices. The global results of these tests demonstrated that the sediment grain-size compositions differed significantly overall among habitat types in zones A and B (p=0.1 and 1.7%, respectively), and those in zone C bordered on differing significantly (p=5.2%; Tables 4.2a-c). However, grain-size composition did not differ significantly among seasons in any zone.

The extent of the significant overall differences among habitat types in the various zones were slightly higher in zone A than B, *i.e.* Global R= 0.288 *vs* 0.215. However, the pairwise results of these ANOSIM tests demonstrated that the basis for the significant overall differences in both of these zones were almost entirely attributable to differences between habitat type 5 and all other habitat types (Tables 4.2a and b). Furthermore, while the global results for data recorded in zone C were not significant, all of the pairwise comparisons between habitat type 5 and the other five habitat types were significant (Table 4.2c). The samples from this relatively exposed and reef-containing habitat type were thus particularly discrete from the majority of samples collected in all other habitat types on the MDS plots constructed separately for the different zones (Figs 4.5b-d). Moreover, in zones A and B, the differences in sediment grain-size were greatest between this habitat type and both habitat types 1 and 2, which are highly and moderately sheltered, respectively, and contain seagrass in their nearshore waters (Tables 4.2a and b, respectively).

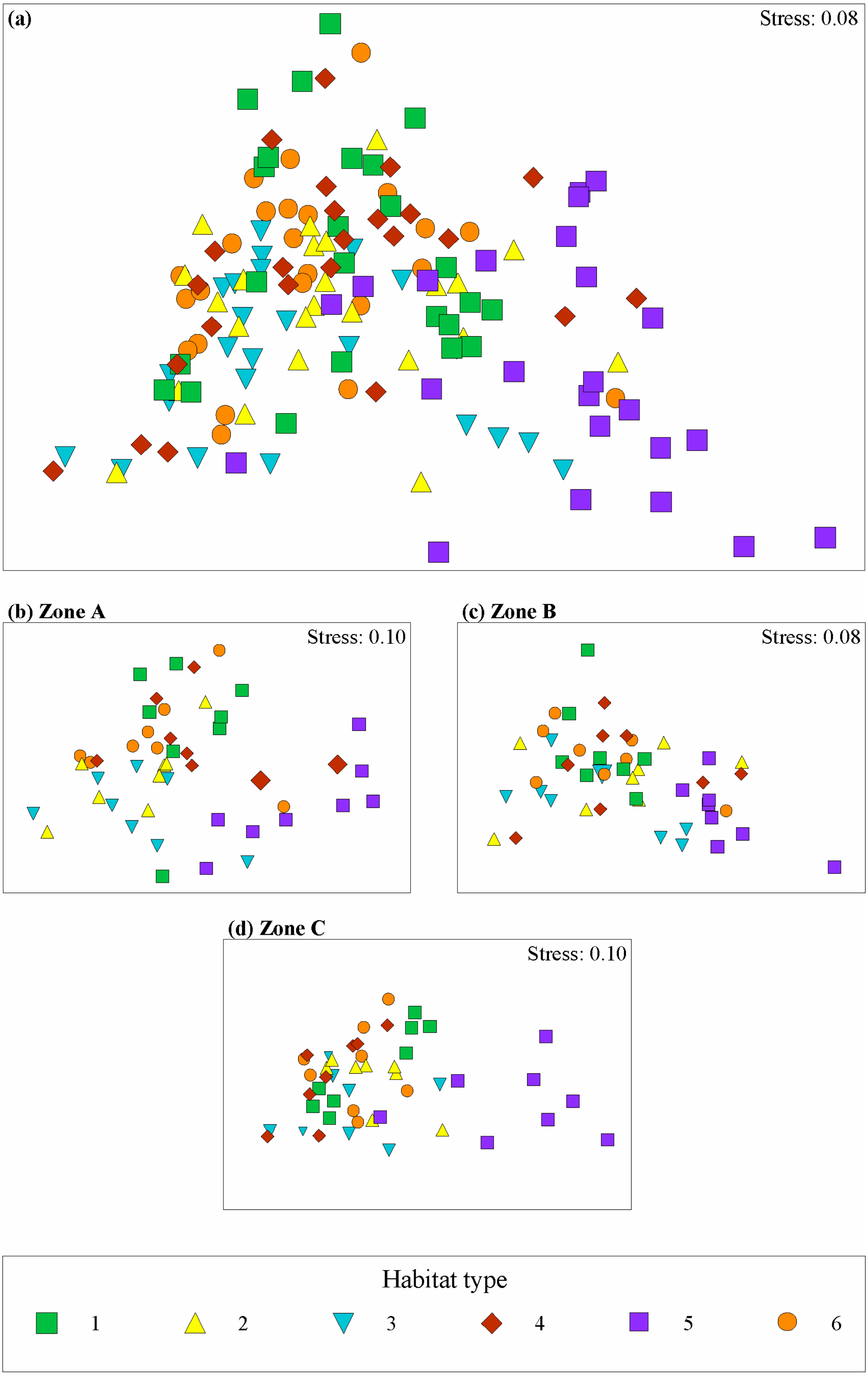


Figure 4.5: Two-dimensional MDS ordination of the contributions of the sediment grain size fractions to samples collected at habitat types 1-6 in each season during 2000 derived using data for samples from (a) zones A, B and C, (b) zone A only, (c) zone B only, and (d) zone C only.

Table 4.2 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in a one-way ANOSIM test of the grain size compositions of the sediment at habitat types 1-6 in (a) zone A, (b) zone B and (c) zone C in 2000. Significant results are highlighted in boldface.

(a) Zone A (p=0.6%; Global R=0.288)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	7.4	0.313										
3	**3.7**	**0.500**	16.0	0.313								
4	88.9	-0.313	38.3	0.063	7.4	0.313						
5	**1.2**	**0.688**	**1.2**	**0.625**	**3.7**	**0.500**	27.2	0.188				
6	33.3	0.125	21.0	0.250	74.1	-0.063	14.8	0.188	**3.7**	**0.563**		

(b) Zone B (p=1.7%; Global R=0.215)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	71.6	-0.125										
3	30.9	0.125	13.6	0.313								
4	63.0	0.000	33.3	0.125	100.0	-0.188						
5	**1.2**	**0.813**	**1.2**	**0.875**	**1.2**	**0.625**	**3.7**	**0.563**				
6	70.4	-0.063	**1.2**	**0.813**	63.0	-0.063	100.0	-0.500	**4.9**	**0.563**		

(c) Zone C (p=5.2%; Global R=0.149)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	97.5	-0.438										
3	58.0	-0.063	22.2	0.188								
4	80.2	-0.188	100.0	-0.250	35.8	0.125						
5	**4.9**	**0.500**	**2.5**	**0.688**	**2.5**	**0.625**	**3.7**	**0.563**				
6	95.1	-0.250	21.0	0.188	19.8	0.188	95.1	-0.250	**1.2**	**0.813**		

SIMPER showed that, in each of the zones, the differences in sediment grain-size composition between habitat type 5 and all other habitat types were due to greater contributions of the >2000, 1000-2000 and 500-1000 μm grain-size fractions in habitat type 5 than in the other habitat types, and greater contributions of the 250–500, 125-250 and 63-125 μm grain-size fractions in habitat types 1, 2, 3, 4 and 6 than in 5.

In order to examine more fully the significant differences in sediment grain-size composition among zones, the data recorded in each of the six habitat types were subjected separately to one-way ANOSIM. It should be noted that the samples collected in the different seasons were used as “replicates” in these analyses as the two-way crossed season x habitat type ANOSIM tests described previously did not detect any significant differences on the basis of this factor. The one-way ANOSIM tests showed that there were significant overall differences in grain-size composition among zones only at habitat type 5 (p= 2.6%, global R= 0.347), and examination of the pairwise comparisons in this test showed that only that between zones A and B was significant (p=3.7%, R=0.688). SIMPER showed that this latter significant difference was attributable to greater contributions of the 125-250 and 250-500 µm grain-size fractions in zone A than B, whereas the reverse was true for the 1000-2000 and >2000 µm fractions.

4.4 Discussion

4.4.1 Spatial and temporal differences in beach and nearshore morphology

Coastal morphologists have produced relatively complex schemes for classifying the beach types present along coastlines in different parts of the world, most of which rely on the ability to distinguish between a series of morphological states (*e.g.* Wright and Short 1983, 1984, Lippmann and Holman 1990, Masselink and Short 1993, Hegge *et al.* 1996, Doucette 2000). The allocation of a beach to a particular morphotype, as defined in those studies, involves collecting detailed measurements on the *in situ* topography, sediment characteristics and/or the wave, current and tidal regimes, which often necessitates the use of sophisticated equipment and a substantial amount of fieldwork. This information is then used to calculate an environmental parameter, the most widely accepted of which is the “dimensionless fall velocity” (*e.g.* see Wright and Short 1983, 1984), which provides the basis for assigning any given beach to one of those morphotypes.

Many of these morphodynamic models have been developed along micro-mesotidal coasts that experience moderate to high levels of oceanic wave activity (*e.g.* Wright and Short 1983, 1984). However, recent research has indicated that the usefulness of the dimensionless fall velocity environmental parameter for categorising beaches along both macrotidal coastlines (*e.g.* in northern Europe; Brown and McLacahlan 1990) and coasts that are sheltered to some extent from oceanic waves by surrounding geophysical structures (*i.e.* the lower west coast of Australia) is, at best, limited (Hegge *et al.* 1996, Masselink and Pattiaratchi 2001b). Thus, the *in situ* geomorphological characteristics of beaches along lower energy coastlines are controlled to a relatively greater extent by local prevailing winds (and thus seas and along-shore current activity), rather than by mainly incident oceanic wave energy, as is the case along exposed shores (Jackson *et al.* 2002, Masselink and Pattiaratchi 2001b).

Hegge *et al.* (1996) identified six categories of beaches along the coast of south-western Australia on the basis of measurements of topographic profiles recorded between mid summer and early autumn during one year. These morphotypes, namely concave, moderately concave, steep, moderately steep, flat and steeped beaches, differed from most of the six beach types that are able to be identified using the dimensionless fall velocity parameter developed by Wright and Short (1983, 1984), *i.e.* reflective or dissipative beach types, or one of four intermediate morphological states. The profiles of several of the beach morphotypes identified by Hegge *et al.* (1996) were comparable to those measured at some of the habitat types in the current study, particularly in the case of the concave and steep beaches, *i.e. cf* those measured at the highly sheltered habitat type 1 and the moderately-fully exposed habitat type 5, respectively, in the current study. Thus, these workers typically recorded the first of these morphotypes, which are relatively narrow beaches with a relatively steep foreshore zone but a markedly flat nearshore area, at those sites that were the most sheltered from wave activity, while steep beaches (*i.e.* steep, linear beach and nearshore areas) were recorded at those locations which are comparatively exposed and experienced turbulent wave swash.

Hegge *et al.* (1996) detected, however, relatively little statistical association between the morphology of most of the beach types and the range of hydrodynamic measurements (*e.g.* wave height, long-shore currents and swash run-up) recorded at each of those sites. Different morphotypes were thus identified under similar hydrodynamic conditions and, in some cases, the morphotype of a particular site varied considerably between sampling occasions within the short period in which the data in that study were recorded. Such results were attributed to the fact that the morphology of many beaches along relatively low energy coastlines, such as those on the lower west coast of Australia, are often those which have been “inherited” from previous high energy storm or strong sea-breeze events (*e.g.* Eliot and Clarke 1986, Masselink and Pattiaratchi 1998) and thus do not reflect accurately their typical nearshore hydrodynamic conditions (Masselink and Pattiaratchi 2001b). Some variability was also detected between the morphology of sites representing the same habitat type in the current study. These factors highlight some of the difficulties associated with using such *in situ* measurements for categorising nearshore sites into groups that reflect appropriately their overall environmental characteristics, and which can thus be used as a basis for interpreting the spatial distribution of nearshore fauna.

The topographic profiles of nearshore sites surveyed in the current study exhibited considerable seasonal variation at some of the habitat types. This was particularly the case at the moderately exposed habitat types 3 and 4 and the relatively exposed habitat type 6. Thus, there were often clear differences in overall beach height and noticeable seaward/landward migrations of berm crest formations (*i.e.* reflecting sediment accretion/erosion, respectively) between particular seasons at these habitat types. However, while overall beach height was greatest and the location of the berm most seaward during summer and/or autumn at some habitat types (*i.e.* thereby indicating sediment accretion during these seasons and erosion during winter/spring), the reverse was true at other habitat types.

Masselink and Pattiaratchi (2001b) also reported marked seasonal changes in the morphology of beaches along the lower west coast of Australia, and ascribed such differences mainly to seasonal reversals in the along-shore sediment transport generated by local wind and thus wave and current activity, rather than to the influence of the seasonal differences in oceanic swell activity that occur along this relatively protected coastline (Lemm *et al.* 1999). While the latter seasonal difference in incident swell activity, and the extent to which sites are exposed, will undoubtedly contribute to both temporal and spatial differences in beach morphology along the lower west coast of Australia, the extent to which sediment is deposited or eroded between seasons at different sites along this coast is influenced heavily by (1) the orientation of those beaches with respect to the strong local sea breezes that occur during summer (Masselink 1996) and storm wind and wave conditions during winter and (2) the physical setting of those beaches in relation to surrounding geophysical structures, *i.e.* barriers to sediment transport such as headlands, rocky outcrops and groynes. Differences in the geophysical setting of the various habitat types identified in the current study would thus explain the inconsistencies among those habitat types in the seasonal patterns of sediment accretion and erosion. Moreover, the beach and nearshore morphology of some of the habitat types identified in this study varied little among seasons, and this was particularly the case at habitat type 1. Such results are probably attributable to the fact that this habitat type is protected to a large extent from both swell and local wind activity (*i.e.* and is thus unlikely to receive large quantities of sediment from other locations along the coast or experience marked erosion), and a substantial proportion of any suspended sediment in the nearshore waters surrounding this habitat type would be likely to become entrapped within the dense seagrass beds that are present in the shallows.

The marked seasonal differences in beach morphology at several of the habitat types along the lower west coast of Australia also make the use of these *in situ* measurements for categorising nearshore sites into groups that appropriately reflect their overall environmental characteristics problematic. Moreover, some workers have suggested that thorough investigations of the morphology of beaches along this coastline require measurements to be undertaken at very frequent intervals, *i.e.* daily in some cases, to encompass the range of differences in their morphologies (*e.g.* Eliot *et al.* 1982, Clarke and Eliot 1983). The resources required to undertake such field measurements would clearly preclude the use of this approach for categorising nearshore sites over regional spatial scales.

4.4.2 Spatial and temporal differences in sediment parameters

Multivariate analysis of the grain-size composition of the sediment collected during this study showed that the contributions of the different grain-size fractions differed significantly among habitat types. However, those differences were almost entirely attributable to the significant differences between the grain-size composition at habitat type 5 and each of the other habitat types. Thus, while the sediment at most habitat types was dominated by medium grain-sizes (*i.e.* those between 250 and 500 µm in size), that in each of the different zones at the moderately to fully exposed habitat type 5, which also contained areas of nearshore reef, comprised significantly greater contributions of larger grain fractions (*i.e.* those between 500 and 2000 µm in size) than was the case at habitat types 1, 2, 3, 4 and 6. This finding is consistent with that of Hegge *et al.* (1996), who recorded the largest mean grain-sizes at beaches assigned to the "steep" morphotype, *i.e.* that morphotype displaying close similarities to the morphological profiles recorded at habitat type 5 in this study. It is also relevant that the differences in the sediment grain-size composition among habitat types were greatest between habitat types 5 and the highly to moderately sheltered habitat types 1 and 2, and that Hegge *et al.* (1996) recorded some of the lowest mean grain-sizes at those morphotypes which matched the morphological profiles recorded at those latter two habitat types.

Several other workers have also recorded particularly coarse sediments in those nearshore areas that are located close to rocky reefs, and have attributed this to the greater extent of wave-breaking activity and thus weathering of consolidated substrates that generally occur in these areas, (*e.g.* Ambrose and Anderson 1990, Posey and Ambrose Jr. 1994, Barros *et al.* 2001). The larger size of the sediment grains at habitat type 5 probably also reflects the fact that there is only a short distance between the main source of these sediments (*i.e.* reef substrata) and the beach area, thereby reducing the potential for physical weathering of those grains by wave action in those waters. Large shell fragments derived from marine invertebrates associated with the nearshore reefs are also likely to contribute to the relatively high proportion of large sediment grains found at habitat type 5. Moreover, the degree to which finer grains remain suspended in the water column is likely to be greater in turbulent nearshore environments such as habitat type 5 than in more sheltered areas such as habitat types 1 and 2, where the greatly reduce water movement enables these small particles to settle. It is thus also relevant that the substrate at habitat type 1 (*i.e.* the most sheltered of all habitat types along the coast and contained the greatest areas of nearshore seagrass) not only contained among the largest proportions of finer sand grains, but also comprised significantly greater proportions of particulate organic matter than that at most of the other habitat types along this coastline and had the shallowest redox discontinuity layer.

Although Hegge *et al.* (1996) generally found reasonably good relationships between the different beach morphotypes and differences in sediment grain-size, they detected considerable variability in the grain-size compositions of sites representing particular morphotypes. These findings, and the lack of marked differences in grain-size among most of the habitat types identified in the current study, may be attributable to the along-shore mixing of sediment by local currents which flow predominantly northwards in summer and southwards in winter (Masselink and Pattiaratchi 2001b). Along-shore homogenisation of the sediments on the lower west coast of Australia by these local currents may also explain the lack of significant seasonal differences in grain-size composition that were detected in all habitat types and zones in the present study.

Significant differences in sediment grain-size compositions among zones were detected only at habitat type 5, where zone B, which includes the turbulent wave swash zone, contained significantly greater proportions of particularly large grains (*i.e.* 1000-2000 and >2000 µm in size), than zone A, the uppermost zone located between the high tide mark and the seaward limit of unsaturated sediments. Several other workers have also recorded greater proportions of larger sediment grains within the wave swash zones of nearshore marine environments (*e.g.* Calliari 1994, Guillén and Hoekstra 1997).

The penetrability of the sediment at the various habitat types was often the greatest in zone A and least in zone B. Such results are probably attributable to fact that the sediment in zone A is exposed to ambient wind conditions during falling and low tides, and the aolian transport of this sediment is likely to reduce the extent to which the interstitial spaces between the sand grains becomes compacted. In contrast, the continual physical impact of wave swash and reworking of the substrate in the turbulent wave swash in likely to compress the interstitial spaces between sediment grains in zone B.

4.4.3 Spatial and temporal differences in detached macrophyte accumulations, water temperature and salinity

The volume of accumulations of detached seagrass and macrophytes on the beach face differed significantly among both habitat types and seasons. Thus, the relatively exposed habitat type 6 contained the lowest volumes of detached macrophytes in each season, and these differences were particularly marked in several cases. The volume of the macrophyte accumulations at the highly sheltered habitat type 1 in summer and autumn were also usually substantially lower than those recorded at habitat types 2-5 in these seasons. While these results would be expected for habitat type 6, which does not contain any attached aquatic macrophytes in the nearshore vicinity and tend to be located along comparatively open stretches of coast (*i.e.* and therefore less likely to be a focal point for converging waves that may carry detached plant material), the results obtained at habitat type 1 are seemingly at odds with the fact that those nearshore waters contain dense seagrass beds and thus a major source of plant material. However, those latter results are most likely attributable to the fact that the extent of the wave activity at that highly sheltered habitat type is insufficient to remove large quantities of senescing seagrass from the beds and transport this material towards the shore.

The remaining four habitat types each contained relatively similar mean volumes of detached macrophytes in each season, except summer when the volume recorded at habitat type 4 was markedly lower than that at habitat type 2, 3 and 5. However, wracks of detached macrophytes tend to accumulate in each of these four habitat types by different processes, reflecting differences in their physical setting in relation to surrounding seagrass or macroalgal beds and geophysical structures. Thus, for example, while the nearshore waters of the moderately sheltered habitat type 2 contain patches of seagrass, the majority of the detached plant material that accumulates at this habitat type (which reached *ca* 38 000 L along a 50 m transect on the beachface on some sampling occasions) is probably derived from the dense seagrass beds which occur offshore along the lower west coast of Australia, *i.e.* on the sandy forelands, Success and Parmelia banks, which have formed in the lee of the Garden Island Ridge (see Fig. 2.1 and subsection 2.4). The predilection for detached macrophytes to accumulate at habitat type 2 from these beds is probably related to the fact that sites representing this habitat type are usually located within the vicinity of sheltering structures such as headlands or shallow sandy spits, and thus represent convergence points for waves or alongshore currents that may be transporting wrack material. Moreover, the detached macrophytes which accumulate at habitat type 4 are most likely derived from the seagrass beds which are located in the slightly deeper waters of this habitat type and that are transported inshore by the relatively high wave activity that occurs in those areas, while the accumulations at the moderately to fully exposed habitat type 5 probably originate mostly from the macroalgae that grows on the limestone reefs located close to shore.

Marked seasonal differences in the volume of detached macrophyte accumulations were also detected at habitat type 2-5, with the mean volumes often being greatest in autumn and least in spring. These results are probably attributable to the strengthening and more frequent onshore winds and the increasing swell wave height that typically occurs along the lower west coast of Australia during the first of those seasons (M.P. Rogers and Associates 1995), *i.e.* thereby providing greater means for transporting senescing plant material that has accumulated close to attached macrophyte beds during the preceding seasons, and a depletion in those stores of detached material during the latter season. However, the extent to which the volume of detached macrophytes varied among seasons was substantially lower at habitat type 1 than at the above habitat types, which probably reflects the relatively small intraannual differences in wave energy at that highly sheltered environment.

Water temperature along the lower west coast of Australia varied to the greatest extent among seasons, then between day and night. Differences among habitat types were relatively minor, and did not exhibit any pronounced trends. As would be expected for coastal areas such as this which experience a Mediterranean climate, the water temperatures were greatest during summer when ambient temperatures and day length are generally greatest and rainfall is least (Gentilli 1971), and lowest in winter when the reverse is usually true for those climatic factors. Likewise, salinity was also generally greatest in the warmer seasons, *i.e.* summer or autumn, and exhibited relatively little difference among habitat types. However, unlike water temperature, the greatest differences in this environmental parameter occurred between years, with salinities in most seasons in 2000 being significantly lower than the corresponding seasons in 2001. Such differences probably reflect interannual variability in the overall volume of rainfall.

In summary, this component of the study emphasises that measurements for the non-enduring environmental characteristics recorded at a diverse range of sites along the coastline, such as sediment grain size and morphology of the beach profile, exhibit little consistent spatial variation along the coastline and/or considerable temporal variation. Indeed, the *in situ* data recorded for sediment grain-size provided no obvious indication that they would be able to distinguish among habitat types, apart from those sites that corresponded to our habitat type 5. Thus, the above types of environmental characteristics, which have been used to distinguish among habitat types of coastal areas elsewhere, do not provide a reliable reflection of differences in nearshore habitat types along the lower west coast of Australia. Moreover, in view of the extent to which these non-enduring environmental characteristics can be affected by short-term changes in climatic and hydrodynamic conditions, the acquisition of data over the spatial and temporal scales required to encompasses this variability and thus be useful for coastal and fisheries managers, would be hugely time-consuming and expensive. This contrasts with the situation regarding our use of quantitative enduring environmental characteristics to identify spatial differences in nearshore marine environment along the lower west coast of Australia. Furthermore, as will be seen from the results presented in the following chapters, the validity of these habitat types is endorsed by the fact that significant statistical relationships are able to be detected between the spatial distribution of the nearshore fauna and spatial differences in the enduring environmental characteristics along the coastline.

Chapter 5. Relationships between fish assemblages and habitat types along the lower west coast of Australia

5.1 Introduction

Temperate nearshore marine waters in both the northern and southern hemispheres contain habitats that are crucial for a diverse range of fish species, many of which are commercially and/or recreationally important. Thus, along the lower west coast of Australia, species such as the King George whiting (*Sillaginodes punctata*), southern school whiting (*Sillago bassensis*), yellow-eye mullet (*Aldrichetta forsteri*), sea mullet (*Mugil cephalus*) tailor (*Pomatomus saltator*), sandy sprat (*Hyperlophus vittatus*) and Australian herring (*Arripis georgiana*) use nearshore marine waters as nursery environments, while others such as yellow-finned whiting (*Sillago schomburgkii*) and blue sprat (*Spratelloides robustus*) remain in these waters throughout the whole of their life. The value of the commercial catch for finfish and baitfish fisheries in this region in 2001 was estimated to be *ca* \$530 K (Penn 2002), while the expenditure during 2000/2001 by recreational fishers on commodities that are associated with undertaking fishing in coastal waters in the west coast bioregion (*i.e.* central to lower Western Australia) was *ca* \$156 M (Henry and Lyle 2003). Moreover, the physical heterogeneity of the nearshore environment along the lower west coast of Australia, and the presence of the warm Leeuwin Current, which facilitates the dispersal of a range of tropical fish species to the temperate inshore waters of this region (Hutchins 1991, Hutchins and Pearce 1994, Ayvazian and Hyndes 1995), has led to the occurrence of a diverse fish fauna in these waters. Such diversity is reflected, in part, by the fact that two Marine Parks have been established in these coastal waters under the Conservation and Land Management Act 1984 (see Fig. 2.1).

Many of the studies that have examined relationships between spatial differences in the composition of nearshore fish assemblages and spatial variability in the environmental characteristics of those waters, have focused specifically on determining the extent to which fish are partitioned amongst areas that can easily be distinguished by extreme differences in a single environmental characteristic, *e.g.* unvegetated substrata *vs* vegetated substrata (*e.g.* Orth and Heck 1980, Vanderklift 1996, Gotceitas *et al.* 1997, Jenkins *et al.* 1997b, Ornellas and Coutinho 1998, Arrivillaga and Baltz 1999, Lazzari and Tupper 2002), reef or rock *vs* sand substrata (*e.g.* Howard 1989, Pihl and Wennhage 2002) and sheltered from *vs* exposed to wave activity (*e.g.* Shaw and Jenkins 1992, Hyndes *et al.* 1996a). However, obvious differences in a single characteristic neither encapsulate the environmental complexity that is present in nearshore waters along temperate coastlines, nor take into account the fact that several inter-connected environmental factors are usually required to adequately characterise different habitat types (Roff and Taylor 2000, O'Hara 2001, Skilleter and Loneragan, in press).

Although some workers have considered the ways in which spatial variation in the composition of nearshore fish assemblages might be explained by differences in several environmental parameters, they have examined those environmental differences in a largely qualitative manner (*e.g.* Gilligan 1980, Ayvazian and Hyndes 1995, Dean *et al.* 2000). This thereby restricts the extent to which such environmental characters can be related statistically to the composition of the biota in an area and makes it difficult for other workers, in the future, to be certain that the type of environmental conditions in their studies are essentially the same as in those earlier studies. Furthermore, while other workers have explored statistically the extent to which the composition of nearshore ichthyofaunas are related to a range of individual quantitative environmental variables (*e.g.* water temperature, degree of exposure to wave activity, the volume of detached macrophytes and the extent of rocky areas; Clark *et al.* 1996a, Mueter and Norcross 1999, Beyst *et al.* 2002), these workers made no attempt to elucidate how the collective differences among such suites of environmental variables reflect differences among the various types of habitat found in those nearshore regions.

The ability to identify, in a consistent manner, the suites of fish species that are likely to occur in the various types of habitat in a nearshore region, is crucial for enabling environmental and fisheries managers to develop plans for conserving both the biodiversity and particular species of interest in those waters. Such an ability would enable managers to develop plans to protect representatives of habitat types that are either typical of a nearshore region or are relatively unique (Allee *et al.* 2000, Roff and Evans 2002, Roff *et al.* 2003). Moreover, a framework for identifying nearshore habitat types and for predicting their likely fauna also provides ecologists with a basis for developing and testing scientific hypotheses regarding the underlying processes that influence the composition of biotic assemblages in those environments.

Accurate prediction of the type of fauna that is likely to characterise a nearshore site on the basis of its environmental characteristics thus requires, firstly, a scheme for classifying habitat types that is based on quantitative environmental criteria, and secondly, sound quantitative data for the composition of faunal assemblages at examples of those habitat types. Thus, during this component of the study, samples of the fish fauna were collected regularly at sites representing each of the nearshore habitat types identified quantitatively along the lower west coast of Australia (see Chapter 3), and the number of individuals of each fish species in those samples were recorded. Acquisition of such data then enabled us to match statistically the complementary faunal and environmental data sets (Clarke and Gorley 2001), and thus provided the means for exploring the extent to which the characteristics of the fish faunas along this coastline are related to habitat type and address the following specific questions.

1) Does each nearshore habitat type along the lower west coast of Australia possess a distinct ichthyofaunal composition and, if so, which species are most characteristic of each of those habitat types?
2) Do any differences in the composition of the fish fauna at the various habitat types recur consistently in all seasons and/or in different years and/or during the day and night?
3) Do the extents of any differences in the ichthyofaunal compositions among the various habitat types parallel those found among the quantitative environmental characteristics that best distinguish each of those habitat types?
4) Are the answers to the above questions influenced by any differences produced by collecting fish samples using two types of seine nets that differ in length, height and mesh size?

5.2 Materials and Methods

5.2.1 Sampling of fish fauna

Fish were collected during each season between summer 2000 and spring 2001 from two representative sites of each of the six nearshore marine habitat types that were identified along the lower west coast of Australia (see Chapter 3, Valesini *et al.* 2003). These sites were the same as those at which detailed *in situ* non-enduring environmental characteristics were measured during this study (see Chapter 4). Two different-sized seine nets were used. The smaller seine net was 21.5 m long and 1.5 m high, and comprised 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m long central bunt (3 mm mesh) and swept an area of 116 m^2. The larger net was 60.5 m long and 2.5 m high, consisted of 29 m long wings made of 25 mm mesh and a 2.5 m long central bunt made of 9 mm mesh, and swept an area of 583 m^2. The smaller net was laid by hand in waters ≥1.5 m deep and stretched parallel to the shoreline before being enclosed in a circle, whereas the large net was deployed in a circle from a dinghy in waters ≤2.5 m deep. Both nets were hauled on to the beach, where the fish were removed and immediately euthanased in an ice slurry and stored frozen.

The small net could be used at each of the 12 sites, whereas high wave activity at habitat types 5 and 6, and also the presence of nearshore reefs at the former habitat type, prevented the use of the large net at the sites representing these two habitat types. Furthermore, the small net was employed during both day and night, whereas the large net was used only during the day, as it was impossible at night to visually detect any large waves approaching the shoreline and thus be able to deploy that latter net safely. Fish could not be sampled with the large net at one of the sites representing habitat type 4 during the winter of 2000 because of the presence of large amounts of detached macrophytes in the nearshore waters at that site throughout that season.

This problem was exacerbated at night due to the inability to visually detect particularly dense accumulations of these macrophytes, and thus prevented fish from being collected at this time with the small net at the same site and at the other site in the same habitat type. Four replicate samples were collected with each of the nets at each site in each season (and during the day and night in the case of the small net), and the timing of the collection of these replicates was staggered over one to two weeks in the middle of each season to reduce the likelihood of samples from a site on a given sampling occasion being unduly influenced by an atypical catch.
A summary of the sampling regime for fish is provided in Table 5.1.

The total number of individuals of each fish species in each sample was recorded. The total length of each individual was measured to the nearest 1 mm, except when a large number of a species was caught, in which case the lengths of a random subsample of 100 of those individuals were measured.

5.2.2 Statistical analyses

The following statistical analyses of the fish data derived from samples collected with the small and large nets were used to ascertain the extent of any significant differences in the composition of the ichthyofauna among the various nearshore habitat types. However, since the sampling of fish at the various habitat types was carried out in each season in two consecutive years (and, in the case of samples collected with the small net, also during the day and night), it was necessary to determine whether any significant differences in ichthyofaunal composition among habitat types were required to be examined separately for each level of the various temporal factors. Thus, whenever possible, the analyses aimed at exploring spatial differences in the compositions of nearshore fish assemblages were carried out separately from those that examined the influence of temporal factors (the latter of which are addressed more fully in Chapter 6). However, since some analyses clearly required consideration of both of these main factors, some of the statistical tests undertaken in this chapter are thus also relevant to the questions addressed in Chapter 6. Appropriate cross-referencing between the chapters has been provided in those cases.

5.2.2.1 Univariate analysis-Density of fish, number of fish species and species relatedness

The total number of individuals of each species in each sample was converted to a density, *i.e.* number of fish 100 m^{-2} and 500 m^{-2} in the case of samples collected with the small and large nets, respectively. All of the species recorded throughout the study were assigned to their respective genera, families, orders, classes and to their common phyla (*i.e.* Chordata), and the average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+), both of which are measures of species relatedness, were calculated for each sample using the DIVERSE

Table 5.1 Summary of the sampling regime for fish in nearshore waters along the lower west coast of Australia. Four replicate samples were collected with each net type at each site on each sampling occasion. S=summer, A=autumn, W=winter and SP=spring; ○ day, ● night; * one site sampled.

	21.5 m seine net								**60.5 m seine net**							
	2000				2001				2000				2001			
Habitat type (each represented by two sites)	S	A	W	SP	S	A	W	SP	S	A	W	SP	S	A	W	SP
1	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○	○	○	○	○	○	○	○
2	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○	○	○	○	○	○	○	○
3	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○	○	○	○	○	○	○	○
4	○ ●	○ ●	○	○ ●	○ ●	○ ●	○ ●	○ ●	○	○	○	○	○	○	○	○
5	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○	○	○*	○	○	○	○	○
6	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○ ●	○	○	○	○	○	○	○	○
Total number of samples	96	96	87	96	96	96	96	96	32	32	28	32	32	32	32	32

routine in the PRIMER 5.2 statistical package (Clarke and Gorley 2001). Average taxonomic distinctness is a measure of species diversity or “taxonomic breadth”, and represents the average phylogenetic path length (ω) between every pair of species in a sample, traced through the levels of a Linnaean taxonomic tree (Clarke and Warwick 1998, 2001b, Warwick and Clarke 2001). Variation in taxonomic distinctness reflects the “evenness” of the distribution of species across the taxonomic tree by determining the variance of ω between each pair of species in a sample (Clarke and Warwick 2001b, Warwick and Clarke 2001). The path lengths between each successive level in the taxonomic tree were weighted equally (*i.e.* ω=1). In order to facilitate comparison of species relatedness in samples collected with the different net types (see later in this subsection), Δ^+ and Λ^+ were both calculated on the basis of whether a species was present or absent. It should be noted that this was the only instance in which presence/absence data were employed to examine spatial or temporal differences in the characteristics of the nearshore fish assemblages. Unlike other univariate measures of species diversity, Δ^+ and Λ^+ are not dependent on sampling effort when based on presence/absence data, and can be meaningfully compared across samples collected by different sampling techniques (Clark and Warwick 1998, 2001b).

Prior to Analysis of Variance (ANOVA), the data for the density of all fish, number of species, average taxonomic distinctness and variation in taxonomic distinctness were each tested to ascertain the type of transformation required (if any) to satisfy the assumptions of constant variance and normality for this analysis. This was achieved by determining, separately for data derived from each net type, the extent to which the variance of groups of replicate samples collected at each site on each sampling occasion were dependent on the mean of those samples. Thus, the log of the standard deviation and the log of the mean of each of the above dependent variables were determined for each group of replicates and the resultant data used to construct scatterplots, *i.e.* log [mean] *vs* log [standard deviation] as the independent and dependent variables, respectively. A regression line was then fitted to the points on each scatterplot to determine the slope of the relationship between these variables. Since this slope was *ca* 1 for total fish density and *ca* 0.5 for number of species in the case of data derived from both net types, these variables were log and square-root transformed, respectively (Clarke and Gorley 2001). A square-root transformation was also shown to be required for both average taxonomic distinctness and variation in taxonomic distinctness in the case of samples collected with the large net, while no transformation and a fourth-root transformation, respectively, were required for these two dependent variables in samples collected using the small net.

The density of fish, number of species, average taxonomic distinctness and variation in taxonomic distinctness derived from replicate samples collected with the large net were subjected to three-way ANOVA to determine whether these four dependent variables differed significantly among the various habitat types, seasons and/or between years. The same dependent variables were subjected to four-way ANOVA in the case of data derived from small net samples, to ascertain whether they differed significantly among habitat types, seasons, years and day *vs* night.

Four-way ANOVA, employing net type, habitat type, season and year as independent factors, was also used to determine the extent of any significant differences in the density of fish, average taxonomic distinctness and variation in taxonomic distinctness, derived from samples collected with the 60.5 and 21.5 m nets at those habitat types and on those sampling occasions where both net types were used, *i.e.* habitat types 1-4 during the day in each season in both years. Prior to subjecting the data for density of fish to this analysis, the number of individuals in samples collected with the small net were expressed as number of fish 500m^{-2}, and thus in the same units as those derived from samples collected using the large net. No such adjustment was required for the values of average taxonomic distinctness and variation in taxonomic distinctness calculated from the samples collected with different net types, since neither of these indices are affected by differences in sampling effort (see earlier in this subsection). In contrast, the number of fish species was not included in the above ANOVA since it is not appropriate to adjust such data in samples collected with the different nets to a common area. This is because the relationship between the cumulative number of species in successive samples and the number of samples is not linear (Clarke and Warwick 2001a), and that the cumulative species curves for the two net types will almost certainly be different.

All replicate samples in each ANOVA were considered to be independent, and all main effects were regarded as fixed. The null hypothesis that the values for a dependent variable did not differ significantly among any of the independent variables was rejected when the significance level (p) was <0.05. When ANOVA detected a significant difference for an interaction term or a main effect that was not involved in any significant interaction, plots containing the marginal means and 95% confidence intervals of each level of the relevant factor(s) were used to ascertain the source of those differences. The data in these plots were back-transformed, where necessary, to allow them to be interpreted more easily. Greater emphasis was placed on those significant main effects or interactions that had the highest mean squares. When ANOVA showed that there were significant differences in the values for a dependent variable among the levels of a main effect that was not involved in any significant interaction, Scheffé's *a posteriori* test was used to determine where those differences occurred.

5.2.2.2 Joint average taxonomic distinctness and variation in taxonomic distinctness analyses

The relationship between the average taxonomic distinctness and variation in taxonomic distinctness of samples collected from the sites representing the various habitat types was determined using the TAXDTEST routine in the PRIMER 5.2 package (Clarke and Gorley 2001). This routine was used both to construct a scatterplot of Δ^+ (independent variable) *vs* Λ^+ (dependent variable) of the samples collected at each site, and to determine the probability that the observed values of these indices were representative (*i.e.* within 95%) of the range of values that would be expected for any subset of fish species (of a comparable size) that could be drawn at random from the data for the entire study region. The 95% confidence limits for the different-sized subsets of species were represented as concentric "ellipses" on the scatterplots, and were calculated from 1000 random simulations of Δ^+ and Λ^+. The sizes of these subsets were chosen specifically to approximate the range in the number of different species recorded at the various sites. Any sites that fell outside their corresponding 95% probability ellipse were considered to represent those at which Δ^+ and/or Λ^+ exhibited significant departure from the values expected for these indices over the entire study region.

Separate scatterplots and 95% probability ellipses of Δ^+ and Λ^+ at the various sites were constructed for samples collected with each of the different net types and for each of the different levels of those temporal factors for which ANOVA detected significant differences in Δ^+ and Λ^+ (see subsection 5.2.2.1).

5.2.2.3 Multivariate Analyses

(i) Composition of fish faunas among habitat types, sampling occasions and between net types

Dispersion-weighting of fish species densities and data transformation

Prior to multivariate analyses, all of which were carried out using routines in the PRIMER 5.2 statistical package (Clarke and Gorley 2001), the density of each species derived from each replicate sample collected with each net type, was rounded to the nearest whole number and weighted according to its observed variability among the various replicate samples, *i.e.* "dispersion-weighted". Since this statistical technique is currently being prepared for publication by K.R. Clarke, M.G. Chapman and P.J. Somerfield, the basic characteristics of the procedure (prepared by K.R. Clarke) are provided below.

The standard treatment of biotic data before subjection to non-parametric multivariate analysis involves initial transformation of the density of each species, followed by computation of Bray-Curtis similarity coefficients between every pair of replicate samples, based on the full set of species. However, a prior ‘fine-tuning’ stage was interpolated into the analysis, in which the densities of the different species are differentially weighted on the basis of their observed variability in the replicate samples. The rationale for this approach is that the individuals of certain fish species, which have a large mean density, may be highly spatially clustered (*i.e.* exhibit a strong tendency to form schools), and thus also exhibit large variation among the replicates. Such species, with low ‘signal to noise ratio’, will be inherently less useful for elucidating the driving environmental factors than another species, which has the same mean density but for which the individuals are less clustered and thus has a greater ‘signal to noise ratio’. The key statistic here is the ‘dispersion index’ of a species, namely the ratio of variance to mean for the number of its individuals in repeated samples. Under certain approximate model conditions for the spatial distribution of organisms of species (*e.g.* a generalised Poisson process; Diggle 1983), it is appropriate to estimate the mean dispersion as the average of the dispersion indices computed for each location (D_i), and to down-weight the contribution of species by dividing each of its counts by D_i. This procedure is performed independently for each species prior to carrying out standard similarity calculations. Note that those species, whose individuals are randomly distributed spatially, have dispersion $D \approx 1$ so that their densities remain unchanged. On the other hand, erratic counts for strongly clustered species ($D>>1$) are down-weighted heavily.

A definitive description of the rationale for dispersion-weighting technique and the spatial process model which motivates and validates its operation, the non-parametric test which is used to determine if a species does exhibit significant clustering, and the benefits of its application to elucidating structure in ordinations and ANOSIM tests, is to be given elsewhere (Clarke KR, Chapman MG, Somerfield PJ, in prep. ‘Modified Bray-Curtis similarity calculations for vanishingly sparse and highly clustered species assemblages’). In the present study, its use does ‘fine-tune’ the Bray-Curtis similarities as hoped, thereby reducing the erratic impact of a high degree of schooling by some species and resulting in a modest but improved link between fish assemblage structure and the enduring environmental variables that best define each of the nearshore habitat types (see part *(ii)* in this subsection). Transformation may still be needed prior to calculation of similarities in order to balance the contribution of abundant species with consistently high counts against those of less common and rare species. The arguments for such transformation are the typical biological ones (Clarke and Green 1988), but are more transparent in this situation where any need to transform densities for purely statistical reasons, *i.e.* to down-weight highly erratic and unreliable counts, has been removed. In practice, having performed initial dispersion-weighting, it is usually only necessary to perform, if at all, a mild transformation.

The dispersion-weighted densities of each species recorded in each group of four replicate samples collected with each net type at each site in each season and each year, and, in the case of samples collected with the small net, also during either the day or night, were meaned and then square-root transformed.

Prior to undertaking multivariate analyses to compare the composition of the ichthyofaunas in samples collected with the large and small nets at those sites and on those sampling occasions when both nets were used, the mean densities of each species in samples collected with the small net (which had previously been adjusted to number of fish 100 m^{-2}), were multiplied by five, prior to transformation, so that they were comparable with those derived from samples collected with the large net, *i.e.* number of fish 500 m^{-2}.

Multidimensional Scaling ordination and associated tests

The Bray-Curtis similarity coefficient was used to construct similarity matrices containing samples collected with either or both of the net types. The matrices were then subjected, depending on the size of the associated stress value, to either two or three-dimensional non-metric Multidimensional Scaling ordination (MDS).

Matrices that had been constructed separately for the samples collected using the different net types were initially subjected to one-way Analysis of Similarities (ANOSIM) to determine whether the compositions of the fish faunas at the various habitat types differed significantly. For each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected when the significance level (p) was <5%, and the extent of any significant differences were determined using the R-statistic value (see subsection 3.2.2.1 for a description of this test statistic). Two-way crossed ANOSIM tests were then used to determine whether any significant differences in ichthyofaunal composition among the various habitat types were required to be interpreted separately for each season, year and, in the case of the small net data, for both day and night, *i.e.* whether there were any significant differences in the composition of the ichthyofauna among the various temporal factors. The particular combinations of factors that were employed in each of the two-way crossed ANOSIM tests are described fully in the Results section of this chapter.

When the pairwise comparisons in any ANOSIM test detected a significant difference between the fish compositions in two habitat types, Similarity Percentages (SIMPER) was used to identify which species typified each of those habitat types (Clarke 1993). These species included both those that were caught consistently (and thus produced a relatively high average similarity to standard deviation ratio in the SIMPER results; Clarke and Warwick 2001a) and those that were caught in large numbers but, due to their tendency to form schools, often had relatively low average similarity to standard deviation ratios. While the frequency of occurrence and hence probability of capturing schooling species during sampling is generally less than that of resident non-schooling species, these species still constituted important components of the fish fauna at some habitat types. Thus, in addition to the SIMPER analyses carried out on the data that had been dispersion-weighted, SIMPER was also performed on the species abundance data that had been log-transformed but not dispersion-weighted. The latter analyses provided a greater ability to identify when schooling species made a substantial contribution to the ichthyofauna of a particular habitat type by enabling of the true abundances of each species to be examined, rather than those which were modified by the weighting procedure. However, it should be noted that while the abundances of these irregularly-occurring schooling species are usually the most heavily down-weighted in the dispersion-weighting procedure (see earlier in this subsection), the average similarity to standard deviation ratios for such species were low, irrespective of whether the data had been dispersion-weighted prior to SIMPER analyses. Moreover, these schooling species were always included in the list of "highest contributing" species when both types of data were used (Clarke and Warwick 2001a). Since SIMPER analyses on the latter data are slightly less conservative in the species they selected as typical of a habitat type, any additional species found to have relatively high average similarity to standard deviation ratios (*i.e.* that were not identified during the same analyses on the dispersion-weighted data), were also considered important for typifying a particular habitat type. These additional species are identified in the Results. If the compositions of fish assemblages in a particular pair of habitat types were not found to be significantly different in an ANOSIM test that was otherwise globally significant, SIMPER was used to determine the species that typified the ichthyofaunal composition of that pair of habitat types collectively.

The similarity matrix that was constructed from data derived from both net types was also subjected to two-way crossed ANOSIM to ascertain whether the composition of the ichthyofaunas collected using the 60.5 and 21.5 m nets were significantly different.
The particular factors used in these ANOSIM analyses are described fully in the following Results section. When ANOSIM detected a significant difference, SIMPER was employed to determine which species were most responsible for distinguishing samples from the different net types.

Similarity in pattern of rank orders between sites in different seasons, years and/or day and night

The second-stage MDS routine (Somerfield and Clarke 1995) was used to determine whether the extent of similarity between each pair of sites, based on their ichthyofaunal compositions, differed among seasons, years and, in the case of small net samples, also between day and night. Thus, separate Bray-Curtis similarity matrices, each containing the ranks of the similarities that were calculated from the mean densities of each fish species at each pair of sites, were constructed for all possible combinations of the different temporal factors (*e.g.* summer 2000, autumn 2001 *etc* in the case of the large net data, and summer 2000-day, autumn 2001-night *etc* in the case of the small net data). The Spearman rank correlation (ρ) was then calculated between the underlying rank orders of each pair of similarity matrices and the resulting values used to produce a second-stage similarity matrix, which was then subjected to MDS ordination (Clarke and Gorley 2001). The distribution of the points on the resultant plot, each of which essentially represented a similarity matrix constructed from the data for the various sites on a particular sampling occasion, enabled detection of whether there were temporal shifts in the degree of ichthyofaunal similarity between the various pairs of sites. For example, in summer 2000, the composition of the fish assemblage at site A may be the most similar to that of site B (and that pair of sites are thus assigned a rank of 1 in the underlying matrix), followed by the comparison between sites A and C (ranked 2), then by that between sites A and D (ranked 3). However, in autumn 2000, the ichthyofauna at sites B and D may be the most similar (ranked 1), followed by that at sites A and D (ranked 2) *etc*.

Each of the matrices employed in this routine are required to contain complementary samples. Thus, on those two occasions when the fish at either one or both of the sites in habitat type 4 could not be sampled with a particular net (see section 5.2.1 and Table 5.1), the data collected either at the other site representing that habitat type, or from the same season and time of day in the other year, were duplicated and used as a replacement. Thus, in the case of samples that could not be collected with the large net at one of the sites in habitat type 4 during winter 2000, the data recorded at the second site in this habitat type on that sampling occasion were duplicated for this analysis. Those samples that could not be collected at night with the small net at either of the sites in habitat type 4 in winter 2000, were likewise replaced with duplicated data collected at each of these sites at night in winter 2001. This prevented the alternative situation in which either all data for habitat type 4 on each sampling occasion, or all data for winter 2000 in each habitat type (and at night in the case of the small net), would have to be removed from the second-stage MDS analysis. The above approaches were justified on the grounds that ANOSIM demonstrated that the composition of the fish fauna at habitat type 4 in each of the other seasons did not differ significantly between sites in the case of samples collected using the large net, or between years with those collected at night with the small net.

The results obtained from the ANOSIM tests referred to earlier in this subsection and those derived from the second-stage MDS analysis were used to determine, respectively, whether the composition of the fish assemblages at the various habitat types and the order of the ranked similarities between each pair of sites, differed significantly among any of the temporal factors. These results, in combination, thus elucidated whether it was appropriate to mean the species density data for samples collected at each site over either seasons and/or years and, in the case of samples collected with the small net, over day and night.

(ii) Relating matrices constructed from ichthyofaunal and enduring environmental data

The RELATE procedure was used to quantify the extent to which the pattern of rank orders between the various pairs of sites in similarity matrices constructed from the ichthyofaunal data in each season and/or year, and, in the case of samples collected using the small net, and/or time of day, paralleled those in the distance matrix derived from data for the selected subset of enduring environmental variables measured at those same sites (see subsection 3.3.1 for environmental variables; Clarke and Gorley 2001). Thus, the Spearman rank correlation coefficient (ρ) was used to correlate the arrangement of the rank orders between the various pairs of sites in (1) the Bray-Curtis matrices constructed from the mean densities of the various fish species at each site (which, if appropriate, had also been averaged over a particular temporal factor or factors), with (2) those in the Euclidean distance matrix constructed from the measurements of the selected environmental variables at the same sites.

The underlying arrangement of the rank orders in any particular fish matrix was considered to be significantly correlated with that of the environmental matrix if the associated p value was <5%. The extent of any significant correlation was gauged by the level of ρ, which can range from -1 (*i.e.* no similarity in arrangement of ranks between samples) to +1 (*i.e.* identical arrangement of ranks between samples; Clarke and Warwick 2001a).

(iii) Identification of species most responsible for distinguishing among habitat types

When the correlation between a fish matrix and the environmental matrix was significant, the BVSTEP routine was used to determine which particular subset of fish species from the initial full suite collected at the various sites on a particular sampling occasion provided the best match with the environmental matrix. This subset of species was thus considered to be that which was the most influential in distinguishing the fish composition at sites representing each of the various habitat types (Clarke and Gorley 2001). This was achieved by restarting the BVSTEP procedure from several different random starting points within the ichthyofaunal data set to maximise the chance of selecting the subset of species which produced the highest correlation (ρ*)* with the environmental distance matrix (see subsection 3.2.2.2 for rationale). The subset of species which produced that maximum ρ was then excluded from the full suite of species, and the BVSTEP procedure restarted to determine whether another subset of species could be found from the remaining species which produced a ρ that was within 95% of that initial maximum value (this represents a modification of the approach of Clarke and Warwick 1998). This procedure was repeated until the maximum ρ that could be calculated was below this limit. The cumulative set of species that produced ρ values within 95% of the initial maximum value was considered to be the most important for distinguishing among the sites representing the different nearshore habitat types at a particular time.

(iv) Life-history categories of fish species in different habitat types

Each fish species that was caught in either net type was assigned to one of the following three life-history categories.

1) Resident, *i.e.* those species that spend their entire life in the nearshore marine environment.
2) Juvenile, *i.e.* those species that occupy nearshore marine waters only during the juvenile phase of their life.
3) Transient, *i.e.* those species which occur irregularly in relatively low numbers in nearshore waters, and are more typically found in waters further offshore or in nearby estuaries.

The classification of species into one of the above life-history categories was based on a combination of their length range, frequency of occurrence and abundance in samples collected during the present study, and the results of other ichthyofaunal studies carried out along the lower west coast of Australia (*e.g.* Hutchins and Swainston 1986, Gommon *et al.* 1994, Ayvazian and Hyndes 1995, Gaughan *et al.* 1996, Hyndes *et al.* 1996a, Platell *et al.* 1998, Fairclough *et al.* 2000). However, since certain marine fish species occur along gradients related to distance from shore and/or water depth, caution should be exercised in considering the category to which they have been assigned in this study as being definitive. Furthermore, the extent to which some species occupy nearshore waters in other regions may differ from that along the lower west coast of Australia.

To determine whether there were significant differences in the affinities of the groups of species representing the various life-history categories for particular types of nearshore habitats, a Bray-Curtis similarity matrix was constructed using each of the species recorded at the different sites (Field *et al.* 1982). Note that this “inverse” approach contrasts with that adopted in the multivariate analyses described in part (*i*) of this subsection, in which the samples collected at the various sites, rather than the species, were used to construct the appropriate similarity matrices. Separate similarity matrices were constructed for the suites of species collected in each net type and for each level of those temporal factors for which the composition of the ichthyofauna was shown by the analyses part (*i*) to differ significantly. This prevented any confounding influences of those factors of the species analyses.

Prior to the construction of each of the above matrices, any species that did not contribute more than 1% to the overall density of fish in samples collected with either net on any sampling occasion were excluded from the analysis, since these very rare species tend to disrupt the patterns in the subsequent MDS ordination analyses (Clarke and Warwick 2001a). The densities for the remaining species were standardised, and thus the species data employed in this inverse analysis were not also dispersion-weighted.

Each of the similarity matrices were subjected to MDS ordination, and one-way ANOSIM was used to determine whether the groups of species representing the various life-history categories differed significantly in terms of the habitat types at which they were the most prevalent.

5.3 Results

5.3.1 Characteristics of the fish fauna collected with the 60.5 m net at habitat types 1-4

5.3.1.1 Mean density and length of each species in each habitat type

The greatest total number of fish recorded in any of the four nearshore habitat types between summer 2000 and spring 2001 (*i.e.* after the number of fish in each sample had been adjusted to 500 m^{-2} and summed), was recorded in the moderately sheltered habitat type 2, *i.e.* 69 252 fish, followed by the 30 432 fish in the moderately exposed habitat type 3 (Table 5.2). In both cases, these relatively high overall abundances were attributable mainly to large catches of the schooling clupeids *Hyperlophus vittatus* and *Spratelloides robustus*, which collectively comprised 87.4 and 77.2% of the total catch in habitat types 2 and 3, respectively. The large size of these schools, and the irregularity of their occurrence is reflected by the large standard deviation associated with the mean density of both of these species in each of these habitat types. The median lengths of *H. vittatu*s and *S. robustus* in habitat types 2 and 3*, i.e.* 33-36 mm in the case of the first species and 43-48 mm for the latter, each of which has a maximum length of *ca* 100 mm (Hutchins and Swainston 1986), demonstrate that they use these habitats mainly during their juvenile stages. Other relatively abundant species in both of these habitat types, *i.e.* those that contributed more than 2% to the total catch, included *Atherinomorus ogilbyi* and *Sillago vittata*. However, whereas *Torquigener pleurogramma* was also relatively abundant in habitat type 2, it was far less abundant in habitat type 3, whereas the reverse was true for *Sillago bassensis.* A considerably greater number of species was recorded in habitat type 2 than 3, and 11 of the 94 species recorded in the large net throughout the study were found only in the first of these habitat types, while only three species were recorded just at habitat type 3 (Table 5.2).

The total of 29 404 fish were recorded in habitat type 1, which was highly sheltered from any wave activity and contained seagrass beds close to shore, was greater than the 18 893

Table 5.2 Life-history category (Lh; R=resident, J=juvenile and T=transient), mean density (M; number of fish 500m^{-2}), standard deviation (±1sd), rank by density (Rk), percentage contribution to the overall catch (%) and length range and median length (lr$^{\text{med}}$) of each fish species in samples collected with the 60.5 m net at habitat types 1-4 in nearshore marine waters along the lower west co of Australia in all seasons between summer 2000 and spring 2001. The number of samples collected and the total number of individuals (after the number of fish in each sample had been adjuste to 500m^{-2}) are also provided for each habitat type.

		1					2					3					4				
	Lh	Rk	M	sd	%	lr$^{\text{med}}$	Rk	M	sd	%	lr$^{\text{med}}$	Rk	M	sd	%	lr$^{\text{med}}$	Rk	M	sd	%	lr$^{\text{med}}$
Leptatherina presbyteroides	R	1	104.9	229.9	22.8	21-73^{53}	27	0.1	0.4	<0.1	45-69^{59}						17	0.2	1.3	0.1	57-65^{60}
Pelates sexlineatus	J	2	100.7	259.6	21.9	7-193^{59}	15	0.6	4.4	0.1	94-163^{147}						18	0.1	0.6	<0.1	58-86^{78}
Sillago burrus	J	3	53.7	76.0	11.7	20-162^{57}	12	1.3	5.4	0.1	31-271^{187}	19	0.2	0.5	<0.1	43-207^{173}					
Atherinomorus ogilbyi	R	4	40.0	113.7	8.7	33-167^{73}	4	36.9	126.9	3.4	21-165^{77}	3	52.0	204.6	10.9	29-168^{97}	6	7.1	21.2	2.3	23-167^{75}
Favonigobius lateralis	R	5	32.2	47.3	7.0	18-81^{38}						23	0.1	1.0	<0.1	38-53^{47}					
Sillago vittata	J	6	31.3	150.3	6.8	27-140^{70}	3	45.8	234.9	4.2	22-273^{58}	5	9.4	19.3	2.0	29-145^{67}	3	47.0	123.4	14.9	23-203^{61}
Torquigener pleurogramma	R	7	19.2	73.8	4.2	53-207^{65}	5	26.1	139.3	2.4	16-186^{63}	12	1.1	5.6	0.2	25-190^{62}	8	1.8	4.3	0.6	35-187^{68}
Apogon rueppellii	R	8	18.4	54.5	4.0	22-88^{38}	31	<0.1	0.2	<0.1	27-28^{28}	28	<0.1	0.2	<0.1	40-45^{43}					
Mugil cephalus	J	9	11.3	43.3	2.5	23-368^{28}	31	<0.1	0.2	<0.1	24-31^{28}	16	0.6	3.3	0.1	25-32^{28}	31	<0.1	0.1	<0.1	26
Sillaginodes punctata	J	10	7.9	18.7	1.7	25-249^{63}	39	<0.1	0.1	<0.1	98	28	<0.1	0.2	<0.1	183-191^{187}					
Aldrichetta forsteri	J	11	7.7	34.8	1.7	26-385^{48}	9	2.7	8.5	0.2	22-311^{121}	9	2.3	6.7	0.5	28-311^{93}	5	8.5	43.2	2.7	36-332^{232}
Gerres subfasciatus	R	12	5.7	15.1	1.2	20-163^{58}	8	3.0	9.5	0.3	97-180^{136}	13	1.0	6.5	0.2	98-167^{118}					
Hyperlophus vittatus	J	13	5.5	23.4	1.2	22-62^{30}	1	768.7	4004.1	69.9	21-88^{33}	1	289.8	1007.0	60.9	22-95^{36}	2	69.5	280.4	22.1	22-93^{41}
Rhabdosargus sarba	J	14	5.3	9.4	1.1	12-190^{52}	13	0.8	3.3	0.1	47-232^{158}	6	5.3	29.1	1.1	118-231^{151}	11	0.4	1.5	0.1	139-268^{182}
Sillago schomburgkii	R	15	4.0	5.1	0.9	47-368^{231}	10	2.2	4.0	0.2	145-370^{243}	7	5.0	16.1	1.1	11-203^{213}	14	0.3	0.7	0.1	202-325^{280}
Haletta semifasciata	R	16	3.5	12.8	0.8	13-294^{118}											22	<0.1	0.2	<0.1	142-160^{143}
Pseudorhombus jenynsii	R	17	1.3	1.7	0.3	30-343^{85}	23	0.1	0.4	<0.1	38-362^{235}	25	0.1	0.3	<0.1	148-297^{186}	23	<0.1	0.2	<0.1	137-299^{218}
Gymnapistes marmoratus	J	18	0.8	1.9	0.2	19-128^{71}	28	0.1	0.2	<0.1	43-69^{54}	20	0.2	0.7	<0.1	37-60^{45}					
Cnidoglanis macrocephalus	R	19	0.7	2.5	0.1	55-562^{93}	31	<0.1	0.2	<0.1	48-83^{66}	11	1.4	6.3	0.3	44-282^{73}	13	0.3	1.0	0.1	54-523^{98}
Callionymus goodladi	R	19	0.7	1.7	0.1	67-160^{99}						32	<0.1	0.1	<0.1	86	18	0.1	0.7	<0.1	52-67^{62}
Scobinichthys granulatus	R	19	0.7	1.8	0.1	39-182^{93}	39	<0.1	0.1	<0.1	42	28	<0.1	0.2	<0.1	30-68^{49}	31	<0.1	0.1	<0.1	76
Ammotretis elongatus	R	22	0.7	1.5	0.1	29-128^{67}	17	0.2	0.5	<0.1	38-121^{78}	18	0.2	0.6	<0.1	68-167^{94}					
Sillago bassensis	J	23	0.4	2.4	0.1	44-108^{67}	6	9.5	32.2	0.9	23-200^{84}	4	23.0	33.8	4.8	12-223^{98}	1	128.9	254.6	40.9	27-197^{77}
Spratelloides robustus	R	24	0.4	1.8	0.1	32-62^{52}	2	192.8	1052.4	17.5	18-93^{43}	2	77.3	244.5	16.3	21-96^{48}	4	45.0	221.5	14.3	17-103^{38}
Enoplosus armatus	J	25	0.3	1.9	0.1	25-65^{32}	31	<0.1	0.2	<0.1	33-68^{51}	22	0.1	0.8	<0.1	43-87^{58}	23	<0.1	0.2	<0.1	31-97^{64}
Cristiceps australis	R	26	0.2	0.7	<0.1	37-157^{93}															
Arripis georgiana	J	26	0.2	1.0	<0.1	214-249^{238}	11	1.6	11.1	0.1	187-284^{215}	15	0.7	2.5	0.1	110-253^{218}	20	0.1	0.3	<0.1	52-239^{221}
Hyporhamphus melanochir	J	28	0.2	1.1	<0.1	27-203^{35}	18	0.2	1.4	<0.1	66-173^{161}	8	2.4	15.2	0.5	57-355^{257}					
Pentapodus vitta	T	28	0.2	0.6	<0.1	37-139^{117}	29	<0.1	0.2	<0.1	135-147^{142}										
Acanthaluteres brownii	R	30	0.1	0.6	<0.1	47-75^{53}															

Table 5.2 continued

Platycephalus speculator	J	31	0.1	0.4	<0.1	77-295^{245}	19	0.2	0.5	<0.1	58-367^{106}	20	0.2	0.5	<0.1	11-304^{127}	23	<0.1	0.2	<0.1	54-185^{120}
Contusus brevicaudatus	R	32	0.1	0.3	<0.1	60-260^{165}	39	<0.1	0.1	<0.1	18-73^{46}	26	0.1	0.2	<0.1	31-77^{41}	31	<0.1	0.1	<0.1	53
Vanacampus poecilolaemus	R	33	0.1	0.3	<0.1	77-190^{179}															
Meuschenia freycineti	J	33	0.1	0.3	<0.1	101-171^{137}															
Acanthaluteres spilomelanurus	R	33	0.1	0.4	<0.1	62-87^{82}															
Pelsartia humeralis	J	36	0.1	0.3	<0.1	35-74^{41}	19	0.2	0.8	<0.1	21-99^{65}	14	0.9	3.1	0.2	24-229^{53}	9	0.9	3.2	0.3	43-143^{81}
Upeneus tragula	J	36	0.1	0.4	<0.1	34-61^{36}	39	<0.1	0.1	<0.1	63						31	<0.1	0.1	<0.1	90
Platycephalus endrachtensis	T	38	0.1	0.2	<0.1	247-525^{344}	25	0.1	0.3	<0.1	200-485^{350}										
Penicipelta vittiger	J	38	0.1	0.3	<0.1	25-86^{55}															
Siphamia cephalotes	R	40	<0.1	0.2	<0.1	21-37^{34}	19	0.2	1.1	<0.1	21-45^{28}	24	0.1	0.5	<0.1	26-37^{35}	15	0.2	0.6	0.1	30-41^{36}
Neoodax balteatus	R	40	<0.1	0.2	<0.1	92-153^{148}	39	<0.1	0.1	<0.1	102										
Stigmatophora argus	R	42	<0.1	0.2	<0.1	164-174^{169}	31	<0.1	0.2	<0.1	105-191^{148}										
Platycephalus inops	J	42	<0.1	0.2	<0.1	221-342^{282}															
Parupeneus fraterculus	J	42	<0.1	0.2	<0.1	40-46^{43}															
Cheilodactylus gibbosus	J	42	<0.1	0.2	<0.1	53-79^{66}															
Pseudolabrus parilus	J	42	<0.1	0.2	<0.1	83-96^{90}	39	<0.1	0.1	<0.1	133	28	<0.1	0.2	<0.1	57-128^{93}	31	<0.1	0.1	<0.1	69
Petroscirtes mitratus	R	42	<0.1	0.2	<0.1	27-70^{49}															
Dactylopus dactylopus	R	42	<0.1	0.2	<0.1	117-118^{118}															
Amoya bifrenatus	R	42	<0.1	0.2	<0.1	63-97^{80}															
Callogobius depressus	R	42	<0.1	0.2	<0.1	68-92^{80}															
Paraplagusia unicolor	R	42	<0.1	0.2	<0.1	130-132^{131}	22	0.2	0.4	<0.1	54-183^{100}	17	0.3	0.9	0.1	35-198^{123}	11	0.4	1.0	0.1	53-226^{100}
Chaetoderma penicilligera	J	42	<0.1	0.2	<0.1	37-219^{128}															
Meuschenia australis	J	42	<0.1	0.2	<0.1	50-52^{51}															
Posidonichthys hutchinsii (A, sp.1)	R	54	<0.1	0.1	<0.1	23															
Atherinosoma elongata	T	54	<0.1	0.1	<0.1	40						32	<0.1	0.1	<0.1	44					
Parapegasus natans	R	54	<0.1	0.1	<0.1	53											31	<0.1	0.1	<0.1	64
Amniataba caudavittatus	T	54	<0.1	0.1	<0.1	88															
Pomatomus saltatrix	J	54	<0.1	0.1	<0.1	41	39	<0.1	0.1	<0.1	63						7	2.4	10.5	0.8	24-154^{105}
Pseudocaranx wrightii	T	54	<0.1	0.1	<0.1	63															
Dactylophora nigricans	J	54	<0.1	0.1	<0.1	57															
Sphyraena obtusata	T	54	<0.1	0.1	<0.1	166											23	<0.1	0.2	<0.1	102-134^{118}
Halichoeres brownfieldi	J	54	<0.1	0.1	<0.1	118															
Siphonognathus radiatus	R	54	<0.1	0.1	<0.1	123															
Parapercis haackei	R	54	<0.1	0.1	<0.1	39															
Lesueurina platycephala	R	54	<0.1	0.1	<0.1	36	14	0.8	1.2	0.1	25-77^{45}	10	1.6	3.0	0.3	30-119^{43}	10	0.9	2.5	0.3	31-77^{48}
Petroscirtes breviceps	R	54	<0.1	0.1	<0.1	31															

Table 5.2 continued

Microcanthus strigatus	J	54	<0.1	0.1	<0.1	28															
Engraulis australis	J						7	3.9	21.7	0.4	32-56^{50}						21	0.1	0.4	<0.1	28-40^{35}
Trygonoptera mucosa	T						16	0.2	0.8	<0.1	133-305^{165}	27	<0.1	0.2	<0.1	180-235^{210}	23	<0.1	0.2	<0.1	155-177^{166}
Torguigener piosae	R						23	0.1	0.3	<0.1	33-79^{55}										
Aptychotrema vincentiana	T						25	0.1	0.4	<0.1	41-417^{93}						23	<0.1	0.2	<0.1	121-123^{122}
Fistularia commersonii	R						29	<0.1	0.2	<0.1	122-147^{129}										
Squatinidae australis	T						31	<0.1	0.2	<0.1	137-273^{205}										
Platycephalus laevigatus	J						31	<0.1	0.2	<0.1	52-64^{58}										
Aracana aurita	T						31	<0.1	0.2	<0.1	108-201^{155}										
Gonorynchus greyi	R						39	<0.1	0.1	<0.1	222										
Hippocampus breviceps	R						39	<0.1	0.1	<0.1	47										
Vanacampus margaritifer	R						39	<0.1	0.1	<0.1	83	32	<0.1	0.1	<0.1	119					
Histiogamphelus cristatus	R						39	<0.1	0.1	<0.1	69										
Schuettea woodwardi	J						39	<0.1	0.1	<0.1	38						15	0.2	0.7	0.1	28-96^{65}
Kyphosus sydneyanus	J						39	<0.1	0.1	<0.1	23										
Scobinichthys sp.	R						39	<0.1	0.1	<0.1	15										
Scorpis georgianus	J						39	<0.1	0.1	<0.1	28										
Trygonorhina fasciata	T											32	<0.1	0.1	<0.1	193	31	<0.1	0.1	<0.1	131
Sardinops neopilchardus	J											32	<0.1	0.1	<0.1	209					
Epinephelides armatus	J											32	<0.1	0.1	<0.1	28					
Cristiceps aurantiacus	R											32	<0.1	0.1	<0.1	93	31	<0.1	0.1	<0.1	130
Eubalichthys sp.	J											32	<0.1	0.1	<0.1	14					
Trachurus novaezelandiae	T																23	<0.1	0.2	<0.1	42-227^{135}
Trachinotus bailloni	J																23	<0.1	0.2	<0.1	213-258^{236}
Iso rhothophilus	R																31	<0.1	0.1	<0.1	34
Mitotichthys meraculus	R																31	<0.1	0.1	<0.1	158
Upeneichthys lineatus	J																31	<0.1	0.1	<0.1	83
Sphyraena novaehollandiae	T																31	<0.1	0.1	<0.1	294
Number of species			**67**					**53**					**39**					**42**			
Overall mean density			**459.4**					**1099.2**					**475.5**					**314.7**			
Number of samples			**64**					**64**					**64**					**60**			
Total no. individuals			**29 404**					**69 252**					**30 432**					**18 893**			

fish derived from samples collected in habitat type 4, which was more exposed to wave activity than any of the other habitat types sampled and contained seagrass beds further offshore (Table 5.2). A far greater overall number of species was recorded in habitat type 1 than in any of the other habitat types, *i.e.* 67 *vs* 53-39 species. *Leptatherina presbyteroides* and *Pelates sexlineatus* made the greatest contributions to the total number of fish recorded at habitat type 1, *i.e. ca* 23 and 22%, respectively, while other relatively abundant species, *i.e. Sillago burrus, A. ogilbyi*, *Favonigobius lateralis*, *S. vittata*, *T. pleurogramma*, *Apogon rueppellii* and *Mugil cephalus,* contributed between 11.7 and 2.5% to the overall catch. The length ranges of each of these species indicate that they used this habitat type during both juvenile and adult life (Table 5.2). Several of the 24 species that were recorded exclusively in habitat type 1 included several that are morphologically adapted to inhabit seagrass beds, *e.g.* sygnathids such as *Vanacampus poecilolaemus* and monocanthids such as *Meuschenia freycineti* and *Acanthaluteres spilomelanurus*.

Sillago bassensis comprised 40.9% of the overall catch in the relatively exposed habitat type 4 (Table 5.2). *Hyperlophus vittatus* ranked second in terms of abundance in this habitat type, and the median length of this species in this habitat type was slightly greater than that recorded in habitat types 2 and 3, *i.e.* 41 *vs* 33-36 mm. *Sillago vittata, S. robustus*, *Aldrichetta forsteri* and *A. ogilbyi* were also relatively abundant in habitat type 4, and contributed between 14.9 and 2.3% to the total catch (Table 5.2). The median lengths of each of these species were, in most cases, slightly less than those for these species in the other three habitat types, except for *A. forsteri,* whose median length in habitat type 4 was far greater than in habitat types 1-3, *i.e.* 232 *vs* 48-121 mm, respectively. Six species were recorded only in habitat type 4, each of which is typically associated either with exposed conditions, *e.g. Trachinotus bailloni* and *Iso rhothophilus*, or with macrophytes, *e.g. Mitotichthys meraculus* (Table 5.2).

5.3.1.2 Density of fish, number of species and species relatedness among habitat types, seasons and between years

ANOVA showed that the density of fish derived from catches obtained using the large net differed significantly among habitat types, seasons and years (p <0.001, 0.01 and 0.05, respectively), and that the mean square was greatest for the first of these factors (Table 5.3). No significant interactions were detected among these main effects. Scheffé's *a posteriori* test demonstrated that the mean density of fish in habitat type 1, *i.e.* 247.9 fish 500m^{-2}, was significantly greater than that in both habitat types 2 and 3, *i.e.* 73.5 and 104 fish 500m^{-2}, respectively (Fig. 5.1a). Moreover, the mean density of fish in autumn, *i.e. ca* 172 fish 500m^{-2}, was significantly greater than in winter, *i.e. ca* 69 fish 500m^{-2} (Fig. 5.1b), and the mean overall density of fish was greater in 2000 than in 2001, *i.e. ca* 149 and 94 fish 500m^{-2}, respectively.

Table 5.3 Mean squares and significance levels for three-way ANOVA of the density of fish, number of fish species, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) in samples collected with the large net at habitat types 1-4 along the lower west coast of Australia in each season in 2000 and 2001. "df"=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	Density of fish	Number of fish species	Δ^+	Λ^+
Main effects					
Habitat type (H)	3	3.185***	15.897***	1.856	70.983
Season (S)	3	2.182**	2.506***	1.671	133.080**
Year (Y)	1	2.404*	0.000	0.272	8.131
Two-way interactions					
H x S	9	0.897	0.723	1.802	32.872
H x Y	3	0.031	0.253	0.198	34.115
S x Y	3	0.295	0.933	0.778	7.682
Three-way interactions					
H x S x Y	9	0.704	0.410	0.384	9.007
Error	219	0.554	0.391	1.593	30.644

The number of species collected in the large net differed significantly among habitat types and seasons (p <0.001), but not between years and there were no significant interactions among these three factors (Table 5.3). The mean square for habitat type was far greater than for season and, as was also the case with the density of fish, the mean number of species was significantly greater at habitat type 1, *i.e. ca* 11 species, than at habitat types 2-4, *i.e.* five to six species (Fig. 5.1c). The mean numbers of species in summer and autumn, *i.e.* 7.9 and 7.6, respectively, were significantly greater than in winter, *i.e.* 5.7 species, and that in summer was also significantly greater than that in spring, *i.e.* 6.2 species (Fig. 5.1d).

ANOVA did not detect any significant differences in the average taxonomic distinctness (Δ^+) of the samples collected with the large net in the various habitat types, seasons or between years, and none of the interaction terms between these three independent factors were significant (Table 5.3). However, the variation in taxonomic distinctness (Λ^+) did differ significantly among seasons (p <0.01). Scheffé's *a posteriori* test, in conjunction with the plot of the mean values of this dependent variable in each season, demonstrated that the taxonomic variability of samples collected during summer and autumn were greater than for samples collected in winter (Fig. 5.1e).

In view of the above significant seasonal differences in Λ^+, scatterplots of Δ^+ *vs* Λ^+ (and the associated 95% confidence ellipses for different-sized subsets of species drawn randomly from the overall list of species recorded during the study), were constructed separately for each season (Figs 5.2a-d). These plots showed that the points for the various sites were particularly tightly grouped during winter, indicating that the values for both Δ^+ and Λ^+ at each of the sites were relatively similar in that season (Fig. 5.2c). In contrast, the Λ^+ at representatives of habitat

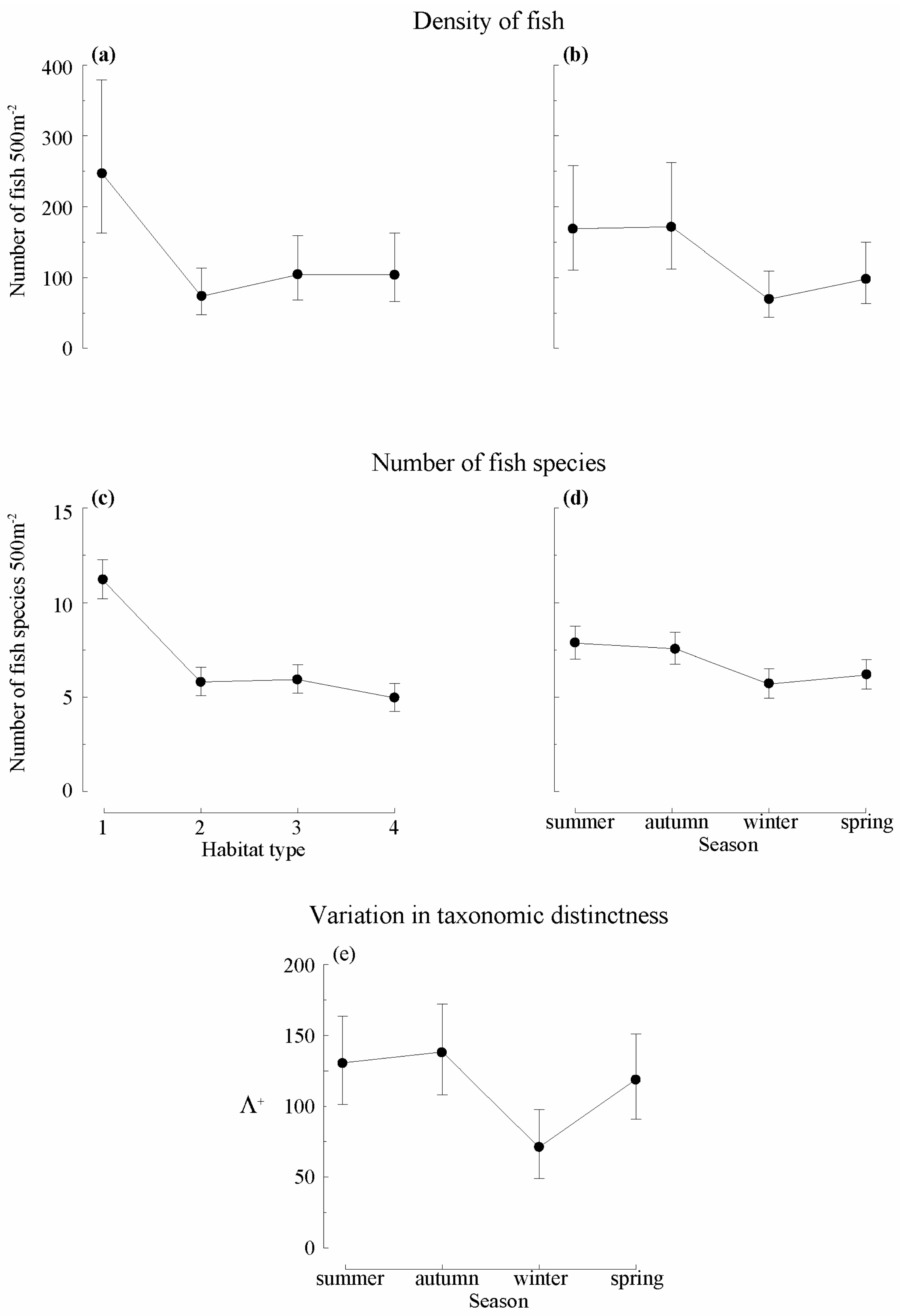


Figure 5.1: Mean (± 95% CI) density of fish in (a) habitat types 1-4 and (b) in each season, mean (± 95% CI) number of species in (c) habitat types 1-4 and (d) in each season, and (e) mean (± 95% CI) variation in taxonomic distinctness in each season in samples collected with the 60.5 m net in 2000 and 2001.

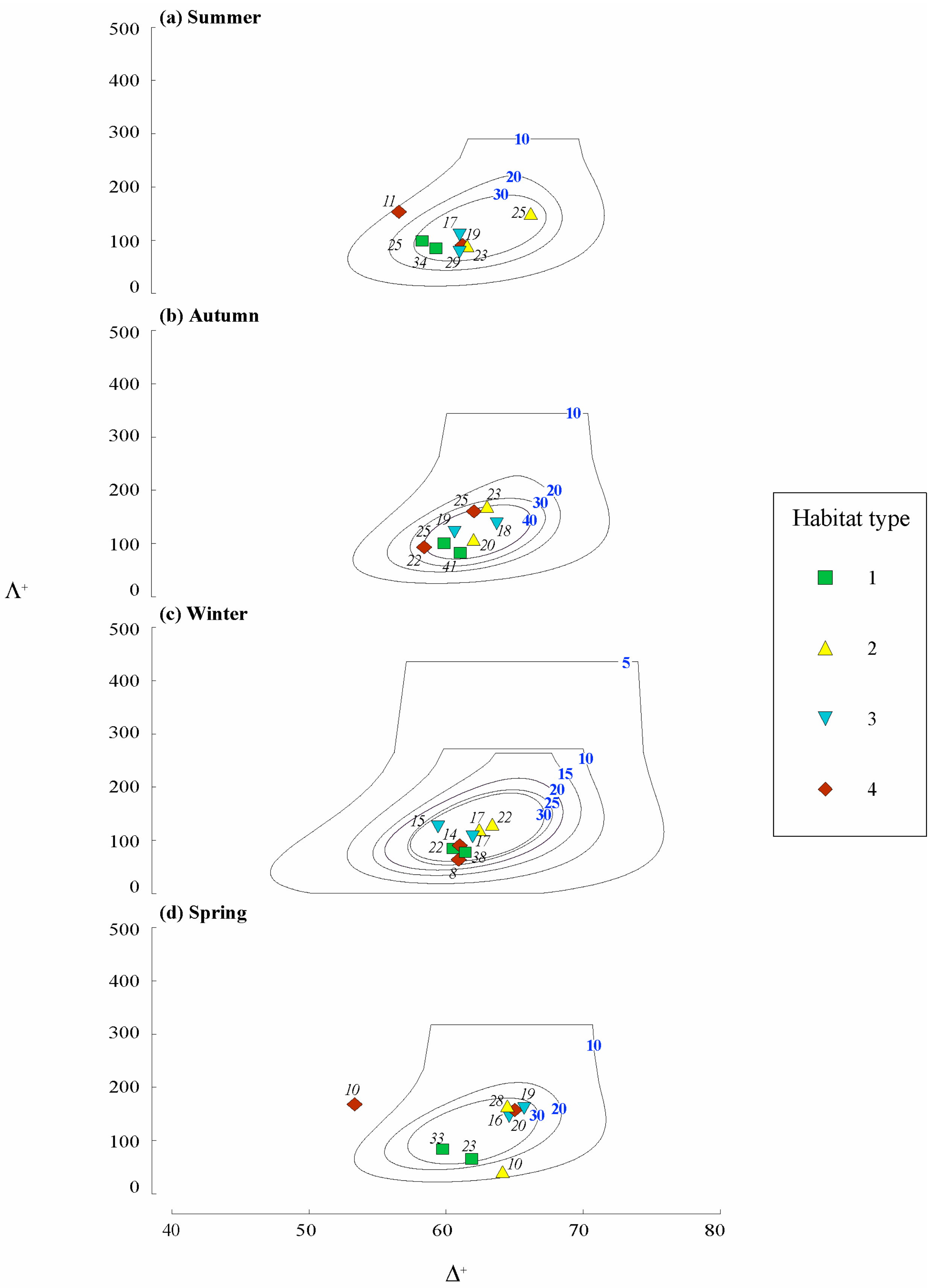


Figure 5.2: Scatterplots of average taxonomic distinctness (Δ^{+}) *vs* variation in taxonomic distinctness (Λ^{+}) of fish in samples collected with the 60.5 m net in habitat types 1-4 in (a) summer, (b) autumn, (c) winter and (d) spring in 2000 and 2001. The number of species recorded at each site in each season and the relevant 95% probability ellipses for simulations of different-sized subsets of species are also provided for each season.

types 2 and 4 were greater than those of the other sites during summer (Fig. 5.2a), while that at sites representing habitat types 1 and 2 were considerably less than at other habitat types during spring (Fig. 5.2d). All of the sites in each season lay within their respective 95% confidence ellipses, except for one site representing the moderately exposed habitat type 4 in spring. This was due to the particularly low Λ^+ of samples collected at that site (Fig. 5.2d).

5.3.1.3 Composition of fish assemblages

(i) Overall differences among habitat types

When the mean densities of the various fish species derived from the samples collected with the large net at each site in each season and in both of years were subjected to MDS ordination, the samples showed a clear tendency to form groups on the basis of habitat type (Fig. 5.3). Thus, samples from the most sheltered habitat type, *i.e.* 1, formed a tight and discrete group that lay the greatest distance from those representing the most exposed habitat type, *i.e.* 4. Samples from habitat types 2 (moderately sheltered) and 3 (moderately exposed) lay between

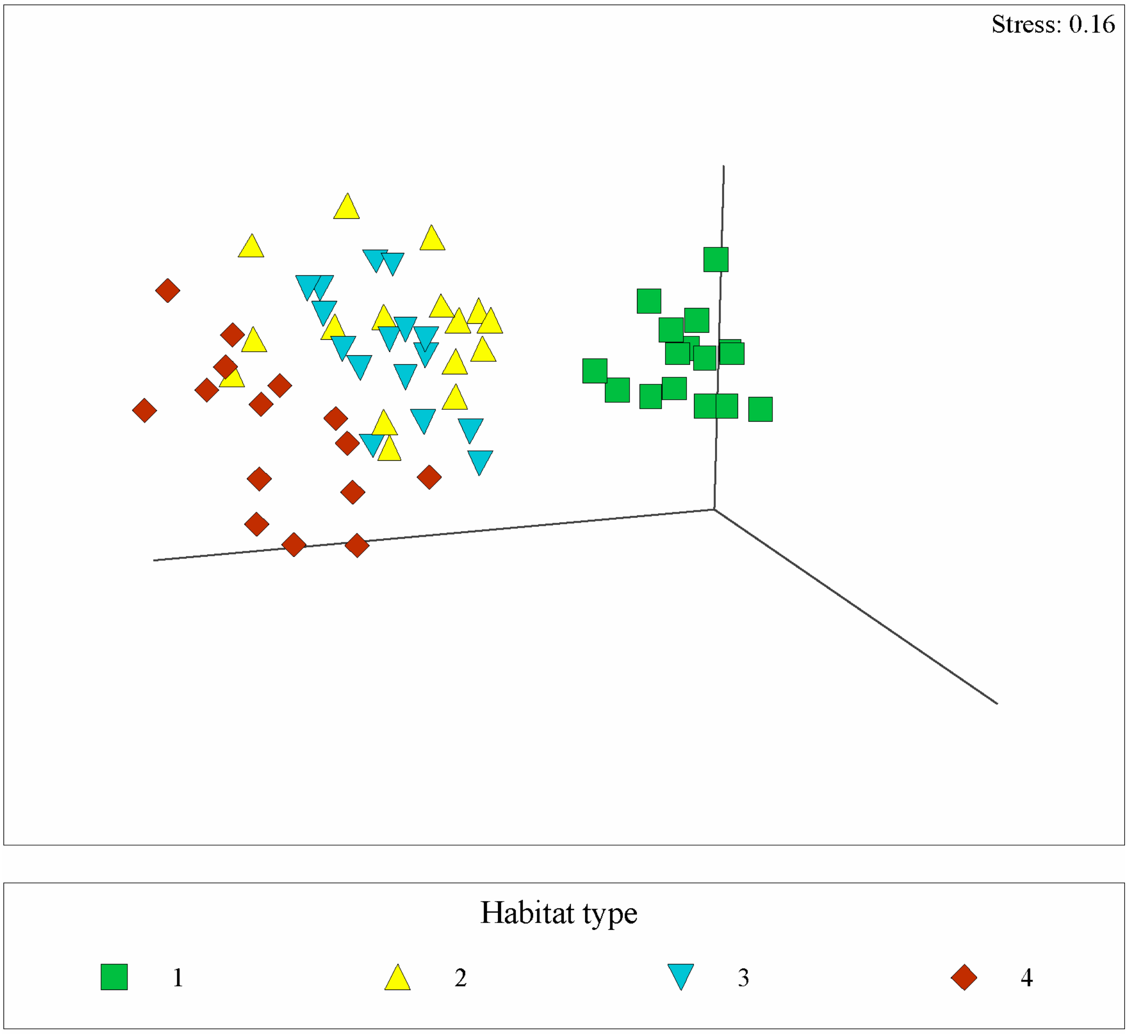


Figure 5.3: Three-dimensional MDS ordination of the mean densities of fish species in samples collected with the 60.5 m net habitat types 1-4 in each season between summer 2000 and spring 2001.

those from 1 and 4, with those from habitat type 3 forming a relatively tight group within the samples from habitat type 2 (Fig. 5.3). One-way ANOSIM showed that the composition of the fish fauna differed significantly overall among habitat types (p=0.1%; Global R=0.530), and that all pairs of habitat were significantly different from each other (p=0.1%), except for habitat type 2 *vs* 3 (p=21.5%). The extent of these pairwise differences was greatest for habitat type 1 *vs* 4 (R=0.925) and least for habitat type 3 *vs* 4 (R=0.293).

The following SIMPER results include those from analyses of both species density data that had been dispersion-weighted, and species density data that had been log-transformed and not dispersion-weighted (the latter of which will be less conservative in the species it selects as typical of a habitat type; see subsection 5.2.2.3 for rationale). Any additional species selected by the latter analyses are identified by an asterisk in each subsequent SIMPER Table .

The species shown by SIMPER to typify each of the habitat types with significantly different ichthyofaunal compositions are listed in Table 5.4. These species include those that were caught regularly in relatively large numbers in the large net and those that were represented by large numbers, but were recorded irregularly due to their tendency to form schools. While some species characterised more than one habitat type (*e.g. Sillago schomburgkii* was regularly abundant at both habitat type 1 and habitat types 2 and 3 collectively, and *S. bassensis* and *H. vittatus* were regularly and irregularly abundant, respectively, at both habitat type 4 and habitat types 2 and 3 collectively), other species typified only one of the habitat types, *e.g. Sillaginodes punctata, S. burrus* and *P. sexlineatus* were regularly abundant only in habitat type 1 (Table 5.4).

(ii) Differences in ichthyofaunal composition among habitat types in different seasons and years

In order to determine whether it was necessary to investigate the above significant differences in ichthyofaunal composition among habitat types 1-4 separately for each season and/or year, two-way crossed ANOSIM tests were used to elucidate whether the compositions of the fish assemblages in each of the four habitat types differed on the basis of one or both of these temporal factors. These tests detected a significant difference among seasons only in habitat type 4 (p=0.1%; Global R=0.79) and did not detect a significant difference between years in any habitat type (p=7.4-92.6%). To accommodate this significant seasonal difference, further comparisons of fish compositions among habitat types were thus carried out separately for each season, but including both years as replicates.

Table 5.4 Regularly and irregularly abundant species, as detected by SIMPER, in samples collected with the 60.5 m net at habitat types 1-4 in each season between summer 2000 and spring 2001. When the compositions of the ichthyofaunas in these habitat types were not significantly different, the data were pooled prior to analysis.

	Regularly abundant	**Irregularly abundant**
1	*S. schomburgkii* *P. jenynsii* *F. lateralis* *S. punctata* *H. semifasciata* *R. sarba* *A. ogilbyi* *P. sexlineatus* *S. burrus* *A. rueppellii* *A. forsteri*	*L. presbyteroides* *T. pleurogramma* *M. cephalus*
2 & 3	*S. bassensis* *L. platycephala* *S. schomburgkii* *S. vittata*	*H. vittatus* *S. robustus* *A. ogilbyi* *T. pleurogramma*
4	*S. bassensis* *L. platycephala** *S. vittata**	*H. vittatus* *S. robustus*

N.B. In this table and subsequent SIMPER tables in this chapter, the irregularly abundant species and additional regularly abundant species (*) were detected using data that was log-transformed but not dispersion-weighted.

When the densities of the various fish species at each of the sites and in the two years were ordinated separately for each season and coded for habitat type, the distribution of the samples paralleled that described above for Fig. 5.3 (*cf* Figs 5.3 and 5.4a-d). One-way ANOSIM demonstrated that the composition of the ichthyofauna differed significantly overall among habitat types in each of the seasons (p=0.1-0.2%), but that the extent of these differences was greatest in summer (Global R=0.701) and least in winter (Global R=0.407). The pairwise comparisons in these ANOSIM tests showed that the composition of the ichthyofauna in each habitat type differed significantly from that in all other habitat types, except in the case of 2 *vs* 3 in each of the four seasons (p=28.6-91.4%), 3 *vs* 4 in autumn (p=11.4%) and 2 *vs* 4 in winter (p=22.9%).

Since the previous two-way crossed ANOSIM tests showed that the fish composition differed significantly among seasons only at habitat type 4, SIMPER was used to determine which species typified the fauna in each season only at this habitat type (Table 5.5). This routine showed that, while some species typified habitat type 4 in all seasons, *e.g. S. bassensis*, others were abundant during only one of the seasons, *e.g. A. forsteri* and *Rhabdosargus sarba* in autumn (Table 5.5).

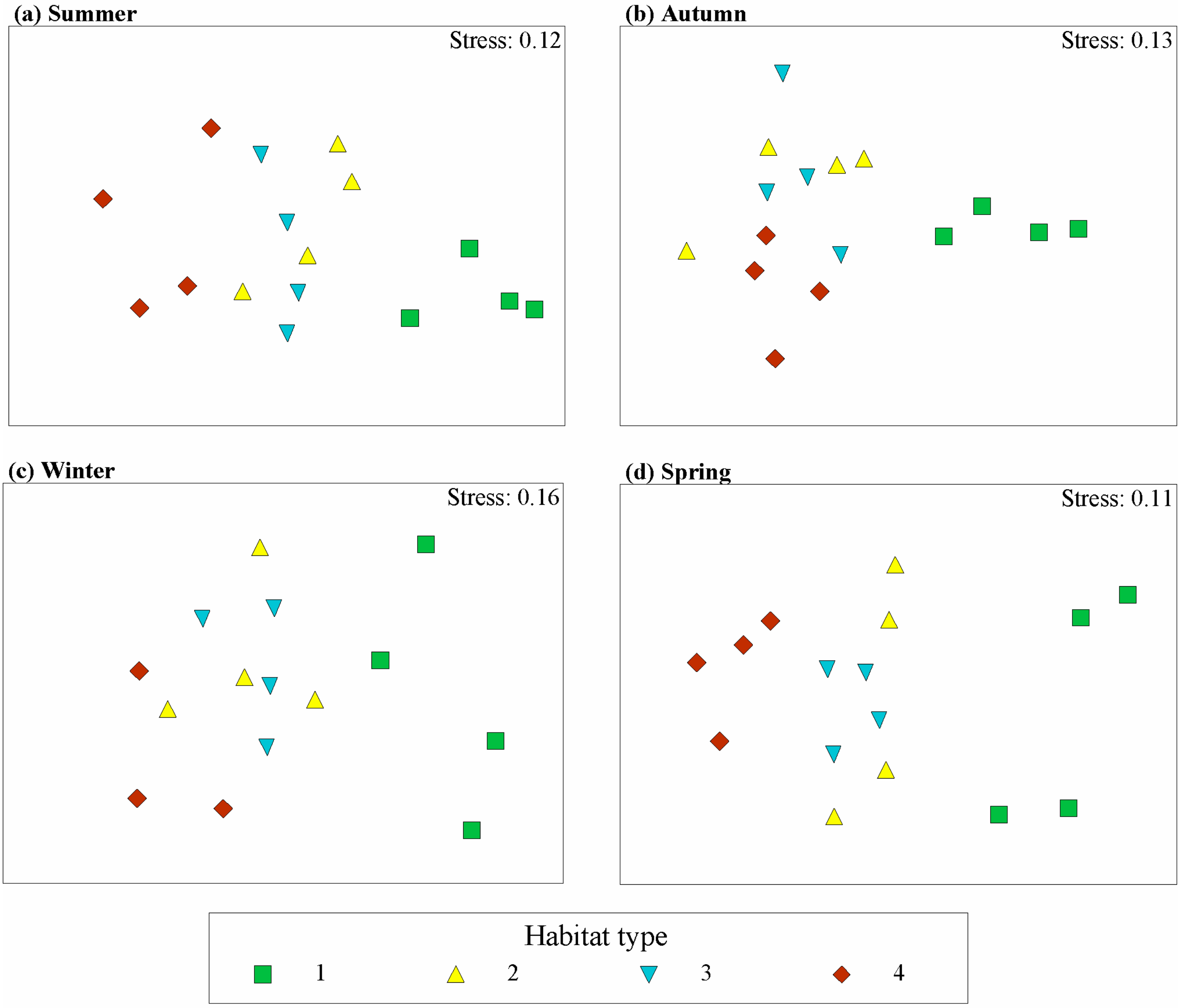


Figure 5.4: Two-dimensional MDS ordination of the mean densities of fish species in samples collected with the 60.5 m net at habitat types 1-4 in (a) summer, (b) autumn, (c) winter and (d) spring of 2000 and 2001.

5.3.1.4 Similarity in pattern of rank orders between sites in different seasons and years

Second-stage MDS was used to elucidate the extent to which the relationships between each pair of sites, based on the degree of similarity of their ichthyofaunal compositions, differed among seasons and/or between years. Although the points representing each season in each year on the resultant second-stage MDS ordination plot were relatively widely dispersed, they were generally arranged according to season and progressed rightwards across the plot from summer and autumn to spring then winter (Fig. 5.5a). These results indicated that there were differences in the arrangement of the rank orders of similarity between pairs of sites in the separate matrices constructed from ichthyofaunal data recorded in each of the different seasons. There was no conspicuous separation of the points on the basis of year (Fig. 5.5b).

Table 5.5 Regularly and irregularly abundant species, as detected by SIMPER, in samples collected with the 60.5 m net at habitat type 4 in each season. Data has been pooled for 2000 and 2001 in this analysis.

	Regularly abundant	**Irregularly abundant**
Summer	*S. bassensis* *S. vittata* *T. pleurogramma* *A. ogilbyi* *L. platycephala*	*S. robustus*
Autumn	*S. bassensis* *P. humeralis* *T. pleurogramma* *C. macrocephalus* *S. woodwardi* *A. forsteri* *R. sarba* *P. unicolor* *S. schomburgkii**	*H. vittatus* *A. ogilbyi* *S. vittata*
Winter	*S. bassensis* *S. robustus* *P. humeralis*	*H. vittatus*
Spring	*L. platycephala* *S. bassensis* *H. vittatus* *S. robustus*	

* additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

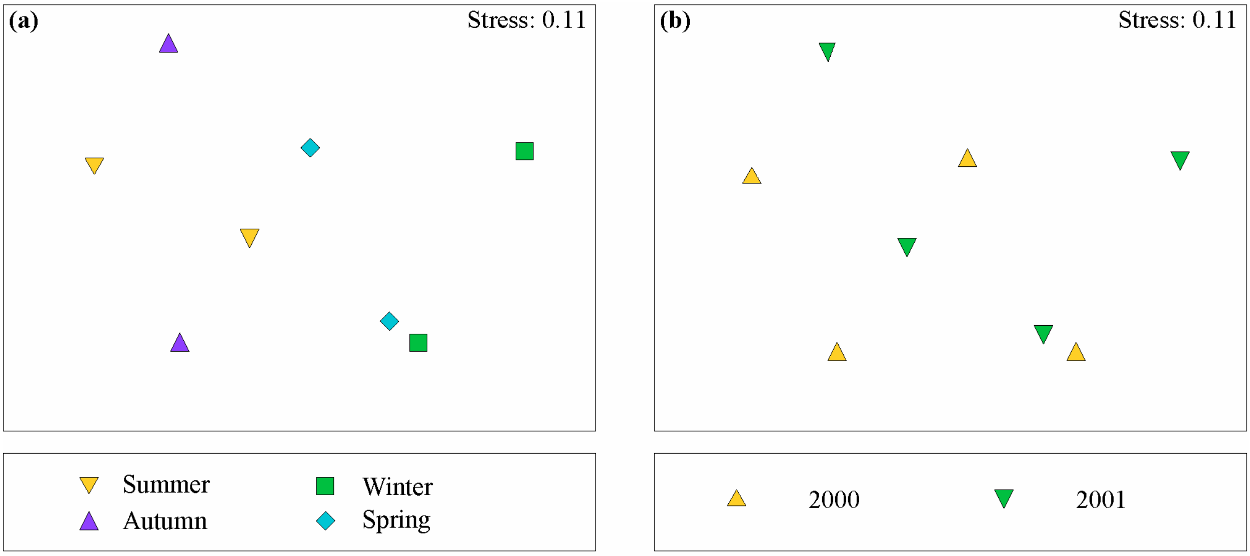


Figure 5.5: MDS ordination of the second-stage similarity matrix containing the correlations between each pair of similarity matrices constructed from the mean densities of fish species in samples collected with the 60.5 m net at habitat types 1-4 during each of the seasons between summer 2000 and spring 2001. The points on the ordination plot have been coded separately for (a) season and (b) year.

5.3.1.5 Relating fish and enduring environmental matrices

RELATE demonstrated that, when the four similarity matrices produced from the fish composition data recorded at the various sites in each season (*i.e.* those used to produce the ordination plots shown in Figs 5.6a-d) were each correlated with the distance matrix constructed from the enduring environmental data for the same sites (*i.e.* that used to produce the ordination plot shown in Fig. 5.7), the ρ values were significant in each case, *i.e.* p=1.2-3.1%. The correlation was highest during autumn (ρ=0.696), followed by spring (ρ=0.598), summer (ρ=0.594) and winter (ρ=0.476). These results demonstrated that the extent of the ichthyofaunal differences between the various sites was significantly correlated, in each season, with the extent of the enduring environmental differences between those same sites.

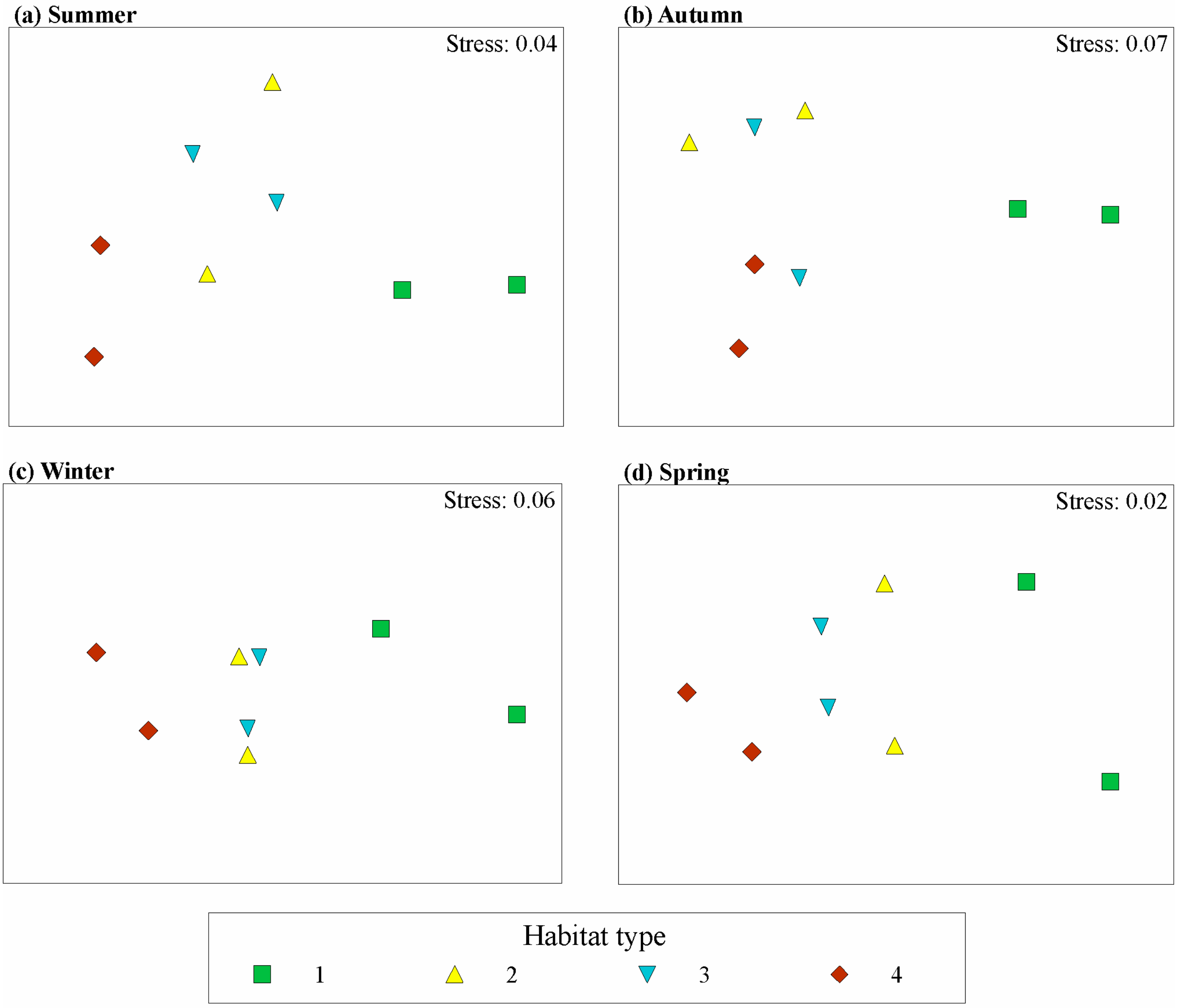


Figure 5.6: Two-dimensional MDS ordination of the mean densities of fish species recorded in samples collected with the 60.5 m net at habitat types 1-4 in (a) summer, (b) autumn, (c) winter and (d) spring. The data have been meaned for samples collected in 2000 and 2001.

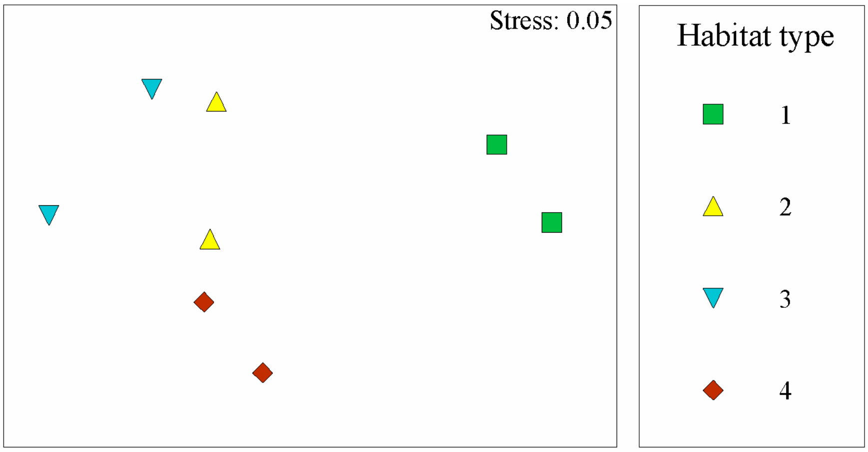


Figure 5.7: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those nearshore sites representing habitat types 1-4 at which fish were sampled with the 60.5 m net.

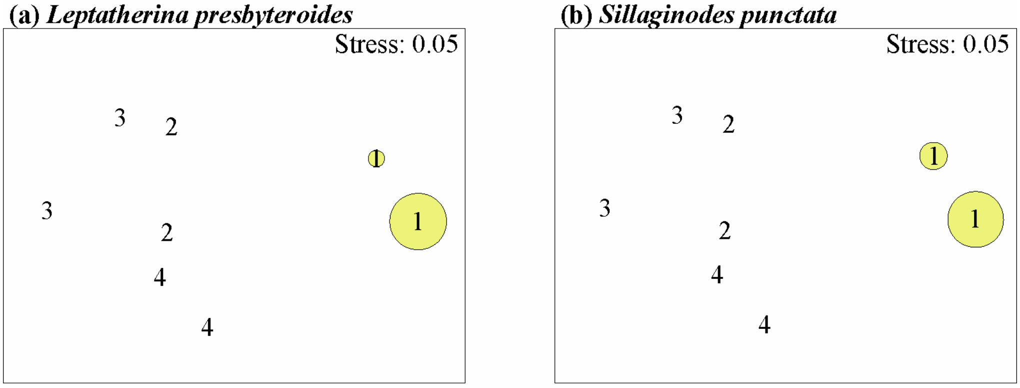
In view of this significant relationship between the ichthyofaunal and environmental data, the BVSTEP procedure was thus employed to ascertain which particular subset of species provided the best correlation with the environmental distance matrix in each season. The selected species are thus those that are most important for distinguishing among the fish faunas at the various habitat types. The suites of species selected by this routine in each of the different seasons are presented in Table 5.6. The maximum ρ values obtained in each season when the selected subsets of fish species were correlated with the environmental distance matrix are also provided.

The relative densities of examples of the species selected in each season were overlaid as circles of proportionate sizes on the points (sites) on the ordination plot produced from the environmental data, *i.e.* that shown in Fig. 5.7 (see Figs 5.8-5.11). These plots thus indicate the ways in which the various species contributed to the differences among habitat types 1-4. For example, species such as *L. presbyteroides* in summer, autumn and winter, *S. punctata* in summer and *Gymnapistes marmoratus* in spring occurred almost exclusively in the highly sheltered habitat type 1 (Figs 5.8a, 5.9a, 5.10a, 5.8b, and 5.11a, respectively). In contrast, other species, such as *Lesueurina platycephala*, *S. bassensis* and *Pelsartia humeralis* were recorded only in the moderately sheltered to moderately exposed habitat types 2-4, and each of these species exhibited marked preferences for one or two of these habitat types, *e.g.* habitat types 2 and 3 in the case of the first species (Figs 5.8d, 5.9e, 5.11b) and habitat 4 in the case of the latter two species (Figs 5.8c, 5.10b and 5.10c, respectively).

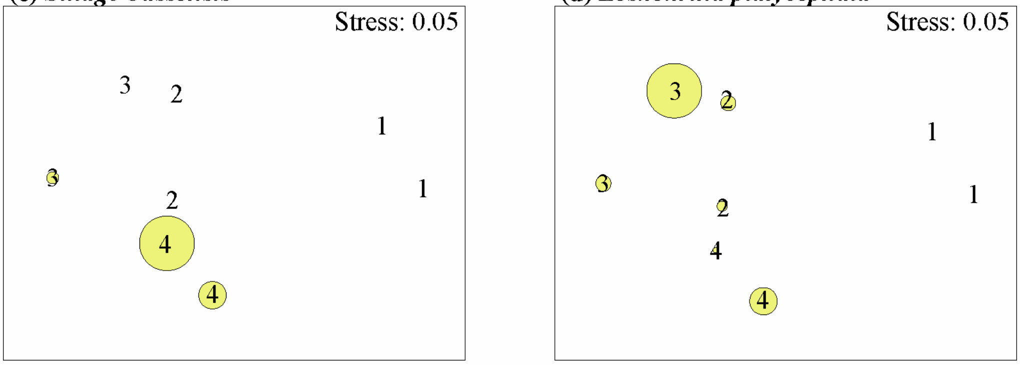
Table 5.6 Subsets of species, derived from samples collected with the 60.5 m net in each season, that were identified by BVSTEP as those which provided the best correlation with the data for the selected suite of environmental characteristics at habitat types 1-4. The maximum correlation value (ρ) between each subset of species and the environmental data is also provided for each season. Data has been pooled for 2000 and 2001 in this analysis.

Summer (max. ρ = 0.847)	**Autumn** (max. ρ = 0.943)	**Winter** (max. ρ = 0.826)	**Spring** (max. ρ = 0.913)
S. bassensis	*S. robustus*	*S. bassensis*	*L. platycephala*
S. punctata	*L. presbyteroides*	*H. vittatus*	*G. marmoratus*
S. burrus	*A. ogilbyi*	*S. robustus*	*H. melanochir*
L. presbyteroides	*S. burrus*	*L. presbyteroides*	*S. cephalotes*
F. lateralis	*S. schomburgkii*	*F. lateralis*	*C. gibbosus*
L. platycephala	*P. sexlineatus*	*P. sexlineatus*	
A. ogilbyi	*L. platycephala*	*P. humeralis*	
P. humeralis	*A. rueppellii*	*En. armatus*	
A. rueppellii	*F. lateralis*	*H. semifasciata*	
M. cephalus	*P. jenynsii*	*S. granulatus*	
T. pleurogramma	*A. forsteri*	*A. rueppellii*	
P. saltatrix	*M. cephalus*	*P. saltatrix*	
M. meraculus	*G. marmoratus*	*P. inops*	
P. natans	*P. saltatrix*		
U. lineatus	*H. melanochir*		
En. armatus	*C. brevicaudatus*		
S. novaehollandiae	*A. vincentiana*		
P. parilus	*V. poecilolaemus*		
H. semifasciata	*P. vitta*		
C. goodladi	*U. tragula*		
Ep. armatus	*H. semifasciata*		
E. australis	*P. fraterculus*		
	A. brownii		
	C. aurantiacus		
	C. goodladi		
	S. woodwardi		
	K. sydneyanus		
	C. australis		

Summer


(a) ***Leptatherina presbyteroides***

(b) ***Sillaginodes punctata***


(c) ***Sillago bassensis***

(d) ***Lesueurina platycephala***

Figure 5.8: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-4 at which fish were sampled with the 60.5m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-4 in summer. Ichthyofaunal data have been meaned for 2000 and 2001.

Autumn

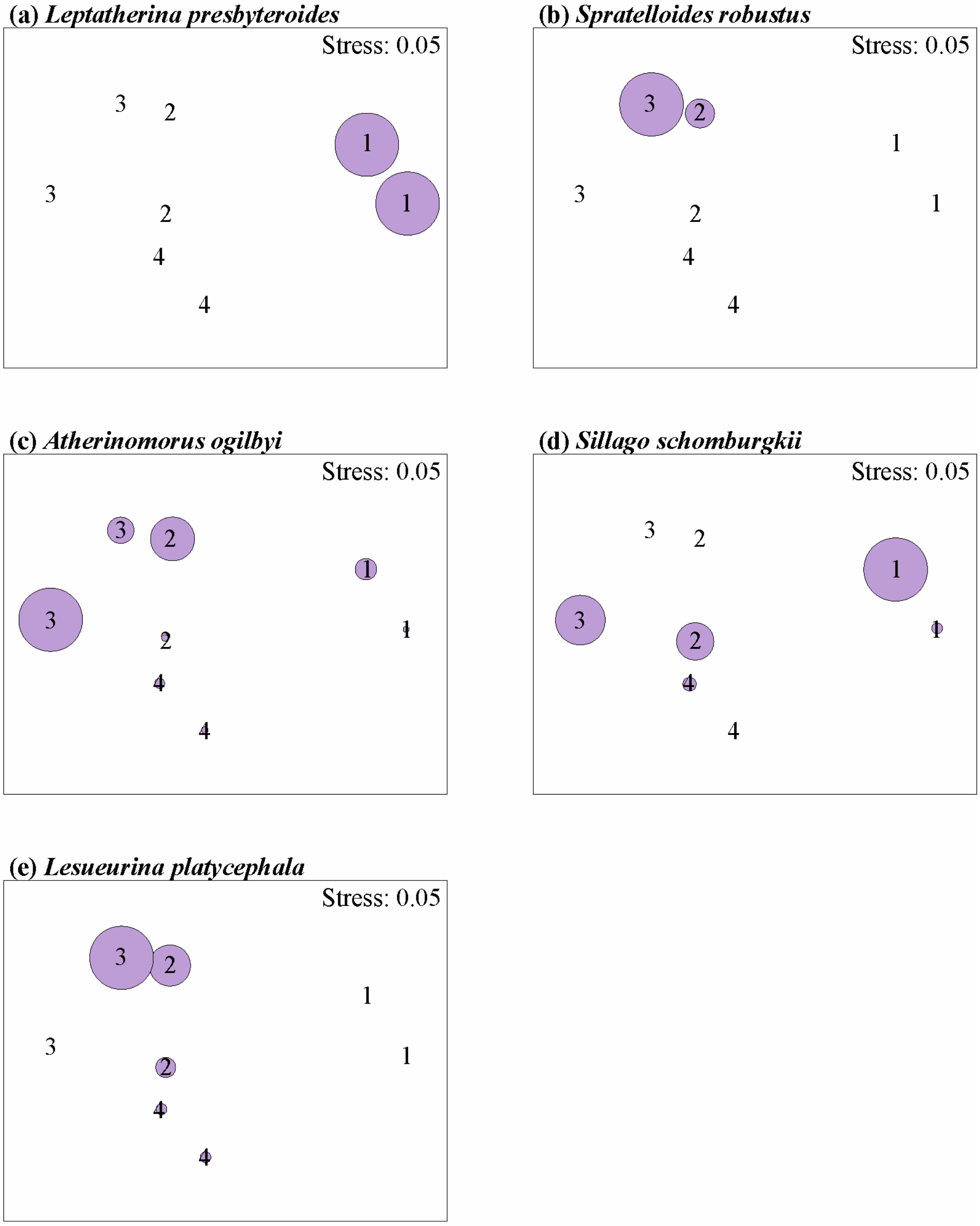
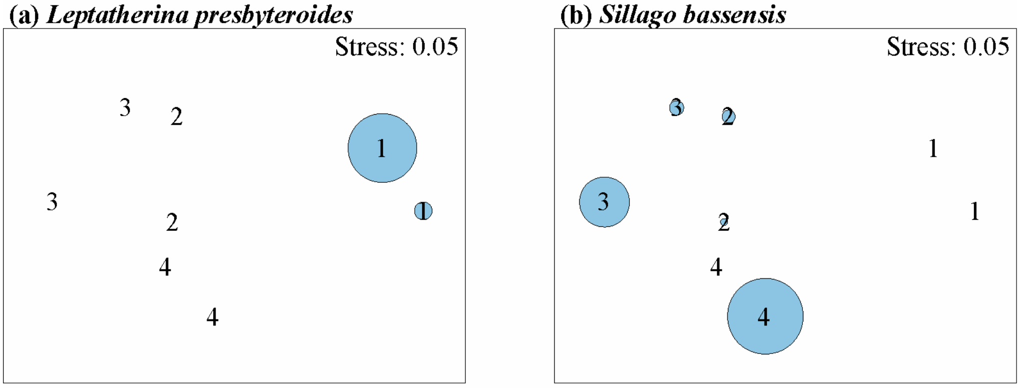


Figure 5.9: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-4 at which fish were sampled with the 60.5m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-4 in autumn. Ichthyofaunal data have been meaned for 2000 and 2001.

Winter


(a) ***Leptatherina presbyteroides***

(b) ***Sillago bassensis***

(c) ***Pelsartia humeralis***

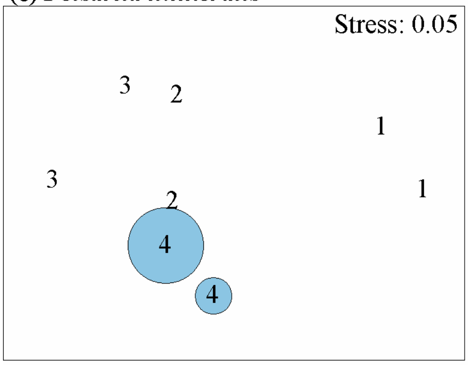


Figure 5.10: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-4 at which fish were sampled with the 60.5m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-4 in winter. Ichthyofaunal data have been meaned for 2000 and 2001.

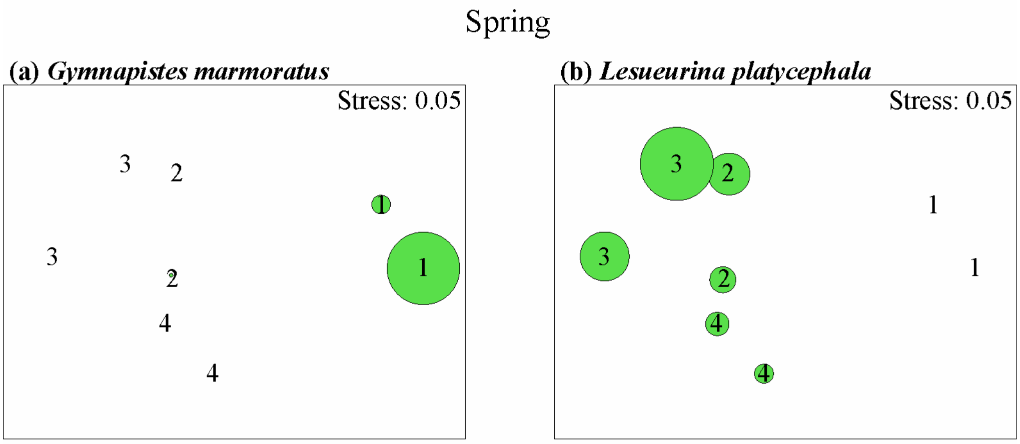


Figure 5.11: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-4 at which fish were sampled with the 60.5m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-4 in spring. Ichthyofaunal data have been meaned for 2000 and 2001.

5.3.2 Characteristics of fish fauna collected with the 21.5 m seine net at each habitat type

The following data for the mean density, lengths and life-history category of each of the fish species caught with the 21.5 m seine net in habitat types 1-6 between summer 2000 and spring 2001 is presented separately for samples collected during the day and night. This facilitates comparisons between the data for fish collected in the large and small nets at habitat types 1-4 during the day.

5.3.2.1 Mean density and length of each species

(i) Characteristics of day-time samples

The total number of fish (*i.e.* after the number of individuals in each sample had been adjusted to 100m^{-2} and summed) in samples collected using the 21.5 m seine net during the day at each of the six nearshore habitat types was greatest at habitat type 3, *i.e.* 16 129 fish, followed by that at habitat types 1 and 2, *i.e.* 9 972 and 8 774 fish, respectively, while the least number of fish was recorded at habitat type 5, *i.e.* 2 867 fish (Table 5.7). As was the case with the samples collected using the large net at habitat types 1-4, those obtained with the small net at habitat type 1 yielded the greatest overall number of species, *i.e.* 45, followed by that at habitat type 2, *i.e.* 45 and 33 species, respectively. The least overall number of species were recorded at habitat type 6, *i.e.* 22 (Table 5.7).

As with samples collected using the large net at habitat type 3, the large overall number of fish recorded in the small net at this habitat type was mainly due to large catches of the schooling clupeid *Hyperlophus vittatus,* which comprised more than 70% of the total catch at this habitat type, and of *Spratelloides robustus* and *Atherinomorus ogilbyi*. These small pelagic species were also the most abundant overall in the samples collected with the small net at habitat type 2, but *S. robustus* was considerably more prevalent in samples from this moderately sheltered habitat type than in those from habitat type 3, whereas the reverse was true for *H. vittatus*. However, at both habitat types 2 and 3, the maximum length of *S. robustus* in samples collected with the small net, *i.e.* 72 and 66 mm, respectively, was considerably lower than that recorded for this species in samples collected with the large net, *i.e.* 93 and 96 mm, respectively (*cf* Tables 5.7 and 5.2). *Lesueurina platycephala* was also relatively abundant in samples collected with the small net at both of these habitat types, and *Aldrichetta forsteri* and *Sillago vittata,* which were represented mainly by their juveniles, were also relatively abundant at habitat type 2.

The samples collected at habitat type 1 were dominated numerically by *A. ogilbyi*, *Leptatherina presbyteroides*, *Sillago burrus*, *Favonigobius lateralis*, *Apogon rueppellii*, *Pelates sexlineatus*, *S. vittata* and *Sillaginodes punctata*, which collectively represented 92.8% of the

Table 5.7 Life-history category (Lh; R=resident, J=juvenile and T=transient), mean density (M; number of fish 100 m^{-2}), standard deviation (±1sd), rank by density (Rk), percentage contribution to the overall catch (%) and length range and median length (lr ^{med}) of each fish species in samples collected with the 21.5 m net during the day at each of the six habitat types (1-6) in nearshore marine waters along the lower west coast of Australia in all seasons between summer 2000 and spring 2001. The number of samples collected and the total number of individuals (after the number of fish in each sample had been adjusted to 100 m^{-2}) are also provided for each habitat type.

	1						**2**					**3**				
	Lh	Rk	M	sd	%	lr ^{med}	Rk	M	sd	%	lr ^{med}	Rk	M	sd	%	lr ^{med}
Atherinomorus ogilbyi	R	1	41.5	220.8	26.6	32-173^{77}	3	9.8	35.2	7.2	23-150^{83}	2	29.5	148.1	11.7	28-160^{124}
Leptatherina presbyteroides	R	2	32.1	85.9	20.6	17-70^{51}	7	1.8	13.3	1.3	26-51^{30}	10	0.8	6.6	0.3	25-48^{29}
Sillago burrus	J	3	25.1	44.3	16.1	16-153^{51}	26	<0.1	0.1	<0.1	162^{162}					
Favonigobius lateralis	R	4	17.3	29.5	11.1	12-69^{30}										
Apogon rueppellii	R	5	10.6	44.5	6.8	19-85^{32}	20	<0.1	0.3	<0.1	42-47^{45}					
Pelates sexlineatus	J	6	10.1	30.7	6.5	21-219^{57}	26	<0.1	0.1	<0.1	151^{151}					
Sillago vittata	J	7	4.8	16.3	3.1	39-163^{77}	6	2.7	8.1	2.0	15-139^{40}	6	2.9	8.7	1.2	31-141^{59}
Sillaginodes punctata	J	8	3.1	8.8	2.0	18-222^{35}										
Haletta semifasciata	R	9	2.3	12.1	1.5	41-149^{92}	26	<0.1	0.1	<0.1	49					
Rhabdosargus sarba	J	10	2.0	5.6	1.3	11-396^{52}	19	0.1	0.4	<0.1	118-150^{137}	8	1.0	5.3	0.4	127-203^{173}
Aldrichetta forsteri	J	11	1.2	3.5	0.8	28-331^{43}	4	5.5	22.4	4.0	20-284^{40}	7	1.6	4.9	0.6	23-296^{223}
Hyperlophus vittatus	J	12	1.1	8.6	0.7	22-43^{32}	2	31.8	179.2	23.2	19-55^{29}	1	177.5	867.2	70.4	23-95^{33}
Gymnapistes marmoratus	J	13	0.8	3.3	0.5	19-83^{38}						18	<0.1	0.2	<0.1	48-50^{50}
Sillago schomburgkii	R	14	0.7	1.8	0.5	45-304^{195}	20	<0.1	0.2	<0.1	228-288^{266}	13	0.2	0.8	0.1	186-278^{217}
Pseudorhombus jenynsii	R	15	0.7	1.0	0.4	26-216^{78}	20	<0.1	0.2	<0.1	179-231^{218}	25	<0.1	0.1	<0.1	224
Torquigener pleurogramma	R	16	0.4	1.3	0.3	55-155^{68}	12	0.3	0.8	0.2	27-203^{73}	17	0.1	0.3	<0.1	63-168^{147}
Ammotretis elongatus	R	17	0.4	1.1	0.3	13-102^{60}	16	0.1	0.4	0.1	59-114^{69}	18	<0.1	0.2	<0.1	67-125^{107}
Gerres subfasciatus	R	18	0.3	0.9	0.2	17-149^{60}	10	0.4	2.5	0.3	126-154^{135}	12	0.2	1.9	0.1	106-127^{114}
Callionymus goodladi	R	19	0.2	0.6	0.1	58-143^{102}	26	<0.1	0.1	<0.1	128					
Mugil cephalus	J	20	0.1	0.9	0.1	27-30^{28}	13	0.2	1.6	0.2	25-31^{27}	11	0.4	3.6	0.2	27-32^{29}
Cristiceps australis	R	21	0.1	0.5	0.1	38-108^{74}										
Cnidoglanis macrocephalus	R	22	0.1	1.0	0.1	70-90^{77}	11	0.4	2.1	0.3	43-147^{90}	15	0.1	0.5	0.1	47-130^{59}
Platycephalus speculator	J	23	0.1	0.3	0.1	72-197^{160}	17	0.1	0.3	0.1	40-220^{63}	18	<0.1	0.2	<0.1	97-164^{131}
Scobinichthys granulatus	R	24	0.1	0.3	0.1	55-117^{77}	26	<0.1	0.1	<0.1	36	23	<0.1	0.2	<0.1	17-27^{22}
Sillago bassensis	J	25	0.1	0.3	<0.1	53-117^{59}	8	1.2	7.1	0.9	27-120^{77}	5	3.3	7.0	1.3	40-188^{84}
Hyporhamphus melanochir	J	25	0.1	0.5	<0.1	98-173^{147}										
Amniataba caudavittatus	T	25	0.1	0.5	<0.1	68-79^{79}										

Table 5.7 continued

Spratelloides robustus	R	28	<0.1	0.2	<0.1	45-67^{55}	1	78.8	563.4	57.5	22-72^{36}	3	25.5	80.2	10.1	18-66^{32}
Sillaginid sp.	J	28	<0.1	0.3	<0.1	14-17^{16}										
Pseudolabrus parilus	J	28	<0.1	0.2	<0.1	31-192^{144}										
Penicipelta vittiger	J	28	<0.1	0.3	<0.1	44-54^{53}										
Vanacampus margaritifer	R	32	<0.1	0.2	<0.1	76-93^{85}										
Pelsartia humeralis	J	32	<0.1	0.2	<0.1	16-17^{16}	9	0.4	1.3	0.3	13-92^{46}	16	0.1	0.6	0.1	37-97^{51}
Arripis georgiana	J	32	<0.1	0.2	<0.1	244-257^{251}	17	0.1	0.5	0.1	45-210^{52}	23	<0.1	0.2	<0.1	115-129^{122}
Upeneus tragula	J	32	<0.1	0.2	<0.1	34-62^{48}										
Lesueurina platycephala	R	32	<0.1	0.2	<0.1	35-52^{44}	5	2.7	3.4	2.0	19-78^{42}	4	7.0	10.0	2.8	20-106^{39}
Dactylopus dactylopus	R	32	<0.1	0.2	<0.1	125-165^{145}										
Acanthaluteres spilomelanurus	R	32	<0.1	0.2	<0.1	52-72^{62}										
Stigmatophora argus	R	39	<0.1	0.1	<0.1	139						25	<0.1	0.1	<0.1	181
Platycephalidae sp.	J	39	<0.1	0.1	<0.1	35	26	<0.1	0.1	<0.1	22					
Platycephalus laevigatus	J	39	<0.1	0.1	<0.1	88										
Neoodax balteatus	R	39	<0.1	0.1	<0.1	52										
Petroscirtes mitratus	R	39	<0.1	0.1	<0.1	80										
Paraplagusia unicolor	R	39	<0.1	0.1	<0.1	129	15	0.1	0.4	0.1	32-119^{105}	13	0.2	0.5	0.1	26-285^{83}
Eubalichthys sp.	J	39	<0.1	0.1	<0.1	18										
Enoplosus armatus	J						14	0.2	1.2	0.1	17-48^{40}	18	<0.1	0.2	<0.1	31-77^{71}
Trygonoptera mucosa	T						23	<0.1	0.2	<0.1	261-309^{285}	25	<0.1	0.1	<0.1	189
Engraulis australis	J						23	<0.1	0.2	<0.1	36-37^{37}	9	0.9	6.7	0.4	21-45^{39}
Siphamia cephalotes	R						23	<0.1	0.2	<0.1	29-37^{33}					
Gonorynchus greyi	R						26	<0.1	0.1	<0.1	146					
Contusus brevicaudatus	R						26	<0.1	0.1	<0.1	28	18	<0.1	0.2	<0.1	39-72^{47}
Odax acroptilus	R											25	<0.1	0.1	<0.1	66
Mitotichthys meraculus	R															
Trachinotus bailloni	J															
Siphonognathus attenuatus	R															
Histiogamphelus cristatus	R															
Philicampus tigris	R															
Platycephalus endrachtensis	T															
Pomatomus saltatrix	J															
Schuettea woodwardi	J															

Iso rhothophilus	R															
Parupeneus fraterculus	J															
Kyphosus sydneyanus	J															
Creedia sp.	R															
Crapatatulus munroi	R															
Scorpis georgianus	J															
Carangidae sp.	J															
Argyrosomus japonicus	T															
Pseudogobius olorum	T															
Number of species			**45**					**33**					**28**			
Overall mean density			**155.8**					**137.1**					**252.0**			
Number of samples			**64**					**64**					**64**			
Total no. individuals			**9 972**					**8 774**					**16 129**			

Table 5.7 continued

		4					**5**					**6**				
	Lh	Rk	M	sd	%	lr ^{med}	Rk	M	sd	%	lr ^{med}	Rk	M	sd	%	lr ^{med}
Atherinomorus ogilbyi	R	4	2.7	12.4	3.8	22-133^{45}	1	21.4	45.0	47.8	30-135^{73}	2	9.7	42.3	14.7	24-108^{81}
Leptatherina presbyteroides	R	19	<0.1	0.1	<0.1	50	3	5.5	36.7	12.4	29-70^{37}					
Sillago burrus	J	15	<0.1	0.2	<0.1	130										
Favonigobius lateralis	R															
Apogon rueppellii	R															
Pelates sexlineatus	J						14	<0.1	0.2	0.1	24-62^{43}	13	<0.1	0.1	<0.1	107
Sillago vittata	J	3	14.2	57.9	19.9	35-143^{58}	8	0.3	1.6	0.7	39-145^{83}	3	7.6	38.6	11.4	28-89^{40}
Sillaginodes punctata	J															
Haletta semifasciata	R															
Rhabdosargus sarba	J	19	<0.1	0.1	<0.1	272										
Aldrichetta forsteri	J	9	0.3	1.3	0.4	19-243^{94}	7	0.5	1.4	1.1	27-100^{39}	6	2.2	11.5	3.4	25-333^{36}
Hyperlophus vittatus	J	5	2.1	9.5	2.9	22-83^{32}	11	0.1	0.7	0.3	28-57^{47}	7	1.3	7.6	1.9	25-83^{30}
Gymnapistes marmoratus	J											13	<0.1	0.1	<0.1	47
Sillago schomburgkii	R	13	0.1	0.3	0.1	275-306^{295}						10	0.1	0.2	0.1	205-250^{219}
Pseudorhombus jenynsii	R	19	<0.1	0.1	<0.1	177										
Torquigener pleurogramma	R	7	1.4	7.6	2.0	34-91^{68}	4	1.9	7.5	4.2	24-76^{35}					

Table 5.7 continued

Ammotretis elongatus	R															
Gerres subfasciatus	R															
Callionymus goodladi	R															
Mugil cephalus	J	15	<0.1	0.2	<0.1	28-29^{29}	15	<0.1	0.1	<0.1	319	13	<0.1	0.1	<0.1	25
Cristiceps australis	R															
Cnidoglanis macrocephalus	R	10	0.2	0.5	0.2	91-42^{133}										
Platycephalus speculator	J	19	<0.1	0.1	<0.1	137	15	<0.1	0.1	<0.1	176	13	<0.1	0.1	<0.1	147
Scobinichthys granulatus	R															
Sillago bassensis	J	2	22.6	88.8	31.6	35-122^{57}	6	0.8	2.6	1.8	34-123^{65}	4	5.7	26.0	8.6	25-130^{53}
Hyporhamphus melanochir	J						15	<0.1	0.1	<0.1	161					
Amniataba caudavittatus	T															
Spratelloides robustus	R	1	24.5	79.9	34.3	18-83^{33}	2	12.3	66.9	27.4	28-90^{57}	1	35.8	232.0	53.9	25-74^{41}
Sillaginid sp.	J															
Pseudolabrus parilus	J						15	<0.1	0.1	<0.1	144					
Penicipelta vittiger	J															
Vanacampus margaritifer	R															
Pelsartia humeralis	J	6	1.9	5.3	2.6	49-272^{93}	10	0.2	0.6	0.4	41-100^{64}	9	0.1	0.3	0.2	97-149^{122}
Arripis georgiana	J															
Upeneus tragula	J															
Lesueurina platycephala	R	8	1.1	1.4	1.5	18-125^{51}	5	1.2	2.8	2.8	28-87^{50}	5	3.6	5.3	5.4	25-137^{52}
Dactylopus dactylopus	R															
Acanthaluteres spilomelanurus	R															
Stigmatophora argus	R											13	<0.1	0.1	<0.1	79
Platycephalidae sp.	J															
Platycephalus laevigatus	J															
Neoodax balteatus	R															
Petroscirtes mitratus	R															
Paraplagusia unicolor	R	11	0.1	0.4	0.1	43-132^{57}	13	0.1	0.4	0.2	83-154^{91}	8	0.1	0.4	0.2	40-321^{154}
Eubalichthys sp.	J															
Enoplosus armatus	J						15	<0.1	0.1	<0.1	37					
Trygonoptera mucosa	T											13	<0.1	0.1	<0.1	312
Engraulis australis	J	11	0.1	0.4	0.1	23-38^{31}						13	<0.1	0.1	<0.1	39
Siphamia cephalotes	R															

Table 5.7 continued

Gonorynchus greyi	R															
Contusus brevicaudatus	R															
Odax acroptilus	R															
Mitotichthys meraculus	R	14	<0.1	0.2	0.1	31-86^{33}										
Trachinotus bailloni	J	15	<0.1	0.2	<0.1	165-171^{168}	12	0.1	0.4	0.2	51-220^{100}	12	<0.1	0.2	0.1	78-118^{83}
Siphonognathus attenuatus	R	15	<0.1	0.2	<0.1	65										
Histiogamphelus cristatus	R	19	<0.1	0.1	<0.1	43										
Philicampus tigris	R	19	<0.1	0.1	<0.1	171										
Platycephalus endrachtensis	T	19	<0.1	0.1	<0.1	384										
Pomatomus saltatrix	J	19	<0.1	0.1	<0.1	47						10	0.1	0.3	0.1	29-96^{90}
Schuettea woodwardi	J	19	<0.1	0.1	<0.1	49										
Iso rhothophilus	R						9	0.3	2.0	0.6	33-55^{43}					
Parupeneus fraterculus	J						15	<0.1	0.1	<0.1	41					
Kyphosus sydneyanus	J						15	<0.1	0.1	<0.1	33					
Creedia sp.	R						15	<0.1	0.1	<0.1	110					
Crapatatulus munroi	R						15	<0.1	0.1	<0.1	49					
Scorpis georgianus	J						15	<0.1	0.1	<0.1	58					
Carangidae sp.	J											13	<0.1	0.1	<0.1	37
Argyrosomus japonicus	T											13	<0.1	0.1	<0.1	346
Pseudogobius olorum	T											13	<0.1	0.1	<0.1	43
Number of species			**27**					**24**					**22**			
Overall mean density			**71.5**					**44.8**					**66.4**			
Number of samples			**63**					**64**					**64**			
Total no. individuals			**4 502**					**2 867**					**4 251**			

total catch. These species, and each of their median lengths, were similar to those that were relatively abundant in the samples collected with the large net at this habitat type (*cf* Tables 5.7 and 5.2). Five of the 14 species that were recorded exclusively in the small net samples collected during the day at habitat type 1 were also recorded only in this habitat type in the large net (*cf* Tables 5.7 and 5.2).

In contrast to habitat types 1-3, the samples collected at habitat type 4 were dominated numerically by almost equal proportions of *S. robustus* and *S. bassensis*, which together comprised 66% of the total number of fish recorded in this habitat type (Table 5.7). While the contribution made by the latter species was similar in those samples collected with the 60.5 m net at this habitat type, that of *S. robustus* was considerably lower in the large net samples (*cf* Tables 5.7 and 5.2). *Sillago vittata* was also relatively abundant in the shallows at habitat type 4 during the day and represented 19.9% of the total number of fish, while *A. ogilbyi*, *H. vittatus*, *Pelsartia humeralis* and *Torquigener pleurogramma* comprised between 3.8 and 2.0% of the overall catch. The median lengths of most of these relatively abundant species indicated that they occurred predominantly as juveniles at this habitat type, and, with the exception of that for *P. humeralis,* these lengths were less than those for these species in samples collected with the large net at this habitat type (*cf* Tables 5.7 and 5.2). Six species were recorded only in this habitat type during the day, of which four are typically associated with seagrass or detached weed, *i.e. Mitotichthys meraculus, Siphonognathus attenuatus, Histiogamphelus cristatus* and *Philicampus tigris* (Hutchins and Swainston 1986).

Approximately 94% of the total number of fish recorded at habitat type 5 during the day were *A. ogilbyi* and *S. robustus, Leptatherina presbyteroides, T. pleurogramma* and *L. platycephala*, the majority of which were represented by the first two of these species. Moreover, the median lengths of *A. ogilbyi* and *S. robustus* were less in this habitat type than in the other habitat types in which these species were relatively abundant (Table 5.7). Three of the six species recorded during the day and found only in habitat type 5 typically occur in shallow reef areas, *i.e. Parupeneus fraterculus, Kyphosus sydneyanus* and *Scorpis georgianus,* while one of the other species is known to have an affinity for nearshore areas which experience turbulent wave activity, *i.e. Iso rhothophilus* (Hutchins and Swainston 1986, Gommon *et al.* 1994).

While *ca* 54% of the overall catch at the exposed habitat type 6 was represented by *S. robustus*, which occurred mainly as juveniles, the large standard deviation associated with the mean density of this species reflected the irregularity of catches of this schooling species at this habitat type. *Atherinomorus ogilbyi, S. vittata, S. bassensis, L. platycephala* and *A. forsteri* were also relatively abundant in this habitat type and contributed between 14.7 and 3.4% to the overall number of fish. The median and maximum lengths of *S. vittata* were considerably lower in habitat type 6 than in most other habitat types in which this species was relatively abundant, while the reverse was true for *L. platycephala*. Three species were found only in this habitat type during the day, two of which were transients, *i.e. Argyrosomus japonicus* and *Pseudogobius olorum* (Table 5.7).

(ii) Characteristics of night-time samples

In contrast to the results obtained during the day, the total number of fish in samples collected with the 21.5 m seine net at night was greatest in habitat type 1, *i.e.* 30 968 fish (Table 5.8). This total was *ca* three times greater than that in the same habitat type during the day, and more than five times the next highest total density of fish recorded at night, *i.e.* 6 001 fish at habitat type 4. This latter total was also higher than that recorded in the same habitat type during the day (*cf* Tables 5.8 and 5.7). The total number of fish recorded at each of other four habitat types at night were each substantially lower than those recorded in the same habitat types during the day. This was particularly the case in habitat type 3, at which the lowest overall number of fish were caught at night, with this total being *ca* one eleventh of that recorded at this habitat type during the day (*cf* Tables 5.8 and 5.7). The total numbers of species recorded in habitat type 1 during the night and day were very similar, whereas the number of species found at night was greater than during the day in each of the other habitat types (*cf* Tables 5.8 and 5.7).

The relatively large overall number of fish recorded at habitat type 1 at night was due mainly to large catches of *L. presbyteroides*, which represented nearly 69% of the total catch in this habitat type. While this species ranked second in terms of overall abundance in habitat type 1 during the day, its contribution to that total was nearly 3.5 times less than that at night. With the exception of *T. pleurogramma,* each of the other species that were relatively abundant at night in this habitat type were also abundant during the day, although the order of their ranking differed between these times in some cases. *Sillaginodes punctata*, which was among the more abundant species recorded at habitat type 1 during the day, was not relatively abundant in at night in this habitat type. However, the mean density of this species was greater at night than during the day (*cf* Tables 5.8 and 5.7). The minimum, maximum and median lengths of most of the species that were relatively abundant during both the day and night were similar during both of those periods. Eleven of the 77 species recorded at night were found exclusively in habitat type 1, two of which were found solely in this habitat type during both the day and night (*cf* Tables 5.8 and 5.7).

Hyperlophus vittatus was the most abundant species recorded in habitat type 2 at night, and contributed *ca* 46% to the total number of fish recorded at that habitat type. However, while

Table 5.8 Life-history category (Lh; R=resident, J=juvenile and T=transient), mean density (M; number of fish 100 m^{-2}), standard deviation (±1sd), rank by density (Rk), percentage contribution to the overall catch (%) and length range and median length (lr ^{med}) of each fish species in samples collected with the 21.5 m net during the night at each of the six habitat types (1-6) in nearshore marine waters along the lower west coast of Australia in all seasons between summer 2000 and spring 2001. The number of samples collected and the total number of individuals (after the number of fish in each sample had been adjusted to 100 m^{-2}) are also provided for each habitat type.

		1					2					3				
	Lh	Rk	M	sd	%	lr ^{med}	Rk	M	sd	%	lr ^{med}	Rk	M	sd	%	lr ^{med}
Leptatherina presbyteroides	R	1	332.8	579.9	68.8	24-74^{54}	27	<0.1	0.1	<0.1	65					
Atherinomorus ogilbyi	R	2	46.7	114.7	9.6	31-143^{68}	8	1.0	3.3	2.6	35-157^{85}	5	1.3	3.1	5.8	38-143^{88}
Torquigener pleurogramma	R	3	21.0	103.8	4.3	39-197^{63}	5	1.9	6.7	5.1	12-185^{63}	15	0.2	0.6	1.0	20-169^{68}
Favonigobius lateralis	R	4	17.6	33.0	3.6	16-75^{34}										
Apogon rueppellii	R	5	15.5	24.4	3.2	17-84^{46}	16	0.1	0.4	0.3	30-58^{41}	6	1.3	5.7	5.5	37-63^{53}
Sillago burrus	J	6	14.9	24.9	3.1	19-227^{47}	15	0.2	0.9	0.5	30-186^{158}	21	0.1	0.3	0.2	133-188^{184}
Pelates sexlineatus	J	7	9.7	37.1	2.0	15-217^{51}	27	<0.1	0.1	<0.1	24	29	<0.1	0.1	0.1	64
Gerres subfasciatus	R	8	6.7	19.2	1.4	18-169^{34}	18	0.1	0.3	0.2	128-163^{136}	17	0.2	0.8	0.8	107-184^{142}
Rhabdosargus sarba	J	9	4.9	9.1	1.0	11-287^{179}	2	5.5	17.8	14.3	19-244^{157}	3	2.2	7.1	9.7	123-283^{173}
Sillaginodes punctata	J	10	4.0	9.3	0.8	23-251^{40}										
Spratelloides robustus	R	11	2.8	6.7	0.6	35-93^{59}	27	<0.1	0.1	<0.1	63	25	<0.1	0.2	0.1	47-50^{49}
Sillago vittata	J	12	2.3	8.2	0.5	31-149^{57}	7	1.0	2.3	2.7	24-141^{46}	4	1.4	3.7	6.1	24-275^{38}
Pseudorhombus jenynsii	R	13	0.8	1.3	0.2	28-212^{77}	27	<0.1	0.1	<0.1	141					
Hyperlophus vittatus	J	14	0.5	1.5	0.1	30-53^{37}	1	17.7	69.9	46.2	18-54^{30}	9	0.5	1.3	2.1	29-69^{38}
Sillago schomburgkii	R	15	0.4	0.8	0.1	47-346^{218}	14	0.3	0.6	0.7	127-293^{213}	7	0.7	1.7	3.2	168-287^{218}
Gymnapistes marmoratus	J	16	0.3	0.9	0.1	18-95^{58}	10	0.6	2.2	1.7	40-96^{62}	15	0.2	1.0	1.0	28-104^{54}
Aldrichetta forsteri	J	17	0.3	1.0	0.1	32-312^{83}	4	2.3	5.1	5.9	24-330^{51}	8	0.6	1.1	2.6	32-287^{184}
Cnidoglanis macrocephalus	R	17	0.3	1.1	0.1	58-525^{87}	6	1.2	2.6	3.2	45-476^{147}	10	0.5	1.0	2.0	54-528^{224}
Arripis georgiana	J	19	0.3	0.9	0.1	65-280^{246}	12	0.4	1.0	0.9	169-245^{214}	12	0.4	1.2	1.7	66-242^{212}
Hyporhamphus melanochir	J	20	0.2	0.7	<0.1	32-249^{92}	20	0.1	0.2	0.1	104-355^{159}	18	0.1	0.5	0.4	74-114^{104}
Ammotretis elongatus	R	21	0.2	0.4	<0.1	30-128^{74}	24	<0.1	0.2	0.1	73-100^{87}	29	<0.1	0.1	0.1	158^{158}
Mugil cephalus	J	22	0.2	0.7	<0.1	26-437^{294}	17	0.1	0.3	0.2	23-307^{28}	25	<0.1	0.2	0.1	26-27^{27}
Engraulis australis	J	22	0.2	0.8	<0.1	75-99^{83}						29	<0.1	0.1	0.1	73
Paraplagusia unicolor	R	24	0.1	0.6	<0.1	74-141^{126}	11	0.5	0.9	1.3	49-300^{168}	13	0.3	0.7	1.5	20-295^{143}
Platycephalus speculator	J	24	0.1	0.4	<0.1	64-409^{198}	18	0.1	0.2	0.2	126-311^{232}	21	0.1	0.3	0.2	118-249^{203}
Lesueurina platycephala	R	24	0.1	0.5	<0.1	23-68^{33}	3	3.7	5.4	9.7	22-80^{42}	1	6.3	8.8	27.6	20-126^{39}
Enoplosus armatus	J	27	0.1	0.8	<0.1	26-33^{29}	20	0.1	0.3	0.1	42-55^{46}					
Haletta semifasciata	R	28	0.1	0.5	<0.1	57-167^{114}										

Table 5.8 continued

Callionymus goodladi	R	29	0.1	0.3	<0.1	76-112^{88}										
Sphyraeana obtusata	T	30	0.1	0.3	<0.1	267-320^{284}	27	<0.1	0.1	<0.1	319					
Cristiceps australis	R	30	0.1	0.2	<0.1	19-82^{53}										
Microcanthus strigatus	J	30	0.1	0.4	<0.1	30-33^{32}										
Pelsartia humeralis	J	33	<0.1	0.2	<0.1	26-191^{73}	13	0.3	1.0	0.9	21-167^{72}	11	0.4	1.7	1.9	49-210^{148}
Sillago bassensis	J	33	<0.1	0.2	<0.1	48-67^{53}	9	0.9	2.0	2.4	33-150^{72}	2	5.3	8.0	23.4	28-192^{88}
Platycephalus endrachtensis	T	35	<0.1	0.2	<0.1	340-375^{358}										
Platycephalus inops	J	35	<0.1	0.2	<0.1	153-358^{256}										
Gonorynchus greyi	R	37	<0.1	0.1	<0.1	306										
Iso rhothophilus	R	37	<0.1	0.1	<0.1	34										
Histiogamphelus cristatus	R	37	<0.1	0.1	<0.1	105						29	<0.1	0.1	0.1	63
Pentapodus vitta	T	37	<0.1	0.1	<0.1	73										
Upeneus tragula	J	37	<0.1	0.1	<0.1	63										
Girella zebra	J	37	<0.1	0.1	<0.1	40										
Cheilodactylus rubrolabiatus	J	37	<0.1	0.1	<0.1	40										
Parapercis haackei	R	37	<0.1	0.1	<0.1	55										
Chaetoderma penicilligera	J	37	<0.1	0.1	<0.1	64										
Contusus brevicaudatus	R	37	<0.1	0.1	<0.1	127	22	<0.1	0.2	0.1	31-60^{45}	25	<0.1	0.2	0.1	37-146^{92}
Schuettea woodwardi	J						22	<0.1	0.2	0.1	40-86^{44}	24	<0.1	0.2	0.2	78-99^{92}
Trygonoptera mucosa	T						24	<0.1	0.2	0.1	221-241^{231}	21	0.1	0.2	0.2	258-368^{292}
Trachurus novaezelandiae	T						24	<0.1	0.2	0.1	205-208^{207}	20	0.1	0.4	0.3	183-217^{214}
Dasyatis brevicaudata	T						27	<0.1	0.1	<0.1	337					
Cirrhimuraena calamus	R						27	<0.1	0.1	<0.1	317					
Stigmatophora argus	R						27	<0.1	0.1	<0.1	173					
*Terapontid.*sp.	J						27	<0.1	0.1	<0.1	12					
Siphamia cephalotes	R						27	<0.1	0.1	<0.1	37	18	0.1	0.4	0.4	27-41^{35}
Pseudocaranx dentex	T						27	<0.1	0.1	<0.1	158					
Pseudolabrus parilus	J						27	<0.1	0.1	<0.1	57					
Kyphosus sydneyanus	J											14	0.2	1.8	1.1	28-60^{47}
Scobinichthys granulatus	R											25	<0.1	0.2	0.1	44-55^{50}
Aptychotremata vincentiana	T											29	<0.1	0.1	0.1	97
Myliobatis australis	T											29	<0.1	0.1	0.1	500
Atherinosoma elongata	T											29	<0.1	0.1	0.1	52
Stigmatophora nigra	R											29	<0.1	0.1	0.1	102
Pomatomus saltatrix	J											29	<0.1	0.1	0.1	88

Petroscirtes breviceps	R											29	<0.1	0.1	0.1	37
Chelidonichthys kumu	J															
Sardinops neopilchardus	J															
Trachinotus bailloni	J															
Pseudocaranx wrightii	T															
Argyrosomus japonicus	T															
Scorpis georgianus	J															
Acanthistius serratus	J															
Vincentia punctata	R															
Carangidae sp.	J															
Kyphosus cornelii	J															
Cheilodactylus gibbosus	J															
Eubalichthys sp.	J															
Number of species			**46**					**38**					**38**			
Overall mean density			**483.9**					**38.3**					**22.7**			
Number of samples			**64**					**64**					**64**			
Total no. individuals			**30 968**					**2 452**					**1 450**			

Table 5.8 continued

		4					**5**					**6**				
	Lh	Rk	M	sd	%	lr$^{\text{med}}$	Rk	M	sd	%	lr$^{\text{med}}$	Rk	M	sd	%	lr$^{\text{med}}$
Leptatherina presbyteroides	R						2	2.9	13.3	11.9	37-70^{57}					
Atherinomorus ogilbyi	R	18	<0.1	0.2	<0.1	95-122^{118}	1	10.0	33.4	41.3	47-105^{75}	18	<0.1	0.2	0.1	27-87^{57}
Torquigener pleurogramma	R	10	0.5	2.0	0.5	48-111^{59}	9	0.6	3.7	2.5	22-73^{32}	11	0.2	1.3	0.5	17-170^{152}
Favonigobius lateralis	R						19	<0.1	0.2	0.1	48-58^{53}					
Apogon rueppellii	R															
Sillago burrus	J						25	<0.1	0.1	0.1	133	14	0.1	0.5	0.2	156-186^{179}
Pelates sexlineatus	J											19	<0.1	0.2	0.1	119-145^{132}
Gerres subfasciatus	R											5	0.8	4.2	1.7	120-164^{140}
Rhabdosargus sarba	J		0.1	0.5	0.1	170-207^{199}	12	0.2	0.8	0.9	153-350^{320}	6	0.7	2.7	1.6	137-297^{180}
Sillaginodes punctata	J						17	0.1	0.5	0.3	178-207^{190}					
Spratelloides robustus	R	21	<0.1	0.1	<0.1	73	4	1.8	5.1	7.2	29-85^{56}	20	<0.1	0.2	0.1	52-80^{66}
Sillago vittata	J	3	4.3	17.1	4.1	27-138^{61}	15	0.2	0.8	0.7	39-239^{87}	9	0.3	1.0	0.7	29-98^{49}
Pseudorhombus jenynsii	R															

Table 5.8 continued

Hyperlophus vittatus	J	1	76.0	375.2	70.9	20-107^{35}	3	2.8	15.8	11.6	22-36^{28}	3	1.7	9.3	3.7	26-92^{36}
Sillago schomburgkii	R	12	0.2	0.4	0.2	249-328^{287}	19	<0.1	0.2	0.1	222-323^{273}	13	0.2	0.5	0.4	212-314^{252}
Gymnapistes marmoratus	J						19	<0.1	0.2	0.1	41-72^{57}	15	0.1	0.3	0.1	53-57^{56}
Aldrichetta forsteri	J	8	0.9	3.7	0.8	26-246^{44}	11	0.3	1.4	1.4	27-247^{44}	12	0.2	0.6	0.5	32-344^{180}
Cnidoglanis macrocephalus	R	4	2.7	6.1	2.5	87-549^{158}	8	0.7	2.4	2.9	62-588^{107}	21	<0.1	0.2	0.1	189-350^{270}
Arripis georgiana	J						19	<0.1	0.2	0.1	70-259^{165}	8	0.4	1.7	0.8	67-249^{148}
Hyporhamphus melanochir	J	18	<0.1	0.2	<0.1	68-88^{78}	13	0.2	0.6	0.8	80-155^{111}					
Ammotretis elongatus	R															
Mugil cephalus	J						25	<0.1	0.1	0.1	29	24	<0.1	0.1	<0.1	30
Engraulis australis	J	9	0.5	3.9	0.5	47-82^{58}										
Paraplagusia unicolor	R	11	0.4	0.7	0.4	61-173^{124}						7	0.4	0.8	0.9	39-323^{219}
Platycephalus speculator	J	21	<0.1	0.1	<0.1	89										
Lesueurina platycephala	R	5	1.5	2.2	1.4	25-107^{43}	5	1.5	2.4	6.4	28-94^{57}	2	3.9	4.6	8.8	22-120^{44}
Enoplosus armatus	J	21	<0.1	0.1	<0.1	97	19	<0.1	0.2	0.1	73-75^{74}					
Haletta semifasciata	R	21	<0.1	0.1	<0.1	68										
Callionymus goodladi	R															
Sphyraeana obtusata	T											16	0.1	0.3	0.1	214-232^{226}
Cristiceps australis	R															
Microcanthus strigatus	J															
Pelsartia humeralis	J	7	1.1	3.2	1.1	42-234^{84}	6	1.0	3.1	4.2	36-175^{73}	10	0.3	0.7	0.7	57-206^{116}
Sillago bassensis	J	2	17.1	63.0	16.0	26-147^{60}	7	0.8	4.1	3.3	42-170^{60}	1	34.3	125.6	76.7	20-128^{40}
Platycephalus endrachtensis	T											25	<0.1	0.1	<0.1	288
Platycephalus inops	J															
Gonorynchus greyi	R															
Iso rhothophilus	R	15	0.1	0.3	0.1	41-55^{53}	18	0.1	0.3	0.2	21-38^{27}					
Histiogamphelus cristatus	R	21	<0.1	0.1	<0.1	73										
Pentapodus vitta	T															
Upeneus tragula	J															
Girella zebra	J															
Cheilodactylus rubrolabiatus	J															
Parapercis haackei	R															
Chaetoderma penicilligera	J															
Contusus brevicaudatus	R															
Schuettea woodwardi	J	6	1.3	4.2	1.2	35-195^{93}	10	0.5	2.1	2.1	23-204^{55}	4	0.9	5.0	2.0	63-222^{183}
Trygonoptera mucosa	T	15	0.1	0.2	0.1	178-266^{201}						22	<0.1	0.2	0.1	213-299^{256}

Table 5.8 continued

Trachurus novaezelandiae	T															
Dasyatis brevicaudata	T											26	<0.1	0.1	<0.1	320
Cirrhimuraena calamus	R						25	<0.1	0.1	0.1	600					
Stigmatophora argus	R															
*Terapontid.*sp.	J															
Siphamia cephalotes	R	14	0.1	0.4	0.1	35-44^{38}										
Pseudocaranx dentex	T															
Pseudolabrus parilus	J	21	<0.1	0.1	<0.1	59										
Kyphosus sydneyanus	J															
Scobinichthys granulatus	R															
Aptychotremata vincentiana	T															
Myliobatis australis	T															
Atherinosoma elongata	T															
Stigmatophora nigra	R															
Pomatomus saltatrix	J	13	0.1	0.6	0.1	60-152^{122}	19	<0.1	0.2	0.1	29-42^{36}	17	<0.1	0.2	0.1	58-93^{60}
Petroscirtes breviceps	R															
Chelidonichthys kumu	J	18	<0.1	0.2	<0.1	62-88^{75}										
Sardinops neopilchardus	J	21	<0.1	0.1	<0.1	37										
Trachinotus bailloni	J	21	<0.1	0.1	<0.1	149	13	0.2	0.7	0.8	45-200^{132}	27	<0.1	0.1	<0.1	77
Pseudocaranx wrightii	T	21	<0.1	0.1	<0.1	44										
Argyrosomus japonicus	T	21	<0.1	0.1	<0.1	347						23	<0.1	0.2	0.1	301-343^{322}
Scorpis georgianus	J	21	<0.1	0.1	<0.1	38	16	0.1	0.5	0.3	39-60^{46}					
Acanthistius serratus	J						25	<0.1	0.1	0.1	88					
Vincentia punctata	R						25	<0.1	0.1	0.1	54					
Carangidae sp.	J						25	<0.1	0.1	0.1	16					
Kyphosus cornelii	J						25	<0.1	0.1	0.1	39					
Cheilodactylus gibbosus	J						25	<0.1	0.1	0.1	51					
Eubalichthys sp.	J						25	<0.1	0.1	0.1	15					
Number of species			**31**					**33**					**27**			
Overall mean density			**107.2**					**24.2**					**44.8**			
Number of samples			**56**					**64**					**64**			
Total no. individuals			**6 001**					**1 548**					**2 867**			

H. vittatus ranked second in terms of abundance during the day in this habitat type and contributed *ca* 23% to that total catch, the mean density of this species during the day was nearly twice that at night (*cf* Tables 5.8 and 5.7). Of the other species that were relatively abundant in habitat type 2 at night, *Rhabdosargus sarba, T. pleurogramma, C. macrocephalus* and *S. bassensis* were not abundant in this habitat type during the day, while *S. robustus*, which was the most abundant species in habitat type 2 during the day and represented 57.5% of the total catch, contributed <0.1% to the total number of fish recorded at night. Moreover, the considerably greater maximum and median lengths of *R. sarba* and *C. macrocephalus* at night than day indicate that the larger individuals of these species were relatively more prevalent at night in this habitat type (Table 5.8).

Lesueurina platycephala and *S. bassensis* were the most abundant species by far at night in habitat type 3. However, while the collective contribution of these species to the overall catch was far higher at night than during the day, (*i.e.* 51 *vs* 4.1%), the mean densities of each of these species were similar during both of these periods. This diel difference in their relative contributions was due to the far greater overall density of fish that was recorded during the day, most of which comprised *H. vittatus*. In contrast, this schooling clupeid accounted for only 2.1% of the catch at night (*cf* Tables 5.7 and 5.8). *Rhabdosargus sarba*, *S. vittata*, *A. ogilbyi*, *A. rueppellii*, *S. schomburgkii, A. forsteri* and *C. macrocephalus* were also relatively abundant species in habitat type 3 at night, and contributed between 9.7 and 2.0% to the total catch. While the median lengths of both *Sillago* species and *H. vittatus* indicated these species were represented mainly by their juveniles in this habitat type at night, those of the other abundant species implied that they occurred mainly as adults (Table 5.8). Seven of the species recorded in the nearshore waters at night occurred solely in habitat type 3, and four of these were not recorded in any habitat type during the day.

The night-time ichthyofauna at habitat type 4 was dominated numerically by *H. vittatus*, with the mean density of this species being much greater at night than that during the day at this habitat type, *i.e.* 76.0 *vs* 2.1 fish 100 m^{-2} (*cf* Tables 5.8 and 5.7). *Sillago bassensis, S. vittata*, and *C. macrocephalus* were also relatively abundant in habitat 4 at night, and contributed between 16.0 and 2.5% to the total catch. The minimum, maximum and median lengths of those species that were abundant during both the day and night in this habitat type were similar between these periods. Three of the species recorded at night were found solely in habitat type 4, *i.e. Chelidonichthys kumu, Sardinops neopilchardus* and *Pseudocaranx wrightii,* all of which were not recorded in any habitat type during the day (*cf* Tables 5.8 and 5.7).

Atherinomorus ogilbyi was the most abundant species by far in habitat type 5 at night, where it represented more than 40% of the total catch. This species made a similar contribution to the total number of fish in this habitat type during the day (*cf* Tables 5.8 and 5.7). *Leptatherina presbyteroides, H. vittatus, S. robustus, L. platycephala, P. humeralis, S. bassensis, C. macrocephalus, T. pleurogramma* and *Schuettea woodwardi* were also relatively abundant in this habitat type at night, and they each contributed between 11.9 and 2.1% to the total catch. *H. vittatus, P. humeralis, C. macrocephalus* and *Schuettea woodwardi* were either not recorded or were present in greatly reduced numbers during the day in habitat type 5, while the *S. robustus* was far more abundant during the day than night in this habitat type. Six of the species recorded at night were caught only in this habitat type, four of which were not recorded in any habitat type during the day, *i.e. Acanthistius serratus, Vincentia punctata, Kyphosus cornelii* and *Cheilodactylus gibbosus* (*cf* Tables 5.8 and 5.7).

Nearly 77% of the fish recorded at habitat type 6 at night were *S. bassensis*, *i.e.* a mean density of 34.3 individuals 100 m^{-2} (Table 5.8). In contrast, this species comprised only 8.6% of the total catch during the day in this habitat type and was represented by a mean density of 5.7 fish 100 m^{-2} (*cf* Tables 5.8 and 5.7). The median length of *S. bassensis* indicated it was represented mainly by its juveniles during both night and day in this habitat type. *Lesueurina platycephala, H. vittatus* and *S. woodwardi* were also relatively abundant at night in habitat type 6. However, *S. robustus*, *A. ogilbyi* and *S. vittata*, which collectively represented 80.0% of the overall catch at this habitat type during the day, comprised only 0.9% of the catch at night (*cf* Tables 5.8 and 5.7).

5.3.2.2 Density of fish, number of species and species relatedness in different habitat types, seasons and years and between day and night

ANOVA demonstrated that the density of fish differed significantly among habitat types and seasons and between years ($p < 0.001$; Table 5.9). Each of the possible combinations for the two-way interactions between day *vs* night, habitat type and seasons were also highly significant ($p < 0.001$), and that between season and year was also significant, but at a lower level, *i.e.* $p < 0.05$. Furthermore, the three-way interactions between diel period, habitat type and season and between habitat type, season and year were also highly significant ($p < 0.001$). The mean squares for the diel period x season and diel period x habitat type interactions were similar in magnitude to those for both the season and year main effects, and between *ca* 2.5 and 4.5 times greater than those for each of the other significant interaction terms. However, the mean square for habitat type was at least five times greater than that for any of the other significant main effects or interactions (Table 5.9).

Table 5.9 Mean squares and significance levels for four-way ANOVA of the total density of fish, number of fish species, average taxonomic distinctness (Δ^+)and variation in taxonomic distinctness (Λ^+) in samples collected with the 21.5 m net during the day and night at habitat types 1-6 along the lower west coast of Australia in each season in 2000 and 2001. “df”=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	Total density of fish	Number of fish species	Δ^+	Λ^+
Main effects					
Diel (D)	1	0.562	41.044***	19346.326***	61.094***
Habitat type (H)	5	21.519***	26.077***	8873.622***	39.202***
Season (S)	3	4.032***	5.963***	1407.023*	28.192***
Year (Y)	1	4.023***	4.239***	2325.671*	4.811
Two-way interactions					
D x H	5	3.601***	0.962**	833.946	1.583
D x S	3	4.239***	4.106***	3812.423***	10.640***
D x Y	1	0.173	0.032	63.150	3.343
H x S	15	1.453***	0.588*	937.564*	2.404
H x Y	5	0.235	0.195	446.592	0.917
S x Y	3	0.900*	1.889***	830.253	4.700*
Three-way interactions					
D x H x S	15	0.947***	0.499	951.680*	2.505
D x H x Y	5	0.246	0.584	784.676	4.432*
D x S x Y	3	0.367	0.278	294.261	1.352
H x S x Y	15	1.353***	0.925***	975.114**	2.474
Four-way interaction					
D x H x S x Y	14	0.376	0.274	477.754	1.712
Error	664	0.339	0.313	490.348	1.564

The mean density of fish in each season at night was markedly higher in habitat type 1 than in each of the other five habitat types, in which the densities were relatively similar. However, while the mean densities of fish in each season during the day also tended to be greater at habitat type 1 than in each of the other five habitat types, this was not always the case. For example, during spring, the density of fish in habitat type 1 was less than in habitat type 2 and far lower than in habitat type 3 (Fig. 5.12a). Furthermore, the mean densities in each season at habitat type 1 were also greater at night than during the day, whereas this did not always apply in the other five habitat types (*cf* Figs 5.12b and a, respectively). The mean densities of fish were least during winter in five of the six habitat types during the day, ranging between 2.3 and 52.2 fish 100m^{-2}, whereas they were the greatest or second greatest in this season at five of the six habitat types at night, during which they ranged between 8.1 and 301.0 fish 100 m^{-2}. However, the reverse was generally true for autumn and summer (Figs 5.12a, b). Moreover, the extent of the variation in mean densities among the various seasons within each habitat type was almost invariably greater during the day than night (Figs 5.12a, b). All of the above differences

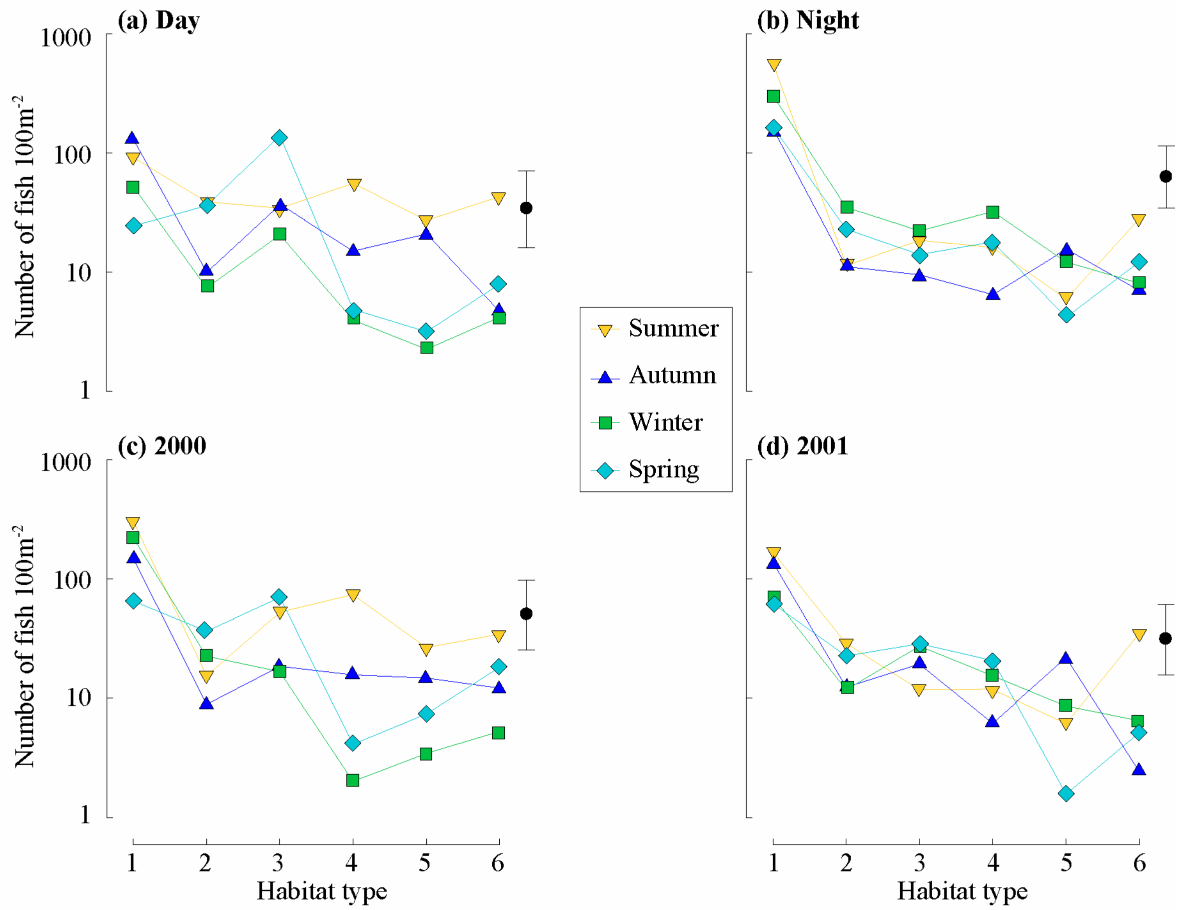


Figure 5.12: Mean (± 95% CI) density of fish at habitat types 1-6 in each season during (a) the day, (b) the night, (c) 2000 and (d) 2001 in samples collected with the 21.5 m net. For the sake of clarity in this figure and in all subsequent figures containing the results of ANOVA, the overall mean (± 95% CI) is provided on each plot (denoted by black symbols and lines)

thus contribute to the significant three-way interaction detected between diel period, habitat type and season.

The mean densities in habitat type 1 in each season during 2001 were greater than those in the corresponding seasons in each of the other habitat types in 2001 and this generalisation was usually also applicable in 2000 (Figs 5.12d and c, respectively). However, the significant interaction among habitat type, season and year was due to the fact that, in 2000, the mean densities of fish were greatest or close to the greatest during summer in five of the six habitat types and least during winter in four of those habitat types, whereas in 2001, the mean density of fish in summer was greatest in only three habitat types and was the second greatest in winter in four of the habitat types (Figs 5.12c and d, respectively).

The number of species was shown by ANOVA to differ significantly between day and night, among habitat types and seasons and between years ($p < 0.001$; Table 5.9). Significant two-way interactions for this dependent variable were detected between diel period and season ($p < 0.001$), season and year ($p < 0.001$), diel period and habitat type ($p < 0.01$) and habitat type and season ($p < 0.05$), and the three-way interaction between habitat type, season and year was also significant ($p < 0.001$). The mean square was greatest for the diel main effect, which contrasted markedly with the situation for the density of fish, for which this factor was not significant. However, as with density of fish, the mean square for habitat type was far greater than for either season or year, and the mean square for the diel x season interaction was greater than that for any other significant interaction term (Table 5.9).

The mean number of species was greater during the night than the day in each season (Fig. 5.13a). However, the extent of these diel differences varied markedly amongst seasons, with a far greater number of species being recorded at night than during the day in winter than in summer. Similar trends with respect to the diel effect were evident in the plot for the mean number of species in the six habitat types during the day and night (Fig. 5.13b). Thus, while the number of species was also greater during the night than day in each habitat type, those diel differences were far greater in habitat type 1 and, to a lesser extent habitat type 2, than in habitat types 3-6 (Fig. 5.13b).

The other significant interactions were explored by plotting the mean number of species in each habitat type and season separately for 2000 and 2001 (Figs 5.13c and d, respectively). Thus, in both years, the mean number of species in each season was typically greater in habitat type 1 than in any of the other five habitat types. However, the relationship between the mean numbers of species in the four seasons was not always the same in each habitat type. For example, in 2001, the mean numbers of species in habitat types 4 and 6 were lower in autumn

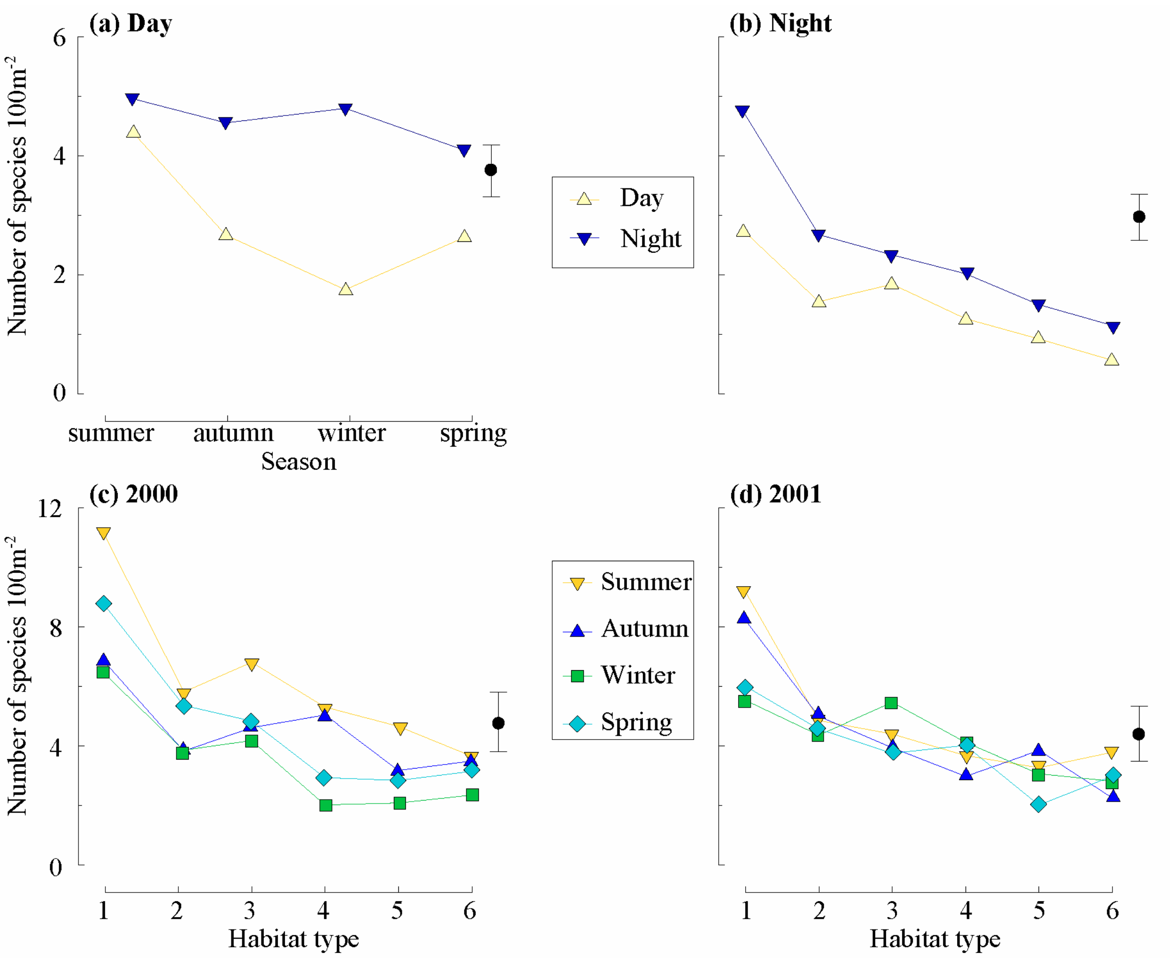


Figure 5.13: Mean (± 95% CI) number of fish species in samples collected with the 21.5 m net during (a) the day and night in each season and (b) the day and night at habitat types 1-6, and in each season and habitat type during (c) 2000 and (d) 2001.

than in any other season, while the reverse was true in this season in habitat type 5 (Fig. 5.13d). Furthermore, the mean number of species in each habitat type was greatest in summer and lowest in winter in 2000, while it was greatest in winter in two habitat types during 2001. The variation in the mean number of species among the different seasons in each habitat type was also greater in 2000 than 2001 (Figs 5.13c, d).

Average taxonomic distinctness differed significantly between day and night and among habitat types ($p < 0.001$) and, to a lesser extent, among seasons and between years ($p < 0.05$; Table 5.9). The diel x season and habitat type x season two-way interactions were also significant ($p < 0.001$ and 0.05, respectively), as was the three-way interaction between these variables and that between habitat type, season and year ($p < 0.05$ and 0.01, respectively). The mean square was far greater for the diel effect than for any of the other significant main effects or interactions, and, as was also the case for density of fish and number of species, the mean square for the diel x season interaction was considerably higher than that for any other significant interaction (Table 5.9).

Plots of the mean values for Δ^+ across the six habitat types in each season in both 2000 and 2001 (Figs 5.14a and b, respectively) showed that, while this dependent variable was generally greatest at habitat type 1 and least at either habitat type 5 or 6 in the various seasons, this was not always the case. For example, Δ^+ was lowest at habitat type 4 in winter 2000 (Fig. 5.14a). Furthermore, the extent of the difference in Δ^+ between consecutive habitat types was greater in some seasons than in others, *e.g.* the marked decline between habitat types 4 and 5 in spring 2001 *vs* the relatively similar values in these two habitat types in summer 2001 (Fig. 5.14b). A similar decreasing trend in Δ^+ from habitat type 1 to 6 was observed in most seasons during both the day and night (Figs 5.14c and d, respectively). However, the significant interaction among these three independent variables is partly due to the fact that, particularly during the day, the values of Δ^+ in summer 2000 were relatively constant across all habitat types, which contrasted with those for autumn, winter and spring. Moreover, while Δ^+ was either lowest or close to the lowest during winter in samples collected during the day, it was highest during this season in four of the six habitat types in samples collected at night (Figs 5.14c, d).

Variation in taxonomic distinctness differed significantly between day and night and among habitat types and seasons ($p < 0.001$; Table 5.9), and the season x diel period, season x year and habitat type, diel period and year interactions were also significant ($p < 0.001$, < 0.05 and < 0.05, respectively). As was the case for Δ^+, the mean square for the first main effect was considerably greater than those for any other significant factor or combination of factors, and that between season and diel period was the most important of the interaction terms. Plots of the mean Λ^+ in each season during both the day and night showed that the significant interaction between these two temporal factors was due to the fact that the values for this dependent variable were greater at night than during the day in autumn, winter and spring, but were very similar during the day and night in samples collected during summer (Fig. 5.14e). The relatively weak interaction between season and year was largely attributable to the slightly higher mean value for Λ^+ recorded in 2001 than 2000 in winter, whereas the reverse was true in all other seasons, and particularly during summer (Fig. 5.14f). Plots of the mean values of Λ^+ during the day and night across each of the six habitat types that were constructed separately for 2000 and 2001, showed that the interaction among these three independent variables was due to the fact that, while the Λ^+ of samples collected at night was usually considerably greater than that of day-time samples at each habitat type, this was not the case at habitat types 5 and 6 in 2000 and habitat types 3 and 5 in 2001, where similar values were recorded during those times (Figs 5.14g and h).

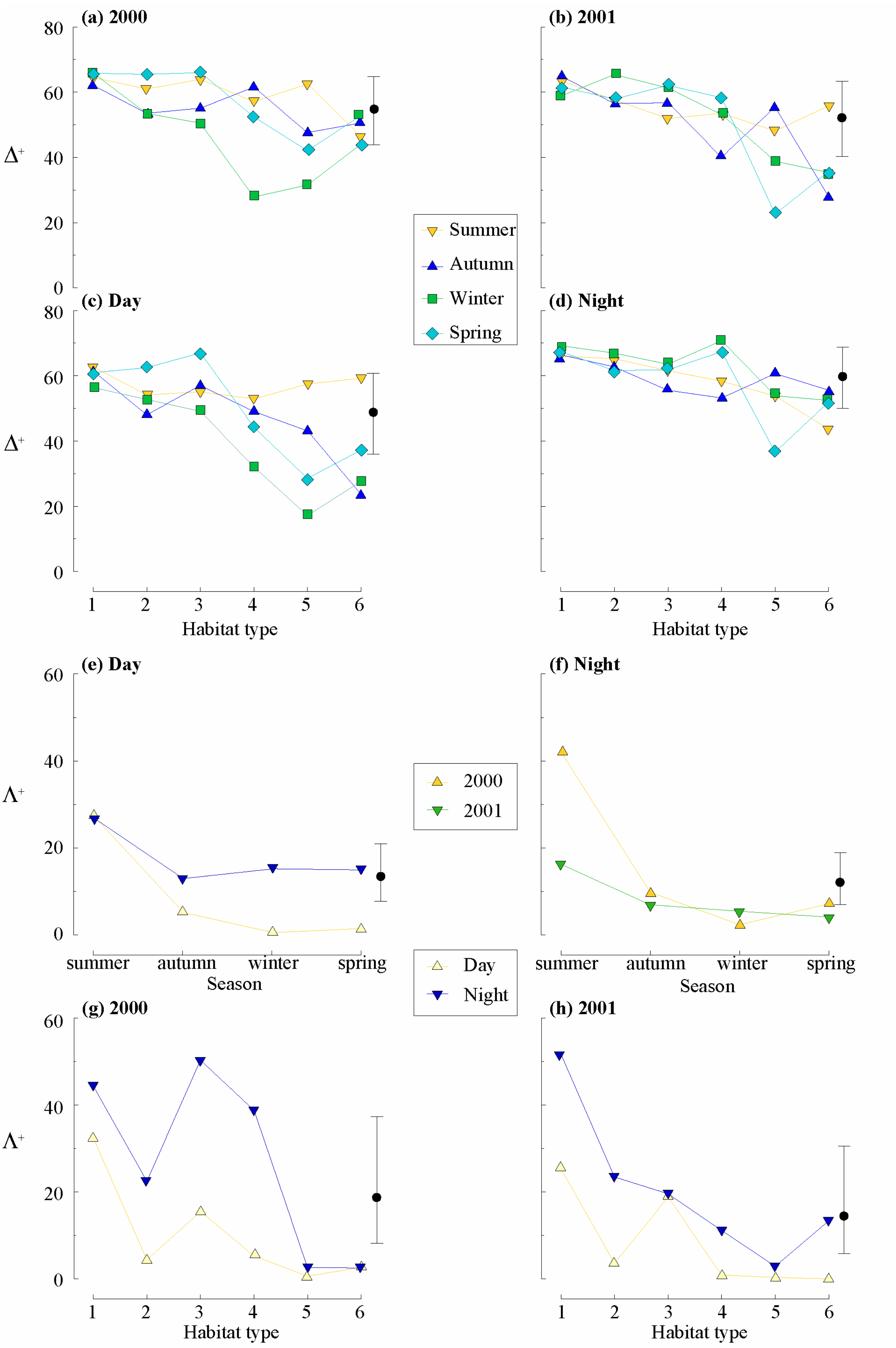


Figure 5.14: (a-d) Mean (± 95% CI) of the average taxonomic distinctness (Δ^+) of samples collected with the 21.5 m net at each habitat type and season during (a) 2000, (b) 2001, (c) the day, (d) the night. (e-f) Mean (± 95% CI) variation in taxonomic distinctness (Λ^+) of samples collected with the 21.5 m net in each season of 2000 and 2001 during (e) day and (f) night, and in each habitat type during the day and night in (g) 2000 and (h) 2001.

In view of the significant and relatively large differences detected by ANOVA in both Δ^+ and Λ^+ among seasons and between day and night, scatterplots of the relationship between these two indicies at the various sites representing habitat types 1-6, and the relevant 95% probability ellipses for different-sized subsets of species, were constructed separately for both of these temporal factors (Figs 5.15a-d and 5.16a-d). In addition to the trends in Δ^+ and Λ^+ detected by ANOVA, these plots showed that each site lay within their relevant 95% confidence ellipse in each season during the day (Figs 5.15a-d). These results demonstrate that the taxonomic diversity and evenness of those samples did not depart significantly from that expected for the fish assemblages in nearshore waters along the lower west coast of Australia. The sites were particularly tightly grouped in spring and were most widely dispersed during winter (Figs 5.15d and c, respectively). The lowest Δ^+ and Λ^+ were also recorded in that latter season, *i.e.* at one of the representatives of habitat types 4 and 5 (Fig. 5.15c). In contrast, the scatterplots of the Δ^+ *vs* Λ^+ in samples collected at night in each season showed that the sites were relatively tightly grouped in winter and were most dispersed in summer (Figs 5.16c and a, respectively). Furthermore, in that latter season, the points for one of the sites representing the most exposed habitat type (6) lay well outside the relevant 95% confidence ellipse (*i.e.* that representing random simulations for five species), and one of the sites representing habitat type 4 lay on the border of its associated expected region (Fig. 5.16a).

5.3.2.3 Composition of fish assemblages

(i) Overall differences among habitat types

MDS ordination of the mean densities of the various fish species derived from samples collected with the 21.5 m seine net during the day and night at each site in each season and in both 2000 and 2001 showed that when the samples were coded for habitat type, those from habitat type 1 formed a tight group that was largely discrete from those representing the other five habitat types (Fig. 5.17). Although the samples from habitat types 2-6 did not form such distinct groups, most of those from habitat types 2 and 3 formed a vertical band that lay adjacent to those from habitat type 1. The majority of samples from habitat type 4 lay on the opposing side of the group containing those from habitat types 2 and 3, and tended to merge with those from habitat type 6, most of which formed a relatively tight group. Most of the samples from habitat type 5 formed a broad group that tended to lie above those from habitat types 2, 3, 4 and 6 (Fig. 5.17). One-way ANOSIM showed that the composition of the fish fauna differed significantly overall among the six habitat types (p=0.1%; Global R=0.426) and that the members of each pair of habitat types were significantly different from each other (Table 5.10). The greatest differences were detected between habitat type 1 and each of the other five habitat types (p=0.1%; R=0.763-0.893), while the least difference was between habitat types 2 and 3 (p=0.6%; R=0.065; Table 5.10).

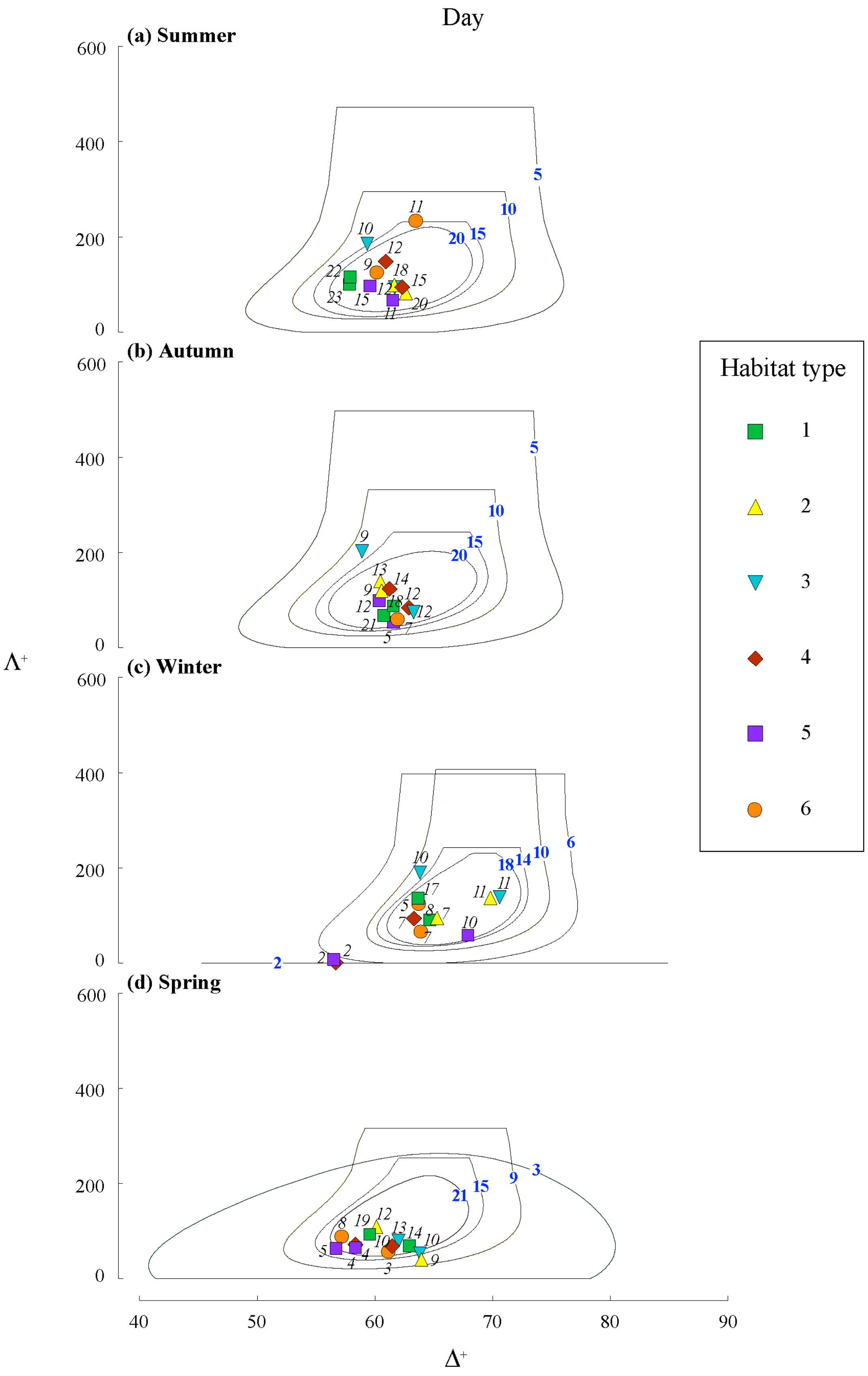


Figure 5.15: Scatterplots of average taxonomic distinctness *vs* variation in taxonomic distinctness of fish in samples collected with the 21.5 m net during the day at habitat types 1-6 in (a) summer, (b) autumn, (c) winter and (d) spring in 2000 and 2001. The number of species recorded at each site and the relevant 95% probability ellipses for simulations of different- sized subsets of species are also provided for each season.

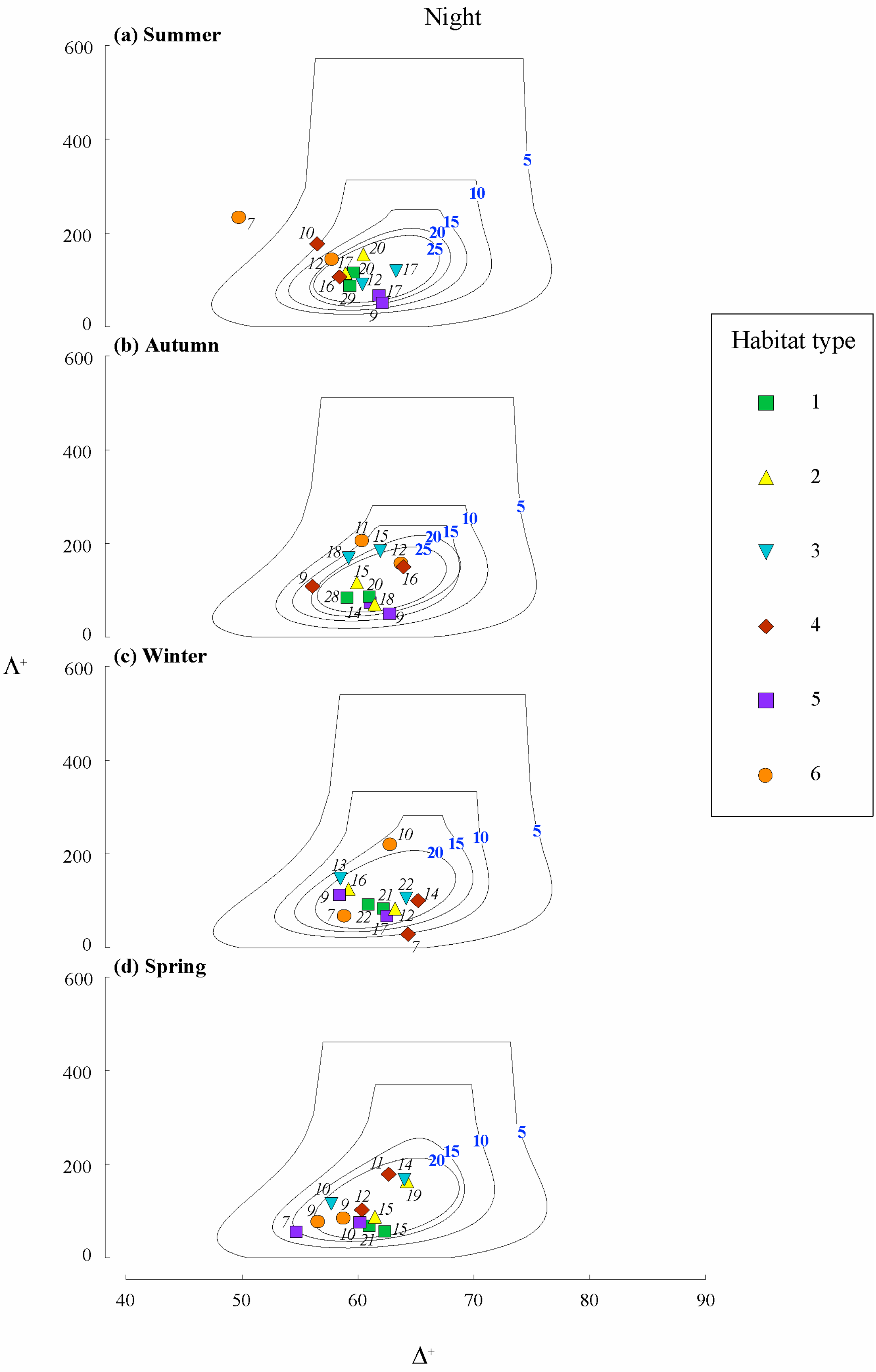


Figure 5.16: Scatterplots of average taxonomic distinctness *vs* variation in taxonomic distinctness of fish in samples collected with the 21.5 m net during the night at habitat types 1-6 in (a) summer, (b) autumn, (c) winter and (d) spring in 2000 and 2001. The number of species recorded at each site and the relevant 95% probability ellipses for simulations of different-sized subsets of species are also provided for each season.

Table 5.10 Significance levels (p; %) and R-statistic values for the global and pairwise comparisons in a one-way ANOSIM test of the ichthyofaunal compositions in samples collected with the 21.5 m net at each of the six habitat types (1-6) during the day and night in all seasons between summer 2000 and spring 2001. Values in boldface represent those that are significant.

Habitat type (p=0.1%; Global R=0.426)

	1		2		3		4		5		6	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.763**										
3	**0.1**	**0.798**	**0.6**	**0.065**								
4	**0.1**	**0.886**	**0.1**	**0.231**	**0.1**	**0.277**						
5	**0.1**	**0.825**	**0.1**	**0.289**	**0.1**	**0.381**	**0.2**	**0.146**				
6	**0.1**	**0.893**	**0.1**	**0.177**	**0.1**	**0.146**	**0.1**	**0.137**	**0.1**	**0.199**		

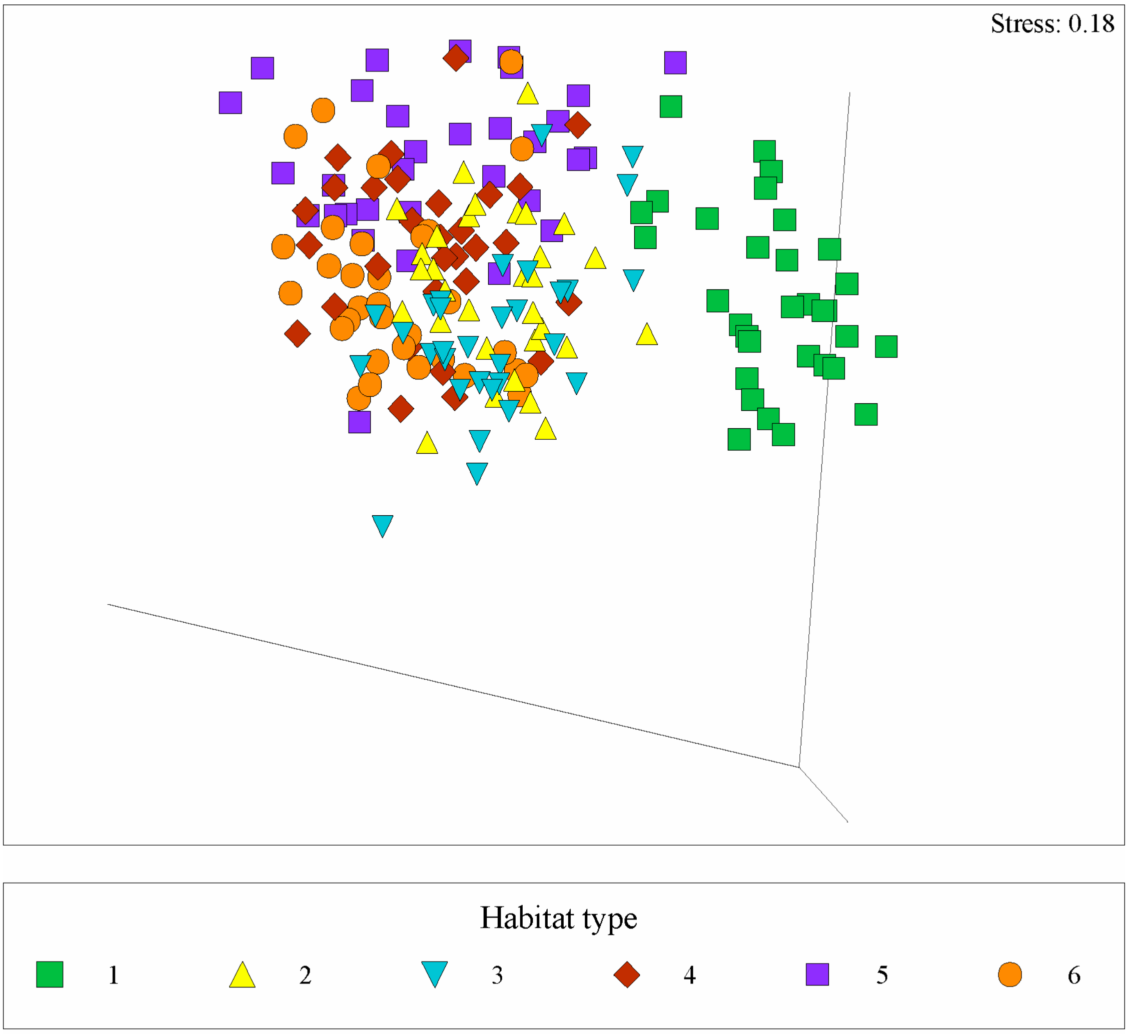


Figure 5.17: Three-dimensional MDS ordination of the mean densities of fish species in samples collected with the 21.5 m net during the day and night at habitat types 1-6 in each season between summer 2000 and spring 2001.

The species identified by SIMPER as typifying each of the six habitat types (over all seasons, both years and during day and night) are listed in Table 5.11. With the exception of *A. ogilbyi and T. pleurogramma*, none of the species that typified the overall fish fauna at habitat type 1 was characteristic of any other habitat type. In contrast, the small resident species *L. platycephala* occurred consistently at habitat types 2-6. Of these five habitat types, *S. bassensis* typified each of the more exposed and predominantly sandy habitat types, *i.e.* 3, 4 and 6, while other species typified the fauna at only one of these habitat types, *e.g. A. forsteri* at habitat type 2 (Table 5.11).

Table 5.11 Regularly and irregularly abundant species, as detected by SIMPER, in samples collected with the 21.5 m net at habitat types 1-6 during the day and night in all seasons between summer 2000 and spring 2001.

	Regularly abundant	**Irregularly abundant**
1	*F. lateralis* *R. sarba* *P. jenynsii* *L. presbyteroides** *A. ogilbyi** *S. burrus** *S. punctata**	*A. rueppellii* *T. pleurogramma*
2	*L. platycephala* *T. pleurogramma* *A. forsteri**	*H. vittatus*
3	*L. platycephala* *S. bassensis* *S. vittata**	*H. vittatus* *A. ogilbyi*
4	*L. platycephala*	*H. vittatus* *S. bassensis* *S. robustus*
5	*L. platycephala*	*A. ogilbyi*
6	*L. platycephala*	*S. bassensis*

(ii) *Differences in ichthyofaunal composition among habitat types in different years, seasons and between day and night*

The next question to be addressed was whether the significant differences in ichthyofaunal composition that were detected globally among habitat types needed to be examined separately for each year, season and/or day and night, or whether it was appropriate to pool the data for one or more of the three temporal factors.

Two-way crossed ANOSIM was thus used to test whether the composition of the fish fauna in each of the six habitat types differed significantly among seasons, between years and between day and night. However, since this test can employ only two factors at a time, it was necessary to separate the data on the basis of one of the three factors, and then subject the data for the remaining two factors in each habitat type to this analysis. It was initially decided to separate the data for each habitat type on the basis of whether it was recorded during day or night. The diel factor was chosen both because one-way ANOSIM detected a significant difference overall between the composition of the ichthyofauna collected during the day and night (*i.e.* p=0.1%), and because the choice of that variable ensured that, through separation into just two components, the maximum number of samples were available for subsequent multivariate analyses.

Two-way crossed ANOSIM tests carried out using ichthyofaunal data recorded during the day in each of the six habitat types and employing seasons and years as factors, demonstrated that the composition of the fish assemblages differed significantly among seasons in habitat types 2, 3, 4 and 5 (p=0.2-1.0%; Global R=0.438-0.573), but not between years in any habitat type (p=16.0-95.1%; Table 5.12a). When the same approach was adopted to analyse the night-time data, the composition of the ichthyofauna was found to differ significantly among seasons only in habitat type 3 (p=0.4%; Global R=0.5) and, as during the day, did not differ significantly between years in any of the six habitat types (p=7.4-100.0%; Table 5.12a).

Table 5.12 Global significance levels (%) for (a) season x year two-way crossed ANOSIM tests for both the day and night and (b) diel period x season two-way crossed ANOSIM tests (data pooled for 2000 and 2001), carried out on ichthyofaunal data in samples collected with the 21.5 m net at habitat types 1, 2, 3, 4, 5 and 6. Values in boldface represent those that are significant.

(a) Season x Year

	Day		**Night**	
Habitat type	season	year	season	year
1	85.1	65.4	80.4	100.0
2	**0.3**	39.5	71.1	98.8
3	**1.0**	95.1	**0.4**	7.4
4	**0.2**	45.7	63.2	88.9
5	**0.6**	16.0	31.4	81.5
6	8.6	42.0	5.9	100.0

b) Diel period x Season

Habitat type	diel	season
1	22.4	12.0
2	**1.8**	**0.1**
3	**0.5**	**0.1**
4	**0.4**	**0.1**
5	**5.0**	**0.1**
6	45.1	**0.1**

Two-way crossed ANOSIM was then used to elucidate whether the composition of the fish fauna differed significantly between day and night in each of the six habitat types. Since the previous season x year ANOSIM tests demonstrated that ichthyofaunal composition did not differ between 2000 and 2001 in any habitat type during either the day or night, this ANOSIM test employed day/night and season as the two factors and regarded the samples collected in each of the years as "replicates". This test demonstrated that the composition of the fish fauna differed significantly between day and night at habitat types 2-5, *i.e.* p=0.4-5.0%; Global R=0.164-0.288 (Table 5.12b). Furthermore, the results for season in this ANOSIM test for each habitat type were the same as those for this factor when day-time data were employed in the above season x year ANOSIM tests, except in the case of habitat type 6. Thus, while the diel x season ANOSIM test also detected significant differences in ichthyofaunal composition among seasons in habitat types 2-5 (p=0.1%, Global R=0.277-0.471), but not in habitat type 1 (p=12.0%), significant differences were also detected among seasons in habitat type 6 (p=0.1%, Global R=0.328). However, it should be noted that the results of the season x year ANOSIM tests for habitat type 6 showed that the composition of the fish faunas were close to differing significantly among the various seasons during both day and night, *i.e.* p=8.6 and 5.6%, respectively.

In view of the global differences in fish composition that were detected by ANOSIM among seasons and/or between day and night in most of the habitat types (Table 5.12a and b), further multivariate analyses of ichthyofaunal differences among habitat types were carried out separately for each level of these two temporal factors, but including the samples collected in both years as replicates.

Day

When the fish assemblage data recorded during the day was ordinated separately for summer, autumn, winter and spring, the extent to which the samples formed groups on the basis of habitat types varied among the four seasons (Figs 5.18a-d, respectively). This was reflected in the results of one-way ANOSIM tests, which showed that, while the compositions of the fish assemblages differed significantly overall among the six habitat types in each season (p=0.1%), the differences were greater in winter and spring than in summer and autumn, *i.e.* Global R=0.505 and 0.492 *vs* 0.396 and 0.353, respectively (Table 5.13c, d, a and b, respectively). The pairwise comparisons of these ANOSIM tests showed that, in each season, the composition of the fish fauna at habitat type 1 differed significantly from that of each of the other habitats (p=2.9%), except in the case of habitat type 3 in autumn. While the ichthyofaunal compositions of the members of few other pairs of habitat types were significantly different in summer and autumn, those of the members of several pairs differed significantly in winter and spring, and most notably between habitat type 3 and the other four habitat types (Table 5.13a-d).

Table 5.13 Significance levels (p; %) and R-statistic values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal compositions in samples collected with the 21.5 m net during the day at each of the six habitat types (1-6) in (a) summer, (b) autumn, (c) winter and (d) spring. Samples collected in 2000 and 2001 have been pooled in these analyses. Significant pairwise comparisons are highlighted in boldface.

(a) Summer (p= 0.1%; Global R=0.396)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.844**										
3	**2.9**	**1.000**	48.6	-0.010								
4	**2.9**	**0.948**	45.7	-0.010	28.6	0.083						
5	**2.9**	**0.979**	22.9	0.208	**2.9**	**0.417**	54.3	-0.042				
6	**2.9**	**0.948**	40.0	0.010	60.0	-0.063	80.0	-0.156	40.0	0.052		

(b) Autumn (p=0.1%; Global R=0.353)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.844**										
3	5.7	0.490	54.3	-0.021								
4	**2.9**	**0.938**	60.0	-0.115	20.0	0.146						
5	**2.9**	**0.906**	42.9	0.042	14.3	0.188	**2.9**	**0.448**				
6	**2.9**	**0.917**	45.7	0.010	22.9	0.177	17.1	0.188	11.4	0.208		

(c) Winter (p=0.1%; Global R=0.505)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.771**										
3	**2.9**	**0.667**	14.3	0.229								
4	**2.9**	**0.896**	8.6	0.521	**2.9**	**0.729**						
5	**2.9**	**0.833**	**2.9**	**0.563**	**2.9**	**0.656**	20.0	0.177				
6	**2.9**	**0.927**	5.7	0.521	**2.9**	**0.448**	28.6	0.115	28.6	0.073		

(d) Spring (p=0.1%; Global R=0.492)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.635**										
3	**2.9**	**0.813**	17.1	0.177								
4	**2.9**	**0.865**	5.7	0.458	**2.9**	**0.885**						
5	**2.9**	**0.792**	**2.9**	**0.625**	**2.9**	**0.958**	**2.9**	**0.385**				
6	**2.9**	**0.688**	14.3	0.240	**2.9**	**0.552**	22.9	0.073	25.7	0.083		

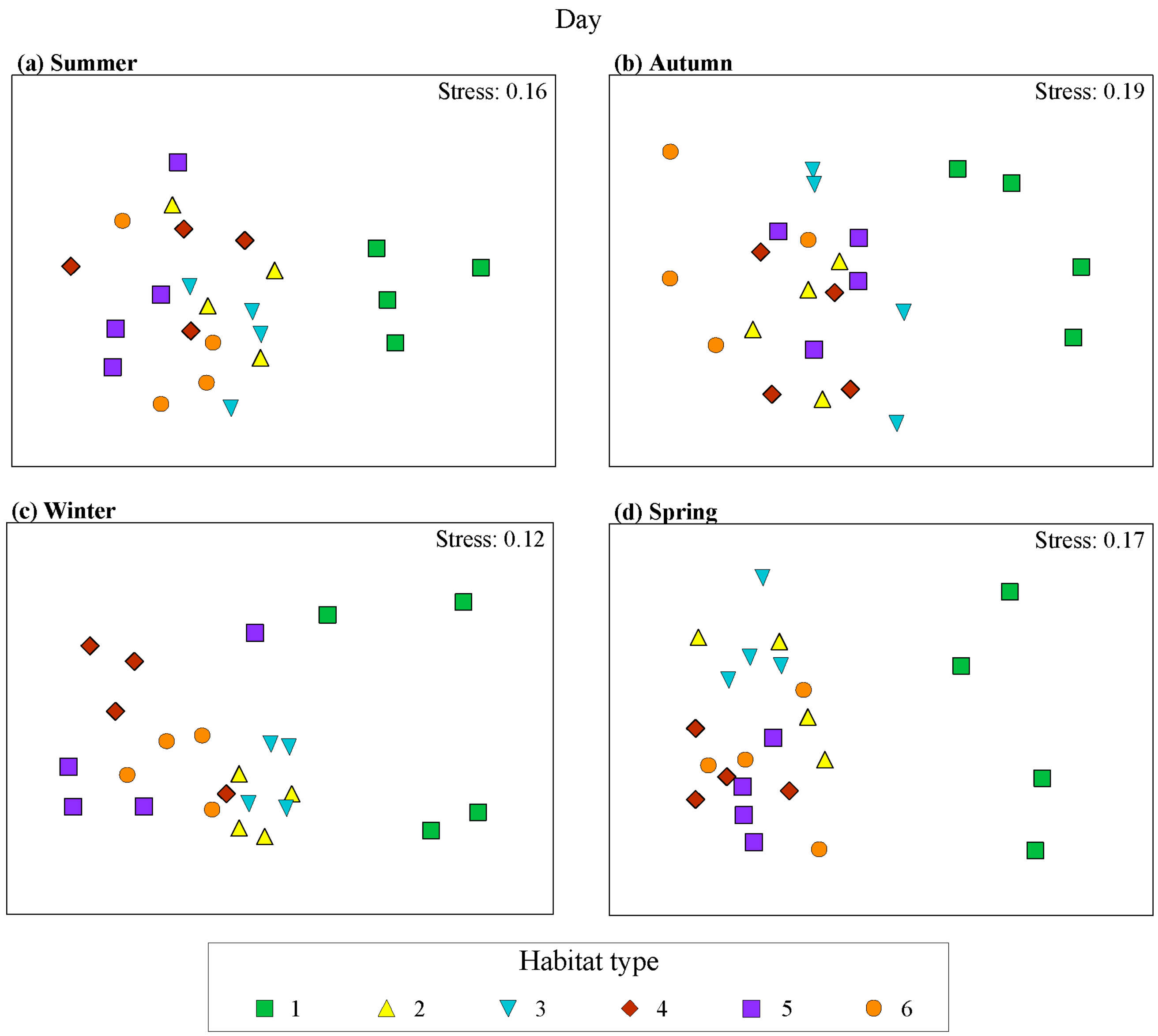


Figure 5.18: Two-dimensional MDS ordination of the mean densities of fish species in samples collected with the 21.5 m net during the day at habitat types 1-6 in (a) summer, (b) autumn, (c) winter and (d) spring of 2000 and 2001.

In accordance with the results of the previous season x year two-way crossed ANOSIM tests carried out on day-time data (Table 5.12a), SIMPER was used to ascertain which species characterised habitat types 2, 3, 4 and 5 separately for summer, autumn, winter and spring (Table 5.14a-d). The pairwise results of the one-way ANOSIM test carried out for each season (see Table 5.13a-d) were used to determine whether SIMPER analyses should be carried out on pooled data for two or more habitat types in any given season. It should be noted that, while the composition of one habitat type (*e.g.* 2) may not have differed from another habitat type (*e.g.* 3), SIMPER was carried out separately for each of those habitats if either was shown by ANOSIM to differ significantly from that of another habitat type, *e.g.* 3 *vs* 4.

Table 5.14 Regularly and irregularly abundant species, as detected by SIMPER, in samples collected with the 21.5 m net during the day at habitat types 2-5 in (a) summer, (b) autumn, (c) winter and (d) spring. When the compositions of the ichthyofaunas in these habitat types were not significantly different (see Table 5.13), the data recorded at those habitat types in that season were combined. Samples collected in 2000 and 2001 have been pooled in these analyses.

(a) Summer					
2 & 4		**3**		**5**	
Regularly abundant	Irregularly abundant	Regularly abundant	Irregularly abundant	Regularly abundant	Irregularly abundant
L. platycephala *S. bassensis* *S. vittata* *P. unicolor*	*S. robustus*	*S. bassensis* *L. platycephala* *S. vittata* *S. schomburgkii* *P. unicolor* *R. sarba**	*S. robustus*	*L. platycephala* *S. bassensis*	*S. robustus* *L.presbyteroides* *A. ogilbyi*

(b) Autumn				
2 & 3		**4**		**5**
Regularly abundant	Irregularly abundant	Regularly abundant	Irregularly abundant	Regularly abundant
L. platycephala *A. ogilbyi*	*S. robustus*	*P. humeralis* *S. bassensis* *L. platycephala* *T. pleurogramma* *A. ogilbyi**	*S. robustus*	*A. ogilbyi* *L. platycephala* *S. robustus*

(c) Winter				
2	**3**		**4**	**5**
Regularly abundant	Regularly abundant	Irregularly abundant	Regularly abundant	Regularly abundant
L. platycephala *A. forsteri*	*L. platycephala* *A. forsteri* *T. pleurogramma*	*A. ogilbyi*	*L. platycephala* *P. humeralis*	*L. platycephala*

(d) Spring			
2 & 3		**4**	**5**
Regularly abundant	Irregularly abundant	Regularly abundant	Regularly abundant
L. platycephala *H. vittatus*	*A. ogilbyi*	*L. platycephala*	*L. platycephala* *A. forsteri*

* additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

Thus, SIMPER showed that, in summer, each of the species that characterised the combined habitat types 2 and 4 were also typical of the fish assemblage at habitat type 3, except that *S. schomburgkii* and *R. sarba* also typified that latter habitat type. Only two species were regularly abundant at habitat type 5 in this season, both of which were among those that typified habitat types 2-4. However, schools of *L. presbyteroides* and *A. ogilbyi* were caught on an irregular basis only at this habitat type and in this season (Table 5.14a). In autumn, the fish assemblage habitat type 4 was relatively distinct, and was characterised by several species that did not typify any of the other three habitat types, *i.e. P. humeralis*, *S. bassensis* and, *T. pleurogramma* (Table 5.14b). SIMPER demonstrated that few species typified each habitat type in both winter and spring (Tables 5.14c and d, respectively). However, in contrast to the situation in summer and autumn, *A. forsteri* was regularly abundant in both habitat types 2 and 3 in winter and in habitat type 5 in spring. Moreover, the schooling clupeid *H. vittatus* occurred regularly at the combined habitat types 2 and 3 in spring (Table 5.14d), which coincides with the time of year at which the 0+ juveniles of this species typically recruit into nearshore waters (Gaughan *et al.* 1996).

Night

Unlike the situation during the day, the composition of the ichthyofauna at night differed significantly among seasons only in habitat type 3 (Table 5.12a). However, separate MDS ordination and one-way ANOSIM tests of the night-time data collected at the various habitat types in summer, autumn, winter and spring (Figs 5.19a-d and Table 5.15, respectively), showed that there were some small seasonal differences in the overall extent to which the composition of the fish assemblages differed among those habitat types. Thus, while the composition of the ichthyofauna differed significantly overall among habitat types in each season (*i.e.* p=0.1%), these differences were slightly greater in winter than in all other seasons, and were least in spring, *i.e.* Global R=0.641 and 0.506, respectively. Moreover, the extents of these global differences were greater than those detected in the corresponding seasons during the day (*cf* Tables 5.15 and 5.13).

Pairwise comparisons in the above ANOSIM tests showed that, at night in each season, the composition of the fish assemblages in habitat type 1 differed significantly from that in each of the other five habitat types (p=2.9%, R=0.625-1.000; Table 5.15a-d). However, it should be recognised that, due to sampling difficulties at night in habitat type 4 in winter (see section 5.2.1 and Table 5.1), the results of all pairwise comparisons involving this habitat type in this season were based on too few samples to provide a sufficient number of possible permutations for the ANOSIM test to produce a reliable result. Thus, such pairwise comparisons were not

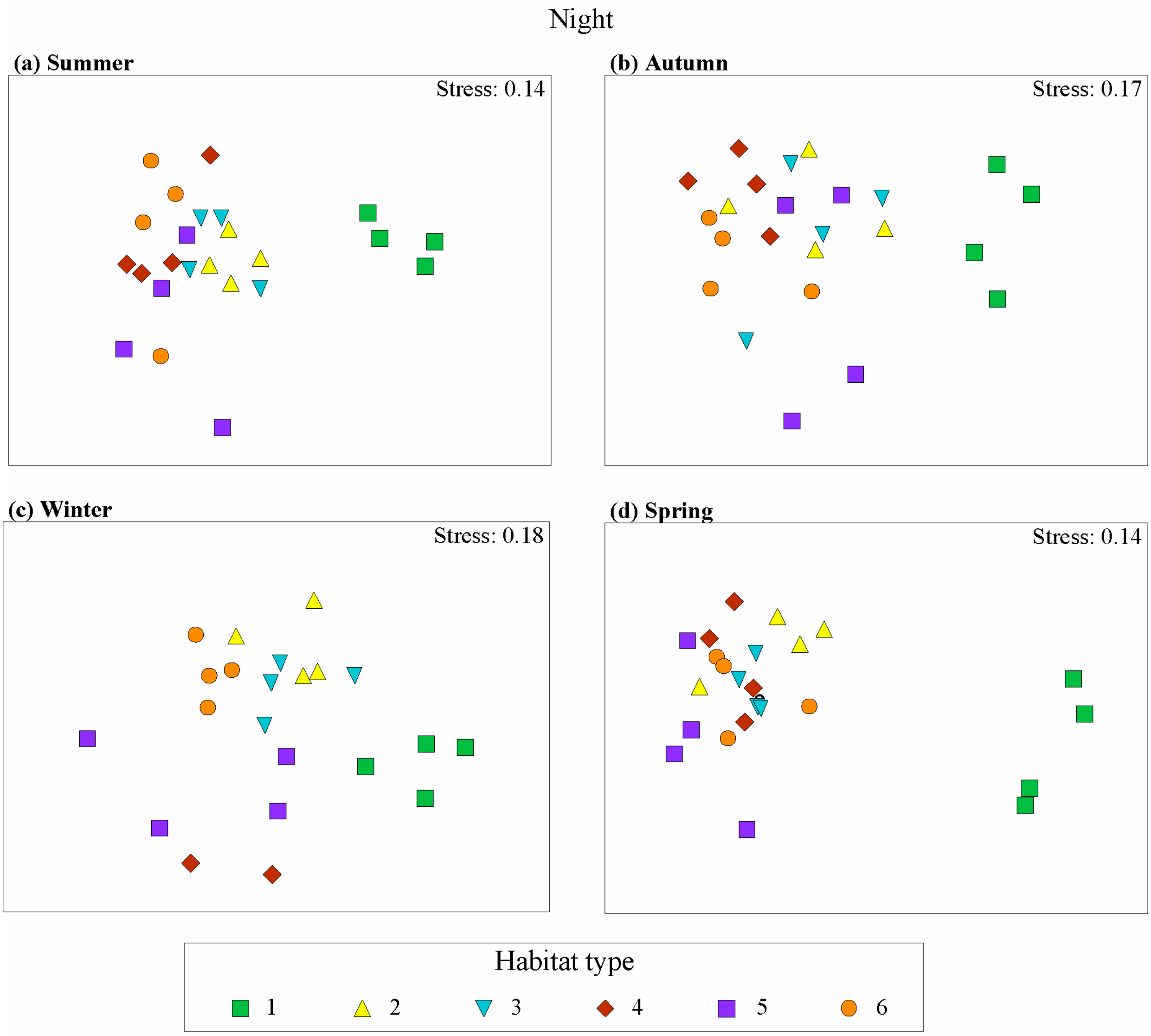


Figure 5.19: Two-dimensional MDS ordination of the mean densities of fish species in samples collected with the 21.5 m net during the night at habitat types 1-6 in (a) summer, (b) autumn, (c) winter and (d) spring of 2000 and 2001.

interpreted. In addition to the significant differences between the ichthyofauna at habitat type 1 and that at all other habitat types in most seasons, the fish compositions in several other pairs of habitat types were shown to differ significantly in the various seasons (see boldface values in Tables 5.15a-d). However, some pairs of habitat types did not differ significantly in any season, *e.g.* 2 *vs* 3 and 3 *vs* 6. It should also be noted that several pairs of habitats bordered on differing significantly (*i.e.* p=5.7%), such as 2 *vs* 6 in summer and winter and 5 *vs* 6 in spring (Table 5.15).

Table 5.15 Significance levels (p; %) and R-statistic values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal compositions in samples collected with the 21.5 m net at night in each of the six habitat types (1-6) during (a) summer, (b) autumn, (c) winter and (d) spring. Samples collected in 2000 and 2001 have been pooled in these analyses. Values in boldface represent those that are significant. Those pairwise comparisons marked with a dash could not be reliably interpreted due to an insufficient number of samples.

(a) Summer (p= 0.1%; Global R=0.569)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**1.000**										
3	**2.9**	**1.000**	34.3	0.083								
4	**2.9**	**0.979**	**2.9**	**0.479**	17.1	0.188						
5	**2.9**	**0.979**	**2.9**	**0.438**	8.6	0.302	28.6	0.104				
6	**2.9**	**1.000**	5.7	0.500	5.7	0.302	34.3	0.104	5.7	0.448		

(b) Autumn (p=0.1%; Global R=0.571)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.927**										
3	**2.9**	**0.875**	65.7	-0.052								
4	**2.9**	**1.000**	8.6	0.271	5.7	0.333						
5	**2.9**	**0.990**	**2.9**	**0.594**	**2.9**	**0.531**	**2.9**	**0.667**				
6	**2.9**	**1.000**	25.7	0.198	28.6	0.104	17.1	0.177	**2.9**	**0.854**		

(c)Winter (p=0.1%; Global R=0.641)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.875**										
3	**2.9**	**1.000**	34.3	0.073								
4	-	-	-	-	-	-						
5	**2.9**	**0.625**	**2.9**	**0.542**	**2.9**	**0.469**	-	-				
6	**2.9**	**1.000**	5.7	0.323	5.7	0.427	-	-	**2.9**	**0.510**		

(d) Spring (p=0.1%; Global R=0.506)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**2.9**	**0.990**										
3	**2.9**	**1.000**	5.7	0.375								
4	**2.9**	**1.000**	22.9	0.146	11.4	0.281						
5	**2.9**	**0.990**	**2.9**	**0.698**	**2.9**	**0.729**	17.1	0.198				
6	**2.9**	**1.000**	14.3	0.313	48.6	-0.031	**2.9**	**0.396**	5.7	0.448		

SIMPER, which was carried out separately for each season on the night-time data for habitat type 3 (Table 5.16) showed that, while the ichthyofauna at this habitat type was characterised by regular occurrences of *L. platycephala* and *S. bassensis* in each season and by *C. macrocephalus* and *S. schomburgkii* in three of those seasons, some species were typical of only two consecutive seasons, *e.g. A. forsteri* in autumn and winter and *R. sarba* during winter and spring (Table 5.16).

Table 5.16 Regularly abundant species, as detected by SIMPER, in samples collected with the 21.5 m net at night in habitat type 3 in summer, autumn, winter and spring. Data has been pooled for 2000 and 2001 in this analysis.

Summer	Autumn	Winter	Spring
T. pleurogramma *L. platycephala* *C. macrocephalus* *S. bassensis* *P. unicolor* *S. vittata**	*S. vittata* *A. forsteri* *S. bassensis* *L. platycephala* *A. georgiana* *S. schomburgkii* *C. macrocephalus**	*R. sarba* *S. bassensis* *L. platycephala* *A. forsteri* *S. schomburgkii* *A. oglibyi**	*L. platycephala* *S. bassensis* *S. schomburgkii* *R. sarba* *C. macrocephalus*

* additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

Since the previous two-way crossed ANOSIM tests demonstrated that the ichthyofaunas at habitat types 2, 4 and 5 each differed significantly between day and night but not among seasons at night (Table 5.12a and b), SIMPER was performed on the night-time data for each of those habitat types that had been the pooled across all seasons and years (Table 5.17). It should also be noted that, although one-way ANOSIM did not detect a significant difference in the overall night-time compositions of habitat types 2 and 3, SIMPER was used to identify the species that characterised each of these habitats to accommodate the above-mentioned seasonal differences in ichthyofaunal composition that had been identified in the latter habitat type. Thus, while SIMPER demonstrated that *L. platycephala* also occurred consistently at night in habitats 2, 4 and 5, several other species occurred regularly in either habitat type 2 or 4 at this time. For example, *A. forsteri, P. unicolor* and *T. pleurogramma* also characterised habitat type 2, while habitat type 4 was typified by species such as *P. humeralis* and *S. woodwardi*. Moreover, relatively large schools of *A. ogilbyi* occurred irregularly only in habitat type 5 (Table 5.17).

Table 5.17 Regularly and irregularly abundant species, as detected by SIMPER, in samples collected with the 21.5 m net at night in habitat types 2, 4 and 5 in all seasons between summer 2000 and spring 2001.

	Regularly abundant	Irregularly abundant
2	*L. platycephala* *A. forsteri* *P. unicolor* *T. pleurogramma* *S. vittata* *C. macrocephalus*	*H. vittatus*
4	*L. platycephala* *C. macrocephalus* *P. humeralis* *S. woodwardi* *S. bassensis*	*H. vittatus*
5	*L. platycephala*	*A. ogilbyi*

Seasonal differences in ichthyofauna at habitat type 6

Since two-way crossed ANOSIM demonstrated that the composition of the fish assemblage at habitat type 6 varied significantly among seasons but not between day and night or years (see Tables 5.12a and b), SIMPER analyses for this habitat type were carried out separately for summer, autumn, winter and spring, but using pooled data for day and night and 2000 and 2001. The resident species *L. platycephala* was characteristic of the fauna at this habitat type in each season, while *S. bassensis* was also regularly abundant in summer and autumn. Furthermore, *S. vittata* occurred in relatively large numbers but irregularly in this habitat type during summer.

5.3.2.4 Similarity in pattern of rank orders between sites in different seasons, years and day vs night

The ichthyofaunal data derived from small net samples collected at the various sites during both the day and night in each season and year were subjected to second-stage MDS ordination to ascertain whether the degree of similarity in fish composition between each pair of the 12 sites differed on the basis of any of those temporal factors.

When the points on the resultant ordination plot were coded separately for day and night, season and year (Figs 5.20a, b and c, respectively), they showed a marked tendency to separate on the basis of the first two of these temporal factors. Thus, when the points were coded for day or night, six of the eight points for day lay to the right and/or below those for night (Fig. 5.20a) and, when the same samples were coded for season, the points for winter, spring, summer and autumn progressed from left to right on the plot (Fig. 5.20b). In contrast,

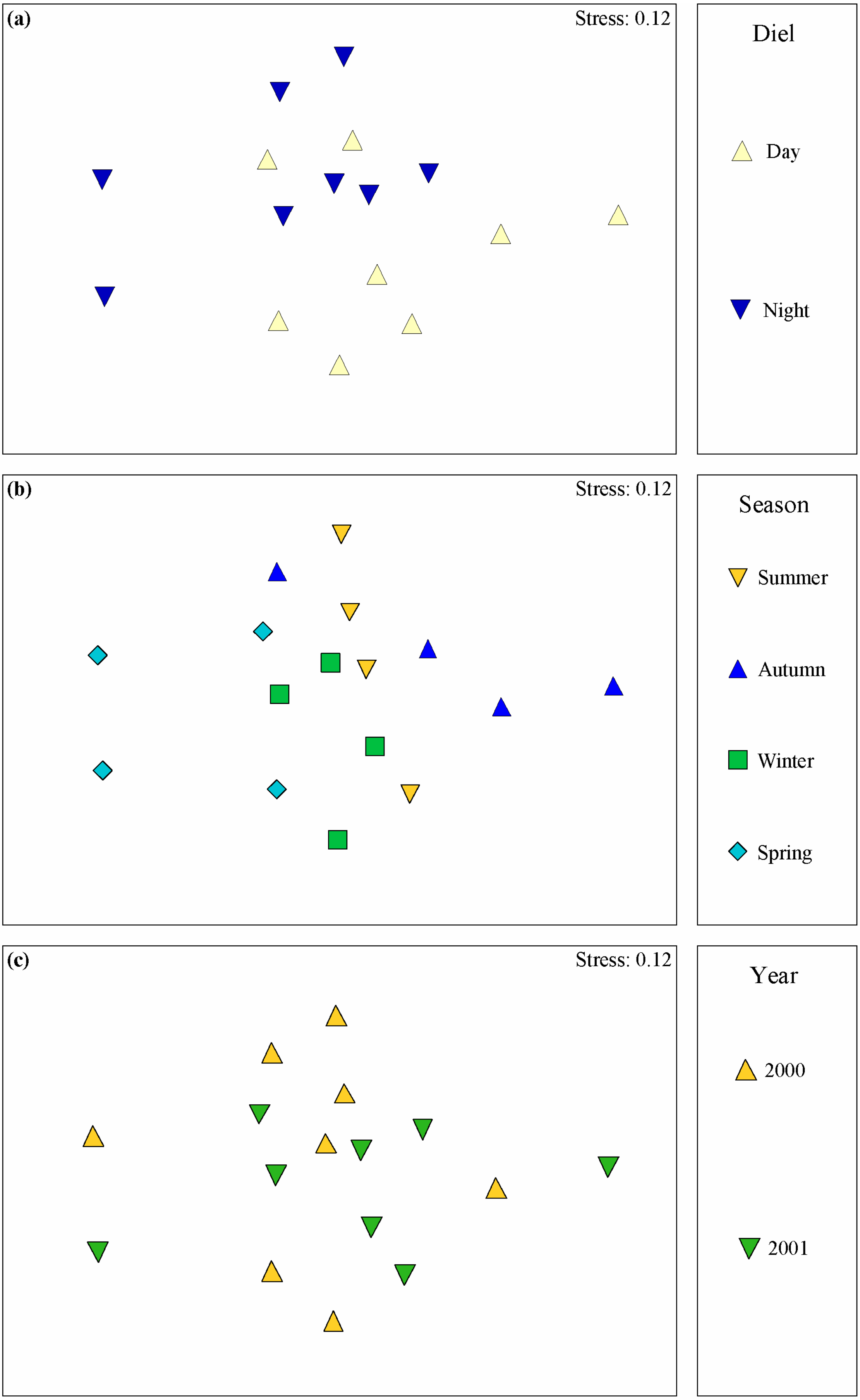


Figure 5.20: MDS ordination of the second-stage similarity matrix containing the correlations between each pair of matrices that were constructed from the mean densities of fish species in samples collected with the 21.5 m net at habitat types 1-6 on each separate sampling occasion, *i.e.* day and night in each season in 2000 and 2001. The points on the ordination plot have been coded separately for (a) diel, (b) season and (c) year.

the points for 2000 and 2001 showed no conspicuous tendency to form separate groups (Fig. 5.20c). These results demonstrate that there were diel and seasonal shifts in the extent of ichthyofaunal similarity between the various sites representing the six habitat types.

The presence of diel and seasonal trends on the second-stage ordination plot shown in Figs 5.20a and b, in conjunction with the significant differences in ichthyofaunal composition detected by ANOSIM on the basis of these two temporal factors in most of the six habitat types (Table 5.12a and b), indicated that it was appropriate to examine the following separately for both the day and night and each season, but using data which had been averaged over years.

1) Whether the extent of ichthyofaunal differences between the sites representing the six habitat types matched differences produced from the enduring environmental data for those sites.
2) If the above correlation was significant, which species were most responsible for distinguishing among the various habitat types.

5.3.2.5 Relating fish and enduring environmental matrices

The RELATE procedure was used to correlate each of the eight Bray-Curtis similarity matrices that were produced from the fish assemblage data at the various sites during both the day and night in each of the different seasons (*i.e.* those used to produce the ordination plots in Figs 5.21a-h), with the distance matrix containing the same sites that was constructed from the subset of enduring environmental data that best discriminated among those habitat types (*i.e.* that used to produce the ordination plot in Fig. 5.22). This resulted in a significant match in all cases (p=0.1-2.8%), except for in autumn during the day (*i.e.* Fig. 5.21b *vs* Fig. 5.22). However, the correlation between that latter similarity matrix and the environmental distance matrix bordered on significance, *i.e.* p=5.5%. It should be noted that since MDS ordination of the matrix produced from the fish composition data recorded in spring at night showed that those sites representing habitat type 1 differed markedly from those representing the other five habitat types (see insert in Fig. 5.21h), these two sites were excluded from both this matrix (see Fig. 5.21h for re-ordination of the sites representing habitat types 2-6) and the environmental matrix prior to undertaking the RELATE procedure for spring at night. The above significant correlations demonstrated that the extent of differences among the six habitat types on the basis of their fish composition data, matched those derived from the enduring environmental data that best discriminated among those habitat types.

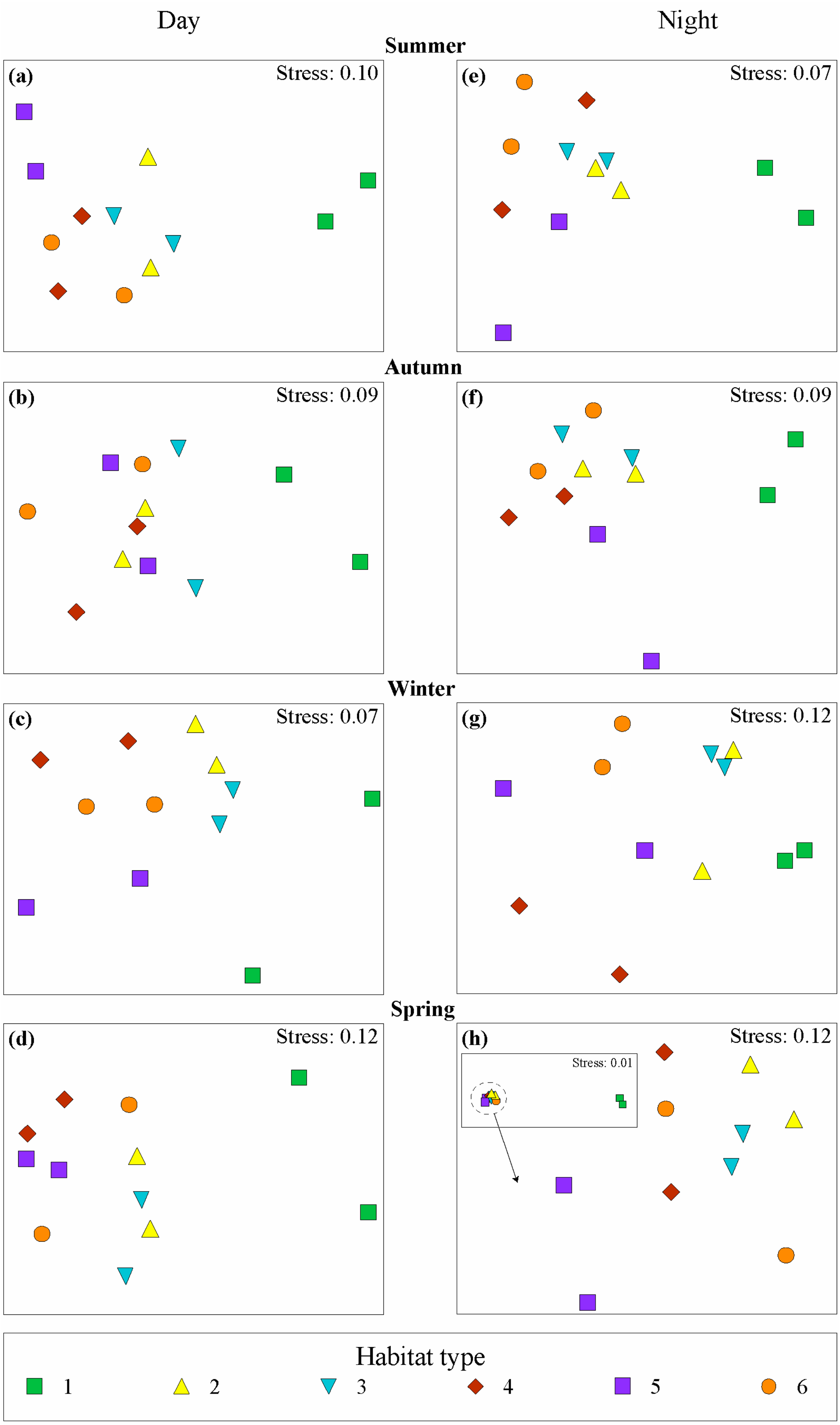


Figure 5.21: Two-dimensional MDS ordination of the mean densities of fish species recorded in samples collected with the 21.5 m net at habitat types 1-6 in summer, autumn, winter and spring during the day (a-d, respectively) and night (e-h, respectively). The data have been meaned for samples collected in 2000 and 2001. N.B. The data recorded during the night in spring (h) was re-ordinated without the samples collected at habitat type 1 to elucidate more fully the relationships among habitat types 2-6.

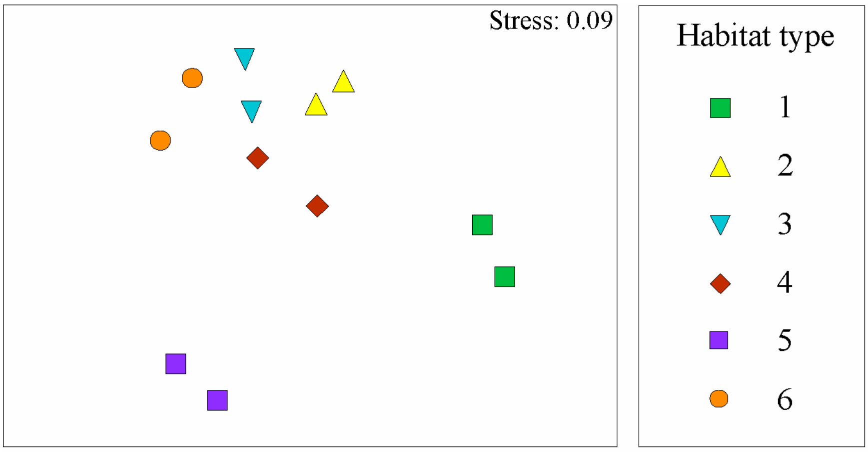


Figure 5.22: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those nearshore sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net.

The extent of the significant correlations between the fish and enduring environmental matrices was lowest in winter at night (ρ=0.345) and greatest in summer during the day (ρ=0.695). The ρ values in each of the remaining cases were relatively similar and ranged between 0.422 and 0.578.

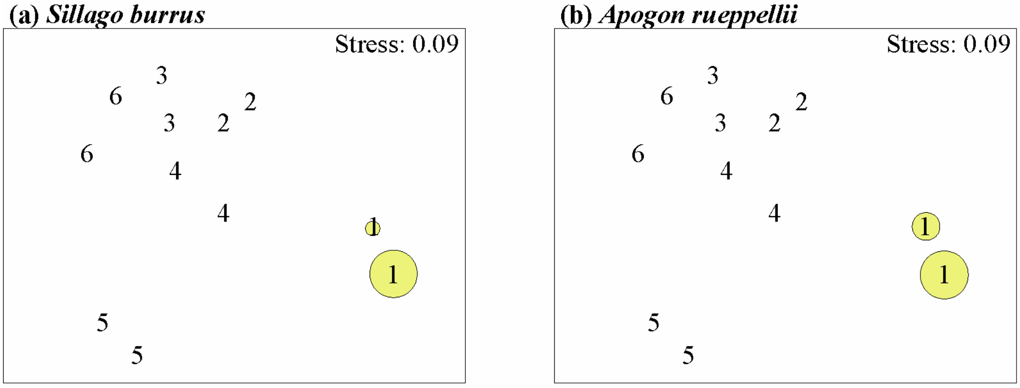
In view of the significant matches between the arrangement of samples in each of the fish matrices and the environmental matrix, BVSTEP was then used to identify the suite of species which collectively provided the best correlation with the enduring environmental matrix in each season during both the day and night. These species are listed in Table 5.18 and represent those most responsible for distinguishing among the fish assemblages at the six habitat types during each of those sampling occasions.

The ways in which examples of these selected species contributed to the differences among the various habitat types during the day and night and in each season are illustrated in the ordination plots shown in Figs 5.23-5.29. These figures showed that some species exhibited a clear affinity for the highly sheltered habitat type 1, *e.g. S. burrus* and *A. rueppellii* during the day in summer, *A. rueppellii* during the night in this season (Figs 5.23a, 5.23b and 5.26a, respectively), and *L. presbyteroides* at night in autumn and winter (Figs 5.27a and 5.28a, respectively). Other species, such as *P. jenynsii* and *Platycephalus speculator* occurred mostly in both this sheltered habitat type and the moderately sheltered habitat type 2 (Figs 5.23c, 5.23d, 5.26b, 5.27b, 5.28b, 5.28c). Some species, such as *P. unicolor* and *L. platycephala,* were distributed mainly in waters that were more exposed to wave activity and in which the substrate close to shore was unvegetated, *i.e.* habitat types 2, 3, 4 and 6 (*e.g.* Figs 5.23e, 5.24a, 5.24b, 5.25a, 5.29a), while *Trachinotus bailloni* occurred mainly in the exposed habitat type 5 which also contained reef areas close to shore, and occasionally in sites representing the moderately to fully exposed habitat types 4 to 6 (Figs 5.23f, 5.24c, 5.25b, 5.28e).

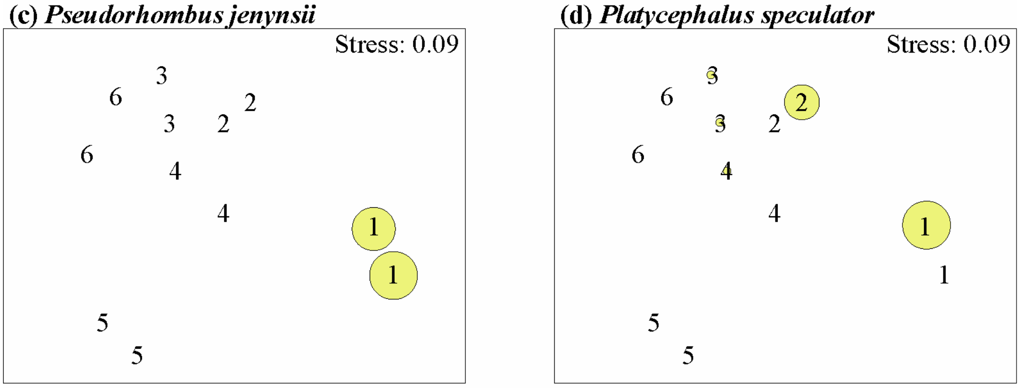
Table 5.18 Subsets of species, derived from samples collected with the 21.5 m net during both the day and night and in each season, that were identified by BVSTEP as those which provided the best correlation with the data for the selected suite of environmental characteristics at habitat types 1-6. The maximum correlation value (ρ) of each subset of species with the environmental data is also provided for each sampling occasion. Data has been pooled for 2000 and 2001 in this analysis.

	Summer	**Autumn**	**Winter**	**Spring**
Day	(max. ρ= 0.830)	(not significant)	(max. ρ = 0.704)	(max. ρ = 0.630)
	S. burrus		*L. presbyteroides*	*C. macrocephalus*
	A. rueppellii		*T. bailloni*	*S. vittata*
	P. sexlineatus		*A. georgiana*	*T. bailloni*
	P. unicolor		*L. platycephala*	*E. armatus*
	P. speculator		*P. unicolor*	*L. platycephala*
	P. jenynsii		*T. pleurogramma*	*P. parilus*
	S. punctata		*A. elongata*	*S. georgianus*
	P. laevigatus			*C. brevicaudatus*
	F. lateralis			
	C. goodladi			
	S. vittata			
	A. forsteri			
	H. semifasciata			
	A. elongata			
	T. pleurogramma			
	T. bailloni			
	H. cristatus			
	P. tigris			
	I. rhothophilus			
	M. meraculus			
	S. attenuatus			
	N. balteatus			
	C. brevicaudatus			
Night	(max. ρ = 0.772)	(max. ρ = 0.807)	(max. ρ = 0.674)	(max. ρ = 0.764)
	H. vittatus	*H. vittatus*	*H. vittatus*	*C. macrocephalus*
	A. rueppellii	*S. robustus*	*S. robustus*	*P. humeralis*
	S. schomburgkii	*L. presbyteroides*	*L. presbyteroides*	*L. platycephala*
	P. sexlineatus	*S. bassensis*	*P. sexlineatus*	*T. pleurogramma*
	L. platycephala	*S. schomburgkii*	*P. humeralis*	*E. armatus*
	A. elongata	*F. lateralis*	*S. burrus*	*A. ogilbyi*
	E. armatus	*A. forsteri*	*S. punctata*	*S. georgianus*
	S. vittata	*E. armatus*	*F. lateralis*	*C. brevicaudatus*
	I. rhothophilus	*P. speculator*	*P. jenynsii*	*A. japonicus*
	P. endrachtensis	*A. georgiana*	*P. speculator*	*C. gibbosus*
	K. cornelii	*A. serratus*	*H. melanochir*	
	S. obtusata	*M. australis*	*L. platycephala*	
			P. unicolor	
			T. bailloni	
			P. endrachtensis	

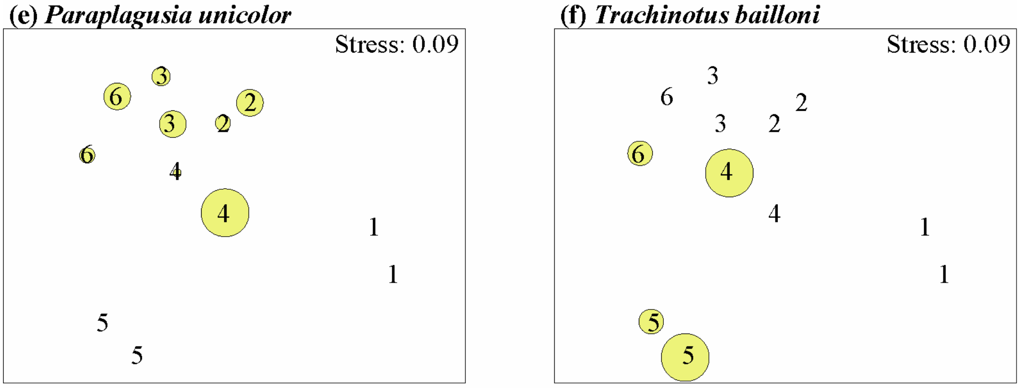
Day, Summer



(a) ***Sillago burrus*** (b) ***Apogon rueppellii***



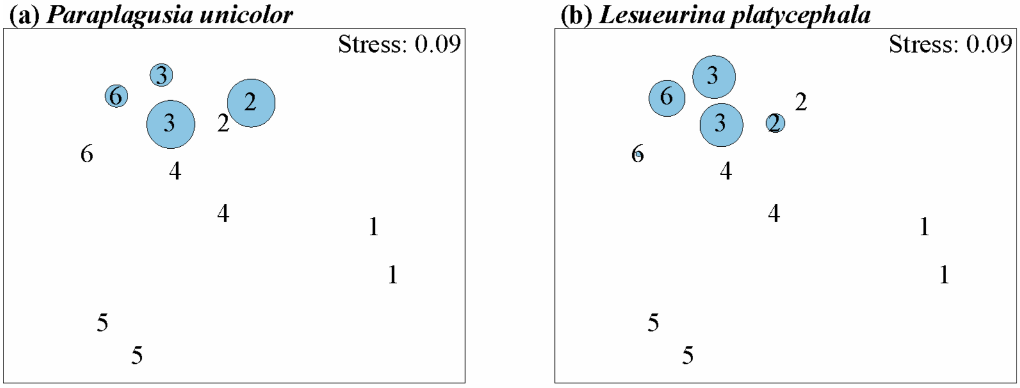
(c) ***Pseudorhombus jenynsii*** (d) ***Platycephalus speculator***



(e) ***Paraplagusia unicolor*** (f) ***Trachinotus bailloni***

Figure 5.23: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-6 during the day in summer. Ichthyofaunal data have been meaned for 2000 and 2001.

Day, Winter


(a) ***Paraplagusia unicolor***

(b) ***Lesueurina platycephala***

(c) ***Trachinotus bailloni***

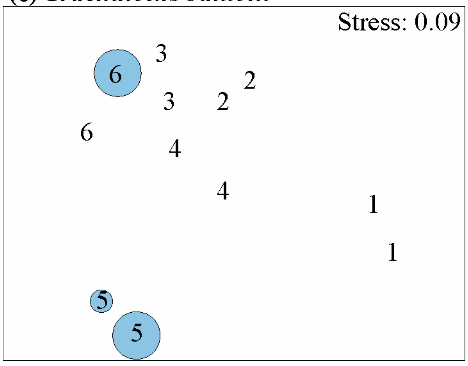
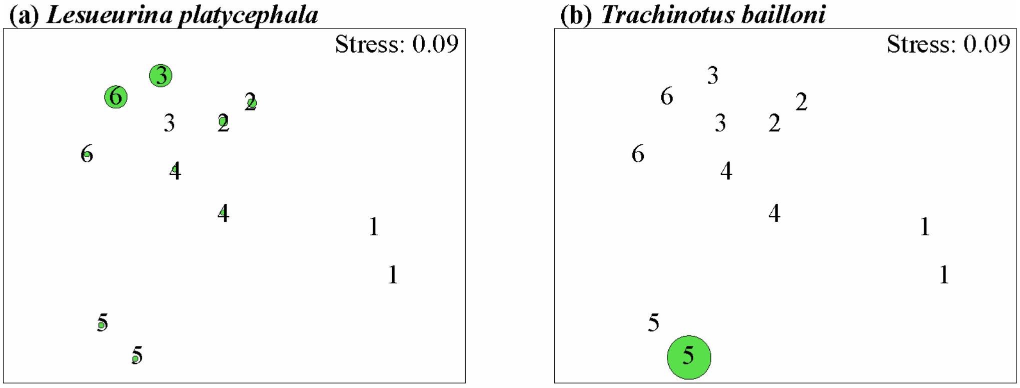


Figure 5.24: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-6 during the day in winter. Ichthyofaunal data has been meaned for 2000 and 2001.

Day, Spring

(a) ***Lesueurina platycephala*** **(b)** ***Trachinotus bailloni***



(c) ***Sillago vittata*** **(d)** ***Enoplosus armatus***

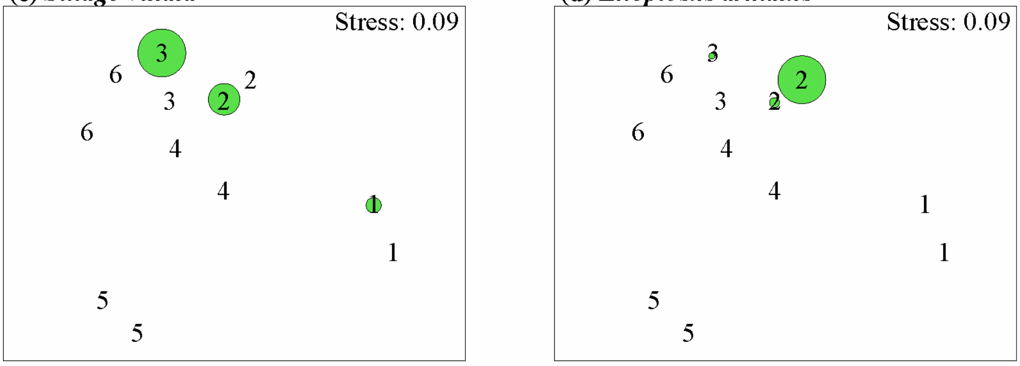
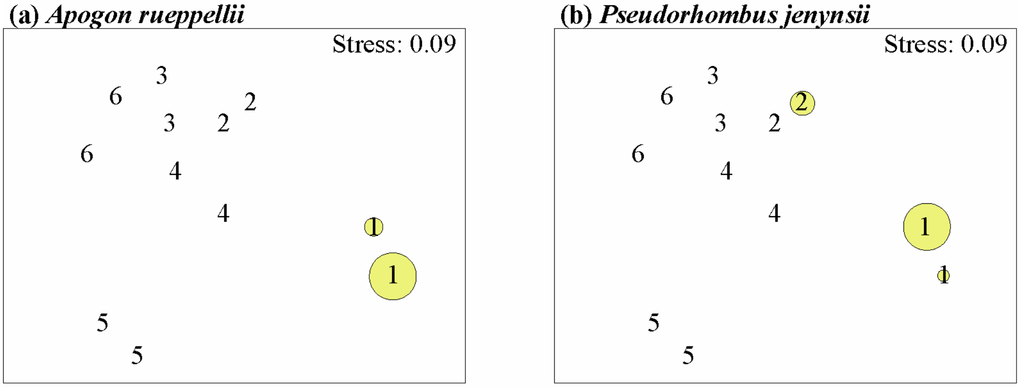
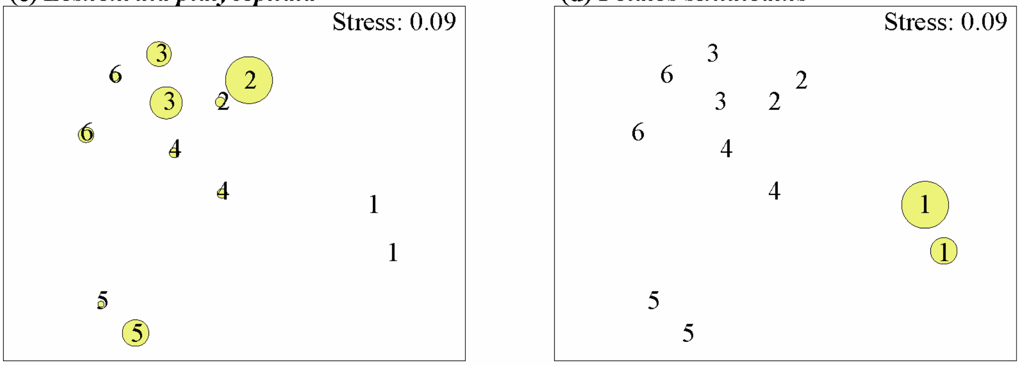


Figure 5.25: Two-dimensional MDS ordination of the values for the selected subset of enduring evironmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas at habitat types 1-6 during the day in spring. Ichthyofaunal data have been meaned for 2000 and 2001.

Night, Summer

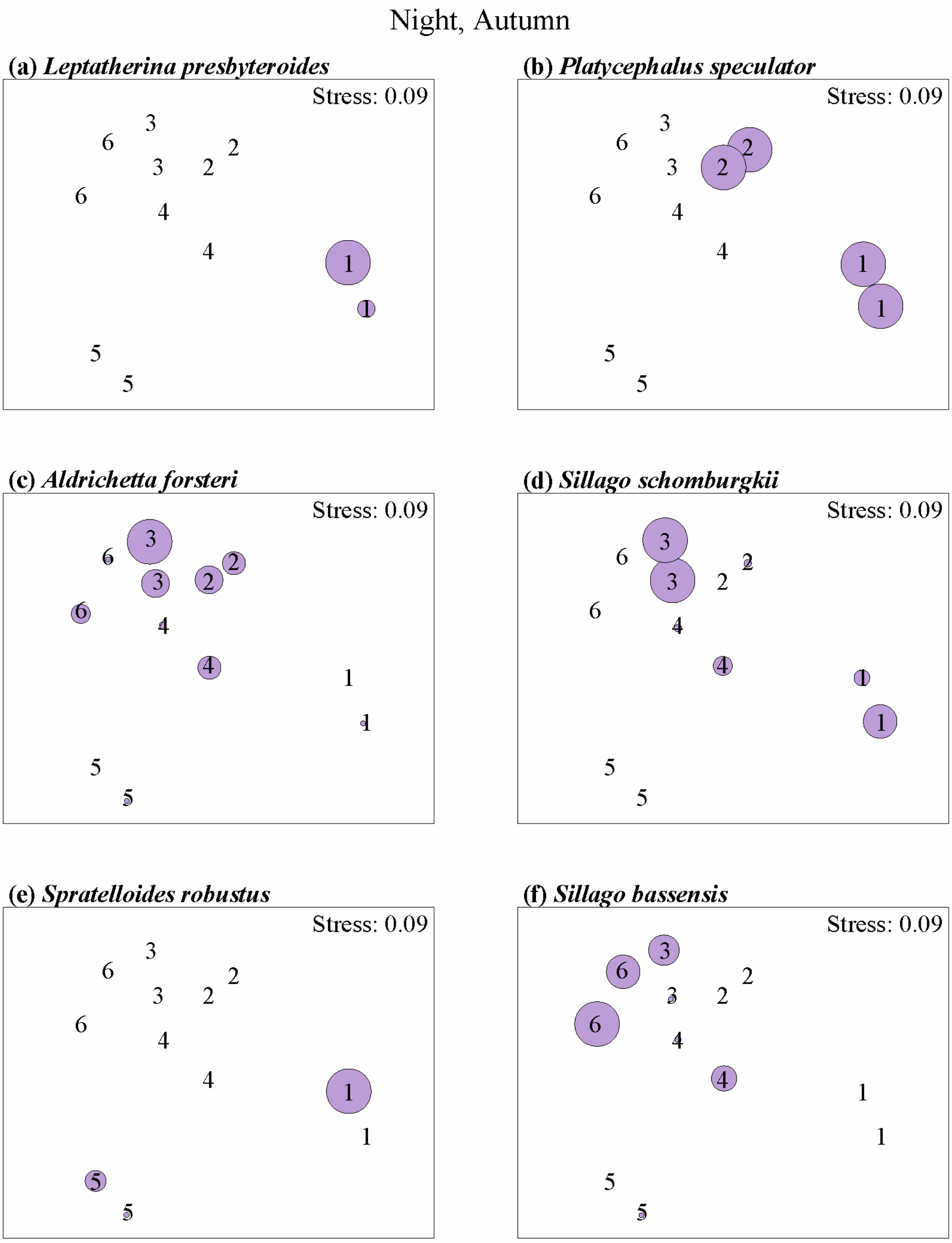

(a) ***Apogon rueppellii***

(b) ***Pseudorhombus jenynsii***


(c) ***Lesueurina platycephala***

(d) ***Pelates sexlineatus***

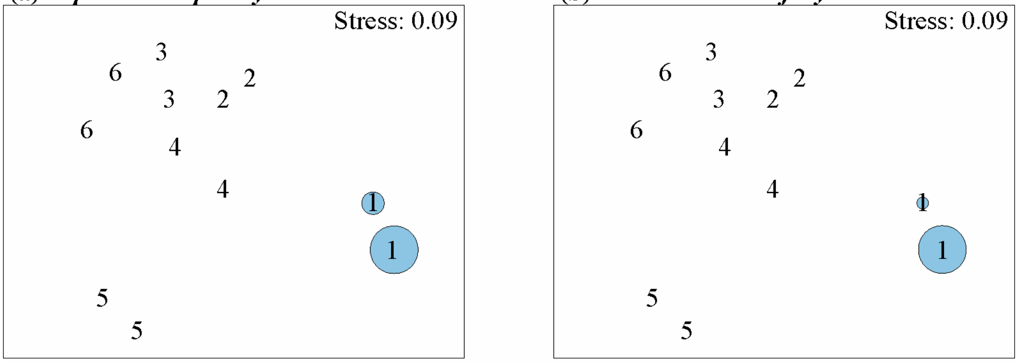
Figure 5.26: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas in habitat types 1-6 at night in summer. Ichthyofaunal data have been meaned for 2000 and 2001.



(a) *Leptatherina presbyteroides* (b) *Platycephalus speculator* (c) *Aldrichetta forsteri* (d) *Sillago schomburgkii* (e) *Spratelloides robustus* (f) *Sillago bassensis*

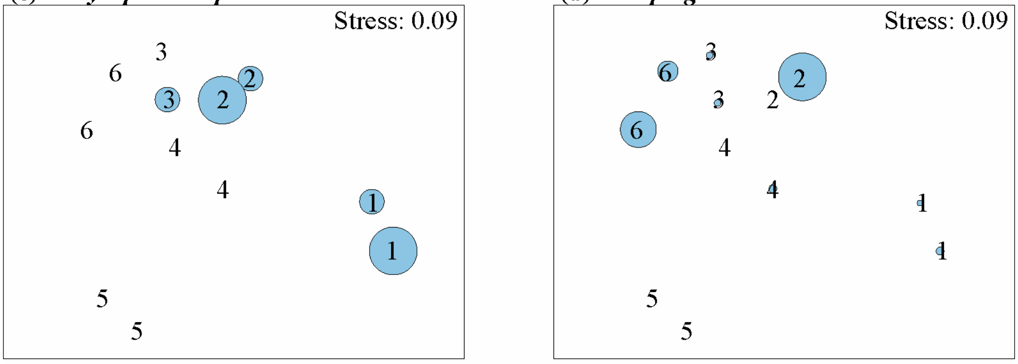
Figure 5.27: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas in habitat types 1-6 at night in autumn. Ichthyofaunal data have been meaned for 2000 and 2001.

Night, Winter



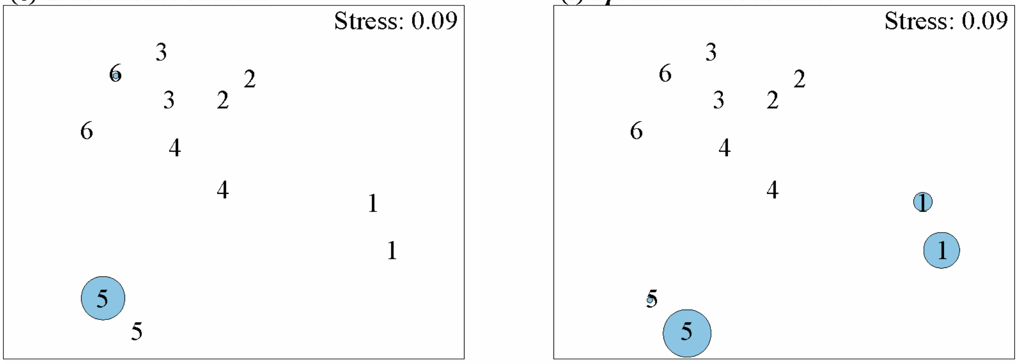
(a) *Leptatherina presbyteroides*

(b) *Pseudorhombus jenynsii*



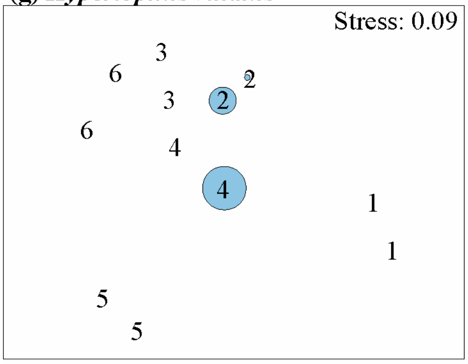
(c) *Platycephalus speculator*

(d) *Paraplagusia unicolor*



(e) *Trachinotus bailloni*

(f) *Spratelloides robustus*



(g) *Hyperlophus vittatus*

Figure 5.28: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas in habitat types 1-6 at night in winter. Ichthyofaunal data have been meaned for 2000 and 2001.

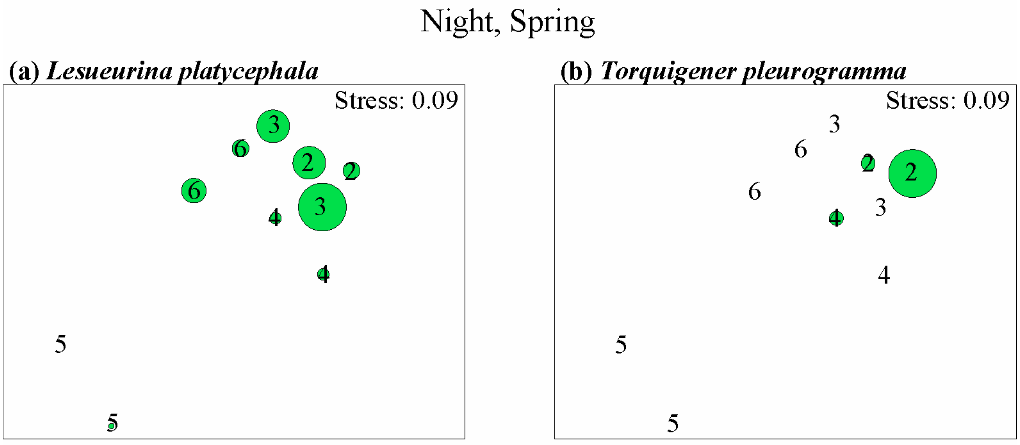


Figure 5.29: Two-dimensional MDS ordination of the values for the selected subset of enduring environmental variables at those sites representing habitat types 1-6 at which fish were sampled with the 21.5 m net. The size of the circles overlaid on each site reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine as those most responsible for distinguishing among the ichthyofaunas in habitat types 1-6 at night in spring. Ichthyofaunal data have been meaned for 2000 and 2001.

5.3.3 Comparison of fish assemblages in samples collected with the 60.5 and 21.5 m nets

5.3.3.1 Density of fish and species relatedness in different net types, habitat types, seasons and years

When the number of fish 500 m^{-2} derived from replicate samples collected with both the 21.5 and 60.5 m seine nets in habitat types 1-4 during the day in each season in 2000 and 2001 were subjected to four-way ANOVA, those densities were shown to differ significantly among habitat types and seasons ($p < 0.001$; Table 5.19). However, the interaction between these variables was significant ($p < 0.001$), as was that between net type and habitat type ($p < 0.01$) and between habitat type, season and year ($p < 0.01$). The mean square was greatest for the first of these interactions, followed closely by that for net type x habitat type. However, the mean squares associated with the habitat type and season main effects were more than three and two times greater, respectively, than that for any of the significant interaction terms (Table 5.19).

The significant net type x habitat type interaction was attributable to the fact that, while the mean densities of fish derived from samples collected using catches obtained with the 21.5 and 60.5 m seine nets were very similar in habitat types 1 and 2, the density calculated from the small net catches was greater than that from the large net catches at habitat type 3, while the reverse was true for habitat type 4 (Fig. 5.30).

Table 5.19 Mean squares and significance levels for four-way ANOVA of the total density of fish, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) derived from samples collected with the 21.5 and 60.5 m seine nets during the day at habitat types 1-4 along the lower west coast of Australia in each season in 2000 and 2001. "df"=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	**Total density of fish**	Δ^+	Λ^+
Main effects				
Net type (N)	1	0.124	132.452***	155.918***
Habitat type (H)	3	9.103***	25.712***	14.700***
Season (S)	3	5.305***	5.099	23.079***
Year (Y)	1	1.743	0.028	0.230
Two-way interactions				
N x H	3	2.041**	15.909*	5.901*
N x S	3	0.502	15.408*	6.610*
N x Y	1	0.790	0.827	2.209
H x S	9	2.752***	3.509	2.692
H x Y	3	0.431		1.925
S x Y	3	0.699	4.987	1.291
Three-way interactions				
N x H x S	9	0.467	4.017	2.941
N x H x Y	3	0.173	2.886	0.208
N x S x Y	3	0.027	5.747	0.070
H x S x Y	9	1.464**	5.821	2.591
Four-way interaction				
N x H x S x Y	9	0.427	4.856	1.494
Error	442	0.521	4.615	1.846

The source of the significant interactions involving habitat type, season and/or year were examined by plotting the values for the mean density of fish in each habitat type and season separately for 2000 and 2001 (Figs 5.30b and c, respectively). Thus, in 2000, the mean densities in autumn were greater than in winter in each of the four habitat types, and those in summer exceeded those in autumn in habitat types 2-4. However, the mean densities in spring 2000 were either lowest or very close to the lowest of any season at habitat types 1 and 4, but were the greatest of any season in habitat types 2 and 3 (Fig. 5.30b). The trends exhibited by the mean densities across habitat types 1-4 in summer, autumn, winter and spring in 2001 did not follow those of the corresponding seasons in 2000 (*cf* Figs 5.30b, c).

In contrast to the results obtained for density, both Δ^+ and Λ^+ were shown by ANOVA to differ significantly between samples collected with the large and small nets ($p < 0.001$), and the mean squares for this main effect were far greater than those for other significant main effects, *i.e.* habitat type for both Δ^+ and Λ^+ and season for Λ^+ ($p < 0.001$). Moreover, for both of these dependent variables, the net type x habitat type and net type x season interactions were also significant, but to a lesser extent, *i.e.* $p < 0.05$ (Table 5.19).

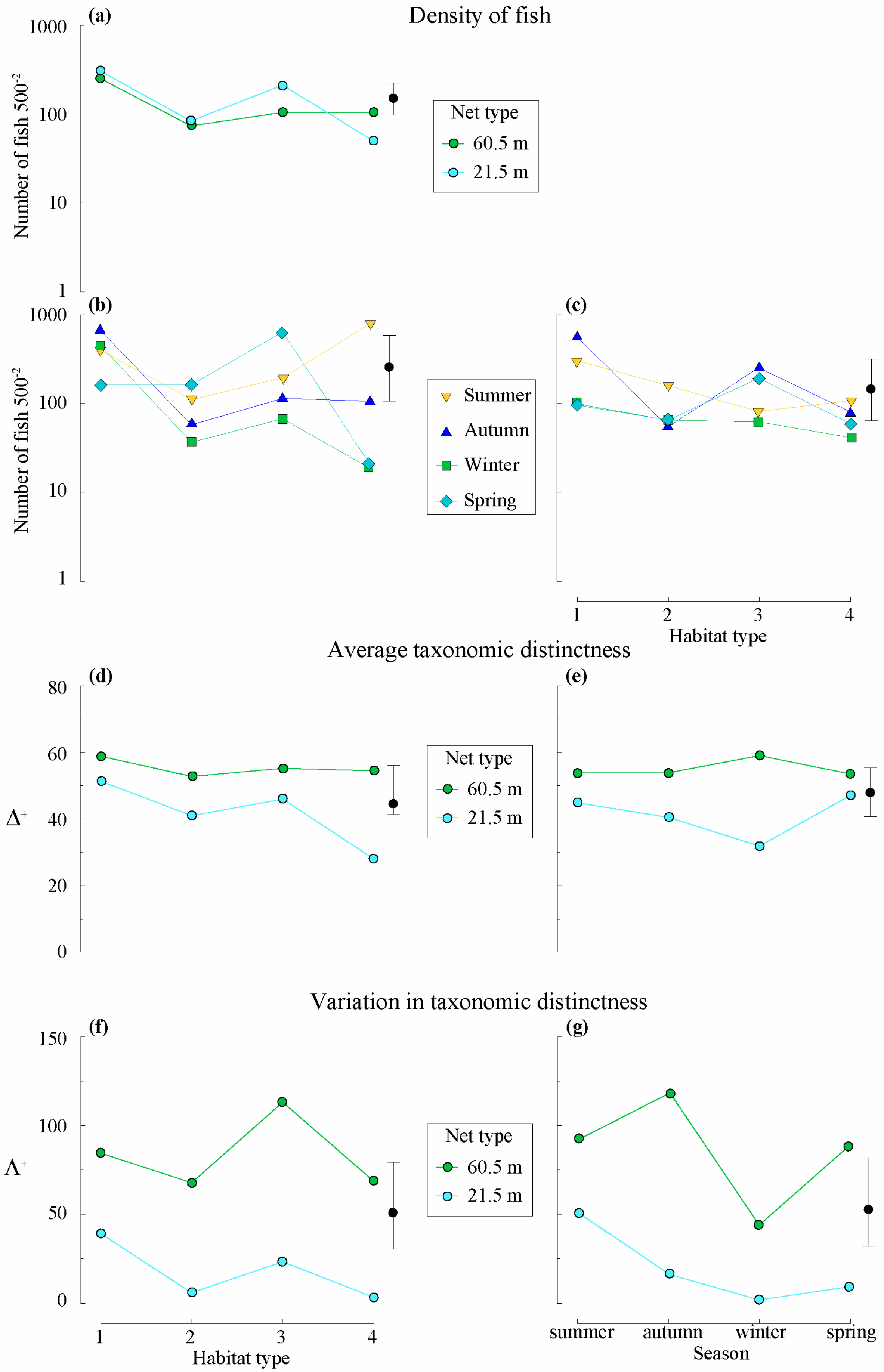


Figure 5.30: Mean (± 95% CI) density of fish in habitat types 1-4 in (a) the 60.5 and 21.5 m nets, and in each season in (b) 2000 and (c) 2001. Mean (± 95% CI) average taxonomic distinctness in samples collected with each net type in (d) habitat types 1-4 and (e) each season. Mean (± 95% CI) variation in taxonomic distinctness in samples collected with each net type in (f) habitat types 1-4 and (g) each season.

Both Δ^+ and Λ^+ were clearly greater in samples collected with the large than small net at each of the four habitat types and in each season (Figs 5.30d, e, f, and g, respectively). However, the extent of the differences in Δ^+ between samples collected with the different nets was considerably greater at habitat type 4 than at the other habitat types (Fig. 5.30d) and during winter than in the other seasons (Fig. 5.30e). Moreover, while the Λ^+ in samples collected with the large net was greatest at habitat type 3, that of the samples collected with the small net was greatest at habitat type 1 (Fig. 5.30f). The extent of the seasonal differences in Λ^+ was also considerably greater in the samples collected with the large than small net. Thus, while mean Λ^+ in the small net samples declined steadily from a maxima in summer to a minima in winter, that of samples collected with the large net was the greatest in autumn (Fig. 5.30g).

5.3.3.2 Comparisons between ichthyofaunal compositions of large and small net samples

In view of the significant differences detected in ichthyofaunal composition among the various habitat types (subsections 5.3.1.3 and 5.3.2.3), the following multivariate analyses used to examine whether the composition of the fish fauna differed significantly between large and small net samples collected at those habitat types and sampling occasions when both net types could be deployed (*i.e.* habitat types 1-4 during the day in each season between summer 2000 and spring 2001), were carried out separately for each habitat type. Moreover, since the analyses in the above subsections also showed that the composition of fish assemblages in samples from both net types differed significantly among seasons in various habitat types but never between years, the former temporal factor was included in subsequent ANOSIM tests, while samples from different years were treated as replicates. It should also be noted that, in all of these analyses, the numbers of individuals in all samples were also adjusted so that they would approximate to the numbers that would have been collected if each net had covered an area of 500 m^{-2}.

When the samples collected in each of the habitat types were subjected to MDS ordination, they showed a marked tendency to separate on the basis of net type in all cases, except habitat type 1 (Figs 5.31a-d). These trends were reinforced by the results of two-way crossed ANOSIM employing net type and season as factors, which demonstrated that the composition of the fish fauna recorded in the two nets differed significantly in habitat types 2, 3 and 4 (p=0.1-1%) but not habitat type 1. Moreover, the extent of the difference between the ichthyofaunal compositions of samples collected with each net type was greatest in habitat type 3 and least in habitat type 4 (Global R=0.547 and 0.271, respectively).

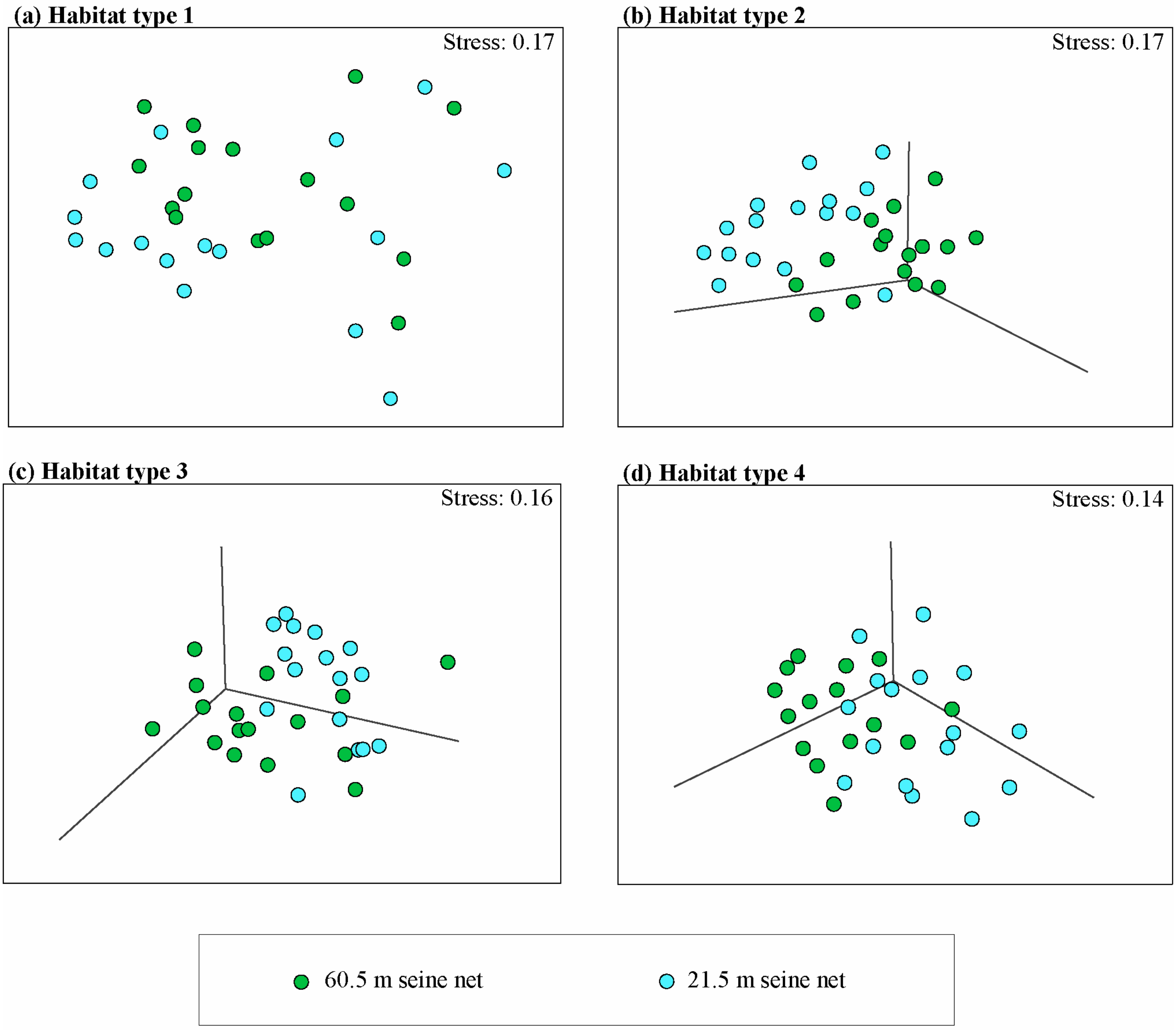


Figure 5.31: MDS ordination of the mean densities of fish species in samples collected with the 21.5 and 60.5 m nets during the day between summer 2000 and spring 2001 in habitat type (a) 1, (b) 2, (c) 3 and (d) 4.

SIMPER showed that the suites of species that were mainly responsible for distinguishing the composition of the fish fauna collected in the large and small seine nets were similar in habitat types 2-4 (Table 5.20). However, some species were collected more consistently in one net type in only one or two of these habitat types, *e.g. Aldrichetta forsteri* and *Arripis georgiana* in habitat types 2 and 3 and *Siphamia cephalotes* in habitat type 4. The net type in which each of the distinguishing species was more regularly abundant was, in several cases, the same in the three habitat types. For example, *Lesueurina platycephala, Spratelloides robustus* and *Atherinomorus ogilbyi* were all relatively more abundant in the 21.5 m net in each of these habitat types, while *Sillago bassensis* was always caught in greater numbers in the 60.5 m net (Table 5.20). However, the net type in which other species were more abundant overall differed among the three habitat types, *e.g. Hyperlophus vittatus* was recorded in greater numbers in the large net in habitat types 2 and 4 and in the small net at habitat type 3 (Table 5.20).

Table 5.20 Regularly abundant species, as detected by SIMPER, that distinguished the composition of the fish faunas recorded in the 60.5 and 21.5 m nets during the day at habitat types 2-4 in all seasons between summer 2000 and spring 2001. The net type in which each species was relatively more abundant is also provided (see superscripts; L=60.5 m net; S=21.5 m net; - little difference in average abundance).

2	3	4
L. platycephala$^{(S)}$	*L. platycephala*$^{(S)}$	*L. platycephala*$^{(S)}$
S. schomburgkii$^{(L)}$	*S. schomburgkii*$^{(L)}$	*S. bassensis*$^{(L)}$
S. vittata$^{(L)}$	*P. unicolor*$^{(S)}$	*P. unicolor*$^{(-)}$
A. ogilbyi$^{(S)}$	*S. bassensis*$^{(L)}$	*S. schomburgkii*$^{(-)}$
A. elongatus$^{(S)}$	*S. vittata*$^{(S)}$	*S. vittata*$^{(S)}$
P. unicolor$^{(S)}$	*A. elongatus*$^{(-)}$	*S. robustus*$^{(S)}$
S. bassensis$^{(L)}$	*A. forsteri*$^{(S)}$	*P. humeralis*$^{(S)}$
A. forsteri$*^{(S)}$	*H. vittatus*$*^{(S)}$	*H. vittatus*$*^{(L)}$
G. subfasciatus$*^{(L)}$	*S. robustus*$*^{(S)}$	*A. ogilbyi*$*^{(S)}$
H. vittatus$*^{(L)}$	*A. ogilbyi*$*^{(S)}$	*T. pleurogramma*$*^{(S)}$
S. robustus$*^{(S)}$	*R. sarba*$*^{(-)}$	*R. sarba*$*^{(L)}$
T. pleurogramma$*^{(L)}$	*T. pleurogramma*$*^{(L)}$	*S. cephalotes*$*^{(L)}$
P. humeralis$*^{(S)}$	*C. macrocephalus*$*^{(L)}$	
A. georgiana$*^{(L)}$	*A. georgiana*$*^{(L)}$	
	P. humeralis$*^{(L)}$	

* additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

5.3.4 *Species analyses: Life-history categories of fish in different habitat types*

5.3.4.1 Large net

Since the ichthyofaunal composition of the samples collected with the large net varied significantly among seasons at one of the habitat types (see subsection 5.3.1.3), the extent of any significant differences in the types of habitat mainly occupied by species that represented the various life-history categories, *i.e.* resident, juvenile or transient, was examined separately for each level of that temporal factor. When the inverse Bray-Curtis similarity matrices constructed from those species that contributed >1% to the total catch at the various habitat types in each season were subjected to MDS ordination, the resultant plots showed that little separation occurred between the groups of species representing the different life-history categories (Figs 5.32a-d). This was reinforced by the fact that ANOSIM did not detect a significant difference, during any season, in the types of habitat occupied by the groups of species assigned to the resident, juvenile or transient categories, *i.e.* Global p=9.1-54.1%.

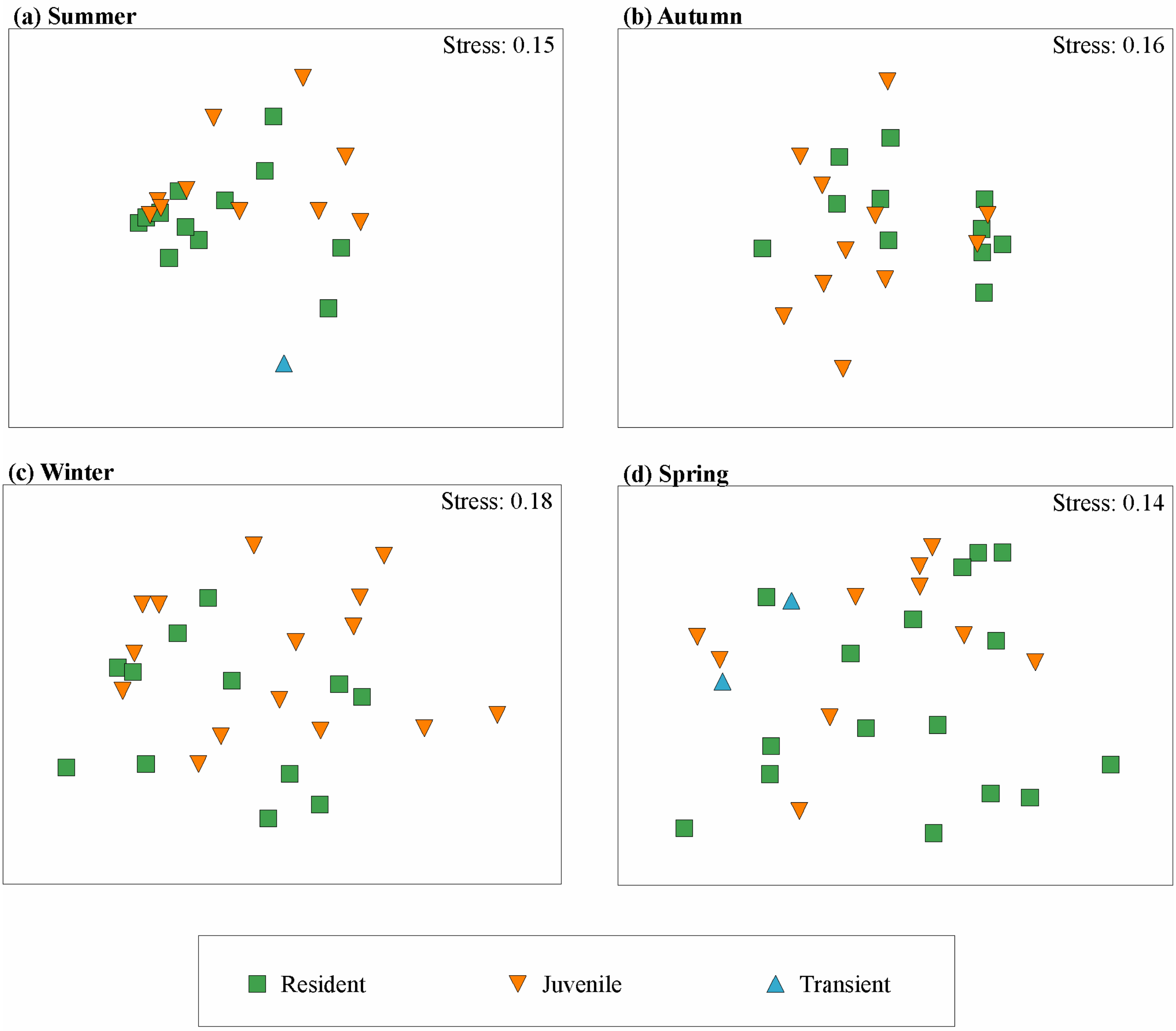


Figure 5.32: Two-dimensional MDS ordination of the species similarity matrices derived from the densities of those species that contributed >1% to the total catch in the 60.5m net at habitat types 1-4 in (a) summer, (b) autumn, (c) winter and (d) spring. Data collected in 2000 and 2001 have been meaned in these analyses. Each species in the above plots is coded for the life-history catogory to which it had previously been assigned.

5.3.4.2 Small net

In view of the significant differences in the ichthyofaunal composition of samples collected with the small net between day and night and among seasons (see subsection 5.3.2.3), the inverse multivariate analyses of the species data were performed separately for each level of both of these temporal factors. When the Bray-Curtis similarity matrices constructed from the more abundant species recorded at the various habitat types during the day and night and in each season were subjected to MDS ordination, the species representing the different life-history categories showed little tendency to form groups (Figs 5.33a-h). Moreover, as was the case with the species caught in the large net,

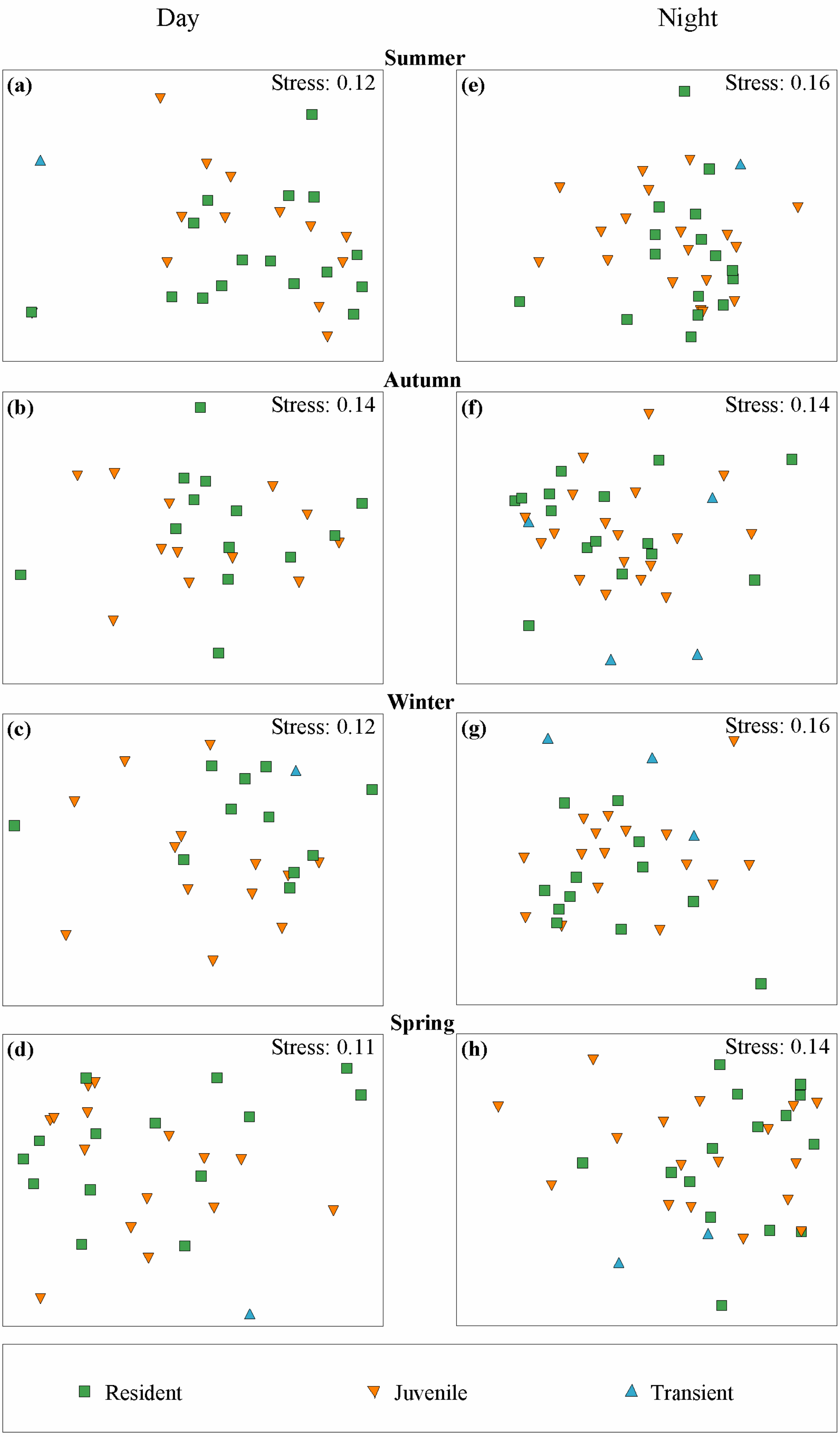


Figure 5.33: Two-dimensional MDS ordination of the species similarity matrices derived from the densities of those species that contributed >1% to the total catch in the 21.5m net at habitat types 1-6 in summer, autumn, winter and spring during the day (a-d, respectively) and night (e-h, respectively). Data collected in 2000 and 2001 have been meaned in these analyses. Each species in the above plots is coded for the life-history catogory to which it had previously been assigned.

ANOSIM failed to detect significant differences among these groups of species on all sampling occasions (Global p=7.6-71.2%). Such results indicate that the species representing the resident, juvenile and transient life-history categories do not tend to exhibit any marked affinity for particular habitat types along this coastline.

5.4 Discussion

5.4.1 Differences in ichthyofaunal composition among habitat types

The results presented in this chapter demonstrate that the overall composition of the fish faunas at the various nearshore habitat types along the lower west coast of Australia were largely, or almost exclusively, significantly different from each other. Thus, the ichthyofaunal composition of the samples collected with the 60.5 m net at habitat types 1-4, after pooling data across seasons and years, were significantly different between each pair of those habitat types, except in the case of the moderately sheltered habitat type 2 *vs* the moderately exposed habitat type 3. Moreover, even when the densities of all of the species from samples collected with the 21.5 m net during the day and night in each season and both years were pooled, the ANOSIM test still demonstrated that the ichthyofaunal compositions in each pair of the six nearshore habitat types were significantly different.

The R-statistic values for pairwise comparisons in the relevant ANOSIM test emphasised that, in the case of both the large and small net samples, the composition of the fish fauna at the highly sheltered habitat type 1, which contains seagrass close to shore, is by far the most distinct of all of the habitat types in this study area. However, in the case of the small net samples, the R-statistic value for the comparison of the ichthyofaunal compositions at habitat types 2 *vs* 3 was particularly low and less than half that for any other pair of habitat types. Thus, caution should be exercised on placing too much importance on the relevance of that particular significant difference in fish composition.

It is noteworthy that, even when the data for samples collected with the large net at habitat types 1-4 were kept separate on the basis of season but pooled for year, the results for each season paralleled, to a large extent, those for all seasons combined, *i.e.* the compositions of the fish assemblage at habitat type 2 did not differ significantly from that at habitat type 3 in any season. In contrast, the composition of the samples collected using the small net in a given season during either the day or night never differed significantly between all pairs of the six habitat types, as they did when the data collected at different times were pooled. Thus, even the usually distinct ichthyofaunal composition at habitat type 1 did not differ significantly from that of one of the other habitat types on one occasion, *i.e.* habitat type 3 during the day in autumn.

The above difference in the results obtained when data from the small net samples was pooled for all sampling occasions *vs* when it was analysed separately for day and night and season, may be partly attributable to the lower number of permutations that are able to be calculated for each comparison between a pair of habitat types in the latter ANOSIM tests, *i.e.* >999 *vs* 35. It should be noted that, although the latter number of possible permutations was relatively low, it still provided sufficient power for that ANOSIM test (K.R. Clarke, pers. comm.). However, the p values in ANOSIM tests involving this number of permutations will be conservative and, in several cases, pairwise comparisons between habitat types in the above tests were close to significance, *i.e.* p=5.7%, *e.g.* the previously-mentioned comparison between habitat types 1 and 3 during the day in autumn. In cases such as these, the R-statistic value still provides a reliable indication of the extent of differences between groups (Clarke and Warwick 2001a), and thus the moderately high R-statistic of 0.490 for that latter comparison demonstrated that their ichthyofaunas did differ in some respects, as was clearly shown by the distribution of the samples for these two habitat types on the MDS ordination plot presented in Fig. 5.18b. Moreover, the individual samples employed in all multivariate analyses of the ichthyofaunal data in this study represent a mean of at least four replicates collected with either net type at a particular site and time. Thus, any significant differences in ichthyofaunal composition detected by ANOSIM will almost certainly reflect real differences in the distributions of the various nearshore fish species in the study area.

The question now arises as to why, in contrast with the relatively consistent results in the pairwise habitat type comparisons that were obtained for large net samples collected in different seasons (for which the same number of permutations could be calculated by ANOSIM between any pair of habitat types in a particular season), the results of pairwise tests between the ichthyofaunas of the different habitat types using small net data were inconsistent among seasons and between day and night. The greater variability in the results obtained from the latter data was usually attributable to the influence of large numbers of small 0+ recruits of one or more species moving into the very shallow waters of certain habitat types for a brief period during a particular season and time of day. Since these 0+ recruits then often moved to waters slightly further from shore after a short time, where they remained for longer periods and increased in size, they were subsequently collected in greatly reduced numbers in the small net, whereas they continued to be caught in the large net. The reasons for differences in the composition of samples collected with the two net types at the various habitat types are discussed later in this section, while those for seasonal and diel changes in ichthyofaunal composition at the various habitat types are considered in more detail in Chapter 6.

5.4.2 Species characterising each habitat type

The species that characterised each of the six nearshore habitat types along the lower west coast of Australia are presented in Table 5.21, which represents the cumulative results of all SIMPER analyses performed throughout this chapter. This table emphasises the distinctiveness of the fish fauna at habitat type 1, which contained several species that were characteristic of only that habitat type. For example, *Sillaginodes punctata, Sillago burrus, Pelates sexlineatus, Leptatherina presbyteroides* and *Favonigobius lateralis* were recorded almost exclusively in this highly sheltered habitat type which contains areas of dense seagrass. Most of the above species occurred consistently in relatively large numbers at habitat type 1, and thus account for the mean density of fish generally being the greatest at this habitat type, irrespective of whether those densities were derived from samples collected using the large or small net. The new recruits of each of these species are known to be associated with either seagrass beds or unvegetated patches interspersed between seagrass beds soon after their settlement, and they generally remain in these areas throughout the juvenile phase of their life (Humphries and Potter 1993, Jenkins *et al.* 1997a, b, Vanderklift and Jacoby 2003). Furthermore, since *F. lateralis* is a permanent resident in nearshore marine waters and deposits its eggs on the substrate, the relatively calm type of environment found in habitat type 1 would maximize the chance of survival of its eggs and newly-hatched larvae (H. Gill, pers. comm.). Numerous other species, many of which are cryptic monocanthids, syngnathids, clinids or odacids that are morphologically adapted for inhabiting seagrass beds (*e.g.* Kikuchi 1980, Orth and Heck 1980, Scott 1981, Jenkins *et al.* 1997b, Travers and Potter 2002), were found exclusively in habitat type 1, *e.g. Cristiceps australis, Acanthaluteres spilomelanurus* and *Penicipelta vittiger*. Although these species usually represented a much smaller proportion of the total catch obtained at this habitat type than the previously-mentioned characteristic species, they contributed to the generally greater average taxonomic distinctness and variation in taxonomic distinctness of samples collected with the small net at this habitat type, and to the significantly higher mean number of species recorded in both net types at this habitat type.

Far fewer species characterised the ichthyofaunas at only one of the other five habitat types. However, one example is provided by *Enoplosus armatus*, which was found regularly only in habitat type 2. This finding is consistent with the fact that this species is

Table 5.21 Regularly and irregularly abundant species, as detected by SIMPER, in habitat types 1-6 along the lower west coast of Australia. These results represent the cumulative list of characteristic species detected by SIMPER analyses performed throughout Chapter 5, using data for both net types during both the day and night in each season between summer 2000 and spring 2001.

Habitat type	Regularly abundant	Irregularly abundant
1	*S. schomburgkii* *P. jenynsii* *F. lateralis* *S. punctata* *H. semifasciata* *R. sarba* *A. ogilbyi* *P. sexlineatus* *S. burrus* *A. rueppellii* *A. forsteri* *R. sarba* *L. presbyteroides**	*L. presbyteroides* *T. pleurogramma* *M. cephalus* *A. rueppellii*
2	*L. platycephala* *A. forsteri* *P. unicolor* *T. pleurogramma* *S. vittata* *C. macrocephalus* *A. ogilbyi* *H. vittatus* *E. armatus* *S. bassensis** *L. presbyteroides**	*H. vittatus* *A. ogilbyi* *S. robustus*
3	*T. pleurogramma* *L. platycephala* *C. macrocephalus* *S. bassensis* *P. unicolor* *S. vittata* *A. forsteri* *A. georgiana* *S. schomburgkii* *R. sarba* *A. oglibyi* *H. vittatus*	*A. ogilbyi* *S. robustus*
4	*S. bassensis* *S. vittata* *T. pleurogramma* *A. ogilbyi* *L. platycephala* *S. woodwardi* *A. forsteri* *R. sarba* *P. unicolor* *S. robustus* *P. humeralis* *H. vittatus* *C. macrocephalus*	*S. robustus* *H. vittatus* *A. ogilbyi*
5	*L. platycephala* *S. bassensis* *A. ogilbyi* *S. robustus* *A. forsteri*	*A. ogilbyi* *S. robustus* *L. presbyteroides*
6	*L. platycephala* *S. bassensis*	*S. vittata*

* additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

usually most abundant in those coastal areas where attached or detached macrophytes occur (Hutchins and Swainston 1986), and that habitat type 2 contained sparsely distributed patches of seagrass and, at particular times of the year, also large accumulations of detached seagrass and algae (see Chapter 4). Furthermore, the fact that *Pelsartia humeralis* was characteristic only of habitat type 4, which is moderately exposed and contains beds of seagrass in adjacent offshore waters, is explained by previous findings that this species is usually associated with detached macrophytes in relatively exposed waters (Robertson and Lenanton 1984, Ayvazian and Hyndes 1995). *Pelsartia humeralis* is particularly well camouflaged for living amongst this detached plant material, which provides shelter from predators and a rich source of invertebrate prey for this species (Robertson and Lenanton 1984).

The frequent lack of a significant difference between the composition of the ichthyofauna at habitat types 2 and 3 in samples collected with both the large and small nets, is consistent with the finding that the same ten species, out of a total of 15, typified each of these consecutive habitat types. However, there were a few occasions when their compositions did differ significantly. This helps account for the fact that *L. presbyteroides* and, as mentioned earlier, *E. armatus*, typify habitat type 2 but not 3, whereas the reverse is true for *Arripis georgiana*, *Sillago schomburgkii* and *Rhabdosargus sarba* (Table 5.21). It is also relevant that, apart from at habitat type 2, *L. presbyteroides* is only otherwise regularly abundant at the highly sheltered habitat type 1.

In contrast to the species discussed in the above paragraphs, several other species typified two or more of the habitat types along the lower west coast of Australia on a regular basis. However, such species often made a greater contribution to the fish fauna in a particular habitat type or types. For example, *S. bassensis* typified the ichthyofaunas at habitat types 2-6, but constituted a far greater proportion of the catch at the moderately to fully exposed sandy habitat types 4 and 6, than at the more sheltered habitat types 2 and 3. This finding is consistent with the results of Hyndes *et al.* (1996a), which showed that this species was far more abundant in relatively exposed nearshore marine waters than in those that were more sheltered from wave activity. Moreover, *L. platycephala* also typified the fish assemblages at habitat types 2-6, but occurred in greater densities and made greater contributions to the samples collected at habitat types 2 and 3.

Some of the species that characterised the fish assemblages at two or more habitat types were recorded in large numbers but on an irregular basis as a result of their tendency to form schools. This accounts for the high degree of variability (standard deviation) that was usually associated with the mean abundances of these species, which was also often very high. Thus, although relatively low average similarity/standard deviation ratios were usually assigned to these schooling species in the results of the SIMPER analyses, their inclusion as species which typify a habitat type is still considered valid since they were recorded in the same habitat types in particular seasons and/or in either the day or night in both years. For example, schools of juvenile *Spratelloides robustus* were caught during the day at habitat types 2-6 during the summer and/or autumn, while the juveniles of another schooling clupeid, *Hyperlophus vittatus*, which spawns in deeper offshore waters along the lower west coast of Australia mainly during winter (Gaughan *et al.* 1996), were also collected irregularly in large numbers at habitat types 2-4. However, the overall densities of these schooling fish were far greater at habitat type 2 in the case of the first of these species and at habitat types 2 and 3 in the case of the latter species. Large schools of both of the above clupeid species were also caught by Valesini *et al.* (1998) and Vanderklift and Jacoby (2003) during the day at particular nearshore sites along the lower west coast of Australia that, on the basis of the current habitat classification scheme, would be assigned to habitat types 2 and 3. The former study also showed that sampling carried out at sites that would be assigned to habitat types 1 or 6 did not yield appreciable numbers of either of these species. The apparent affinity of juvenile *H. vittatus* for moderately exposed and predominantly sandy nearshore environments may be related to the protection that is provided for these small transparent fish from visual predators by the wave swash and suspended sand (Goh 1992, Vanderklift 1996, D. Winters, pers. comm.). Moreover, unlike the more exposed habitat types 5 and 6, the moderate degree of wave activity at habitat types 2 and 3 would be less likely to cause physical damage to the relatively fragile bodies of these juvenile fish. Furthermore, the planktonic invertebrates which comprise the majority of the diet of both of these clupeid species (Goh 1992, Schafer *et al.* 2002), are approximately 18 times more abundant during the day at habitat type 2 than at the highly sheltered habitat type 1 (Chapter 8).

A number of other species collected in either the large or small net which were not identified by SIMPER as characteristic of one or more habitat type(s), were selected by BVSTEP as important for distinguishing among the ichthyofaunal compositions of the various habitat types in particular seasons and during either the day and night in the case of the small net samples. Several of these species were responsible for distinguishing the fish assemblages at habitat type 1 from those at the other habitat types, and included those that are adapted morphologically and/or in their coloration for living in seagrass beds, *e.g. Gymnapistes marmoratus, Callionymus depressus, Acanthaluteres brownii* and *Pseudolabrus parilus*. However, some of these weed-associated species were also found among detached macrophyte accumulations at habitat type 4, *e.g. Mitotichthys meraculus, Histiogamphelus cristatus* and *Siphonognathus attenuatus,* and were thus important for distinguishing the ichthyofauna at this habitat type from those at the other habitat types. *Platycephalus speculator*, which is known to inhabit sheltered sand and weed areas in nearshore marine waters (Hutchins and Swainston 1986), was generally important for distinguishing the ichthyofaunas of both habitat types 1 and 2 from those of the other habitat types, while juvenile *Pomatomus saltatrix* also contributed to the distinctiveness of the fish samples collected by the large net at habitat type 4 in three of the four seasons. Furthermore, *Trachinotus bailloni* was important for distinguishing the fish assemblages in habitat type 5, which differs from all other habitat types in that it contains areas of reef close to shore. The occurrence of this reef-dwelling tropical species at habitat type 5 is almost certainly brought about by the southwards transfer of its eggs and larvae by the warm Leeuwin Current that flows along the continental shelf of this coastline. The subsequent transport of such larvae to nearshore areas along the coast is facilitated by local onshore winds (Hutchins 1991).

5.4.3 Consistency of differences in ichthyofaunal compositions among habitat types in different seasons and/or years and/or between day and night

When the composition of the fish fauna collected in either net type was shown to differ significantly among seasons and, in the case of samples collected with the small net, between day and night, separate analyses for each level of that temporal factor(s) showed that, in all cases, the overall ichthyofaunal composition differed significantly among habitat types. Furthermore, no significant differences in the composition of the fish fauna were detected between years in any habitat type, thus indicating that the assemblages of fish at those habitat types recur consistently on an interannual basis.

However, the extent of the overall differences in ichthyofaunal composition among habitat types varied to some degree among seasons and, in the case of the small net, also between day and night. The composition of the fish assemblages in large net samples exhibited the greatest difference amongst the four habitat types in summer and the least in winter, *i.e.* the Global R-statistics for one-way ANOSIM tests for data recorded in these two seasons were 0.707 and 0.407, respectively. The seasonal variation in the extent of these overall habitat type differences was almost entirely attributable to the samples collected at habitat type 4, since this was the only one of the four habitat types sampled with this net type in which the fish composition differed significantly among seasons. The marked difference in overall ichthyofaunal compositions among habitat types during summer was mainly due to the contrast between the consistently large numbers of small juvenile *S. bassensis* that were caught in the large net at habitat type 4 in that season, and the far lower numbers of this species in the samples from the other three habitat types. Further details of temporal differences in the ichthyofaunal compositions of the various habitat types are provided in Chapter 6.

In the case of samples collected using the 21.5 m net, greater overall differences among the fish compositions at the various habitat types were generally detected at night in each season than during the day. This was often attributable to one or more species migrating into the shallows of particular habitat types at night. For example, *Schuettea woodwardi* was caught regularly at night only in habitat type 4, and *A. georgiana* only typified the night-time samples collected in autumn at habitat type 3 (*i.e.* the only habitat type in which the ichthyofaunal compositions at night differed significantly among seasons). Furthermore, *R. sarba* was consistently abundant only at night in habitat type 3, and this was the case in both winter and spring.

The extent to which the overall composition of the small net samples differed among habitat types was slightly greater in winter and spring during the day, and in winter at night. The diel and seasonal differences in the composition of the ichthyofauna at the various habitat types are explored in more detail in the following chapter.

5.4.4 Relationships between differences in ichthyofaunal compositions and enduring environmental characteristics at the various habitat types

The extent of the differences among the various habitat types on the basis of their ichthyofaunal assemblages (*i.e.* sampled using each net type in each season and during the day and night) were, in all but one case, significantly correlated with those for the collective suite of seven quantitative environmental variables that had been statistically selected as providing the best discrimination among those habitat types. Although the extent of the correlations between the ichthyofaunal and environmental data in winter were usually lower than in the other seasons (presumably reflecting, in part, the significantly lower densities of fish and often also the mean numbers of species), those correlations were each still statistically significant. Furthermore, in the single case in which the correlation was not significant, *i.e.* for the data derived from day-time samples collected in autumn using the 21.5 m net, the level was very close to significance, *i.e.* p=5.5%.

The significant relationships between the matrices constructed from the fish and enduring environmental data recorded at the various nearshore habitat types along the lower west coast of Australia, indicate that the consistently recurring differences in the compositions of the various fish assemblages reflect the differences among the enduring physical characteristics of those habitat types. It is thus now possible to use measurements of the selected seven environmental variables at any site along this coastline to predict the type of fish fauna likely to be found at that site in any season during the day and/or night.

The demonstration that the composition of fish assemblages in different nearshore habitat types is statistically related to differences in the physical characteristics of those habitat types supports the views of Dethier (1992), Allee *et al.* (2000) and Roff and Taylor (2000) that differences in biotic composition in marine waters can be adequately explained by heterogeneity in the physical environment. It thus also validates the use of predominantly enduring physical attributes to classify marine habitats. These results contrast with the conclusions of Robinson and Levings (1995) that nearshore habitat classification schemes, which are based on physical features, cannot be used for identifying differences among the characteristics of fish assemblages.

5.4.5 Does the type of net influence the extent of differences in ichthyofaunal composition among habitat types?

As discussed in the preceding subsections, the compositions of the fish samples collected with the large and small nets at habitat types 1-4 during the day were shown to (1) differ significantly overall among habitat types, (2) remain significantly different overall among habitat types in each season in both years and (3) match statistically, in each season, the manner in which the selected subset of enduring environmental variables discriminated among the various nearshore habitat types.

Despite the above similarities in the results of analyses of the catch data obtained using the small and large nets, the compositions of the fish faunas in samples obtained with the two nets from each of habitat types 2-4 were significantly different. These differences reflect mainly the fact that, due to the steepness of the slope in the subtidal regions of habitat types 2-4, the small net (1.5 m high) could not be used as far offshore and in as deep water as the large net (2.5 m high). Moreover, it is also likely that the differences in mesh size between the 60.5 and 21.5 m nets (*i.e.* 9 *vs* 3 mm, respectively, in the central pocket and 25 *vs* 9 mm, respectively, in the wings), would have influenced the composition of the fish samples collected using those two net types.

Although only a few of the species recorded at habitat types 2-4 were caught exclusively in either the 21.5 or 60.5 m seine net, several species, and usually particular life-cycle stages of those species, were caught more consistently and in relatively greater numbers in one of the net types. For instance, the use of the large seine net enabled those fish that typically occupy slightly deeper waters in areas further from the shoreline to be caught more consistently than was the case with the small net, *e.g.* adult *S. schomburgkii* and *A. georgiana* at habitat types 2 and 3 and large *R. sarba* in habitat type 4. Thus, the median lengths of *A. georgiana* collected in the large net at habitat types 2 and 3 were 215 and 218 mm, respectively, and thus far greater than the 52 and 122 mm, respectively, for this species in the small net in these habitat types. Moreover, the individuals of *R. sarba* caught at the moderately exposed habitat type 4 were relatively large, and all of these fish, with the exception of one individual, were caught in the large net.

In contrast, some fish species were caught in relatively greater numbers and/or more consistently in the small net, which, through its manner of deployment, is likely to catch a relatively greater number of individuals that inhabit those waters close to the shoreline. Several of these species were typically represented in these catches by their small juveniles, including *S. robustus* in habitat types 2-4 and *A. forsteri* in habitat type 2. The median lengths of these two species in samples collected with the 21.5 m net at the above habitat types (*i.e.* 32-36 mm in the case of the first of these species and 43 mm in the case of the latter), were less than in samples collected with the large net, especially in the case of *A. forsteri*, *i.e.* 38-43 and 121 mm, respectively. Several small resident species were also more prevalent in the samples collected with the small net at particular habitat types, *e.g. Atherinomorus ogilbyi* and *L. platycephala* at habitat types 2-4. For the latter of these species, such results most likely reflect its greater affinity for the particularly shallow waters close to shore, rather than a lack of retention of these small fish by the larger mesh in the 60.5 m net. This is supported by the fact that the median lengths of *L. platycephala* at habitat types 2, 3 and 4 were similar in the small and large net samples, and that the preferred invertebrate prey of its juveniles, *i.e.* amphipods (Chapter 11), occur in considerably greater numbers in the shallower intertidal zones along the lower west coast of Australia, rather than in the subtidal waters (Chapter 7).

Unlike the situation at habitat types 2-4, the compositions of the samples collected with the two net types at habitat type 1 were not significantly different. This was almost certainly related to differences in the slopes of the subtidal area in these habitat types. Thus, the far shallower slope of the subtidal area at habitat type 1 enabled the small net to be deployed in waters that were the same depth and distance from shore as the large net. This difference in bathymetry among the habitat types was reflected by the fact that the wave shoaling margin (*i.e.* 2 m depth contour), which was one of the seven environmental variables selected for discriminating among the six habitat types, was located much further from shore at habitat type 1 than at the other habitat types (see Fig. 3.2). The similar waters that were sampled by the different net types in this highly sheltered habitat type also account for the fact that the minimum, maximum and median lengths of the relatively abundant species in samples collected with both the small and large nets in habitat type 1 were similar. The above differences between the results obtained using the large and small nets at habitat types 2-4 *vs* 1 indicate that differences in the water depths sampled by the 21.5 and 60.5 m seine nets are probably more important than mesh size in influencing the extent to which different species contribute to the samples collected with the two net types.

As with ichthyofaunal composition, the mean fish densities derived from samples collected in habitat type 1 did not differ significantly between the two net types, whereas they did differ significantly between the large and small nets at habitat types 3 and 4. The significantly greater densities of fish in samples collected with the small net than large net at habitat type 3 were almost entirely due to the capture of large schools of *H. vittatus* on several sampling occasions. In contrast, the significantly lower density of fish and the particularly low average taxonomic distinctness in samples collected with the small net at habitat type 4 was almost certainly attributable to the fact that, due to the relatively steep subtidal slope at this habitat type, the small net was usually deployed in the energetic wave-breaking zone that characterised this habitat type, whereas the large net sampled the waters beyond that zone. As would be expected, the densities and diversity of fish were not as great in that breaker zone as in the calmer waters immediately seaward of that zone. The proposed influence of the presence of an energetic breaker zone on the number of fish caught by the two net types is supported by the lack of a significant difference between the densities of fish in samples obtained with the two net types at the relatively sheltered habitat types 1 and 2, where the breaker zone is either virtually absent or relatively small. Fish in those latter waters are thus likely to be distributed more evenly in the nearshore area.

Chapter 6. Temporal differences in the ichthyofaunal characteristics of different habitat types along the lower west coast of Australia

6.1 Introduction

The different nearshore habitat types that have been identified in this study along the lower west coast of Australia are able to be distinguished on the basis of a suite of geophysical characteristics that exhibit little or no variability with time and are thus enduring. However, many abiotic characteristics of the surrounding environment, such as light intensity, climatic factors and oceanographic processes, undergo temporal changes and are therefore non-enduring. These latter environmental characteristics change over differing temporal scales, *e.g.* daily, seasonally and/or annually, and at varying levels of predictability, *e.g.* the regular switch in light intensity between day and night *vs* unpredictable changes in the velocity of onshore winds.

Temporal differences in non-enduring environmental characteristics can influence the composition of nearshore fish fauna by affecting the timing of reproduction and success of juvenile recruitment, food availability, the likelihood of predation and/or the suitability of physico-chemical conditions for survival and growth. For example, diel changes in the characteristics of nearshore fish assemblages typically reflect the movements of small fish to and from these shallow waters, which reduces the risk for these small fish of being preyed upon by piscivorous birds and fish (*e.g.* Modde and Ross 1981, Ross *et al.* 1987, Wright 1989, Burrows *et al.* 1994, Layman 2000), and enables them to exploit their invertebrate prey, which also typically undertake diel migrations between the water column and substrate surface (*e.g.* Alldridge and King 1980, 1985, Mees and Jones 1997, Jacoby and Greenwood 1989, Chapter 10) at the time when they are most available. Seasonal differences in the composition of fish assemblages in nearshore waters are often the result of the time-staggered recruitment of large numbers of the juveniles of those species that utilise these environments as nursery areas, and their emigration to deeper waters as they become mature. These recruitment events frequently coincide with particular environmental conditions that favour the growth and survival of those species, such as warmer temperatures during spring and summer (*e.g.* Gibson *et al.* 1993, Clark *et al.* 1996b, Kokita and Nakazono 2000, Kuo *et al.* 2001, Hakala *et al.* 2003) and lower wave activity (*e.g.* Clark *et al.* 1996b).

Differences in the intrinsic, enduring characteristics of the various nearshore habitat types will lead, however, to differences in the ways in and extents to which temporal changes in non-enduring environmental conditions influence those habitat types and thus their faunas. For example, with respect to less predictable changes in the environmental characteristics of nearshore waters, wracks of detached macrophytes are more likely to accumulate in those habitat types that contain seagrass beds than in those which are not located within the vicinity of such beds.

Moreover, the aspect of and degree to which a nearshore site is sheltered by surrounding landforms will influence the extent to which onshore winds from prevailing directions generate wave activity at that site. The influence of highly regular temporal changes in characteristics of the environment on nearshore fish faunas can also vary among habitat types. For example, the times at which small fish undertake any inshore/offshore movements in response to diel changes in light intensity are likely to vary between those habitat types that contain structures such as seagrass beds or reefs and which thus provide a refuge from piscivores (*e.g.* Robblee and Zieman 1984, Howard 1989, Travers and Potter 2002) and those that are unvegetated and thus do not provide the same type of protection from predation.

From the above, it follows that investigation of the influence of temporal changes in environmental conditions on the nearshore fish faunas needs to be undertaken separately for each habitat type in a region. A similar conclusion was reached by Clark *et al.* (1996b) in their study along the south-western coast of Africa, who found that differences in the underlying physical features of nearshore sites, and thus their fish faunas, led to differences in the ways in which those fish responded to temporal changes in the nearshore environment. This component of the project is thus aimed at determining the extent to which the characteristics of the fish assemblages at each nearshore habitat type along the lower west coast of Australia vary in relation to three temporal factors, namely day *vs* night, season and year. Following on from the broad results of the temporal differences in ichthyofaunal characteristics described in Chapter 5, the following specific hypotheses are explored in detail in this chapter.

1) The characteristics of the fish fauna in the shallow waters of the various habitat types during the day will differ from those at night due to onshore/offshore movements of certain fish species between those times.
2) The extent to which the characteristics of the fish fauna differ between day and night will vary among habitat types as a result of differences in the intrinsic, enduring environmental characteristics of those habitat types.
3) Differences in the timing of recruitment of the juveniles of certain species into nearshore waters will lead to seasonal changes in the composition of the nearshore ichthyofauna at the various habitat types.
4) The extent of seasonal differences in ichthyofaunal composition that result from the recruitment of juveniles at certain times of the year will differ among habitat types due to differences in the suitability of those habitats for juveniles of the various fish species.
5) The characteristics of the fish fauna in the samples collected with the 21.5 m net will differ more markedly among seasons than that obtained with the 60.5 m net. This hypothesis is based on the fact that since the 21.5 m seine net has a finer mesh and

samples predominantly the shallowest waters, it is more likely to catch large numbers of the small 0+ juveniles of species that recruit into nearshore waters along the lower west coast of Australia at particular times of the year.

6.2 Materials and Methods

6.2.1 Sampling of fish fauna

Fish were sampled using a 60.5 and 21.5 m seine net at two sites representing each of the various habitat types identified along the lower west coast of Australia in each season between summer 2000 and spring 2001. Sampling was undertaken only during the day and at habitat types 1-4 with the larger of these two nets, while the small net was used to collect fish during both the day and night at habitat types 1-6. A full description of the sampling regime for fish is provided in subsection 5.2.1 and Table 5.1.

6.2.2 Measurement of non-enduring environmental characteristics

Water temperature and the collective volume of any accumulations of detached seagrass and macroalgae on the beach face were measured at the same sites and times at which fish were collected. A full description of the methods used to measure these environmental characteristics in the field is provided in Chapter 4, subsection 4.2.1.

6.2.3 Statistical Analyses

The following descriptions of the statistical techniques used to analyse the ichthyofaunal data represent an extension of those described in Chapter 5. As outlined in subsection 5.2.2 of that chapter, full examination of the extent to which the composition of the ichthyofauna differed among habitat types required separate analyses to be carried out for each level of the various temporal factors, *i.e.* seasons, years and, in the case of samples collected using the small net, between day and night. Likewise, in the current chapter, full investigation of the extent of temporal differences in ichthyofaunal composition necessitated separate analyses for each habitat type. Thus, several of the data analyses described in subsection 5.2.2 are also relevant to the questions addressed in this chapter. Moreover, as one of the objectives of the current chapter is to examine whether temporal differences in the composition of the ichthyofauna in the study area are correlated with temporal variations in particular non-enduring environmental characteristics (*i.e.* water temperature and the collective volume of any accumulations of detached seagrass and macroalgae on the beach face), the descriptions of the statistical methods used to analyse that environmental data, which are provided in Chapter 4 (see subsection 4.2.2), are also relevant to the current chapter. Appropriate cross-referencing has been provided where necessary.

The following descriptions of the statistical methods that were required to examine (1) the extent of any significant temporal differences in the composition of the ichthyofauna in the various habitat types and (2) whether the temporal trends in the ichthyofaunal data are significantly related to those in the non-enduring environmental characteristics, are thus provided in detail only when those methods are additional to those described in previous chapters.

6.2.3.1 Univariate analyses

(i) Density of fish, number of species and species relatedness

The density of fish, number of species, average taxonomic distinctness and variation in taxonomic distinctness derived from replicate samples collected with the 60.5 and 21.5 m nets were subjected to three and four-way ANOVA, respectively, to determine whether these four dependent variables differed significantly among the various habitat types, seasons and/or between years and, in the case of samples collected with the small net, between day and night. A full description of the methodology for this analysis is provided in subsection 5.2.2.1.

(ii) Non-enduring environmental characteristics

The replicate values for water temperature and the volume of detached macrophytes were subjected to four and three-way Analysis of Variance (ANOVA), respectively, to ascertain whether these two dependent variables differed significantly among habitat types, seasons and between years and, in the case of the former environmental variable, also between day and night. A full description of the methodology for this analysis is provided in subsection 4.2.2.1.

6.2.3.2 Multivariate Analyses

(i) Temporal differences in ichthyofaunal composition and non-enduring environmental characteristics

The Bray-Curtis similarity coefficient was used to construct similarity matrices from the dispersion-weighted mean densities of the various fish species derived from samples collected with each net type at the different habitat types on the various sampling occasions between summer 2000 and spring 2001. Matrices were produced using data from samples collected both at all habitat types and at each habitat type individually. Matrices were subjected to non-metric Multidimensional Scaling (MDS) ordination (Clarke and Gorley 2001), and Analysis of Similarities (ANOSIM; Clarke 1993) was used to ascertain whether the composition of the fish assemblages differed significantly among seasons and/or between years and, in the case of the samples collected with the 21.5 m net, between day and night. When ANOSIM detected a significant difference between groups of samples from different temporal periods, SIMPER (Clarke 1993) was used to elucidate which fish species best characterised each of those groups temporal groups. Full descriptions of the above multivariate analyses are provided in subsection 5.2.2.3, part (*i*).

When a significant difference in the ichthyofaunal composition at a particular habitat type was detected on the basis of one or more of the temporal factors by the multivariate analyses described fully in subsection 5.2.2.3, mean water temperatures and volumes of detached macrophytes at that habitat type were used or ascertain whether those ichthyofaunal differences were significantly related to temporal differences in one or both of those non-enduring environmental characteristics. Thus, the untransformed data for mean water temperatures recorded during the various sampling occasions were used to construct separate Euclidean distance matrices for each of those habitat types. The same procedure was employed for the $\log_{10}$ (n+1) transformed data for the mean volumes of detached macrophytes. All of the above Euclidean distance matrices were subjected to non-metric MDS ordination (Clarke and Gorley 2001).

(ii) Relating matrices constructed from ichthyofaunal and non-enduring environmental data

RELATE was used to determine, separately for each of those habitat types at which significant differences in the composition of the ichthyofauna were detected on the basis for one or more temporal factor(s), the extent of any significant correlation between (1) the Bray-Curtis similarity matrix constructed from the densities of the various fish species in samples collected with either the large or small net during the various sampling occasions, and (2) the complementary Euclidean distance matrix constructed from either mean water temperature or detached macrophyte data during the same sampling occasions. The Spearman rank correlation (ρ) between ichthyofaunal and non-enduring environmental matrices was considered significant if the associated p value was <5% (Clarke and Gorley 2001).

(iii) Identification of species most responsible for matching patterns in complementary matrices

Species distinguishing among temporal periods at each habitat type

When ANOSIM identified significant temporal differences in the ichthyofaunal composition of groups of samples collected with either net at a particular habitat type, BVSTEP was used to identify the subset of species which provided the best correlation (ρ) with the Bray-Curtis similarity matrix constructed from the full suite of species recorded at that habitat type (Clarke and Gorley 2001). The selected subset of species were thus those that were most important for distinguishing the groups of samples which had been shown to differ significantly on the basis of a particular temporal factor. This was achieved by matching the similarity matrix constructed from the densities of the full suite of species recorded at that habitat type with the corresponding densities of species recorded at the same habitat type (Clarke and Gorley 2001). This matching procedure was repeated until no further subsets of species could be drawn from the data that provided a suitable match with the similarity matrix derived from the full suite of species. A full description of the restarting procedure for the BVSTEP routine is provided in subsection 5.2.2.3 part (*iii*).

Species matching temporal differences in non-enduring environmental characteristics at each habitat type

When RELATE detected a significant correlation between a similarity matrix constructed from the ichthyofaunal data derived from samples collected in a particular net and habitat type, and the complementary distance matrix constructed from either the water temperature or the volume of detached macrophytes (*i.e.* those described in (1) and (2), respectively, in part (*ii*) above), BVSTEP was used to identify the subset of species within the full suite recorded at that habitat type that provided the best match with each of the corresponding environmental matrices. This matching procedure was repeated until no further subsets of species could be drawn from the data that provided a suitable match with the Euclidean matrices constructed from each of the non-enduring environmental characteristics. A full description of the restarting procedure for the BVSTEP routine is provided in subsection 5.2.2.3 part (*iii*).

6.3 Results

6.3.1 Characteristics of ichthyofauna collected with the 60.5 m net in different seasons and years

6.3.1.1 Mean density and length of each species

The mean densities and median lengths of each species collected with the 60.5 m seine net during the day in each season at habitat types 1, 2, 3 and 4 are provided in Appendix 1.

6.3.1.2 Density of fish, number of species and species relatedness

The results of ANOVA, which employed density of fish, number of species, average taxonomic distinctness and variation in taxonomic distinctness as dependent variables, and habitat types, seasons and years as independent variables, are provided in Table 5.3. A description of the results of this analysis is provided in subsection 5.3.1.2.

6.3.1.3 Composition of fish fauna

MDS ordination of the mean densities of the various fish species in large net samples in each season in both 2000 and 2001 at habitat types 1-4 showed that when the samples on the 3-d ordination plot were coded according to season (Fig. 6.1a) and year (Fig. 6.1b), there was little overall tendency for the samples to form discrete groups on the basis of either of these temporal factors. One-way ANOSIM showed that while the ichthyofaunal composition differed significantly among seasons overall (p=0.2%), the extent of this difference was relatively small (Global R=0.122). Moreover, the extent of the difference in the composition of the fish fauna between 2000 and 2001 was far lower, *i.e.* Global R= -0.005. The lack of separation of groups of samples in Figs 6.1a and b contrasts with that in Fig. 5.3, which showed that when the samples on the same ordination plot were coded for habitat type, they exhibited a far greater overall tendency to form groups. This was reinforced by the results of one-way ANOSIM for that factor (*i.e.* p=0.1%; Global R=0.530).

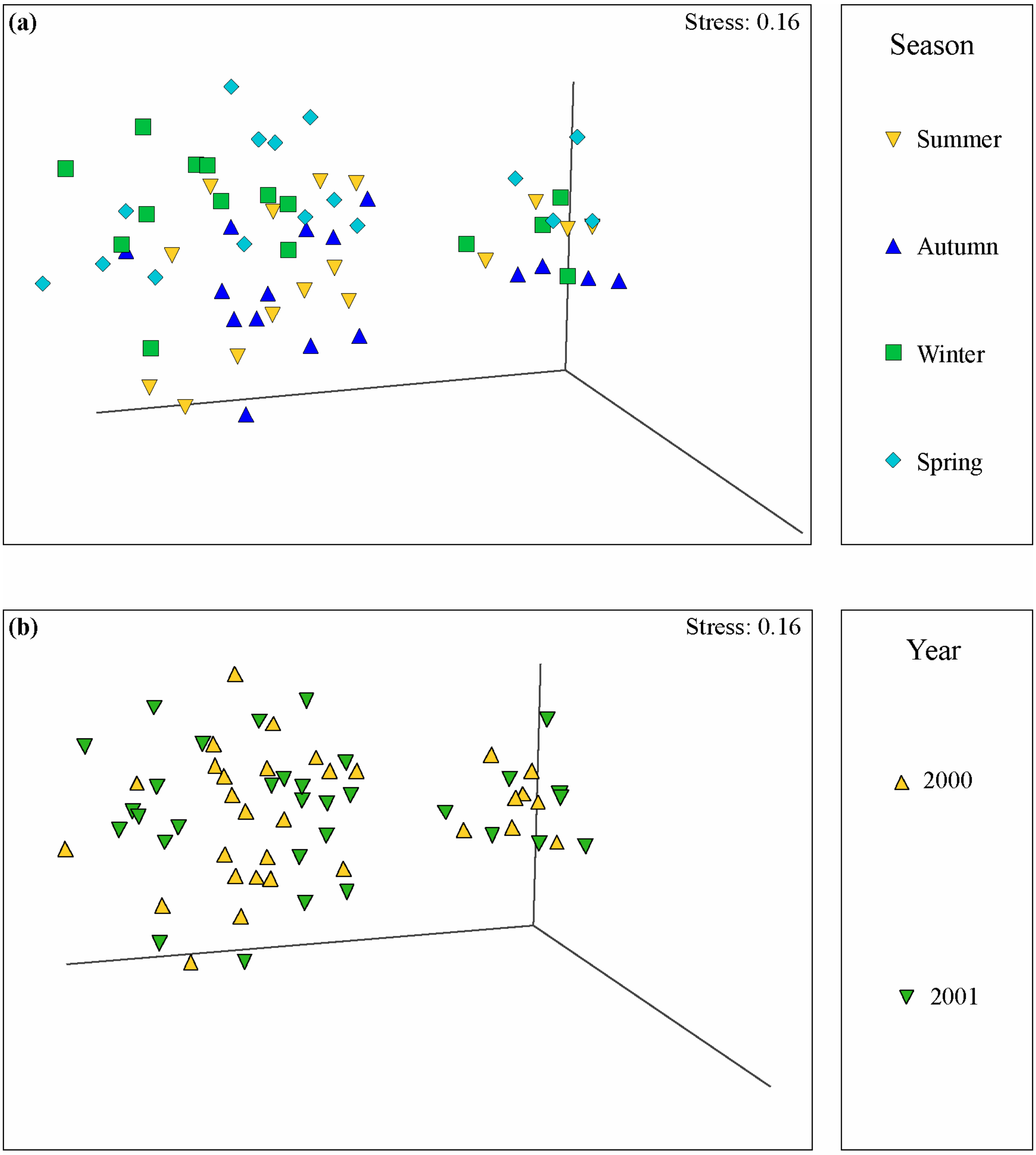


Figure 6.1: Three-dimensional MDS ordination of the mean densities of fish species in samples collected with the 60.5 m net at habitat types1-4 in each season between summer 2000 and spring 2001. Samples on the ordination plot have been coded for (a) season and (b) year.

In view of the strong tendency for the samples collected with the large net to form significantly different groups on the basis of habitat type, the data were thus analysed separately for each level of this factor to ascertain whether the composition of their fish assemblages differed significantly among seasons and/or between years at this finer level. The appropriate two-way crossed season x year ANOSIM tests for data recorded in each of the four habitat types, which were carried out as part of the analyses in the previous chapter and are described fully in subsection 5.3.1.3, showed that the composition of the fish fauna differed significantly among seasons only in habitat type 4 and did not differ significantly between years in any habitat type.

When the ichthyofaunal data recorded for habitat type 4 were subjected to MDS ordination, the samples collected in summer lay on the left side of the plot and adjacent to those from spring, which formed a particularly tight group (Fig. 6.2). The samples for autumn lay below those for spring, while those for winter lay either just to the right of or among those from autumn (Fig. 6.2). One-way ANOSIM demonstrated that the ichthyofaunal composition at this habitat type differed to the greatest extent between autumn and spring (p=2.9%; R=0.625), followed closely by summer *vs* winter (p=2.9%; R=0.611) and then autumn *vs* summer (p=2.9%; R=0.563). Although the remaining pairwise comparisons between seasons were not significantly different, SIMPER was used to identify which species characterised each individual season since the ichthyofaunas in one season in each of those comparisons always differed significantly from that of another season. The results of this routine, which were presented in Table 5.5 in the previous chapter, showed that some species typified the fish fauna at habitat type 4 only during a particular season*, e.g. Sillago vittata* during summer and *Cnidoglanis macrocephalus, Schuettea woodwardi, Aldrichetta forsteri, Rhabdosargus sarba* and *Paraplagusia unicolor* during autumn.

The species selected by BVSTEP as those most responsible for distinguishing among the ichthyofaunas in the samples collected seasonally at habitat type 4 were *Hyperlophus vittatus, Spratelloides robustus, C. macrocephalus, Pelsartia humeralis, Siphamia cephalotes, Sillago bassensis, S. vittata, Pomatomus saltatrix, Arripis georgiana, S. woodwardi, A. forsteri, Lesueurina platycephala* and *P. unicolor* (ρ=0.95). The relative densities of selected examples of these species, represented by circles of proportionate sizes, were overlaid on the samples in the ordination plot shown in Fig. 6.2 and are presented in Figs 6.3a-d. These plots showed, for example, that *S. bassensis* and *S. vittata* were relatively more abundant in summer than in any other season at this habitat type, while *C. macrocephalus* was most abundant in autumn and *A. georgiana* was most abundant in winter (Figs 6.3a, b, c and d, respectively).

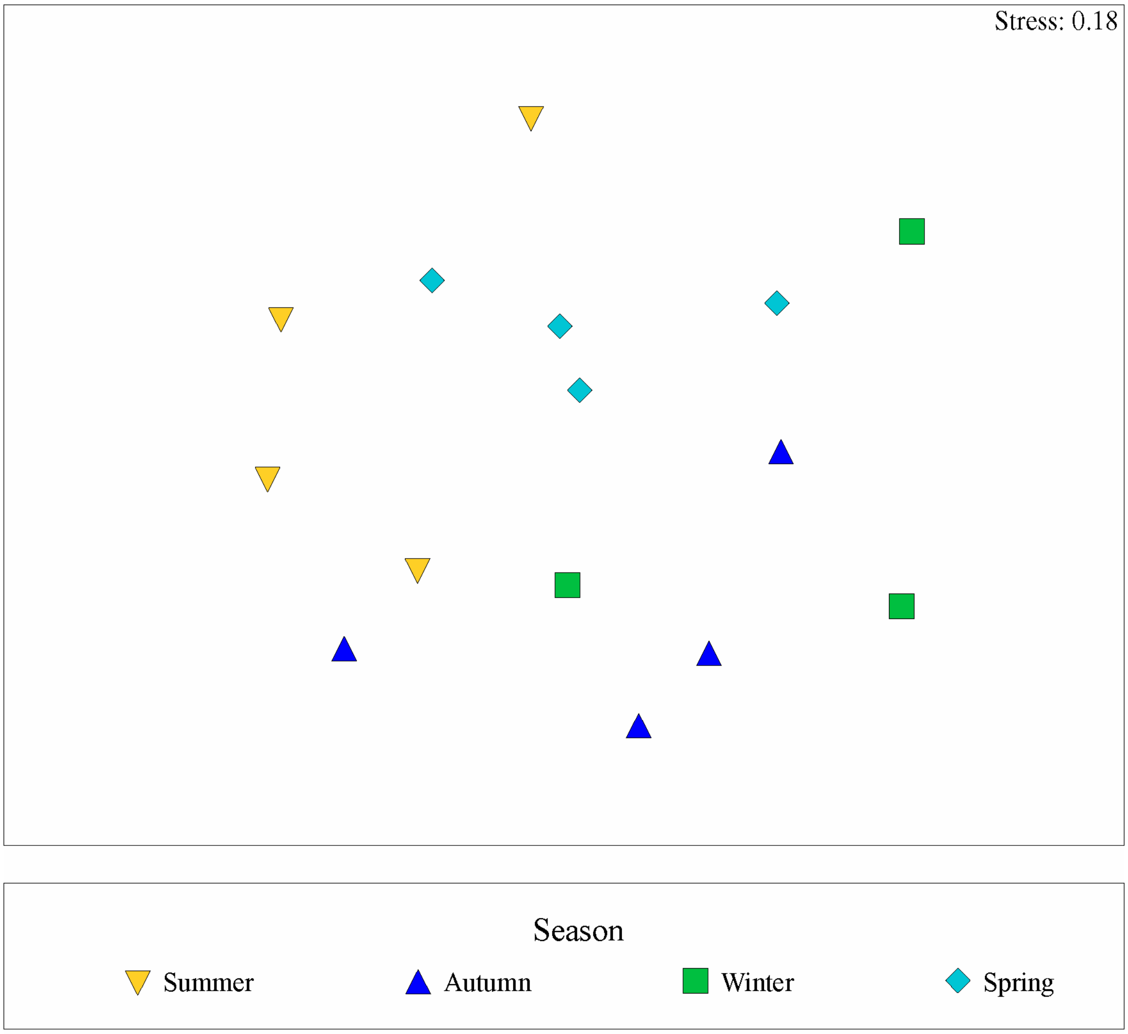


Figure 6.2: Two-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 60.5 m net at habitat type 4 between summer 2000 and spring 2001.

6.3.2 Characteristics of ichthyofauna collected with the 21.5 m seine net in different seasons, years and between day and night

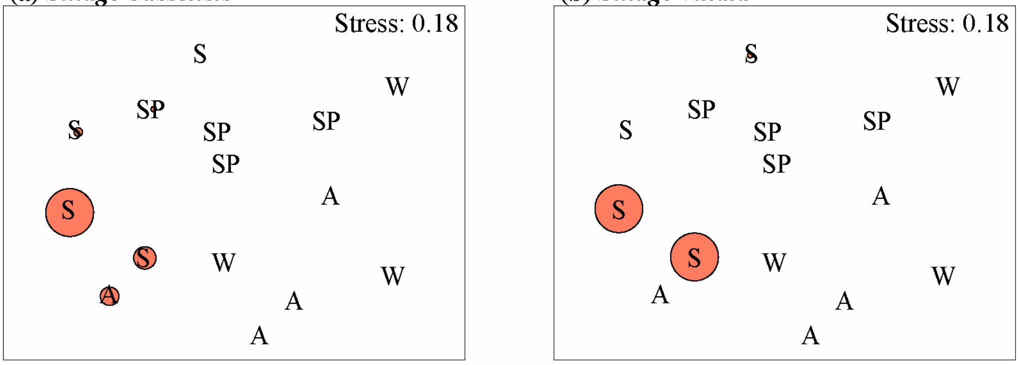
6.3.2.1 Mean density and length of each species

The mean densities and median lengths of each species collected using the 21.5 m net in each season at each of the six habitat types are provided for data recorded during the day in Appendix 2 and at night in Appendix 3.

6.3.2.2 Density of fish, number of species and species relatedness

ANOVA of the density of fish, number of species, average taxonomic distinctness and variation in taxonomic distinctness in samples collected with the 21.5 m net at each habitat type during both the day and night in each season in 2000 and 2001 was carried out in the previous chapter. The results of this analysis are presented in Table 5.9 and described in subsection 5.3.2.2.

(a) ***Sillago bassensis*** **(b)** ***Sillago vittata***



(c) ***Cnidoglanis macrocephalus*** **(d)** ***Arripis georgiana***

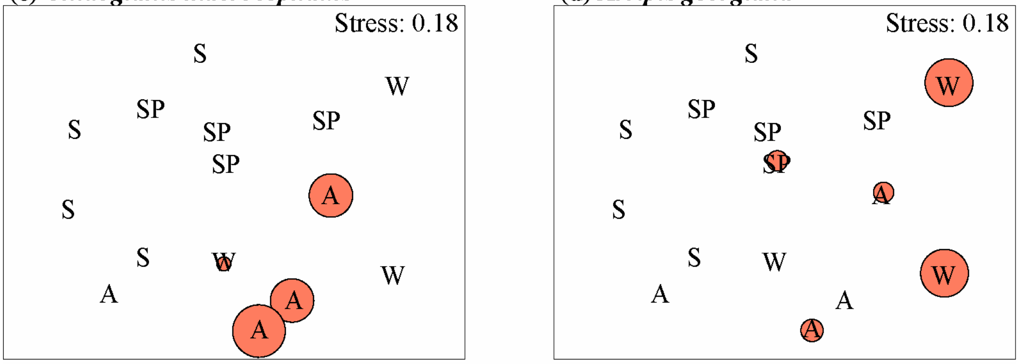


Figure 6.3: Two-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 60.5 m net at habitat type 4 in each season between summer 2000 and spring 2001. Each sample has been coded for season (S=summer, A=autumn, W=winter and SP=spring). The size of the circles overlaid on each sample reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine.

6.3.2.3 Composition of fish fauna

The mean densities of the various fish species in samples collected with the 21.5 m net during the day and night in each season in 2000 and 2001 at habitat types 1-6 were subjected to MDS ordination, and the samples on the resultant plot were coded for each of these temporal factors to explore the overall extent to which they tended to form groups on the basis of those factors (Figs 6.4a-c). These plots showed that the samples did not form any conspicuous groups on the basis either day *vs* night, season or year. The 3-d plot in Figs 6.4a-c has been presented from the same perspective in each case to facilitate appropriate comparisons between the distributions of the samples according to each temporal factor, and also to enable comparisons to be made between these three plots and that coded for habitat type (Fig. 5.17). However, it should be noted that the samples representing each level of the three temporal factors did not exhibit a greater tendency to separate into more distinct groups when the plot was viewed from other perspectives. Moreover, while one-way ANOSIM demonstrated that the composition of the ichthyofauna differed significantly overall between day and night and also among seasons (p=0.1%), the extents of those differences were relatively small (Global R=0.078 and 0.130, respectively), and that between year

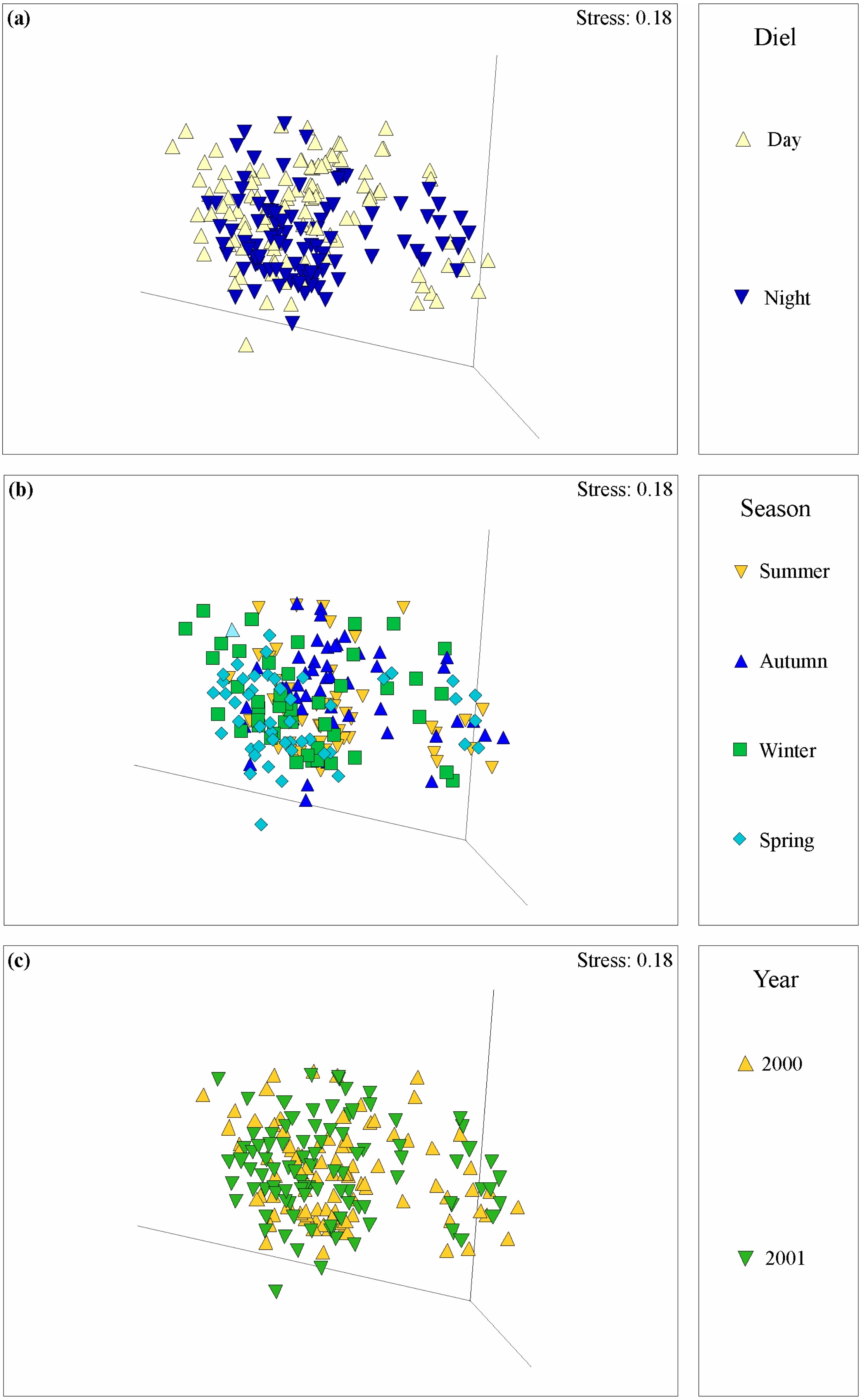


Figure 6.4: Three-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 21.5 m net during the day and night in each season between summer 2000 and spring 2001 at habitat types 1-6. Samples have been coded separately for (a) day *vs* night, (b) season and (c) year.

was considerably lower, *i.e.* Global R=-0.002. As with samples collected using the large net, the extents of the differences in ichthyofaunal composition among the levels of each of the temporal temporal factors were far lower than that among the various habitat types, *i.e.* p=0.1%; Global R=0.426 (see subsection 5.3.2.3).

Given the important overall influence of habitat type on the composition of the fish fauna collected in the small net, the data were thus analysed separately for each of the six habitat types to ascertain whether, at this finer level, the extents of any temporal differences in ichthyofaunal composition were greater than when examined globally as above. The appropriate season x year and season x diel two-way crossed ANOSIM tests, carried out on data recorded in each of the six habitat types, were also required to investigate whether differences in the composition of the fish fauna among habitat types should be explored separately for any or all of these temporal factors. A full description of the results of these tests is thus provided in the previous chapter (see subsection 5.3.2.3 and Tables 5.12a and b). Generally, the global results of these two-way crossed ANOSIM tests showed that the composition of the fish fauna in the samples collected with the small net differed significantly between the day and night in habitat types 2, 3, 4 and 5. The ichthyofaunas in samples collected during the day also differed significantly among seasons at each of those four habitat types, whereas those of samples collected at night differed significantly among seasons only at habitat type 3. Furthermore, while the composition of the fish fauna at habitat type 6 did not differ significantly between the day and night, significant differences were detected among seasons for the pooled day/night data. The composition of the ichthyofauna at habitat type 1 did not differ significantly on the basis of any temporal factor, and no significant differences were detected between years in any of the other habitat types.

(i) Diel differences in ichthyofaunal composition

In order to investigate more fully the basis for the significant diel differences that were detected in the ichthyofaunal composition at habitat types 2-5, separate MDS ordinations were carried out on the data recorded at each of these habitat types (Figs 6.5a-d). The resultant plots showed that, in each case, the samples collected during the day tended to from a separate group from those collected at night, especially at habitat type 4 (Fig. 6.5c). The results for the diel factor in the diel x season two-way crossed ANOSIM tests performed using data collected in each of these habitat types, showed that the ichthyofauna recorded during the day differed to the greatest extent from that at night in habitat types 4 (p=0.4%; Global R=0.288) and 3 (p=0.5%; Global R=0.286), and were least at habitat type 5 (p=5.0%; Global R=0.164).

The species that were detected by SIMPER as most responsible for distinguishing between the day and night-time ichthyofaunas in habitat types 2-5 are listed in Table 6.1. It should be noted that while the compositions of the fish assemblages at these habitat types also differed

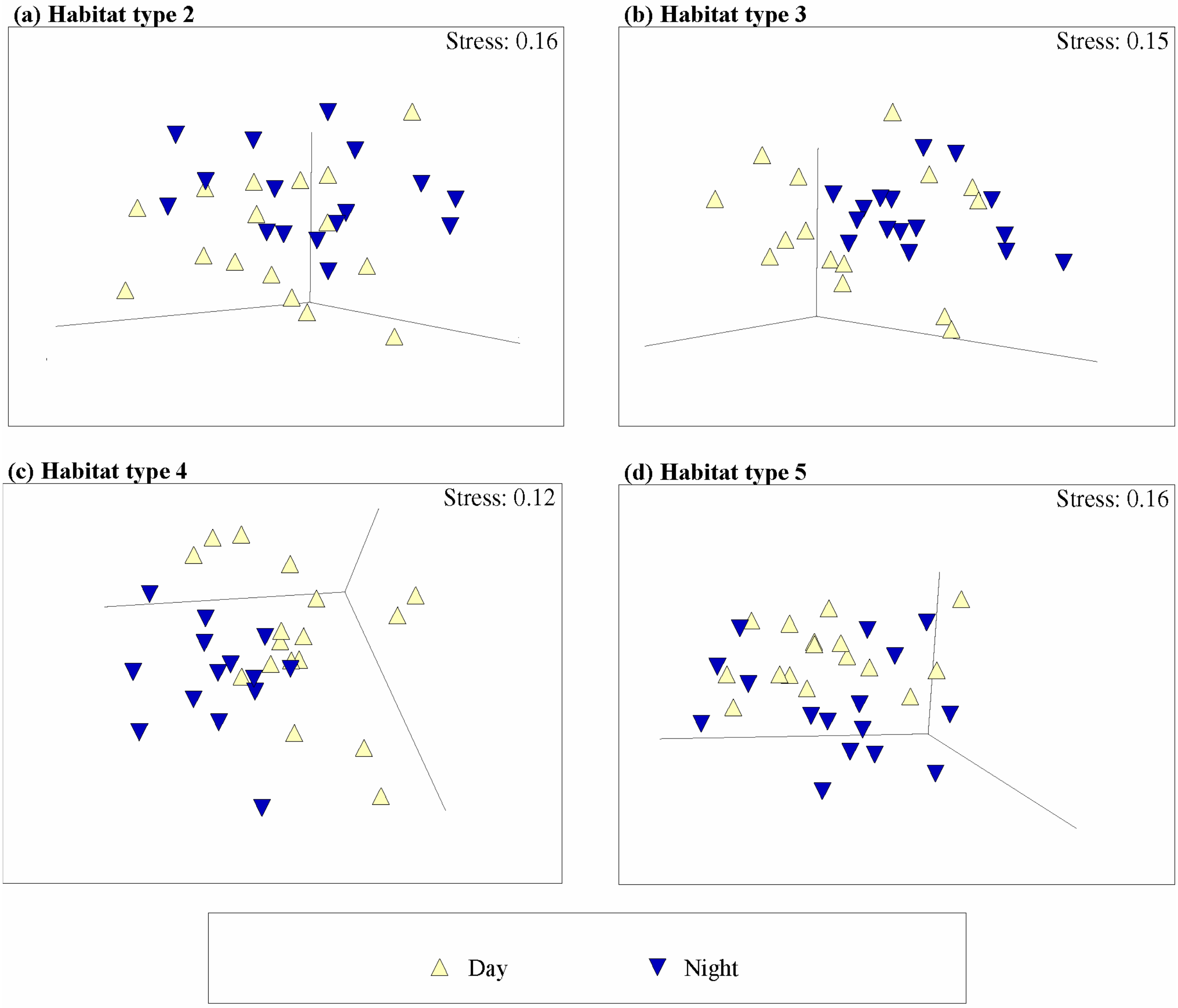


Figure 6.5: Three-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 21.5 m net during the day and night between summer 2000 and spring 2001 at habitat type (a) 2, (b) 3, (c) 4 and (d) 5.

significantly among seasons, these analyses were restricted only to day *vs* night as the species responsible for seasonal differences are investigated fully in the following subsection. Some species were caught more consistently and in greater numbers at night in three or all four of these habitat types, *e.g. Cnidoglanis macrocephalus* and *Sillago schomburgkii*, while others were invariably, or almost invariably, caught in greater numbers during the day, *e.g. Spratelloides robustus, Sillago vittata* and *Atherinomorus ogilbyi* (Table 6.1). Other species distinguished the day and night-time ichthyofaunas only at two consecutive habitat types, *e.g. Paraplagusia unicolor*, *Arripis georgiana* and *Rhabdosargus sarba* were consistently more abundant at night in habitat types 2 and 3, and the same was true for *Schuettea woodwardi* in habitat types 4 and 5. Moreover, some species were more abundant during the day than night in some habitat types, while the reverse was true for those species in other habitat types, *e.g. Hyperlophus vittatus*, which was more abundant during the day at habitat types 2 and 3 but was regularly more abundant at night in habitat type 4 (Table 6.1).

Table 6.1 Regularly and irregularly abundant species, as detected by SIMPER, that distinguished between the composition of the fish faunas collected in the small net during the day and night at habitat types 2-5. The diel period in which each species was more consistently abundant is also provided (see superscripts; D=day, N=night). Data collected in each season between summer 2000 and spring 2001 has been pooled in this analysis.

	REGULARLY ABUNDANT	Irregularly abundant
2	*L. platycephala* $^{(D)}$	*S. robustus* $^{(D)}$
	S. vittata $^{(D)}$	*H. vittatus* $^{(D)}$
	C. macrocephalus $^{(N)}$	
	P. unicolor $^{(N)}$	
	A. forsteri $^{(D)}$	
	A. ogilbyi $^{(D)}$	
	R. sarba $^{*(N)}$	
	S. bassensis $^{*(D)}$	
	T. pleurogramma $^{*(N)}$	
	S. schomburgkii $^{*(N)}$	
	A. georgiana $^{*(N)}$	
3	*L. platycephala* $^{(D)}$	*H. vittatus* $^{(D)}$
	S. bassensis $^{(N)}$	*S. robustus* $^{(D)}$
	C. macrocephalus $^{(N)}$	
	S. vittata $^{(D)}$	
	P. unicolor $^{(N)}$	
	S. schomburgkii $^{(N)}$	
	A. forsteri $^{(D)}$	
	T. pleurogramma $^{(N)}$	
	R. sarba $^{(N)}$	
	A. ogilbyi $^{*(D)}$	
	A. georgiana $^{*(N)}$	
4	*C. macrocephalus* $^{(N)}$	*S. robustus* $^{(D)}$
	S. woodwardi $^{(N)}$	
	L. platycephala $^{(N)}$	
	P. humeralis $^{(N)}$	
	S. bassensis $^{(D)}$	
	S. schomburgkii $^{(N)}$	
	H. vittatus $^{*(N)}$	
	S. vittata $^{*(D)}$	
	A. forsteri $^{*(N)}$	
5	*L. platycephala* $^{(N)}$	
	A. ogilbyi $^{(D)}$	
	S. woodwardi $^{(N)}$	
	A. forsteri $^{(D)}$	
	S. robustus $^{(D)}$	
	P. humeralis $^{(N)}$	
	C. macrocephalus $^{(N)}$	
	L. presbyteroides $^{*(D)}$	

* additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

(ii) Seasonal differences in ichthyofaunal composition

The significant seasonal differences in ichthyofaunal composition detected by two-way crossed ANOSIM at habitat types 2-6 (Table 5.12) were explored in more detail by performing separate multivariate analyses for each of those habitat types using data collected in the relevant diel period. Thus, separate MDS ordinations were carried out on data recorded during the day at habitat types 2, 3, 4 and 5 (Figs 6.6a, b, c and d, respectively), at night in habitat type 3 (Fig. 6.6e) and during the day and night collectively at habitat type 6 (Fig. 6.6f). When the samples in each of the resulting 2-d plots were coded for season, they tended to form groups that progressed rightwards from summer to autumn to spring and then winter across the plot.

One-way ANOSIM demonstrated that, during the day, the seasonal differences in ichthyofaunal composition were greatest overall in habitat type 3 (p=0.1%; Global R=0.547) and least in habitat type 2 (p=0.5%; Global R=0.367; Table 6.2a). These results were reflected in the results of MDS ordination, which showed that the samples collected in each season at the first of these habitat types formed tight and discrete groups, with the exception of those from autumn (Fig. 6.6b), whereas some of the samples from the various seasons intermingled to some extent on the plot constructed from the ichthyofaunal data recorded at habitat type 2 (Fig. 6.6a). The pairwise seasonal comparisons showed that the greatest differences in ichthyofaunal composition during the day occurred between summer and winter at habitat types 2-4, whereas this pairwise comparison was not significant at habitat type 5. Relatively large differences were detected between the fish faunas recorded in autumn and spring at habitat types 4 and 5, whereas the fish compositions in the first of these seasons did not differ significantly from those recorded in summer in any habitat type, or from those recorded in winter in habitat types 2, 4 and 5 (Table 6.2a).

SIMPER was carried out on the day-time data recorded at habitat types 2, 3, 4 and 5 either for each season or using data that had been pooled across particular pairs of seasons, depending on the pairwise results of the ANOSIM tests in each of those habitat types. Thus, if the comparison between two seasons was not significant and those seasons did not vary in whether or not they were significantly different from any of the other seasons, the data for that pair were pooled. The results of these analyses, which are provided in Table 6.3a-d, showed that some species characterised the day-time ichthyofauna in a particular season in most or all of these habitat types, *e.g. S. bassensis*, *S. vittata* and *S. robustus* during summer in habitat types 2, 3 and 4 and, in the case of the latter species, also 5. However, other species characterised only one season or two consecutive seasons in just one habitat type (*e.g. Enoplosus armatus* in spring at habitat type 2 and *Pelsartia humeralis* during autumn and winter at habitat type 4). In contrast, some species characterised the fish assemblages in most seasons in all of these habitat types, such as the resident *L. platycephala* (Table 6.3a-d).

Table 6.2 Significance levels (p; %) and R-statistic values for global and pairwise comparisons in one-way ANOSIM tests of the ichthyofaunal compositions in samples collected with the 21.5 m net in each season during (a) the day at habitat types 2-5, (b) the night at habitat type 3 and (c) during the day and night at habitat type 6. Values in boldface represent those that are significant. Data recorded in 2000 and 2001 have been pooled in these analyses. S=summer, A=autumn, W=winter and SP=spring.

(a) Day

		S		A		W		SP	
		p	R	p	R	p	R	p	R
Habitat type 2	**S**								
(p=0.5%; Global R=0.367)	**A**	51.4	0.000						
	W	**2.9**	**0.750**	8.6	0.354				
	SP	5.7	0.385	**2.9**	**0.323**	**2.9**	**0.427**		
Habitat type 3	**S**								
(p=0.1%; Global R=0.547)	**A**	25.7	0.167						
	W	**2.9**	**0.792**	**2.9**	**0.406**				
	SP	**2.9**	**0.750**	**2.9**	**0.552**	**2.9**	**0.583**		
Habitat type 4	**S**								
(p=0.2%; Global R=0.457)	**A**	5.7	0.292						
	W	**2.9**	**0.844**	11.4	0.250				
	SP	**2.9**	**0.542**	**2.9**	**0.750**	17.1	0.250		
Habitat type 5	**S**								
(p=0.2%; Global R=0.387)	**A**	20.0	0.156						
	W	20.0	0.198	14.3	0.365				
	SP	**2.9**	**0.510**	**2.9**	**0.719**	**2.9**	**0.365**		

(b) Night

Habitat type 3 (p=0.1%; Global R=0.395)

	S		A		W		SP	
	p	R	p	R	p	R	p	R
S								
A	**2.9**	**0.354**						
W	5.7	0.542	**2.9**	**0.365**				
SP	**2.9**	**0.542**	**2.9**	**0.510**	17.1	0.229		

(c) Day and Night

Habitat type 6 (p=0.1%; Global R=0.299)

	S		A		W		SP	
	p	R	p	R	p	R	p	R
S								
A	**0.9**	**0.230**						
W	**0.3**	**0.481**	**0.3**	**0.326**				
SP	**0.1**	**0.428**	**0.2**	**0.392**	88.8	0.072		

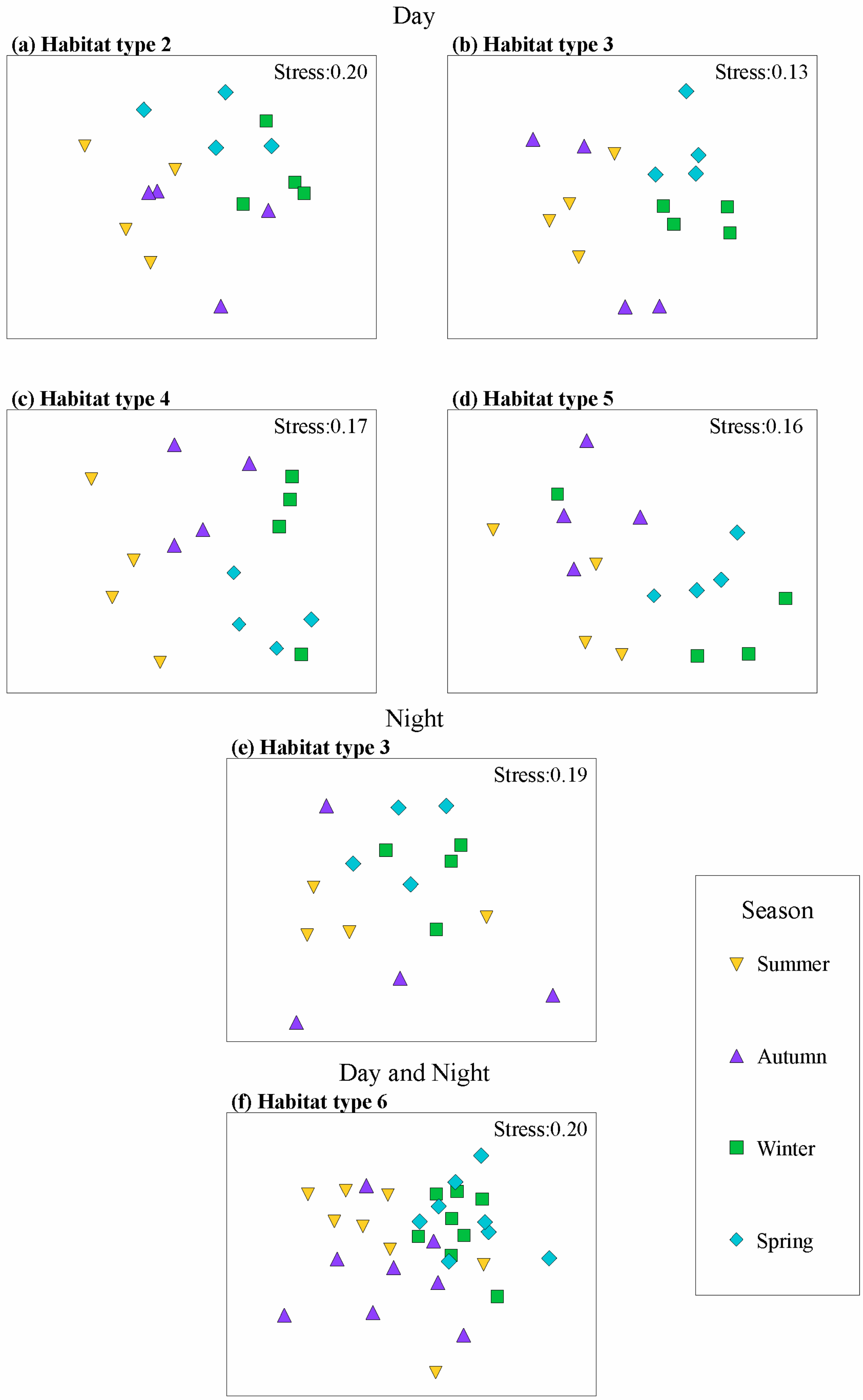


Figure 6.6: Two-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 21.5 m net in each season between summer 2000 and spring 2001 during the day at habitat type (a) 2, (b) 3, (c) 4 and (d) 5 at night in habitat type (e) 3, and during the day and night at habitat type (f) 6.

Table 6.3 Regularly and irregularly abundant species, as detected by SIMPER, in samples collected in the 21.5 m net during the day in summer, autumn, winter and spring at habitat types (a) 2, (b) 3, (c) 4 and (d) 5. When the compositions of the ichthyofaunas at those habitat types did not differ significantly between two or more seasons, SIMPER was performed on the pooled data for those seasons. Data collected in 2000 and spring 2001 have been pooled in these analyses.

(a) Habitat type 2

Summer		**Autumn**	**Winter**	**Spring**	
Regularly abundant	Irregularly abundant	Regularly Abundant	Regularly abundant	Regularly abundant	Irregularly abundant
S. bassensis *L. platycephala* *S. vittata* *P. unicolor* *L. presbyteroides**	*S. robustus* *A. ogilbyi*	*L. platycephala* *T. pleurogramma* *A. forsteri* *A. ogilbyi*	*L. platycephala* *A. forsteri*	*L. platycephala* *E. armatus* *H. vittatus* *A. forsteri*	*A. ogilbyi*

(b) Habitat type 3

Summer & Autumn		**Winter**		**Spring**
Regularly abundant	Irregularly abundant	Regularly abundant	Irregularly abundant	Regularly abundant
S. bassensis *S. vittata* *L. platycephala* *R. sarba**	*S. robustus* *A. ogilbyi*	*L. platycephala* *A. forsteri* *T. pleurogramma*	*A. ogilbyi*	*L. platycephala* *H. vittatus* *S. bassensis*

(c) Habitat type 4

Summer		**Autumn**		**Winter**	**Spring**
Regularly abundant	Irregularly abundant	Regularly Abundant	Irregularly abundant	Regularly abundant	Regularly abundant
L. platycephala *S. robustus* *S. bassensis* *P. unicolor**	*S. vittata*	*P. humeralis* *S. bassensis* *L. platycephala* *T. pleurogramma* *A. ogilbyi**	*S. robustus*	*L. platycephala* *P. humeralis*	*L. platycephala*

(d) Habitat type 5

SUMMER, AUTUMN & WINTER		**SPRING**
Regularly abundant	Irregularly abundant	Regularly abundant
L. platycephala	*A. ogilbyi* **S. robustus**	*L. platycephala* *A. forsteri*

*additional species detected by SIMPER on species abundance data that was log-transformed but not dispersion-weighted.

BVSTEP was used to identify the subset of species that provided the best match with the similarity matrix constructed from all species recorded during the day at a particular habitat type. These species are thus those that were most important for distinguishing among the ichthyofaunas of the groups of samples which had been shown previously by ANOSIM to differ significantly among seasons at that habitat type, and are listed in Table 6.4a for habitat types 2, 3, 4, and 5. The densities of examples of these selected species were represented as circles of proportional sizes overlaid on the samples in the ordination plot of the day-time data recorded at each of the above habitat types, *i.e.* those shown in Figs 6.6a-d, and are presented in Figs 6.7a-d. These plots showed, for example, that *Aldrichetta forsteri* was the most consistently abundant in winter at habitat type 3 and in spring at habitat type 5 (Figs 6.7b*i* and d*i*, respectively). Moreover, while SIMPER demonstrated that *L. platycephala* characterised the day-time ichthyofauna at habitat types 2-5 during all seasons, the plot presented in Fig. 6.7b*ii* demonstrated that, at habitat type 3, this species made a considerably greater contribution to the catches in winter and spring than in summer and autumn.

MDS ordination of the data collected seasonally at night in habitat type 3 showed that the samples collected in each season intermingled to some extent on the resultant plot, with those samples collected in autumn being particularly widely dispersed (Fig. 6.6e). One-way ANOSIM demonstrated that the extent of the overall seasonal differences in ichthyofaunal composition was less at night than that during the day in this habitat type, *i.e.* Global R=0.395 *vs* 0.547. However, the night-time samples collected in spring formed a relatively tight group and remained discrete from those collected in summer (Fig. 6.6e), and ANOSIM detected the greatest differences in ichthyofaunal composition between these seasons (p=2.9%; R=0.542; Table 6.2b). ANOSIM also detected significant differences between the fish compositions in autumn and those in each of the other seasons (p=2.9%; R=0.354-0.510; Table 6.2b). The species identified by SIMPER as characterising the night-time ichthyofauna in each season at this habitat type are listed in Table 5.16 and described fully in subsection 5.3.2.3. This routine showed that several of the species that typified the night-time ichthyofauna in particular seasons at habitat type 3 were not recorded regularly in any season during the day, *e.g. C. macrocephalus* in summer, autumn and spring and *S. schomburgkii* in autumn, winter and spring (*cf* Tables 5.16 and 6.3b). BVSTEP showed that a subset of 16 species provided the best correlation with the full suite of species recorded at night in this habitat type (Table 6.4b), of which *S. bassensis* and *S. vittata* made greater contributions to the seasonal catches in summer, while *S. schomburgkii* was relatively more abundant in winter (Figs 6.8a-c, respectively).

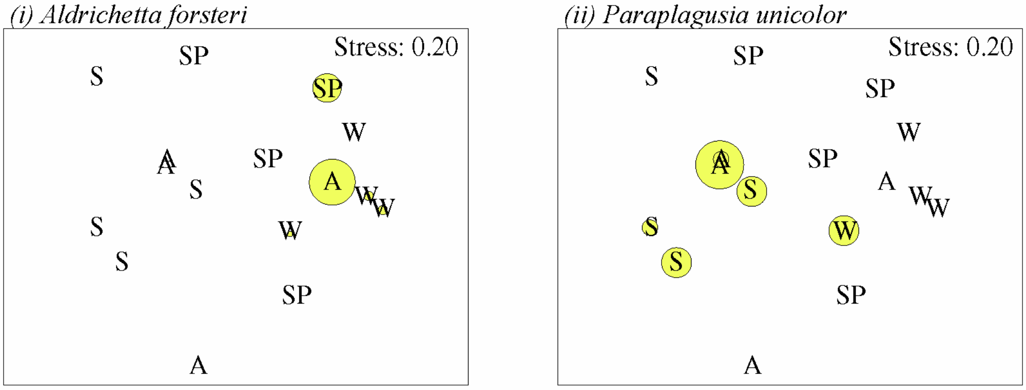
When the samples collected during the day and night at the most exposed habitat type (*i.e.* 6) were subjected to MDS ordination, they tended to separate less on the basis of season than

Table 6.4 The subsets of species recorded in the 21.5 m net in (a) habitat types 2-5 during the day, (b) habitat type 3 at night and (c) habitat type 6 during both the day and night, that were identified by BVSTEP as those most responsible for distinguishing among the samples which had been shown previously by ANOSIM to differ significantly among seasons at each of those habitat types and times (see Tables 6.2a-c). The maximum correlation (ρ) between each subset of species and the similarity matrix constructed from the full suite of species in each habitat type and diel period is also provided.

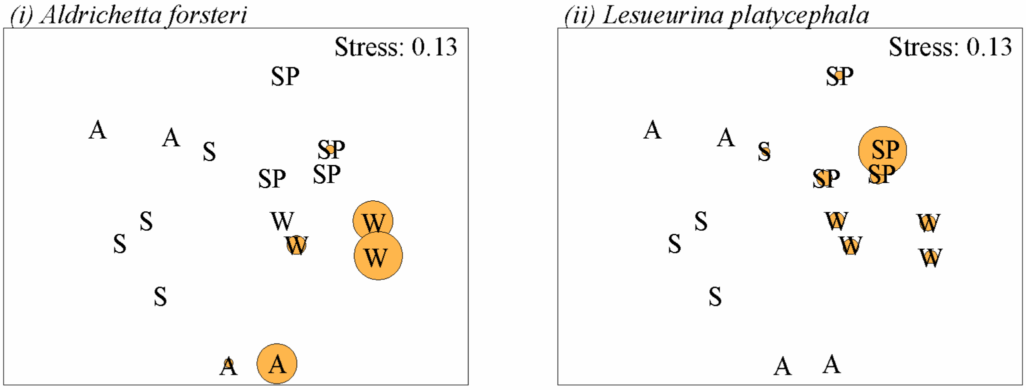
	2	**3**	**4**	**5**	**6**
(a) Day	(max. $\rho = 0.898$)	(max. $\rho = 0.957$)	(max. $\rho = 0.955$)	(max. $\rho = 0.951$)	
	H. vittatus ***C. macrocephalus*** ***A. ogilbyi*** *P. speculator* *P. humeralis* *A. rueppellii* *S. bassensis* *S. schomburgkii* *E. armatus* *A. forsteri* *A. elongata* **P. unicolor**	***H. vittatus*** ***S. robustus*** ***A. ogilbyi*** ***S. bassensis*** ***S. vittata*** ***R. sarba*** ***A. forsteri*** ***L. platycephala*** *P. unicolor*	***S. robustus*** ***C. macrocephalus*** ***A. ogilbyi*** ***P. humeralis*** ***S. bassensis*** *A. forsteri* ***L. platycephala*** *P. unicolor* ***E. australis***	***S. robustus*** *A. ogilbyi* *P. humeralis* *T. bailloni* *A. forsteri* *L. platycephala* **T. pleurogramma** ***I. rhothophilus***	
(b) Night		(max. $\rho = 0.951$)			
		A. ogilbyi *P. humeralis* *S. cephalotes* ***S. bassensis*** *S. schomburgkii* *S. vittata* *A. georgiana* *P. saltatrix* *R. sarba* *M. cephalus* *L. platycephala* *P. unicolor* *S. granulatus* *T. pleurogramma* ***A. vincentiana*** ***T. mucosa***			
(c) Day & Night					(max. $\rho = 0.959$)
					S. robustus ***A. ogilbyi*** *P. humeralis* ***S. bassensis*** *S. schomburgkii* ***S. vittata*** ***G. subfasciatus*** ***R. sarba*** *A. forsteri* ***L. platycephala*** ***P. unicolor***

Day

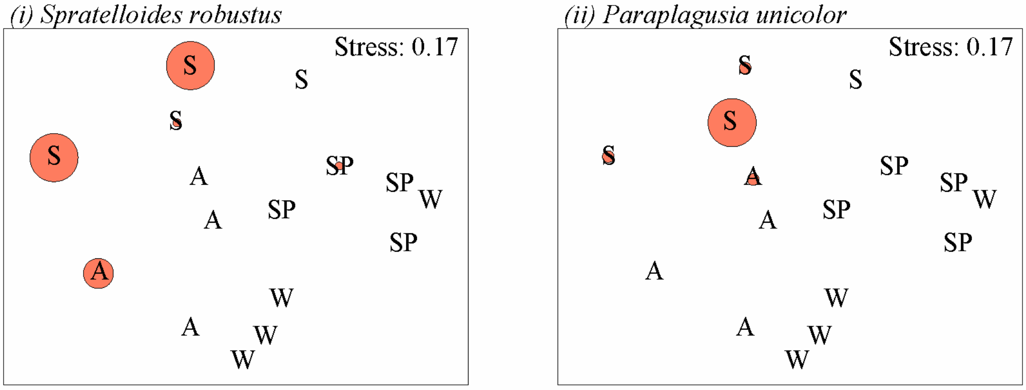
(a) Habitat type 2



(b) Habitat type 3



(c) Habitat type 4



(d) Habitat type 5

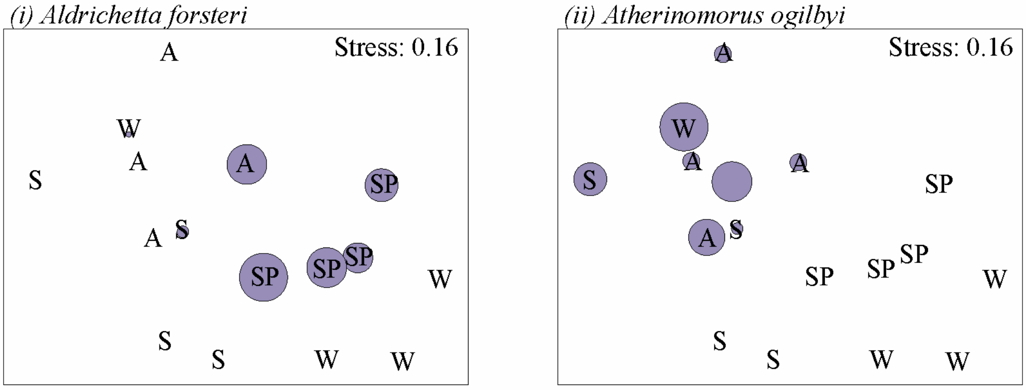


Figure 6.7: Two-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 21.5 m net during the day in each season between summer 2000 and spring 2001 at habitat type (a) 2, (b) 3, (c) 4 and (d) 5. Each sample has been coded for season (S=summer, A=autumn, W=winter and SP=spring). The size of the circles overlaid on each sample reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine.

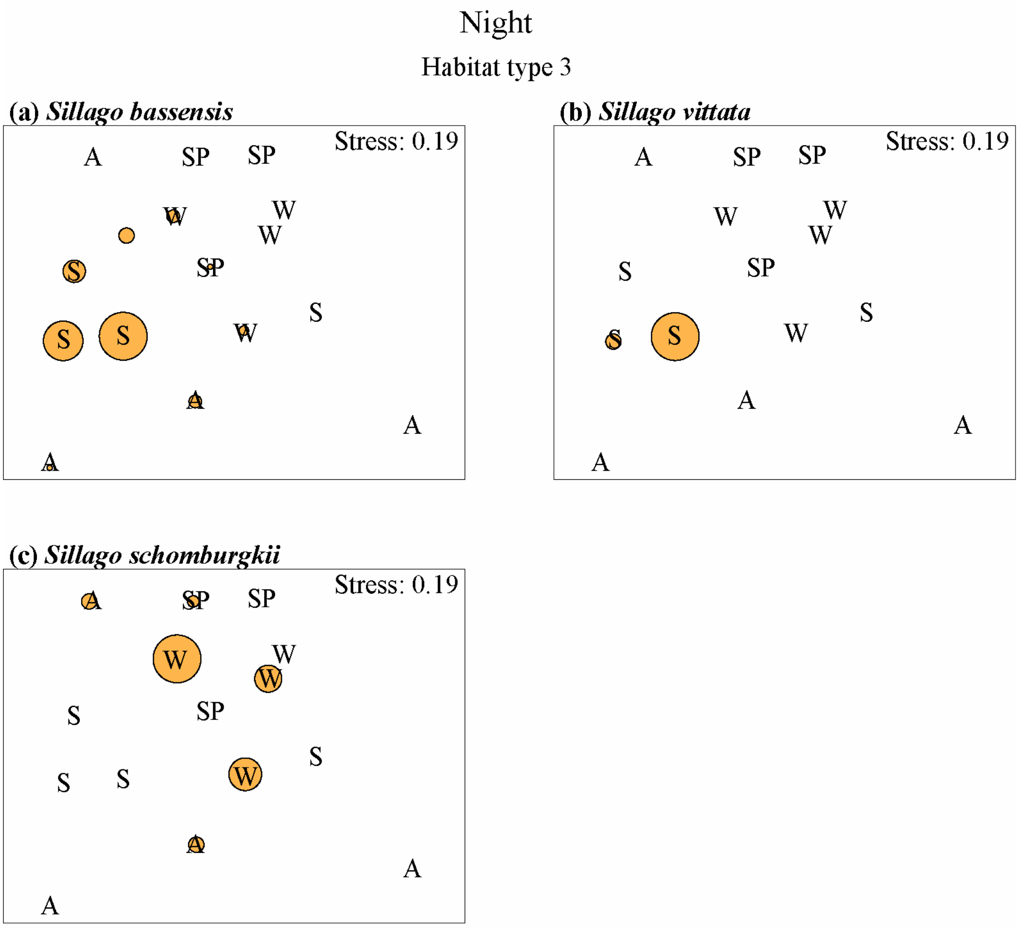


Figure 6.8: Two-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 21.5 m net during the night in each season between summer 2000 and spring 2001 at habitat type 3. Each sample has been coded for season (S=summer, A=autumn, W=winter and SP=spring). The size of the circles overlaid on each sample reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine.

those collected during either the day or night at habitat types 2-5 (*cf* Figs 6.6f and a-e). These results were reinforced by the relatively low Global R-statistic in the one-way ANOSIM test for this habitat type, *i.e.* 0.299 *vs* 0.547-0.367 (Table 6.2c *vs* a and b). However, six of the eight samples collected during summer at this habitat type formed a tight group that was largely discrete from those collected in winter and spring. Moreover, the samples for winter also formed a relatively tight group that lay almost entirely within those from spring (Fig. 6.6f). As was the case in other habitat types, the samples collected during autumn were the most dispersed (Fig. 6.6f). However, ANOSIM showed that all pairwise comparisons between the various seasons were significant (p=0.1-0.9%), except for that between winter and spring (p=88.8%), and that the greatest differences in ichthyofaunal composition were between summer and winter (R=0.481; Table 6.2c). SIMPER showed that the ichthyofauna in each of the different seasons at this habitat type was typified by between one and three species, which invariably included *L. platycephala*. *Sillago bassensis* was also caught regularly in summer and autumn, and schools of *S. vittata* were prevalent in the first of these seasons. The results of this analysis are described fully in subsection 5.3.2.3. The subset of species that were most important for distinguishing the ichthyofauna in the samples collected seasonally at habitat type 6 is provided in Table 6.4c, and the densities of examples of these species are overlaid on the points in the ordination plot containing the samples from this habitat type. These plots showed that *S. bassensis* and *S. vittata* were both caught almost entirely in summer (Figs 6.9a and b, respectively).

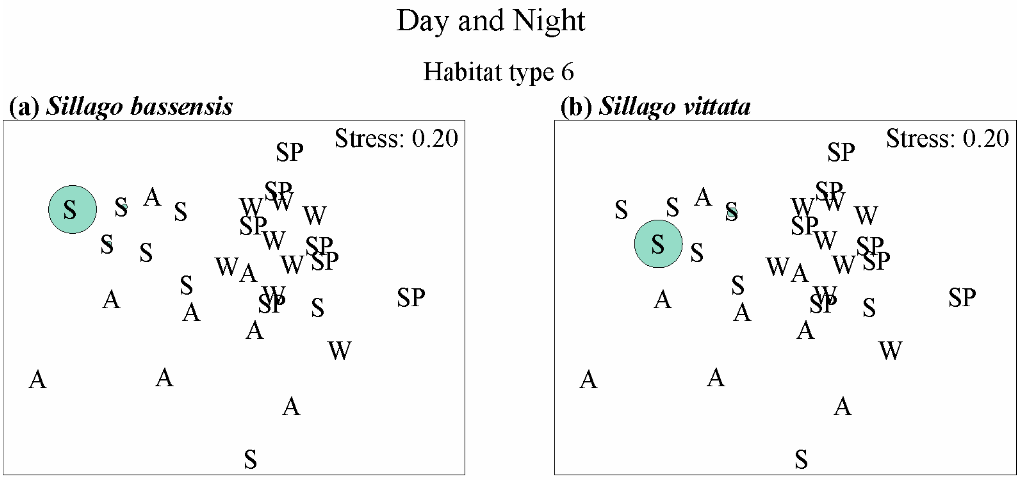


Figure 6.9: Two-dimensional MDS ordination of the mean densities of the various fish species in samples collected with the 21.5 m net during the day and night in each season between summer 2000 and spring 2001 at habitat type 6. Each sample has been coded for season (S=summer, A=autumn, W=winter and SP=spring). The size of the circles overlaid on each sample reflect the magnitude of the mean density of examples of species selected by the BVSTEP routine.

6.3.3 Differences in non-enduring environmental characteristics in different seasons, years and/or between day and night

The results of ANOVA of the data for water temperature and volume of detached macrophytes on the beach face recorded at the six habitat types during the day and/or night in each season between summer 2000 and 2002 are presented in Table 4.1c and described fully in subsection 4.3.2. In general, these analyses showed that the differences in water temperature were greatest among seasons, followed by day *vs* night then habitat type, and that several of the interactions between these three factors, and also year, were also significant. The volume of detached macrophytes differed to the greatest extent among habitat types, followed by season, and the interaction between these two main effects was significant.

6.3.4 Relationships between temporal differences in ichthyofaunal composition and non-enduring environmental characteristics

6.3.4.1 Water temperature

The extent of any significant relationships between temporal differences in the composition of the ichthyofauna and those in water temperature were examined separately for each of those habitat types at which significant seasonal and/or diel differences in ichthyofaunal composition had previously been detected, *i.e.* habitat type 4 in the case of samples collected with the large net and habitat types 2-6 for samples collected with the small net. Although ANOVA also detected significant differences in water temperature for some interaction terms that included year, separate plots of the mean temperatures for 2000 and 2001 showed that the source of those interannual differences were either small or due to a single atypical value (see Fig. 4.4). Furthermore, the composition of the fish faunas collected in both the large and small nets did not differ significantly between years in any habitat type, season or diel period (see subsections 5.3.1.3 and 5.3.2.3, respectively). The samples collected in both years were thus treated as "replicates" in the following analyses.

RELATE was used to determine the extent of any significant correlation between (1) a Bray-Curtis similarity matrix constructed from the densities of the various fish species in samples collected with either the small or large net at a particular habitat type in the various seasons and, where appropriate, during either the day or night (*i.e.* those used to produce the ordination plots shown in Figs 6.2 and 6.6a-f), and (2) the complementary Euclidean distance matrix constructed from the mean water temperatures recorded at the same habitat type on the same sampling occasions (*i.e.* those used to produce the ordination plots shown in Figs 6.11a-f). In those cases in which RELATE detected a significant and relatively high correlation between the above matrices, BVSTEP was then used to ascertain which subset of species from the initial full suite recorded in a particular net and habitat type provided the best match with the corresponding temperature matrix. These species thus represented those whose seasonal differences in abundance best matched the seasonal differences in water temperature at that habitat type.

RELATE demonstrated that the extent of the ichthyofaunal differences between samples collected seasonally with the large net at habitat type 4 was significantly correlated with the seasonal differences in the day-time water temperatures at that habitat type, *i.e.* $p=0.1\%$; $\rho=0.440$ (*cf* ordination plots in Fig. 6.2 and 6.10c, respectively). BVSTEP demonstrated that a subset of 13 species were most responsible for providing this significant match between the above matrices, *i.e. Spratelloides robustus, Cnidoglanis macrocephalus, Pelsaria humeralis, Siphamia cephalotes, Platycephalus speculator, Sillago vittata, Arripis georgiana, Rhabdosargus sarba,*

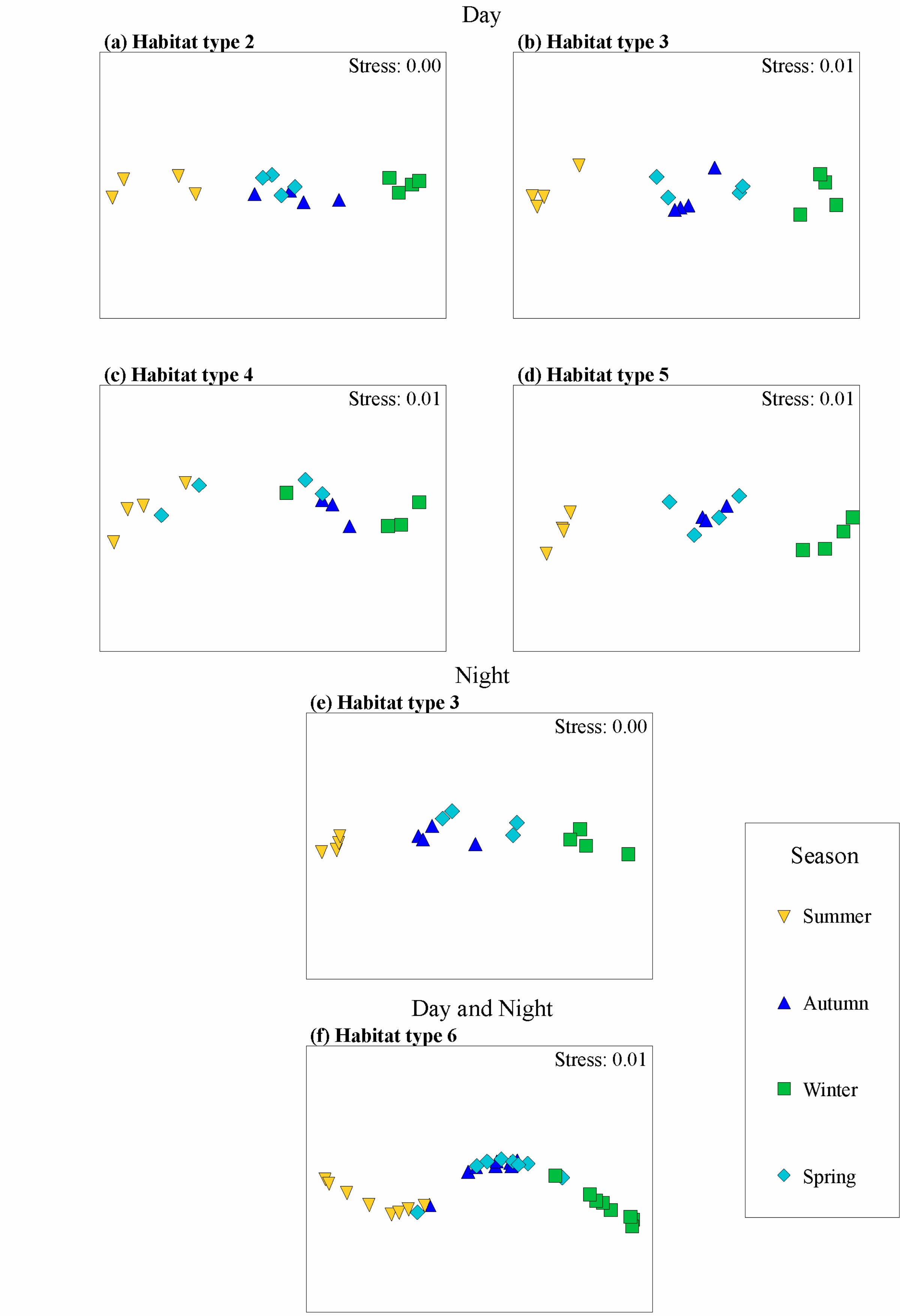


Figure 6.10: Two-dimensional MDS ordination of the mean water temperatures recorded during the day at habitat type (a) 2, (b) 3, (c) 4 and (d) 5, (e) at night at habitat type 3, and (f) during the day and night at habitat type 6 between summer 2000 and spring 2001.

Mugil cephalus, Callionymus goodladi, Sphyraeana obtusata and *Pseudorhombus jenynsii*. Moreover, the correlation between this subset of species and the temperature matrix was considerably higher than that when all species recorded at habitat type 4 in the large net were used (*i.e.* ρ=0.668 *vs* 0.440). The relative densities of examples of the above species are overlaid as circles on the samples in the ordination plot of the seasonal temperatures at this habitat type in Figs 6.11a-d. Thus, the greatest catches of species such as *S. vittata* at habitat type 4 were clearly associated with water temperatures recorded in summer, while greater numbers of *C. macrocephalus* and *R. sarba* were associated with the intermediate temperatures recorded in autumn. *Arripis georgiana* was caught in higher numbers in winter when water temperatures had declined to their annual minima (Figs 6.11a, b, c and d, respectively).

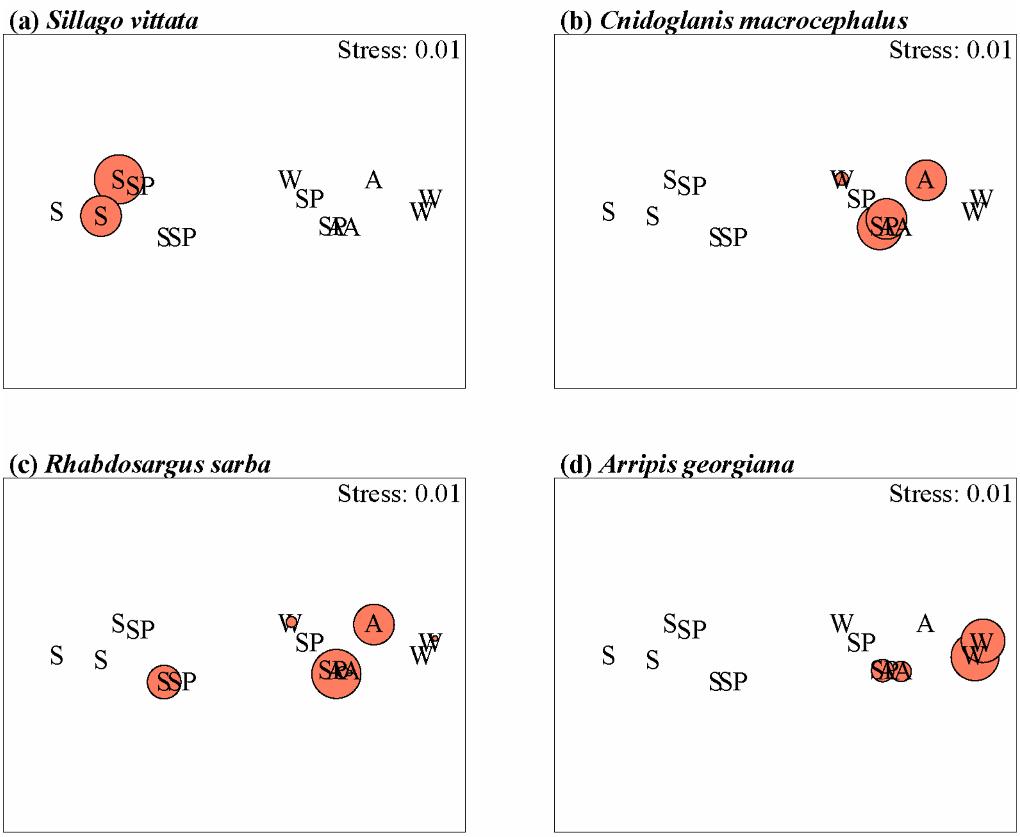


Figure 6.11: Two-dimensional MDS ordination of the mean water temperatures recorded at habitat type 4 during the day in each season between summer 2000 and spring 2001. The mean density of examples of species selected by the BVSTEP routine from samples collected with the 60.5 m net at the same habitat type, are overlaid as circles of proportionate sizes on the points representing each sampling occasion.

When the similarity matrices that were produced from the ichthyofaunal samples collected with the small net during the day in each season at habitat types 2, 3, 4 and 5 were matched with the complementary matrices constructed from the day-time water temperatures at those habitat types, a significant correlation was detected only in the case of habitat types 2 and

4, *i.e.* p=2.9 and 2.0%, respectively. However, the extents of these significant correlations were low, *i.e.* ρ=0.230 and 0.198, respectively. Likewise, when the similarity matrices constructed using the ichthyofaunal data from small net samples collected in each season at night in habitat type 3 and during the day and night at habitat type 6 were each matched with the complementary temperature matrices, a significant correlation was detected only in the case of the latter habitat type (p=4.9%), and the extent of that correlation was low, *i.e.* ρ=0.126. The use of BVSTEP in the above cases where a significant correlation was detected between a fish and temperature matrix showed little improvement in the extent of ρ.

6.3.4.2 Detached macrophytes

RELATE detected a significant but relatively low correlation between the similarity matrix constructed using the ichthyofaunal data from samples collected seasonally with the large net at habitat type 4 (see Fig. 6.2) and the complementary distance matrix constructed from the detached macrophyte data recorded at that habitat type (see Fig. 6.12c), *i.e.* p=1.3%, ρ=0.247. The use of BVSTEP showed that this correlation was improved when a selected subset of 14 species was used to construct a similarity matrix, rather than the initial full suite of species, *i.e.* ρ=0.529. These species were *C. macrocephalus, Sillago schomburgkii, Scobinichthys granulatus, Cristiceps aurantiacus, S. vittata*, *S. robustus, Mitotichthys meraculus, Pomatomus saltatrix, Upeneichthys lineatus, Upeneus tragula, Sphyraena novaehollandiae, Parapegasus natans, Lesueurina platycephala* and *Contusus brevicaudatus,* and the relative densities of examples of these species are superimposed as circles of proportionate sizes on the samples in the MDS plot of the detached macrophyte data at habitat type 4 (Figs 6.13a-d). These plots showed that greater densities of weed-associated species such as *C. macrocephalus* and *S. granulatus* were recorded in autumn and winter (*i.e.* when the greatest volumes of detached macrophytes were recorded at this habitat type; Figs 6.13a and b, respectively), while others such as *S. vittata* were most abundant in summer when the volume of detached weed was low (Fig. 6.13d).

No significant correlations were detected between the matrices produced from the small net data collected during the day in each season at habitat types 2-5 and the complementary matrices constructed from the detached macrophyte data.

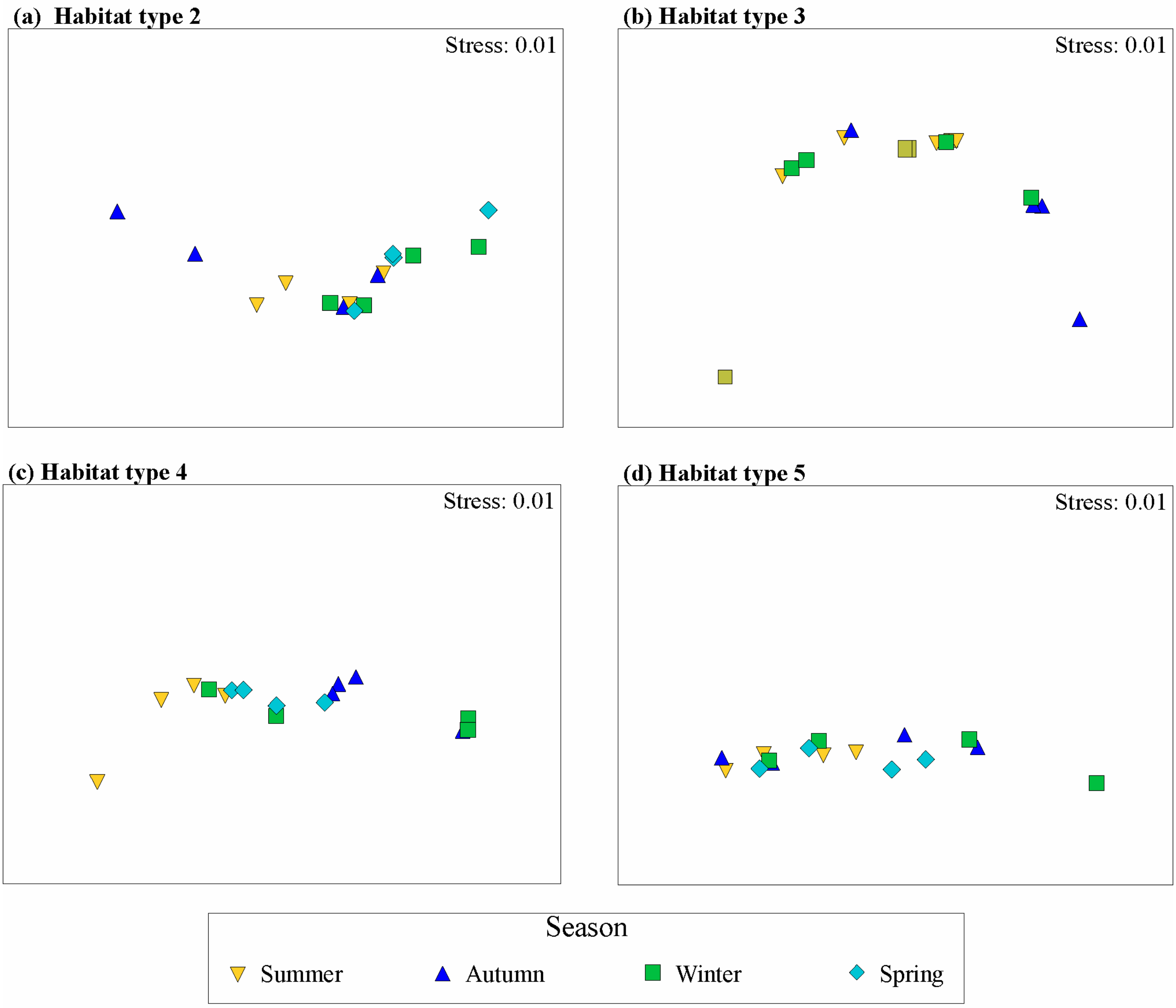
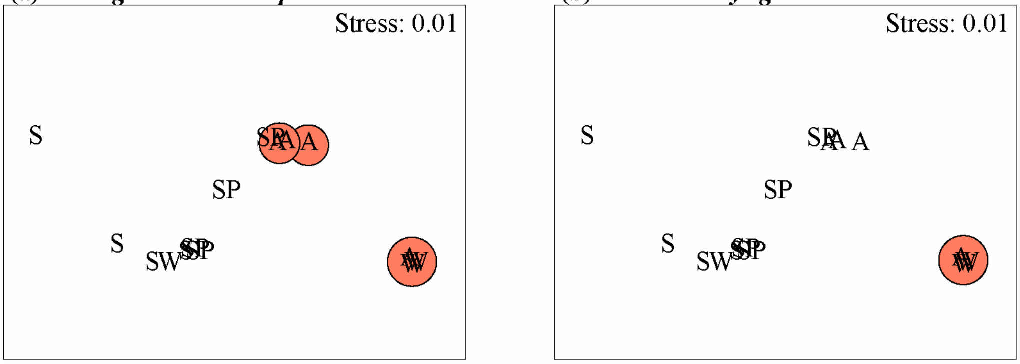


Figure 6.12: Two-dimensional MDS ordination of the mean volume of detached macrophytes recorded during the day at habitat type (a) 2, (b) 3, (c) 4 and (d) 5 between summer 2000 and spring 2001.

(a) ***Cnidoglanis macrocephalus*** **(b)** ***Scobinichthys granulatus***



(c) ***Sillago schomburgkii*** **(d)** ***Sillago vittata***

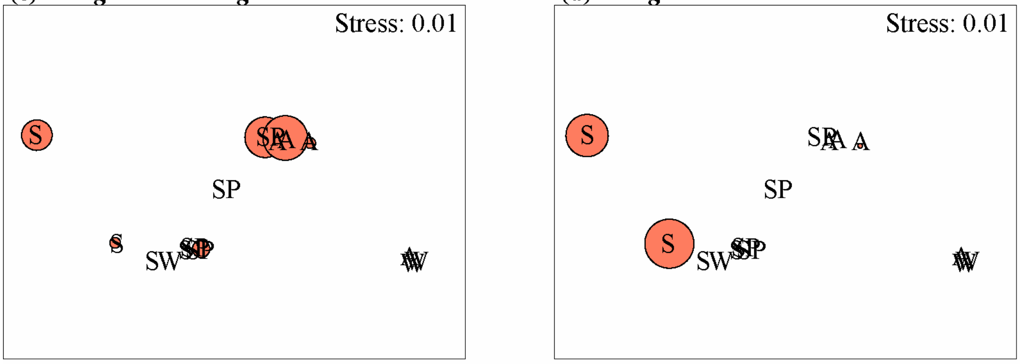


Figure 6.13: Two-dimensional MDS ordination of the mean volume of detached macrophytes recorded at habitat type 4 during the day in each season between summer 2000 and spring 2001. The mean density of examples of species selected by the BVSTEP routine from samples collected with the 60.5 m net at the same habitat type, are overlaid as circles of proportionate sizes on the points representing each sampling occasion.

6.4 Discussion

6.4.1 Extent of diel differences in ichthyofaunas at different habitat types

6.4.1.1 Diel differences in ichthyofaunal compositions at habitat types 2-5

On the basis of samples collected using the 21.5 m seine net, the compositions of the nearshore fish fauna, differed significantly between the day and night in four of the six habitat types, *i.e.* 2-5. These significant diel differences were attributable to one or both of the following.

1) Large influxes of small 0+ recruits of particular species into the shallow waters close to shore at those habitat types during the day, and their emigration offshore to slightly deeper waters at night.
2) Nocturnal migration inshore of the adults and sometimes juveniles of other species at night, and their emigration offshore during the day.

Thus, small 0+ *Spratelloides robustus, Sillago vittata* and *Atherinomorus ogilbyi* were each caught in far greater numbers during the day than night in the shallows close to shore in particular seasons at habitat types 2-4, and small juvenile *Hyperlophus vittatus* and *Aldrichetta forsteri* were also far more abundant in samples collected during the day than night at habitat types 2 and 3. For example, the mean density of *S. robustus* at habitat type 2 in any season was as high as 313.2 fish 100 m^{-2} during the day, but only 0.1 fish 100 m^{-2} at night. Furthermore, the maximum mean seasonal density of *H. vittatus* at habitat type 3 was 706.5 fish 100 m^{-2} during the day, compared to 1.4 fish 100 m^{-2} at night. The nocturnal emigration of the juveniles of the above species to slightly deeper waters at habitat types 2, 3 and/or 4 is likely to be related to one or more of the following.

(i) A reduction at night in both the availability of prey and the ability to detect prey visually.

The major prey items of juveniles of the pelagic species *S. robustus, S. vittata* and *A. ogilbyi* at the moderately sheltered to exposed habitat types along the lower west coast of Australia, *i.e.* calanoid copepods and/or cladocerans (Schafer *et al.* 2002, Hourston *et al.* submitted, Chapter 11), are most available in the water column during the day (Chapters 8 and 10). Thus, the abundant day-time catches of these juvenile fish at particular habitat types, which also accounted for the tendency of the overall number of fish at those habitat types to be greater during the day than night, coincides with the time when large numbers of these invertebrates migrate vertically from the substrate into the water column. Furthermore, as each of the above fish species have well-developed eyes and are thus presumably visual predators, their ability to locate these small and transparent prey would be greatly reduced at night.

(ii) *Avoidance of piscivorous fish.*

Some piscivorous fish were consistently more abundant in the shallow inshore waters at night (*e.g.* adult *Arripis georgiana* at habitat types 2 and 3), and others, although not caught regularly or in large numbers at habitat types 2-5, were only recorded at night, *e.g.* adult *Pseudocaranx dentex* and *Sphyraena novaehollandiae* at habitat type 2, and *Trachurus novaezelandiae* at habitat types 2 and 3. The concomitant emigration undertaken by small fish to slightly deeper waters would thus reduce the risk of being subjected to predation by these larger species. The nocturnal onshore movement of these piscivorous fish contributed to the consistently greater mean number of species, average taxonomic distinctness and variation in taxonomic distinctness in samples collected at night than during the day in habitat types 2-5. It should also be recognised that, due to the ability of these larger fish to swim fast, their numbers in those night-time samples probably do not represent their true relative abundance in the shallows at that time. Numerous other workers have also reported a greater occurrence of larger piscivorous fish in nearshore marine waters at night (*e.g.* Ross *et al.* 1987, Wright 1989, Gibson *et al.* 1998, Layman *et al.* 2000). However, in contrast with the results obtained in the present study, some workers have recorded greater numbers of small juvenile fish in the shallows at night than during the day, *e.g.* Modde and Ross 1981, Burrows *et al.* 1994, Gibson *et al.* 1998. This difference in findings is partly attributable to the differences in the morphology and position within the water column occupied by the fish in these studies. Thus, while the latter two of the above studies focused on the diel movements of benthic-dwelling flatfish, which would be able to occupy the very shallow waters close to the shoreline at night and thus be inaccessible to larger piscivorous fish, the juvenile fish that exhibited nocturnal emigrations from the shallows in the current study are pelagic and would not be able to occupy such shallow water.

(iii) *More suitable environmental conditions when not feeding.*

The less turbulent waters slightly offshore of the wave-breaking zone in nearshore areas are likely to be less physically demanding for small fish to maintain a suitable position in the water column while they are inactive (Clark *et al.* 1996b, Layman 2000).

Although the diel movement patterns of juvenile *S. vittata, A. ogilbyi* and *A. forsteri* were similar at each of the habitat types in which they were abundant, those of juvenile *H. vittatus* and *S. robustus* differed at particular habitat types. Thus, although the first of these clupeid species was caught in much greater numbers during the day than night in the small net at habitat types 2 and 3, the reverse was true at habitat type 4. It is noteworthy that the largest night-time catches of these juveniles at habitat type 4 were almost always associated with large volumes of detached and broken weed, which would presumably provide these fish with shelter from nocturnally-active piscivores. Moreover, while juvenile *S. robustus* were present in large numbers during the day in the shallows at habitat types 2-4, but were virtually absent from those waters at night, the reverse was true at habitat type 1 and, to lesser extent, at habitat type 5. The fact that *S. robustus* was caught in only low numbers in both net types during the day at habitat type 1, both of which were used to sample over the seagrass beds and bare substrate present in those waters, suggests that this species resided a considerable distance from shore at that time, *i.e.* among seagrass beds in slightly deeper waters. The difference in the diel pattern of occurrence of *S. robustus* between habitat types is probably related to the fact that the susceptibility of this small species to predation by birds during the day would be far greater in the especially shallow and sheltered waters found at habitat type 1 than at other more exposed habitat types that contain a wave-breaking zone and thus provide shelter for those small fish among suspended sand and wave swash. Furthermore, the risk for *S. robustus* of being preyed upon at night is substantially less in habitat type 1, since the shallowness of these waters precludes the occurrence of many large piscivorous fish. It is also probable that the nearshore reefs at habitat type 5 would also provide shelter for *S. robustus* during the day, and the moderate number of this species recorded over adjacent sand areas at night in this habitat type may reflect their use of these areas for foraging.

Other species, which are not predominantly piscivorous, were caught more consistently and in greater numbers in the shallow waters close to shore at night in habitat types 2, 3, 4 and/or 5, *i.e. Rhabdosargus sarba* and *Paraplagusia unicolor* at habitat types 2 and 3, *Sillago schomburgkii* at habitat types 2-4, *Cnidoglanis macrocephalus* at habitat types 2-5 and *Pelsartia humeralis* and *Schuettea woodwardi* at habitat types 4 and 5. A major value of the nocturnal onshore migration undertaken by these species, many of which were adults or large juveniles, is that it exposes these species to a greater availability of their preferred invertebrate prey. For example, polychaetes represent a major component of the diet of *S. schomburgkii* (Hyndes *et al.* 1997, Chapter 11), the more errant forms of which are usually more active at night (Alldridge and King 1980, 1985, Jacoby and Greenwood 1989). Furthermore, when the tidal height along this coastline is higher at night, *i.e.* during spring, summer and the first half of autumn (Department for Planning and Infrastructure 2003), these larger fish are more able to access sedentary invertebrate prey located in the intertidal zone that is covered only by wave swash during the day. Bivalves, for example, which comprise a large proportion of the diet of *C. macrocephalus* at night (Robertson and Lenanton 1984), occur in the greatest densities in the swash zone of the more exposed habitat types along the lower west coast of Australia (Chapter 7), and would be more accessible for this fish species during higher tides. Foraging over bare sand areas at night also reduces the risk of predation by avian piscivores in the case of species such as *C. macrocephalus* and *P. humeralis,* both of which are known to be preyed on by cormorants along the lower west coast of Australia (Robertson and Lenanton 1984).

6.4.1.2 Lack of diel differences in ichthyofaunal compositions at habitat types 1 and 6

The lack of a significant diel difference in ichthyofaunal composition at habitat type 1 was probably attributable to the fact that seagrass and sand substrates were both sampled with the small net during the day and night at this habitat type. Thus, species that tend to exhibit diel movements between these vegetated and unvegetated areas (*e.g.* to forage over bare sand at night or to shelter within seagrass beds during the day) would have been collected at both times. Yet, the fact that both the mean number of species and the two species relatedness indices were greater in night-time samples implies that some species are more active and thus particularly susceptible to capture at this time. However, as most of these species (which include several that usually shelter within seagrass beds during the day, *e.g. Parapercis haackei* and *Histiogamphelus cristatus*) tend to be solitary, they were not present in sufficient numbers at night to lead to a significant diel difference in the overall composition of the ichthyofauna at this habitat type. Other workers have also reported a significantly greater number of fish species at night over nearshore unvegetated areas that are adjacent to seagrass, and have attributed such results to the nocturnal feeding activity of species that inhabit vegetated areas during the day, *e.g.* Travers and Potter (2002). Moreover, the overall density of fish in habitat type 1 was considerably greater at night than during the day, which was due mainly to very large catches of *Leptatherina presbyteroides* in all seasons. The nocturnal increase in abundance of this pelagic species is probably attributable to the fact that a large proportion of its diet consists of small benthic crustaceans (Prince *et al.* 1982), many of which migrate into the water column at night in this habitat type (Chapters 8 and 10). However, while this species was less abundant during the day at this habitat type, it was still present in relatively high numbers in most seasons, thereby reducing the tendency for such results to produce significant differences between the day and night-time fish assemblages.

In contrast to the situation at habitat type 1, the lack of significant diel differences in composition of the ichthyofauna at the exposed habitat type 6 is largely attributable to the fact that the majority of the samples collected from this habitat type during both the day and night contained few fish and a small number of species that, in most cases, were not taxonomically diverse. Indeed, most samples collected at habitat type 6 were characterised almost entirely by *Lesueurina platycephala* and, to a lesser extent, *Sillago bassensis*, both of which are typically found in more exposed nearshore waters (Gommon *et al.* 1994, Ayvazian and Hyndes 1995, Hyndes *et al.* 1996a), In the case of the first of these species, the apparent lack of diel onshore/offshore movements is probably related to the fact that its cryptic coloration, small size and tendency to burrow into the sand would make it very difficult to be detected by visual predators such as *Sphyraeana obtusata* and *A. georgiana,* which were caught only at night in this exposed habitat type. Moreover, while *S. robustus* and *S. vittata* were both recorded in large numbers during the day at habitat type 6 and were both either virtually absent or present in much lower numbers at night in this habitat type, the failure of such results to produce significant diel differences in the ichthyofaunal composition at this habitat type is almost certainly due to the fact that most of these individuals were caught in a very restricted number of samples, *e.g.* 97% of *S. robustus* recorded at habitat type 6 were collected in just two replicate samples. The contribution of such atypical catches to the overall ichthyofauna at a habitat type would thus be heavily down-weighted in the dispersion-weighting procedure that was carried out prior to multivariate analyses.

6.4.2 Seasonal differences in ichthyofaunal characteristics

The seasonal differences that were detected in the mean density of fish and the composition of the ichthyofauna in particular habitat types along the lower west coast of Australia were related mainly to the far greater abundances of the juveniles of various species that occurred at certain times of the year. These included the recruits of those fish species that use nearshore environments as nursery areas, and of others that are nearshore residents but are particularly abundant in the season(s) following their spawning. However, the extent of seasonal differences in the composition of fish assemblages in these coastal waters varied with habitat type and usually also with whether the samples were collected using the 60.5 or 21.5m seine net. Moreover, in the case of samples collected with the smaller net, the extent of seasonal differences in ichthyofaunal composition at the various habitat types also differed between day and night. The following subsections explore the basis for the significant seasonal differences in the composition of the nearshore fish assemblages in the study region, and in the number of fish species, species diversity and taxonomic structure of the samples in those waters.

6.4.2.1 Seasonal differences in ichthyofaunal characteristics of large net samples

The marked seasonal differences that were detected in the ichthyofaunal composition of samples collected with the 60.5 m net at habitat type 4 were due either to large catches of the juveniles of particular species in one or two seasons, or to more consistent catches of some species at certain times of the year. The ichthyofauna during summer at this habitat type was particularly distinctive and was characterised by large catches of juvenile *S. bassensis, S. vittata* and *S. robustus*, which contributed to the significantly greater overall density of fish recorded in samples collected during this season. The large summer-time catches of small juveniles of the former two whiting species is consistent with the fact that, along the lower west coast of Australia, the adults of these species spawn between October and March (Hyndes and Potter 1996, Hyndes *et al.* 1996a, b). The timing of such spawning events also coincides with the presence of particularly high abundances of planktonic calanoid copepods and/or cladocerans, which are the preferred invertebrate prey of the juvenile fish in nearshore waters along the lower west coast of Australia (Chapters 8, 10 and 11, Schafer *et al.* 2002). Large catches of other species also typified the fish fauna in large net samples at habitat type 4 in seasons other than summer. For example, *A. forsteri* was caught in relatively large numbers only during autumn, while schools of *H. vittatus* characterised the ichthyofauna in all seasons except summer. However, while the latter species was represented mainly by adults in autumn, its juveniles were far more abundant in winter and spring. The occurrence of new 0+ recruits of *H. vittatus* in winter and spring reflects the fact that the spawning period of this species along the lower west coast of Australia peaks in June and July (Gaughan *et al.* 1996).

It has been widely reported that intraannual changes in water temperature are one of the most important environmental influences on the time of spawning of many fish species (*e.g.* Clark *et al.* 1996b, Hyndes and Potter 1996, Fairclough *et al.* 2000, Kokita and Nakazono 2000). The peak spawning time of many fish species along the lower west coast of Australia coincides with those times of the year at which water temperatures are either declining most rapidly, *i.e.* late autumn/early winter, *e.g. A. georgiana* (Fairclough *et al.* 2000), *Sillaginodes punctata* (Hyndes *et al.* 1998), *H. vittatus* (Gaughan *et al.* 1996), and *A. forsteri* (Chubb *et al.* 1981), or rising towards the annual maxima, *i.e.* late spring/early summer, *e.g. S. vittata* and *S. bassensis* (Hyndes and Potter 1996, Hyndes *et al.* 1996b). The significant and relatively high correlation between the seasonal changes in water temperature at habitat type 4 and the seasonal differences in the ichthyofaunal composition of samples collected with the large net at this habitat type thus concurs with these previously reported findings.

Several other species were caught more consistently in the large net during particular seasons at habitat type 4, although not in especially large numbers. For example, *P. humeralis, C. macrocephalus* and *S. woodwardi,* which are particularly well camouflaged for living in floating accumulations of detached macrophytes, where they feed on amphipods associated with this plant material (*e.g.* Lenanton *et al.* 1982, Robertson and Lenanton 1984, Ochieng and Erftemeijer 1999), were characteristic of the fish assemblage at this habitat type only during autumn. The more consistent catches of these species in this season coincides with the particularly large volume of detached seagrass and algae that were deposited on the beach face at habitat type 4 in this season, the majority of which would probably have originated from the extensive seagrass and macroalgal beds located slightly offshore at this habitat type (Hansen 1984). The association of seasonal differences in the composition of the ichthyofauna with seasonal differences in the quantities of detached macrophytes at habitat type 4 was also supported by the significant correlation between these data at this habitat type.

The lack of significant seasonal differences in ichthyofaunal composition at the other three habitat types sampled with the large net was attributable to two main reasons. Firstly, some of the species whose abundance varied markedly among seasons at habitat type 4 were far less prevalent in the other habitat types. For example, the density of *S. bassensis* during summer at habitat type 4 was between six and 215 times greater than in habitat types 1-3 in the same season, presumably reflecting the affinity of this species for nearshore waters that are relatively exposed to wave activity (Hyndes *et al.* 1996a) and the fact that amphipods, which have been found to represent a large part of the diet of juvenile *S. bassensis* (Hyndes *et al.* 1997), are strongly associated with more exposed coastal waters (Chapter 7) and contain detached macrophytes (Lenanton *et al.* 1982). Secondly, many of the species that characterised the assemblages in each of the other three habitat types were relatively numerous throughout the year. For some of these species, the lack of marked seasonal variation in the abundance is due to their being resident in those habitats, *e.g. Favonigobius lateralis, Pseudorhombus jenynsii, L. presbyteroides* and *Haletta semifasciata*, each of which typified the highly sheltered habitat type 1. However, several of the other species that characterised the fish assemblages at habitat types 1-3 included those that use nearshore waters as nursery areas, *e.g. R. sarba* and *Sillago burrus* in habitat type 1 and *S. vittata* at habitat types 2 and 3. While the young juveniles of such species recruited into these habitat types during particular seasons, they then usually remained in those areas for the rest of the year, and thus their numbers did not undergo marked intraannual fluctuations. The fact that *S. vittata* occurred consistently in at least three of the four seasons in the samples collected at the latter habitat types, whereas it was only abundant in summer at habitat type 4, indicates that, although the small juveniles of this species recruit into the nearshore waters of that relatively exposed habitat type, they have a greater affinity for and/or chance of survival in the less exposed waters at habitat types 2 and 3. These findings concur with those of Hyndes *et al.* (1996a).

6.4.2.2 Seasonal differences in ichthyofaunal characteristics of small net samples

(i) Day

As with the samples collected in the large net, the number and diversity of fish species in samples collected using the small net during the day were generally greater in summer than winter at most habitat types, probably reflecting the more favourable conditions for growth for a greater range of species at that time of year, *e.g.* warmer water temperatures and lower wave activity. Moreover, significant differences in the ichthyofaunal composition of samples collected with the small net during the day were detected among seasons at habitat type 4, and no such differences were detected at habitat type 1. However, in contrast to the situation with the fish fauna caught using the 60.5 m net, the composition of the day-time samples collected with the 21.5 m net also differed significantly among seasons at habitat types 2 and 3.

Several of the species that were responsible for the significant seasonal differences in composition of the day-time samples obtained with the small net at habitat type 4 were similar to those that produced seasonal differences in the large net samples at this habitat type. Thus, juvenile *S. robustus* and *S. bassensis, S. vittata* were each abundant in summer and were either not recorded, or were recorded in appreciably lower numbers, in the other seasons. However, juvenile *A. ogilbyi* and *H. vittatus* were also relatively abundant in the small net samples collected in summer and spring at habitat type 4, and these small fish, like the juveniles of the above species, feed extensively on cladocerans and calanoid copepods during the day (Goh 1992, Chapter 11), which are particularly abundant in the nearshore waters along the lower west coast of Australia during this season (Chapters 8 and 10). Both of these species were caught more consistently throughout the year in the large net at this habitat type.

The significant seasonal differences in the composition of the fish fauna collected in the small net during the day at habitat types 2 and 3 were also mainly attributable to marked influxes of juveniles of each of the above species during the same seasons. However, the abundance of some of these species, such as *H. vittatus* and *A. ogilbyi*, were markedly greater in these two less exposed habitat types than at habitat type 4. Moreover, juvenile *A. forsteri* recruited into the shallows of habitat types 2 and 3 from autumn to spring, while juvenile *L. platycephala* were particularly abundant in winter and spring in the samples collected at the moderately exposed habitat type 3. While these results for the latter species presumably reflects its affinity for more exposed nearshore waters (Gommon *et al.* 1994, Ayvazian and Hyndes 1995), the greater abundance of its juveniles at habitat type 3 than the more exposed habitat type 4 most likely reflects the greater survival of these small 0+ fish in waters that are not too exposed.

Although each of the above species were also relatively abundant in samples collected with the large net at habitat types 2 and 3, they were caught more consistently throughout the year in that net rather than mainly in particular seasons. For some of these species, this suggests that after their small juveniles have recruited into the shallower waters close to shore in particular seasons (*i.e.* where they were captured mainly in the small net), they emigrate after a relatively short time into slightly deeper waters (*i.e.* where they were caught mainly in the large net) and remain there for much of the year. For example, newly-recruited *S. robustus* (median lengths of *ca* 35 mm) were caught in large numbers during summer at habitat type 2 in both the 21.5 and 60.5 m nets, but were considerably more abundant in the shallower waters sampled with the smaller of these nets, *i.e.* mean densities of 1566 and 525.3 fish 500 m^{-2}, respectively. However, few *S. robustus* were caught in the small net in subsequent seasons at this habitat type (*i.e.* mean densities of 1.0-6.5 fish 500 m^{-2}), whereas mean densities of 116.8 and 117.8 fish 500 m^{-2} (with median lengths of 37 and 67 mm, respectively), were recorded in samples collected with the large net in autumn and winter, respectively.

The fact that significant seasonal differences were detected in the ichthyofaunal composition of the day-time samples collected with the large and small nets at habitat type 4, but were detected only in samples collected with the latter net at habitat types 2 and 3, indicates that the newly-recruited juveniles of some species use both the deeper and shallower waters at the former habitat type in a similar way, whereas only the shallow waters closer to shore are used in a particularly seasonal manner by juveniles of certain species at the less exposed habitat types 2 and 3. These results are probably related to the more energetic wave-breaking and swash zones found at habitat type 4 than at those other two habitat types, which probably would have deterred, to some extent, the small 0+ recruits of certain species from occupying mainly those shallower areas close to shore. Thus, juvenile fish that recruit into this habitat type are also inclined to inhabit the slightly deeper and calmer waters seaward of the breaker zone, *i.e.* those waters sampled by the 60.5 m net on a more seasonal basis than at habitat types 2 and 3. This view is supported by the fact that, while high numbers of newly-recruited *S. bassensis* and *S. vittata* were recorded in both the small and large nets at habitat type 4 in summer, both species were caught much more consistently in the latter net type in this season. In contrast, both of these species were caught very consistently in each net type during summer at habitat types 2 and 3. Moreover, the marked decline in the catches of species such as *S. vittatus* and *S. robustus* after summer in both the small and large nets at habitat type 4 suggests that the juveniles of these species either emigrated to other nearshore habitats or did not survive. However, the relatively high and more consistent catches of both *S. vittatus* and *S. robustus* in the large net at the less exposed habitat types 2 and 3 throughout the year indicates that these habitats provide more suitable environments for these species.

(ii) *Night*

In contrast to the samples obtained during the day with the small net in the shallow waters close to shore, the composition of the fish fauna collected in these waters at night differed significantly among seasons only at habitat type 3. Moreover, the extent of the seasonal difference in ichthyofaunal composition at that latter habitat type was less at night than during the day. These results were attributable to the fact that, as mentioned earlier in subsection 6.4.1.1, many of the species that differed markedly in abundance among seasons during the day at habitat types 2-5, occurred in much lower numbers and/or more consistently in these habitat types at night.

However, juvenile *S. bassensis*, which occurred in relatively high numbers in summer at habitat type 3 during the day, were also particularly abundant in this season at night in this habitat type. Moreover, juvenile *L. platycephala*, which were recorded in relatively high numbers in winter and spring at habitat type 3 during the day, were also abundant in these seasons in the shallow waters at this habitat type at night. This finding is possibly related to the fact that cumaceans, which comprise part of the diet of the juveniles of this benthic species (Chapter 11), are particularly abundant in the shallows at habitat type 3 (Chapter 7) and are present in far greater numbers on the substrate surface at night (Chapter 10). Other species responsible for producing significant seasonal changes in the composition of the ichthyofauna at night in habitat type 3 included *S. schomburgkii* and *R. sarba*, both of which occurred more regularly in winter, and *C. macrocephalus*, which characterised the night-time ichthyofauna in each season in this habitat type except winter. Juvenile *P. unicolor* were also caught more consistently in autumn and summer, respectively. Possible reasons for the nocturnal onshore migration of many of the above species were provided in subsection 6.4.1.1.

(iii) *Day and night*

The overall extent of the seasonal differences in the composition of the ichthyofauna collected during the day and night at habitat type 6 was also relatively small, and many of these differences were due to relatively large influxes of juvenile *S. bassensis* and *S. vittata* in summer (*i.e.* median lengths of 53 and 40 mm, respectively). The distinct seasonality in the occurence of *S. vittata* in this exposed habitat type (*i.e.* 99% of the total catch was recorded in summer) paralleled that of this species in the moderately exposed habitat type 4, and it is probable that the physical conditions at habitat type 6 were also unsuitable for this species. Large numbers of juvenile *S. robustus* were also caught at habitat type 6 in summer and, while this species was the most abundant overall at this habitat type, it was not identified as a characteristic species by SIMPER. As mentioned in subsection 6.4.1.2, such results are attributable to the highly atypical occurrence of this species in these waters.

Chapter 7. Characteristics of the benthic macroinvertebrate assemblages in different habitat types

7.1 Introduction

Benthic macroinvertebrates are those invertebrates that inhabit the substrate of aquatic environments and are retained by a 500 µm sieve (Howard *et al.* 1989, Bennett 1992). They are a major source of food for fish in nearshore waters and thus constitute a very important component of the food webs in that type of environment (Hyndes *et al.* 1997, Platell and Potter 1998, Schaefer *et al.* 2002). The number of species, densities and diversity of intertidal and shallow subtidal benthic macroinvertebrate assemblages in the soft sediments of nearshore marine waters are typically inversely correlated with the extent to which those waters are exposed to wave action (*e.g.* Bally 1981, Dexter 1984, Defeo *et al.* 1992, Jaramillo and McLachlan 1993) and positively correlated with the extent to which the substrate supports attatched and detatched macrophytes (Edgar 1990, Frost 1999, Hutchings and Jacoby 1994). The values for these biotic variables in nearshore waters also vary with the degree to which the substrate is covered by water during a tidal cycle, typically increasing from the supralittoral to the subtidal zone (Knott *et al.* 1983, Fleischack and de Freitas 1989, McArdle and McLachlan 1992). The benthic macroinvertebrate assemblages in sheltered habitats tend to be dominated by soft-bodied deposit-feeding species, whereas those in relatively exposed habitats tend to contain more hard-bodied suspension-feeders (McLachlan *et al.* 1994, Barnes and Hughes 1998, Muniz and Pires 1999).

Seasonal changes in environmental variables, such as water temperature, sediment grain size and the amount of sedimentary organic material, are considered to influence the number of species, densities and diversity of macrobenthic assemblages either directly through affecting the species survival or indirectly through the timing of recruitment (Dexter 1979, Hutchings and Jacoby 1994). In reality, relatively few attempts have been made to examine seasonal variation in benthic macroinvertebrate assemblages, particularly among different types of sandy beach habitats within a geographical region, and previous studies have not detected strong seasonal trends (Dexter 1984, Morrisey *et al.* 1992, Constable 1999). Such results have been ascribed to a combination of inadequate replication within a season, *i.e.* one sampling time per season, coupled with limited knowledge regarding many of the species reproductive cycles and life history strategies, which in turn, has resulted in seasonal changes in benthic macroinvertebrate assemblages being confounded with finer-scale temporal changes and/or interannual changes (Dexter 1984, Morrisey *et al.* 1992).

The diversity of benthic macroinvertebrate assemblages has traditionally been measured using indices based on the number of species (*e.g.* Margalefs' index, Pielou's evenness index, Shannon-Weiner diversity index). However, the values derived for these indices do not account for differences in the overall taxonomic structure amongst various assemblages. This problem can be overcome by using average taxonomic distinctness and variation in taxonomic distinctness indices (Warwick and Clarke 1995), which consider diversity in terms of richness and evenness throughout the taxonomic hierarchy, respectively. The studies that have produced data on these two indices have focused on meiobenthic nematode assemblages and to a lesser extent macrobenthic invertebrate assemblages and have used these indices to explore the influence of environmental degradation or large-scale spatial variation on these components of the biota (Warwick and Clarke 1995, 1998, Clarke and Warwick 2001b, Arvanitidis *et al.* 2002, Warwick *et al.* 2002). In the case of such assemblages, the average taxonomic distinctness has been shown to reflect the extent of trophic diversity, as gauged by differences in feeding mechanisms. It is thus relevant that average taxonomic distinctness has been shown to vary amongst different types of habitat, with the values being lower for assemblages that inhabit sheltered muddy habitats than for those that live in clean well-flushed sands, since these differences reflect variations in the composition of the species in terms of their modes of feeding (Warwick and Clarke 1995).

Most of the limited numbers of studies aimed at determining the characteristics of the benthic macroinvertebrate assemblages of sandy beaches in Australia have been undertaken in the high-energy environments found on the east coast of this continent (Dexter 1983, 1984, 1985, James and Fairweather 1996, Barros *et al.* 2002, Rossi and Underwood 2002). However, the only one of these studies that incorporated seasonal sampling was that of Dexter (1984) on the lower east coast of Australia. The only published studies on the benthic macroinvertebrate assemblages of the low wave energy beaches of south-western Australia have focused on restricted aspects of those assemblages and/or their habitats, *i.e.* on overall densities or the densities of selected species (McLachlan and Hesp 1984, Shepherd *et al.* 1988) or on comparing assemblages in different habitats that were defined only by a single environmental variable (McLachlan 1985). The development of certain multivariate statistical methods, and in particular multidimensional scaling ordination and associated tests, now provide biologists with the tools to explore, in depth, the ways in which the species compositions of benthic macroinvertebrate assemblages differ among habitats, which have been defined in terms of a range of environmental variables, as well as between zones and seasons, and to be able to tease out which species contribute most to any such differences (Clarke and Gorley 2001).

During the present study, the densities of each of the benthic macroinvertebrate taxa in three zones in each of the six nearshore habitat types identified on the lower west coast of Australia (see Chapter 3, Valesini *et al.* 2003) were recorded seasonally for one year. The resultant data were used to test the following hypotheses. 1) The number of species and density of benthic macroinvertebrates will be greatest in the habitat type that is the least exposed to wave activity and contains dense seagrass beds, and in the subtidal zone in each habitat type. 2) The average taxonomic distinctness and the variation in taxonomic distinctness of the benthic macroinvertebrate fauna will vary among habitat types as a result of differences among the trophic characteristics of the species in those habitat types. 3) The benthic macroinvertebrate assemblages in habitats that are most sheltered from wave exposure will contain relatively high densities of soft-bodied, *e.g.* polychaetes and oligochaetes, than hard-bodied organisms, *e.g.* crustaceans and molluscs, and relatively high densities of deposit feeders than suspension feeders, whereas the reverse will be true in more exposed habitats. 4) The extent of differences among each of the various habitat types, based on the compositions of their benthic macroinvertebrate assemblages, will be significantly correlated with the extent of differences among those habitat types based on their enduring environmental characteristics. 5) The compositions of the benthic macroinvertebrate assemblages will differ among seasons due to differential responses of the various species to seasonal changes in environmental variables such as temperature, sediment grain size and food availability.

7.2 Materials and Methods

7.2.1 Study Area

Benthic macroinvertebrates were sampled at two sites representing each of the six nearshore habitat types identified along the lower west coast of Australia. These sampling sites, which differed in the extent to which they were exposed to wave activity and in the presence and location of seagrass and nearshore reefs, were the same as those at which fish were collected (see Chapter 5). Habitat type 1 was highly sheltered from wave activity with areas of dense seagrass within 50 m of the shoreline, while habitat type 2 was moderately sheltered from wave activity with areas of sparse seagrass within 50 m of the shoreline and further offshore. Habitat types types 3 and 4 were moderately exposed to wave activity and contained no seagrass in the vicinity and offshore seagrass beds, respectively, whereas habitat type 5 was moderately exposed to wave activity with reefs present within 50 m of the shoreline and habitat type 6 was relatively exposed to wave activity with no seagrass in the vicinity.

Three zones were sampled at each site. Zone A was the zone between the most recent high tide mark, as reflected in the presence of a drift line on the upper shore, and the effluent line (the point at which groundwater outflow occurs). Zone B was the zone between the effluent line and the lower swash line, *i.e.* the point at which the swash curls before breaking on to the beach, and which is thus characterised by saturated sediment (McLachlan and Jaramillo 1995). Zone C was located further offshore, where the average water depth was approximately 1 m.

7.2.2 Sampling regime

Five randomly located sediment cores were collected from each of the three zones at each of the 12 sites during the day in each season between the summer and spring of 2000. The collection of samples from each site was staggered over a 2-3 week period in the middle of each season to reduce the chances of the resultant data being unduly affected by an atypical sample.

The cylindrical corer, which was 11 cm in diameter and had a surface area of 96 cm^2, sampled to a depth of 15 cm. The sediment samples were preserved in 5% formalin buffered in sea water and subsequently wet sieved through a 500 µm mesh. A dissecting microscope was used to remove the invertebrates from any sediment that was also retained on the mesh and these were then identified to the lowest possible taxon and stored in 70% ethanol. The number of each macroinvertebrate taxon in each replicate sample was converted to a density, *i.e.* number of individuals m^{-2}.

7.2.3 Statistical Analysis

7.2.3.1 Univariate Analyses

Prior to subjecting the number of species and densities of benthic macroinvertebrates to Analysis of Variance (ANOVA), the relationships between the means and associated standard deviations for both variables at each habitat type in each zone in each season were examined to ascertain which type of transformation, if any, was required to satisfy the assumptions of normality and constant variance (Clarke and Gorley 2001). This procedure showed that both of these biotic variables required a log (n+1) transformation. Each benthic macroinvertebrate species was classified according to its respective genus, family, order, class and phylum, thus providing a list with inherent taxonomic structure of the benthic macroinvertebrate assemblages present along the lower west coast of Australia. The average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) were calculated for the species in each of the samples collected from each zone in each habitat type in each season using the DIVERSE routine in the PRIMER 5.2 statistical package (Clarke and Gorley 2001). Average taxonomic distinctness is defined as the average path length connecting all pairs of species in a sample, based on their hierarchical classification in a standard Linnaean tree (Clarke and Warwick 2001b). Each hierarchical level in the classification is a “weighted” step in the total path length connecting each pair of species and each step length in the present study was weighted equally. Variation in taxonomic distinctness is a measure of the evenness of the distribution of species across the hierarchical categories of the taxonomic tree (Clarke and Warwick 2001b). Examination of the relationships between the means and standard deviations for both of these biodiversity indices showed that they each required a log (n+1) transformation. The density of all species, the number of species and the Δ^+ and Λ^+ of the samples collected in each zone at each habitat type and in each season were subjected to three-way ANOVA to determine whether they differed significantly among habitat types, zones and/or seasons.

7.2.3.2 Joint Δ^+ and Λ^+ analyses

Initially, 95% probability ellipses were constructed from 1000 simulated values of Δ^+ and Λ^+, calculated for each of a specified range of subsets of species of varying sizes (m) that were drawn at random from the regional species list. The ranges of m were chosen to approximate the range in size of the number of species at each of the habitat types for each of the zones, individually, so that the appropriate 95% probability ellipses could be constructed. These 95% confidence ellipses defined the range of values for Δ^+ and Λ^+ for each of the expected different-sized subsets of species. Observed Δ^+ and Λ^+ co-ordinates that fell outside their relevant probability ellipses indicated significant departure from that expected for the benthic macroinvertebrate fauna along the lower west coast of Australia.

7.2.3.3 Multivariate analyses

The following multivariate analyses were carried out using the PRIMER 5.2 statistical package (Clarke and Gorley 2001). The Bray-Curtis similarity coefficient was employed to construct a similarity matrix from the log (n+1) transformed densities of the various macroinvertebrate species recorded in each zone at each habitat type in each season. This matrix was then subjected to non-metric multidimensional scaling (MDS) ordination. One-way and two-way crossed Analysis of Similarities (ANOSIM) (Clarke 1993) were carried out to ascertain whether the compositions of the benthic macroinvertebrate assemblages differed significantly among habitats, zones and/or seasons. The factors employed in each of these tests are specified in detail in the Results. In each test, the null hypothesis that there were no significant differences among groups was rejected if the significance level (p) was <5%. The R-statistic value was used to ascertain the extent of any significant differences (Clarke 1993). Any R-statistic values <0.1 were regarded as negligible. Where ANOSIM detected a significant difference among a priori groups and the R-statistic was >0.1, Similarity Percentages (SIMPER) (Clarke 1993) was used to identify which species made the greatest contributions to those differences.

The second-stage MDS routine was used to determine whether the arrangement of the rank orders of similarity between each of the habitat types in the separate Bray-Curtis similarity matices constructed for each season and zone differed on the basis of each of those factors. RELATE was used to determine whether the arrangement of the rank orders of similarity in the Bray-Curtis matrix constructed from the densities of the benthic macroinvertebrate species in each each zone at each habitat type and in each season was significantly correlated with those in the complementary Euclidean distance matrix calculated from the values for the seven environmental variables that best distinguished those habitat types (see Chapter 3).

7.3 Results

The sampling of benthic macroinvertebrates in the three zones at the six habitat types in each season in 2000 yielded 4181 individuals, which corresponds to a total of 435 521 individuals, when each sample is adjusted to 1 m^{-2} and summed. These samples contained 121 species from eight phyla, namely Annelida, Crustacea, Mollusca, Sipuncula, Uniramia, Nematoda, Turbellaria and Porifera. The Polychaeta, Malacostraca and Bivalvia, which were the most speciose classes, were represented by 41, 35 and 21 species, respectively and contributed 37.7, 22.6 and 10.1%, respectively to the total number of individuals.

The number of species and total number of individuals recorded at habitat type 1 were greater by factors of at least five and two, respectively, than those at each of the other five habitat types (Table 7.1). Six annelid species contributed approximately 60% to the individuals collected in habitat type 1, while approximately 30% of those in habitat type 2 comprised the bivalve *Donacilla* sp. 1 (Table 7.1). The cumacean, *Leptocuma* sp., ranked first in terms of abundance at habitat types 3 and 4, comprising approximately 30 and 18% of the individuals obtained at each, respectively. An insect, *i.e.* coelopid sp., comprised *ca* 45% of the benthic macroinvertebrates recorded in habitat type 5, while the amphipod, phoxocephalopsid sp. 1, and the bivalve *Donax columbella* made up approximately 50% of the benthic macroinvertebrates collected at the exposed habitat type 6.

7.3.1 Number of species, densities of benthic macroinvertebrates and species relatedness among habitat types, zones and seasons.

Three-way ANOVA showed that the mean number of species differed significantly among habitat types and zones but not among seasons and that there was a significant two-way interaction between habitat type and zone (Table 7.2). The mean squares were greatest for zone and least for the interaction. The mean number of species was greatest in zone C at habitat types 1, 2, 5 and 6 and was least in this zone in habitat type 4 (Fig. 7.1a). However, there was no clear trend for the number of species in either zones A or B to be consistently greater across the six habitat types. For each zone, the mean number of species was greatest in habitat type 1 and essentially second greatest in habitat type 2, while in zones A and B it was least in habitat type 5 (Fig. 7.1a).

Table 7.1 Mean density (M; number of individuals 1 m^{-2}), standard deviation (±1sd), percentage contributions to the sum of the mean densities (%) and the rank by density (Rk) of each benthic macroinvertebrate taxon in samples collected in all zones at habitat types 1-6 in nearshore waters along the lower west coast of Australia in all seasons during 2000. Each taxon has been classified into its appropriate phyla (Ph) (A-Annelida, C-Crustacea, M-Mollusca, S-Sipuncula, Un-Uniramia, N-Nematoda, Pl- Platyhelminthes and Po-Porifera) and predominant feeding mode (F) (Dp-deposit feeder, Dt-detritus feeder, S-suspension feeder, P-predator, U-Unknown). The number of taxa, number of samples collected and the total number of individuals (after the number of individuals in each sample had been adjusted to that in 1 m^{-2}) are also provided for each habitat type.

			1				2				3				4				5				6			
	Ph	F	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Enchytraid sp. 3	A	Dt	291.7	942.4	14.0	1													6.1	29.8	1.5	7				
Capitella sp. 1	A	Dp	256.9	535.6	12.3	2									3.5	17.0	1.9	8								
Capitella sp. 2	A	Dp	244.8	402.5	11.8	3																	1.7	5.9	0.5	16
Enchytraid sp. 1	A	Dt	173.6	525.3	8.3	4													18.2	80.6	4.5	4	1.7	8.5	0.5	16
Eusyllinae spp.	A	Dt	158.9	333.8	7.6	5	6.1	25.7	1.9	11	1.7	8.5	0.6	17												
Enchytraid sp. 2	A	Dt	153.6	382.6	7.4	6																				
Aricidea sp.	A	Dp	72.9	287.7	3.5	7																				
Pseudopolydora sp.	A	Dp	63.4	222.1	3.0	8																	12.2	51.4	3.3	6
Phylo sp. 1	A	Dp	59.9	289.0	2.9	9	1.7	8.5	0.5	20													1.7	8.5	0.5	16
Exogoninae spp.	A	Dp/C	56.4	127.0	2.7	10																				
Notomastus sp.	A	Dp	55.6	204.4	2.7	10					0.9	4.3	0.3	23									2.6	12.8	0.7	12
Donacilla sp. 2	M	S	53.8	180.0	2.6	12									1.7	8.5	1.0	17					6.9	17.0	1.9	9
Kalliapseudid sp.	C	S/Dp	45.1	156.3	2.2	13																				
Muscid sp.	Un	Dt	39.9	195.6	1.9	14																				
Sipunculan sp. 2	S	Dp	38.2	120.5	1.8	15									0.9	4.3	0.5	24								
Coelopid sp.	Un	Dt	37.3	99.4	1.8	15									0.9	4.3	0.5	24	182.3	844.9	45.5	1	0.9	4.3	0.2	19
Mysella sp. 1	M	S	35.6	103.3	1.7	17					0.9	4.3	0.3	23												
Spio sp.	A	Dp	33.0	129.6	1.6	18	0.9	4.3	0.3	25	1.7	8.5	0.6	17	1.7	8.5	1.0	17								
Leptocuma sp.	C	Dp/S	27.8	87.5	1.3	19	39.1	166.1	12.3	2	82.5	339.5	29.1	1	32.1	157.3	17.7	1					22.6	84.9	6.2	5
Pontodrilus litoralis	A	Dt	17.4	48.6	0.8	20	2.6	9.3	0.8	14									5.2	21.5	1.3	9				
Staphilinid sp.	Un	Dt	16.5	52.8	0.8	20													1.7	8.5	0.4	15				
Polydora sp.	A	Dp	14.8	41.4	0.7	22	0.9	4.3	0.3	25													0.9	4.3	0.2	19
Tanais sp.	C	Dp	14.8	54.4	0.7	22																				
Polydorella sp.	A	Dp	8.7	28.1	0.4	24																				
Capitellid sp. 4	A	Dp	8.7	30.0	0.4	24																				
Oniscid sp. 1	C	Dt	7.8	21.1	0.4	24					0.9	4.3	0.3	23	1.7	5.9	1.0	17	59.9	217.4	14.9	3	30.4	83.3	8.3	4
Marphysa sp.	A	P	7.8	19.2	0.4	24																				
Exoediceroides sp. 1	C	U	6.1	15.6	0.3	28	6.9	25.8	2.2	9									0.9	4.3	0.2	20	2.6	9.3	0.7	12
Exoediceroides sp. 2	C	U	6.1	29.8	0.3	28					3.5	13.3	1.2	13	0.9	4.3	0.5	24					0.9	4.3	0.2	19
Phoxocephalopsid sp. 1	C	U	5.2	25.5	0.3	30	28.6	84.6	9.0	4	18.2	60.3	6.4	6	23.4	110.5	12.9	3	1.7	5.9	0.4	15	104.2	192.1	28.6	1

Table 7.1 continued

			1				2				3				4				5				6			
	Ph	F	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Prionospio sp.	A	Dp	5.2	25.5	0.3	30	2.6	12.8	0.8	14																
Capitellid sp. 1	A	Dp	5.2	14.1	0.3	30																				
Nephtys gravereii	A	P	4.3	15.0	0.2	33																				
Soletolina biradiata	M	Dp	4.3	12.3	0.2	33																				
Phoxocephalopsid sp. 2	C	U	3.5	17.0	0.2	33	13.9	31.1	4.4	7					6.9	25.8	3.8	6	4.3	13.7	1.1	10	53.0	237.7	14.5	3
Sipunculan sp. 1	S	Dp	3.5	17.0	0.2	33	1.7	5.9	0.5	20					1.7	8.5	1.0	17								
Linga crassilirata	M	S	3.5	17.0	0.2	33	0.9	4.3	0.3	25																
Lysidice sp.	A	P	3.5	13.3	0.2	33																				
Corophium minor	C	Dt/S	2.6	12.8	0.1	39																	0.9	4.3	0.2	19
Scoloplos sp.	A	Dt	2.6	9.3	0.1	39	19.1	65.0	6.0	5					2.6	12.8	1.4	10								
Diopatra sp.	A	P	2.6	9.3	0.1	39																				
Oniscid sp. 2	C	Dt	1.7	8.5	0.1	42													2.6	9.3	0.6	11				
Septifer sp.	M	S	1.7	8.5	0.1	42					0.9	4.3	0.3	23												
Mysella sp. 2	M	S	1.7	5.9	0.1	42																				
Psammobiid sp.	M	Dp	1.7	5.9	0.1	42																				
Cyamid sp.	M	S	1.7	8.5	0.1	42																				
Pisionidens sp.	A	Dp	0.9	4.3	<0.1	47									2.6	12.7	1.4	10	6.9	4.3	1.7	6	12.2	28.8	3.3	6
Transorchestia sp.	C	Dt	0.9	4.3	<0.1	47													0.9	4.3	0.2	20	0.9	4.3	0.2	19
Gomphina sp.	M	S	0.9	4.3	<0.1	47																	0.9	4.3	0.2	19
Mandalotus sp.	Un	Dt	0.9	4.3	<0.1	47									1.7	5.9	1.0	17	1.7	8.5	0.4	15				
Haplostylus sp.	C	S	0.9	4.3	<0.1	47	5.2	15.4	1.6	12	3.5	10.0	1.2	13	1.7	8.5	1.0	17								
Poriferan sp.	Po	S	0.9	4.3	<0.1	47													1.7	8.5	0.4	15				
Microspio sp.	A	Dp	0.9	4.3	<0.1	47	2.6	9.3	0.8	14	18.2	72.8	6.4	6					0.9	4.3	0.2	20				
Sipunculid sp.	S	Dp	0.9	4.3	<0.1	47	0.9	4.3	0.3	25	1.7	8.5	0.6	17												
Ceratonereis aquisetis	A	Dt/Dp	0.9	4.3	<0.1	47	0.9	4.3	0.3	25	0.9	4.3	0.3	23												
Phylo sp.2	A	Dt	0.9	4.3	<0.1	47																				
Capitellid sp. 2	A	Dp	0.9	4.3	<0.1	47																				
Capitellid sp. 3	A	Dp	0.9	4.3	<0.1	47																				
Decamastus sp.	A	Dp	0.9	4.3	<0.1	47																				
Caullierella sp.	A	Dp	0.9	4.3	<0.1	47																				
Dodecaceria sp.	A	Dp	0.9	4.3	<0.1	47																				
Waitangi sp.	C	S	0.9	4.3	<0.1	47																				
Orthorrhapha sp.	Un	Dt	0.9	4.3	<0.1	47																				

Table 7.1 continued

			1				**2**				**3**				**4**				**5**				**6**			
	Ph	F	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Trachyselis sp.	Un	Dt	0.9	4.3	<0.1	47																				
Ochthebius sp.	Un	Dt	0.9	4.3	<0.1	47																				
Colon sp.	Un	Dt	0.9	4.3	<0.1	47																				
Lucinid sp.	M	S	0.9	4.3	<0.1	47																				
Tellina sp. 2	M	S/Dp	0.9	4.3	<0.1	47																				
Tellina sp. 1	M	S/Dp	0.9	4.3	<0.1	47																				
Nucula sp.	M	S	0.9	4.3	<0.1	47																				
Donacilla sp. 1	M	S					92.9	177.5	29.2	1	6.9	21.9	2.5	8	3.5	7.9	1.9	8					0.9	4.3	0.2	19
Donax columbella	M	S					29.5	49.9	9.3	3	27.8	68.9	9.8	3									77.3	181.6	21.2	2
Scolelepis carunculata	A	S					18.2	36.5	5.7	6	6.1	11.5	2.1	10	29.5	73.2	16.3	2	1.7	5.9	0.4	15	2.6	12.8	0.7	12
Exoediceroides sp. 3	C	U					13.0	39.2	4.1	8	20.0	71.5	7.1	5	9.5	42.6	5.3	5	0.9	4.3	0.2	20				
Uldanamia pillare	C	U					6.9	24.3	2.2	9	1.7	5.9	0.6	17												
Atheta sp.	Un	Dt					3.5	7.9	1.1	13	34.7	141.4	12.3	2	5.2	15.4	2.9	7	2.6	7.0	0.6	11	0.9	4.3	0.2	19
Hippa australis	C	S/Dt					2.6	12.8	0.8	14	0.9	4.3	0.3	23	2.6	9.3	1.4	10	0.9	4.3	0.2	20	5.2	9.2	1.4	10
Haploscoloplos sp.	A	Dt					2.6	9.3	0.8	14					2.6	7.0	1.4	10								
Gynodiastylid sp. 2	C	U					2.6	7.0	0.8	14																
Amphipod sp. 1	C	U					1.7	5.9	0.5	20									6.1	25.7	1.5	7				
Leptonereis sp.	A	Dt/Dp					1.7	8.5	0.5	20																
Nereis diversicolor	A	Dt/Dp					1.7	5.9	0.5	20																
Rhyncospio sp.	A	Dp					0.9	4.3	0.3	25																
Capitomastus sp.	A	Dp					0.9	4.3	0.3	25																
Heteromastus sp.	A	Dp					0.9	4.3	0.3	25																
Ophelid sp	A	Dp					0.9	4.3	0.3	25																
Cypridinodes sp.	C	S					0.9	4.3	0.3	25																
Gynodiastylid sp. 1	C	U					0.9	4.3	0.3	25																
Gynodiastylid sp. 3	C	U					0.9	4.3	0.3	25																
Scolelepis lamellicincta	A	S									20.8	65.0	7.4	4	23.4	53.7	12.9	3	66.0	140.2	16.5	2				
Isocladus sp.	C	Dt									6.9	17.0	2.5	8	0.9	4.3	0.5	24	2.6	7.0	0.6	11				
Golgingid sp.	S	Dp									5.2	21.5	1.8	11					0.9	4.3	0.2	20				
Nematode sp	N	U									4.3	17.4	1.5	12												
Gastrosaccus sorrentoensis	C	S									2.6	12.8	0.9	15									9.5	30.7	2.6	8
Donax deltoides	M	S									2.6	9.3	0.9	15	0.9	4.3	0.5	24								
Turbellarian sp.	Pl	U									1.7	5.9	0.6	17	2.6	7.0	1.4	10								

Table 7.1 continued

			1				2				3				4				5				6			
	Ph	F	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Ogyridid sp.	C	Dt									1.7	8.5	0.6	17												
Magelona sp.	A	Dp									0.9	4.3	0.3	23									2.6	9.3	0.7	12
Amphipod sp. 3	C	U									0.9	4.3	0.3	23	2.6	12.8	1.4	10	17.4	59.8	4.3	5				
Dirimus sp.	C	U									0.9	4.3	0.3	23	0.9	4.3	0.5	24								
Glycera sp.	A	Dp									0.9	4.3	0.3	23												
Amphipod sp. 2	C	U													2.6	4.3	1.4	10	0.9	4.3	0.2	20				
Orbinia sp.	A	Dt													1.7	8.5	1.0	17								
Portunis pelagicus	C	P/Dt													0.9	4.3	0.5	24	2.6	12.8	0.6	11				
Talitrid sp. 1	C	Dt													0.9	12.8	0.5	24	0.9	4.3	0.2	20				
Abraeinae sp.	Un	Dt													0.9	4.3	0.5	24	0.9	4.3	0.2	20				
Mactrid sp.	M	S													0.9	4.3	0.5	24					0.9	4.3	0.2	19
Eunice sp.	A	P													0.9	4.3	0.5	24								
Mycopod sp.	C	S													0.9	4.3	0.5	24								
Birubius sp.	C	U													0.9	4.3	0.5	24								
Exoediceroides sp. 4	C	U													0.9	4.3	0.5	24								
Decapod sp.	C	U													0.9	4.3	0.5	24								
Exosphaeroma sp.	C	Dt													0.9	4.3	0.5	24								
Talitrid sp. 2	C	Dt																	0.9	4.3	0.2	20				
Sphaeromatid sp.	C	Dt																	0.9	4.3	0.2	20				
Haustorioidea sp.	C	U																					3.5	7.9	1.0	11
Conchostracan sp.	M	S																					0.9	4.3	0.2	19
Epicodakei tatei	M	S																					0.9	4.3	0.2	19
Glycymeris radians	M	U																					0.9	4.3	0.2	19
Glycymeris sp.	M	U																					0.9	4.3	0.2	19
Musculista sp.	M	S																					0.9	4.3	0.2	19
Number of taxa			**70**				**36**				**32**				**39**				**30**				**32**			
Overall mean density			**2082.5**				**317.7**				**283.0**				**181.4**				**401.0**				**364.6**			
Number of samples			**120**				**120**				**120**				**120**				**120**				**120**			
Total no. individuals			**249 900**				**38 124**				**33 960**				**21 786**				**48 120**				**43 728**			

Table 7.2 Mean squares and significance levels for three-way ANOVA of the number of taxa, density, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of benthic macroinvertebrates in samples collected in zones A, B and C at habitats 1-6 in each season in 2000. "df"=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	No. of taxa	Density	Δ^+	Λ^+
Main effects					
Habitat type (H)	5	0.212***	3.272***	1.480**	0.211***
Zone (Z)	2	0.361***	0.642	3.213***	0.365***
Season (S)	3	0.082	0.961	0.575	0.080
Two-way interactions					
H x Z	10	0.133***	0.380	0.644*	0.132***
H x S	15	0.032	0.380	0.221	0.031
Z x S	6	0.034	0.221	0.310	0.031
Three-way interactions					
H x Z x S	30	0.011	0.172	0.165	0.011
Error	72	0.033	0.394	0.320	0.031

The mean density of benthic macroinvertebrates was significantly influenced by habitat type, but not by zone or season (Table 7.2). Scheffé's *a posteriori* tests showed that the mean density of benthic macroinvertebrates was significantly greater in habitat type 1 than in the other five habitat types and that the mean densities in habitat types 2-6 were not significantly different from each other. The mean density of benthic macroinvertebrates was approximately ten times greater in habitat type 1 than in habitat types 3, 4 and 5 and about six times greater than in habitat types 2 and 6 (Fig. 7.1 b).

The mean average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) were significantly influenced by both habitat type and zone, but not by season, and there was a significant two-way interaction between habitat type and zone (Table 7.2). The mean squares were greatest for zone and least for the interaction in both cases. The mean Δ^+ was greatest in zone C in five of the six habitat types (1, 2, 3, 4, 6) and least in zone A in each of those habitat types except habitat type 4, but was greatest in zone A in habitat type 5 (Fig. 7.1c). For zones A and B, the mean Δ^+ was greatest in habitat type 6 and was least in habitat type 5, while for zone C it was greatest in habitat type 1 and least in habitat type 4 (Fig. 7.1c). The mean Λ^+ was greatest in zone C and least in zone B in all habitat types, except in habitat type 1 where it was slightly lower in zone A than zone B (Fig. 7.1d). This variable was greatest for each zone in habitat type 1 and was least for each zone in habitat type 5.

7.3.2 *Joint Δ^+ and Λ^+ analyses*

Since ANOVA demonstrated that for both mean Δ^+ and mean Λ^+ there was a significant habitat x zone interaction, 95% probability ellipses for joint Δ^+ and Λ^+ values were calculated for a specified range of subsets of species in each zone and superimposed with the observed Δ^+ and

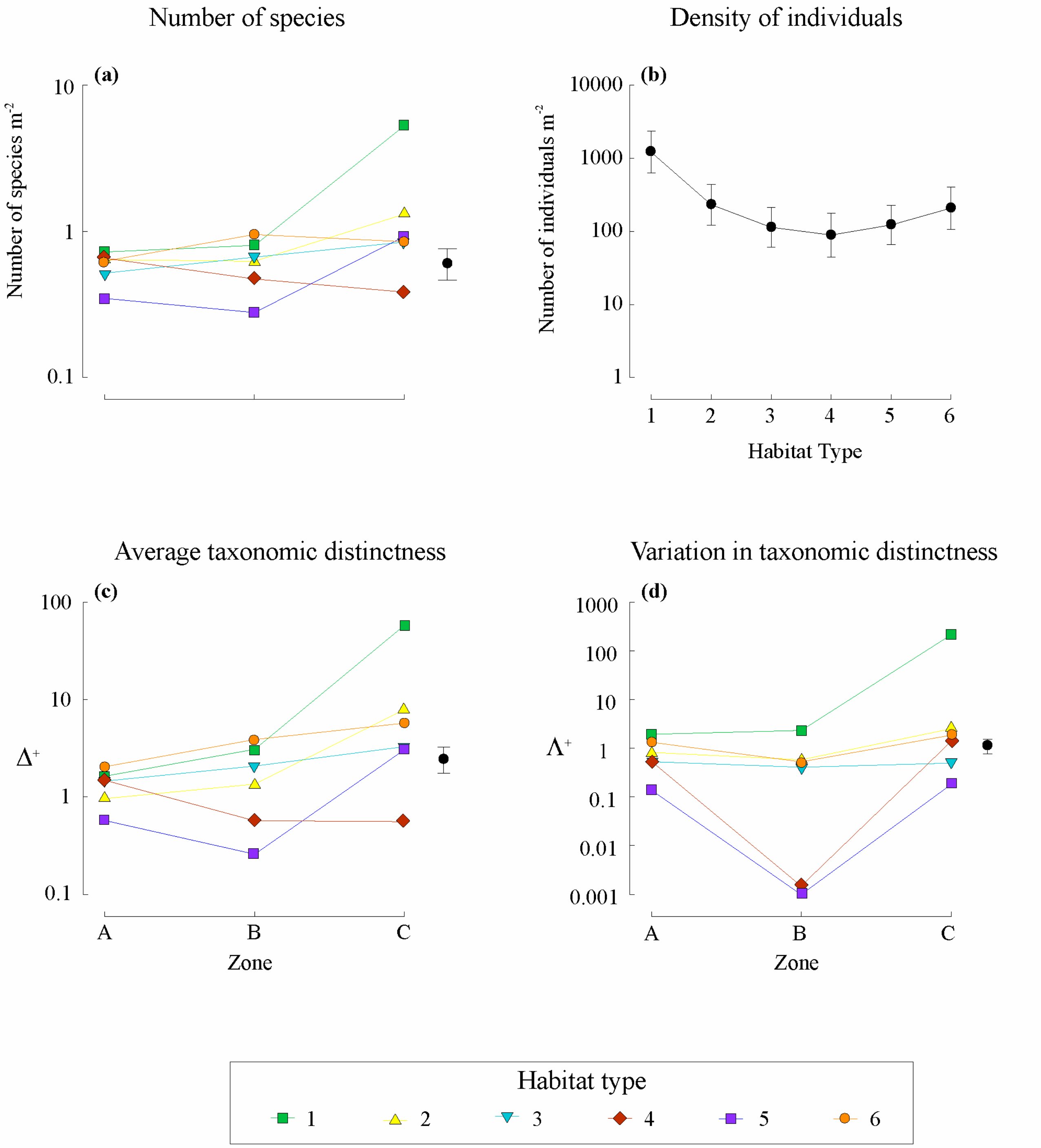


Figure 7.1: Mean (± 95% CI) (a) number of species (c) average taxonomic distinctness (Δ^+) and (d) variation in taxonomic distinctness (Λ^+) of benthic macroinvertebrates in zones A, B and C at habitats 1-6, and (b) densities of benthic macroinvertebrates at habitats 1-6. Data derived from samples collected seasonally in 2000. For the sake of clarity the overall mean (± 95% CI) is provided on each plot (denoted by black symbols and lines).

Λ^+ values for the species lists of each habitat type, in each zone separately (Figs 7.2a-d). In zones A and B all of the points representing the joint Δ^+ and Λ^+ values for each of the habitat types fell within their respective 95% probability ellipses indicating that the taxonomic structure of the species assemblages at each was representative of that for the entire region (Fig. 7.2a, b). In zone C, none of the points representing the joint Δ^+ and Λ^+ values for the various habitat types fell outside of their respective ellipses (Fig. 7.2c), except in the case of habitat type 1, which fell outside its respective ellipse in the direction of decreased Δ^+ and increased Λ^+ (Figs 7.2d).

7.3.3 Community Analyses

7.3.3.1 Differences in benthic macroinvertebrate assemblages among habitat types.

One-way ANOSIM showed that the benthic macroinvertebrate species compositions differed significantly among habitat types, zones and seasons. The global R-statistic value was greater for habitat type than for zone (0.222 *vs* 0.126, respectively), but was negligible for season (R-statistic<0.1). Emphasis is thus now placed on comparing the compositions according to habitat type.

When the mean densities of the benthic macroinvertebrate species in each zone at each site and in each season were subjected to MDS ordination and coded for habitat type, the majority of the samples collected from habitat type 1 formed a group on the left side of the three-dimensional plot, whereas the majority of those from habitat type 5 lay towards the upper right of that plot and those from habitat types 2 and 3 occupied intermediate positions (Fig. 7.3a). Half of the samples from habitat type 4 lay in the bottom right half of the plot, while the other half lay amongst those for habitat type 5. Those for habitat type 6 were scattered through much of the plot (Fig. 7.3a). Pairwise ANOSIM comparisons between the various habitat types showed that the species compositions at each of the habitat types were significantly different from each other in all cases except for habitats 2 *vs* 3, 3 *vs* 4 and 4 *vs* 5. However, whereas the global R-statistics for all of the pairwise comparisons involving habitat type 1 were at least 0.316, those for all possible pairs among habitat types 2-6 exceeded 0.18 only in the cases of habitat types 5 *vs* 2, 3 and 6 and 4 *vs* 6 and otherwise exceeded 0.1 only with habitat types 6 *vs* both 2 and 3 (Table 7.3).

SIMPER showed that the benthic macroinvertebrate species composition in habitat 1 was typified by five polychaete taxa (Table 7.4). Two of these taxa, *Capitella* sp. 2 and eusyllinae spp., distinguished habitat type 1 from all other habitat types. *Donacilla* sp. 1 and *Scolelepis carunculata* were among the most important typifying species of the assemblages in habitat types 2, 3, and 4. Similarly, the assemblages in habitat types 4 and 5 were both typified primarily by *Scolelepis lamellicincta* (Table 7.4). Greater densities of *Donacilla* sp. 1 and

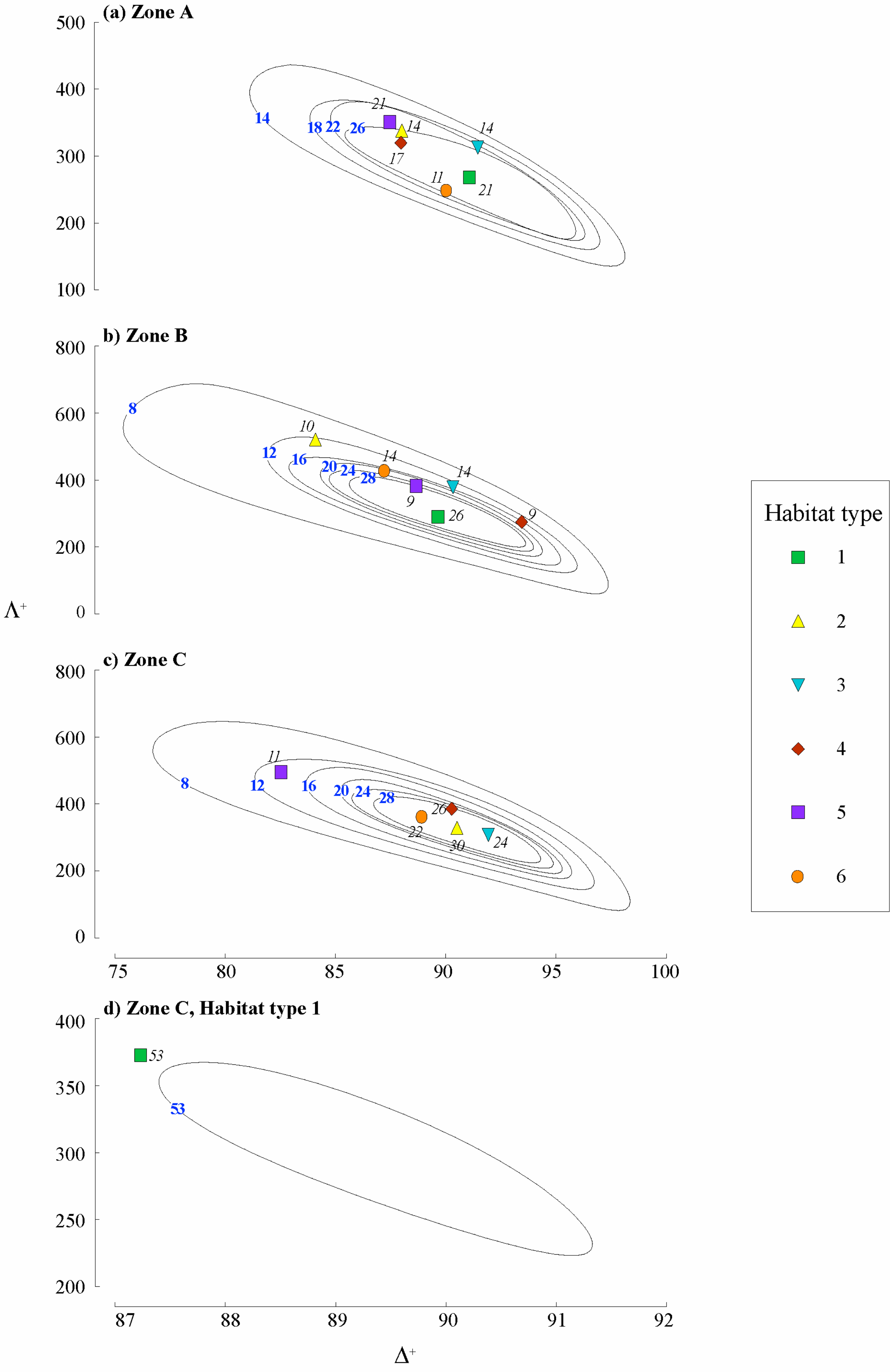


Figure 7.2: Scatterplots of average taxonomic distinctness *vs* variation in taxonomic distinctness of macrobenthic species in samples collected at each of habitat types 1-6 in all seasons in (a) zone A, (b) zone B, (c) habitat ypes 1-5 in zone C and (d) habitat type 1 in zone C. The number of species recorded at each habitat type and the relevant 95% probability ellipses for simulations of different-sized subsets of species are also provided for each zone

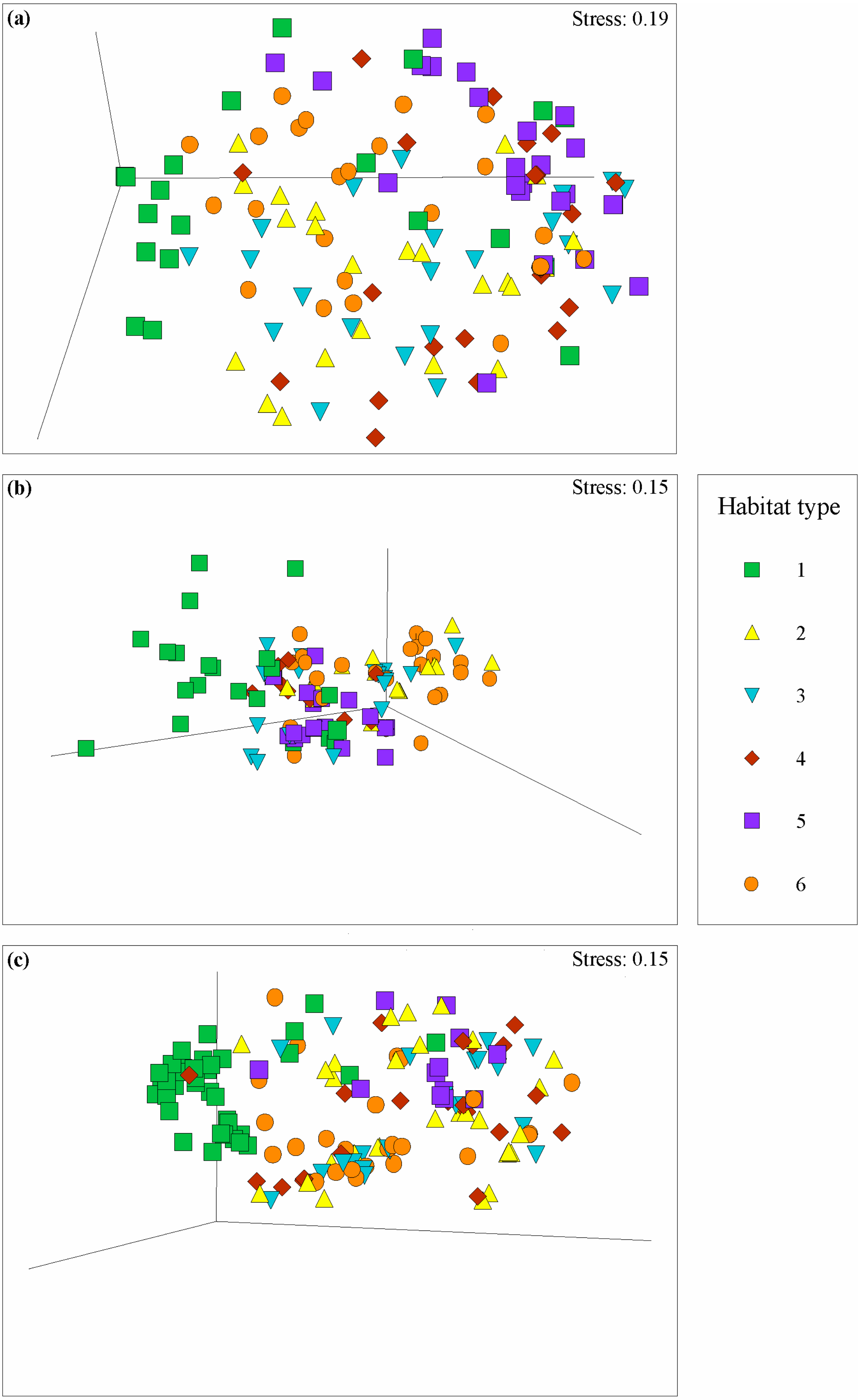


Figure 7.3: Three-dimensional MDS ordination of the densities of benthic macroinvertebrate species derived using data from habitat types 1-6 during the summer, autumn, winter and spring for (a) zones A, B and C, (b) zone B and (c) zone C and coded for habitat type.

Table 7.3 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in a one-way ANOSIM test of the benthic macroinvertebrate assemblages at habitat types 1-6. Samples collected in the different zones and seasons have been pooled in this analysis. Significant and non-negligible results (*i.e.* R >0.1) are highlighted in boldface.

Habitat type (p=0.1%; Global R=0.222)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.377**										
3	**0.1**	**0.393**	8.6	0.043								
4	**0.1**	**0.385**	0.9	0.095	4.0	0.059						
5	**0.1**	**0.368**	**0.1**	**0.279**	**0.1**	**0.182**	9.7	0.038				
6	**0.1**	**0.316**	**0.3**	**0.123**	**0.4**	**0.127**	**0.1**	**0.224**	**0.1**	**0.271**		

D. columbella at habitat type 2 distinguished the species composition at this habitat type from those in both habitat types 4 and 5, which contained greater densities of *S. lamellicincta* (Table 7.4). The assemblages at habitat types 3 and 5 were also distinguished by greater densities of *D. columbella* and *S. lamellicincta* at each habitat type, respectively. The species composition at habitat type 6 was typified primarily by phoxocephalopsid sp. 1 and *D. columbella* (Table 7.4). These two species were present in the greatest densities in habitat type 6 and were primarily responsible for distinguishing this habitat type from all others.

7.3.3.2 Composition of assemblages among different habitat types in each zone and/or season.

Since one-way ANOSIM demonstrated that, after habitat type, the species compositions of the samples differed to the greatest extent among zones, attention is now focused on examining the extent of differences among the habitat types but now considering each zone separately and taking season into account.

Two-way crossed ANOSIM, employing habitat type and season as factors, showed that, in the case of zone C, the species composition differed significantly among habitat types and seasons (Global R=0.327 and 0.161, respectively), whereas for zone B it differed significantly only among habitat types (Global R=0.116), and for zone A did not differ significantly among either habitat types or seasons (p >5%). SIMPER showed that zone A was typified by oniscid sp.1, *Isocladus* sp., coelopid sp., *Atheta* sp, and several species of enchytraid.

Following separate ordinations of the densities of benthic macroinvertebrates in zones B and C, the majority of the samples from habitat type 1 lay in the left side of the plot (Figs 7.3 b, c) and formed a particularly discrete group in the case of zone C (Fig. 7.3 c). The samples for habitat types 2-6 were less widely distributed on the ordination plot for zone B than zone C.

Table 7.4 Species detected by SIMPER as those most responsible for typifying the benthic macroinvertebrate fauna at habitat types 1-6 (see taxa arranged along diagonal cells) and distinguishing each pair of those habitat types (see taxa arranged along vertical cells). Samples collected in the different zones and seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided in each case (see superscripts). Grey shading represents those pairs of habitat types that did not contain significantly different faunal compositions (see Table 7.3).

	1	**2**	**3**	**4**	**5**	**6**
1	*Capitella* sp. 1 *Capitella* sp. 2 Eusyllinae spp. Exogoninae spp. *Aricidea* sp.					
2	*Donacilla* sp. 1$^{(2)}$ *Capitella* sp. 2$^{(1)}$ Eusyllinae spp.$^{(1)}$	*Donacilla* sp. 1 *Donax columbella* *Scolelepis carunculata* Phoxocephalopsid sp. 1 *Exoediceroides* sp. 3				
3	*Capitella* sp. 2$^{(1)}$ Eusyllinae spp. $^{(1)}$ *Donax columbella*$^{(3)}$ *Leptocuma* sp. $^{(3)}$ *Capitella* sp. 1$^{(1)}$	▨	*Scolelepis carunculata* *Isocladus* sp. *Leptocuma* sp. *Donacilla* sp. 1			
4	*Capitella* sp. 2$^{(1)}$ Eusyllinae spp. $^{(1)}$ *Capitella* sp. 1$^{(1)}$	*Donacilla* sp. 1$^{(2)}$ *Scolelepis carunculata*$^{(4)}$ *Donax columbella*$^{(2)}$ Phoxocephalopsid sp. 1$^{(2)}$ *Scolelepis lamellicincta*$^{(4)}$	▨	*Scolelepis lamellicincta* *Scolelepis carunculata* *Hippa australis* *Donacilla* sp. 1 *Atheta* sp.		
5	*Capitella* sp. 2$^{(1)}$ *Scolelepis lamellicincta*$^{(5)}$ Eusyllinae spp. $^{(1)}$ *Capitella* sp. 1$^{(1)}$	*Donacilla* sp. 1$^{(2)}$ *Scolelepis lamellicincta*$^{(5)}$ *Scolelepis carunculata*$^{(2)}$ *Donax columbella*$^{(2)}$	*Scolelepis lamellicincta*$^{(5)}$ *Donax columbella*$^{(3)}$ *Leptocuma* sp.$^{(3)}$ Oniscid sp. 1$^{(5)}$ *Isocladus* sp.$^{(3)}$	▨	*Scolelepis lamellicincta* *Pisionidens* sp. Oniscid sp. 1 *Isocladus* sp.	
6	*Capitella* sp. 2$^{(1)}$ *Donax columbella*$^{(6)}$ Phoxocephalopsid sp. 1$^{(6)}$ Eusyllinae spp. $^{(1)}$	*Donax columbella*$^{(6)}$ *Donacilla* sp. 1$^{(2)}$ Phoxocephalopsid sp. 1$^{(6)}$ *Leptocuma* sp. $^{(2)}$ *Scolelepis carunculata*$^{(2)}$ Oniscid sp. 1$^{(6)}$	*Donax columbella*$^{(6)}$ Phoxocephalopsid sp. 1$^{(6)}$ *Leptocuma* sp.$^{(3)}$ Oniscid sp. 1$^{(6)}$	Phoxocephalopsid sp. 1$^{(6)}$ *Donax columbella*$^{(6)}$ Oniscid sp. 1$^{(6)}$ *Leptocuma* sp.$^{(4)}$ *Scolelepis carunculata*$^{(4)}$ *Scolelepis lamellicincta*$^{(4)}$	*Scolelepis lamellicincta*$^{(5)}$ *Donax columbella*$^{(6)}$ Oniscid sp. 1$^{(5)}$ Phoxocephalopsid sp. 1$^{(6)}$ *Pisionidens* sp.$^{(6)}$	Phoxocephalopsid sp. 1 *Donax columbella* Oniscid sp. 1 *Hippa australis* *Leptocuma* sp. 1 *Pisionidens* sp.

For zone B, each of the pairwise comparisons between habitat types was significant except for that between habitat types 2 and 3. However, the R-statistic values never exceeded 0.221 for any comparison and were <0.1 between habitat type 2 *vs* 4, 2 *vs* 6 and 3 *vs* 6 and were thus considered negligible (Table 7.5a).

Table 7.5 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in two-way crossed habitat type x season ANOSIM tests of the benthic macroinvertebrate assemblages at habitat types 1-6 in (a) zone B and (b) zone C. Only the results for the habitat type component of these two-way crossed analyses are presented in the following tables. Significant and non-negligible results (*i.e.* R >0.1) are highlighted in boldface.

(a) Zone B (p=0.1%; Global R=0.116)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.2**	**0.112**										
3	**0.1**	**0.139**	23.6	0.018								
4	**0.1**	**0.116**	3.6	0.054	**0.2**	**0.114**						
5	**0.1**	**0.144**	**0.1**	**0.123**	**0.1**	**0.159**	**0.2**	**0.105**				
6	**0.1**	**0.178**	3.8	0.064	2.2	0.080	**0.1**	**0.221**	**0.1**	**0.215**		

(b) Zone C (p=0.1%; Global R=0.327)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.689**										
3	**0.1**	**0.739**	**0.2**	**0.109**								
4	**0.1**	**0.731**	15.1	0.028	0.3	0.086						
5	**0.1**	**0.831**	**0.1**	**0.174**	**0.1**	**0.178**	2.4	0.057				
6	**0.1**	**0.642**	0.6	0.095	0.8	0.073	**0.2**	**0.110**	**0.1**	**0.147**		

In zone C, the global R-statistic was greater for habitat type than for season (data for season not shown). Furthermore, the differences among the faunas at habitat type 1 and those at each of the other habitat types were far greater in zone C than in zone B (see Tables 7.5 a, b). In zone C, the composition of the benthic macroinvertebrate assemblage in each habitat type differed significantly from that in each other habitat type, except in the case of habitat type 2 *vs* 4. However, as in zone B, the R-statistic value showed that some of these differences were negligible, i.e those between habitat types 2 *vs* 6, 3 *vs* 4, 3 *vs* 6 and 4 *vs* 5 (Table 7.5b).

SIMPER showed that, in zone B, the species composition in habitat type 1 was both characterised and distinguished from those in the other habitat types by greater densities of *Capitella* sp. 2, eusyllinae spp. and exogoninae spp. (Table 7.6a). The species composition in

Table 7.6a Species detected by SIMPER as those most responsible for typifying the benthic macroinvertebrate fauna in zone B at habitat types 1, 2 & 3, 4, 5 and 6 (see taxa arranged along diagonal cells) and distinguishing each pair of those habitat types (see taxa arranged along vertical cells). Samples collected in the different seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided in each case (see superscripts). Data from two habitat types have been pooled in those cases in which the compositions of their benthic macroinvertebrate faunas were not significantly different from each other, but where both of those faunas differed significantly from those at other habitat types in the same manner (see Table 7.5a).

	1	**2 & 3**	**4**	**5**	**6**
1	*Capitella* sp. 2 Eusyllinae spp. Exogoninae spp.				
2 & 3	*Donax columbella*$^{(2\&3)}$ *Capitella* sp. 2$^{(1)}$ *Donacilla* sp. 1$^{(2\&3)}$ Eusyllinae spp. $^{(1)}$ *Scolelepis carunculata*$^{(2\&3)}$ Exogoninae spp. $^{(1)}$	*Donax columbella* *Scolelepis lamellicincta* *Donacilla* sp. 1			
4	*Capitella* sp. 2$^{(1)}$ Eusyllinae spp. $^{(1)}$ *Scolelepis carunculata*$^{(4)}$ Exogoninae spp. $^{(1)}$ *Capitella* sp. 1$^{(1)}$	*Donax columbella*$^{(2\&3)}$ *Scolelepis carunculata*$^{(4)}$ *Donacilla* sp. 1$^{(2\&3)}$ *Scolelepis lamellicincta*$^{(2\&3)}$ *Exoediceroides* sp. 3$^{(4)}$ *Atheta* sp. $^{(2\&3)}$ Phoxocephalopsid sp.1$^{(2\&3)}$	*Scolelepis carunculata* *Exoediceroides* sp. 3		
5	*Scolelepis lamellicincta*$^{(5)}$ *Capitella* sp. 2$^{(1)}$ Eusyllinae spp. $^{(1)}$ *Pisionidens* sp$^{(5)}$ Exogoninae spp. $^{(1)}$	*Scolelepis lamellicincta*$^{(5)}$ *Donax columbella*$^{(2\&3)}$ *Scolelepis carunculata*$^{(2\&3)}$ *Donacilla* sp. 1$^{(2\&3)}$ *Pisionidens* sp$^{(5)}$ *Atheta* sp. $^{(2\&3)}$ Phoxocephalopsid sp.1$^{(2\&3)}$	*Scolelepis lamellicincta*$^{(5)}$ *Pisionidens* sp$^{(5)}$ *Scolelepis carunculata*$^{(4)}$ *Exoediceroides* sp. 3$^{(4)}$ *Atheta* sp. $^{(5)}$	*Scolelepis lamellicincta*	
6	*Donax columbella*$^{(6)}$ Phoxocephalopsid sp.1$^{(6)}$ *Pisionidens* sp$^{(6)}$ *Capitella* sp. 2$^{(1)}$ Eusyllinae spp. $^{(1)}$	*Donax columbella*$^{(6)}$ Phoxocephalopsid sp.1$^{(6)}$ *Pisionidens* sp. $^{(6)}$ *Donacilla* sp. 1$^{(2\&3)}$ *Hippa australis*$^{(6)}$ Phoxocephalopsid sp. 2$^{(6)}$ *Scolelepis carunculata*$^{(2\&3)}$	*Donax columbella*$^{(6)}$ Phoxocephalopsid sp.1$^{(6)}$ *Pisionidens* sp. $^{(6)}$ *Hippa australis*$^{(6)}$ *Donacilla* sp. 2$^{(6)}$ *Scolelepis carunculata*$^{(4)}$ Phoxocephalopsid sp. 2$^{(6)}$	*Scolelepis lamellicincta*$^{(5)}$ *Donax columbella*$^{(6)}$ *Pisionidens* sp. $^{(6)}$ Phoxocephalopsid sp.1$^{(6)}$ *Hippa australis*$^{(6)}$ *Donacilla* sp. 2$^{(6)}$	*Donax columbella* Phoxocephalopsid sp. 1 Phoxocephalopsid sp. 2 *Pisionidens* sp.

Table 7.6b Species detected by SIMPER as those most responsible for typifying the benthic macroinvertebrate fauna at habitat types 1, 2 & 4, 3, 5 and 6 (see taxa arranged along diagonal cells) and distinguishing each pair of those habitat types (see taxa arranged along vertical cells) in zone C. Samples collected in the different seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided in each case (see superscripts). Data from two habitat types have been pooled in those cases in which the compositions of their benthic macroinvertebrate faunas were not significantly different from each other, but where both of those faunas differed significantly from those at other habitat types in the same manner (see Table 7.5b).

	1	**2 & 4**	**3**	**5**	**6**
1	*Capitella* sp. 2 *Capitella*sp. 1 Eusyllinae *Aricidea* sp. *Marphysa* sp.				
2 & 4	*Capitella* sp. 2$^{(1)}$ *Capitella*sp. 1$^{(1)}$ Eusyllinae$^{(1)}$ *Leptocuma* sp. $^{(2\&4)}$	*Scolelepis carunculata* *Leptocuma* sp.			
3	*Capitella* sp. 2$^{(1)}$ *Capitella*sp. 1$^{(1)}$ Eusyllinae$^{(1)}$ *Leptocuma* sp. $^{(3)}$	*Leptocuma* sp.$^{(3)}$ *Scolelepis carunculata*$^{(2\&4)}$ *Scolelepis lamellicincta*$^{(2\&4)}$	*Leptocuma* sp.1		
5	*Capitella* sp. 2$^{(1)}$ *Capitella*sp. 1$^{(1)}$ Eusyllinae$^{(1)}$ *Scolelepis lamellicincta*$^{(5)}$	*Scolelepis lamellicincta*$^{(5)}$ *Scolelepis carunculata*$^{(2\&4)}$ Phoxocephalopsid sp. 2$^{(5)}$ *Scoloplos* sp. $^{(2\&4)}$ *Leptocuma* sp. $^{(2\&4)}$	*Scolelepis lamellicincta*$^{(5)}$ *Leptocuma* sp.$^{(3)}$	*Scolelepis lamellicincta* Phoxocephalopsid sp. 2	
6	*Capitella* sp. 2$^{(1)}$ *Capitella*sp. 1$^{(1)}$ Eusyllinae$^{(1)}$ *Leptocuma* sp. $^{(6)}$	*Leptocuma* sp. $^{(2\&4)}$ Phoxocephalopsid sp. 1$^{(2\&4)}$ *Scolelepis carunculata*$^{(2\&4)}$ *Donax columbella*$^{(6)}$	*Leptocuma* sp. $^{(6)}$ Phoxocephalopsid sp. 1$^{(6)}$ *Donax columbella*$^{(6)}$	*Scolelepis lamellicincta*$^{(5)}$ *Leptocuma* sp. $^{(6)}$ Phoxocephalopsid sp. 1$^{(6)}$ Phoxocephalopsid sp. 2$^{(5)}$ *Donax columbella*$^{(6)}$	*Leptocuma* sp.1 Phoxocephalopsid sp. 1

habitat type 5 was always distinguished from the other habitat types by greater densities of *S. lamellicincta*, while that in habitat type 6 was distinguished from all other habitat types by greater densities of *D. columbella*, phoxocephalopsid spp. 1 and 2 and *Pisionidens* sp. The species compositions in habitat types 2 and 3 in this zone were characterised by *D. columbella, S. lamellicincta* and *Donacilla* sp. 1, while that in habitat type 4 was characterised by *S. carunculata* and *Exodiceroides* sp. 3. The species composition at habitat type 3 was distinguished from all other habitat types by greater densities of *Donacilla* sp., while that in habitat type 4 was distinguished from all others by greater densities of *S. carunculata* (Table 7.6a).

SIMPER showed that in zone C, the species composition at habitat type 1 was characterised by eusyllinae spp., *Capitella* spp. 1 and 2, *Aricidea* sp. and *Marphysa* sp., and that the first three species distinguished it from the species composition at each of the other habitat types (Table 7.6b). As in zone B, the species composition at habitat type 5 was characterised by and distinguished from those at habitat types 2 and 4 collectively and 3 and 6 by its greater densities of S. lamellicincta. However, in zone C, *Leptocuma* sp. was important in characterizing the species compositions at habitat types 2 and 4 collectively and 3 and 6 (Table 7.6b).

Since the species composition in zone C differed significantly among seasons, one-way ANOSIM was used to determine in which seasons the species compositions in that zone differed significantly among habitat types. These tests showed that the species compositions in zone C differed significantly among habitat types in each season and that the extent of these differences was greatest in spring and least in autumn (Table 7.7a-d).

Following MDS ordination of the densities of benthic macroinvertebrates in zone C in each season, the samples for habitat type 1 in each season formed a tight group that was almost entirely separated from those of all other habitat types (Figs 7.4 a, b, c and d). In each season, most of the samples for habitat types 5 and 6 tended each to form well-defined groups in a different part of the plot and the samples for habitat type 3 also formed a relatively tight group in autumn and spring (Fig. 7.4b, d).

Pairwise ANOSIM comparisons showed that the composition of the assemblage at habitat type 1 was the most distinct of all habitat types and that the extent of the difference between habitat types was greatest in spring and least in autumn (Table 7.7a-d).

The suites of species that, in each season, typified each habitat type or groups of habitat types which did not differ significantly in composition, showed little overlap (Table 7.8a-d).

Table 7.7 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in a one-way ANOSIM test of the benthic macroinvertebrate assemblages in zone C at habitat types 1-6 during (a) summer, (b) autumn, (c) winter and (d) spring. Significant and non-negligible results (*i.e.* R >0.1) are highlighted in boldface.

(a) Summer (p=0.1%; Global R=0.256)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.707**										
3	**0.1**	**0.762**	7.3	0.079								
4	**0.1**	**0.732**	26.1	0.021	77.4	0.021						
5	**0.1**	**0.730**	**0.2**	**0.144**	38.0	0.002	69.8	0.025				
6	**0.1**	**0.691**	**1.5**	**0.130**	29.5	0.017	43.9	0.001	6.4	0.052		

(b) Autumn (p=0.1%; Global R=0.224)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.558**										
3	**0.2**	**0.461**	27.8	0.022								
4	**0.2**	**0.543**	7.0	0.049	10.2	0.031						
5	**0.2**	**0.558**	2.7	0.074	2.8	0.075	48.3	0.005				
6	**0.5**	**0.363**	**3.7**	**0.117**	**3.4**	**0.136**	**0.3**	**0.188**	**0.4**	**0.208**		

(c) Winter (p=0.1%; Global R=0.326)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.799**										
3	**0.1**	**0.894**	**0.3**	**0.168**								
4	**0.1**	**0.858**	34.6	0.008	**2.0**	**0.120**						
5	**0.1**	**0.896**	**0.2**	**0.165**	68.7	0.017	**0.7**	**0.136**				
6	**0.1**	**0.898**	**0.3**	**0.160**	28.9	0.002	**0.7**	**0.134**	13.2	0.026		

(d) Spring (p=0.1%; Global R=0.374)

	1		**2**		**3**		**4**		**5**		**6**	
	p	R	p	R	p	R	p	R	p	R	p	R
1												
2	**0.1**	**0.720**										
3	**0.1**	**0.566**	**3.90**	**0.15**								
4	**0.1**	**0.710**	12.90	0.09	**0.5**	**0.228**						
5	**0.1**	**0.924**	**0.10**	**0.25**	**0.1**	**0.595**	7.7	0.102				
6	**0.1**	**0.665**	50.20	0.01	**1.0**	**0.168**	6.0	0.128	**0.1**	**0.236**		

Table 7.8 Species detected by SIMPER as those most responsible for typifying the benthic macroinvertebrate fauna in zone C at habitat types 1-6 in (a) summer, (b) autumn, (c) winter and (d) spring 2000. Data has been pooled for those habitat types between which ANOSIM did not detect a significant difference in the composition of the benthic macroinvertebrates, but where the faunas at all of those habitat types differed significantly in the same manner from those at the remaining types (see Table 7.7). * indicates a particular taxon is most abundant in a particular habitat type in a particular season.

(a) Summer			
1	**2, 3 & 4**	**5**	**6**
Capitella sp. 1 *Aricidea* sp. *Pseudopolydora* sp. Exogoninae spp. Eusyllinae spp. *Phylo* sp. *Capitella* sp. 2	Phoxocephalopsid sp. 1 *Donacilla* sp.1 *Uldanamia pillare*	*Scolelepis lamellicincta*	*Donax collumbella*

(b) Autumn			
1	**2, 3 & 4**	**5**	**6**
Eusyllinae spp. *Capitella* sp. 2 *Capitella* sp. 1 *Donacilla* sp. 2 *Aricidea* sp.	*Scoloplos* sp. *Haplostylus* sp. *Atheta* sp.	Enchytraid sp.	Phoxocephalopsid sp. 1* *Leptocuma* sp. *Magelona* sp. *Gastrosaccus sorrentoensis*

(c) Winter		
1	**2 & 4**	**3, 5 & 6**
Capitella sp. 1* *Capitella* sp. 2 Eusyllinae spp.	*Scolelepis carunculata*	*Scolelepis lamellicincta* Amphipod sp. 3 Phoxocephalopsid sp. 1

(d) Spring			
1	**2, 4 & 6**	**3**	**5**
Mysella sp* *Capitella sp. 2** Eusyllinae spp. *Tanais* sp.*	*Leptocuma* sp. *Scoloplos* sp.* *Scolelepis carunculata** *Scolelepis lamellicincta*	*Leptocuma* sp.* Golgingid sp. Phoxocephalopsid sp. 1	*Scolelepis lamellicincta**

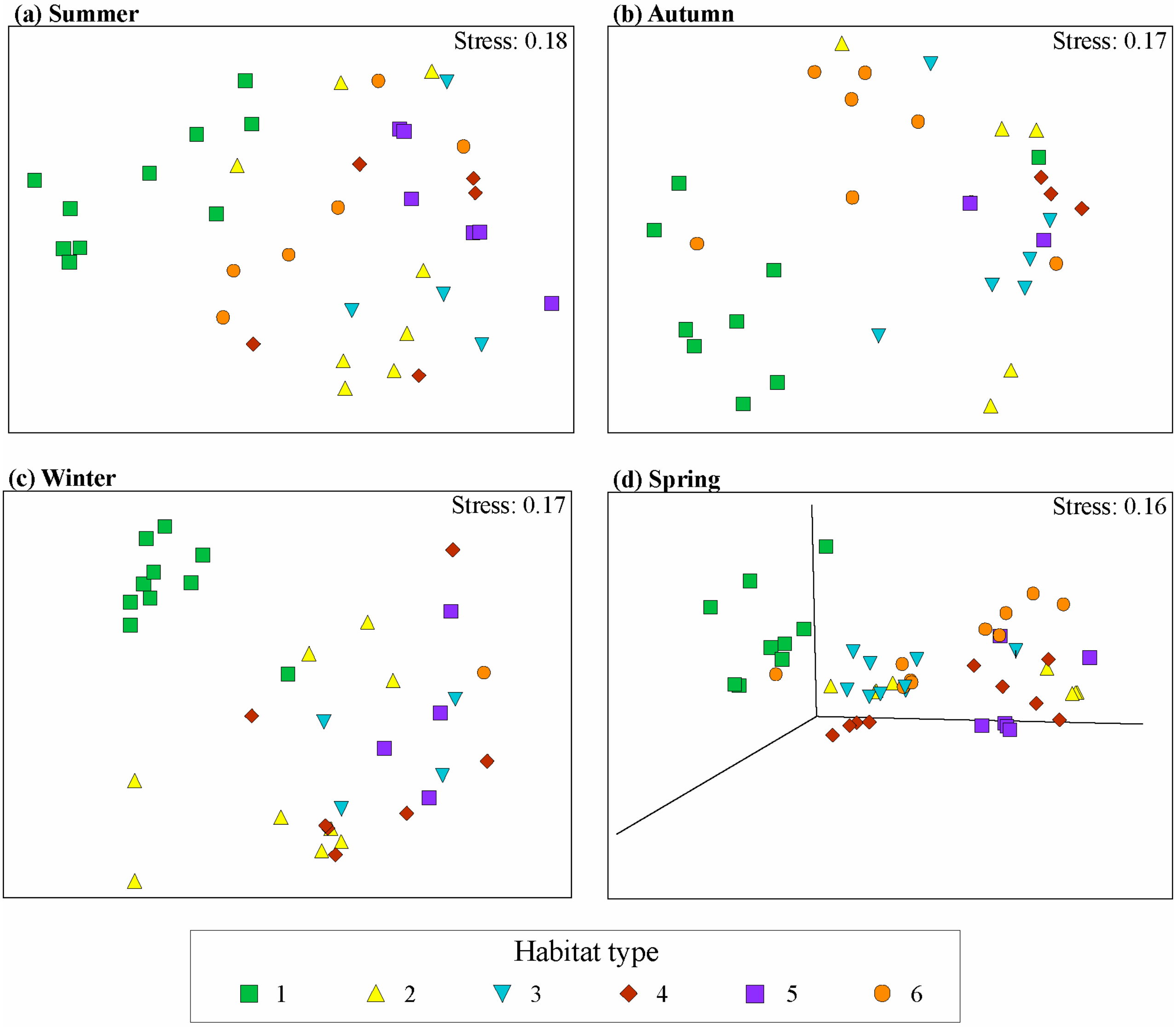


Figure 7.4: MDS ordination of the densities of benthic macroinvertebrate species in zone C at habitat types 1-6 during a) summer, b) autumn c) winter and d) spring of 2000, coded for habitat type.

7.3.4 Matching of multivariate patterns

The order of the rank similarities between each of the habitat types in each of the season/zone combinations were compared by generating a 2nd stage similarity matrix based on Spearman rank correlations calculated between all pairs of season/zone similarity matrices. There was no tendency for the points to group according to season or zone (Fig. 7.5a, b) and one-way ANOSIM demonstrated that there were no significant differences in the pattern of the rank similarities between each of the habitat types in either seasons or zones ($p>0.05$). Thus the RELATE procedure was applied to the rank similarities between each zone in each habitat type in each season, based on the densities of their benthic macroinvertebrate assemblages. The results demonstrated that the rank similarities between habitat types 1-6 were significantly correlated with the rank similarities calculated using data obtained for each of the seven environmental variables which best distinguished those habitat types ($p<0.01$, $\rho = 0.572$).

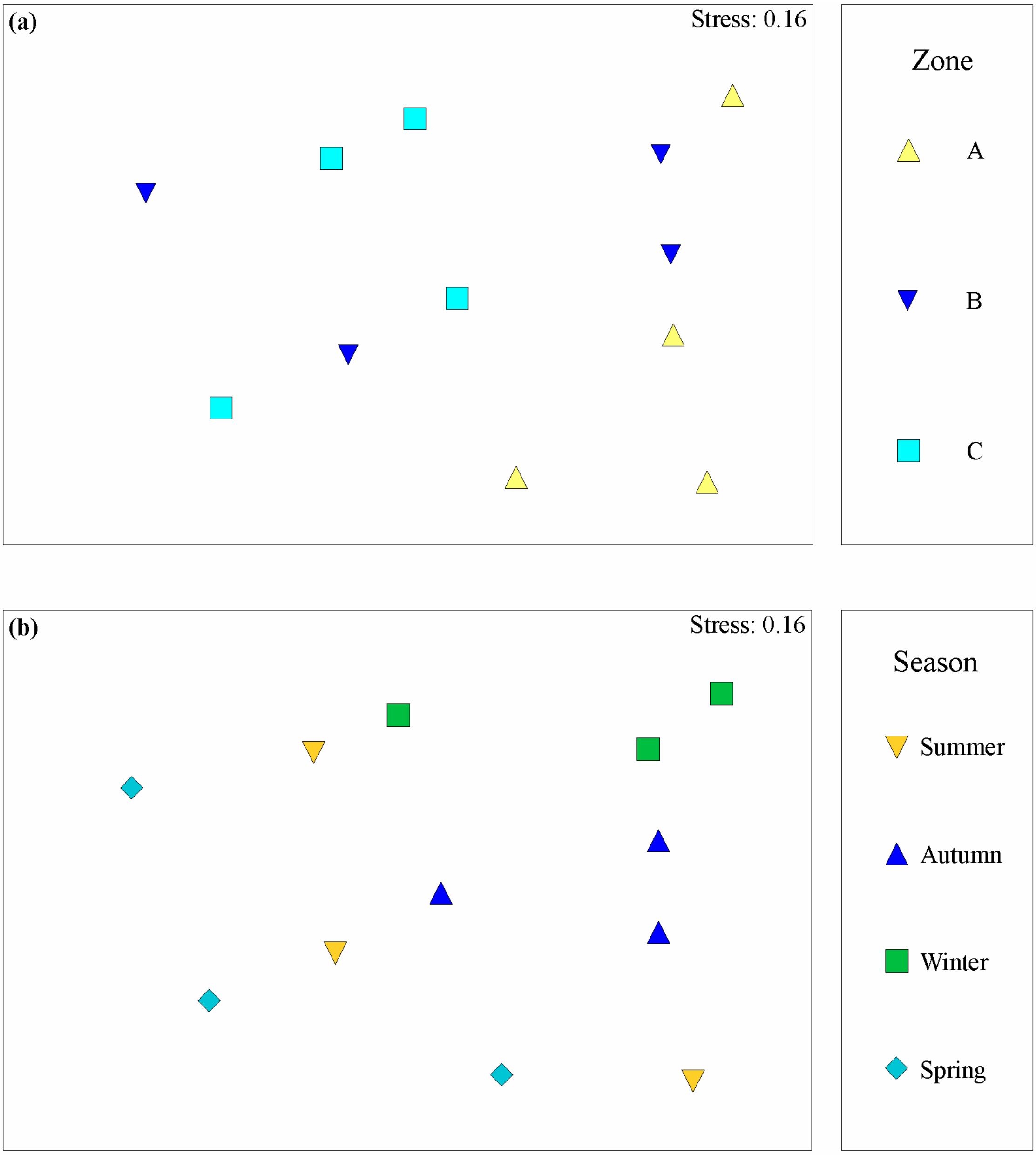


Figure 7.5: Two-dimensional MDS ordination of the second-stage similarity matrix containing the correlations between each pair of similarity matrices constructed from the densities of macrobenthic species in samples collected at habitat types 1-6 in each zone in each of the seasons between summer and spring 2000. The points on the ordination plot have been coded separately for (a) zone and (b) season.

7.3.5 *Differences in benthic macroinvertebrate assemblages among zones and seasons in each habitat type*

Since the results of ANOSIM tests reported previously demonstrated that the compositions of the benthic macroinvertebrate assemblages differed to a greater extent among habitat types than either zone or season, the influence of both zone and season in each habitat type are now examined.

Two-way crossed ANOSIM tests showed that the species composition differed significantly among zones and seasons at each of the six habitat types. The species composition varied to a greater degree among zones rather than seasons in habitat type 1 (Table 7.9a, b). However, global R-statistic values were <0.1 in all other cases, showing that the overall differences in composition among both zones and seasons were negligible in habitat types 2 to 6.

Table 7.9 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in a two-way crossed zone x season ANOSIM test of the benthic macroinvertebrate assemblages at habitat type 1. Results for each of these factors are presented in tables (a) and (b), respectively. S=summer, A=autumn, W=winter and SP=spring. Significant and non-negligible results (*i.e.* R >0.1) are highlighted in boldface.

(a) Zone (p=0.1%; Global R=0.424)

	A		**B**		**C**	
	p	***R***	p	R	p	R
A						
B	5.3	0.051				
C	**0.1**	**0.719**	**0.1**	**0.502**		

(b) Season (p=0.1%; Global R =0.113)

	S		**A**		**W**		**SP**	
	p	R	p	R	p	R	p	R
S								
A	57.2	0.013						
W	**0.1**	**0.132**	31.4	0.010				
SP	**0.1**	**0.234**	**2.0**	**0.110**	**0.1**	**0.18**		

On the three-dimensional MDS ordination plot derived using the densities of the various benthic macroinvertebrate species in habitat type 1, the majority of the samples for zone C formed a group in the right of the plot, that lay to the right of most of those from zone B, while most of those for zone A lay towards the bottom of the middle part of the plot (Fig. 7.6a). When the data were coded for season, the samples for spring formed a group on the right of the three-dimensional plot and most of those for summer formed a relatively tight group (Fig. 7.6b).

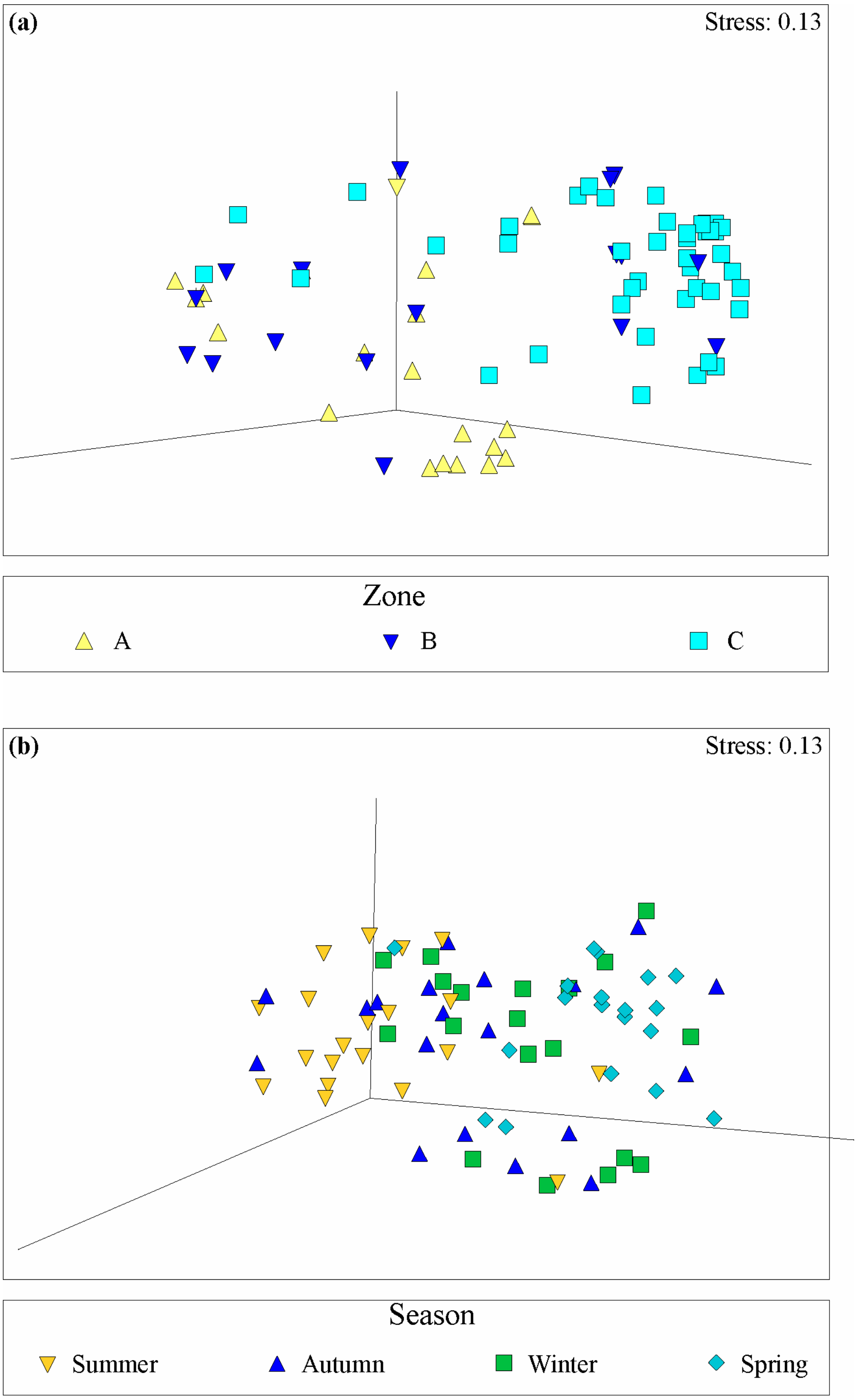


Figure 7.6: Three-dimensional MDS ordination of the densities of benthic macroinvertebrate species in zones A, B and C at habitat type 1 during the summer, autumn, winter and spring in 2000, coded for a) zone and b) season.

Pairwise comparisons among the samples for the three zones in habitat type 1 showed that the species composition in zone C differed significantly from that in both zones A and B (Table 7.9a). Pairwise comparisons among the samples for the various seasons in habitat type 1 showed that the species compositions differed significantly between summer *vs* winter and spring *vs* the other three seasons, that the greatest of these differences were between spring *vs* both summer and winter, but that these differences were relatively small (R-statisic=0.232 and 0.180, respectively) (Table 7.9b).

SIMPER showed that, in habitat type 1 the species assemblage in zone A was typified by enchytraid spp. 3 and 4, coelopid sp. and staphilinid sp, whereas that in zones B and C were typified by *Capitella* spp. 1 and 2, and eusyllinae spp (Table 7.10a). The latter three species also distinguished between zones B and C, as their densities were far greater in the latter zone. SIMPER also showed that, in habitat type 1, the compositions of the samples in spring were distinguished from all other seasons by greater densities of *Capitella* sp. 2 and *Mysella* sp. 1, while those in summer were distinguished from those in winter by greater densities of exogoninae spp. in the summer and *Capitella* spp. 1 and 2 in the winter (Table 7.10b).

Table 7.10 Species detected by SIMPER as those most responsible for typifying the benthic macroinvertebrate fauna (see taxa arranged along diagonal cells) and distinguishing the faunas (see taxa arranged along vertical cells) in (a) zones A, B and C and (b) summer (S), autumn (A), winter (W) and spring (SP) at habitat type 1. The zone or season in which distinguishing taxa were most abundant is also provided in each case (see superscripts). Grey shading represents those pairs of zones or seasons that did not contain significantly different compositions (see Table 7.9).

(a) Zone

	A	**B**	**C**
A	Enchytraid sp. 3 Enchytraid sp. 2 Coelopid sp. Staphilinid sp.		
B		*Capitella* sp. 2 Exogoninae spp. Enchytraid sp. 3 Eusyllinae spp. Enchytraid sp. 2	
C	*Capitella* sp. 2$^{(C)}$ *Capitella* sp. 1$^{(C)}$ Eusyllinae spp.$^{(C)}$	*Capitella* sp. 2$^{(C)}$ *Capitella* sp. 1$^{(C)}$ Eusyllinae spp.$^{(C)}$	*Capitella* sp. 2 *Capitella* sp. 1 Eusyllinae spp.

(b) Season

	S	**A**	**W**	**SP**
S	*Capitella* sp. 1 Exogoninae spp. *Capitella* sp. 2 *Pseudopolydora* sp. *Aricidea* sp.			
A		Eusyllinae spp. *Capitella* sp. 2 *Capitella* sp. 1		
W	*Capitella* sp. 1$^{(W)}$ *Capitella* sp. 2$^{(W)}$ Exogoninae spp.$^{(S)}$		*Capitella* sp. 2 *Capitella* sp. 1 Eusyllinae spp.	
SP	*Capitella* sp. 2$^{(SP)}$ Eusyllinae spp. $^{(SP)}$ Exogoninae spp.$^{(S)}$ *Capitella* sp. 1.$^{(S)}$ *Mysella* sp. 1$^{(SP)}$	*Capitella* sp. 2$^{(SP)}$ Eusyllinae spp. $^{(SP)}$ *Mysella* sp. 1$^{(SP)}$	*Capitella* sp. 2$^{(SP)}$ Eusyllinae spp. $^{(SP)}$ *Mysella* sp. 1$^{(SP)}$ *Capitella* sp. 1$^{(W)}$ Enchytraid sp. 3$^{(W)}$	*Capitella* sp. 2 *Mysella* sp. 1 Eusyllinae spp.

7.4 Discussion

The number of benthic macroinvertebrate species recorded in the six habitat types identified in nearshore waters on the lower west coast of Australia ranged from 30-70, whereas that found by Dexter (1984) during seasonal sampling of four different habitats at a similar latitude on the east coast of Australia ranged from 12-48. These comparisons provide strong indications that the diversity of the benthic macroinvertebrate fauna in nearshore coastal waters is greater on the lower west coast than lower east coast of Australia. In contrast, the overall mean density of benthic macroinvertebrates we recorded for our sampling sites on the lower west coast of Australia (604.9 individuals m^{-2}) was far less than the 941.2 individuals m^{-2} recorded by Dexter (1984) for nearshore waters along the east coast of Australia. The relatively low densities of benthic macroinvertebrates on the lower west coast of Australia are almost certainly related to the fact that the waters along this coast are nutrient poor (Caputi *et al.* 1996), which limits the production of the plankton and microphytobenthos that constitute the diet of benthic macroinvertebrates (Whitlatch 1981, Creach *et al.* 1997, Bouillon *et al.* 2002). Furthermore, the diversity and densities of the benthic macroinvertebrate fauna in nearshore waters were typically greater and less, respectively, than in comparable waters elsewhere in the world, *e.g.* southern U.S.A., South Africa, South America and the Middle East (McLachlan 1990, McLachlan *et al.* 1998, Dugan *et al.* 2000, Jaramillo *et al.* 2001).

7.4.1 Differences in benthic macroinvertebrate assemblages among habitat types

The results of this component of the study demonstrated that the compositions of benthic macroinvertebrate assemblages at sites on the lower west coast of Australia were influenced markedly by the type of habitat in which the site was located. Indeed, the influence of habitat type was shown to be far greater than that of either zone or time of year. Since habitat type 1 contained the greatest number of species, density and taxonomic diversity and the most distinct fauna, it is highly relevant that this habitat type was the most sheltered and possessed the greatest amount of sedimentary organic material, a potential food source both for themselves and their prey (see Chapter 4). The tendency for the above three variables to be greatest in the most protected habitat in a region, particularly if it includes some seagrass, is consistent with the results of a number of other studies (*e.g.* Hutchings 1981, Dexter 1984, Edgar 1990, Edgar and Shaw 1995b, Brazeiro 2001).

The benthic macroinvertebrate assemblage in habitat type 1 was characterised by five polychaete taxa that were among the ten most abundant species in this habitat type and were rarely found in the other five habitat types, *i.e. Capitella* spp. 1 and 2 (Capitellidae), eusyllinae spp. and exogoninae spp. (Syllidae), *Aricidea* (Paraonidae). These polychaetes are sub-surface deposit-feeders (Fauchauld and Jumars 1979) and thus belong to a trophic group that attains its greatest densities in environments where turbulence is low and substantial amounts of organic matter, and thus the food of these organisms, are allowed to settle and become incorporated into the subsurface sediment layer (Dexter 1984, 1989, Harkantra and Parulekar 1984, Defeo *et al.* 1992). Furthermore, the absence of marked turbulence provides optimal conditions for deposit-feeders, by allowing these organisms to remain within their burrows without risk of becoming dislodged (Sanders 1958, Whitlatch 1981, Barnes and Hughes 1998). Moreover, the presence of a substantial amount of sedimentary organic matter as a food source allows different species of deposit-feeding macroinvertebrates to coexist and attain elevated densities (Levinton 1979, Glasby *et al.* 2000).

Hutchings (1981) provided several possible explanations for increased density and diversity in areas where seagrass is present as opposed to areas of bare substrate. Firstly, seagrasses stabilise sediments and dampen current and wave action, which may allow for increased larval settlement and also prevent resuspension of adults and juveniles. Secondly, the presence of seagrass may provide a physical barrier or shelter from predators. It is therefore likely that the protection offered by seagrasses at habitat type 1 accounts, in part, for the greater numbers of species and densities of benthic macroinvertebrates at these sites. Thirdly, the presence of seagrass provides a greater degree of structural complexity to the nearshore environment, which may increase the number and variety of available niches for the organisms to inhabit (Hutchings 1981). Although the samples collected at habitat type 1 were not taken directly amongst the seagrass beds, the stabilising, protective and structural effects of seagrass beds are likely to extend outwards towards the shore (Krebs 1994). Hutchings (1981) also stated that seagrass beds may increase the supply of food to the benthos in the form of detritus. Seagrass detritus is a major source of organic input to the nearshore zone in Western Australia, and while recent evidence suggests that invertebrate species do not use seagrass detritus directly as a food source they have been shown to assimilate epiphytic microalgae that are associated with it (Vizzini and Mazzola 2003).

Habitat type 6, the most exposed to wave action, also contained a particularly distinct assemblage of benthic macroinvertebrates, which was characterised by four species of crustaceans, *i.e.* phoxocephalopsid sp. 1 (Amphipoda), oniscid sp. (Isopoda), *Hippa australis* (Decapoda) and *Leptocuma* sp. (Cumacea), and by the bivalve mollusc *Donax collumbella* (Donacide) and the polychaete *Pisionidens* sp. (Pisionidae). The possession by these species of either hard exoskeletons, shells or a cuticle and appreciable mobility enable them to cope with the problems posed by the relatively turbulent conditions found in this type of habitat (McLachlan and Hesp 1984, Barnes 1987). Turbulence leads to suspension of organic material in the water column, which together with zooplankton, can then be filtered as a food source by certain macroinvertebrates (Barnes and Hughes 1998, McLachlan 1990, Defeo *et al.* 1992). In this context, it is relevant that the density of zooplankton was greater at Leighton Beach, a representative of habitat type 6, than at Penguin Island, a representative of habitat type 1 (see Chapter 8) and that most, if not all of the above six macroinvertebrate taxa are capable of filtering food from the water column. Moreover, the frequent flushing of interstitial spaces that occurs in the substrate of exposed habitats maintains the sediments in those habitat types clean, and thereby provides conditions that are crucial for the maintenance of the fine feeding structures of filter-feeders (McLusky and Elliot 1981).

Although the composition of the benthic macroinvertebrate assemblages at the most sheltered habitat (type 1) was the most distinct of all habitat types and clearly very different from that at the most exposed habitat (type 6), the compositions in some sequential pairs of habitat types, *i.e.* 2 *vs* 3, 3 *vs* 4 and 4 *vs* 5, were not significantly different from each other. It is thus relevant that the bivalve *Donacilla* sp. 1 and the polychaetes *Scolelepis carunculata* and *Scolelepis lamellicincta* were all among the suite of species that typified habitat types 2, 3, 4 and 5. These filter-feeding and burrowing species thus apparently have an affinity for habitats where the moderate wave activity will lead to a sufficient suspension of organic material as a food source, and yet turbulence is not sufficiently strong to dislodge the organisms from the sediment. Soft-bodied species of *Scolelepis* in similar environments in Tahiti have been observed rapidly retracting into the sediment at the approach of a wave and protruding their palps into a shallow film of water as the wave receded, and thereby intercepting organic material in the water column (Frouin *et al.* 1998). Although *Donacilla* sp. 1, *S. carunculata* and *S. lamellicincta* were each part of the suite of typifying species for habitat types 2-5, the densities of the first two species decreased from habitat types 2 to 5, whereas the density of the third species exhibited the opposite trend. Those changes thus contributed to the gradational change that occurred in the composition of the benthic macroinvertebrate fauna between habitats types 2 and 5.

When the compositions of the benthic macroinvertebrate assemblages in each corresponding zone of the six habitat types were compared using ANOSIM, and considering that an R-statistic value <0.1 reflects a negligible difference, no conspicuous differences were found among the faunal compositions of zone A in those habitat types. However, differences were found among the faunal compositions of both zones B and C in the different habitat types, particularly in the case of zone C in habitat type 1 *vs* that zone in all other habitat types. It is not surprising that the difference among habitat types was most marked in zone C as this zone, unlike the other two zones, is covered by water throughout the tidal cycle. Thus, during the course of a tidal cycle, it is more stable than zones A and B and therefore its assemblage, within a given habitat type, is less likely to vary.

The joint Δ^+ and Λ^+ tests revealed that for each of the corresponding zones, the taxonomic structure of the assemblages at the majority of the habitat types was reflective of that of the regional benthic macroinvertebrate species list. The only exception was the assemblage in zone C at habitat type 1, which fell outside its 95% confidence interval in the direction of greater Λ^+, but lesser Δ^+, despite the fact that it contained the greatest mean numbers of species, mean Δ^+ and mean Λ^+ of all the habitat types. This was due to the fact that deposit feeders from the class polychaeta dominated the fauna at habitat type 1, and there were proportionally fewer representatives of other higher taxa at this habitat type, relative to its number of species, than was recorded for the region. It follows that this habitat type, with its high sedimentary organic content being indicative of a detritus based food web, is capable of supporting a wide range of higher taxa relative to the other five habitat types, but which comprise only those functional feeding groups that are suited to such a food base. Thus, the influence of the physical characteristics of certain habitats is such that their inhabitant fauna are relatively specialized and consequently not representative of the suite of fauna found in the region.

The results of the RELATE procedure used in this study demonstrated that differences in the enduring environmental characteristics that distinguished the various habitat types identified along the lower west coast of Australia accounted for approximately 58% (ρ=0.572) of the variation in the benthic macroinvertebrate assemblages among those habitat types. The compositions of benthic macroinvertebrate assemblages on sandy beaches are thought to be regulated primarily by species responses to variations in physical factors (McLachlan 1983, McLaclan *et al.* 1993). There is however, a noticeable lack of information regarding the extent to which they are influenced by biological factors, *e.g.* competition and predation. The interaction between such complex factors may account for considerable variation amongst such assemblages and may help to explain the remaining variation among those in the present study (Defeo 1993, 1996, Defeo *et al.* 1997).

7.4.2 Comparisons among the assemblages in different zones and seasons in each habitat type.

The global R-statistic values demonstrated that the compositions of the benthic macroinvertebrate fauna only differed markedly among zones in the most sheltered habitat type (1) and that any zonal differences in the other 5 habitat types were negligible. It is highly relevant that the zonal differences in habitat type 1 were greatest between zone A, which receives swash only during high tide, and zone C, which is always fully submerged. In zone A, which typically contains relatively damp or dry sediment and deposits of macrophytes, the fauna was characterised by a number of air-breathing and detritivorous oligochaetes and insects. These taxa are adapted to living in drier conditions, *i.e.* a protective exoskeleton enables insects to withstand desiccation, while marine oligochaetes are adapted for burrowing into damp subsurface sediment layers on the upper beach level, where rotting macrophytes are often found and can thus be used as a food source (Barnes 1987, Gierre and Pfannkuche 1992, James and Fairweather 1996, Rossi and Underwood 2002). It is noteworthy, that, the accumulations of macrophytes in zone A at habitat type 1 were relatively consistent throughout the year and tended to exhibit long residence periods (see Chapter 4), thereby providing a more stable environment and food source for these organisms at this habitat.

Zone C in habitat type 1, which contained the greatest number of species, density and taxonomic diversity of any zone in any habitat type, was characterised by relatively large densities of deposit-feeding polychaetes. These organisms are able to thrive in this particular zone because the relative lack of turbulence results in the deposition of an abundant source of food. Although the fauna in zone B, the region in which the beach face was subjected to fluctuating swash, was also characterised by these species, their densities were far lower. The fact that species with the above morphological and deposit-feeding characteristics also typify zone B in habitat type 1, reflects the fact that even the swash zone is never subjected to heavy wave action in this habitat type.

The compositions of the benthic macroinvertebrate assemblages along the lower west coast of Australia also underwent seasonal changes in habitat type 1. The composition was most distinct in spring, due to the presence of particularly large densities of *Capitella* sp. 2, a eusyllinae species and *Mysella* sp. 1. These increases in density presumably reflect marked increases in reproductive activity in response to the increases in water temperature and light intensity that occur in this season (Leber 1982, Barnes 1987).

The lack of a significant difference in the composition of the benthic macroinvertebrate fauna among the different zones and seasons at habitat types 2 to 6 parallels the situation recorded for habitats elsewhere in the world, where there is turbulence (Dexter 1984, Defeo *et al.* 1992, McLachlan 1990, James and Fairweather 1996). The above authors have attributed the lack of such differences to a greater small-scale spatial and temporal variation in the fauna of less stable environmental conditions in exposed habitats. Such small-scale variation can be attributed to the transportation of fauna between zones in response to the substantial wave activity that is found in habitat types 2-6.

The results of this component of the study have demonstrated that the composition of the benthic macroinvertebrate assemblage in the most protected habitat type along the lower west coast of Australia differed markedly from those in the other five habitat types, which were more exposed to wave activity.

Chapter 8. Characteristics of zooplankton assemblages in nearshore waters along the lower west coast of Australia

8.1 Introduction

Zooplankton are small planktonic fauna and are found in almost all nearshore waters (*e.g.* see review by McLachlan 1983, van der Spoel and Heyman 1983, Brown and McLachlan 1990, Kingsford 1995, Noda *et al.* 1998, Shaw and Robinson 1998, Lund and Davis 2000). Practically all nearshore fauna are represented in the zooplankton during at least one stage in their life cycle, *i.e.* at the egg, larval or adult stage (Newell and Newell 1963), and the assemblages of these planktonic organisms are thus highly diverse. Zooplankton typically range between 53 µm to greater than 1 mm in size, and can be broadly classified on the basis of the proportion of their life that is spent in the water column. Thus, holoplanktonic organisms remain in the plankton throughout their lives and include many species of copepods, cladocerans and rotifers, meroplankton spend only the early stages of their lives as pelagic organisms and comprise the larvae of many benthic invertebrates, benthic chordates and ichthyoplankton, while tychoplankton are those organisms that are benthic-dwellers but migrate periodically into the water column for feeding, reproduction or dispersal purposes (Brown and McLachlan 1990, Kennish 1990).

Zooplankton are the main grazers of phytoplankton, which are the world's most important source of primary production (Kennish 1990, Helleren and John 1997), and are a major source of food for larval, juvenile and adult fish in nearshore waters (*e.g.* Gaughan 1992, Hyndes *et al.* 1997, Jenkins *et al.* 1998, Schafer *et al.* 2002). Studies on the characteristics of zooplankton assemblages are thus crucial for interpreting the trophic inter-relationships that occur in nearshore marine waters (Maloney *et al.* 1991, Gaughan and Potter 1994). Moreover, while the distribution of these planktonic organisms is known to be inherently patchy (which has been attributed to schooling, co-active clustering for trophic interactions and/or spawning activity, *e.g.* Hamner and Carlton 1979, Davis *et al.* 1992, Noda *et al.* 1998), spatial differences in the characteristics of nearshore zooplankton assemblages are also useful indicators of variability in the surrounding physical environment (Karjalainen *et al.* 1996, Helleren and John 1997, Shaw and Robinson 1998, Pagés and Gili 1991, Gaughan and Fletcher 1997, Archambault *et al.* 1998).

Many zooplankters are distributed passively, and differences in hydrodynamic regimes thus play a major role in influencing where they occur. Spatial differences in zooplankton composition have therefore been related largely to differences in oceanographic and climatic conditions at global and national scales, *e.g.* prevailing ocean currents and water temperature (van der Spoel and Heyman 1983), and variability in wave activity and local current patterns at regional and local scales (Mileikovsky 1973, Mills and D'Adamo 1995, Jenkins *et al.* 1998, Shanks *et al.* 2003). However, since these planktonic assemblages usually also contain the early life-cycle stages of benthic organisms, their characteristics are also likely to be influenced by the geophysical characteristics of the nearshore substrate and the extent to which that substrate contains vegetation (Jones and Short 1995). Several workers have identified significant differences in the assemblages of these organisms among nearshore locations that differ both in their hydrodynamic and geophysical characteristics (*e.g.* Archambault *et al.* 1998, Shanks *et al.* 2003).

The distribution of zooplankton is also known to vary over a range of temporal scales, the most well-documented of which is the vertical migration between the substrate and water column that is undertaken by many taxa between day and night (*e.g.* Alldredge and King 1980, Jacoby and Greenwood 1989, Department of Environmental Protection 1996, Mauchline 1998, Shaw and Robinson 1998). Such migrations have been attributed to diel changes in a range of environmental conditions, such as light intensity, temperature and hydrostatic pressure (Huntley 1985). Differences in lunar and tidal phases have also been shown to influence the extent and frequency of vertical migrations undertaken by zooplankton in nearshore marine waters (*e.g.* Alldredge and King 1980, Heath *et al.* 1988, Rowe and Epifanio 1994). Moreover, several other workers have identified longer-term changes in the characteristics of zooplankton in coastal waters, such as among seasons (*e.g.* Jacoby and Greenwood 1989, Webber *et al.* 1996, Helleren and John 1997, Calbet *et al.* 2001) and years (*e.g.* D'Adamo 1992, Gaughan and Fletcher 1997). These temporal differences have been attributed to changes in water temperature, currents, wave action, salinity and advection patterns.

Despite the importance of zooplankton in nearshore waters, both as a component of the food web and as indicator of habitat type, the large majority of research on the assemblages of these organisms has been carried out in either deeper offshore waters, rivers or estuaries (*e.g.* Emery 1968, Gaughan and Potter 1994, 1995, Gaughan and Fletcher 1997, Havens 1998, Kobayashi *et al.* 1998, Lund and Davis 2000). Moreover, of the small number of studies that have been carried out on zooplankton that occur in waters along the lower west coast of Australia (*i.e.* Environmental Resources of Australia 1971a, b, McLachlan and Hesp 1984, Department of Environmental Protection 1996), none have attempted to determine whether spatial differences in those assemblages were related to differences in nearshore marine habitat type.

The main objective of this component of the study was thus to ascertain whether the characteristics of the zooplankton assemblages in the nearshore marine waters along the lower west coast of Australia differed significantly among a selection of the different habitat types that were identified quantitatively by Valesini *et al.* 2003 (also see Chapter 3), and which differed broadly in the extent to which they were exposed to wave activity and the presence of any submerged vegetation. The extent of any diel, seasonal and interannual differences in the characteristics of these zooplankton assemblages were also examined at each of these habitat types. Collection of such data provided a basis to test the following specific hypotheses.

1) The habitat type(s) that are least exposed to wave activity will contain the greatest density of zooplankton and the highest number of taxa.
2) The zooplanktonic assemblage at the habitat type that is most exposed to wave activity will be characterised, to a far greater extent than the most sheltered habitat type, by taxa that are hard-bodied and/or good swimmers.
3) The density of zooplankton and number of taxa will be greater at night than during the day due to the nocturnal migrations of meroplanktonic and tychoplanktonic organisms from the benthos into the water column. Such vertical migrations will also lead to significant differences in the composition of the zooplankton assemblages between day and night.
4) The number of taxa and density of zooplankton will be greater in summer than in winter due to more favourable conditions for reproduction, growth and survival, *e.g.* warmer water temperatures and lower wave activity.
5) The extent of diel and seasonal differences in the composition of the nearshore zooplankton will be greatest at the most sheltered habitat type, where the low level of water turbulence and thus mixing of the water column will facilitate greater detection of those taxa that migrate vertically between day and night, and the shallowness of those waters will lead to more extreme seasonal changes in water temperature.

8.2 Materials and Methods

8.2.1 Sampling regime

Zooplankton were sampled at three of the six nearshore habitat types that had been identified quantitatively by Valesini *et al.* (2003) along the lower west coast of Australia, *i.e.* habitat types 1, 2 and 6 (also see Chapter 3), which differ mainly in the extent to which they are exposed to wave activity and the presence of seagrass. Thus, habitat type 1 is highly sheltered from wave activity and contains dense seagrass close to shore, habitat type 2 is moderately sheltered to wave activity and contains patches of nearshore seagrass and habitat type 6 is relatively exposed to wave action and has no seagrass growing on its sandy substrate.

Zooplankton were collected at water depths of *ca* 1 m in each of the three habitat types during both the day and night in each season between summer 2000 and spring 2001. Five replicate samples were collected at each site on each sampling occasion. Moreover, to reduce the chance of the resultant data being unduly affected by any atypical samples, the timing of collection of these replicates was staggered over one to two weeks in the middle of each season. A conical 150 µm mesh plankton net with a mouth diameter of 0.36 m and length of 1.50 m, was used to sample the zooplankton. The net tapered to a 0.12 m wide cod-end, to which a canister, 0.14 m in height, was attached. The canister contained a small window covered with 150 µm mesh, which thus allowed water to filter through the net, yet retained all zooplankton. A mesh size of 150 µm was specifically chosen for this study, as it was sufficiently small to retain the large majority of zooplankters that would be able to be detected by fish (*i.e.* meso-zooplankton and macro-zooplankton, which are greater than 202 µm in size; Brown and McLachlan 1990, Kennish 1990), yet large enough to maintain an efficient rate of water filtration by enabling the passage of very small suspended sediment particles.

Each replicate sample was collected by hand-towing the net along a 100 m transect that lay parallel to the shoreline. During each tow, the net was held just below the surface of the water column to reduce the potential for sediment to clog the net. The volume of water filtered through the net during each tow was measured by a flowmeter that was fitted, off centre, in the mouth of the net (Jacoby and Greenwood 1989, Jenkins *et al.* 1998). The zooplankton retained in each sample were immediately fixed in 5% formalin buffered in seawater.

In the laboratory, each zooplankton sample was passed through a 500 µm sieve to remove any large debris, such as detached plant matter. All material retained on the sieve was transferred to a container and the sample diluted to a standard volume of 200 ml using 70% ethanol. On the small number of occasions when the volume of material retained on the sieve exceeded 200 ml, the sample was split either by half or quarters using a folsom plankton splitter (Wickstead 1976), and one portion of the sample was then diluted to the standard volume of 200 ml. If a considerable amount of sand remained in a sample, Ludox (TM-50 colloidal silica) was used to extract the organic matter, *i.e.* including zooplankton, from the inorganic material. Samples were then stained with Rose Bengal to improve the ability to detect zooplankters.

After agitating each 200 ml sample to suspend all zooplankton, three replicate subsamples were extracted without replacement. The volume of these subsamples was either 0.5, 1 or 2 ml, depending on the density of zooplankton in the original sample. Zooplankers in each subsample were then identified to the lowest possible taxon using dissecting and compound microscopes. The numbers of zooplankters of each taxon in each subsample were corrected to that found in a constant volume of 1 ml and, where necessary, were multiplied by the number of times the original sample had been split. The numbers of each taxon were then converted to a density (*i.e.* number of zooplankters 1 m^{-3}), and the mean density of each taxon in each replicate sample calculated.

8.2.2 Statistical analyses

8.2.2.1 Univariate analyses

In order to ascertain the type of transformation (if any) the data for zooplankton density and number of taxa required to broadly satisfy the assumptions of constant variance and normality for Analysis of Variance (ANOVA), the extent of any linear relationship between the mean in each habitat type on each sampling occasion (dependent variable) and the associated standard deviation (independent variable) was determined for each of these factors (Clarke and Gorley 2001). The results of these regression analyses indicated that the data for zooplankton density required a log (n+1) transformation, while that for number of taxa did not require transformation.

Four-way ANOVA was then used to determine whether the density of all zooplankton and the number of taxa in the replicate samples differed significantly between habitat types, seasons, day and night and/or years. Each replicate sample was independent of all other samples and all main effects were considered fixed. The null hypothesis that the values for the above dependent variables did not differ significantly among any of the independent variables was rejected when the significance level (p) was <0.05. When ANOVA detected a significant difference for an interaction term or a main effect not involved in a significant interaction, plots of the marginal means (back-transformed where necessary) and 95% confidence intervals of each level of the relevant factor(s) were used to ascertain the source of those differences.

8.2.2.2 Multivariate analyses

All of the following multivariate analyses were carried out using the PRIMER 5.2 statistical package (Clarke and Gorley 2001).

The Bray-Curtis similarity coefficient was employed to produce a similarity matrix from the log (n+1) transformed mean densities of the various zooplankton taxa recorded in each habitat type, season, year and during the day or night. This matrix was subjected to two-dimensional non-metric Multidimensional Scaling (MDS) ordination, and was employed in one-way Analysis of similarities (ANOSIM) tests to ascertain whether the composition of the zooplankton assemblages differed significantly overall on the basis of habitat type, season, year and/or time of day. In each of these ANOSIM tests, the null hypothesis that the zooplanktonic composition did not differ significantly on the basis of either of these factors was rejected if the significance level (p) was <5%, and the extent of any significant differences was determined by the size of the associated R-statistic (Clarke 1993).

In order to more fully elucidate the extent of differences in the zooplankton composition on the basis of the various independent factors, the log (n+1) transformed densities of the zooplankton taxa in the replicate samples were separated on the basis of two of those factors and used to produce Bray-Curtis similarity matrices. These matrices were then subjected to two-way crossed ANOSIM to test whether the zooplankton assemblages differed significantly among the remaining two independent factors. The particular factors used in these ANOSIM tests are provided in detail in subsection 8.3.3.2. The densities of the various zooplankton taxa in the replicate samples were employed in these analyses, rather than data which had been meaned to represent any one habitat type on any one sampling occasion, to ensure that a sufficient number of permutations were able to be calculated in each test to produce results that could be interpreted reliably.

When one or two-way crossed ANOSIM detected significant differences in zooplankton composition among the levels of a factor(s), Similarity Percentages (SIMPER; Clarke 1993) was used to ascertain which taxa were most responsible for such differences.

8.3 Results

8.3.1 Mean density of zooplankton taxa in each habitat type

A total of 1 613 486 zooplankters were recorded during this study, after the density of individuals in each sample had been adjusted to number of individuals 1 m^{-3}. These zooplankton were represented by 60 taxa and belonged to 11 identifiable phyla (Table 8.1). The greatest number of individuals was recorded at the relatively exposed habitat type 6, followed closely by that at the moderately sheltered habitat type 2. The total number of zooplankters recorded at the highly sheltered habitat type 1 was *ca* eight times lower than that recorded at the other two habitat types (Table 8.1).

Calanoid copepods were the most abundant taxa by far at habitat types 2 and 6, where they comprised *ca* 63 and 54%, respectively, of the overall number of zooplankton caught (Table 8.1). While these invertebrates were less abundant at habitat type 1, they still contributed *ca* 28% to the total number of individuals and ranked second in terms of abundance at that habitat type. Moreover, *Penilia avirostris* ranked second at the two more exposed habitat types, but the mean density and percentage contribution of this taxon was far greater at habitat type 6. This taxon was also relatively abundant at habitat type 1 (*i.e.* contributed at least 2% to the overall number of zooplankton recorded), but to a lesser extent (Table 8.1). Other taxa that were relatively abundant at all habitat types included the larvacean *Oikopleura* spp. and cyclopoid spp., with the first of these taxa making the greatest contribution to the zooplankton assemblage at habitat type 2, while the latter species was most prevalent at habitat type 6 (Table 8.1). In contrast, harpacticoid spp. contributed 30.5% to the total number of zooplankters recorded at habitat type 1, whereas they represented only 4.4% of the overall number of individuals at habitat type 2 and were not among the taxa that were relatively abundant at habitat type 6.

Table 8.1 Phyla (Ph) (C=Crustacea, N=Nematoda, Ch=Chordata, M=Mollusca, Cn=Cnidaria, A=Annelida, E=Echinodermata, Sa=Sarcodina, Ct=Chaetognatha, Cl=Chelicerata, Un=Uniramia and O=Other), mean density (M; number of individuals 1 m^{-3}), standard deviation (±1sd), rank by density (Rk) and percentage contribution to the sum of the mean densities (%) of each zooplankton taxon in samples collected at habitat types 1, 2 and 6 in nearshore marine waters along the lower west coast of Australia during the day and night in all seasons between summer 2000 and spring 2001. The number of taxa, number of samples collected and the total number of individuals (after the number of zooplankters in each sample had been adjusted to that in 1 m^{-3}) are also provided for each habitat type.

		1				**2**				**6**			
	Ph	Mean	sd	%	Rk	Mean	sd	%	Rk	Mean	sd	%	Rk
Harpacticoid spp.	C	357.4	743.7	30.5	1	415.4	649.1	4.4	4	181.2	167.1	1.8	8
Calanoid spp.	C	323.5	467.0	27.6	2	6047.9	11837.8	63.3	1	5463.4	8056.8	53.6	1
Gammarid spp.	C	105.4	225.2	9.0	3	326.4	702.0	3.4	5	20.2	57.9	0.2	16
Penilia avirostris	C	76.0	343.8	6.5	4	945.0	2554.3	9.9	2	2358.1	7585.8	23.1	2
Nematode spp.	N	68.6	350.2	5.8	5	3.4	14.7	<0.1	40	3.3	17.8	<0.1	34
Decapod larvae (mysis) spp.	C	40.4	85.0	3.4	6	16.6	41.1	0.2	24	7.9	23.9	0.1	27
Oikopleura spp.	Ch	33.5	105.5	2.9	7	461.4	1067.1	4.8	3	257.7	389.4	2.5	6
Cyclopoid spp.	C	24.1	40.4	2.1	8	254.9	372.3	2.7	6	422.9	635.5	4.2	3
Gastropod sp. 1	M	16.2	35.3	1.4	9	73.6	143.8	0.8	11	70.6	145.3	0.7	13
Gastropod sp. 4	M	15.0	40.0	1.3	10	7.6	31.8	0.1	33	18.0	79.8	0.2	19
Cumacean spp.	C	10.3	28.0	0.9	11	11.0	32.3	0.1	29	4.9	15.2	0.1	32
Bivalve spp.	M	9.5	23.3	0.8	12	108.2	258.7	1.1	8	274.1	913.8	2.7	5
Obelia spp.	Cn	9.3	29.4	0.8	13	88.5	287.5	0.9	10	183.0	451.7	1.8	7
Copepod nauplii spp.	C	9.3	24.4	0.8	14	45.9	121.9	0.5	14	47.2	120.2	0.5	14
Polychaete (late stage larvae) spp.	A	9.0	17.8	0.8	15	165.0	256.2	1.7	7	81.4	129.0	0.8	12
Spionid spp.	A	8.3	19.2	0.7	16	51.5	131.0	0.5	13	42.6	106.9	0.4	15
Ostracod spp.	C	7.5	25.3	0.6	17	64.7	227.5	0.7	12	16.3	48.0	0.2	22
Gastropod sp. 3	M	6.2	12.6	0.5	18	23.2	94.4	0.2	20	17.3	59.4	0.2	20
Sagitta spp.	Ct	5.5	22.9	0.5	19	21.2	55.4	0.2	22	4.5	19.3	<0.1	33
Gastropod sp. 2	M	3.8	8.8	0.3	20	25.4	52.5	0.3	19	98.8	343.4	1.0	10
Decapod zoea spp.	C	3.7	10.8	0.3	21	7.9	22.7	0.1	32	8.2	19.0	0.1	25
Cirripedia nauplii spp.	C	3.3	13.2	0.3	22	100.2	284.8	1.1	9	302.7	916.2	3.0	4
Echinopluteus larvae spp.	E	3.3	16.6	0.3	23	8.6	43.5	0.1	30	0.5	2.8	<0.1	41
Polychaete (early stage larvae) spp.	A	3.0	11.4	0.3	24	12.9	46.1	0.1	26	5.0	20.4	0.1	31
Eggs	O	2.7	9.5	0.2	25	20.9	39.1	0.2	23	18.6	104.2	0.2	18
Unidentified a	O	2.1	9.6	0.2	26	5.9	20.3	0.1	35	5.3	21.1	0.1	30
Hydramedusa spp.	Cn	2.1	8.4	0.2	27	35.7	156.2	0.4	16	82.8	176.1	0.8	11
Hydroid sp. 1	Cn	1.9	5.3	0.2	28	36.4	82.8	0.4	15	12.2	33.2	0.1	23
Halacarid spp.	Cl	1.8	10.8	0.1	29	0.8	3.0	<0.1	44	0.8	4.1	<0.1	39

Table 8.1 continued

Cladoceran spp.	C	1.5	7.2	0.1	30	11.2	35.6	0.1	27	114.8	259.7	1.1	9
Serolid spp.	C	1.3	6.1	0.1	31	13.2	51.3	0.1	25	8.2	64.4	0.1	26
Fish larvae	O	1.3	3.4	0.1	32	8.1	26.5	0.1	31	5.7	21.7	0.1	29
Isopod sp. 1	C	1.2	3.6	0.1	33	21.7	59.3	0.2	21	18.7	46.3	0.2	17
Hyperid spp.	C	0.7	4.8	0.1	34	1.0	4.2	<0.1	42	0.2	2.1	<0.1	48
Megalopae sp 1	C	0.6	3.4	<0.1	35	0.4	3.7	<0.1	45				
Lucifer sp.	C	0.5	3.1	<0.1	36	0.3	2.3	<0.1	48	0.3	2.7	<0.1	46
Tanaid spp.	C	0.5	3.1	<0.1	37								
Culicid spp.	Un	0.5	3.2	<0.1	38								
Radiolarian spp.	S	0.4	2.5	<0.1	39								
Gnathid spp.	C	0.4	2.3	<0.1	39	0.3	2.3	<0.1	50				
Ascidian larvae spp.	Ch	0.3	2.0	<0.1	41	11.2	35.5	0.1	28	9.5	42.2	0.1	24
Cavoliniid spp.	M	0.3	1.5	<0.1	42	34.7	158.1	0.4	17	16.4	54.0	0.2	21
Siphonophore spp.	Cn	0.2	1.4	<0.1	43	3.5	14.0	<0.1	39	2.1	9.1	<0.1	35
Oribatid spp.	Cl	0.1	1.1	<0.1	44								
Decapod larvae (nauplii) spp.	C					32.2	130.3	0.3	18	6.9	22.1	0.1	28
Ophiopluteus larvae	E					7.5	35.5	0.1	34	1.6	9.9	<0.1	37
Hydroid sp. 2	Cn					5.2	14.1	<0.1	36	0.3	2.4	<0.1	47
Unidentified b	O					4.79	35.2	<0.1	37	0.5	3.0	<0.1	43
Thaliacea spp.	Cn					4.10	25.3	<0.1	38	0.2	1.6	<0.1	49
Megalopae sp. 2	C					3.23	21.6	<0.1	41				
Sphaeromatid spp.	C					0.93	5.3	<0.1	43	0.3	2.0	<0.1	45
Abylopsis spp.	Cn					0.41	2.5	<0.1	46				
Cephalopod spp.	M					0.36	1.8	<0.1	47	0.2	1.4	<0.1	50
Echinoderm spp.	E					0.32	2.8	<0.1	49	2.1	10.2	<0.1	35
Caprellid spp.	C					0.24	1.5	<0.1	51				
Cirripedia larvae spp.	C					0.11	1.0	<0.1	52	0.5	2.8	<0.1	40
Podon sp.	C									1.3	11.2	<0.1	38
Unidentified sp. 4	O									0.5	4.2	<0.1	42
Unidentified sp. 3	O									0.4	3.1	<0.1	44
Isopod sp. 2	C									0.1	0.9	<0.1	51
Number of taxa		**45**				**53**				**51**			
Overall mean density		**1172.5**				**9551.09**				**10199.39**			
Number of samples		**79**				**77**				**77**			
Total no. individuals		**92 668**				**735 464**				**785 354**			

However, while the relative contribution of these copepods was far higher at habitat type 1, their mean density was greatest at habitat type 2 (Table 8.1). Gammarid spp. were also relatively abundant at both the highly and moderately sheltered habitat types 1 and 2, respectively, but were not abundant at the most exposed habitat type (6). Moreover, nematode spp., which are soft-bodied, and decapod larvae (mysis) spp. were abundant only at habitat type 1, whereas bivalve spp., which are hard-bodied, and cirripedia nauplii spp. were abundant only at habitat type 6 (Table 8.1).

8.3.2 Density of zooplankton and number of taxa in different habitat types, seasons, years and between day and night

Four-way ANOVA showed that density of zooplankton differed significantly among habitat types and seasons and between day and night (p <0.001). The two-way interactions between season and year and between habitat type and season were also significant (p <0.001), as were the habitat type x season x year and habitat type x season x diel period three-way interactions (p <0.01). The mean square for habitat type was far greater than those for the other significant main effects, which were, in turn, greater than those for the above interactions (Table 8.2).

Table 8.2 Mean squares and significance levels for four-way ANOVA of the density of zooplankton and number of taxa in samples collected at habitat types 1, 2 and 6 along the lower west coast of Australia during the day and night in each season in 2000 and 2001. "df"=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	Density of zooplankton	Number of taxa
Main effects			
Habitat type (H)	2	16.791***	731.783***
Season (S)	3	6.271***	642.822***
Year (Y)	1	0.579	18.709
Diel (D)	1	3.568***	34.778
Two-way interactions			
H x S	6	1.400***	67.790***
H x Y	2	0.396	36.012*
S x Y	3	2.271***	58.908**
H x D	2	0.071	10.076
S x D	3	0.258	18.033
Y x D	1	0.493	27.713
Three-way interactions			
H x S x Y	6	0.710**	29.127*
H x S x D	6	0.705**	50.781***
H x Y x D	2	0.245	10.609
S x Y x D	3	0.285	17.660
Four-way interaction			
H x S x Y x D	6	0.459	34.499**
Error	185	0.217	11.100

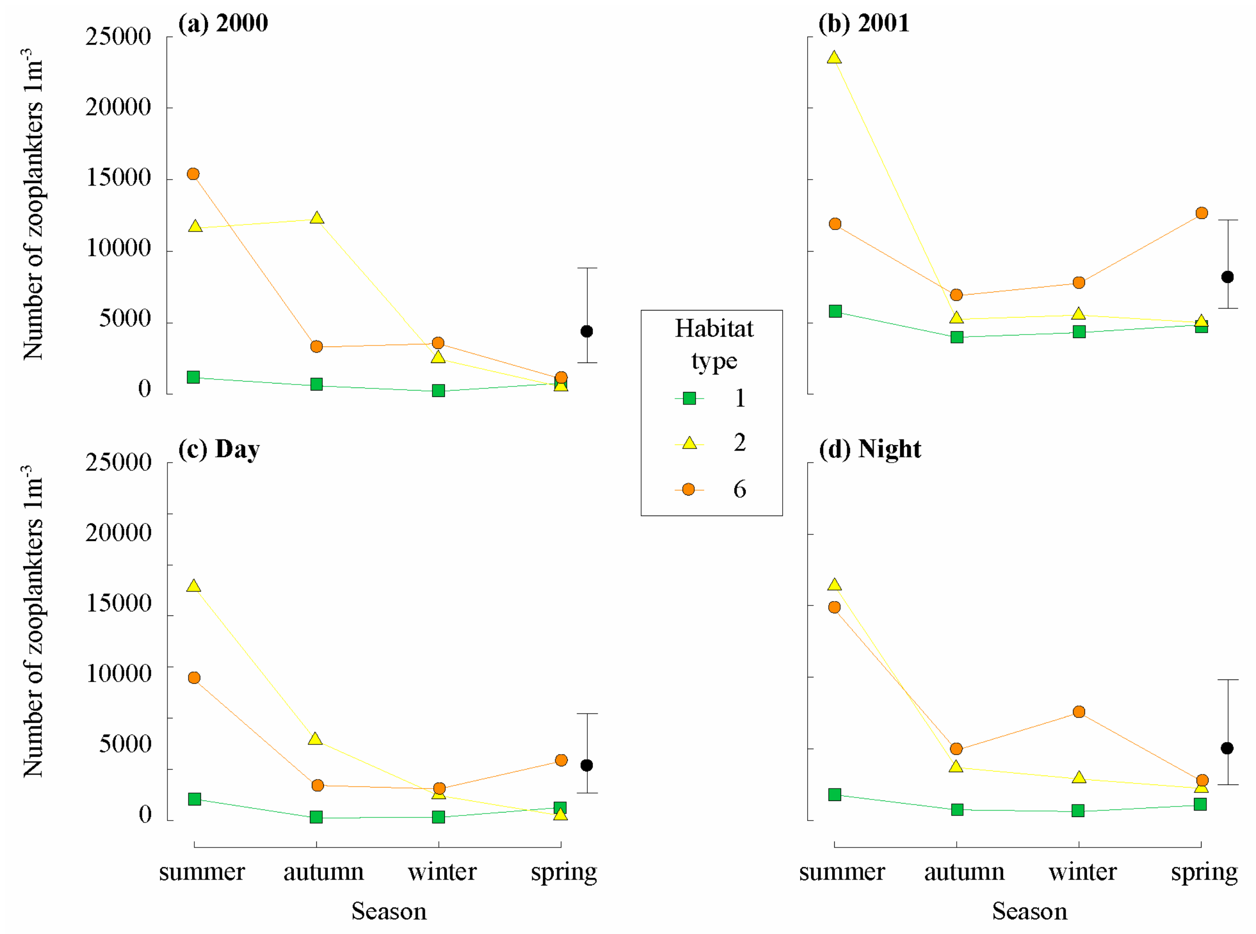


Figure 8.1: Mean (± 95% CI) density of zooplankton at each habitat type and season during (a) 2000, (b) 2001, (c) the day and (d) the night. For the sake of clarity in this figure and Fig. 8.2, the overall mean (± 95% CI) is provided on each plot (denoted by black symbols and lines).

The mean density of zooplankton was almost always greater at habitat types 2 and 6 than at habitat type 1 (Figs 8.1a-d). However, the significant interactions involving habitat type that were detected by ANOVA were due to the fact the extent of the differences in mean zooplankton density among habitat types varied markedly on the basis of each of the three temporal factors. For example, the significant interactions that included habitat type, season and/or year were attributable , in part, to the fact that while the densities of zooplankton at both habitat types 2 and 6 declined markedly from summer and/or autumn to a minimum in spring during 2000 and either autumn or spring in 2001, that at habitat type 1 exhibited very little seasonal variation throughout both of these years (Figs 8.1a and b). Moreover, whereas the mean density of zooplankton at habitat type 2 was greatest in autumn in 2000, it was almost the lowest during this season in 2001 (Figs 8.1a and b). The causes of the significant interactions that involved habitat type, season and/or diel period were exemplified by the fact that while the mean densities recorded during the day at habitat type 2 in summer were markedly greater than those at habitat type 6 in this season, very similar mean densities were recorded at both of these habitat types during summer at night. Moreover, while similar mean densities were recorded at habitat types 2 and 6

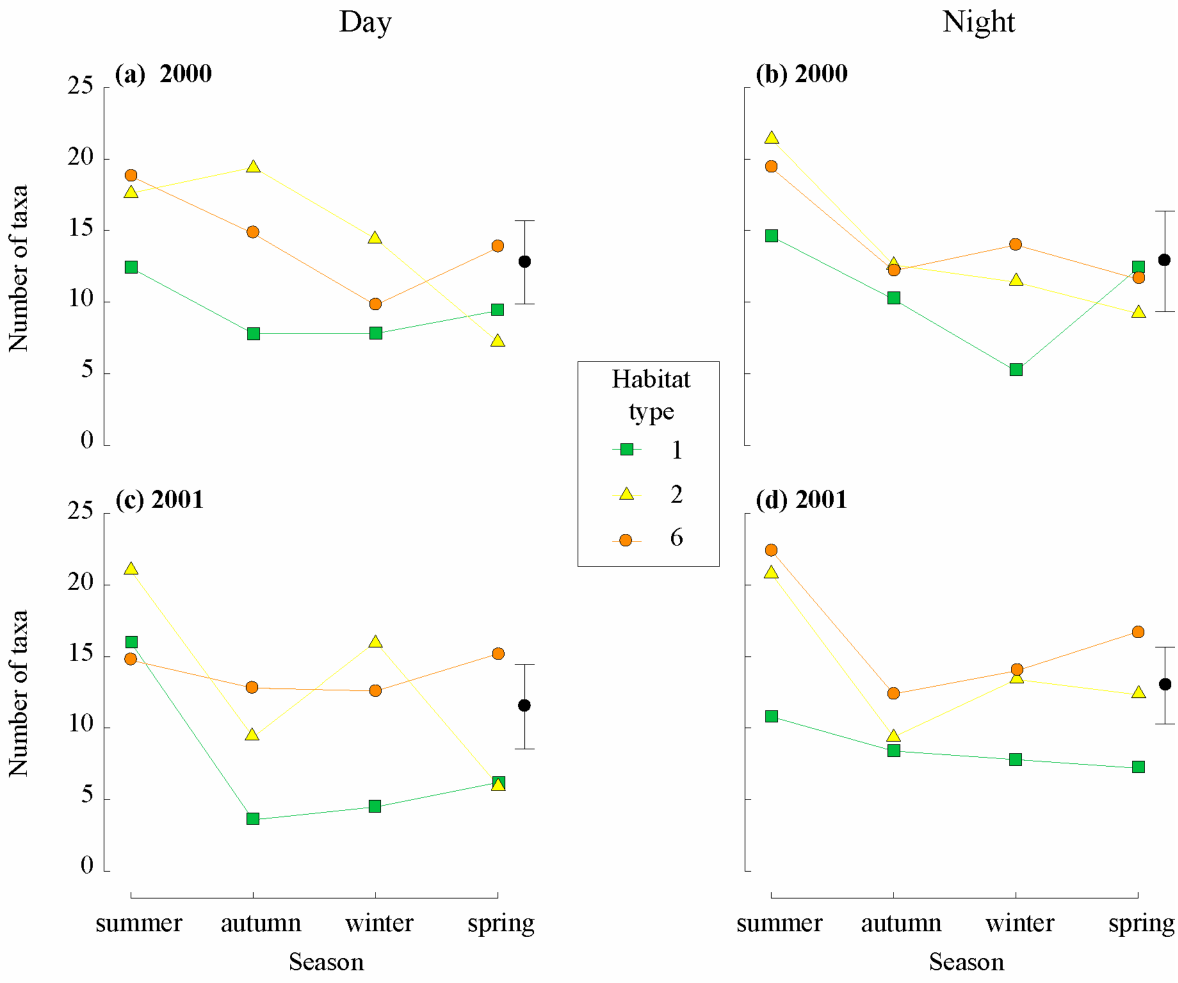


Figure 8.2: Mean (± 95% CI) number of zooplankton taxa at each habitat type and season during the day and night in 2000 (a and b, respectively) and day and night in 2001 (c and d, respectively).

in winter during the day, that at habitat type 6 was considerably higher than that at habitat type 2 in this season at night (Figs 8.1c and d).

Four-way ANOVA showed that the number of zooplankton taxa differed significantly among habitat types and seasons ($p < 0.001$; Table 8.2). The two-way interactions between habitat type and season, season and year and habitat type and year were also significant ($p < 0.001$, 0.01 and 0.05, respectively), as were the habitat type x season x diel period and habitat type x season x year three-way interactions ($p < 0.001$ and 0.05, respectively) and the four-way interaction ($p < 0.01$). The mean squares for habitat type and season were far greater than those for all of the significant interactions, followed by that for the two-way interaction between these two independent variables (Table 8.2).

Plots of the mean number of taxa recorded at each of the habitat types in the various seasons during both the day and night in 2000 and 2001 showed that while the values for this dependent variable fluctuated considerably on the basis of all four independent variables, they were usually the lowest at the highly sheltered habitat type 1 (Figs 8.2a-d). Moreover, the greatest number of taxa was often recorded in summer (Figs 8.2a-d).

8.3.3 *Composition of zooplankton assemblages among habitat types*

8.3.3.1 Overall differences among habitat types

When the mean densities of the various zooplankton taxa recorded at the three habitat types during the day and night and in all seasons between summer 2000 and spring 2001 were subjected to two-dimensional MDS ordination and plotted, the samples from habitat type 6 formed a particularly tight group that lay at one end of the relatively dispersed group of samples from the moderately sheltered habitat type 2. Samples from the latter habitat type intermingled with those from habitat type 1, which were even more widely dispersed (Fig. 8.3).

One-way ANOSIM demonstrated that the composition of the zooplanktonic assemblages differed significantly overall among habitat types (p=0.1%; Global R=0.277), and that the extent of these differences were greatest between the most exposed habitat type 6 and the least exposed habitat type 1 (p=0.1%; R=0.465), and least between habitat types 2 and 6

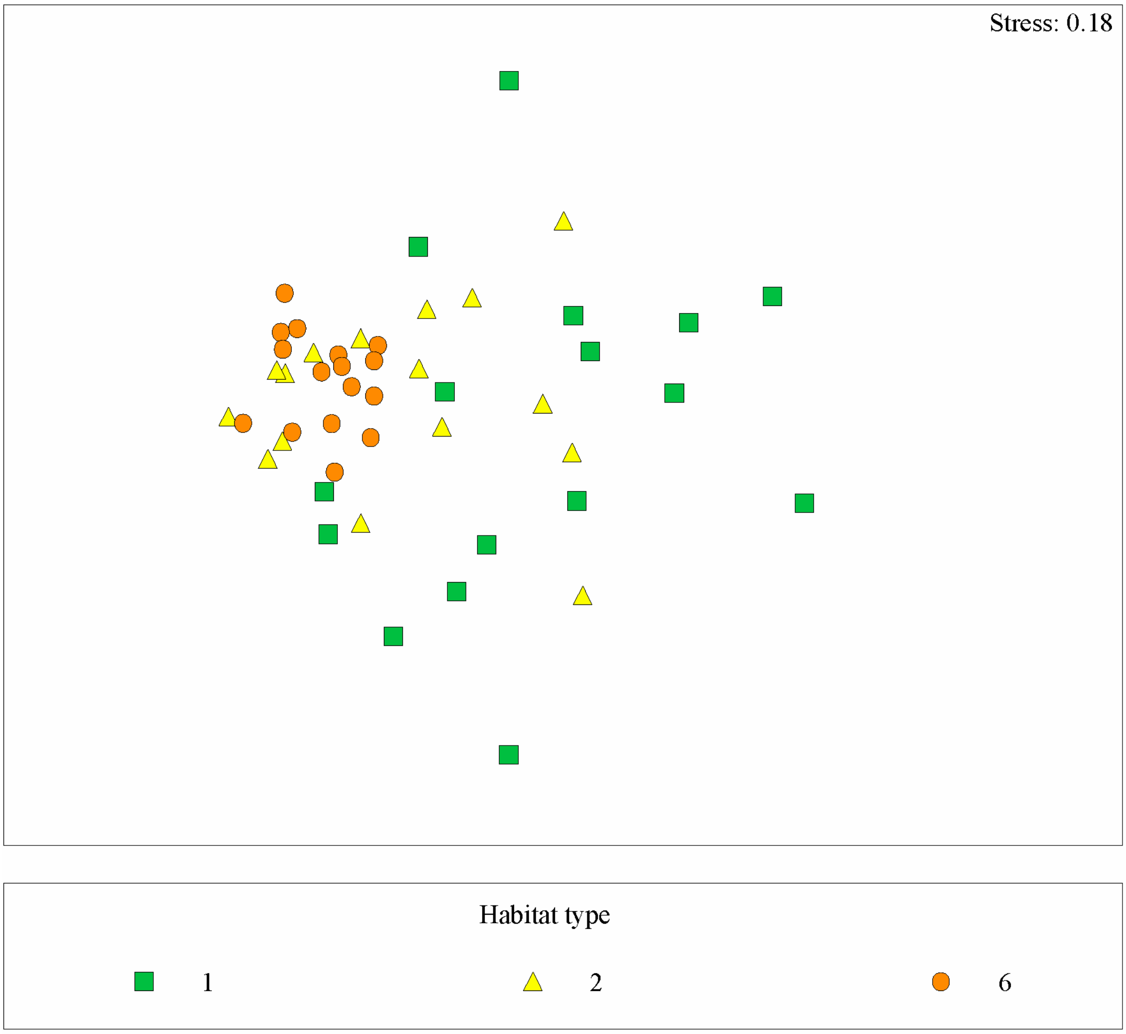


Figure 8.3: Two-dimensional MDS ordination of the mean densities of zooplankton taxa recorded at habitat types 1, 2 and 6 during the day and night in each season between summer 2000 and spring 2001.

(p=0.1%; R =0.143). Similar results were obtained when the densities of the various zooplankton taxa in each replicate sample collected at the three habitat types were subjected to MDS ordination and one-way ANOSIM (data not shown).

The species identified by SIMPER as those that were most responsible for typifying and/or distinguishing the composition of the zooplanktonic assemblages at the various habitat types are presented in Table 8.3. The planktonic fauna at habitat type 6 was shown to be typified by a relatively large number of taxa, while that at habitat type 1 was typified only by consistent occurrences of harpacticoid copepods. While each of the taxa that typified habitat type 2 were also among those that typified habitat type 6, their faunas were distinguished by more regular occurrences and greater numbers of gammarid spp. and ostracod spp. at the first of these habitat types (Table 8.3). The zooplanktonic assemblage at habitat type 1 was distinguished from those at both habitat types 2 and 6 by several of the same taxa, all of which were found in greater numbers at those latter two habitat types. However, some differences did occur, *e.g.* ostracod spp. and isopod sp. 1 distinguished the faunas at habitat types 1 *vs* 2 and not those at habitat type 1 *vs* 6, while the reverse was true for *Obelia* spp. and cladoceran spp. (Table 8.3).

Table 8.3 Species detected by SIMPER as those most responsible for typifying the zooplankton assemblages at habitat types 1, 2 and 6 along the lower west coast of Australia (see taxa arranged along diagonal cells) and distinguishing each pair of those habitat types (see taxa arranged along vertical cells). The habitat type at which each of the distinguishing taxa were most abundant is also provided (see superscripts). "l.s.l."=late stage larvae.

	1	**2**	**6**
1	Harpacticoid spp.		
2	Bivalve spp.(2) *Oikopleura* spp.(2) Polychaete (l.s.l. larvae) spp.(2) Cyclopoid spp.(2) *Penilia avirostris*(2) Ostracod spp.(2) Isopod sp. 1(2) Gastropod sp. 1(2)	Calanoid spp. Harpacticoid spp. Polychaete (l.s.l.) spp. Cyclopoid spp.	
6	*Penilia avirostris*(6) Hydramedusa spp.(6) *Obelia* spp.(6) Polychaete (l.s.l.) spp.(6) *Oikopleura* spp.(6) Cladoceran spp.(6) Bivalve spp.(6) Cyclopoid spp.(6) Calanoid spp.(6)	Gammarid spp.(2) Ostracod spp.(2)	Calanoid spp. Polychaete (l.s.l.) spp. Penilia avirostris Harpacticoid spp. *Oikopleura* spp. Cyclopoid spp. *Obelia* spp. Hydramedusa spp. Bivalve spp.

8.3.3.2 Differences in zooplankton composition among habitat types during the day and night, each season and in both years

The following detailed analyses were focused on determining whether it was necessary to examine the differences in zooplankton composition among habitat types that were described in the previous subsection separately for day and night, season and/or year (*i.e.* to remove the influence of any other confounding factors), or whether it was appropriate to pool the data for one or more of those temporal factors. Two-way crossed ANOSIM was thus used to elucidate whether there were any significant temporal differences in zooplankton composition within any of the habitat types. The densities of the various taxa in the replicate samples were used in these detailed analyses, rather than those that had been meaned across replicates collected at a particular habitat type on a particular sampling occasion, to ensure that a sufficient number of samples were available to provide results that could be interpreted reliably. Moreover, since this ANOSIM test can only employ two factors at a time, it was necessary initially to separate the data on the basis of one of the three temporal factors. The data was thus first separated on the basis of year, since one-way ANOSIM demonstrated that the extent of the overall differences in zooplankton composition were the next greatest on the basis of this factor (see subsection 8.3.4).

Two-way crossed season x diel period ANOSIM tests were thus carried out separately for data recorded in each habitat type and year. The global results of these tests showed that, in all cases, the composition of the zooplankton differed significantly on the basis of both season (p=0.1%; Global R=0.556-0.882) and day *vs* night (p=0.1-0.7%; Global R=0.200-0.726). It was then necessary to determine whether the composition of the zooplankton differed between the two years in the various habitat types. In view of the significant results detected by the above two-way crossed season x diel period ANOSIM tests, the data was separated on the basis of both day and night and habitat type, and two-way crossed season x year ANOSIM tests carried out for each of these subsets of data. The results of these tests demonstrated that the zooplankton composition in each habitat type during both the day and night also differed significantly between years (p=0.1%; Global R=0.518-0.874) and seasons (p=0.1%, Global R=0.552-0.817). Subsequent multivariate analyses to investigate differences in the composition of zooplankton among habitat types were thus carried out separately for day and night, each season and both years.

When the densities of the various zooplankton taxa in the replicate samples were ordinated separately for each combination of the three temporal factors, the samples exhibited a pronounced tendency to form separate groups on the basis of habitat type in most cases (Figs 8.4a-h and 8.5a-h). One-way ANOSIM showed that the zooplankton composition differed significantly among habitat types in each case (p=0.1-0.2%), and that the overall extent of these differences were usually high, *i.e.* Global R >0.500 in all but one case (Table 8.4).

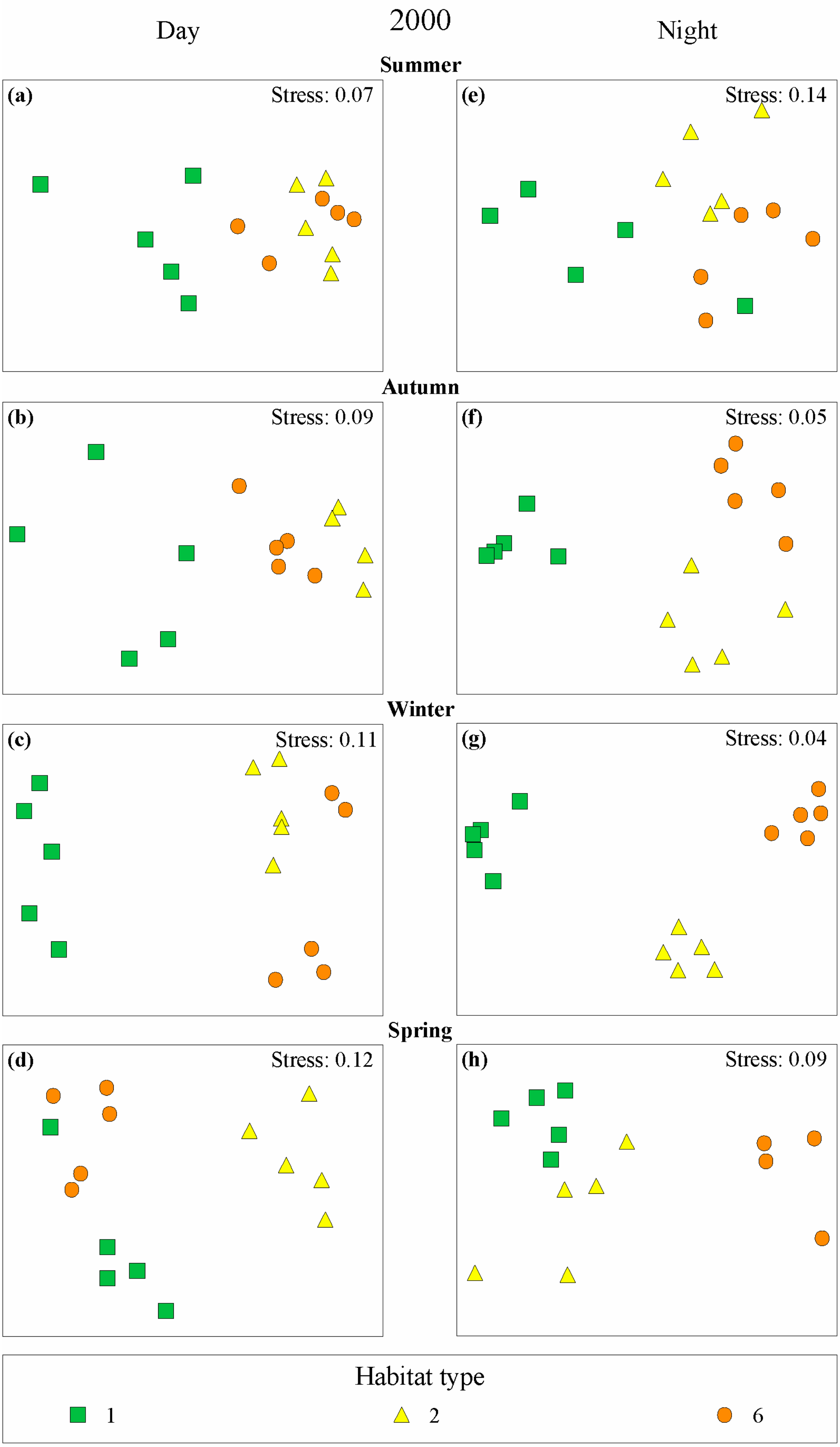


Figure 8.4: Two-dimensional MDS ordination of the densities of zooplankton taxa in replicate samples collected at habitat types 1, 2 and 6 in summer, autumn, winter, and spring 2000 during the day (a-d, respectively) and in each of these seasons at night (e-h, respectively).

Table 8.4 Significance levels (p; %) and R-statistic values for global and pairwise comparisons in one-way ANOSIM tests of the zooplankton compositions at habitat types 1, 2 and 6 during the day and night in summer, autumn, winter and spring in 2000 and 2001. Values in boldface represent those that are significant.

		2000						2001				
Day				1		2			1		2	
				p	R	p	R		p	R	p	R
	Summer	**p=0.2%; Global R=0.550**						**p=0.1%; Global R =0.716**				
			2	**0.8**	**0.828**				**0.8**	**0.724**		
			6	**0.8**	**0.696**	7.1	0.232		**0.8**	**1.000**	**0.8**	**0.419**
	Autumn	**p=0.1%; Global R =0.626**						**p=0.2%; Global R =0.325**				
			2	**0.8**	**0.794**				**0.8**	**0.581**		
			6	**0.8**	**0.680**	**0.8**	**0.750**		**4.0**	**0.344**	6.3	0.188
	Winter	**p=0.1%; Global R =0.787**						**p=0.1%; Global R =0.573**				
			2	**0.8**	**0.984**				**0.8**	**0.763**		
			6	**0.8**	**0.988**	**1.6**	**0.456**		**0.8**	**0.819**	**1.6**	**0.388**
	Spring	**p=0.1%; Global R =0.848**						**p=0.1%; Global R =0.778**				
			2	**0.8**	**0.932**				**4.0**	**0.400**		
			6	**1.6**	**0.656**	**0.8**	**0.984**		**0.8**	**0.932**	**0.8**	**0.850**
Night												
	Summer	**p=0.1%; Global R =0.549**						**p=0.1%; Global R =0.834**				
			2	**0.8**	**0.568**				**0.8**	**1.000**		
			6	**0.8**	**0.660**	**0.8**	**0.448**		**0.8**	**1.000**	**0.8**	**0.548**
	Autumn	**p=0.1%; Global R =0.971**						**p=0.1%; Global R =0.781**				
			2	**0.8**	**0.980**				**0.8**	**0.564**		
			6	**0.8**	**1.000**	**0.8**	**0.884**		**0.8**	**1.000**	**0.8**	**0.688**
	Winter	**p=0.1%; Global R =0.998**						**p=0.1%; Global R =0.749**				
			2	**0.8**	**1.000**				**0.8**	**0.856**		
			6	**0.8**	**1.000**	**0.8**	**1.000**		**0.8**	**1.000**	13.5	0.169
	Spring	**p=0.1%; Global R =0.802**						**p=0.1%; Global R =0.754**				
			2	**0.8**	**0.524**				**5.4**	**0.600**		
			6	**0.8**	**1.000**	**0.8**	**0.925**		**0.8**	**1.000**	8.6	0.500

The pairwise comparisons between habitat types were significant in all cases in each of those ANOSIM tests (p=0.8-4.0%), with only a few exceptions, *e.g.* habitat type 2 *vs* 6 during the day in summer 2000 and autumn 2001 and during the night in winter and spring 2001.

The extents of the significant differences between habitat types 1 and 2 or 1 and 6 were usually higher than those between habitat types 2 and 6 (Table 8.4). The distribution of the samples on the ordination plots presented in Figs 8.4a-h and 8.5a-h showed that while the samples from habitat type 1 were often the most dispersed, they tended to form a particularly discrete group that lay the greatest distance from those representing the other two habitat types, *e.g.* Figs 8.4a and c and Figs 8.5a, c and e. In contrast, most of the samples from habitat types 2 and 6 usually lay adjacent to each other, and formed relatively tight groups in several cases, *e.g.* Figs 8.4b and 8.5a, b, c and e.

The taxa that were shown by SIMPER to characterise the zooplankton assemblages in each of the three habitat types during the day and night in each season and in both years are presented in Tables 8.5a-h. The number of taxa that typified the zooplanktonic assemblages at habitat types 2 and 6 were often greater than at habitat type 1, especially in the case of those samples collected during the day. Some taxa typified the zooplankton in each of the three habitat types on most sampling occasions, *e.g.* harpacticoid spp. and calanoid spp., while others usually characterised only one of the habitat types on several sampling occasions, *e.g.* decapod larvae (mysis) spp. in habitat type 1 at night and bivalve spp. in habitat type 6 during the day and/or night. Other taxa exhibited pronounced affinities for either the highly and moderately sheltered habitat types (*e.g.* gammarid spp.), or the moderately sheltered and relatively exposed habitat types (*e.g.* cyclopoid spp.; Tables 8.5a-h.).

8.3.4 Composition of zooplankton assemblages in different seasons, years and between day and night

When the samples on the MDS ordination plot that was constructed from the mean densities of the various zooplankton taxa recorded at the three habitat types during the day and night in all seasons between summer 2000 and spring 2001 (*i.e.* that presented in Fig. 8.3) were coded separately for day *vs* night, season and year (Figs 8.6a, b and c, respectively), they showed an obvious tendency to form separate groups only on the basis of the latter of those temporal factors (Fig. 8.6c). One-way ANOSIM detected significant differences overall on the basis of both season and year (p=0.1%), and the extent of these differences were slightly higher for year (*i.e.* Global R=0.168 *vs* 0.145). The extents of these significant temporal differences in zooplankton composition were lower than those detected by ANOSIM on the basis of habitat type (*i.e.* Global R=0.277).

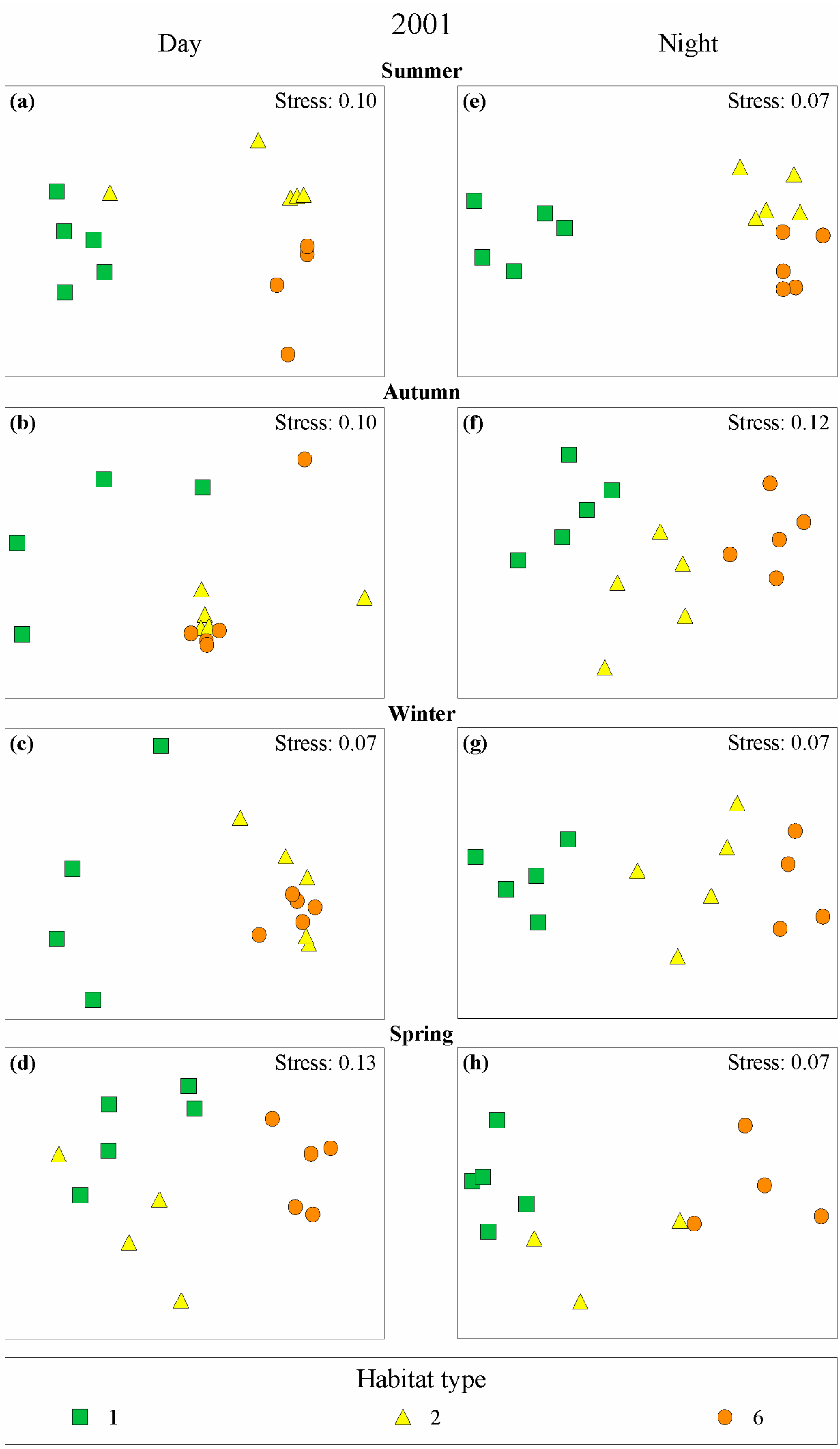


Figure 8.5: Two-dimensional MDS ordination of the densities of zooplankton taxa in replicate samples collected at habitat types 1, 2 and 6 in summer, autumn, winter, and spring 2001 during the day (a-d, respectively) and in each of these seasons at night (e-h, respectively).

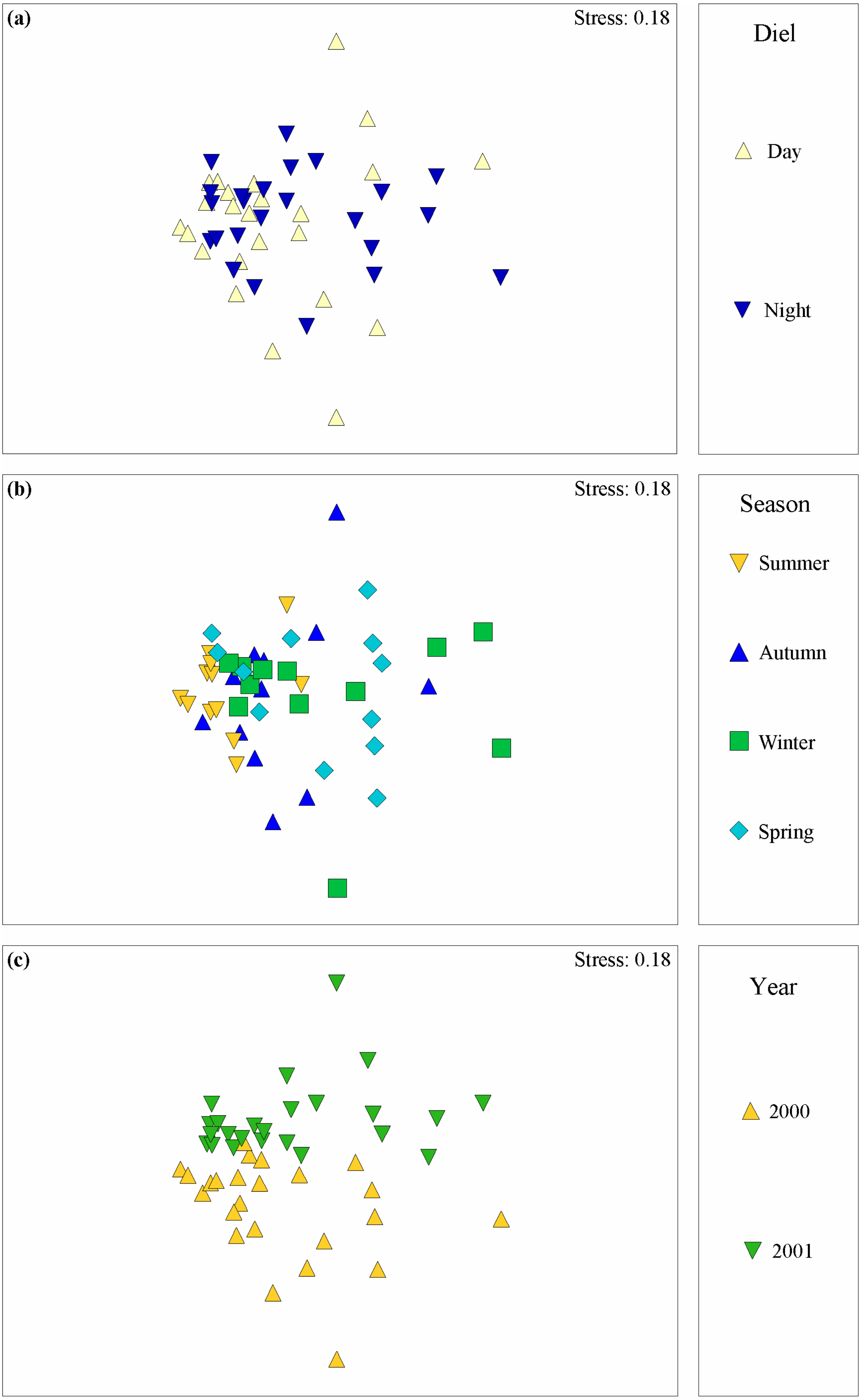


Figure 8.6: Two-dimensional MDS ordination of the mean densities of zooplankton taxa recorded at habitat types 1, 2 and 6 during the day and night in each season between summer 2000 and spring 2001. The samples on the plot have been coded separately for (a) day *vs* night, (b) season and (c) year.

Table 8.5 Regularly abundant zooplankton taxa, as detected by SIMPER, in samples collected at habitat types 1, 2 and 6 during the day and night in (a) summer, (b) autumn, (c) winter and (d) spring in 2000 and in each season in 2001 (e-h, respectively). “l.s.l.”= late stage larvae; “juv.”=juvenile.

(a) Summer 2000

1		**2**		**6**	
Day	Night	Day	Night	Day	Night
Gastropod sp. 1	Calanoid spp.	Bivalve spp.	Polychaete (l.s.l.) spp.	Calanoid spp.	Cirripedia nauplii spp.
Oikopleura spp.	*Oikopleura spp.*	Spionid spp.	Harpacticoid spp.	Cladoceran spp.	Harpacticoid spp.
Cyclopoid spp.	Dec. larvae (mysis) spp.	*Oikopleura spp.*	*Sagitta* spp.	Cyclopoid spp.	*P. avirostris*
Harpacticoid spp.	Cyclopoid spp.	Calanoid spp.	Calanoid spp.	Gastropod sp. 2	Calanoid spp.
Calanoid spp.	Gastropod sp. 1	*P. avirostris*	*P. avirostris*	*P. avirostris*	*Oikopleura spp.*
		Polychaete (l.s.l.) spp.	Gastropod sp. 1	Dec. larvae nauplii	Cyclopoid spp.
		Cyclopoid spp.	Cyclopoid spp.	Polychaete (l.s.l.) spp.	*Obelia spp.*
		Cirripedia nauplii spp.	Dec. larvae (mysis) spp	Harpacticoid spp.	
		Harpacticoid spp.	Decapod zoea spp.	Spionid spp.	
			Polychaete (l.s.l.) spp.		
			Oikopleura spp.		

(b) Autumn 2000

1		**2**		**6**	
Day	Night	Day	Night	Day	Night
Harpacticoid spp.	Bivalve spp.	Harpacticoid spp.	Cyclopoid spp.	Cavoliniid spp.	Calanoid spp.
	Dec. larvae (mysis) spp.	Calanoid spp.	Polychaete (l.s.l.) spp.	Harpacticoid spp.	*P. avirostris*
	Harpacticoid spp.	Cyclopoid spp.	Harpacticoid spp.	Calanoid spp.	Harpacticoid spp.
	Spionid spp.	Polychaete (l.s.l.) spp.	Calanoid spp.	*P. avirostris*	*Oikopleura spp.*
		Oikopleura spp.	Gammarid spp.	Polychaete (l.s.l.) spp.	Cavoliniid spp.
		P. avirostris		Cladoceran spp.	Cyclopoid spp.
		Ostracod spp.		Bivalve spp.	

Table 8.5 continued

(c) Winter 2000

1		2		6	
Day	Night	Day	Night	Day	Night
Harpacticoid spp. Gastropod sp. 1	Gammarid spp. Harpacticoid spp.	Ostracod spp. Calanoid spp. Harpacticoid spp.	Harpacticoid spp. Hydroid sp. 2 Calanoid spp. Ostracod spp. Gammarid spp. Hydroid sp. 1	Calanoid spp.	Harpacticoid spp. Calanoid spp. *Oikopleura spp.* *Obelia spp.* Cyclopoid spp. Spionid spp. Polychaete (l.s.l.) spp.

(d) Spring 2000

1		2		6	
Day	Night	Day	Night	Day	Night
Gastropod sp. 1 Calanoid spp.	Gammarid spp. Harpacticoid spp. Calanoid spp.	Hydroid sp. 1 Harpacticoid spp. Calanoid spp.	Calanoid spp. Gammarid spp. Hydroid sp. 1	*Oikopleura spp.* Calanoid spp. Cyclopoid spp. Gastropod sp. 4	Calanoid spp. Bivalve spp. Cyclopoid spp.

(e) Summer 2001

1		2		6	
Day	Night	Day	Night	Day	Night
Polychaete (juv.) spp Calanoid spp. Harpacticoid spp. Gastropod sp. 1 Copepod nauplii spp.	Cyclopoid spp. Harpacticoid spp. Calanoid spp.	Polychaete (l.s.l.) spp. Calanoid spp. Gastropod sp. 1 Harpacticoid spp. Cyclopoid spp. Copepod nauplii spp. *P. avirostris*	Harpacticoid spp. Polychaete (l.s.l.) spp. Cyclopoid spp. Calanoid spp. *P. avirostris*	Cyclopoid spp. Calanoid spp. Bivalve spp. Isopod a *Obelia spp.* Gastropod sp. 1 Copepod nauplii spp. Harpacticoid spp.	Calanoid spp. Cyclopoid spp. *Obelia spp.* Gastropod sp. 1 Gastropod sp. 2 Bivalve spp. *P. avirostris*

Table 8.5 continued

(f) Autumn 2001

1		**2**		**6**	
Day	Night	Day	Night	Day	Night
Harpacticoid spp.	Calanoid spp. Harpacticoid spp. Gammarid spp. Dec. larvae (mysis) spp.	Calanoid spp. Harpacticoid spp.	Gammarid spp. Cyclopoid spp. Harpacticoid spp.	Calanoid spp. *P. avirostris*	Cyclopoid spp. Calanoid spp. Harpacticoid spp. *Oikopleura spp.* *P. avirostris*

(g) Winter 2001

1		**2**		**6**	
Day	Night	Day	Night	Day	Night
Gammarid spp. Harpacticoid spp.	Harpacticoid spp. Gammarid spp. Nematode spp.	Calanoid spp. Polychaete (l.s.l.) spp. Cyclopoid spp.	Calanoid spp. Gammarid spp. Harpacticoid spp. Cyclopoid spp.	Calanoid spp. Hydramedusa spp. *P. avirostris* Polychaete (l.s.l.) spp. Cyclopoid spp. *Oikopleura spp.*	*Oikopleura spp.* Cyclopoid spp. Polychaete (l.s.l.) spp. *P. avirostris* Calanoid spp.

(h) Spring 2001

1		**2**		**6**	
Day	Night	Day	Night	Day	Night
Calanoid spp.	Harpacticoid spp. Calanoid spp. Gammarid spp.	Calanoid spp. Harpacticoid spp.	Calanoid spp. Gammarid spp.	Bivalve spp. *P. avirostris* Calanoid spp. Polychaete (l.s.l.) spp. Harpacticoid spp.	Bivalve spp. *Oikopleura spp.* Calanoid spp. Fish larvae

In order to more fully investigate the extent of temporal differences in the composition of the zooplankton assemblages, separate multivariate analyses were carried out for each of the three habitat types in view of the significant and large differences that were identified previously on the basis of this factor (see subsection 8.3.3), and also for both years. The replicate samples collected in habitat types 1, 2 and 6 in both 2000 and 2001 were thus subjected separately to MDS ordination, and the samples on the resultant plots coded for both season and day *vs* night (Figs 8.7a-f). These plots showed that, during 2000, the samples from habitat type 2 exhibited a strong overall tendency to form separate groups on the basis of both season and day *vs* night (Fig. 8.7b), while those from habitat type 1 formed particularly discrete seasonal groups only in the case of samples collected at night (Fig. 8.7a). The samples collected at habitat type 6 in 2000 showed relatively little tendency to separate on the basis of day *vs* night (either overall or within most seasons), but formed relatively tight and discrete groups on the basis of season, with the exception of a few samples from winter (Fig. 8.7c). During 2001, the samples from habitat type 1 showed some overall tendency to separate on the basis of season (especially in the case of samples collected during summer and spring), and, within each season, on the basis of day *vs* night (Fig. 8.7d). The samples collected at both habitat types 2 and 6 in 2001 exhibited less overall tendency to form separate groups on the basis of season than was the case in each of these habitats during 2000, and showed little tendency to separate on the basis of day *vs* night (Figs 8.7e and f).

The appropriate two-way crossed ANOSIM tests for investigating fully the extent to which the composition of the zooplankton assemblages differed significantly on the basis of day *vs* night, season and/or year in any or all of the three habitat types were carried out in subsection 8.3.3.2, *i.e.* to determine whether it was necessary to examine the spatial differences in zooplankton composition separately for any or all the three temporal factors. The detailed results of these season x diel ANOSIM tests for data recorded in both 2000 and 2001 are presented in Tables 8.6a-f. The global results of these analyses reinforced the temporal trends exhibited by samples on the MDS plots for each of the three habitat types in the two years (*i.e.* Figs 8.7a-f), and showed that in 2000, the greatest overall differences in zooplankton composition on the basis of both season and day *vs* night occurred at habitat type 2 (*i.e.* Global R=0.882 and 0.726, respectively), while the least overall difference on the basis of both of these temporal factors occurred at habitat type 6 (*i.e.* Global R=0.647 and 0.262, respectively; Tables 8.6b and c). The extent of the overall seasonal and diel differences in zooplankton composition at habitat type 2 in 2001 were markedly lower than in this habitat type during 2000 (*cf* Tables 8.6e and b). However, while the overall seasonal differences detected at habitat types 1 and 6 were also smaller in 2001 than at those habitat types in 2000, the reverse was true for diel differences (Tables 8.6d, f, a and c, respectively).

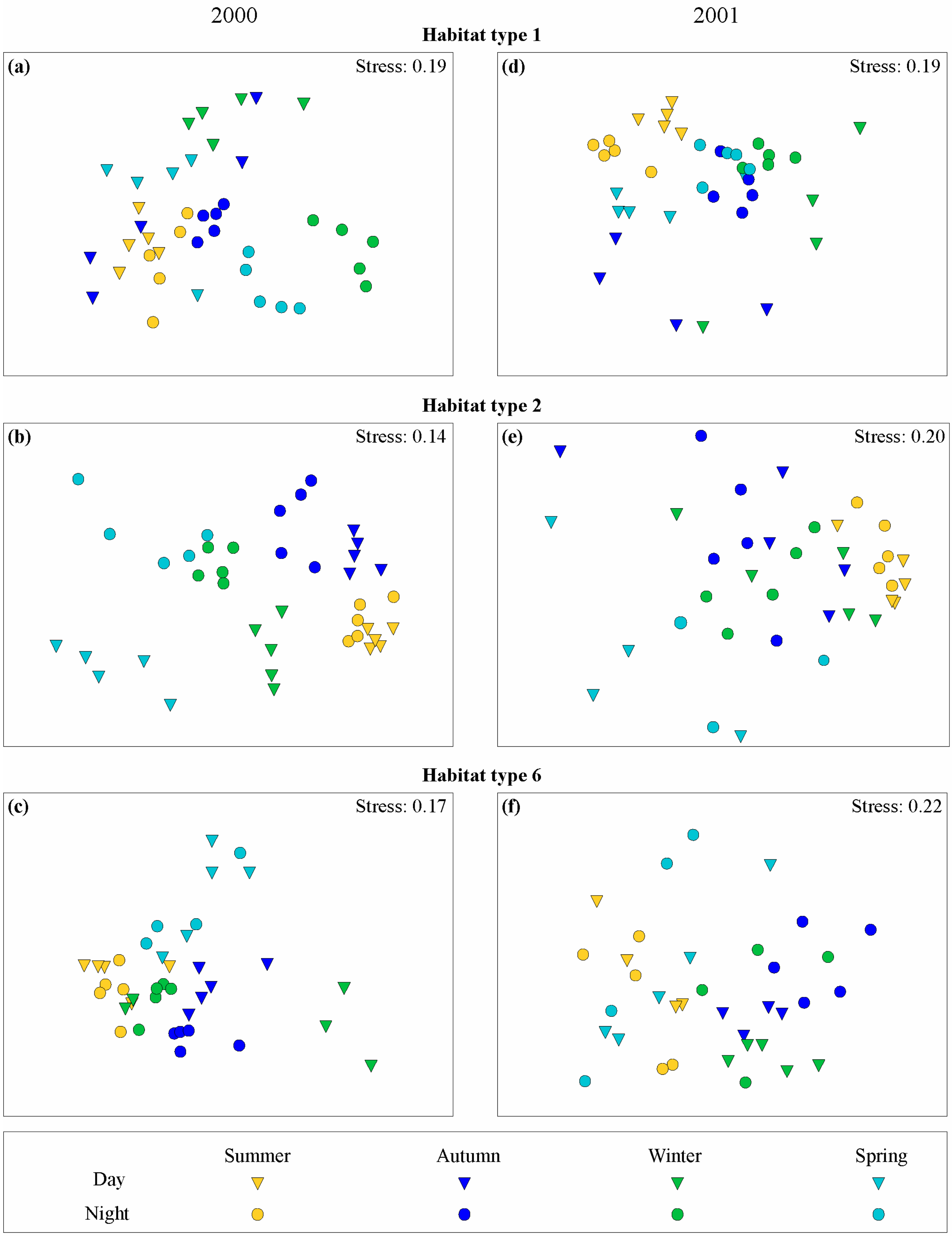


Figure 8.7: Two-dimensional MDS ordination of the density of the various zooplankton taxa in replicate samples collected during the day and night in each season at habitat type 1, 2 and 6 in 2000 (a, b and c, respectively) and at each of these habitat types in 2001 (d, e and f, respectively).

Table 8.6 Significance levels (p; %) and R-statistic values for global and pairwise comparisons in two-way crossed season x diel period ANOSIM tests of the zooplankton collected in 2000 and 2001 at habitat types (a) 1, (b) 2 and (c) 6. Values in boldface represent those that are significant.

(a) Habitat type 1

	2000						**2001**					
Season	**p=0.1%; Global R=0.744**						**p=0.1%; Global R=0.666**					
	S		**A**		**W**		**S**		**A**		**W**	
	p	R	p	R	p	R	p	R	p	R	p	R
A	**0.1**	**0.448**					**0.1**	**0.856**				
W	**0.1**	**0.924**	**0.1**	**0.742**			**0.2**	**0.898**	**0.4**	**0.440**		
SP	**0.1**	**0.802**	**0.1**	**0.828**	**0.1**	**0.842**	**0.1**	**0.914**	**0.5**	**0.261**	**0.1**	**0.545**
Day *vs* Night	**p=0.1%; Global R=0.587**						**p=0.1%; Global R=0.660**					

(b) Habitat type 2

	2000						**2001**					
Season	**p=0.1%; Global R=0.882**						**p=0.1%; Global R=0.566**					
	S		**A**		**W**		**S**		**A**		**W**	
	p	R	p	R	p	R	p	R	p	R	p	R
A	**0.1**	**0.936**					**0.1**	**0.678**				
W	**0.1**	**0.982**	**0.1**	**0.910**			**0.1**	**0.422**	**0.4**	**0.288**		
SP	**0.1**	**0.996**	**0.1**	**0.910**	**0.1**	**0.722**	**0.1**	**0.889**	**0.2**	**0.526**	**0.1**	**0.638**
Day *vs* Night	**p=0.1%; Global R=0.726**						**p=0.2%; Global R=0.700**					

(c) Habitat type 6

	2000						**2001**					
Season	**p=0.1%; Global R=0.647**						**p=0.1%; Global R=0.590**					
	S		**A**		**W**		**S**		**A**		**W**	
	p	R	p	R	p	R	p	R	p	R	p	R
A	**0.1**	**0.834**					**0.1**	**0.728**				
W	**0.1**	**0.554**	**0.1**	**0.608**			**0.1**	**0.741**	**0.1**	**0.409**		
SP	**0.1**	**0.836**	**0.1**	**0.764**	**0.1**	**0.581**	**0.1**	**0.447**	**0.1**	**0.566**	**0.1**	**0.675**
Day *vs* Night;	**p=0.3%; Global R=0.262**						**p=0.1%; Global R=0.318**					

All of the pairwise comparisons between seasons were significant in each habitat type and year. During 2000, the extent of these differences were particularly high for data recorded at habitat type 2, *i.e.* R=0.910-0.996 in all cases except spring *vs* winter (R=0.722; Table 8.6b). The seasonal differences in the composition of the zooplankton collected at habitat type 1 were greatest between summer and winter and least between summer and autumn (Table 8.6a), while at habitat type 6, the size of the R values for those pairwise comparisons that included winter were notably lower than those for the other comparisons (Table 8.6c). These latter results were attributable to the particularly distinctive composition of three of the samples collected in winter during the day (see Fig. 8.7c). During 2001, the greatest seasonal differences in each of the three habitat types were between summer and at least one of the other seasons, while the least difference was detected for autumn *vs* winter and/or autumn *vs* spring (Tables 8.6d-f).

The SIMPER analyses carried out for each of the habitat types during the day and night in each season and in each year in the previous subsection (see Tables 8.5a-h) also facilitated the identification of those taxa that were most responsible for the significant temporal differences in the composition of the zooplanktonic assemblages in the nearshore waters along the lower west coast of Australia. Thus, some taxa were shown by this analysis to characterise the planktonic fauna at a habitat type during only the day or night. For example, gammarid spp. typified the zooplankton at habitat types 1 and 2 only at night during several seasons in both years, with only one exception (Tables 8.5a-h). Furthermore, the taxa that were most typical of the zooplanktonic assemblages in particular habitat types varied seasonally. For example, the zooplankton recorded at habitat type 2 during the day in 2000 was characterised to the greatest extent by bivalve spp. in summer, harpacticoid spp. in autumn, ostracod spp. in winter, and hydroid sp. 1 in spring (Tables 8.5a-d). Interannual differences were exemplified by the fact that in habitat type 1, gastropod sp. 1 typified the day-time assemblages in three of the four seasons in 2000, but characterised the fauna at this habitat type during only one season in 2001 (Tables 8.5a-h).

8.4 Discussion

A total of 60 zooplankton taxa, which belonged to 11 identifiable phyla and represented 1 613 486 individuals (after the numbers in each sample had been adjusted to number of individuals 1 m^{-3}), were recorded along the lower west coast of Australia during both the day and night in each season between summer 2000 and spring 2001. However, comparison of these results with those obtained in other shallow nearshore marine waters is hindered not only by the paucity of research of zooplankton assemblages in those environments, but also by differences in the sampling regimes employed by other workers and the taxonomic level to which the zooplankters recorded in those studies have been classified. In view of the latter two factors, the following comparisons between the results of this study and those obtained by other workers are thus restricted mainly to the number of broad taxonomic groups, *i.e.* phyla.

The number of phyla that were represented by the zooplankton recorded in the current study was slightly greater than that recorded by Kimmerer *et al.* (1985) in shallow coastal waters along the central west Australian coastline, *i.e.* 8 *vs* 10 phyla, but substantially higher than the three phyla recorded by Rios-Jara (1998) in coastal waters along the Puerto Rican coastline. Samples of the zooplankton assemblages in the slightly offshore waters along the lower west coast of Australia collected by the Department of Environmental Protection (1996) revealed the presence of 13 phyla, while a study carried out in the lower reaches of the nearby Swan Estuary showed that the zooplanktonic fauna was represented by nine phyla (Gaughan and Potter 1994). In this study and all the above studies, the phylum Crustacea was the most abundant by far, frequently comprising more than 70% of the total numbers of individuals caught.

8.4.1 Differences in zooplankton assemblages among habitat types

The characteristics of the zooplankton assemblages differed markedly among the three habitat types in the nearshore waters along the lower west coast of Australia. Most notably, the overall density of zooplankters at the highly sheltered habitat type 1 was *ca* eight times lower than that recorded at the moderately sheltered and relatively exposed habitat types 2 and 6, respectively. Furthermore, the mean number of taxa recorded during any particular sampling occasion was almost always the lowest at habitat type 1. These findings were in direct contrast to the first of the hypotheses proposed at the beginning of this study (see subsection 8.1).

The relatively low number of taxa and density of zooplankton at this highly sheltered habitat type is almost certainly due, in part, to the comparatively low volumes of nutrient-rich water that it receives from the two permanently-open estuaries that are located along the lower west coast of Australia (*i.e.* the Swan and Peel-Harvey estuaries; see Fig. 2.1). These plumes of low salinity water, which are discharged from the mouths of these estuaries into the nearshore marine environment during the highly seasonal rainfall events that occur along this coastline in winter and spring, carry high loads of land-derived nutrients and thus support particularly high densities of phytoplankton, *i.e.* the main source of food for zooplankton (Department of Environmental Protection 1996). Variation among nearshore habitat types in the volume of discharge they typically receive from the Swan and Peel-Harvey estuaries is due both to differences in their vicinity to these systems and their local geophysical characteristics. Thus, the site representing habitat type 6 at which zooplankton were sampled is located within 4 km of the mouth of the Swan River Estuary, and local-scale hydrodynamic modeling of the coastal waters along the lower west coast of Australia has demonstrated that the buoyant winter discharge from this estuary is forced readily towards that nearshore site by the strong south-westerly and westerly winds that occur along the lower west coast of Australia at that time of year (Department of Environmental Protection 1996) (see Chapter 2, subsection 2.3.1). Moreover, the site representing habitat type 2 at which zooplankton were sampled lies the closest of three sampling sites to the Peel-Harvey Estuary, and the nutrient-rich winter discharge from this system reaches that site within 12-24 hours under south-westerly wind conditions (Department of Environmental Protection 1996). However, the nearshore site representing habitat type 1 is located almost at the midpoint between the Swan and Peel-Harvey estuaries, and thus lies the greatest distance of each of the three sampling sites from these two systems. The volume of estuary discharge and the concentrations of nutrients that reach that nearshore site is thereby likely to be substantially less than at those sites representing habitat types 2 and 6. Moreover, the causeway construction joining Garden Island to the mainland that is located just to the north-east of the site representing habitat type 1 (see Fig. 2.1), and the very shallow sand spit that joins the southern-eastern end of that sampling site to the mainland, both function as physical barriers to estuary discharge from the Swan and Peel-Harvey estuaries, respectively. The supply of local currents to habitat type 1 is further restricted by the greater frictional resistance to water flow that is caused by the shallowness of the waters and dense seagrass beds that characterise that habitat type.

In addition to disparities in the supply of suspended nutrients among nearshore habitat types, differences in the extent of wave activity are also likely to play a role in the significantly lower density of zooplankton at the highly sheltered habitat type 1 than at the more exposed habitat types 2 and 6. Thus, several other workers have detected greater abundances of zooplankton in more exposed coastal environments, *e.g.* see review by McLachlan (1983), McLachlan and Hesp (1984). Such results have been attributed to the greater densities of phytoplankton in the turbulent wave-breaking and swash zones of those waters, where the nutrients required by those organisms for growth are kept in suspension and are thus more available.

The composition of the zooplankton assemblages also varied markedly among the three habitat types, with the greatest differences occurring between habitat type 1 and the two more exposed habitat types. While the assemblage at habitat type 1 during any particular time of day, season and year was usually characterised by fewer taxa than was the case at habitat types 2 and 6 on comparable sampling occasions, taxa such as decapod larvae (mysis) spp. exhibited clear affinities for that highly sheltered habitat type. Moreover, gammarid amphipods frequently typified the night-time fauna at habitat types 1 and 2, but were never recorded consistently at the relatively exposed habitat type 6. These invertebrates are known to be particularly associated with seagrass and macroalgae (*e.g.* Edgar 1990, Duffy and Hay 2000, Sanchez-Jerez *et al.* 2000, Schreider *et al.* 2003), and the above findings are consistent with the fact that habitat types 1 and 2 contain dense meadows and patches of seagrass, respectively, and that wracks of detached macrophytes commonly accumulate in those nearshore waters (see Chapter 4). In contrast, taxa such as bivalve spp. occurred regularly at habitat type 6, but never characterised the fauna at habitat type 1. It is relevant that the bivalve species *Donax collumbella* also characterised the distinctive benthic macroinvertebrate assemblage that was found at habitat type 6 (see Chapter 7), and it is thus likely that the bivalve spp. recorded in the plankton at this habitat type comprise their juveniles, at least in part. These organisms possess a hard protective shell and are thus particularly well-adapted to cope with the relatively turbulent conditions at this habitat type, and the continual flushing of the water column and interstitial spaces by water turbulence would ensure that their fine filter-feeding structures are kept clean (McLusky and Eliot 1981). Moreover, the affinity of cyclopoid spp. for the two more exposed habitat types in this study reflects the particularly good swimming ability of this copepod taxa, which would thus enable it to actively maintain an appropriate position in the water column in these more turbulent environments (Barnes 1987).

8.4.2 Temporal differences in zooplankton assemblages

Significant differences in the characteristics of the zooplankton assemblages along the lower west coast of Australia also were detected between day and night, seasons and years. However, the nature and extent of those temporal differences varied markedly among the different habitat types. Thus, while the overall density of zooplankton at habitat type 1 exhibited very little variation on the basis of any temporal factor, that at habitat types 2 and 6 differed widely among seasons and, to a lesser extent, between day and night and years. In contrast, the composition of the zooplanktonic assemblages varied markedly among seasons in all three habitat types, particularly during 2000. Moreover, while pronounced diel differences in zooplankton composition occurred at habitat type 1 in both years, the composition of the assemblage at habitat type 2 differed markedly between day and night only during 2000, and that at habitat type 6 exhibited relatively little diel variation in both 2000 and 2001.

The markedly higher density of zooplankters recorded during summer and/or autumn than during the remainder of the year at habitat types 2 and 6 is most likely attributable to the combined influences of the distinct seasonality of water discharge from the Swan and Peel-Harvey estuaries that is received by those nearshore habitat types, and the seasonal differences in water temperature that occur along the lower west coast of Australia. Thus, the volume of discharge from these systems increases markedly in winter and spring due to highly seasonal rains in those seasons, and transports high levels of land-derived nutrients into the surrounding nearshore marine waters. As outlined in subsection 8.4.2, these nutrient-rich waters are received readily by the sites representing habitat types 2 and 6 and, when combined with the significantly warmer water temperatures that occur along the lower west coast of Australia in summer (see Chapter 4) and the greater number of daylight hours in that season, provide ideal conditions for rapid phytoplankton growth (*e.g.* Department of Environmental Protection 1996, John 2000, Horner Rosser and Thompson 2001). The peak in zooplankton density at these habitat types during these warmer seasons thus almost certainly reflects marked increases in their main source of food. Moreover, the distinct lack of seasonal differences in zooplankton density at habitat type 1 is almost certainly a consequence of the fact that the site representing this highly sheltered habitat type receives little of the nutrient-rich waters from the two estuaries along this coastline. Other workers have also recorded greater densities of zooplankton in summer, and have attributed such findings to seasonal vertical migration into the water column for reproductive and dispersal purposes (*e.g.* Knox 1994, Jacoby and Greenwood 1989). While those latter factors probably contribute to the seasonal differences in zooplankton density recorded in the current study, the minimal intraannual variability in the density of these organisms at habitat type 1 implies that seasonal differences in phytoplankton abundance is the main cause of the intraannual differences recorded at habitat type 2 and 6 along the lower west coast of Australia.

The greatest seasonal differences in zooplankton composition at each of the three habitat types were usually detected between summer and at least one of the other seasons. In most cases, this was attributable to a greater abundance of several taxa and/or the more regular occurrence of a greater number of taxa in this season than during the remainder of the year. These results most likely reflect a greater rate of growth, survival and reproduction of many zooplankters due to the warmer water temperatures, greater abundance of food and calmer water conditions that occur in the nearshore waters along this coastline during summer. For example, *Penilia avirostris* occurred in markedly higher densities and more regularly during summer in all habitat types during 2000. This cladoceran is known to be particularly abundant in the nearshore waters of tropical and sub-tropical regions (Wong *et al.* 1992), and several other workers have also reported peaks in the abundance of *P. avirostris* during summer in nearshore marine waters elsewhere (*e.g.* Wong *et al.* 1992, Kingsford 1995, Onbé and Ikea 1995). Moreover, cirripedia nauplii spp. occurred more regularly in this season at both habitat types 2 and 6 in 2000. Adults of this taxon typically inhabit those areas that contain hard substrata, *e.g.* the large offshore reef chain system that is present along the lower west coast of Australia, and the greater presence of their planktonic larvae during summer may reflect the passive onshore transport of these organisms by the strong seabreezes that occur along this coastline in this season. Some taxa were more prevalent in seasons other than summer at particular habitat types, such as gammarid amphipods during autumn at habitat type 2. The greater abundance of this weed-associated taxa most likely reflects the particularly large volume of detached macrophytes that were recorded at this habitat type in this season (see Chapter 4).

The marked differences in the composition of the zooplankton assemblages between day and night that were detected at the highly and moderately sheltered habitat types 1 and 2, respectively, reflect the migration of several taxa from the substrate surface into the water column at night, and their subsequent return to the benthos during the day. Thus, the mean number of taxa recorded at these habitat types in any particular season and year was often greater at night than that recorded during the day, and SIMPER demonstrated that zooplankters such as decapod larvae (mysis) spp. and gammarid spp. (which are typically benthic-dwelling), were consistently more prevalent at night than during the day at habitat types 1 and/or 2. The nocturnal migration of gammarid amphipods into the water column at particular habitat types along the lower west coast of Australia is consistent with the markedly greater contribution made by these invertebrates to the diet of the planktivorous fish *Atherinomorus ogilbyi* at night in these nearshore waters (see Chapter 11). Such diel migratory patterns have been recorded by many other workers (*e.g.* Alldredge and King 1980, 1985, Jacoby and Greenwood 1989, Shaw and Robinson 1998), and these findings have been attributed both to active movements, *i.e.* to exploit food sources at the time when they are most available, avoid predation, facilitate dispersion or increase the chance of reproduction, and also to passive causes that result from physico-chemical changes in the characteristics of the water column between day and night, *e.g.* changes in tidal state, hydrostatic pressure, turbulence and temperature (Heath *et al.* 1988, Rowe and Epifanio 1994). The relatively small diel differences in the characteristics of the zooplankton assemblages recorded at habitat type 6 is most likely a reflection of the greater water turbulence at that habitat type, which would thus lead to greater mixing of the water column and make it more difficult to detect differences in the vertical migration patterns of zooplankters.

Differences in the characteristics of the zooplankton assemblages along the lower west coast of Australia were also detected between 2000 and 2001. Thus, while the overall density of zooplankton at each habitat type and in each season was often greater during 2001 than 2000, the number of taxa that typified those assemblages was usually greater in 2000, especially in the case of habitat types 2 and 6 in summer and autumn. Moreover, while some taxa occurred consistently in a habitat type during one of the years, they were less prevalent in the other year. The presence of such interannual differences in the characteristics of the nearshore zooplankton assemblages is not surprising, given the extent to which the distribution of these planktonic organisms can be influenced by variations in hydrodynamic and climatic factors such as oceanic and local current patterns, local wind regimes and volume of annual rainfall. However, despite the differences in the characteristics of zooplankton assemblages detected between 2000 and 2001 in this study, the composition of those assemblages still exhibited significant and large differences among habitat types in both of those years.

Chapter 9. Characteristics of the meiofaunal assemblages in different habitat types

9.1 Introduction

Meiofauna, *i.e.* benthic metazoans that pass through a 500 µm sieve but are retained on meshes of 40-63 µm (Coull 1999), are often the most abundant metazoans in the soft sediments of estuaries and nearshore marine waters (Gierre 1993). Since these invertebrates make a substantial contribution to the diets of the juveniles of many fish species, they constitute, in these waters, a crucial component of food chains and play an important role in nutrient recycling (Gee 1989, Kennedy and Jacoby 1997). Despite their importance, our knowledge of the diversity and ecology of meiofauna is far less than that of the macrofauna (Gierre 1993). This can largely be attributed to a bias towards focusing on animals that are sufficiently large to recognise and identify with relative ease (Gierre 1993). The most numerically important component of the meiofauna in nearshore marine and estuarine waters is the Nematoda, whose individuals often outnumber those of all other meiofaunal taxa collectively (Coull 1999).

The factors that are considered to influence the abundance and composition of meiofaunal assemblages include sediment grain size (Wieser 1959b, Warwick 1971, Coull 1988), organic content (Warwick 1971, McLachlan *et al.* 1981, Huys *et al.* 1992, Moens *et al.* 1999), extent of oxygenation of the sediment (McLachlan 1978, Coull 1988) and degree of exposure to wave action (Wieser 1959a, b). Attempts to relate the characteristics of meiofaunal assemblages to environmental characteristics have usually focused on one or at most two of those factors. Moreover, no attempt has been made to relate statistically the composition of meiofauna with particular habitat types that have been identified on the basis of a suite of environmental features.

Although numerous studies of the meiofauna have been undertaken in the macrotidal waters of temperate regions of the northern hemisphere (Blome *et al.* 1999, Danovaro 2002, Grémare *et al.* 2002, Menn 2002, Tita *et al.* 2002, Warwick *et al.* 2002), there have been relatively few studies of these invertebrates in the microtidal environments of nearshore marine waters in temperate regions of the southern hemisphere (*e.g.* Nicholas and Hodda 1999). For example, the only studies that have focused on the ecology of meiofauna in nearshore marine waters in temperate Australia are those of McLachlan and Hesp (1984) and McLachlan (1985) in Western Australia and of Warwick *et al.* (1990), Nicholas (2001) and Nicholas and Hodda (1999) in eastern Australia. Furthermore, McLachlan and Hesp (1984) only examined the distribution of meiofaunal taxa at a broad level within a single cusp system on a beach face, *i.e.* within an area of a few square meters, and McLachlan (1985) estimated biomass rather than the densities of the entire meiofaunal assemblage and made no attempt to distinguish taxa at a lower taxonomic level.

The different habitats found in nearshore marine waters along the microtidal lower west coast of Australia vary mainly in the extent to which they are exposed to wave action and contain seagrass meadows and reefs (Valesini *et al.* 2003, chapter 3). The taxonomic diversity and ubiquity of nematodes (Wieser 1959a, b) would be likely to make these organisms a particularly useful candidate for assessing the validity of these habitat type distinctions for biota.

The main aim of this study was to determine whether the characteristics of the meiofaunal community along the lower west coast of Australia, and particularly of its nematode component, vary in relation to the differences of habitat type as defined by a suite of enduring environmental characteristics. The sites chosen for study represent the habitat type that is least exposed to wave activity and which contains seagrass (habitat type 1) and that which is most exposed to wave activity and containes no seagrass (habitat type 6) and also an intermediate habitat type (2) (see Valesini *et al.* 2003, Chapter 3 for further details of these habitat types). The study also focused on determining whether any differences in the meiofaunal characteristics among the different habitat types were maintained throughout the year and also among zones on the beach that varied in the duration and the extent to which they were covered by water during each tidal cycle. More specifically, the following hypotheses were tested at two taxonomic levels, namely a broad level using major meiofaunal taxa and then at a species level using only nematodes. 1) The density of meiofauna and the density, number of taxa and taxonomic diversity of nematodes will be greatest in the habitat type that is most sheltered from wave energy and contains areas of dense seagrass. 2) The compositions of the meiofaunal and nematode assemblages will vary among habitat types due to the affinity of certain taxa for particular environmental conditions. 3) The compositions of the meiofaunal and nematode assemblages will vary seasonally and amongst intertidal zones as a result of variations in reproductive success and mortality. Particular focus will be directed towards the results of the studies of nematodes as that taxon was separated at the species level and is considered particularly useful for discriminating between different environments.

9.2 Materials and methods

9.2.1 Sampling regime and laboratory procedures

The meiofauna in the sandy substrates of three zones (A, B, C) in habitat types 1, 2 and 6, which varied in the extent to which they were exposed to wave activity and contained seagrass (see Introduction for brief details and Chapter 4 for full details of the characteristics of those habitat types), were sampled seasonally between the summers of 2000 and 2001. Zone A was located between the high-tide water mark on the beach face and the effluent line, *i.e.* the highest point of groundwater discharge on the beach face, and was thus submerged for at least part of each tidal cycle. Zone B was situated between the effluent line and the lower limit of the wave swash and thus, in contrast to the situation in Zone A, its interstitial environment was saturated. Zone C was located in approximately 1 m of water and was thus permanently submerged. Five randomly-located sediment cores were collected from each zone in each habitat type during the day in each of the five seasons. The perspex corer was 3.2 cm in diameter, 11 cm high and sampled an area of *ca* 8 cm^2. Each sediment core was immediately fixed in 5% formalin / seawater solution.

The sediment from each core was passed through two sieves, the first made of 500 µm mesh and the second of 63 µm mesh, a procedure which excluded benthic macroinvertebrates but retained meiofauna. The meiofauna were removed from the remaining fine sediment using the colloidal silica solution Ludox ™, which separated out the organic fraction of the sample, and these were then rinsed in water and preserved in 70% ethanol. Each sample was then diluted to a standard 20 ml, from which five 1 ml subsamples were extracted without replacement. The organisms in each subsample were isolated, identified and assigned to one of 10 broad taxonomic groups under a binocular dissecting microscope and pooled. The nematodes were separated from the other organisms and placed in a 10% glycerol / water solution and the solution evaporated for 12 h at 60 ºC. These nematode samples were then mounted on slides in anhydrous glycerol and each slide was sealed with paraffin wax and slide sealant (Platt and Warwick 1988).

Nematodes were identified to the lowest possible taxon (*i.e.* nominal species level) using a compound microscope at a magnification of 100-1000 times and employing mainly the keys provided in Platt & Warwick (1988) and Warwick *et al.* (1998).

9.2.2 Statistical analyses

9.2.2.1 Univariate analyses

Each nematode species was assigned to its respective genus, family, suborder, order, subclass and class for subsequent analyses of the average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+), which were calculated using the DIVERSE routine in PRIMER 5.2. Average taxonomic distinctness is defined as the average path length through a hierarchical classification based on a Linnaean tree, connecting each pair of species in a sample, and Λ^+ is the variance of those path lengths, which gives a measure of the evenness of the distribution of the species across the taxonomic tree (Clarke and Warwick 2001).

The densities of individuals in the meiofauna and of its nematode component, and the number of species, Δ^+ and Λ^+ of nematodes only, were subjected to Analysis of Variance (ANOVA) to determine whether those variables differed significantly among habitat types, zones and seasons. The results of a test for heteroscedasticity (Clarke and Gorley 2001) demonstrated that, prior to subjecting the data for these variables to ANOVA, the first three variables required log transformation to satisfy the assumptions of normality and constant variance for that test, while the last two required no transformation. The null hypothesis for ANOVA, that values for each of the above dependent variables did not differ significantly among the independent variables was rejected when the significance level (p) was <0.05. Each sample was considered to be independent of all other samples, and all main effects were regarded as fixed. When a significant difference was detected for any main effect not involved in a significant interaction, Scheffè's *a posteriori* test was used to ascertain the source of those differences.

9.2.2.2 *Joint Δ^+ and Λ^+ analyses for nematodes.*

The relationship between the values for Δ^+ and Λ^+, derived from the nematode assemblages from samples collected in each habitat type in the different zones and seasons was determined using the TAXDTEST routine in the PRIMER 5.2 statistical package (Clarke and Gorley 2001). This routine was used both to construct scatter plots of the values for Δ^+ *vs* Λ^+ (as independent and dependent variables, respectively) and to determine the probability that the observed values of these indices were representative (*i.e.* within 95%) of the range of values that would be expected for any subset of species (of comparable size) that could be drawn at random from the data for the entire study region. The procedure for calculating each 95% confidence ellipse involved generating 1000 random subsamples of a set number of species taken from the regional taxa list, calculating the values Δ^+ and Λ^+ for each and constructing an ellipse on the bivariate plot to encompass 95% of the variation of the generated samples. The observed values of Δ^+ and Λ^+ were then superimposed on the plots and any samples that lay outside their corresponding 95% confidence ellipse were considered to exhibit a significant departure from the expected values of Δ^+ and Λ^+. These biodiversity indices were calculated only for the nematode taxa as the other meiofaunal taxa were classified at a broad level.

9.2.2.3 *Multivariate analyses*

The following analyses of the compositions of the meiofaunal assemblages and their nematode components were carried out using routines in the PRIMER 5.2 statistical package (Clarke and Gorley 2001). The log-transformed densities of both the meiofaunal taxa and of the various nematode species, derived from replicate samples collected in each habitat type, zone and season, were used to construct separate Bray-Curtis similarity matrices. These matrices were subjected to non-metric multidimensional scaling (MDS) ordination. Note that the MDS ordination and associated tests used mean data when there were a sufficient number of samples, as in the case of the global analyses for the influence of habitat type, season and zone, and replicate data when there was a reduced number of samples. Since the stress levels of each of the two-dimensional MDS ordination solutions almost invariably exceeded 0.2, plots of the three-dimensional solutions are presented in the results. One and two-way crossed Analysis of Similarity (ANOSIM) tests were used to ascertain whether the faunal composition of samples collected from the various habitat types, zones and seasons differed significantly among those *a priori* groups. In each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected if the significance level (p) was <5%. When significant differences were detected among *a priori* groups, the R-statistic was used to determine the extent of those differences and Similarity Percentages (SIMPER) was employed to elucidate which species typified each of those groups. The second-stage MDS routine was used to determine whether the extent of the Bray-Curtis similarity in nematode compositions between each pair of habitat types differed among the various zones and/or seasons.

9.3 Results

9.3.1 Meiofaunal assemblages

The total number of meiofaunal organisms was greatest in the highly sheltered habitat type 1, and similar in the moderately sheltered habitat type 2 and the exposed habitat type 6 (Table 9.1). Nematodes dominated the meiofauna in habitat types 1 and 6, where they comprised over half of the total number of individuals. Although nematodes were also abundant in habitat type 2, about 50% of the meiofauna in that habitat type were polychaetes. In contrast, polychaetes represented only 12.5 and 2.3% of the meiofauna in habitat types 1 and 6, respectively. The meiofauna in habitat type 6 contained a substantial amount of crustaceans, representing 26.5% of the total number of individuals, which were dominated by interstitial harpacticoids. In contrast, crustaceans contributed less to the meiofauna in habitat types 1 (9.5%) and 2 (12%). Turbellarians were also relatively abundant in habitat types 1 and 6 (Table 9.1).

9.3.2 Density of meiofauna in different zones, habitat types and seasons

Three-way ANOVA showed that the density of the meiofauna differed significantly among habitat types and seasons (p <0.001), and that there were significant interactions between these two variables and also between habitat type and

Table 9.1 Mean density (M; number of individuals 10 cm^{-2}), standard deviation (±1 sd), percentage contributions to the sum of the mean densities (%) and the rank by density (Rk) of each of the major meiofaunal taxa in samples collected in all zones at habitat types 1, 2 and 6 in nearshore marine waters along the lower west coast of Australia in all seasons between summer 2000 and summer 2001. The number of taxa, number of samples collected and the total number of individuals (after the number of individuals in each sample had been adjusted to that in 10 cm^{-2}) are also provided for each habitat type. *=taxa used in subsequent multivariate analyses.

	1				**2**				**6**			
	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Crustaceans	**38.0**	**70.7**	**9.5**		**32.0**	**53.0**	**12.0**		**70.6**	**157.1**	**26.5**	
*Harpacticoids-interstitial	25.2	68.4	6.3	**5**	23.3	49.6	8.7	**3**	68.9	157.0	25.9	**2**
*Harpacticoids-burrowing	12.7	24.6	3.2	**6**	8.7	19.0	3.2	**6**	1.6	4.2	0.6	**5**
*Others	0.1	0.8	<0.1	**9**	0.1	0.8	<0.1	**9**	0.2	0.9	<0.1	**9**
***Other arthropods**	**2.7**	**19.6**	**0.7**	8	**0.1**	**0.8**	<0.1	10	**0.3**	**2.9**	**0.1**	8
***Nematodes**	**211.1**	**251.6**	**53.8**	1	**80.9**	**86.6**	**30.3**	2	**145.7**	**142.4**	**54.9**	1
***Turbellarians**	**63.7**	**138.1**	**16.0**	2	**18.5**	**50.7**	**7.0**	4	**41.6**	**71.5**	**15.7**	3
Polychaetes	**50.3**	**82.0**	**12.5**		**134.4**	**331**	**50.3**		**6.2**	**17.5**	**2.3**	
*Capitellids	40.5	82.1	10.2	**3**	122.3	325.7	45.8	**1**	4.8	17.3	1.8	**4**
*Protrodrillids					9.7	36.0	3.6	**5**	0.1	0.6	<0.1	**10**
*Others	9.4	15.7	2.3	**7**	2.4	10.8	0.9	**7**	1.4	4.2	0.5	**6**
***Oligochaetes**	**30.0**	**98.5**	**7.5**	4	**1.3**	**3.8**	**0.5**	8	**0.9**	**4.3**	**0.3**	7
Number of major taxa	**9**				**10**				**10**			
Overall mean density	**395.4**				**267.3**				**265.5**			
Number of samples	**75**				**75**				**75**			
Total no. individuals	**29 958**				**20 039**				**19 913**			

zone (p <0.001; Table 9.2). The mean squares were far greater for each of the significant main effects than the interaction terms. The habitat x season interaction was attributable to the fact that, while the mean density of meiofauna was least in winter at each habitat type and greatest in summer 2001 at both habitat types 1 and 2, it reached a maximum during spring at habitat type 6. Although the mean density of meiofauna was greatest in zone A at both habitat types 1 and 2, it was greatest in zone C at habitat type 6.

Table 9.2 Mean squares and significance levels for three-way ANOVA of the density of meiofauna in samples collected in zones A, B and C at habitats 1, 2 and 6 in each season between summer 2000 and summer 2001. "df"=degrees of freedom. ***p <0.001.

	df	**Density**
Main effects		
Habitat type (H)	2	2.00***
Zone (Z)	2	0.07
Season (S)	4	2.80***
Two-way interactions		
H x Z	4	0.68***
H x S	8	0.85***
Z x S	8	0.16
Three-way interactions		
H x Z x S	16	0.13
Error	180	0.09

9.3.3 Comparisons of meiofaunal assemblages among habitat types, seasons and zones

When the mean densities of the meiofauna in the three zones at each of the three habitat types in each of the five seasons were subjected to MDS ordination, the samples from habitat type 1 were located in a band that extended virtually the full width of the 3D ordination plot, while those for habitat type 2 lay mainly in the centre of the plot and those for habitat type 6 lay predominantly on the right of the plot (Fig. 9.1a). When the samples were coded for season, those for winter formed a relatively discrete group on the right of the plot, while those for summer 2001, autumn and spring formed relatively tight but overlapping groups and those for summer 2002 were widely dispersed (Fig. 9.1b). When coded for zone, the points on the MDS ordination exhibited no tendency to form discrete groups (Fig. 9.1c). One way-ANOSIM demonstrated that the composition of the meiofauna differed significantly among habitats (p=0.1%, R=0.163) and seasons (p=0.1%, R=0.168).

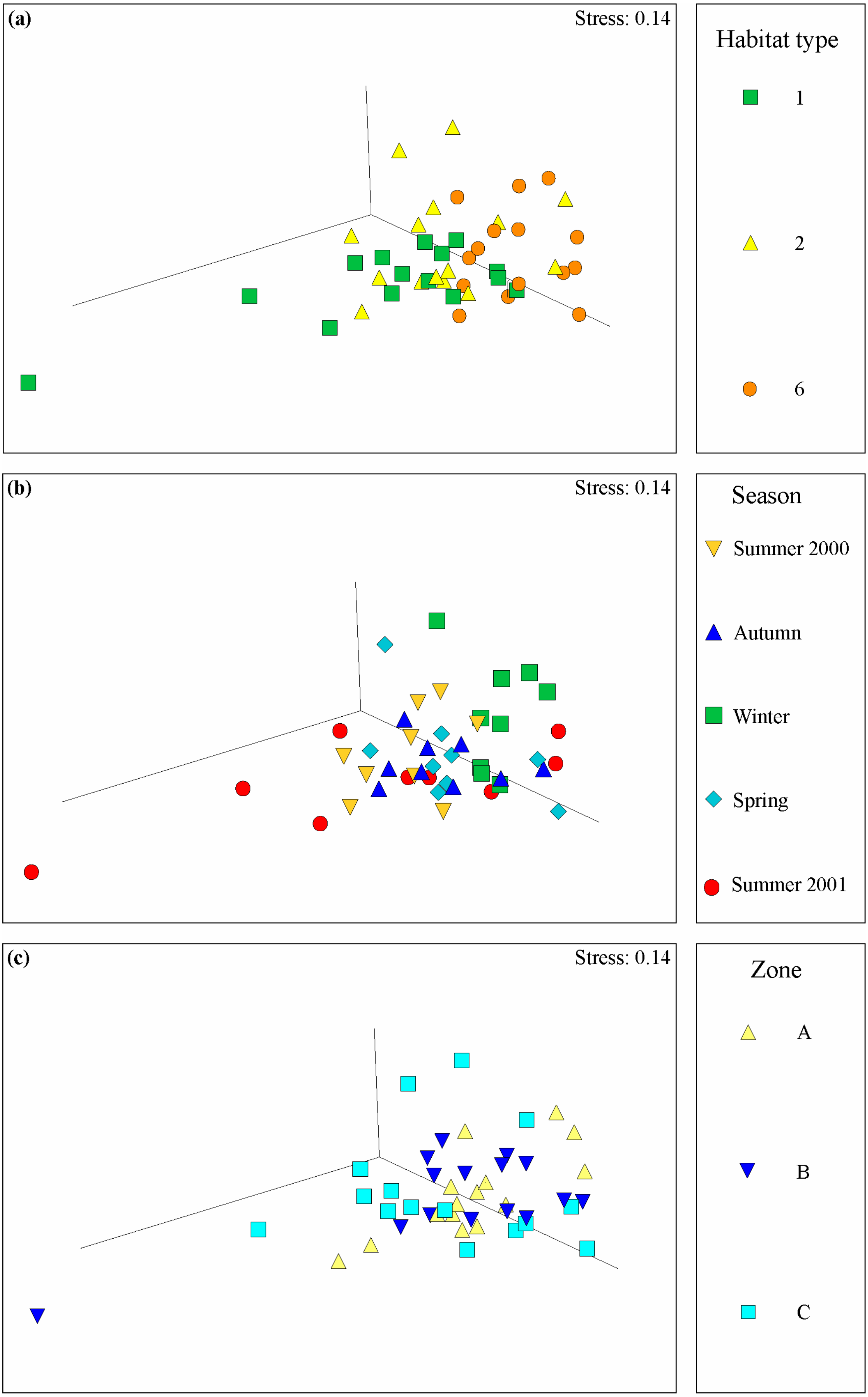


Figure 9.1:Three-dimensional MDS ordination of the densities of benthic meiofaunal organisms at habitat types 1, 2 and 6 during summer 2000, autumn, winter and spring and summer 2001 coded for (a) habitat type, (b) season and (c) zone.

SIMPER showed that the meiofauna at habitat type 1 was distinguished from those at habitat types 2 and 6 by the regular occurrence of relatively large numbers of nematodes, “other polychaetes” and burrowing harpacticoids. Moreover, unlike the situation in habitat type 1, relatively high densities of capitellid polychaetes and interstitial harpacticoids were recorded consistently and in high densities at habitat types 2 and 6, respectively. The compositions of the meiofauna in both summers were distinguished from those in other seasons by the occurrence of consistently high densities of nematodes, capitellid polychaetes and both interstitial and burrowing harpacticoids, while those in winter and autumn contained consistently higher densities of turbellarians than in other seasons.

In order to investigate more fully the extent of the significant differences in meiofaunal composition among habitat types, the densities for each replicate sample in each zone in each habitat type were ordinated separately for each season. The majority of samples for one or more of the habitat types formed relatively tight and often discrete groups in each season. This applied, for example, with habitat type 1 in autumn, winter and summer 2001, with habitat type 2 in summer 2000 and 2001, and with habitat type 6 in spring and summer 2001 (Fig. 9.2).

Two-way crossed ANOSIM, employing habitat type and zone as factors, demonstrated that the composition of the meiofauna differed significantly among habitat types in all seasons (Table 9.3) and that the differences were greatest in summer 2001 (Global R=0.810), followed by summer 2000 and spring (Global R=0.482 and 0.483, respectively). Pairwise comparisons showed that, in all seasons except winter, the meiofaunal composition differed significantly between each pair of habitat types, and that the differences were usually greatest between habitat types 1 and 6 (Table 9.3). SIMPER demonstrated that the meiofauna at the highly-sheltered habitat type 1 was distinguished from that at the exposed habitat type 6 by the regular occurrence of burrowing harpacticoids during both summers, but was distinguished from that at both of the other habitat types by greater abundances of turbellarians in spring (Table 9.4). Moreover, capitellid polychaetes and “other polychaetes” and/or nematodes were important in distinguishing the meiofauna at one or both of the other habitat types in autumn, spring and summer 2001. In contrast, turbellarians were recorded more regularly and in higher numbers at habitat type 6 than at one or both of the other habitat types in all seasons except spring and summer 2001 (Table 9.4).

The composition of the meiofauna also differed significantly among zones in summer 2000 and spring and particularly summer 2001. However, the global R-statistics were usually low and always considerably less than those detected for habitat type in each corresponding season.

Table 9.3 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in two-way crossed habitat type x zone ANOSIM tests of the meiofaunal assemblages at habitat types 1, 2 and 6 and zones A, B and C in (a) summer 2000 (b) autumn, (c) winter, (d) spring and (e) summer 2002. Only the results for the habitat type component of these two-way crossed analyses are presented in the following tables. Significant results are highlighted in boldface.

(a) Summer 2000 (p=0.1%; Global R=0.482)

	1		**2**	
	p	R	p	R
2	**0.2**	**0.299**		
6	**0.1**	**0.568**	**0.1**	**0.619**

(b) Autumn 2000 (p=0.1%; Global R=0.326)

	1		**2**	
	p	R	p	R
2	**0.7**	**0.317**		
6	**0.1**	**0.455**	**1.2**	**0.227**

(c) Winter 2000 (p=0.5%; Global R=0.126)

	1		**2**	
	p	R	p	R
2	**2.0**	**0.132**		
6	**3.6**	**0.083**	**1.9**	**0.158**

(d) Spring 2000 (p=0.1%; Global R=0.483)

	1		**2**	
	p	R	p	R
2	**0.1**	**0.456**		
6	**0.1**	**0.625**	**0.2**	**0.340**

(e) Summer 2001 (p=0.1%; Global R=0.810)

	1		**2**	
	p	R	p	R
2	**0.1**	**0.749**		
6	**0.1**	**0.912**	**0.1**	**0.689**

Table 9.4 Species detected by SIMPER as those most responsible for typifying the benthic meiofaunal assemblages at habitat types 1, 2 and 6 (see taxa arranged along diagonal cells) and distinguishing each pair of those habitat types (see taxa arranged along vertical cells) in each season between summer 2000 and summer 2001. Samples collected in the different zones have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided in each case (see superscripts).

		1	**2**	**6**
Summer 2000	**1**	Nematodes		
	2	Capitellids$^{(2)}$	Nematodes Capitellids	
	6	Turbellarians$^{(6)}$ Epibenthic harpacticoids$^{(1)}$	Capitellids$^{(6)}$ Turbellarians$^{(6)}$	Nematodes Turbellarians
Autumn	**1**	Nematodes Capitellids Other polychaetes		
	2	Capitellids$^{(1)}$ Other polychaetes$^{(1)}$ Nematodes$^{(1)}$	Nematodes	
	6	Capitellids$^{(1)}$ Other polychaetes$^{(1)}$	Turbellarians$^{(6)}$ Interstitial harpacticoids$^{(6)}$	Nematodes
Winter	**1**	Nematodes		
	2	Turbellarians$^{(1)}$	Nematodes	
	6	Interstitial harpacticoids$^{(1)}$ Turbellarians$^{(6)}$	Turbellarians$^{(6)}$	Turbellarians
Spring	**1**	Nematodes		
	2	Turbellarians$^{(1)}$ Nematodes$^{(1)}$ Capitellids$^{(2)}$	Nematodes	
	6	Interstitial harpacticoids$^{(6)}$ Turbellarians$^{(1)}$	Interstial harpacticoids$^{(6)}$ Nematodes$^{(6)}$	Nematodes Interstitial harpacticoids
Summer 2001	**1**	Nematodes Epibenthic harpacticoids		
	2	Epibenthic harpacticoids$^{(1)}$ Capitellids$^{(2)}$ Other polychaetes$^{(1)}$ Nematodes$^{(1)}$	Capitellids Nematodes	
	6	Other polychaetes$^{(1)}$ Epibenthic harpacticoids$^{(1)}$ Nematodes$^{(1)}$	Capitellids$^{(2)}$	Nematodes

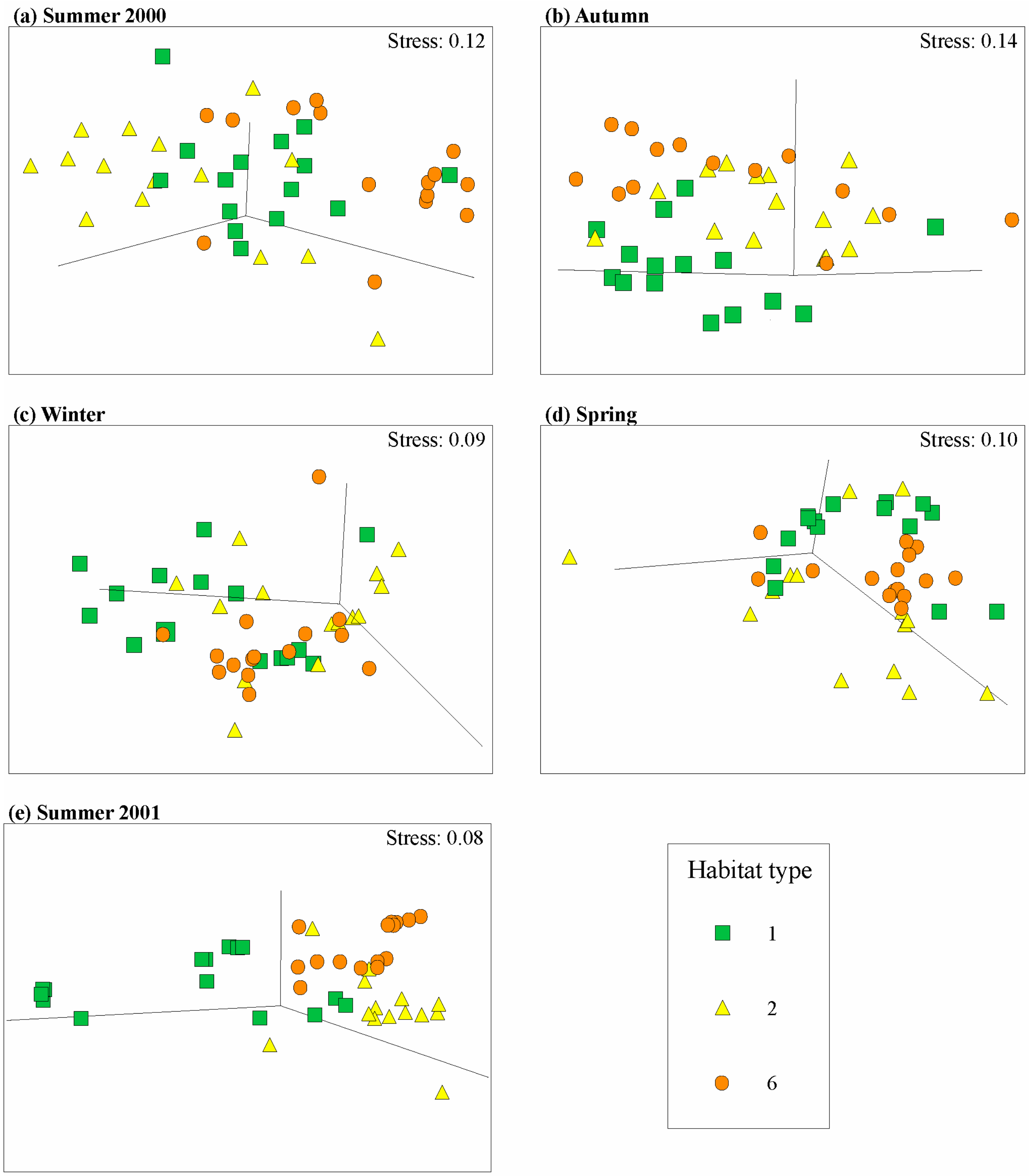


Figure 9.2: Three-dimensional MDS ordination of the densities of benthic meiofaunal taxa athabitat types 1, 2 and 6 during (a) summer 2000, (b) autumn, (c) winter, (d) spring and (e) summer 2001.

9.3.4 *Comparisons of meiofaunal assemblages among different seasons and zones in each habitat type*

In order to investigate more fully the significant overall differences that were detected in meiofaunal composition among seasons, the data recorded in each of the three habitat types were subjected separately to MDS ordination (Fig. 9.3). The resultant plots showed that, while the samples for the five seasons tended to overlap, those for certain seasons showed little or no overlap, *e.g.* winter *vs* summer 2001 in habitat type 1 and winter *vs* both summer 2000 and summer 2001 in habitat types 1 and 6. ANOSIM demonstrated that the composition of the assemblages differed significantly among seasons at each habitat type ($p < 0.1\%$, Global R=0.319-0.427; Table 9.5), and that those differences were slightly greater at habitat type 1 than at habitat types 2 and 6. Pairwise seasonal comparisons within each habitat type showed

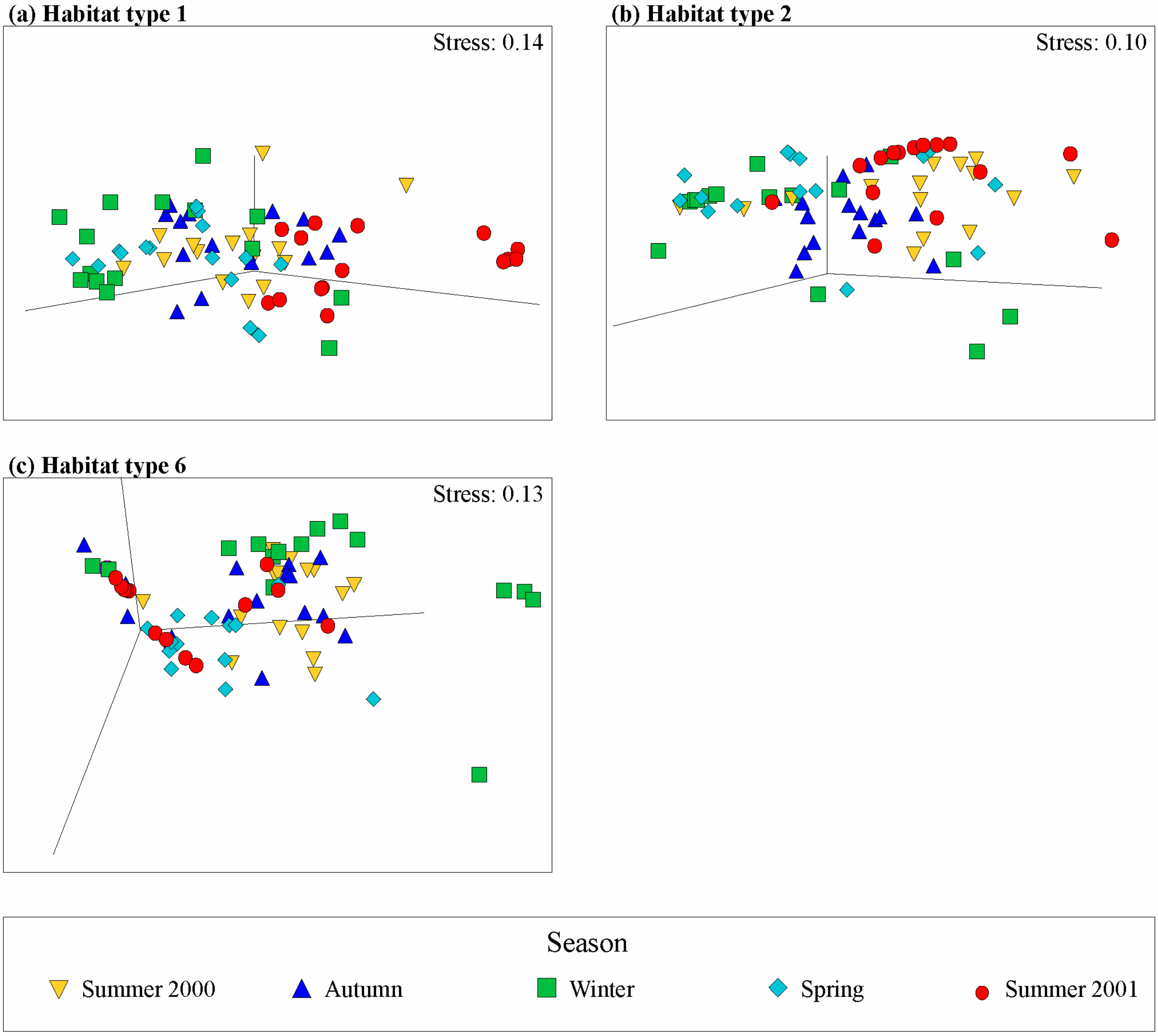


Figure 9.3: Three-dimensional MDS ordination of the densities of benthic meiofaunal taxa in each season between summer 2000 and summer 2001 at (a) habitat type 1, (b) habitat type 2 and (c) habitat type 6.

that, although the composition in each season was significantly different from every other season in all but two cases, the R-statistics were often low. However, the R-statistic for winter *vs* summer 2001 at each habitat type, and autumn *vs* summer 2001 at habitat types 1 and 2 were relatively high, ranging from 0.303 to 0.734. SIMPER demonstrated that in each habitat type, the meiofaunal assemblages in winter were distinguished from those in summer 2001 by relatively greater densities of turbellarians and lower densities of nematodes and either burrowing or interstitial harpacticoids. Furthermore, relatively greater densities of nematodes and harpacticoids distinguished

Table 9.5 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in one-way ANOSIM tests of the benthic meiofaunal assemblages in each season between summer 2000 and summer 2001 at habitat types 1, 2 and 6 (S2000=summer 2000, A=autumn, W=winter, SP=spring and S2001=summer 2001). Significant results are highlighted in boldface.

Habitat type 1 (p=0.1%; Global R=0.427)

	S2000		**A**		**W**		**SP**		**S2001**	
	p	R	p	R	p	R	p	R	p	R
S2000										
A	32.1	0.033								
W	**2.2**	**0.184**	**1.5**	**0.249**						
SP	**0.7**	**0.220**	**0.2**	**0.301**	**0.1**	**0.364**				
S2001	**0.1**	**0.633**	**0.1**	**0.667**	**0.1**	**0.734**	**0.1**	**0.661**		

Habitat type 2 (p=0.1%; Global R=0.324)

	S2000		**A**		**W**		**SP**		**S2001**	
	p	R	p	R	p	R	p	R	p	R
S2000										
A	**0.5**	**0.257**								
W	**0.2**	**0.363**	**0.1**	**0.377**						
SP	**0.1**	**0.314**	**0.1**	**0.409**	5.4	0.140				
S2001	**0.2**	**0.281**	**0.2**	**0.469**	**0.1**	**0.463**	**0.1**	**0.287**		

Habitat type 6 (p=0.1%; Global R=0.319)

	S2000		**A**		**W**		**SP**		**S2001**	
	p	R	p	R	p	R	p	R	p	R
S2000										
A	**1.8**	**0.187**								
W	**0.2**	**0.321**	**1.6**	**0.179**						
SP	**0.1**	**0.531**	**0.7**	**0.256**	**0.1**	**0.593**				
S2001	**0.4**	**0.345**	**0.4**	**0.303**	**0.1**	**0.539**	**5.0**	**0.145**		

summer 2001 from autumn. Although the meiofaunal assemblages differed significantly among zones within each habitat type (p =0.1-0.4%), as was determined within each season, the extent of those differences was relatively minor (Global R-statistics=0.135-0.324).

9.3.5 Nematode assemblages

A total of 75 nematode species represented by 14107 individuals in 202 cores, which corresponds to a total of 17552 individuals when the samples had each been adjusted to 10 cm^{-2} and then summed, were recorded during this study. Sixty two of those species were found at the most protected habitat type (1), while 49 and 42 species were recorded at habitat types 2 and 6, respectively (Table 9.6). However, only seven species contributed more than 5% to the total number of individuals in habitat types 1 and 2, and just four species exceeded this level in habitat type 6. The dominant species, *i.e.* those contributing >10% to the overall number of nematodes, differed among the three habitat types. Thus, at habitat type 1, *Paracomesoma* sp. (14.5%), *Mesacanthion* sp. (13.3%) and *Daptonema* sp. (11.5%) dominated the nematode assemblage, whereas *Chromadorita* sp. (21.9%) and *Trileptium* sp. (11.9%) were the most abundant species at habitat type 2, and *Gonionchus australis* (34.8%), *Theristis* sp.1 (17.1%) and *Onyx* sp.1 (11.8%) constituted the majority of nematodes found at habitat type 6 (Table 9.6).

9.3.6 Number of species, density, and species relatedness of nematodes in different zones, habitat types, and seasons

Three-way ANOVA demonstrated that both the density and number of species of nematodes differed significantly among habitat types, seasons and zones (p <0.001) and that there was a significant two-way interaction between habitat type and season (p <0.01; Table 9.7). The mean squares for both of these variables were far greater for habitat type than for the other two other main effects, which, in turn, were far greater than that for the interaction. Scheffè's *a posteriori* test showed that the mean number of species and mean densities of nematodes in zone C (4.5 and 381 nematodes 10 cm^{-2}, respectively) were significantly greater than those in both zones A (3.4 and 167 nematodes 10cm^{-2}, respectively) and B (2.7 and 112 nematodes 10cm^{-2}, respectively), which were not significantly different from each other (Figs 9.4a, c). The mean number of species and mean densities in each season were greater in habitat type 1 than in either of the other two habitat types and, in four of the five seasons, were greater or the same in habitat type 6 as in habitat type 2 (Figs 9.4b, d). The mean density and mean number of species were both least in winter in each habitat type.

Table 9.6 Mean density (M; number of individuals 10 cm^{-2}), standard deviation (±1sd), percentage contributions to the sum of the mean densities (%) and the rank by density (Rk) of each nematode species in samples collected in all zones at habitat types 1, 2 and 6 in nearshore waters along the lower west coast of Australia in all seasons between summer 2000 and summer 2001. The number of taxa, number of samples collected and the total number of individuals (after the number of individuals in each sample had been adjusted to that in 10 cm^{-2}) are also provided for each habitat type.

	1				**2**				**6**			
	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Paracomesoma sp.	26.9	69	15	1	2.2	4.4	7	6	1.6	4.6	3.9	5
Mesacanthion sp.	24.7	54	13	2	0.4	1.7	1.4	12	0.4	1.3	0.9	12
Daptonema sp.	21.2	48	12	3	2.3	7	7.5	3	0.6	2.1	1.5	11
Chromadorita sp.	12.3	29	6.6	4	6.9	24	22	1	0.2	1.1	0.6	21
Neochromadora sp.	12.3	31	6.6	4	0.1	0.8	0.5	24	0.1	0.6	0.2	30
Dichromadora sp.	10.6	22	5.7	6	0.4	1.3	1.2	16	0.3	1.2	0.8	15
Pheronus sp.	10.1	32	5.4	7	0.1	0.8	0.5	24	0.2	0.9	0.4	24
Theristus sp. 1	8.4	15	4.6	8	2.3	4.7	7.2	4	7	15	17	2
Marylynnia sp.	7.4	14	4	9	0.1	0.6	0.2	31	0.3	1.2	0.8	15
Metalinhomoeus sp.	5.0	24	2.7	10					0.1	0.6	0.2	30
Parapinnanema sp.	3.8	13	2	11					0.1	0.6	0.2	30
Pomponema sp.	3.3	7.4	1.8	12	0.1	0.6	0.2	31	0.1	0.6	0.2	30
Leptonemella sp.	3.0	8.6	1.6	13								
Microlaimus sp. 1	3.0	7	1.6	13	0.7	4.1	2.3	10	0.2	1.1	0.6	21
Chromadorina sp.	2.2	10	1.2	15	0.1	0.8	0.5	24				
Bathylaimus sp. 1	2.1	5	1.1	16	0.8	2.4	2.6	9	1.1	2.2	2.6	6
Trefusia sp.	2.0	4.2	1.1	16					0.2	1.1	0.6	21
Trochaimus sp.	2.1	6.6	1.1	16					0.1	0.6	0.2	30
Spirinia sp. 1	1.9	5	1	19	0.1	0.6	0.2	31	0.2	0.9	0.4	24
Rhabditis sp. 1	1.8	6.8	1	20	0.4	1.4	1.4	12	2.7	13	6.6	4
Graphonema sp. 2	1.7	4.3	0.9	21	0.4	1.9	1.4	12	0.3	1.2	0.8	15
Microlaimus sp. 2	1.2	6.1	0.7	22	0.1	0.6	0.2	31				
Gonionchus australis	1.2	4.6	0.6	23	0.4	2.5	1.2	16	14	44	35	1
Theristus sp. 2	1.2	3.5	0.6	23	0.2	1.3	0.7	20	0.1	0.6	0.2	30
Gomphionema sp.	1.0	2.9	0.5	25								
Spirinia sp. 2	1.0	3.1	0.5	25					0.1	0.6	0.2	30
Paralinhomoeus sp. 1	0.9	2.3	0.5	27	0.2	1	0.7	20				
Metadesmolaimus sp.	0.9	3	0.5	28	1.4	4	4.4	8	0.8	2.7	1.9	9
Viscosia sp. 2	0.9	2.4	0.5	28	0.6	2	1.9	11	0.7	2.3	1.7	10
Camacholaimus sp.	0.8	4.4	0.4	30	0.2	1.3	0.7	20	0.1	0.6	0.2	30
Prochromadorella sp.	0.7	2	0.4	31	0.1	0.6	0.2	31				
Diplopeltula sp.	0.6	5.4	0.4	32								
Paralinhomoeus sp. 2	0.6	2.4	0.4	32								
Viscosia sp. 1	0.6	2.8	0.4	32	1.7	4.1	5.4	7	0.4	1.8	0.9	12
Cephalanticoma sp.	0.6	1.8	0.3	35								
Synonchium sp. 1	0.6	2.3	0.3	35								
Graphonema sp. 1	0.6	2.8	0.3	35	0.4	1.6	1.2	16				
Hypodontolaimus sp.	0.6	2.6	0.3	35	0.1	1.2	0.5	24				
Metoncholaimus sp.	0.6	1.8	0.3	35	0.1	0.6	0.2	31	0.3	1.2	0.8	15
Odontophora sp.	0.5	1.7	0.3	40	0.1	0.6	0.2	31				
Setosabatieria sp.	0.5	1.7	0.3	40					0.2	0.9	0.4	24
Chromadoridae sp.	0.4	1.9	0.2	42								
Halalaimus sp.	0.4	1.6	0.2	43								
Microlaimus sp. 3	0.4	2	0.2	43	0.2	1.8	0.7	20				
Haliplectus sp.	0.3	1.2	0.2	45								
Choniolaimus sp.	0.3	1.2	0.2	45	0.1	0.6	0.2	31				
Onyx sp. 1	0.3	1.2	0.2	45	0.4	1.7	1.4	12	4.8	12	12	3

Table 9.6 continued

	1				2				6			
	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Ascolaimus sp.	0.3	1.2	0.2	45					0.9	3.2	2.3	7
Tripyloididae sp.	0.2	1.8	0.1	49								
Actinonema sp.	0.2	1.3	0.1	49	0.1	0.8	0.5	24	0.1	0.6	0.2	30
Rhynchonema collare	0.2	1	0.1	49	0.1	0.6	0.2	31	0.1	0.6	0.2	30
Rhabditis sp. 2	0.1	0.8	0.1	52								
Spilophorella sp.	0.1	1.2	0.1	52	0.1	0.6	0.2	31	0.2	0.9	0.4	24
Bathylaimus sp. 2	0.1	1.2	0.1	52					0.1	0.6	0.2	30
Enoplus sp.	0.1	0.8	0.1	52	2.3	5.8	7.2	4	0.1	0.6	0.2	30
Metadasynemella sp.	0.1	0.6	0	56								
Oxystomina sp.	0.1	0.6	0	56								
Synonchium sp. 2	0.1	0.6	0	56								
Euchromadora sp.	0.1	0.6	0	56	0.1	1.2	0.5	24				
Enoplolaimus sp.	0.1	0.6	0	56	0.1	0.6	0.2	31	0.9	4	2.3	7
Parodontophora sp.	0.1	0.6	0	56					0.2	0.9	0.4	24
Gammanema sp.	0.1	0.6	0	56					0.1	0.6	0.2	30
Halanonchus sp.					0.4	2.5	1.2	16				
Cobbia sp.					0.1	0.6	0.2	31				
Elzalia sp.					0.1	0.6	0.2	31				
Eurystomina sp.					0.1	0.6	0.2	31				
Leptosomatum sp.					0.1	0.6	0.2	31				
Onyx sp. 2					0.1	0.6	0.2	31				
Rhynchonema sp. 2					0.1	0.6	0.2	31				
Subsphaerolaimus sp. 2					0.1	0.6	0.2	31				
Xenolaimus sp.					0.1	0.6	0.2	31				
Nudora sp.					0.1	1.2	0.5	24	0.4	2	0.9	12
Epacanthion sp.									0.3	1.2	0.8	15
Trileptium sp.					3.7	12	12	2	0.2	1.4	0.6	20
Subsphaerolaimus sp. 1									0.2	0.9	0.4	24
Number of taxa	**62**				**49**				**42**			
Overall mean density	**185**				**31**				**41**			
Number of samples	**69**				**68**				**65**			
Total no. individuals	**12765**				**2135**				**2652**			

ANOVA showed that Δ^+ and Λ^+ both differed significantly among habitat types and seasons ($p < 0.001$) and that, in both cases, the mean squares were slightly higher for the former independent variable (Table 9.7). There was a small but significant interaction between habitat type and zone for Δ^+ and between habitat type and season for Λ^+ ($p < 0.05$; Table 9.7). The mean values for Δ^+ were significantly lower in winter than in all other seasons (Fig. 9.5a). Although the mean values for Δ^+ in zones A, B and C were each greater in habitat type 1 than in habitat types 2 and 6, those in zones B and C were greater in habitat type 6 than 2, whereas the reverse was the case in zone A (Fig. 9.5b). The values for Λ^+ were greater in habitat type 1 than habitat type 6 in all seasons and were greater than those in habitat type 2 in each season except summer 2000. Variation in taxonomic distinctness was less in habitat type 6 than in habitat type 2 in three of the five seasons (Fig. 9.5c).

Table 9.7 Mean squares and significance levels for three-way ANOVA of the number of taxa, density, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of nematodes in samples collected in zones A, B and C at habitats 1, 2 and 6 in each season between summer 2000 and summer 2001. "df"=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	No. of species	Density	Δ^+	Λ^+
Main effects					
Habitat type (H)	2	4.112***	20.448***	8916.428***	380848.155***
Zone (Z)	2	0.476***	4.774***	1726.039	53361.280
Season (S)	4	1.582***	10.954***	7880.480***	304392.990***
Two-way interactions					
H x S	8	0.176**	1.378**	1476.137	75810.493*
H x Z	4	0.118	1.234	2028.225*	25144.344
Z x S	8	0.096	0.942	718.252	33148.348
Three-way interactions					
H x Z x S	16	0.047	0.359	578.497	36497.223
Error	157	0.060	0.532	758.058	34266.420

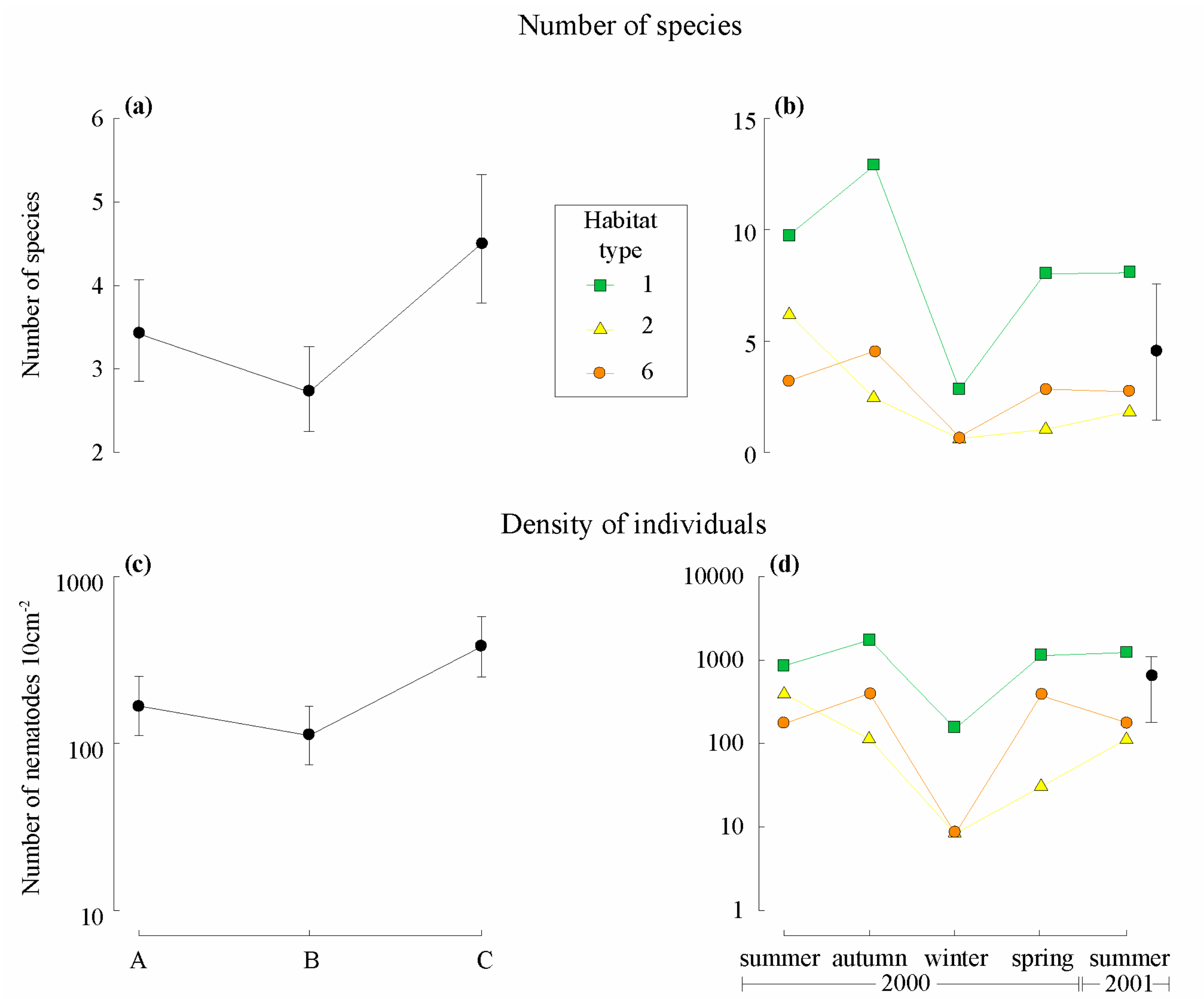


Figure 9.4: Mean (± 95% CI) number of nematode species in (a) zones A, B and C and (b) at habitat types 1,2 and 6 in each season, and mean (± 95% CI) density of nematodes in (c) zones A, B and C and (d) at habitat types a, 2 and 6 in each season. For the sake of clarity, in this figure and Fig. 9.5, the overall mean (± 95% CI) is provided on each plot (denoted by black symbols and lines).

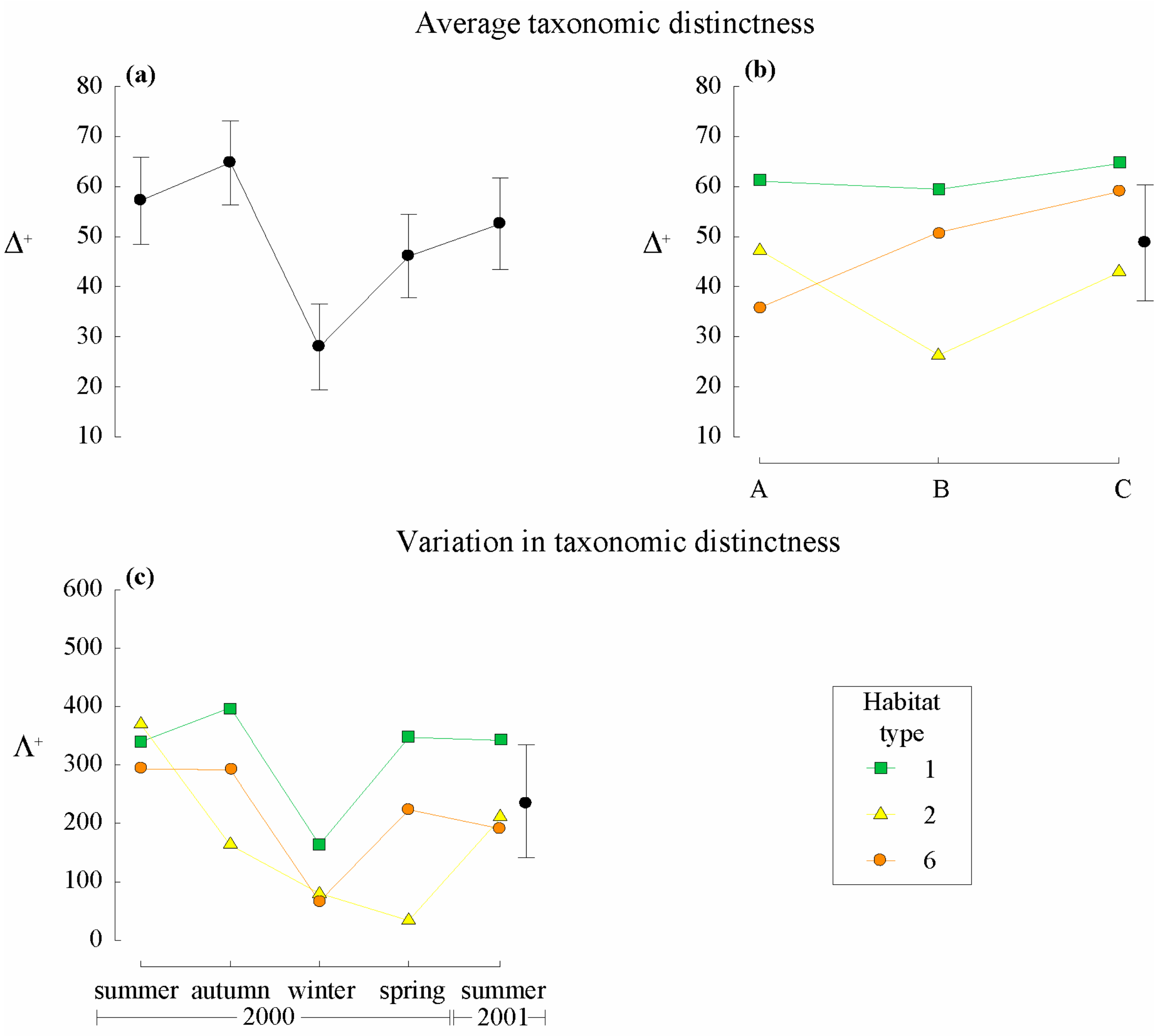


Figure 9.5: Mean (±95% CI) of the average taxonomic distinctness (Δ^+) for (a) each season between summer 2000 and summer 2001 and (b) zones A, B and C at each habitat type and (c) variation in taxonomic distinctness (Λ^+) in habitat types 1, 2 and 6 in each season.

9.3.7 Joint biodiversity analyses

Scatter plots of Δ^+ *vs* Λ^+ constructed for each of the five seasons and three zones showed that, in almost all cases, the points for all three habitat types lay within their relevant 95% confidence ellipses. This demonstrates that, apart from the point representing habitat type 1 in zone B (Fig 9.6g), the observed values for Δ^+ and Λ^+ lay within those expected for the nematode assemblages in the nearshore waters along the lower west coast of Australia (Figs 9.6a-h). The reason for this single exception is a higher than expected Λ^+. While the points for the assemblages from habitat type 1 on the plots for zones A and C remained inside their respective confidence ellipses, they were also close to the highest Λ^+ expected for samples of their size (Fig 9.6f-h).

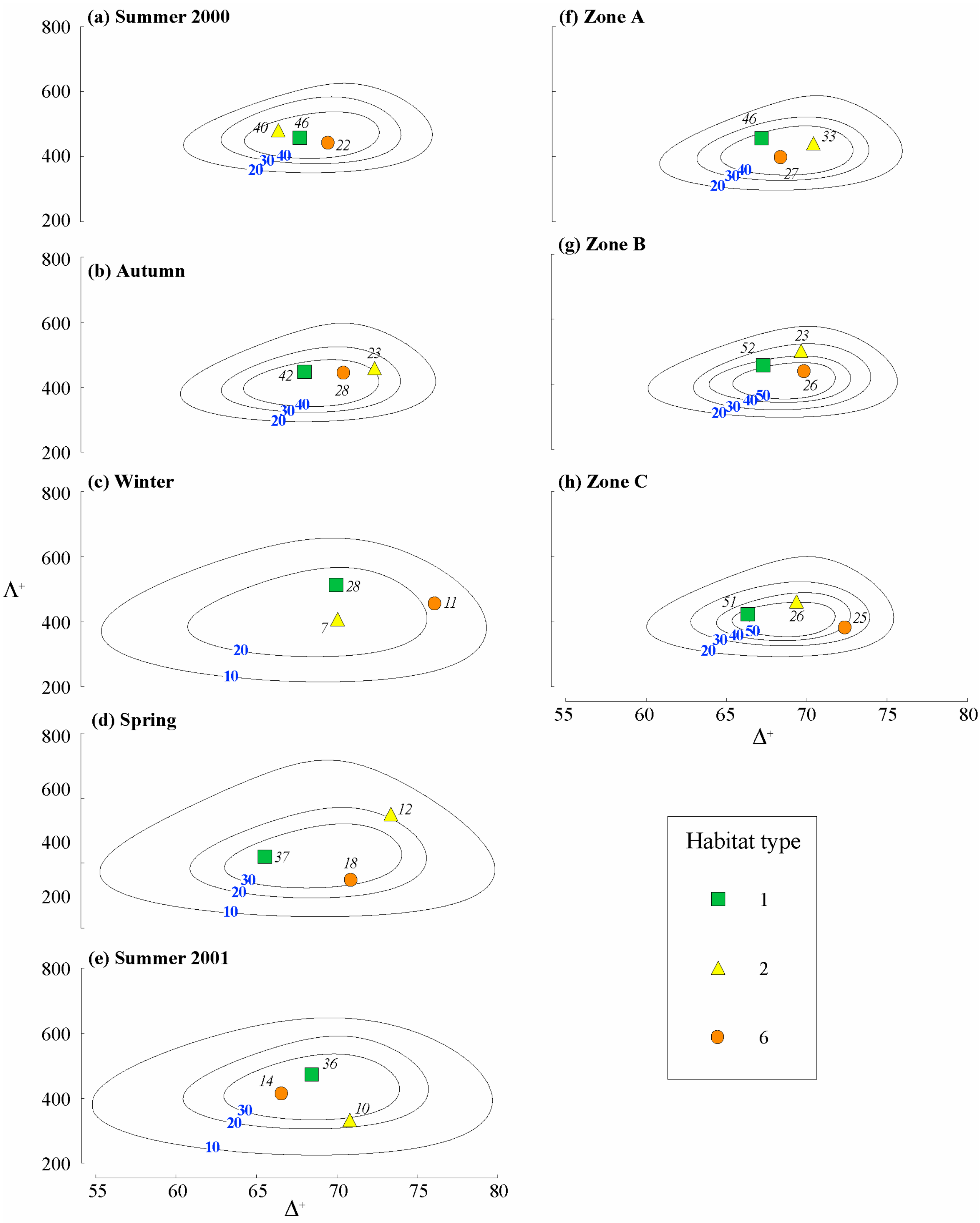


Figure 9.6: Scatterplots of average taxonomic distinctness *vs* variation in taxonomic distinctness of nematodes in samples collected at habitat types 1, 2 and 6 in (a) summer 2000, (b) autumn, (c) winter (d) spring and (e) summer 2001, and in zones (f) A, (g) B and (h) C. The number of species recorded at each habitat type and the relevant 95% probability ellipses for simulations of different-sized subsets of species are also provided for each season and zone.

9.3.8 Comparisons among the nematode assemblages in different habitat types.

When the densities of the various nematode species, derived from the means of the replicate samples collected in each zone at each habitat type during each season, were subjected to MDS ordination, all but one of the samples from habitat type 1 formed a tight and essentially discrete group that lay in the bottom left hand part of the 3D ordination plot below and/or to the left of all but one of those from habitat type 2 and to the left of all of those from habitat type 6 (Fig. 9.7a). When the samples on the same ordination plot were coded for season, the samples from the different seasons tended to intermingle (Fig. 9.7b). However, most of the samples for winter did lie above those for summer 2001. When the samples were coded for zone, the samples for no zone exhibited a conspicuous tendency to lie in a different part of the plot to those of the other two zones (Fig. 9.7c).

One-way ANOSIM showed that the compositions of the nematode assemblages differed significantly among habitat types ($p < 0.1\%$; Global R=0.424) and seasons ($p < 0.1\%$; Global R=0.176). Pairwise comparisons demonstrated that the species composition in each habitat type was significantly different from that in each of the other habitat types ($p < 0.1\%$), with the R-statistic values being greatest for habitat types 1 *vs* 6 (R=0.595) and habitat types 1 *vs* 2 (R=0.416) and least for habitat types 2 *vs* 6 (R=0.269).

SIMPER showed that *Paracomesoma* sp.1 and *Theristis* sp.1 were important in typifying the nematode assemblage at habitat types 1 and 2, while *Mesacanthion* sp. and *Daptonema* sp. typified that at habitat type 1 but not habitat type 2, whereas the reverse applied to *Enoplus* sp.. Although *Theristis* sp.1 also typified habitat type 6, the other two typifying species for the assemblage at this habitat type, *Gonionchus australis* and *Onyx* sp.1, were not found regularly in either of the other two habitat types.

9.3.9 Comparisons of nematode assemblages among different habitat types in each season

Since nematode compositions differed significantly among seasons, MDS analyses were carried out using the densities of the various nematode species for each of the five seasons separately in order to explore more fully the extent to which the compositions of the nematode assemblages in each of the three habitat types varied within each season. The resultant plots showed that the extent to which the samples from the different habitat types formed separate groups on the ordination plot varied with season (Figs 9.8a-e). Thus, for example, in spring, the groups of samples collected from each habitat type formed almost completely discrete groups (Fig. 9.8d), whereas those from the three habitat types overlapped markedly and were widely spaced in winter (Fig. 9.8c). Samples from habitat type 1 formed a relatively tight group in the plots for summer 2000, autumn, spring and summer 2001 (Figs 9.8a, b d and e, respectively).

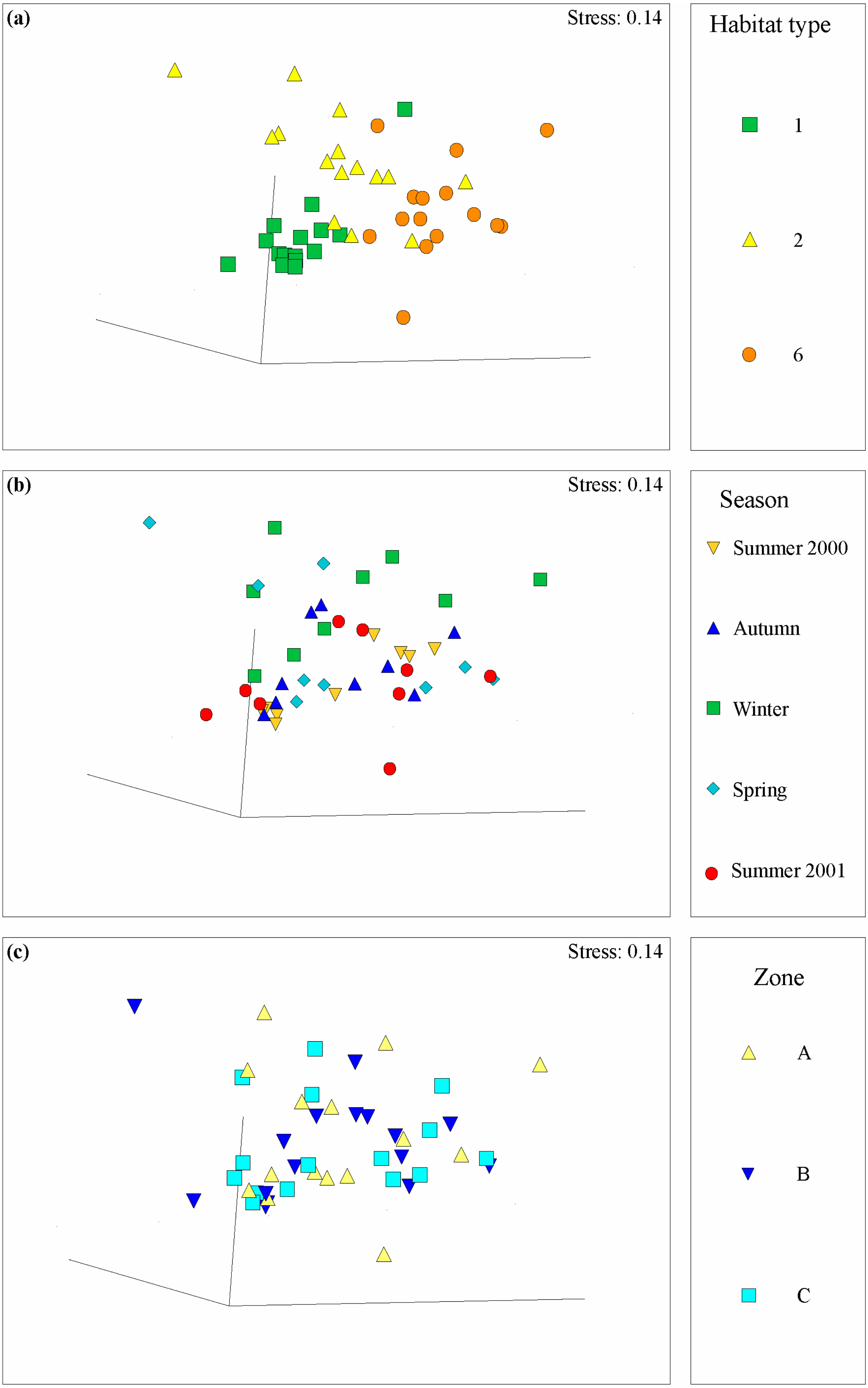


Figure 9.7: Three-dimensional MDS ordination of the mean densities of nematode species in samples collected in zones A, B and C at habitat types 1, 2 and 6 in all seasons between summer 2000 and summer 2001. Samples on the plot have been coded for (a) habitat type, (b) season and (c) zone.

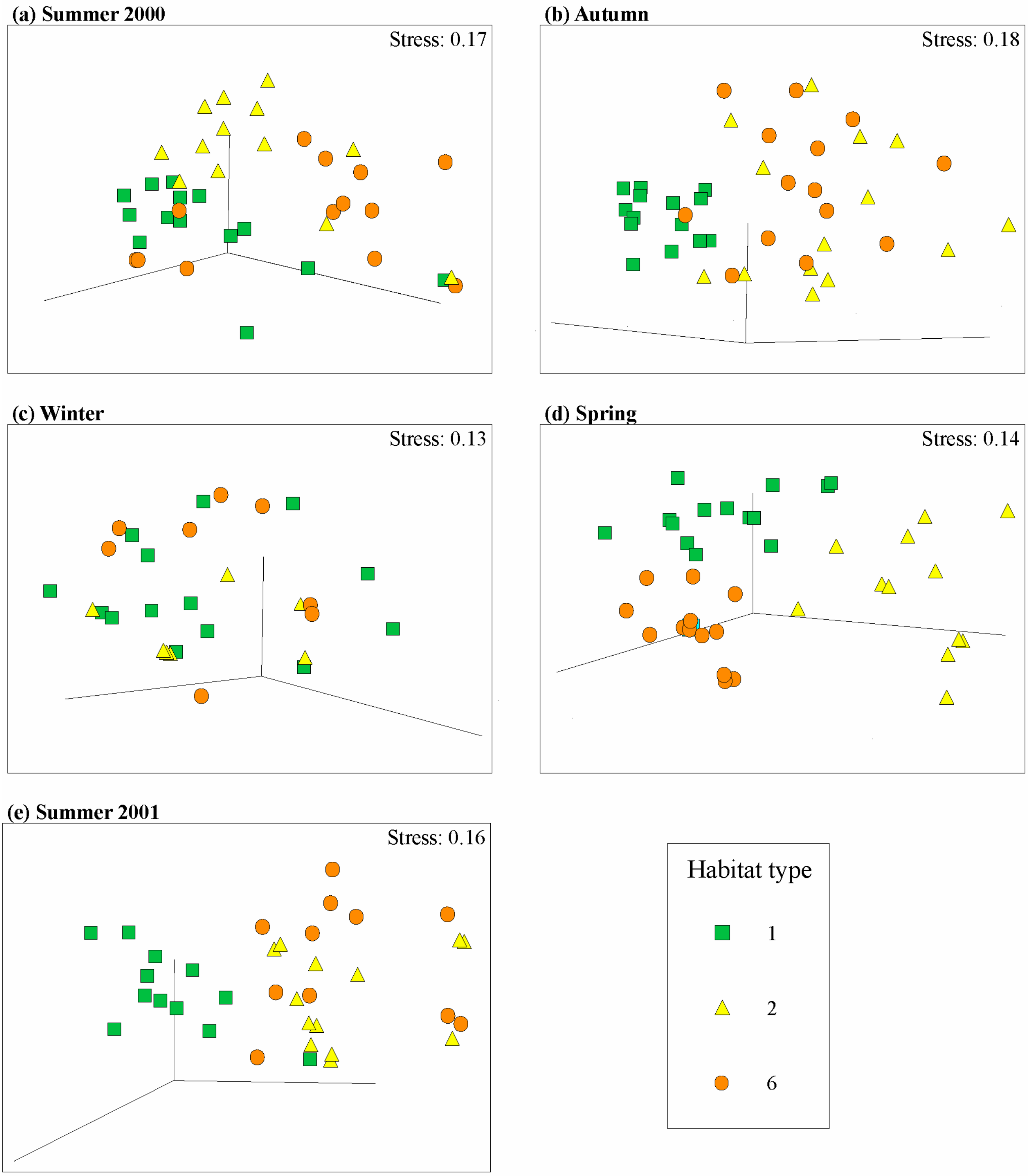


Figure 9.8: Three-dimensional MDS ordination of the densities of nematode species taxa at habitat types 1, 2 and 6 during (a) summer 2000, (b) autumn, (c) winter, (d) spring and (e) summer 2001.

Although the majority of samples for habitat type 2 formed a relatively discrete group in the summers of 2000 and 2001, the samples for that habitat type overlapped markedly those of habitat type 6 in autumn.

Two-way crossed ANOSIM tests, employing habitat type and zone as factors, showed that, in each season, the compositions of the nematode assemblages differed significantly among habitat types (p=1.3% in winter and 0.1% in all other seasons). However, the differences between habitat types were far greater in spring, autumn and the summers of 2000 and 2001 (Global R=0.678-0.409) than in winter (Global R= 0.282). Pair-wise comparisons in the two-way crossed ANOSIM tests showed that the compositions of the nematode assemblages in habitat types 1 and 2 differed significantly from that in habitat type 6 in all seasons, and that those in the former two seasons were significantly different from each other in all seasons except winter.

The results of SIMPER analyses shown in Table 9.8 highlight the species that typifying the nematode assemblages in the various habitat types in each season. Attention is drawn to the fact that, while a particular species was one of the typifying species for the assemblage at a habitat type in each season, *e.g. Paracomesoma* sp. in habitat type 1, the suite of other typifying species varied among seasons.

9.3.10 Differences in the arrangement of rank orders of similarity among habitat types

Ordination of the similarity matrix derived from the second-stage MDS routine, which was constructed from the nematode compositions in the various habitat types in each season and zone showed that, when the samples were coded for each of those factors (Fig. 9.9a and b, respectively), the points exhibited little tendency to form groups. These results show that the extent of similarity in the composition of the nematodes assemblages between the three habitat types did not show consistent change among zones or seasons.

9.3.11 Comparisons between nematode assemblages in different seasons and zones in each habitat type

Two-way ANOSIMs demonstrated that the compositions of the nematode assemblages in each habitat type underwent significant seasonal changes and differed significantly among zones. The samples on the three-dimensional MDS ordination plots for the nematode assemblages at habitat type 2 showed clear evidence of some degree of seasonal separation. Thus, the samples for summer 2001 lay on the right of the plot and to the right and/or below those for summer 2000, while all of those for autumn lay in the left of the plot (Fig. 9.10b). The separations between seasons were less pronounced in habitat types 1 and 6 (Fig. 9.10a-c). In the plot for habitat type 1 the samples for zone C formed a tight group that lay above and/or to the left of those for zones A and B (Fig. 9.10d). Such zonal differences were not as pronounced at habitat types 2 and 3 (Fig. 9.10 e, f, respectively).

Table 9.8 Species detected by SIMPER as those most responsible for typifying the nematode fauna at habitat types 1, 2 and 6 in (a) summer 2000, (b) autumn, (c) winter, (d) spring and (e) summer 2001. Data has been pooled for those habitat types between which ANOSIM did not detect a significant difference in nematode assemblage composition.

(a) Summer 2000		
1	**2**	**6**
Dichromadora sp. *Daptonema* sp. *Paracomesoma* sp.	*Enoplus* sp. *Viscosia* sp. 1	*Theristis* sp. 1 *Bathylaimus* sp. 1 *Gonionchus australis*

(b) Autumn		
1	**2**	**6**
Paracomesoma sp. *Daptonema* sp. *Mesacanthion* sp.	*Paracomesoma* sp. *Rhabditis* sp. 1	*Theristis* sp. 1 *Gonionchus australis*

(c) Winter	
1 & 2	**6**
Paracomesoma sp. *Mesacanthion* sp.	*Theristis* sp. 1

(d) Spring		
1	**2**	**6**
Mesacanthion sp. *Bathylaimus* sp. 1 *Paracomesoma* sp.	*Daptonema* sp. 1	*Gonionchus australis* *Theristis* sp. 1

(e) Summer 2001		
1	**2**	**6**
Chromadorita sp *Paracomesoma* sp *Mesacanthion* sp.	*Chromadorita* sp. *Theristis* sp. 1	*Onyx* sp. 1 *Gonionchus australis*

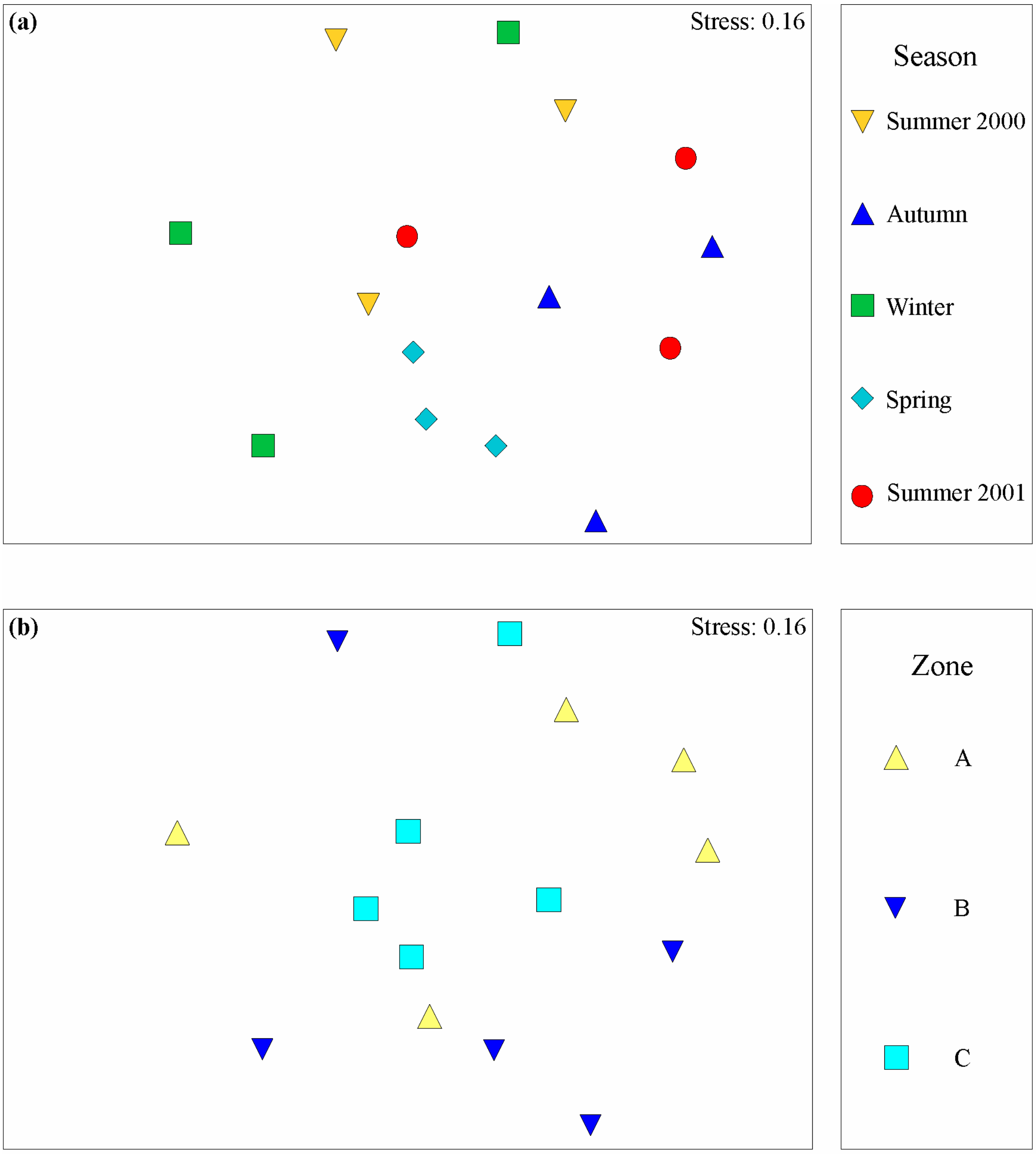


Figure 9.9: MDS ordination of the second-stage similarity matrix containing the correlations between each pair of similarity matrices constructed from the densities of nematode species at habitat types 1, 2 and 6 during each of the seasons between summer 2000 and summer 2001. The points on the ordination plot have been coded separately for (a) zone and (b) season.

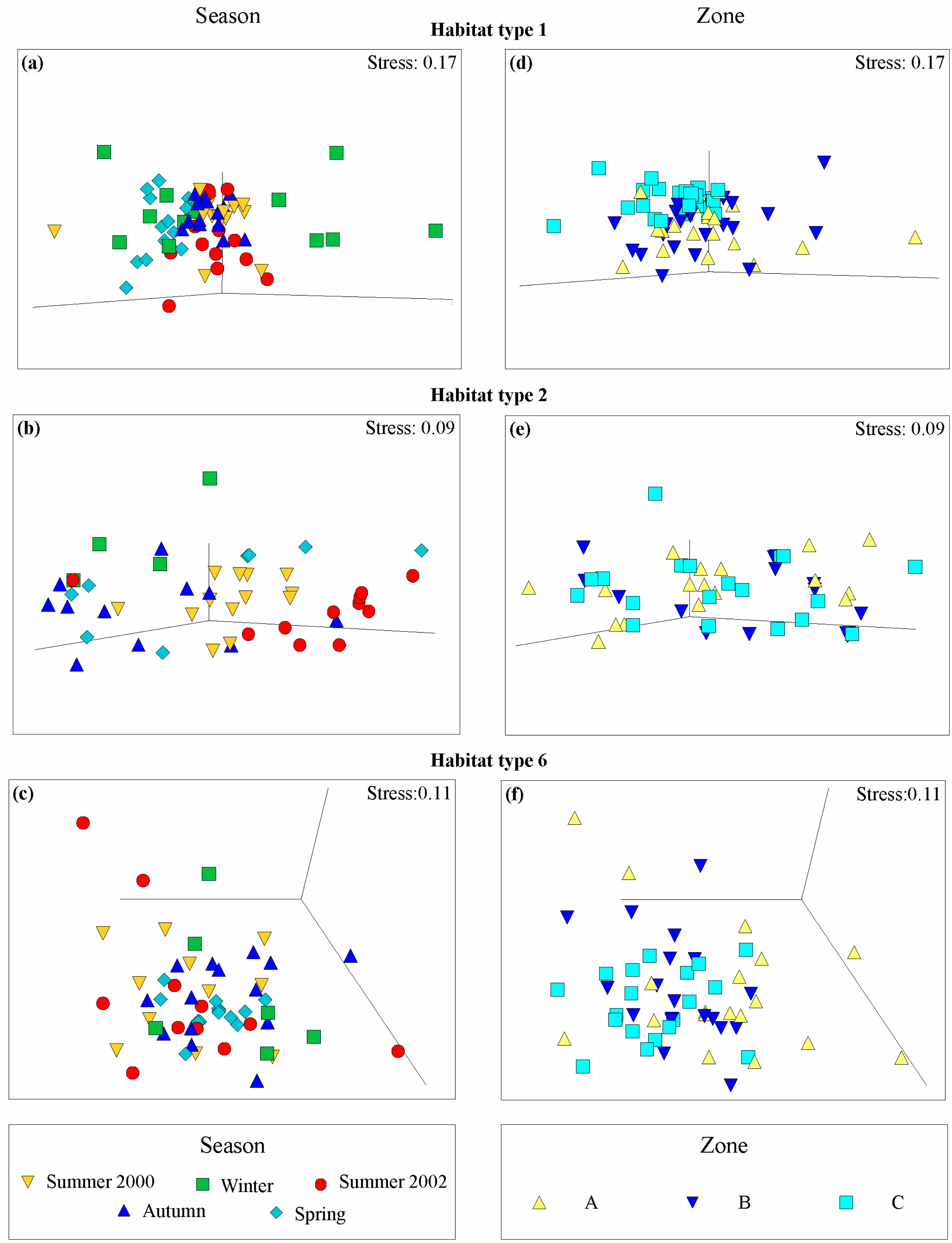


Figure 9.10: Three-dimensional MDS ordination of the densities of nematode species at habitat types 1, 2 and 6 in each season between summer 2000 and summer 2001 (a-c, respectivley) and each zone (d-f, respectivley).

In each habitat type, the Global R-statistics were greater for season (0.231-0.314) than for zone (0.103-0.190). Furthermore, differences among both seasons and zones were most distinct at habitat type 1 ($p < 0.1\%$, Global R=0.314 and $p < 0.1\%$, Global R=0.190, respectively) and least at habitat type 2 ($p < 0.1\%$, Global R=0.231 and p=4.5%, Global R=0.103, respectively).

Pairwise tests revealed that, at habitat type 1, the composition of the nematode assemblage in each season was significantly different from that in each of the other seasons (R =0.268-0.461) and that the composition in summer 2001 was often the most distinct. At habitat types 2 and 6, most pairwise seasonal comparisons were significant and those involving winter had the greatest R-statistic values (R=0.536-0.610 and R=0.193-0.743, respectively). Pairwise comparisons determined that the composition of the nematode assemblage in zone C was significantly different from those in zones A and B at habitat type 1 (R=0.325 and 0.160, respectively), and that in zone A was significantly different from those in B and C at habitat type 6 (R=0.218 and 0.253, respectively). The extent of any differences was always greatest between zones A and C.

SIMPER identified that, at habitat type 1, the composition of the nematode assemblage in summer 2001 was distinguished from those in the other seasons by relatively greater densities of *Chromadorita* sp. and *Mesacanthion* sp.. The composition in winter at habitat type 2 was mainly distinguished from those of both summers by far lower densities of *Chromadorita* sp., and the composition of the samples from habitat type 6 during the winter were distinguished from those from autumn, spring and summer 2001 by relatively lower densities of *Gonionchus australis* and *Theristis* sp.1, both of which were identified at a global level as typifying that habitat type. The samples from zone A were distinguished from those from zone C through the presence of far greater densities of *Dichromadora* sp. and *Mesacanthion* sp. at habitat type 1 and of *Onyx* sp.1 and *Gonionchus australis* at habitat type 6.

9.4 Discussion

9.4.1 Meoifaunal assemblages

The overall densities of the meiofauna in the three habitat types studied on the lower west coast of Australia, which ranged from 265 to 395 organisms 10 cm^{-2}, fall within the lower end of the range of those reported for sandy intertidal habitats in South Africa (McLachlan 1977, 1978). The density of the meiofauna was greatest in the most sheltered habitat type (1), and was essentially the same in the moderately sheltered habitat type (2) and the most exposed habitat type (6). The difference between the densities at habitat type 1 *vs* both habitat types 2 and 6 presumably reflects the fact that, as exposure to wave action increases, the surface sediments, in which the meiofauna are concentrated (Coull and Bell 1979, Coull 1988), become more disturbed and thus less conducive for colonisation by the meiofauna (Bell and Sherman 1980, Palmer 1986). Furthermore, habitat type 1 was located close to seagrass beds, which would have provided detrital material that, through the relative lack of water turbulence, would be able to settle and accumulate and act as a substantial source of food for the meiofauna. The shallow, sheltered conditions characteristic of habitat type 1 would also favour the growth and accumulation of microphytobenthos (Jorgensen and Revsbech 1983), another food source of meiofauna (Hicks and Coull 1983, Marcotte 1983). The densities of the meiofauna have been found to be positively correlated with the amount of organic material in the sediment in other areas (McLachlan *et al.* 1981, Huys *et al.* 1992, Moens *et al.* 1999).

The taxa, that are typically most abundant in meiofaunal communities, namely, nematodes, turbellarians, harpacticoid copepods and polychaetes (Coull 1988, Gierre 1993), were also prevalent in the meiofauna of the three habitat types studied on the Western Australian coast. Nematodes dominated the meiofauna in habitat types 1 and 6, where they comprised >50% of the total number of individuals, thereby paralleling the situation in other nearshore waters (McLachlan and Hesp 1984, Phillips and Fleeger 1985, Gierre 1993, Netto *et al.* 1999, Schratzberger *et al.* 2000). However, the Polychaeta was the dominant group at habitat type 2 (>50% contribution). Although harpactiocid copepods are often numerically the second most dominant meiofaunal taxa (McLachlan and Hesp 1984, Phillips and Fleeger 1985, Gierre 1993, Netto *et al.* 1999, Schratzberger *et al.* 2000), this was the case only in habitat type 2. Turbellarians and nematodes ranked second in terms of abundance in habitats types 1 and 2, respectively.

9.4.2 Compositions of meiofaunal assemblages among habitat types

The marked differences in the composition and densities of the meiofauna among habitat types are presumably related, in part, to the influence of differences in wave exposure, as has been found to occur elsewhere (Wieser 1959b, McLachlan 1977, 1980, McLachlan 1985, Palmer 1986). The composition at habitat type 1 was distinguished from that at the other two habitat types by relatively higher densities of nematodes, and the composition at habitat type 2 was distinguished from that at habitat type 6 by a relatively higher density of capitellid polychaetes and a relatively lower density of interstitial harpacticoids. Sediment grain size influences the meiofaunal composition, with nematodes tending to be the dominant taxa in finer sediments and harpacticoid copepods being more abundant in coarser sediment types (Coull 1988). Although habitat type 1 is the most sheltered of the habitat types and would therefore have been expected to contain finer sediments than the other two habitat types, we were unable to detect any significant difference among the particle size composition of the sediments at the three habitat types. Thus, the above differences in faunal compositions may reflect differences in the extent of oxygenation of the sediments at the three habitat types. Such a view would be consistent with the fact that, through the presence of greater turbulence, the sediments at habitat type 6 would be particularly well oxygenated and therefore account for the high densities of harpacticoid copepods at that site. The conclusion that the sediment was far better oxygenated at habitat type 6 than habitat type 1 is borne out by the fact that the redox discontinuity layer was much deeper at the former than latter habitat type (Chapter 4). The prevalence of such crustaceans in well oxygenated sediments elsewhere is considered to reflect the fact that these organisms are particularly susceptible to low oxygen levels in the interstices of the substrate (McLachlan 1978, Coull 1988).

9.4.3 Compositions of meifaunal assemblages among seasons and zones

The density and composition of the meiofauna both underwent marked changes during the year in each habitat type, with densities generally being greatest in the warmer months and least in winter, a trend often found with meiofaunal communities (Coull 1988). This presumably reflects, at least in part, a decrease in reproductive activity at low temperatures (Heip *et al.* 1985). However, turbellarians attained relatively higher densities in winter than in the warmer months, thereby paralleling the situation elsewhere (Faubel 1976).

Although the densities and composition of the meiofauna varied among zones, those differences were far less pronounced than those associated with habitat type, and would appear to be less than those found with meiofaunal communities elsewhere (Heip *et al.* 1985, Armonies and Reise 2000). The relatively weak zonal differences in our study area are presumably related to the presence of a very small tidal amplitude. However, some taxa were more prevalent in a particular zone. For example, turbellarians, a taxa commonly associated with intertidal areas and swash zones (Gierre 1993), distinguished our zone B, and capitellid polychaetes, which are often found in the upper regions of the tidal gradient (Gierre 1993) distinguished our zone A. Furthermore, these taxa were also prevalent in comparable zones in another microtidal sandy beach in Western Australia (McLachlan and Hesp 1984).

9.4.4 Nematode assemblages

During the present study, only two of the 75 species of nematodes recorded in samples collected from sites representing three different habitat types in nearshore waters along the lower west coast of Australia during five successive seasons could be assigned to a previously described species. The presence of such a large number of undescribed nematode species on this coast of Australia highlights the urgent need for taxonomic studies on this important component of the meiofaunal community in this region. In contrast to the situation at the species level, all but two of the 73 putative species could be allocated to a particular genus.

Only one third of the 59 genera recorded in nearshore waters along the lower west coast of Western Australia during this study were also found in a comparable environment at a similar latitude on the east coast of Australia (Nicholas and Hodda 1999, Nicholas 2001). Furthermore, as many as 27 of the 48 genera found in the latter region were not recorded on the lower west coast of Australia. However, 85% of the genera recorded on the lower west coast have been previously found in one or other of a wide range of marine and estuarine environments in Australia (Greenslade 1989). Comparisons between our list of nematode species and a checklist of marine nematode species from around the world (Gerlach and Riemann 1973/1974), emphasises the highly cosmopolitan nature of the genera encountered during our study.

The 75 nematode species found during the present study on beaches on the lower west coast of Australia is far more than the 34 and 58 species recorded by Warwick *et al.* (1990) and Nicholas & Hodda (1999) in nearshore marine habitats in Tasmania and south-eastern mainland Australia, respectively. However, 104 and 77 species of nematode were recorded by McIntyre and Murison (1973) and Blome *et al.* (1999) in nearshore coastal beaches of Scotland and the East Frisian Wadden Sea, respectively. Although the number of species recorded during this study is within the range recorded by other workers, the densities recorded during the present study are relatively low, even at the least exposed habitat type *i.e.* habitat type 1 (*cf* Heip *et al.* 1985, Alongi 1986). This suggests that the nearshore waters along the lower west coast of Australia are not particularly productive.

9.4.5 Compositions of nematode assemblages among habitat types

Our seasonal data demonstrate that the number of species, diversity (Δ^+ and Λ^+) and density of nematodes were consistently greater at habitat type 1 than at habitat types 2 and 6, which were far less protected and contained far less seagrass or no seagrass. The greater number of species and density is like to be due to fact that the relatively lower exposure to wave energy provides an environment, which is more stable and productive than the other two habitat types. The higher values of Δ^+ indicate that the assemblages at habitat type 1 contain representatives of a greater number of higher taxa than the other two habitat types, while the greater values of Λ^+ indicate that the taxonomic composition is uneven, *i.e.* contain both species which have many congeners, and higher taxa which are represented by only a few species. It is thus relevant that the taxonomic structure of the assemblage in zone B at habitat type 1 showed significant departure from that expected specifically in the direction of greater Λ^+, which is likely to have been caused by the cumulative effect of the assemblage at habitat type 1 having high values Λ^+

and zone B receiving the greatest amount of scouring, and thus would introduce selection for those organisms adapted for that environment.

The results of the above analyses concur with the results of SIMPER, which determined that habitat type 1 was distinguished from the other two habitat types primarily by species that were closely related, *i.e. Chromadorita* sp., *Neochromadora* sp., *Dichromadora* sp. and *Marylinnia* sp.. Examination of the morphology of these species highlights the fact that all four of the above species are diatom grazers, as are two of the other species determined to be diagnostic of habitat type 1, *i.e. Paracomesoma* sp. and *Pheronus* sp. (Moens and Vincx 1997). The greater densities of these species of nematodes at habitat type 1 than at either habitat types 2 or 6 strongly suggest that the amount of microphytobenthic diatoms was greater in this habitat type. Such a conclusion would be consistent with the fact that, in the study area, the density of such algae is greatest in those waters where turbulence is particularly low, as is the case in habitat type 1 (Kendrick *et al.* 1998) In contrast to the situation at habitat type 1, the two most important diagnostic species of the nematode assemblage at habitat type 6, *i.e. Theristis* sp.1 and *Gonionchus australis*, belong to genera which are regarded as bacterial grazers (Moens and Vincx 1997). Thus, at this habitat type, where the far more turbulent wave action would presumably discourage the growth of microphytobenthos, there appears to have been selection for nematodes that are adapted to ingesting bacteria rather than diatoms.

The composition of the nematode assemblage at the moderately sheltered habitat type 2, at which patches of seagrass were present, contained relatively large numbers of species that typified habitat type 1, *e.g. Paracomesoma* sp., and also species which typified habitat type 6, *e.g. Theristis* sp.1. Thus, in this respect, the composition of nematode assemblages at habitat type 2 was intermediate between those at the highly sheltered habitat type 1 and the relatively exposed habitat type 6. This implies that algal food sources are more readily available at habitat type 2 than 6, but that bacteria still comprise a substantial portion of the diet of nematodes in this environment. Several other species, which characterised neither of the other two habitat types, were found relatively consistently at habitat type 2, *e.g. Enoplus* sp. and *Viscosia* sp.1. The above comparisons, allied with the results of ANOSIM tests, demonstrate that the compositions of the nematode assemblages differ significantly among habitat types in nearshore waters along the lower west coast of Australia, and thus provide further evidence that differences in the relative abundances of key nematode species amongst sites provide reliable indications that the environmental conditions at those sites differ (Alongi 1986, Warwick *et al.* 1990, Dittmann 2000, Fisher 2003).

9.4.6 Compositions of nematode assemblages among seasons and zones

The number of species and densities of nematodes at each of the habitat types underwent a pronounced decline in winter. Indeed, a number of cores collected in this season yielded no nematodes, particularly in the case of those taken in zones A and B at the two most exposed habitat types. The declines in the above two biotic parameters in winter, which parallels those found in a similar environment on the east coast of Australia (Nicholas and Hodda 1999) suggest that, during this season, a large number of nematodes die and/or their reproductive success declines dramatically. This view is consistent with that of Heip *et al.* (1985) who, on the basis of laboratory studies, concluded that the generation time of some nematode species was increased at low water temperatures. Although a marked reduction in water temperature is probably the major factor that brought about the decline in the number of species and density in winter, it is noteworthy that the seasonal declines in these variables were particularly marked at habitat type 1. It would thus appear especially relevant that the majority nematodes in this highly protected habitat feed predominantly on microphytobenthos and that, in microtidal sandy nearshore environments, the amount of this component of the biota declines precipitously during winter (Sundbäck *et al.* 2000).

In the case of habitat types 2 and 6, which are more exposed to wave action than habitat type 1, the marked declines in the numbers of species and densities of nematodes in winter were probably also related, in part, to a reduction in the stability of the interstitial environment in which nematodes live. The increased instability of the substrate at habitat types 2 and 6 in this season is caused by a pronounced increase in wave swash turbulence. The latter increase in turbulence is reflected in the width of the wave swash zone, which encompasses both zones A and B, being two to three times greater in winter than in any other season (F. Valesini, unpublished data). The fact that the impact of the changes in turbulence was greatest in zones A and B would account for the prevalence of cores with no nematodes being greater in these two zones than in zone C.

The marked increase that occurred in the densities and number of species of nematodes in each habitat type during spring demonstrates that the assemblages of nematodes in these environments are capable of rapid recovery when environmental conditions become favourable. It is thus noteworthy that the compositions of the assemblages at the three habitat types were most discrete in spring. This is due to the fact that the diagnostic species of each habitat type in spring, *e.g. Mesacanthion* sp., *Bathylaimus* sp.1 and *Paracomesoma* sp. at habitat type 1, *Daptonema* sp. at habitat type 2 and *Gonionchus australis* and *Theristis* sp1. at habitat type 6, each underwent particularly rapid growth in population size in this season.

The mean number of species and mean densities were significantly greater in zone C than in zones A and in particular B. This presumably reflects the fact that the substrate in zone C, which is permanently covered by water, provides a more stable and hence more favourable environment for nematodes than that in either zones A or B, which are both exposed for part of the tidal cycle. Nicholas and Hodda (1999) recorded similar trends among zones for nematode assemblages in nearshore waters in eastern Australia. However, in their review, Heip *et al.* (1985) reported that the densities of nematodes are often greatest near the effluent line, *i.e.* at a position equivalent to the interface that separates zones A and B in our study. The above differences in the location of maximum densities presumably reflect differences between the microtidal conditions on the lower west and east coasts of Australia and the largely macrotidal areas on which Heip *et al.* (1985) derived the results for their review. It would thus appear relevant that, in macrotidal waters, areas further up the beach are likely to be relatively less disturbed by tidal and wave action than areas further down the beach

The composition of the nematode assemblages along the lower west coast of Australia showed at best only slight variation among zones. In contrast, Nicholas and Hodda (1999) found that the composition of the nematode communities changed significantly along a transect perpendicular to the length of the beach. It may be relevant that, although both the lower west and east coasts are microtidal, the mean tidal height on the coast studied by Nicholas and Hodda (1999) is still about 60% greater than in the area where our study was conducted. Consequently, the conditions in the different zones on the lower east coast of Australia may be sufficiently different to favour slightly different suites of species.

The results of the current study indicate that meiofaunal densities and composition, at both a broad taxonomic level, and in the case of nematode assemblages a species level, are strongly influenced by differences in the enduring physical characteristics that are associated with the different habitat types. The environmental differences among seasons and zones exert a relatively smaller influence on meiofaunal densities

Chapter 10. Characteristics of the hyperbenthic faunal assemblages in different habitat types.

10.1 Introduction

The hyperbenthic fauna, also termed suprabenthic or epibenthic fauna, benthic boundary layer macrofauna, demersal zooplankton or benthopelagic plankton, includes all swimming bottom-dependent animals that undergo daily or seasonal vertical migrations between the sea floor and the water column (Dauvin *et al.* 1994, Mees and Jones 1997). The hyperbenthos typically contains taxa such as amphipods, cumaceans, isopods, polychaetes and copepods, which, depending on the time of day, may also be recorded as either benthic macroinvertebrates or zooplankters (Mees and Jones 1997, Vallet and Dauvin 1998). The hyperbenthic fauna is important in marine environments as its members often act as a link in the trophic interactions between benthic and pelagic organisms (Perissinotto and McQuaid 1990) and provide an important food source for many demersal and pelagic fish species (Sorbe 1981, Möller *et al.* 1985, Pihl 1985, Dauvin *et al.* 1994, Wang and Dauvin 1994, Edgar and Shaw 1995a, Cunha *et al.* 1997).

The density and number of species of hyperbenthic organisms have been found to be negatively correlated with the extent of wave activity in certain areas (Lock and Mees 1999, San Vicente and Sorbe 1999) and positively correlated with the extent of seagrass coverage on the substrate (Pihl 1996, Mattila *et al.* 1999). The hyperbenthic fauna in exposed coastal habitats, that are subjected to heavy wave action, strong currents and surge, typically comprise species with good swimming ability and a protective exoskeleton (Lock and Mees 1999), while those in more sheltered habitats contain relatively greater densities of soft-bodied organisms (Mees and Jones 1997).

The number of taxa and species composition of the hyperbenthic fauna vary between day and night, with densities typically being greater at night than during the day. This diel difference has been attributed to the vertical migration that is undertaken by many taxa (Cahoon and Tronza 1992, Dauvin *et al.* 1994, Wang and Dauvin 1994, Mees and Jones 1997, Takahashi and Kawaguchi 1997, Maquart-Moulin 1999, Dauvin *et al.* 2000), and which optimises their chances of encountering an abundant food source and of avoiding predation (Alldredge and King 1980, Cunha *et al.* 1997, Azeiteiro and Marques 1999). The density of the hyperbenthic fauna tends to be greatest in spring and summer, reflecting an increase in reproductive activity in response to an increase in temperature and consequently in the level of recruitment (Jones 1986, San Vicente and Sorbe 1999).

The majority of studies on hyperbenthic fauna have been conducted in the northern hemisphere, and particularly in the English Channel and western Europe and most of those studies have been conducted in depths ranging from 5 m to 75 m (*e.g.* Mees and Jones 1997, Dauvin *et al.* 1994, Vallet and Dauvin 1998, 1999, Dauvin *et al.* 2000). The few studies that have been undertaken on the hyperbenthic fauna in coastal waters with water depths of less than 5 m include those by Pihl (1986) and Takahashi and Kawaguchi (1995). The only studies on the hyperbenthic fauna in Australia are those by Young and Wadley (1979) and Jones (1986) in nearshore waters in north-eastern Australia. These studies focused on the influence of temporal factors, *i.e.* seasonal and diel effects, on selected taxa of the hyperbenthic faunal community found within a marine embayment.

This component of this FRDC report was aimed at determining the extent to which the characteristics of the hyperbenthic fauna in nearshore waters along the lower west coast of Australia varied among habitat types that had been distinguished on the basis of a suite of enduring environmental criteria. Moreover, the study was also aimed at determining the extent to which any such differences in the hyperbenthic assemblages varied over several different temporal scales. In particular we tested the following hypotheses:

1) The number of taxa and overall density of the hyperbenthic fauna will be greatest at those habitat types that are most sheltered from wave activity and contain dense seagrass beds.
2) The composition of the hyperbenthic fauna at the most highly sheltered habitat type will contain relatively greater numbers of soft-bodied taxa, while that at relatively exposed habitat types will contain relatively greater numbers of hard-bodied taxa.
3) The number of species, density and composition of hyperbenthic faunal assemblages will differ between day and night due to diel vertical migrations by these organisms.
4) The compositions of the hyperbenthic fauna will vary seasonally and the number of species and densities of hyperbenthic organisms will be greatest in summer and least in winter.

10.2 Materials and methods

10.2.1 Sampling regime

The hyperbenthic fauna was sampled in subtidal waters, *i.e. ca* one meter depth, at the same three nearshore beaches at which the zooplankton and meiofauna were collected, *i.e* habitat types 1, 2 and 6. Habitat type 1 was highly sheltered from wave activity, with seagrass beds being located close to the shoreline, while habitat type 2 was moderately sheltered from wave activity with seagrass beds within 50 m of the shoreline but further offshore than at habitat type 1. Habitat type 6 was relatively exposed to wave activity and no seagrass was present in the vicinity.

Five replicate samples of the hyperbenthic fauna at each of the three habitat types were collected during both the day and night in the middle of each season between summer 2001 and summer 2002. Collection of the replicate samples at each habitat type in each season was staggered over 3 to 4 weeks in order to reduce the chance that the data for a season would be unduly influenced by an atypical sample. The hyperbenthic fauna was collected using a sled that comprised a metal rectangular frame (50 cm in width and 25 cm in height) to which a plankton net was attached. The sled was mounted on two runners that maintained its base at a height of *ca* 3 cm above the substrate. The plankton net, which was 1.45 m in length and tapered to a width of 7 cm, comprised 150 µm mesh. A cod-end, that was made of PVC tube with a diameter of 11 cm, was attached to the tapered end of the net. The cod-end had a 4.5 cm diameter draining port, over which a piece of 150 µm mesh was attached, enabling water to flow out of the cod-end while the sled was being towed. Samples were collected by towing the sled manually along a 50 m transect that lay parallel to the shoreline and in which the water was approximately one meter in depth. The sample retained in the cod-end was fixed with 5% formalin buffered in seawater.

10.2.2 Laboratory processing

Each sample of hyperbenthic fauna was wet sieved through nested 500 µm and 150 µm mesh sieves and the resultant size fractions removed and stored separately in 70% ethanol. This separated the fauna by size and facilitated comparisons between the composition of the hyperbenthic fauna and that of both the zooplankton (pelagic organisms ≥150 µm : see Chapter 8) and benthic macroinvertebrates (organisms ≥500 µm, see Chapter 7).

The 500 µm sieve fraction of each sample was stained with Rose Bengal. All organisms were then separated from the sediment, sorted to the lowest possible taxon using a dissecting microscope and counted. In those cases in which a sample was particularly large, a Folsom plankton splitter was used to produce a representative subsample of manageable size, *i.e.* either a quarter, an eighth or one sixteenth of the full sample.

The organisms retained on the 150 µm sieve were separated from the remaining sediment using colloidal silica (Ludox TM-50). Each sample was covered with sufficient Ludox TM-50 to double its volume and stirred mechanically for 15 min. The organisms that were separated from the sediment during this period were decanted and stained with Rose Bengal. This procedure was repeated until all organisms had been removed from the sediment. The organisms were then stored in 200 ml of 70% ethanol. Each sample was stirred thoroughly and three 1 ml subsamples were removed using a pipette. Organisms were removed from each subsample and, using a dissecting microscope, sorted to the lowest possible taxon and into juvenile and adult stages, which were then counted separately.

10.2.3 Data treatment

When the samples collected on the 500 µm mesh had been separated into subsamples, the number of individuals of each hyperbenthic taxon in that subsample was multiplied by the number of times the original sample had been split. In the case of the three subsamples collected using the 150 µm mesh, the ratio of the volume of these three subsamples to the volume of the original sample were used, in conjunction with the number of individuals in each subsample, to estimate the number of individuals of each hyperbenthic taxa that would have been present in the original sample. The collective number of individuals of each hyperbenthic taxon in the 500 and 150 µm fractions represent the number of hyperbenthic organisms that were collected in the whole sample. These numbers were then converted to a density (number of individuals m^{-3}) by using the measurements of the net entrance and the distance travelled during each tow.

10.2.4 Univariate analyses

Each hyperbenthic organism was assigned to its lowest possible taxon, and to each successive broader level of classification, based on the Linnaean tree (see Chapter 5, subsection 5.2.2.1). Two biodiversity measures, the average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+), which are based on the taxonomic relatedness of the various taxa, were then calculated for each sample using the TAXDTEST routine in PRIMER 5.2 (Clarke and Gorley 2001) (see Chapter 5, subsection 5.2.2.2 for a definition of these indices).

Prior to subjecting the numbers of taxa, densities, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of hyperbenthic fauna to Analysis of Variance (ANOVA), the relationships between the means and associated standard deviations for each of those variables during both the day and night in each season at each habitat type were examined to ascertain the type of transformation that was required (if any) to satisfy the assumptions of normality and constant variance. This demonstrated that a $\log_{10}$ transformation were required in all four cases. The log-transformed values for the above four biotic variables were then subjected to three-way ANOVA, in order to ascertain whether they differed significantly among habitat types, seasons and/or between day and night.

10.2.5 Bivariate analyses

Ninety-five percent probability ellipses were constructed from 1000 simulated values of Δ_m^+ and Λ_m^+ for each of a range of subsets of species of varying sizes ($_m$) that were drawn randomly from the overall taxa list. The ranges of $_m$ were chosen to approximate the range in size of the number of species in each habitat type, in the day and night and in each season so that the appropriate 95% probability ellipse could be constructed. These 95% confidence ellipses defined the range of values for Δ^+ and Λ^+ for each of the expected different sized subsets of species. Observed Δ^+ and Λ^+ co-ordinates were superimposed onto the 95% confidence ellipses and those that fell outside their respective envelope indicated significant departure from that expected for the hyperbenthic fauna on the lower west coast of Australia.

10.2.6 Multivariate analyses

The multivariate analyses, which used the density of both the juveniles and adults of each hyperbenthic taxon in each sample in each season during the day and night at each habitat type, were carried out using the PRIMER 5.2 statistical package (Clarke and Gorley 2001). Note that mean values were used when there were a sufficient number of points and that the values for replicates were used when there were an insufficient number of points. The data were $\log_{10}(n+1)$ transformed and the Bray-Curtis similarity coefficient was used to construct similarity matrices for use in multi-dimensional scaling (MDS) ordination. Analysis of similarities (ANOSIM), were used to determine whether the composition of the hyperbenthic faunal assemblages differed significantly among the different habitat types, seasons and diel period and similarity percentages (SIMPER) were used to identify the suites of taxa that were responsible for any significant differences detected among *a priori* groups by ANOSIM (Clarke 1993).

The 2nd-stage MDS routine and associated one-way ANOSIM tests in PRIMER 5.2 (Clarke and Gorley 2001) were used to determine whether the rank order of similarity between each of the habitat types in the separate Bray-Curtis similarity matrices for each season/diel combination differed on the basis of either season or time of day.

10.3 Results

10.3.1 Composition of taxa

Sampling of the hyperbenthic fauna at the three habitat types during the day and night in each season in 2001 and the summer of 2002 yielded a total of 906 322 adult individuals that represented 147 taxa. This corresponded to a total of 129 002 adults when the numbers in each sample had been adjusted to the number of individuals m^{-3} and summed. Sixteen hyperbenthic taxa were represented by juveniles of which there were a total of 15 927 individuals. This corresponded to a total of 2 507 individuals after the number in each sample had been adjusted to the number m^{-3} and summed. Of the 14 phyla recorded, the phylum Arthropoda made the greatest contribution to the total number of taxa (57%) and total number of individuals (93.3%), and comprised mainly crustaceans such as cladocerans, copepods, cumaceans, tanaids, mysids and decapods (Table 10.1). Other numerically abundant taxa included juvenile polychaetes, ascidians and larvaceans.

Table 10.1 Mean density (M; no. individuals 1 m^{-3}), standard deviation (±1sd), percentage contributions to the sum of the mean densities (%) and the rank by density (Rk) of each hyperbenthic taxon in samples collected at habitat types 1, 2 and 6 in nearshore waters along the lower west coast of Australia during the day and night in all seasons between summer 2001 and summer 2002. Each taxon has been classified into its respective phyla (Ph) (A-Annelida, C-Crustacea, Ch-Chordata, Cl-Chelicerata, Cn-Cnidara, Ct-Chaetognatha, M-Mollusca, N-Nematoda, Ne-Nemertean, Pl-Platyhelminthes, Po-Pogonophora, S-Sipunculan, Sa-Sarcodina and Un-Uniramia). The number of taxa, number of samples collected and the total number of individuals (after the number of individuals in each sample had been adjusted to that in 1 m^{-3}) are also provided for each habitat type.

		1				**2**				**6**			
	Ph	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Nematode spp.	N	911.64	225.78	38.32	1	20.10	2.75	0.10	17	2.52	0.25	0.06	32
Exoediceroides sp. 4	C	325.77	56.78	13.69	2	37.95	8.28	0.20	12	10.10	1.50	0.25	18
Harpacticoid spp.	C	213.40	27.34	8.97	3	27.50	3.14	0.14	15	59.43	13.03	1.47	7
Exoediceroides sp. 1	C	170.31	20.04	7.16	4	691.58	101.84	3.57	3	87.38	19.96	2.16	5
Calanoid spp.	C	134.57	13.49	5.66	5	12533.10	2531.58	64.68	1	1946.97	185.15	48.13	1
Petalophthalmid sp.	C	119.57	11.83	5.03	6	207.71	42.13	1.07	5	18.05	4.26	0.45	13
Lyssianassid sp. 2	C	57.90	7.48	2.43	7	2.06	0.65	0.01	37				
Cyclopoid spp.	C	56.97	4.26	2.39	8	91.40	7.13	0.47	9	508.43	69.02	12.57	3
Capitella sp.	A	53.16	12.16	2.23	9	2.35	0.40	0.01	37	0.18	0.04	<0.01	67
Cumacean sp. 2	C	44.69	5.05	1.88	10	29.33	8.70	0.15	14	3.59	0.60	0.09	26
Cumacean sp. 1	C	41.39	4.01	1.74	11	96.53	12.26	0.50	8	43.67	4.49	1.08	9
Cyproideid sp. 1	C	21.14	3.42	0.89	12	0.51	0.16	<0.01	57	1.15	0.36	0.03	39
Enchytraid sp.	A	17.41	5.50	0.73	13	0.51	0.16	<0.01	57				
Polycopid sp.	A	16.10	3.34	0.68	14								
Cumacean sp. 3	C	15.62	4.51	0.66	15								
Penilia avirostris	C	15.57	2.76	0.65	16	4351.15	1253.13	22.46	2	923.44	120.43	22.83	2
Tanaid sp. 1	C	14.48	1.63	0.61	17	2.83	0.49	0.01	37	0.52	0.16	0.01	46
Exogoninae spp.	A	13.90	1.98	0.58	18	3.34	0.52	0.02	28	0.80	0.15	0.02	41
Syllinae spp.	A	9.83	1.49	0.41	19	7.50	1.16	0.04	23	0.51	0.09	0.01	46
Chaetognath spp.	Ct	9.82	1.81	0.41	19	105.10	24.84	0.54	7	31.69	5.75	0.78	10
Penaeus latisulcatus	C	9.50	2.04	0.40	21	5.12	1.45	0.03	26	28.26	8.81	0.70	11
Foram sp. 1	Sa	8.04	2.24	0.34	22	0.01	0.00	<0.01	57				
Ischyrocerid sp. 2	C	6.97	1.28	0.29	23	30.23	7.01	0.16	13	3.58	0.73	0.09	26
Serpulid sp.	A	6.66	1.93	0.28	24					0.45	0.10	0.01	46
Tipulid sp.	Un	5.45	1.02	0.23	25								
Ampithoid sp. 1	C	4.90	0.80	0.21	26	49.19	13.59	0.25	10	1.75	0.25	0.04	35
Tanaid sp. 2	C	4.87	1.34	0.20	27	47.02	13.32	0.24	11	10.70	1.77	0.26	17

Table 10.1 continued

		1				2				6			
	Ph	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Cingulopsid sp.	M	4.76	1.02	0.20	27	3.55	0.37	0.02	28	19.58	4.87	0.48	12
Erythropini sp.	C	4.10	1.21	0.17	29	672.86	182.33	3.47	4	65.73	14.04	1.62	6
Hydromedusa spp.	Cn	3.93	0.80	0.17	29	26.86	2.59	0.14	15	45.85	5.70	1.13	8
Cypridinid sp. 2	C	3.59	0.79	0.15	31					0.54	0.11	0.01	46
Rhyncospio sp. 2	A	3.58	1.05	0.15	31	0.02	0.01	<0.01	57				
Cypridinid sp. 1	C	3.23	0.35	0.14	33	0.01	0.00	<0.01	57	10.26	1.25	0.25	18
Trochid sp.	M	3.07	0.97	0.13	34					0.37	0.08	0.01	46
Sphaeromatid sp. 1	C	2.34	0.31	0.10	35	1.57	0.48	0.01	37	16.28	2.75	0.40	14
Exoediceroides sp. 2	C	2.30	0.49	0.10	35	0.02	0.00	<0.01	57	14.59	2.46	0.36	15
Cirripedid spp.	C	2.16	0.64	0.09	37	1.19	0.20	0.01	37	1.51	0.23	0.04	35
Oikopleura spp.	Ch	2.06	0.62	0.09	37	173.73	30.47	0.90	6	100.47	10.41	2.48	4
Polyclad sp.	Pl	2.02	0.43	0.08	39	4.67	0.96	0.02	28	1.71	0.40	0.04	35
Ampithoid sp. 2	C	1.79	0.34	0.08	39	1.28	0.32	0.01	37	1.02	0.32	0.03	39
Eusyllinae spp.	A	1.63	0.33	0.07	41	7.59	0.85	0.04	23	4.51	0.62	0.11	25
Phoxocephalopsid sp. 1	C	1.63	0.40	0.07	41	0.86	0.19	<0.01	57	3.81	0.53	0.09	26
Pseudoampharete sp.	A	1.54	0.35	0.06	43					0.26	0.08	0.01	46
Ctenodrillid sp.	A	1.54	0.32	0.06	43	3.58	0.80	0.02	28	0.14	0.04	<0.01	67
Calliostoma australe	M	1.54	0.35	0.06	43								
Donacilla sp.	M	1.40	0.32	0.06	43	3.96	0.35	0.02	28	8.36	2.20	0.21	21
larval Ascidian spp.	Ch	1.36	0.16	0.06	43	1.66	0.26	0.01	37	13.26	2.78	0.33	16
Chrysopetalid sp.	A	1.31	0.22	0.06	43								
Polyplacophorid sp.	M	1.29	0.22	0.05	49								
Ovulid sp.	M	1.28	0.40	0.05	49								
Valviferid sp.	C	1.12	0.24	0.05	49	2.35	0.42	0.01	37	0.51	0.16	0.01	46
Lyssianassid sp. 1	C	0.91	0.15	0.04	52	0.51	0.16	<0.01	57				
Phoxocephalopsid sp. 2	C	0.80	0.18	0.03	53	4.67	1.29	0.02	28	10.31	1.36	0.25	18
Sipunculan sp.	S	0.77	0.17	0.03	53					0.77	0.17	0.02	41
Oribatid sp. 2	Cl	0.77	0.17	0.03	53								
Eunicid sp.	A	0.68	0.17	0.03	53	1.80	0.42	0.01	37	0.03	0.01	<0.01	67
Caprellid sp.	C	0.67	0.11	0.03	53	1.02	0.22	0.01	37	0.70	0.11	0.02	41
Exoediceroides sp. 3	C	0.57	0.16	0.02	58	13.95	3.43	0.07	19	2.99	0.70	0.07	29
Sepiolid sp.	A	0.54	0.16	0.02	58	0.51	0.16	<0.01	57				
Colomaastigid sp.	C	0.51	0.16	0.02	58	1.54	0.49	0.01	37				

Table 10.1 continued

		1				2				6			
	Ph	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Acathurus sp.	Ch	0.51	0.16	0.02	58	1.02	0.32	0.01	37				
Alluaudellid sp.	A	0.51	0.16	0.02	58								
Callionymid sp.	Ch	0.51	0.16	0.02	58								
Oribatid sp. 3	Cl	0.51	0.16	0.02	58								
Parapercis haackii	Ch	0.51	0.16	0.02	58								
Platycopid sp. 1	C	0.51	0.16	0.02	58								
Portunus pelagicus	C	0.51	0.11	0.02	58								
Halacarid sp. 3	Cl	0.44	0.13	0.02	58	0.56	0.16	<0.01	57	0.03	0.01	<0.01	67
Sillaginid spp.	Ch	0.38	0.09	0.02	58	4.61	1.46	0.02	28				
Eusirid sp. 1	A	0.27	0.08	0.01	70	1.79	0.24	0.01	37	0.26	0.08	0.01	46
Ampithoid sp. 3	C	0.26	0.08	0.01	70	0.13	0.04	<0.01	57	6.66	2.10	0.16	23
Hyalellid sp.	C	0.26	0.08	0.01	70	0.51	0.16	<0.01	57	2.85	0.80	0.07	29
juvenile *Magelona* sp.	A	0.26	0.08	0.01	70					2.06	0.43	0.05	34
Philippia radiata	M	0.26	0.08	0.01	70	0.26	0.08	<0.01	57	0.64	0.16	0.02	41
Serolid sp.	C	0.26	0.08	0.01	70	0.01	0.00	<0.01	57	0.38	0.09	0.01	46
Dexaminid sp. 2	C	0.26	0.08	0.01	70					0.26	0.08	0.01	46
Ischyrocerid sp. 1	C	0.26	0.08	0.01	70					0.26	0.08	0.01	46
Rhyncospio sp. 1	A	0.26	0.08	0.01	70	1.54	0.35	0.01	37	0.03	0.01	<0.01	67
Rullierinereis sp.	A	0.26	0.08	0.01	70	0.51	0.16	<0.01	57				
larval Pogonophore sp.	P	0.26	0.08	0.01	70								
Mysidellinae sp.	C	0.26	0.08	0.01	70								
Opheliid sp.	A	0.26	0.08	0.01	70								
Pelates octolineatus	Ch	0.26	0.08	0.01	70								
Foram sp. 2	Sa	0.21	0.05	0.01	70	0.09	0.02	<0.01	57	0.03	0.01	<0.01	67
Platycopid sp. 2	C	0.15	0.03	0.01	70								
Aplysia dactylomela	M	0.13	0.04	0.01	70	2.18	0.37	0.01	37				
Cladoceran sp.	C	0.07	0.02	<0.01	87	11.28	2.30	0.06	22	7.92	1.41	0.20	22
Halacarid sp. 1	Cl	0.06	0.02	<0.01	87	0.03	0.01	<0.01	57				
Podon sp.	C	0.03	0.01	<0.01	87	13.26	2.99	0.07	19	0.32	0.06	0.01	46
Callianassid sp.	C	0.03	0.01	<0.01	87	0.06	0.02	<0.01	57	2.53	0.46	0.06	32
Atherinid spp.	Ch	0.03	0.01	<0.01	87	0.51	0.16	<0.01	57				
Arcturid sp.	C	0.03	0.01	<0.01	87								

Table 10.1 continued

		1				2				6			
	Ph	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Rutidermatid sp.	C	0.02	0.01	<0.01	87					0.51	0.16	0.01	46
Halocypridid sp. 2	C	0.02	0.01	<0.01	87					0.03	0.01	<0.01	67
Thaliacean sp.	Ch	0.01	0.00	<0.01	87	13.25	2.52	0.07	19	0.46	0.10	0.01	46
Gnathid sp.	C	0.01	0.00	<0.01	87					0.03	0.01	<0.01	67
Eusirid sp. 2	A	0.01	0.00	<0.01	87								
Nebalia longicornis	C	0.01	0.00	<0.01	87								
Terebellid sp.	A	0.01	0.00	<0.01	87								
Corophium sp.	C	0.01	0.00	<0.01	87								
Culicid sp.	Un	0.01	0.00	<0.01	87								
Podocopid sp.	C	0.01	0.00	<0.01	87								
Cyproideid sp. 3	C	0.01	0.00	<0.01	87	0.03	0.01	<0.01	57				
Insect sp.	Un	0.01	0.00	<0.01	87								
Leptomysini sp.	C					15.87	4.33	0.08	18	4.99	1.41	0.12	24
Gnathophausid sp.	C					8.19	2.59	0.04	23				
Carid sp.	C					6.40	1.31	0.03	26	0.77	0.16	0.02	41
Nemertean sp.	Ne					4.10	0.90	0.02	28				
Bivalve sp. 1	M					3.62	0.77	0.02	28				
Dexaminid sp. 1	C					2.43	0.65	0.01	37				
Prionospio sp.	A					1.59	0.50	0.01	37	0.27	0.05	0.01	46
Uldanimia pillare	C					1.54	0.35	0.01	37	0.03	0.01	<0.01	67
Clupeid spp.	Ch					1.06	0.32	0.01	37				
Poecilochaetid sp.	A					1.02	0.22	0.01	37				
Gymnapistes marmoratus	Ch					0.77	0.24	<0.01	57				
Asteroid spp.	Ch					0.52	0.17	<0.01	57	1.62	0.36	0.04	35
Cyproideid sp. 2	C					0.51	0.16	<0.01	57	0.03	0.01	<0.01	67
Cumacean sp. 4	C					0.51	0.16	<0.01	57				
Enigmapereis reducta	Ch					0.51	0.16	<0.01	57				
larval pholoidid sp.	A					0.51	0.16	<0.01	57				
Polychaete sp. 1	A					0.51	0.16	<0.01	57				
Rhabdocoel sp.	Pl					0.51	0.16	<0.01	57				
Scoloplella sp.	A					0.51	0.16	<0.01	57				
Sparid sp.	Ch					0.51	0.16	<0.01	57				

Table 10.1 continued

		1				**2**				**6**			
	Ph	M	sd	%	Rk	M	sd	%	Rk	M	sd	%	Rk
Syngnathid sp. 1	Ch					0.51	0.16	<0.01	57				
Lesueurina platycephala	Ch					0.26	0.08	<0.01	57	0.13	0.04	<0.01	67
Sphaeromatid sp. 2	C					0.26	0.08	<0.01	57				
Raricirrus sp.	A					0.14	0.04	<0.01	57				
Diogenid sp.	C					0.03	0.01	<0.01	57				
Halacarid sp. 2	Cl					0.03	0.01	<0.01	57				
Nebalia sp. 1	C					0.03	0.01	<0.01	57				
Philomedid sp.	C					0.02	0.01	<0.01	57	0.42	0.09	0.01	46
Dipteran sp. 2	Un					0.01	0.00	<0.01	57				
Oribatid sp. 4	Cl					0.01	0.00	<0.01	57				
Oribatid sp. 1	Cl					0.01	0.00	<0.01	57	0.13	0.04	<0.01	67
larval stomatopod sp.	C									2.94	0.81	0.07	29
Leucothoid sp.	C									0.38	0.09	0.01	46
Aorid sp.	C									0.26	0.08	0.01	46
Dipteran sp. 1	Un									0.26	0.08	0.01	46
Microspio sp.	A									0.26	0.08	0.01	46
Syngnathid sp. 2	Ch									0.26	0.08	0.01	46
Gastropod sp. 1	M									0.16	0.05	<0.01	67
Gammarid sp. 1	C									0.06	0.02	<0.01	67
Hydroid spp.	Cn									0.06	0.02	<0.01	67
Anthurid sp.	C									0.03	0.01	<0.01	67
Corophiid sp.	C									0.03	0.01	<0.01	67
Halocypridid sp. 1	C									0.03	0.01	<0.01	67
No. of taxa			**104**				**97**				**84**		
Overall mean density			**2 379.3**				**19 376.0**				**4 045.1**		
Number of samples			**50**				**50**				**50**		
Total no. individuals			**11 897**				**96 880**				**20 226**		

The number of taxa (104) were greatest at habitat type 1, followed by habitat type 2 (97) and habitat type 6 (84). In contrast, the overall density of individuals at habitat type 1 was approximately half that at habitat type 6 and approximately one eighth of that at habitat type 2 (Table 10.1). The hyperbenthic fauna at habitat type 1 was dominated by nematode spp., the amphipod *Exoediceroides* sp. 4 and harpacticoid spp., which contributed 38.3, 13.7 and 9.0%, respectively, to the total number of individuals collected at this habitat. At habitat type 2 approximately 65, 22.5 and 3.5% of the total number of individuals were represented by calanoid spp., the cladoceran *Penilia avirostris* and the amphipod, *Exoediceroides* sp. 1. The hyperbenthic fauna at habitat type 6 was dominated by calanoid spp., *P. avirostris* and cyclopoid spp., which contributed 48.1, 22.8 and 12.6%, respectively to the total number of individuals at this habitat type (Table 10.1).

10.3.2 Number of taxa, densities of hyperbenthic taxa and species relatedness

Three-way ANOVA showed that the mean number of hyperbenthic taxa differed significantly between day and night and among seasons and that there was a significant two-way interaction between habitat type and season (Table 10.2). The mean square was greatest for the diel effect and least for season. The mean number of taxa was greater at night, 18, than during the day, 15 (Fig. 10.1a). The mean number of taxa at both habitat types 1 and 2 were greatest in the summers of both 2001 and 2002 and were least in winter in habitat type 1 and in autumn in habitat type 2 (Fig. 10.1b). In contrast, the mean number of taxa at habitat type 6 was greatest in autumn and least in the summer of 2002 (Fig. 10.1b).

Table 10.2 Mean squares and significance levels for three-way ANOVA of the number of taxa, density, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of hyperbenthic fauna in samples collected at habitats 1, 2 and 6 during the day and night in each season between summer 2001 and summer 2002. "df"=degrees of freedom. ***p <0.001; **p <0.01; *p <0.05.

	df	No. of taxa	Density	Δ+	Λ+
Main effects					
Habitat type (H)	2	12.1	2.8***	67.8***	25218.2***
Diel (D)	1	337.5***	3.9***	268.1***	119951.9***
Season (S)	4	97.8***	1.4***	9.1	4125.7
Two-way interactions					
H x S	8	138.2***	3.3***	24.3**	10259.9**
H x D	2	20.5	0.1	2.1	841.2
S x D	4	20.1	0.3	9.1	3584.4
Three-way interactions					
H x S x D	8	31.4	1.4***	15.8	4756.9
Error	120	16.0	0.2	8.7	3234.6

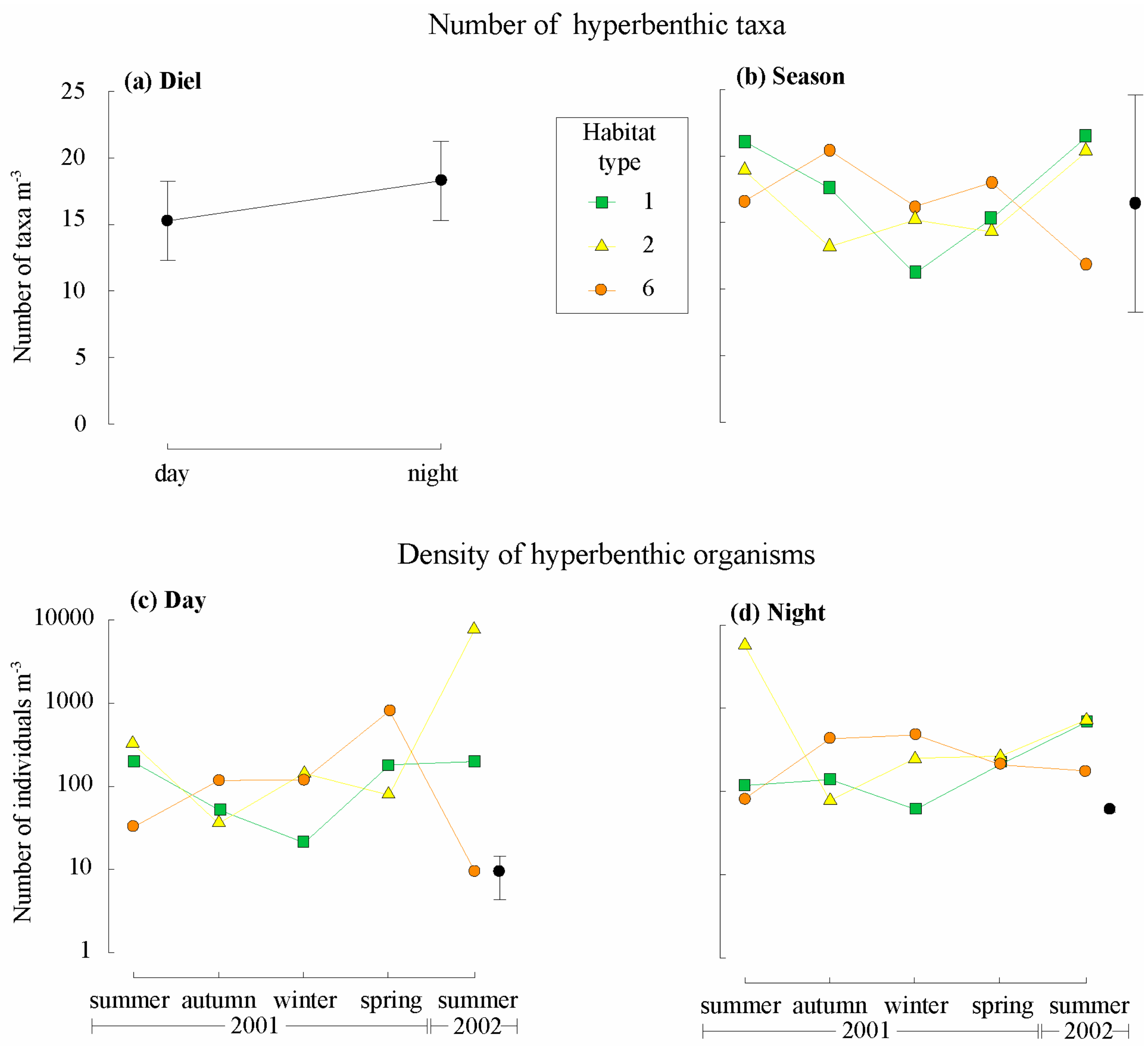


Figure 10.1: Mean (± 95% CI) number of taxa of adult hyperbenthic organisms (a) during the day and night (b) in each season at each habitat type, and the mean density of organisms (c) during the day and night and (d) in each season at each habitat type. For the sake of clarity, in this figure and Fig. 10.2, the overall mean (± 95% CI) is provided on each plot (denoted by black symbols and lines).

The mean densities of hyperbenthic organisms differed significantly among habitat types, seasons and between day and night, and there were significant interactions between habitat type and season, and between habitat type, season and day *vs* night (Table 10.2). The mean squares were greatest for the diel effect and least for season and the three-way interaction. During the day, the mean densities at habitat type 1 and 2 were greatest during the two summers, whereas they were least in the two summers at habitat type 6 (Fig. 10.1c). In contrast, the densities in habitat type 6 were lowest in the two summers and greatest in the spring. While, as during the day, the densities during the night were also at their maxima at habitat type 1 in summer 2002, they were appreciably higher at habitat type 2 at summer 2001. The mean densities at habitat type 6 were less during the autumn and winter during the day, whereas the reverse situation occurred during the night (Figs 10.1c, d).

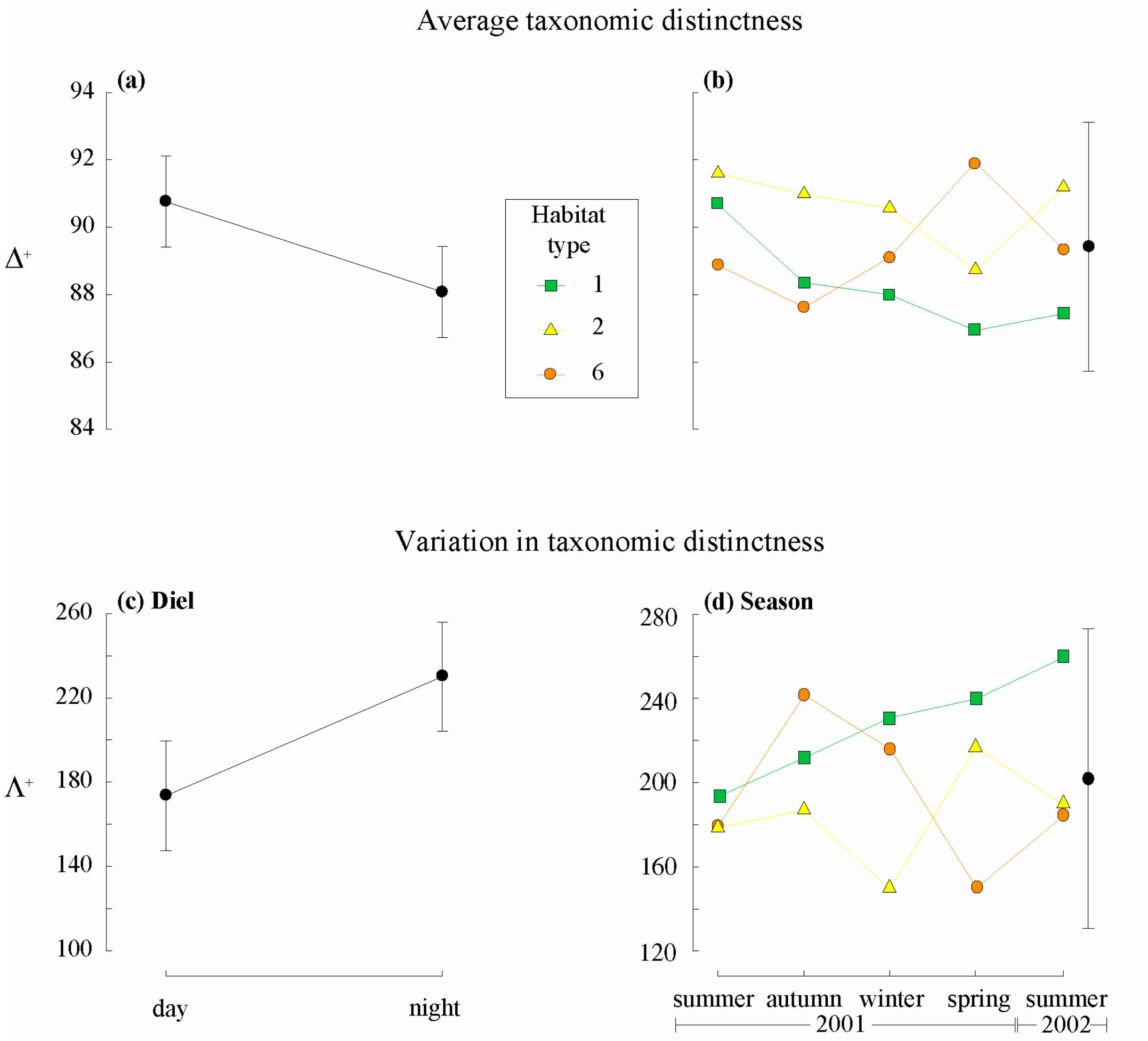


Figure 10.2: Mean (± 95% CI) average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of the adult taxa in the hyperbenthic assemblages during (a and c) the day and night and (b and d) at each habitat type in each season between summer 2001 and summer 2002.

The average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of the hyperbenthic faunal community differed significantly among habitat types and between day and night ($p < 0.001$), and there was a significant two-way interaction between habitat type and season for both variables ($p < 0.01$) (Table 10.2). For both of these dependent variables, the mean squares for diel period were far greater than that for habitat type, which was greater, in turn, than that for the significant interaction (Table 10.2). The mean Δ^+ was greater during the day than night, whereas the reverse was true for Λ^+ (Figs 10.2a, c). These results thus demonstrate that a greater diversity of taxa were recorded during the day than at night, and that the distribution of the various taxa across the levels of the hierarchical phylogenetic tree was more even during the day. Plots of the mean Δ^+ in each habitat type and season showed that the values for habitat type 1 were always lower than those for habitat type 2, and that in both of these habitat types, the mean Δ^+ declined gradually to a minima in spring, and then increased in summer 2002 (Fig. 10.2b). However, the significant interaction between these independent variables was attributable to the fact that the Δ^+ of samples collected at habitat type 6 was the lowest of any habitat type during summer and autumn 2001, but was markedly higher than those of both habitat types 1 and 2 in spring (Fig. 10.2b). Moreover, unlike the situation in habitat types 1 and 2, the mean Δ^+ at habitat type 6 was greatest during that latter season, and then declined in the following summer. In contrast, the significant habitat x season interaction for Λ^+ was due to the fact that the mean values for this dependent variable fluctuated widely among seasons at habitat types 2 and 6, while those at habitat type 1 exhibited a strong positive trend from summer 2001 to summer 2002. Thus, the Λ^+ at that highly sheltered habitat type was the greatest of any habitat type during winter and spring 2001 and summer 2002 (Fig. 10.2d).

10.3.3 Joint biodiversity analyses

Investigation of the relationships between Δ^+ and Λ^+ at the various habitat types was carried out separately for both the day and night and each of the seasons, since the results of ANOVA of these two indices demonstrated that they differed significantly on the basis of both of those temporal factors (see previous subsection). Thus, separate scatterplots of Δ^+ *vs* Λ^+ containing the samples from each habitat type during both the day and night were constructed for each season, and the relevant 95% probability ellipses for the number of taxa contained in each of those samples were also constructed for each plot (Figs 10.3a-e). The distribution of the samples on each plot exhibited a negative trend, which was attributable to the fact that the Δ^+ of samples collected during the day were generally greater than those of samples from the respective habitat types at night, while the reverse was true for Λ^+. Moreover, each sample fell within its relevant 95% confidence ellipse, thus demonstrating that the Δ^+ and Λ^+ of those samples did not depart significantly from that expected for any sample drawn at random from along this coastline.

10.3.4 Overall community analysis

One-way ANOSIM showed that the densities of the hyperbenthic fauna overall differed between habitat types (p=0.1%; Global R-statistic=0.513) and between day and night (p=2.4%; Global R=0.115).

When the mean densities of the various hyperbenthic taxa during both the day and night in each season at each habitat type were subjected to MDS ordination, the samples from habitat type 1 formed a group on the left side of the plot, that was entirely discrete from those from habitat type 6 on the right of the plot (Fig. 10.4). The samples for habitat type 2 lay between the

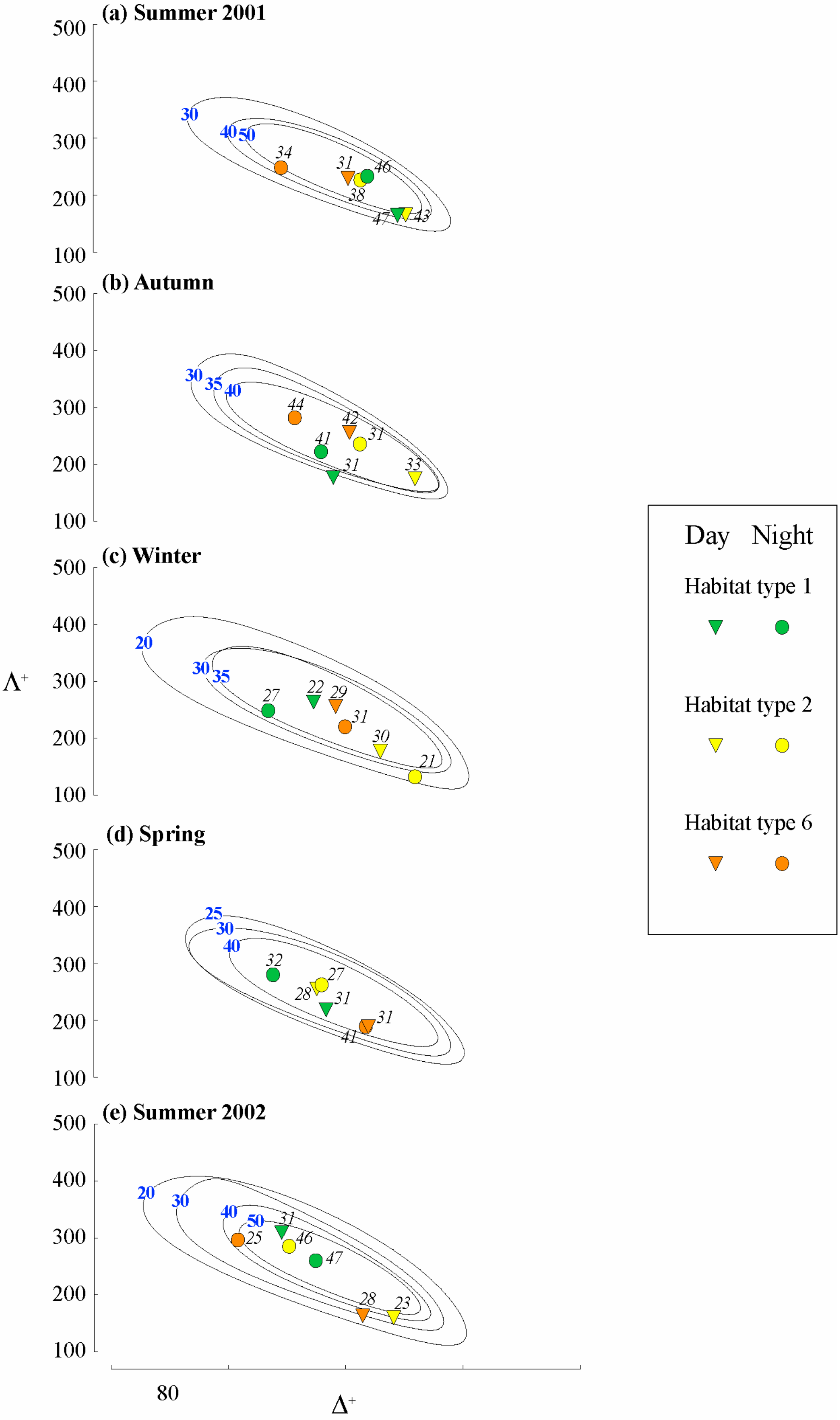


Figure 10.3: Scatterplots of average taxonomic distinctness *vs* variation in taxonomic distinctness of adult hyperbenthic taxa in samples collected at each of habitat types 1, 2 and 6 in (a) summer 2001, (b) autumn, (c) winter, (d) spring and (e) summer 2002. The number of species recorded at each site and the relevant 95% probability ellipses for simulations of different-sized subsets of species are also provided for each season.

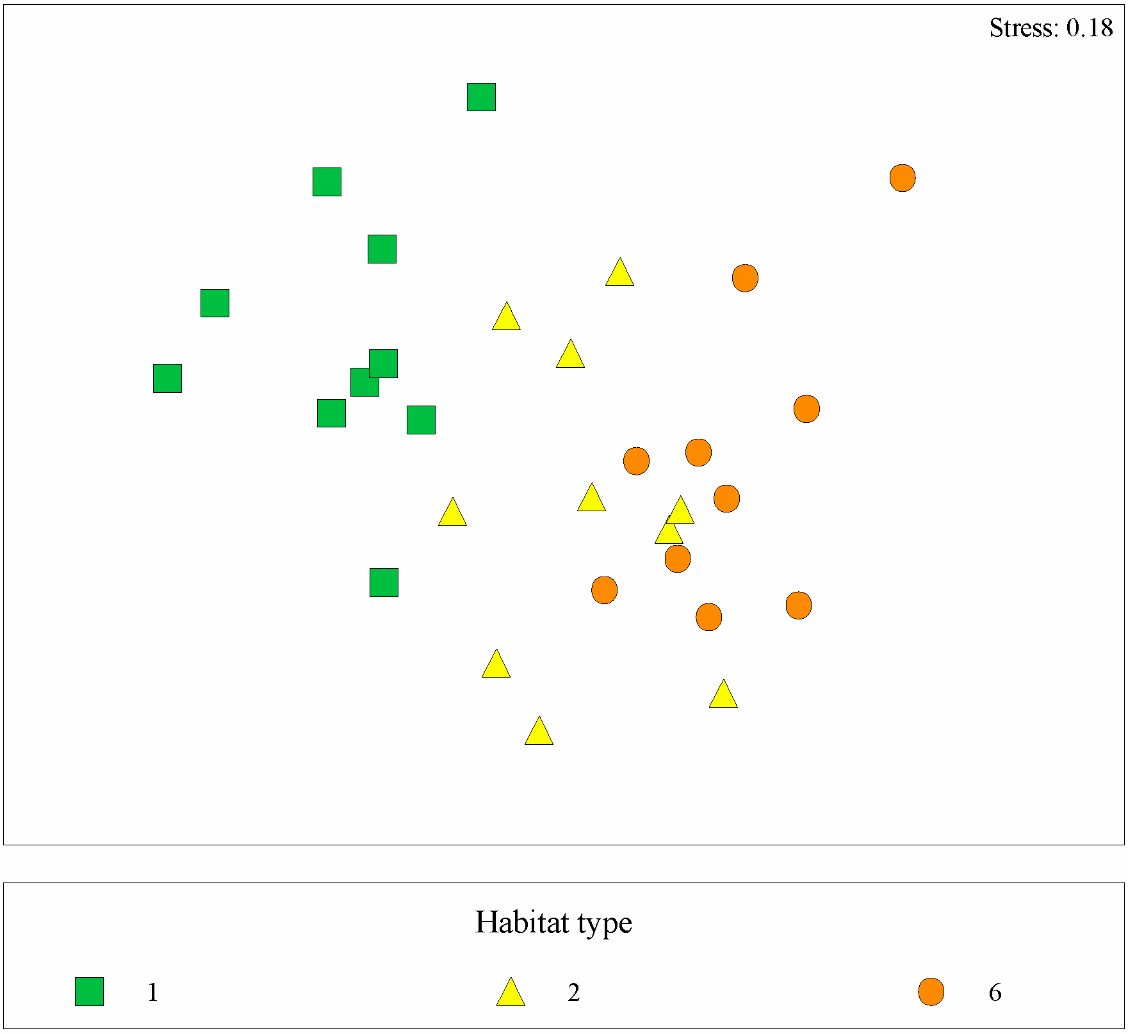


Figure 10.4: Two-dimensional MDS ordination of the mean densities of the adult hyperbenthic taxa recorded at habitat types 1, 2 and 6 in the day and night between the summer of 2001 and summer of 2002.

groups of samples from habitat types 1 and 6 or just inside the group of samples from habitat type 6 (Fig. 10.4). Pairwise comparisons in the ANOSIM test demonstrated that there were significant differences among the compositions of the hyperbenthic fauna in each of the habitat types (p=0.1-1.6%), and that the differences were greatest between habitat types 1 and 6 (R=0.779) and least between habitat types 2 and 6 (R=0.170).

SIMPER showed that the faunal composition at habitat type 1 was distinguished from that at both habitat types 2 and 6 by greater densities of nematode spp. at the former habitat type and greater densities of calanoid spp. and *P. avirostris* at the latter two habitat types. The faunal compositions at habitat type 2 were distinguished from those at habitat type 6 by, in particular, relatively greater densities of *P. avirostris*, calanoid spp. and *Exoediceroides* sp. 1 and relatively lower densities of cyclopoid spp. (Table 10.3).

Table 10.3 Species detected by SIMPER as those most responsible for typifying the hyperbenthic fauna at habitat types 1, 2 and 6 (see taxa arranged along diagonal cells) and distinguishing each pair of those habitat types (see taxa arranged along vertical cells). Samples collected during the day and night and in the different seasons have been pooled in this analysis. The habitat type at which distinguishing taxa were most abundant is also provided (see superscripts).

	1	**2**	**6**
1	Nematode spp. Calanoid spp. Harpacticoid spp. *Exoediceroides* sp. 1 Cyclopoid spp. Petalophthalmid sp Cumacean sp. 1		
2	Calanoid spp.$^{(2)}$ *Penilia avirostris*$^{(2)}$ *Exoediceroides* sp. 1$^{(2)}$ Nematode spp.$^{(1)}$	Calanoid spp. *Exoediceroides* sp. 1 Cyclopoid spp. *Penilia avirostris* Cumacean sp. 1 Petalophthalmid sp. *Oikopleura* spp.	
6	Calanoid spp.$^{(6)}$ *Penilia avirostris*$^{(6)}$ Nematode spp.$^{(1)}$ *Exoediceroides* sp. 1$^{(1)}$	*Penilia avirostris*$^{(2)}$ Calanoid spp. $^{(2)}$ *Exoediceroides* sp. 1$^{(2)}$ Cyclopoid spp.$^{(6)}$ *Oikopleura* spp. $^{(2)}$ Cumacean sp. 1$^{(2)}$	Calanoid spp. Cyclopoid spp. *Penilia avirostris* *Oikopleura* spp.

10.3.5 Composition of assemblages among different habitat types in the day and night and among seasons

Since two-way crossed ANOSIM, employing season and the diel effect as factors for each habitat type separately, showed that the faunal compositions differed significantly between day *vs* night and seasons in each habitat type (test not shown), the extent of differences among habitat types was examined separately for the day and night in each season. One-way ANOSIM showed that the composition of the hyperbenthic fauna differed significantly among habitat types in each season during both the day and night (Table 10.4).

MDS ordination of the densities of the hyperbenthic fauna at each habitat type showed that, in the majority of cases, the samples from the three habitat types formed discrete groups during the day and night in each season, with those from habitat types 1 and 6 forming groups on the left and right sides of each plot, respectively, and those for habitat type 2 lying either between, below and/or above these groups (Figs 10.5a-j).

Table 10.4 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in one-way ANOSIM tests of the hyperbenthic assemblages at habitat types 1, 2 and 6 during the day and night in each season between summer 2001 and summer 2002. Significant results are highlighted in boldface.

		1		**2**	
Summer 2001, Day (p=0.3%; Global R=0.367)		p	R	p	R
	2	11.9	0.232		
	6	**2.4**	**0.436**	**3.2**	**0.464**
Summer 2001, Night (p=0.1%; Global R=0.814)					
	2	**0.8**	**0.940**		
	6	**1.6**	**0.660**	**0.8**	**0.844**
Autumn, Day (p=0.2%; Global R=0.420)					
	2	**1.6**	**0.336**		
	6	**0.8**	**0.636**	**0.8**	**0.308**
Autumn, Night (p=0.1%; Global R=0.652)					
	2	**1.6**	**0.448**		
	6	**0.8**	**0.988**	**0.8**	**0.568**
Winter, Day (p=0.1%; Global R=0.538)					
	2	**0.8**	**0.680**		
	6	**0.8**	**0.756**	**4.0**	**0.384**
Winter, Night (p=0.1%; Global R=0.817)					
	2	**0.8**	**0.904**		
	6	**0.8**	**1.000**	**0.8**	**0.800**
Spring, Day (p=0.1%; Global R=0.875)					
	2	**0.8**	**0.616**		
	6	**0.8**	**0.912**	**0.8**	**1.000**
Spring, Night (p=0.1%; Global R=0.671)					
	2	**0.8**	**0.792**		
	6	**0.8**	**0.628**	**1.6**	**0.552**
Summer 2002, Day (p=0.1%; Global R=0.768)					
	2	**0.8**	**1.000**		
	6	**0.8**	**0.772**	**0.8**	**0.760**
Summer 2002, Night (p=0.1%; Global R=0.960)					
	2	**0.8**	**1.000**		
	6	**0.8**	**1.000**	**0.8**	**0.844**

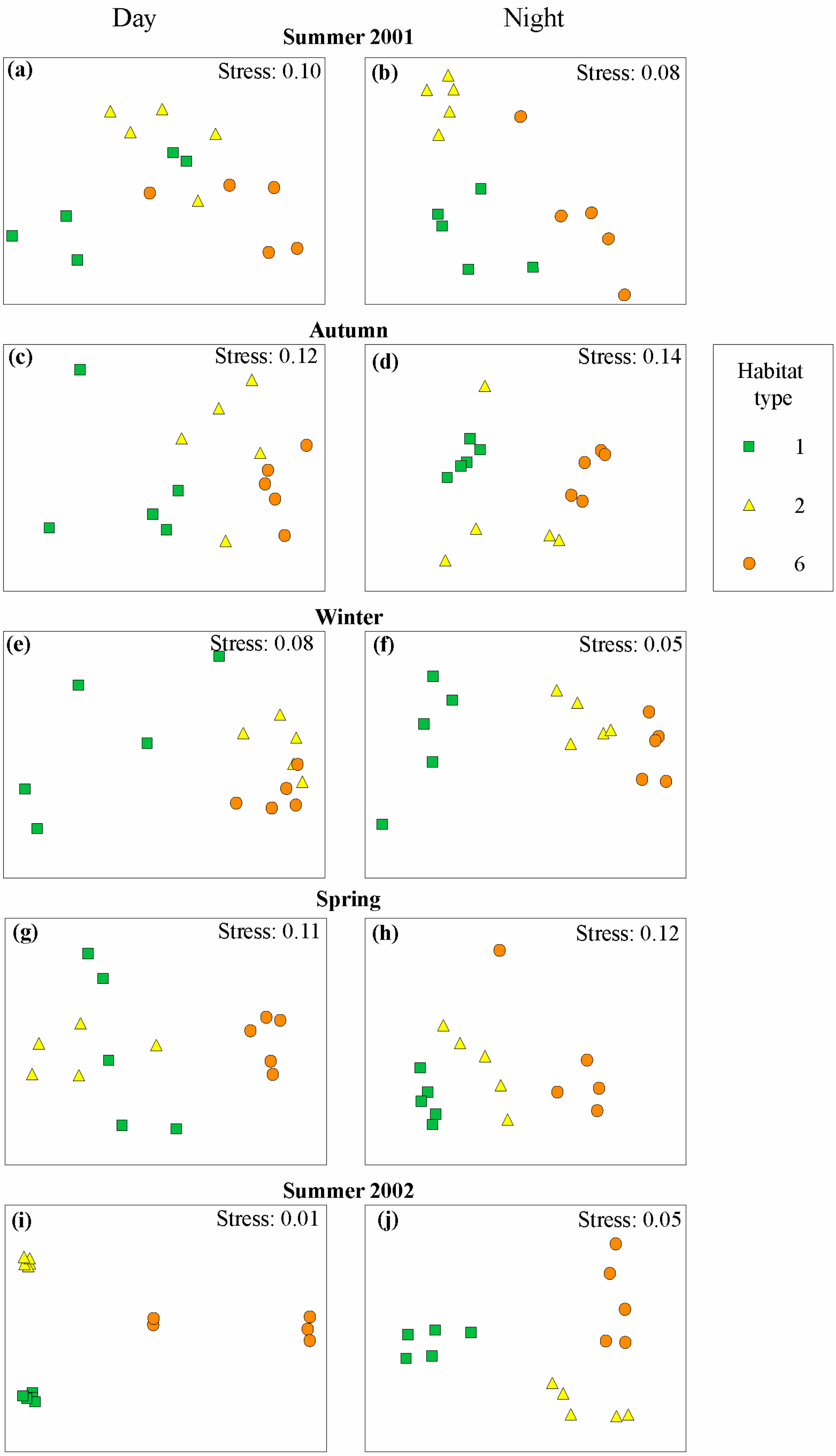


Figure 10.5: Two-dimensional MDS ordination of the densities of adult hyperbenthic taxa at habitat types 1, 2 and 6 in each season between summer 2001 and summer 2002 during the day (a,c,e,g and i) and the night (b,d,f,h and j).

Pairwise ANOSIM comparisons showed that, during both the day and night, the composition of the hyperbenthic fauna in each habitat type were significantly different from each other in each season, except in the case of those in habitat types 1 *vs* 2 in the day in summer 2001 (Table 10.4). There were greater differences among the compositions of the faunas in habitat types at night than during the day in each season except spring (Table 10.4). Although the differences between the faunal compositions in habitat types were greatest between types 1 and 6, there were also often relatively large differences between the compositions in habitat types 1 and 2.

The suite of taxa that typified each habitat type during the day and night in each season contained some of the same species, *i.e.* calanoid spp. and cyclopoid spp. However, some taxa typified only one habitat type, *e.g.* nematode spp. at habitat type 1 (Table 10.5).

10.3.6 Differences in the rank orders of similarity among habitat types between day and night in different seasons

The points on the 2nd stage MDS plot, each of which represented a similarity matrix constructed from the compositions of the hyperbenthos at habitat types 1, 2 and 6 on a sampling occasion, *e.g.* summer 2001 day, summer 2001 night, autumn day *etc.,* were arranged in a seasonal manner (Fig. 10.6a). However, when the points were coded for day and night, they did not show an obvious tendency to form separate groups (Fig. 10.6b). One-way ANOSIM confirmed that there were significant seasonal differences (Global R=0.430), and that there was not a significant difference between day and night. This demonstrates that the extent of the similarity in the hyperbenthic composition between the various habitat types changes with season but not between day and night.

10.3.7 Differences in hyperbenthic communities between day and night and among seasons in each habitat type

Since one-way ANOSIM demonstrated that the compositions of the hyperbenthic fauna differed to a greater extent among habitat types than between day and night and among seasons, the influence of the latter two variables on composition are now examined separately for each habitat type.

Two-way crossed ANOSIMs showed that the composition of the hyperbenthic fauna at habitat types 1, 2 and 6 each differed significantly between day and night and among seasons, but that the overall extent of the seasonal differences at each habitat type (Table 10.6a, b, c) were greater than those between day and night (Table 10.6d).

Table 10.5 Taxa detected by SIMPER as those most responsible for typifying the hyperbenthic fauna at habitat types 1, 2 and 6 during the day and night in each season between summer 2001 and summer 2002. Where a taxon typified the hyperbenthic fauna in more than one habitat type during the day or night in a given season, that marked with an asterisk indicates the habitat type in which it was most abundant.

	Day			**Night**		
	1	**2**	**6**	**1**	**2**	**6**
Summer 2001	Calanoid spp. Cyclopoid spp. Harpacticoid spp.* Nematode spp. *Exoediceroides* sp. 2	Calanoid spp.* Cyclopoid spp.* Hydromedusa spp. Harpacticoid spp. Syngnathid sp. 2 *Penilia avirostris*	Calanoid spp. Cyclopoid spp. Cypridinid sp. 1	Harpacticoid spp. Calanoid spp. Cyclopoid spp. *Exoediceroides* sp. 2 Carid sp. Cumacean sp. 1 Larval ascidian spp. Nematode spp.	Calanoid spp.* Petalophthalmid sp. *Exoediceroides* sp. 2* Leptomysini sp. Larval ascidian spp.* Cyproideid sp. 1 Cumacean sp. 2	Calanoid spp. Cyclopoid spp.* Cingulopsid sp. *Penilia avirostris* Cumacean sp. 1* Carid sp.*
Autumn	*Exoediceroides* sp. 2 Nematode spp. Calanoid spp. Cyclopoid spp. Harpacticoid spp. Capitella sp.	Calanoid spp. (2) Cyclopoid spp. *Exoediceroides* sp. 2 *Penilia avirostris*	*Penilia avirostris** Calanoid spp.* Cyclopoid spp.* Syngnathid sp. 2 *Exoediceroides* sp. 2*	*Phoxocephalopsid* sp. 1 *Exoediceroides* sp. 2 Leptomysini sp.* Calanoid spp. Cumacean sp. 1 Tanaid sp. 2 Cyclopoid spp. Harpacticoid spp.*	*Exoediceroides* sp. 2 Calanoid spp. Cyclopoid spp. Harpacticoid spp. Leptomysini sp. *Penilia avirostris* Nemertean sp.	Calanoid spp.* *Penilia avirostris** *Exoediceroides* sp. 2* Cyclopoid spp.* Cumacean sp. 1 Petalophthalmid sp.
Winter	Nematode spp. Leptomysini sp. Calanoid spp. Harpacticoid spp. Cyclopoid spp.	Calanoid spp. Cyclopoid spp.* *Penilia avirostris* Eusyllinae spp. *Exoediceroides* sp. 2 Cumacean sp. 1 Cladoceran sp.	*Penilia avirostris** Calanoid spp.* Syngnathid sp. 2 Cyclopoid spp.* Cumacean sp. 1	Leucothoid sp. Leptomysini sp.* *Exoediceroides* sp. 2 Nematode spp. Cumacean sp. 2 Cumacean sp. 1 Harpacticoid spp. *Phoxocephalopsid* sp. 1	*Exoediceroides* sp. 2* *Penilia avirostris* Calanoid spp. Cumacean sp. 1* Cyclopoid spp. Leptomysini sp.	Calanoid spp.* Petalophthalmid sp. *Penilia avirostris** Cyclopoid spp.* Cumacean sp. 1 Syngnathid sp. 2 *Exoediceroides* sp. 3 *Exoediceroides* sp. 2

Table 10.5 continued

	Day			Night		
	1	**2**	**6**	**1**	**2**	**6**
Spring	Calanoid spp.	Cumacean sp. 1*	Calanoid spp.*	*Exoediceroides* sp. 2	*Exoediceroides* sp. 2*	Calanoid spp.*
	Phoxocephalopsid sp. 1	*Exoediceroides* sp. 2*	*Penilia avirostris*	Leptomysini sp.	Cumacean sp. 1	*Penilia avirostris*
	Leptomysini sp.	Calanoid spp.	Cyclopoid spp.*	Cyclopoid spp.	Calanoid spp.	Cyclopoid spp.*
	Cumacean sp. 1	Cyclopoid spp.	Cingulopsid sp.	*Phoxocephalopsid* sp. 1	Leptomysini sp.	Syngnathid sp. 2*
	Nematode spp.		Hydromedusa spp.	Calanoid spp.	Eusirid sp. 1	*Exoediceroides* sp. 2
	Harpacticoid spp.		Syngnathid sp. 2	Cumacean sp. 1	Syngnathid sp. 2	Hydromedusa spp.
	Leucothoid sp.			Harpacticoid spp.	Petalophthalmid sp.*	Petalophthalmid sp.
	Exoediceroides sp. 2					
	Cyclopoid spp.					
Summer 2002	Nematode spp.*	*Penilia avirostris*	*Uldanimia pillare*	Nematode spp.	Calanoid spp.*	Calanoid spp.
	Calanoid spp.	Calanoid spp.*	Calanoid spp.	Harpacticoid spp.	*Penilia avirostris*	Petalophthalmid sp.
	Ampithoid sp. 2	Syngnathid sp. 2	Cingulopsid sp.	Leucothoid sp.	Petalophthalmid sp.*	Cyclopoid spp.
	Tanaid sp. 1	Larval ascidian sp.	Cyclopoid spp.	Ampithoid sp. 2	Leptomysini sp.	Hydromedusa spp.
	Harpacticoid spp.	Nematode spp.	*Donacilla* sp.	Polycopid sp.	*Exoediceroides* sp. 2	Larval ascidian sp.
				Cyclopoid spp.*		
				Cumacean sp. 3		

Table 10.6 Significance levels (p; %) and R-statistic values for global and pairwise comparisons in two-way crossed season x diel period ANOSIM tests of the hyperbenthic fauna collected at habitat types (a) 1, (b) 2 and (c) 6. Values in boldface represent those that are significant.

(a) Habitat type 1

Season (p= 0.1%; Global R=0.566)

	S2001		A		W		SP		S2002	
	p	R	p	R	p	R	p	R	p	R
S2001										
A	0.2	0.442								
W	0.1	0.688	0.2	0.376						
SP	0.2	0.458	0.2	0.304	0.4	0.340				
S2002	0.1	0.790	0.1	0.798	0.1	0.790	0.1	0.846		

Day *vs* Night (p=0.1%; Global R= 0.322)

(b) Habitat type 2

Season (p= 0.1%; Global R=0.671)

S2001										
A	0.1	0.652								
W	0.1	0.706	0.1	0.364						
SP	0.1	0.900	0.1	0.530	0.1	0.640				
S2002	0.1	0.680	0.1	0.730	0.1	0.852	0.1	0.954		

Day *vs* Night (p=0.1%; Global R=0.423)

(c) Habitat type 6

Season (p= 0.1%; Global R=0.523)

S2001										
A	0.1	0.560								
W	0.1	0.692	1.6	0.252						
SP	0.2	0.600	0.1	0.486	0.1	0.614				
S2002	0.1	0.486	0.1	0.674	0.1	0.738	0.1	0.628		

Day *vs* Night (p=0.1%; Global R=0.334)

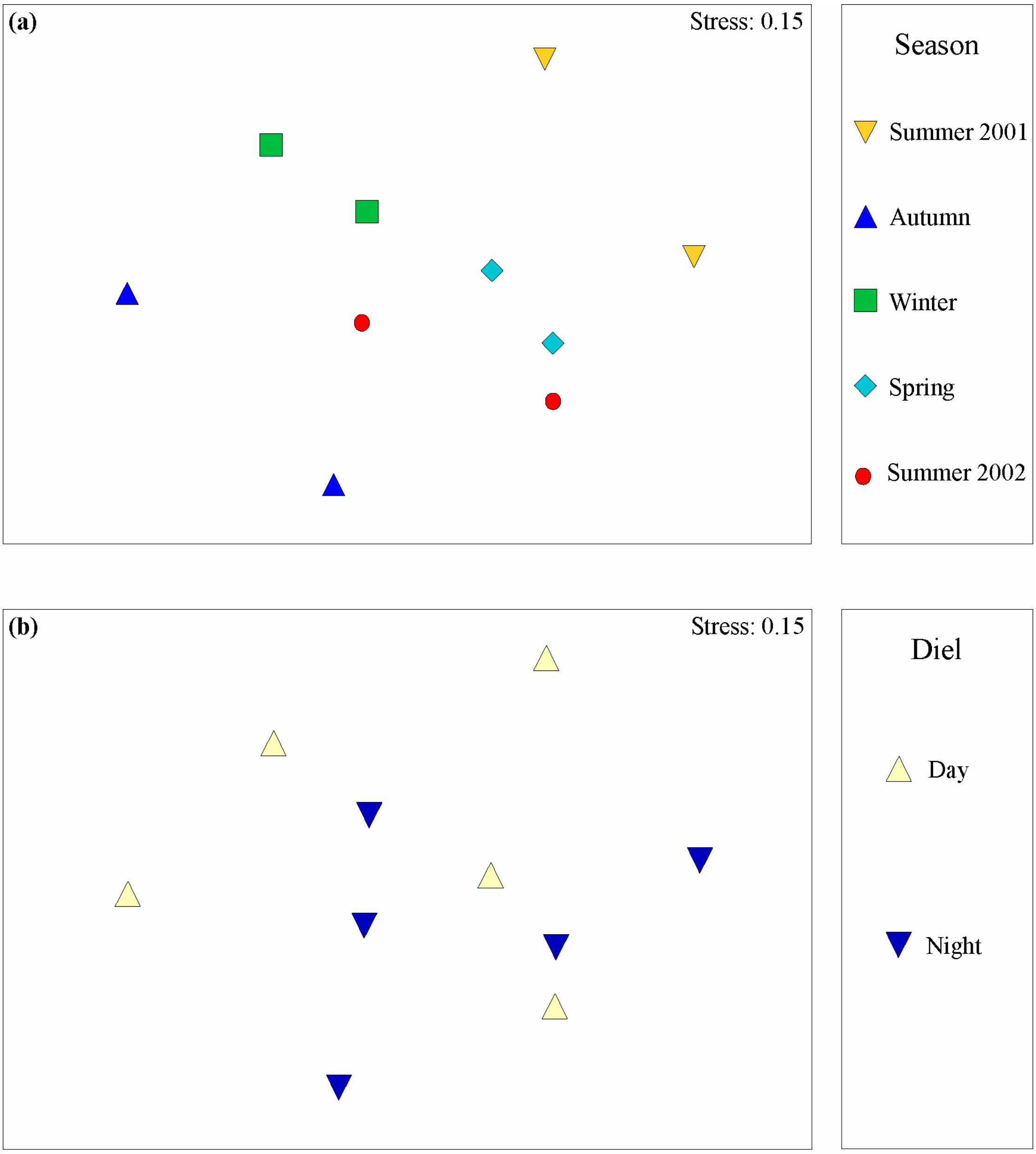
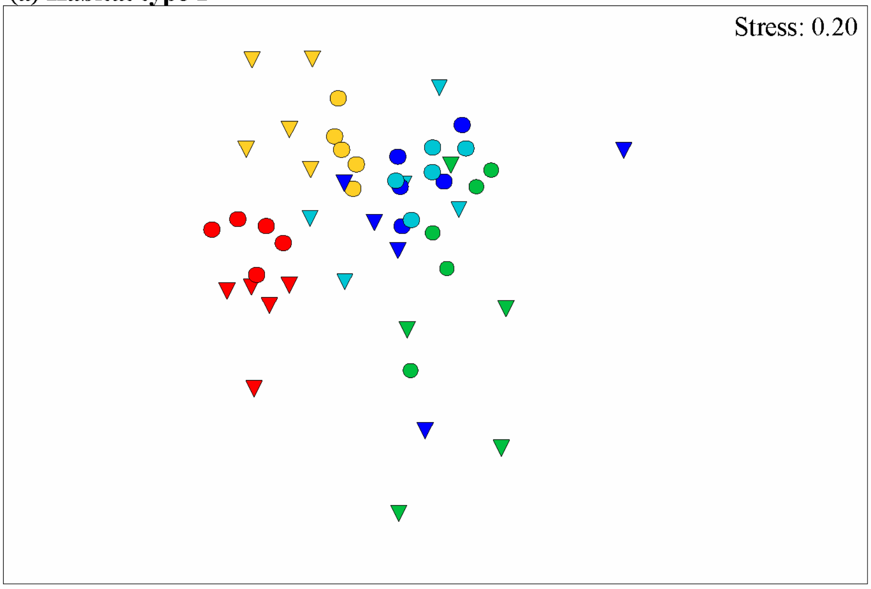


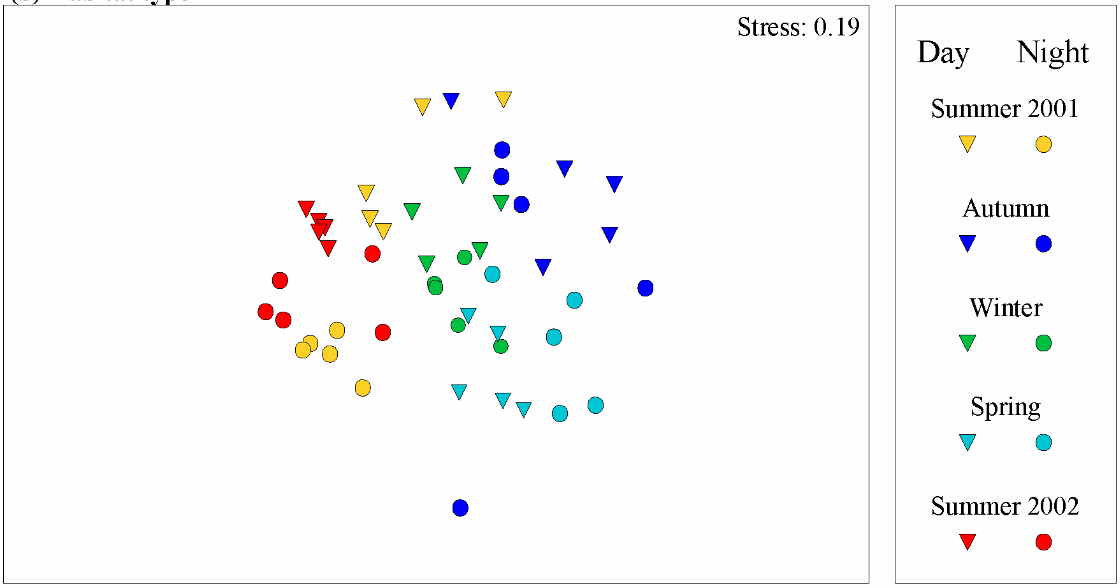
Figure 10.6: MDS ordination of the second-stage similarity matrix containing the correlations between each pair of similarity matrices constructed from the densities of adult hyperbenthic taxa in samples collected at habitat types 1, 2 and 6 during each of the seasons between summer 2001 and summer 2002. The points on the ordination plot have been coded separately for (a) season and (b) diel.

MDS ordinations of the densities of the hyperbenthic fauna at habitat types 1, 2 and 6 showed that the samples exhibited a pronounced tendency to form separate groups on the basis of season. Thus, in each case, the samples in both summers (2001 and 2002) tended to form separate groups on the left of the plots, those for autumn and spring on the right of the plots, while the majority of those for winter lay in a group either amongst or below the former groups of points (Figs 10.7a, b, c). Pairwise ANOSIM comparisons showed that, in each habitat type, the compositions of the hyperbenthos in each season differed significantly from that in all other seasons (Table 10.6a, b, c). These differences were greatest between the compositions in spring *vs* summer 2002 at both habitat types 1 and 2 and between those in winter *vs* summer 2002 at habitat type 6.

(a) Habitat type 1



(b) Habitat type 2



(c) Habitat type 6

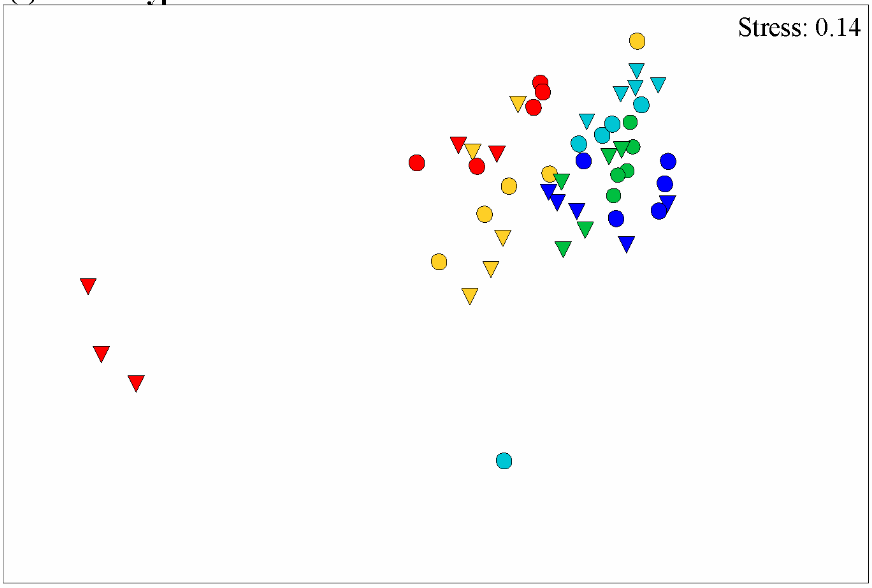


Figure 10.7: Two-dimensional MDS ordination of the densities of adult hyperbenthic taxa in replicate samples from the day and night bewteen summer 2001 and summer 2002 at (a) habitat type 1, (b) habitat type 2 and (c) habitat type 6.

SIMPER showed that, at habitat type 1, the composition in spring was distinguished from that in summer 2002 by relatively greater densities of *Exoediceroides* sp. 1 and 4, and petalophthalmid sp. and relatively lower densities of nematode spp. At habitat type 2, the composition in spring was distinguished from that in summer 2002 by relatively greater densities of cumacean sp. 1 and relatively lower densities of *P. avirostris* and calanoid spp. (Table 10.7a, b). At habitat type 6, the densities of cyclopoid spp., erythropini sp. and cumacean sp. 1 were relatively greater in winter than in summer 2002 (Table 10.7c).

On the MDS ordination plot, derived from the densities of hyperbenthic fauna during the day and night in each season, the samples collected during the day in each habitat type were largely discrete from those collected at night in the corresponding habitat type (Figs 10.7a, b, c).

SIMPER showed that, at habitat types 1, 2 and 6, the majority of the taxa that distinguished the hyperbenthic faunal assemblage in the day from that at night, the majority of those taxa were more abundant at night, except for *Exoediceroides* sp. 4 at habitat type 1, *P. avirostris* at habitat type 2 and *Oikopluera* spp. at habitat type 6 (Table 10.8a, b, c).

10.3.8 Juvenile stages

One-way ANOSIM showed that the compositions of the juveniles in the hyperbenthic fauna differed significantly among habitat types during both the day and night of each season, except for during the day in spring (Table 10.9).

Following MDS ordination of the densities of the juvenile stages of the hyperbenthic fauna, the samples for each habitat type during both the day and night in each season generally formed discrete groups (Figs 10.8a-j). Pairwise ANOSIM comparisons showed that the greatest difference in faunal composition was generally that which occurred between habitat types 1 and 6 (Table 10.9).

Although decapod larvae often typified the composition of each habitat type in each season, other taxa typified the composition of one of the habitat types in a number of seasons and only rarely those of the other two habitat types, *e.g.* capitellid spp. (Table 10.10).

Table 10.7 Taxa detected by SIMPER as those most responsible for typifying the hyperbenthic fauna in summer 2001 (S1), autumn (A), winter (W), spring (SP) and summer 2002 (S2) at habitat types (a) 1, (b) 2 and (c) 6 (see taxa arranged along diagonal cells) and distinguishing each pair of those seasons in each habitat type (see taxa arranged along vertical cells). Samples collected during the day and night and in the different seasons have been pooled in this analysis. The season during which distinguishing taxa were most abundant is also provided (see superscripts).

(a) Habitat type 1

	S1	**A**	**W**	**SP**	**S2**
S1	Calanoid spp. Harpacticoid spp. Cyclopoid spp. *Exoediceroides* sp. 1 Nematode spp. Chaetognath spp.				
A	Harpacticoid spp. $^{(S1)}$ *Exoediceroides* sp. 4$^{(A)}$	*Exoediceroides* sp. 1 Calanoid spp. Nematode spp. Cyclopoid spp. Petalophthalmid sp. Harpacticoid spp. *Exoediceroides* sp. 4 Cumacean sp. 1 Capitella sp.			
W	Calanoid spp. $^{(S1)}$ Harpacticoid spp. $^{(S1)}$ Petalophthalmid sp.$^{(W)}$ *Exoediceroides* sp. 1$^{(S1)}$ Cyclopoid spp. $^{(S1)}$	Petalophthalmid sp. $^{(W)}$ *Exoediceroides* sp. 4$^{(A)}$ *Exoediceroides* sp. 1$^{(A)}$ Calanoid spp. $^{(A)}$ Harpacticoid spp. $^{(A)}$	Nematode spp. Petalophthalmid sp. *Exoediceroides* sp. 1 Harpacticoid spp. Lyssianassid sp. 2 Cyclopoid spp. *Exoediceroides* sp. 4 Cumacean sp. 1		
SP	*Exoediceroides* sp. 4$^{(SP)}$ *Exoediceroides* sp. 1$^{(SP)}$ Petalophthalmid sp.$^{(SP)}$ Harpacticoid spp. $^{(S1)}$	*Exoediceroides* sp. 4$^{(SP)}$ *Exoediceroides* sp. 1$^{(SP)}$ Petalophthalmid sp.$^{(SP)}$ Lyssianassid sp. 2$^{(SP)}$ Harpacticoid spp.$^{(SP)}$ Cumacean sp. 1$^{(SP)}$	*Exoediceroides* sp. 4$^{(SP)}$ *Exoediceroides* sp. 1$^{(SP)}$ Calanoid spp.$^{(SP)}$ Petalophthalmid sp.$^{(W)}$ Lyssianassid sp. 2$^{(SP)}$ Cyclopoid spp.$^{(SP)}$ Cumacean sp. 1$^{(SP)}$ Harpacticoid spp.$^{(SP)}$	*Exoediceroides* sp. 1 Calanoid spp. Petalophthalmid sp. *Exoediceroides* sp. 4 Cumacean sp. 1 Cyclopoid spp. Harpacticoid spp. Nematode spp.	
S2	Nematode spp.$^{(S2)}$	Nematode spp.$^{(S2)}$ *Exoediceroides* sp. 4$^{(A)}$	Nematode spp.$^{(S2)}$ Petalophthalmid sp. $^{(W)}$ Cyproideid sp. 1$^{(S2)}$ Harpacticoid spp.$^{(S2)}$ Calanoid spp.$^{(S2)}$	Nematode spp.$^{(S2)}$ *Exoediceroides* sp. 4$^{(SP)}$ *Exoediceroides* sp. 1$^{(SP)}$ Petalophthalmid sp. $^{(SP)}$	Nematode spp. Harpacticoid spp. Cyproideid sp. 1 Calanoid spp. Tanaid sp. 1 Lyssianassid sp. 2

Table 10.7 continued

(b) Habitat type 2

	S1	A	W	SP	S2
S1	Calanoid spp. Cyclopoid spp. *Exoediceroides* sp. 1 *Oikopleura* spp. Hydromedusa spp. *Penilia avirostris* Erythropini sp. Harpacticoid spp. Petalophthalmid sp.				
A	Calanoid spp.(S1) Erythropini sp.(S1) *Exoediceroides* sp. 1(S1) Petalophthalmid sp.(S1) *Oikopleura* spp.(S1) *Penilia avirostris*(S1)	Calanoid spp. *Exoediceroides* sp. 1 Cyclopoid spp. *Penilia avirostris* Harpacticoid spp. Petalophthalmid sp.			
W	Calanoid spp.(S1) *Exoediceroides* sp. 1(S1) Erythropini sp.(S1) Petalophthalmid sp.(S1) *Oikopleura* spp.(S1) *Penilia avirostris*(S1) Cumacean sp. 1(W) Chaetognath spp.(S1)	*Exoediceroides* sp. 1(W) Cumacean sp. 1(W) *Penilia avirostris*(W) Calanoid spp.(W) Petalophthalmid sp.(W) Cladoceran sp.(W) Cyclopoid spp.(W) *Oikopleura* spp.(W)	Calanoid spp. *Penilia avirostris* Cyclopoid spp. *Exoediceroides* sp. 1 Cumacean sp. 1 Petalophthalmid sp.		
SP	Calanoid spp.(S1) Cumacean sp. 1(SP) *Exoediceroides* sp. 1(SP) Erythropini sp.(S1) Petalophthalmid sp.(S1) *Penilia avirostris*(S1) *Oikopleura* spp.(S1) Cyclopoid spp.(S1)	Cumacean sp. 1(SP) *Exoediceroides* sp. 1(SP) Petalophthalmid sp.(SP) Calanoid spp.(SP)	*Penilia avirostris*(W) *Exoediceroides* sp. 1(SP) Cyclopoid spp.(W) Calanoid spp.(W) *Oikopleura* spp.(W) Cumacean sp. 1(SP) Petalophthalmid sp.(W) Cladoceran sp.(W)	Cumacean sp. 1 *Exoediceroides* sp. 1 Calanoid spp. Cyclopoid spp.	
S2	*Penilia avirostris*(S2) Erythropini sp.(S1) *Exoediceroides* sp. 1(S1)	*Penilia avirostris*(S2) Calanoid spp.(S2) Erythropini sp.(S2)	*Penilia avirostris*(S2) Calanoid spp.(S2) Chaetognath spp.(S2) Erythropini sp.(S2)	*Penilia avirostris*(S2) Calanoid spp.(S2) Cumacean sp. 1(SP)	Calanoid spp. *Penilia avirostris* *Oikopleura* spp. *Exoediceroides* sp. 1 Chaetognath spp. Erythropini sp. Nematode spp.

Table 10.7 continued

(c) Habitat type 6

	S1	**A**	**W**	**SP**	**S2**
S1	Calanoid spp. Cyclopoid spp. Cypridinid sp. 1				
A	*Penilia avirostris*(A) *Exoediceroides* sp. 1(A) Cumacean sp. 1(A) *Oikopleura* spp.(A) Calanoid spp.(A)	*Penilia avirostris* Calanoid spp. Cyclopoid spp. *Exoediceroides* sp. 1 Cumacean sp. 1 *Oikopleura* spp.			
W	*Penilia avirostris*(W) *Oikopleura* spp.(W) Erythropini sp.(W) Calanoid spp.(W) Cumacean sp. 1(W) Cyclopoid spp.(W)	Erythropini sp.(W) *Exoediceroides* sp. 1(A) *Oikopleura* spp.(W) Calanoid spp.(W) *Penilia avirostris*(A) Cyclopoid spp.(W)	Calanoid spp. *Penilia avirostris* *Oikopleura* spp. Cyclopoid spp. Cumacean sp. 1 Erythropini sp.		
SP	*Penilia avirostris*(SP) Calanoid spp.(SP) Cyclopoid spp.(SP) *Oikopleura* spp.(SP) Hydromedusa spp.(SP)	Cyclopoid spp.(SP) Calanoid spp.(SP) *Penilia avirostris*(A) *Exoediceroides* sp. 1(A) Hydromedusa spp.(SP)	Cyclopoid spp.(SP) Calanoid spp.(W) Erythropini sp.(W) *Penilia avirostris*(SP) Cumacean sp. 1(W)	Calanoid spp. *Penilia avirostris* Cyclopoid spp. *Oikopleura* spp. Hydromedusa spp.	
S2	Calanoid spp.(S2) Cyclopoid spp.(S1) Erythropini sp.(S2) Harpacticoid spp.(S1) Cypridinid sp. 1(S1) Hydromedusa spp.(S1)	*Penilia avirostris*(A) Calanoid spp.(S2) *Exoediceroides* sp. 1(A) Cumacean sp. 1(A) *Oikopleura* spp.(A)	*Penilia avirostris*(W) *Oikopleura* spp.(W) Calanoid spp.(W) Cyclopoid spp.(W) Erythropini sp.(W) Cumacean sp. 1(W)	*Penilia avirostris*(SP) Cyclopoid spp.(SP) Calanoid spp.(SP) *Oikopleura* spp.(SP)	Calanoid spp. *Phoxocephalopsid* sp. 2 Cyclopoid spp. Erythropini sp.

Table 10.8 Taxa detected by SIMPER as those most responsible for typifying the hyperbenthic fauna during the day (D) and night (N) in at habitat types (a) 1, (b) 2 and (c) 6 (see taxa arranged along diagonal cells) and distinguishing each pair of those seasons in each habitat type (see taxa arranged along vertical cells). Samples collected in the different seasons have been pooled in this analysis. The time of day during which distinguishing taxa were most abundant is also provided (see superscripts).

		Day	**Night**
(a) Habitat type 1	**Day**	Nematode spp. Calanoid spp. Harpacticoid spp. Cyclopoid spp. *Exoediceroides* sp. 1	
	Night	*Exoediceroides* sp. 4$^{(D)}$ *Exoediceroides* sp. 1$^{(N)}$ Petalophthalmid sp.$^{(N)}$ Nematode spp.$^{(N)}$ Harpacticoid spp.$^{(N)}$	*Exoediceroides* sp. 1 Harpacticoid spp. Petalophthalmid sp. Cyclopoid spp. Nematode spp. Calanoid spp. Cumacean sp. 1 *Exoediceroides* sp. 4
(b) Habitat type 2	**Day**	Calanoid spp. Cyclopoid spp. *Exoediceroides* sp. 1 *Penilia avirostris* *Oikopleura* spp.	
	Night	*Penilia avirostris*$^{(D)}$ Calanoid spp.$^{(N)}$ *Exoediceroides* sp. 1$^{(N)}$ Petalophthalmid sp.$^{(N)}$ Erythropini sp.$^{(N)}$ Cumacean sp. 1$^{(N)}$	Calanoid spp. *Exoediceroides* sp. 1 Petalophthalmid sp. Cyclopoid spp. *Penilia avirostris* Erythropini sp. Cumacean sp. 1
(c) Habitat type 6	**Day**	Calanoid spp. Cyclopoid spp. *Penilia avirostris* *Oikopleura* spp.	
	Night	Calanoid spp. $^{(N)}$ *Penilia avirostris*$^{(N)}$ Cyclopoid spp. $^{(N)}$ Erythropini sp. $^{(N)}$ *Oikopleura* spp.$^{(D)}$ Cumacean sp. 1$^{(N)}$	Calanoid spp. Cyclopoid spp. *Penilia avirostris* Erythropini sp. Cumacean sp. 1 *Oikopleura* spp.

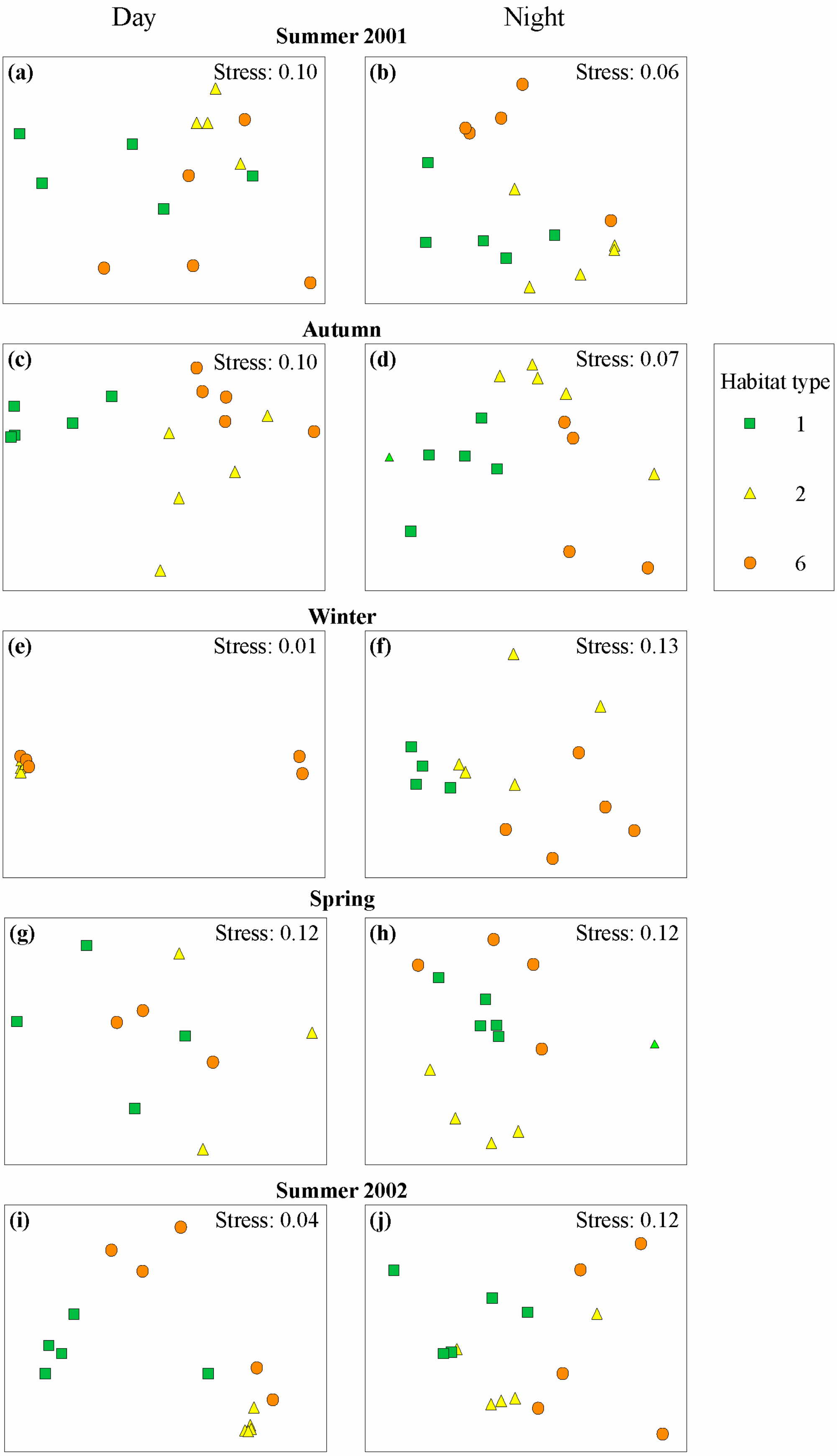


Figure 10.8: Two-dimensional MDS ordination of the densities of juvenile hyperbenthic taxa at habitat types 1, 2 and 6 in each season between summer 2001 and summer 2002 during the day (a,c,e,g and i) and night (b,d,f,h and j).

Table 10.9 Significance levels (p; %) and R-statistic values for both global and pairwise comparisons in one-way ANOSIM tests of the juvenile hyperbenthic assemblages at habitat types 1, 2 and 6 during the day and night in each season between summer 2001 and summer 2002. Significant results are highlighted in boldface.

		1		**2**	
Summer 2001, Day (p=2.4%; Global R=0.263)		p	R	p	R
	2	**4.0**	**0.438**		
	6	19.0	0.136	7.1	0.219
Summer 2001, Night (p=0.2%; Global R=0.484)					
	2	**4.8**	**0.320**		
	6	**2.4**	**0.468**	**1.6**	**0.600**
Autumn, Day (p=0.1%; Global R=0.665)					
	2	**0.8**	**0.868**		
	6	**0.8**	**0.924**	13.5	0.136
Autumn, Night (p=0.1%; Global R=0.484)					
	2	**0.8**	**0.552**		
	6	**0.8**	**0.638**	7.1	0.269
Winter, Day (p=0.2%; Global R=0.614)					
	2	**1.8**	**1.000**		
	6	**5.0**	**0.426**	**0.8**	**0.408**
Winter, Night (p=0.2%; Global R=0.486)					
	2	**2.4**	**0.338**		
	6	**1.6**	**0.813**	**3.2**	**0.412**
Spring, Day (p=41.7%; Global R=0.022)					
	2	42.1	0.019		
	6	8.7	0.225	50.8	0.052
Spring, Night (p=0.1%; Global R=0.413)					
	2	**0.8**	**0.831**		
	6	23.0	0.076	**1.6**	**0.631**
Summer 2002, Day (p=0.2%; Global R=0.602)					
	2	**0.8**	**0.920**		
	6	**4.0**	**0.348**	**0.8**	**0.512**
Summer 2002, Night (p=1.3%; Global R=0.284)					
	2	**3.2**	**0.292**		
	6	**0.8**	**0.430**	9.5	0.176

Table 10.10 Taxa detected by SIMPER as those most responsible for typifying the juvenile hyperbenthic fauna at habitat types 1, 2 and 6 during the day and night in each season between summer 2001 and summer 2002. Where a taxon typified the hyperbenthic fauna in more than one habitat type during the day or night in a given season, that marked with an asterisk indicates the habitat type in which it was most abundant. "juv."=juvenile.

	Day			**Night**		
	1	**2**	**6**	**1**	**2**	**6**
Summer 2001	Capitellid (juv.) spp. Decapod larvae Fish eggs*	Decapod larvae* Fish larvae	Decapod larvae Fish eggs Syllid (larvae) spp. Copepod (nauplii) spp.	Decapod larvae Capitellid (juv.) spp. Fish eggs	Decapod larvae* Fish larvae Spionid (juv.) spp.	Decapod larvae Spionid (larvae) spp.
Autumn	Capitellid (juv.) spp.	Spionid (juv.) spp. Insect (larvae) spp. Fish eggs*	Spionid (juv.) spp.* Fish eggs	Decapod larvae* Capitellid (juv.) spp.	Spionid (juv.) spp.* Decapod larvae Insect (larvae) spp.	Decapod larvae Fish eggs Spionid (juv.) spp.
Winter		Spionid (juv.) spp.* Fish larvae Fish eggs*	Spionid (juv.) spp. Fish eggs Copepod (nauplii) spp.	Decapod larvae*	Decapod larvae Mysid (juv.) spp. Spionid (juv.) spp.	Fish eggs Copepod (nauplii) spp.
Spring				Decapod larvae* Fish eggs*	Fish eggs Fish larvae	Decapod larvae Nebalia (juv.) spp.
Summer 2002	Capitellid (juv.) spp.*	Decapod larvae* Fish larvae	Capitellid (juv.) spp. Decapod larvae	Capitellid (juv.) spp. Decapod larvae	Decapod larvae*	Decapod larvae Fish eggs Copepod (nauplii) spp.

10.4 Discussion

The 147 hyperbenthic taxa recorded in three nearshore habitat types along the lower west coast of Australia was slightly less than the 172 taxa recorded by Beyst *et al.* (2001b) in nearshore waters along the coast of Belgium, using the same sampling technique. Most other studies of the hyperbenthos in relatively shallow waters have been conducted in estuaries, where the number of taxa was far lower than in coastal waters (Mees *et al.* 1993, Tararam *et al.* 1996, Azeiteiro and Marques 1999).

10.4.1 Differences in hyperbenthic fauna among habitat types

The density, number of taxa, species relatedness (*i.e.* Δ^+ and Λ^+) and composition of the hyperbenthic fauna collected along the lower west coast of Australia differed significantly among the three habitat types, and the influence of these spatial environmental differences on the hyperbenthic fauna was much greater than those for either time of day or season with respect to the composition of those assemblages. Moreover, the faunal compositions differed significantly among the three habitat types, these differences were greatest between the two habitat types that were most extreme in terms of their physical characteristics, *i.e.* habitat type 1, which was highly protected from wave action and contained areas of dense seagrass, and habitat type 6, which was relatively exposed to wave action and contained no seagrass. The members of the hyperbenthic fauna have been categorised on the basis of the "hardness" of their bodies, *e.g.* the majority of crustaceans are hard-bodied, whereas polychaetes are soft-bodied (*sensu* Dexter 1992). The fauna at habitat types 1 and 6 contained greater densities of soft-bodied and hard-bodied taxa, respectively, while that at habitat type 2 was intermediate in these respects. Such differences are consistent with the conclusions from the results of other studies that soft-bodied organisms are far better adapted to living in the hyperbenthos in areas where water turbulence is low (Dexter 1992, McLachlan *et al.* 1994, Barnes and Hughes 1998).

The densities of calanoid copepods and the cladoceran *Penilia avirostris* were greater at habitat type 2 than 6, at which the turbulence of water was not as pronounced. It is thus relevant that these crustaceans have been found by other workers to form swarms in relatively sheltered environments (Alldredge and King 1985). Thus, while these crustaceans require some water turbulence for the suspension of phytoplankton, the relatively exposed environment at habitat type 6 may be less than optimal for these organisms. Moreover, the presence of greater densities of amphipods at habitat type 1, which were greater, in turn, than those recorded at habitat types 2 and 6, is consistent with the fact that the microphytobenthos upon which amphipods feed is more likely to be abundant in more sheltered conditions.

The greatest number of hyperbenthic taxa was recorded at the highly sheltered habitat type 1 while the least was recorded at the relatively exposed habitat type 6. These findings are most likely attributable to the greater structural heterogeneity and food provided by the seagrass in the nearshore waters at habitat type 1, and the large extent to which those waters are protected from wave activity. Such results are consistent with those of other studies that have been carried out in other similar nearshore environments (*e.g.* Pihl 1986, Mattila *et al.* 1999). However, the fact that the overall number of taxa was greatest at habitat type 1 but that the Δ^+ of the hyperbenthos was usually the least in this highly sheltered environment, indicates that the majority of the taxa comprising the assemblage at that habitat type were members of a relatively small number of orders. This is exemplified by the fact that 38% of the taxa at this habitat type belong to the class malacostraca, which was represented mainly by 2 orders, *i.e.* amphipoda and leptostraca. In contrast, the malacostracans recorded at habitat type 6 were also represented by the orders mysidacea, decapoda and stomatopoda.

The overall density of hyperbenthos at habitat type 1 was markedly lower than those at the other two habitat types, where seagrass was far more sparse or absent and this finding contrasted directly with one of the hypotheses constructed prior to undertaking this study. It also contrasts with the results of other studies on the hyperbenthos in which vegetated and unvegetated areas have been compared (Pihl 1986, Mattila *et al.* 1999). It is possible that the relatively low densities of hyperbenthic fauna at habitat type 1 reflect low levels of nutrients in the water column as a consequence of the relatively poor exchange of water between this site and the surrounding nearshore environment. Thus, while many other areas along the lower west coast of Australia receive seasonal influxes of nutrient-rich water from the permanently-open Swan and Peel-Harvey estuaries, the site representing habitat type 1 in this study is protected from this estuary discharge by a very shallow sand-bank to the south, and a large causeway construction (*i.e.*) adjoining Garden Island to the mainland, to the north (see Fig. 2.1) (Department of Environmental Protection 1996). Indeed, a relative lack of nutrients and thus phytoplankton in the water column at this habitat type would account for fact that the densities of small crustaceans such as copepods and cladocerans, which feed almost entirely on these planktonic organisms, were lower at this habitat type than at the other two habitat types, where, as a result of wave action and greater water circulation, nutrient availability would have been greater (Mees and Jones 1997).

10.4.2 Differences in hyperbenthic fauna among seasons

The overall densities, number of taxa and faunal composition differed among different seasons at each of the three habitat types, and were most distinct in summer. Thus, the densities of hyperbenthic organisms were greater in summer than in other seasons, which is consistent with the results of studies elsewhere (Jones 1986, Mees *et al.* 1993, Dauvin *et al.* 1994, Azeiteiro and Marques 1999, Lock and Mees 1999, Vallet and Dauvin 1999, Dauvin *et al.* 2000). This is likely to reflect faster generation times of hyperbenthic organisms at higher water temperatures (Dauvin *et al.* 1994). Taxa, such as harpacticoid spp., are present in particularly high densities at all habitat types in summer, which corresponds to the results of many studies conducted in comparable environments in the northern hemisphere (Mees *et al.* 1993, Dauvin *et al.* 1994, Azeiteiro and Marques 1999, Lock and Mees 1999, Vallet and Dauvin 1999, Dauvin *et al.* 2000).

Although the densities were expected to have been lowest in winter, when water temperatures were least, this was not the case. The presence of relatively large densities of copepods, mysids and amphipods in winter is probably related to the deposition of detached macrophytes in this season as this material would act as a source of food and also of shelter in the case of amphipods (Lenanton and Caputi 1989, Vallet and Dauvin 1999, Edgar 2001).

10.4.3 Differences in hyperbenthic fauna between day and night

The relatively greater overall densities of hyperbenthic organisms in the night than during the day presumably reflect, as has been found to be the case elsewhere, the migration of certain taxa from the substrate into the water column at night (*e.g.* Alldredge and King 1980, 1985, Wang and Dauvin 1994, Zouhiri and Dauvin 1995, Dauvin and Zouhiri 1996, Cunha *et al.* 1997, Mees and Jones 1997, Takahashi and Kawaguchi 1997, Vallet and Dauvin 1998, San Vicente and Sorbe 1999). Such nocturnal migrations are likely to be induced by diel changes in light intensity, which is considered to be one of the main environmental factors responsible for initiating such changes (San Vicente and Sorbe 1999). The far greater densities of amphipods in the water column during the night at habitat types 1 and 2 largely accounts for the fact that, while the teleost *Atherinomorus ogilbyi* feeds to a large extent on planktonic crustaceans, it ingests predominantly amphipods during the night (Chapter 11). The average taxonomic distinctness was higher during the day than at night, indicating that the day was represented by a large range of taxa that were found further down the phylogenetic tree, *i.e.* members from family and genus levels. However, the opposite was true for the variation in taxonomic distinctness, which was greater in the night than the day. This is shown by the fact that the night was dominated by mysidacea, amphipoda and perciformes, with only one or two representatives from other orders of taxa.

10.4.4 Early stages of members of the hyperbenthic fauna

In contrast to the situation with the adults of the taxa found in the hyperbenthos, season had a greater influence on the densities and composition of the earlier stages in the life cycles of the components of that fauna. For example, fish eggs were in their greatest densities during spring and in their lowest densities in summer, a trend which is entirely consistent with the marked rise that occurs in the densities in fish larvae between spring and summer. The same type of trend was exhibited by spionid polychaetes. Thus, the densities of the larvae of these invertebrates were low during winter and relatively high in summer, while the opposite trend occurred with those of juvenile spionids.

Chapter 11. Diets of selected teleost species in nearshore, shallow marine waters

11.1 Introduction

The fish faunas found over bare sand in nearshore shallow marine waters typically comprise small species that spend the whole of their life cycles in these environments, such as members of the Atherinidae and Gobiidae, and/or larger species which use these waters predominantly as nursery areas, such as certain members of the Clupeidae, Pleuronectidae, Bothidae and Sillaginidae (*e.g.* Blaber and Blaber 1980, Modde and Ross 1981, Ayvazian and Hyndes 1995, Clark *et al.* 1996, Gibson *et al.* 1996, see Chapter 4). Although these ichthyofaunas are often relatively diverse in composition, they tend to be dominated by a small number of species, which frequently attain high densities in these waters (Brown and McLachlan 1990, Chapter 5). These high densities of fish reflect, in part, the presence of relatively large densities of both planktonic prey, *e.g.* copepods and cladocerans, and benthic macroinvertebrate prey, *e.g.* polychaetes, which collectively constitute by far the most important food source for fish in nearshore waters (*cf* Dexter 1983, Modde and Ross 1983, Lasiak 1986, Jacoby and Greenwood 1989, Jaramillo and McLachlan 1993, Edgar and Shaw 1995a,b).

Since the composition of potential invertebrate prey in nearshore areas varies with extremes in habitat type and, in particular, the extent to which they are exposed to wave activity (*e.g.* Dexter 1983, 1984, Jacoby and Greenwood 1989, Jaramillo and McLachlan 1993, Edgar *et al.* 1994, Hutchings and Jacoby 1994, Chapters 7, 8 and 10), these differences are likely to be reflected in the diets of fish that inhabit those environments. Moreover, due to differences in the peak breeding times and short life cycles of the major prey taxa, the species composition of these prey changes during the year and can also vary in their abundance between day and night (*e.g.* Leber 1982, Dexter 1984, Jacoby and Greenwood 1989, Chapters 7, 8 and 10), which can likewise be reflected in the dietary compositions of those species. However, it should be kept in mind that the ability of certain fish species to persist in different habitat types, which presumably house different suites of invertebrate prey, or to be able to feed on prey which become seasonally abundant, can be directly related to the degree to which they are a generalist feeder and the degree of dietary opportunism that each of those species exhibits, *i.e.* tendency to feed on different prey in response to differences in prey abundance.

Ross (1986) concluded that, when marine fish species co-occur in the same general area, food and then habitat are the resources that are most commonly partitioned among those species, and that one and/or the other of these resources may also be partitioned at a temporal level. Such interspecific resource partitioning is considered to reduce the possibility of competition for food sources. However, it should also be recognized that, for any given species, both morphological and maturational changes as those fish increase in size, can also mean that resources such as food and habitat may be partitioned within that species. Indeed, many studies demonstrate clear and often progressive changes in both the dietary compositions and size of prey ingested by the individuals of species as they increase in size (*e.g.* Werner and Gilliam 1984, Labropoulou *et al.* 1998, Platell *et al.* 1998, Linke *et al.* 2001). When determining the extent to which food resources are partitioned within and among species, the extent of dietary specialisation and opportunism of that species (see above) should be taken into account.

There have apparently been no attempts to investigate the extent to which the food sources ingested by fish living in nearshore sandy areas in the same geographical region vary among habitats that differ in their level of exposure to wave activity, and whether any such variation is greater or less than that attributable to a seasonal and/or diel effect. Furthermore, the extent of any size-related changes in the diets of fish species, and how they may relate to the above factors, has likewise not been explored.

During the present study, we have determined the dietary compositions of eight teleost species that belong to morphologically divergent families (Clupeidae, Atherinidae, Leptoscopidae, Sillaginidae, Bothidae and Pleuronectidae) in three habitat types, *i.e.* very sheltered (habitat type 1), moderately sheltered (habitat type 2) and relatively exposed (habitat type 6), that contain different suites of prey and lie in nearshore waters on the lower west coast of Australia. Species were selected for such dietary comparisons on the basis that they were moderately abundant in at least two of the three habitat types or were characteristic of certain habitat types. Emphasis was also placed on those species for which there was no known dietary information since, at the time, it was considered that dietary data available for other species in similar environments would be available for comparisons with the data collected in the present project. Five of the selected species, *Atherinomorus ogilbyi* (Atherinidae), *Spratelloides robustus* (Clupeidae), *Sillago bassensis, Sillago schomburgkii* and *Sillago vittata* (Sillaginidae) are relatively mobile and swim above the substrate, while the other three, *Lesueurina platycephala* (Leptoscopidae), *Ammotretis elongatus* (Pleuronectidae) and *Pseudorhombus jenynsii* (Bothidae), are benthic and frequently burrow within the substrate. Moreover, the relative size, orientation and degree of protrusiveness of the mouths and the relative sizes of the eyes vary markedly amongst those eight species (see Fig. 11.19 in Discussion). Further contrast amongst these species is provided by the fact that four of these species, *i.e. S. robustus, A. ogilbyi, L. platycephala, S. schomburgkii* and *P. jenynsii*, are capable of completing their life cycles in nearshore waters (Chapter 5), while the two other sillaginids (*S. bassensis* and *S. vittata*) and the pleuronectid *A. elongatus* use such habitats as nursery areas.

Particular emphasis has been placed on testing the following hypotheses. (1) The divergent modes of life and mouth characteristics of those eight teleost species will result in the ingestion of different types of prey. (2) Increases in body size, mouth dimensions and the swimming ability of the eight teleost species will be accompanied by changes in the main prey ingested by those species. (3) The variations known to occur in the density of potential prey among habitat types and seasons and day and night (Chapters 7, 8 and 10) will be reflected in the dietary compositions of the different species, depending on the extent to which they are generalist or opportunistic feeders.

11.2 Materials and methods

11.2.1 Sampling regime

The three sampling sites, which are representative of three habitat types in nearshore waters, were located close to 32°S and 115°45'E along a 40 km stretch of heterogeneous coastline on the lower west coast of Western Australia. Habitat type 1 is very sheltered from wave activity and contains substantial seagrass meadows (*Posidonia australis* and *Posidonia sinuosa*) close to the shore, while habitat type 6 is relatively exposed to wave activity and contains no attached macrophytes. Habitat type 2 is intermediate between these two habitat types in terms of both exposure and extent of seagrass meadows.

The unvegetated areas in nearshore waters at the three habitat types were sampled for *Spratelloides robustus, Sillago bassensis, Sillago vittata* and *Pseudorhombus jenynsii* during the day on three to five occasions spread over four weeks in the middle of each season between summer 2000 and spring 2001. In the case of *Atherinomorus ogilbyi, Sillago schomburgkii, Lesueurina platycephala* and *Ammotretis elongatus*, sampling was carried out as for the previous four species, but during both day and night and in the following year, *i.e.* summer 2001 to summer 2002. Thus, all three habitat types were sampled during the day, *i.e.* between 0900 and 1500 h, using a 21.5 m long seine net, with a 3 mm mesh in the central pocket. The two more sheltered habitat types were also sampled during the day using a 60.5 m long seine net with 9 mm mesh in the central pocket. All three habitat types during the second year of the study were also sampled at night, *i.e.* between 2000 and 2400 h, using the 21.5 m seine net. Note that, because of difficulties in deploying this larger seine net in heavy waves and after nightfall, it could not be used either at the most exposed habitat type, *i.e.* habitat type 6, or during the night. The two seine nets were always deployed in areas where there were little or no detached macrophytes. N.B. Although sampling for fish was also carried out during the night in the first year (see Chapter 5), the four fish species selected for comparisons during that year were not sufficiently abundant to permit dietary analyses of those species. Fish were euthanased by placing them in an ice slurry immediately after capture and then frozen.

In the laboratory, up to 25 individuals of each of the eight species collected at each habitat type in each season during the day (and also during night for *A. ogilbyi, S. schomburgkii, L. platycephala* and *A. elongatus*) were retained for dietary analyses. In order to explore the type of size-related changes in dietary composition that are exhibited by a species, additional fish, and particularly very large and very small individuals, were collected and added to this total to ensure that there was a wide size range of fish for study. Each fish was measured to the nearest 1 mm (total length) and its entire digestive tract removed and stored in 70% ethanol. Since the tracts of six of the species contained a distinct stomach, *i.e. S. robustus, L. platycephala*, *S. bassensis, S. schomburgkii* and *S. vittata*, while those of *A. elongatus* and *A. ogilbyi* instead possessed a slightly enlarged foregut, these two different regions, which typically contained food, were subjected to dietary analysis.

11.2.2 Dietary data

The number of individuals of each species with empty guts, *i.e.* stomach or foregut, was recorded and the fullness of each gut with food was scored on a scale of 1 (almost empty) to 10 (full). The gut contents were examined under a dissecting microscope using reflected light and each dietary item identified to the lowest possible taxon. An examination of the distribution of the dietary items then enabled those items to be allocated to an appropriate series of broader taxonomic groups, subsequently referred to as dietary categories. The percentage frequency of occurrence of each dietary category in the guts of all individuals of each fish species (%F) and the percentage volumetric contribution made by each dietary category to the gut contents of each individual of each fish species (%V), which was determined using the points method that takes into account gut fullness (Hynes 1950, Hyslop 1980), were calculated. Note that analyses of the dietary compositions have focused on volumetric contributions because this variable provides the most reliable data for such analyses (Hyslop 1980), and the extent to which some prey had become masticated or digested made it difficult to obtain reliable counts of certain prey items. Since unidentifiable material and unidentifiable crustaceans may contain the remnants of one or more dietary categories and thus have the potential to bias the results, they were not included in the multivariate analyses of dietary compositions. The contributions made by sediment to the gut contents of each species are shown in Table 11.1, but were not used in dietary analyses as sediment consisted predominantly of inorganic material and was thus not considered a *bona fide* dietary category.

11.2.3 Dietary analyses

The gut contents of each individual fish typically contained only a few of the total number of dietary categories recognised in this study, as is commonly the case in this type of study where a substantial number of dietary categories were found (Linke *et al.* 2001, Platell and Potter 2001). Thus, as in those latter studies, the gut contents of small groups of fish were pooled (see later) in order to decrease the number of dietary categories represented by zero values in each group of guts.

The percentage volumetric dietary data were prepared in the following ways prior to analyses using non-metric Multidimensional Scaling (MDS) ordination as described in Clarke and Gorley (2001). To elucidate the relative extents to which the dietary compositions of the eight fish species were influenced by overall differences amongst species, habitat types and seasons, the percentage volumetric contributions of the various dietary categories in the guts of each species at each habitat type in each season, using data collected only during the day, were first randomly allocated into groups of five. Such analyses were not undertaken on the dietary compositions of the four species during the night, since the diet of only one species (see later) exhibited diel differences. The means were then calculated for the percentage volumetric contributions of the various dietary categories in each group (= dietary sample) and square root transformed, as is appropriate for such data (Platell and Potter 2001). The same approach was adopted for determining the ways in which the dietary compositions of the different species varied with habitat type, season and/or time of day (where possible), except that the data were separated into groups of three, rather than five. The above transformed data were used to construct Bray-Curtis similarity matrices, which were then subjected to non-metric multidimensional scaling (MDS) ordination, as described in Clarke and Gorley (2001).

One-way Analysis of Similarity (ANOSIM) was initially employed to test whether the dietary compositions of fish differed significantly overall amongst species, habitat types and seasons (Clarke 1993). Further one-way and two-way crossed ANOSIM tests were then applied to the data for the different species to determine whether habitat type, season and/or time of day significantly influenced the dietary composition of each species. The diets of one species (*A. elongatus*) could not be further analysed using ANOSIM tests as there were insufficient numbers of dietary samples. N.B. The results of pairwise ANOSIM comparisons are presented only when the number of possible permutations exceeds 35, which means that a significant difference could be detected if it was present (K. Clarke, personal communication). Similarity percentages (SIMPER) was used to determine which dietary categories typified particular groups and were most responsible for any dissimilarities between groups (Clarke 1993).

To explore whether the dietary composition of each species changed with body size in the different habitat types, the mean volumetric conributions of the various dietary categories of individuals in each sequential length class, after pooling for season and time of day (except for *A. ogilbyi*, which was kept separate for day and night), were calculated and plotted as histograms. These analyses employed the dietary data for both the individuals that were randomly chosen from the catches at each habitat type in each season and the additional fish that were selected specifically to ensure that a wide size range of fish was represented (see earlier). The mean volumetric contributions of the various dietary categories of the individuals in each sequential length class for those four species which occurred in each of the three habitat types, *i.e. S. robustus, A. ogilbyi, S. schomburgkii* and *S. vittata*, were subjected to MDS ordination, as described above.

Note that each point on the ordination plots, which represents a mean value for volumetric dietary data for a group or size class as described above, is considered to represent a dietary sample.

11.2.4 Head and mouth morphology analyses

The following measurements were made on 15 individuals of each species and which encompassed the full size range recorded for those species during the sampling period; namely standard length, head length, premaxilla length, dentary length, length from the tip of the upper and lower jaws in extended positions to the posterior of the operculum, and the maximum width and height of the mouth when fully open. All measurements were recorded to the nearest 0.1 mm using vernier calipers (Platell and Potter 2001).

The head and mouth measurements of each fish were expressed as a ratio of its standard length. The standardised measurements were then subjected to Principal Component Analysis (PCA) to determine whether head and mouth morphology differed among species and, if so, to what extent (Clarke and Gorley 2001).

11.3 Results

11.3.1 Overall comparisons of dietary compositions and head and mouth morphologies

The number of guts examined ranged from 35 and 75 for *Pseudorhombus jenynsii* and *Ammotretis elongatus*, respectively, to 233 and 244 for *Sillago schomburgkii* and *Atherinomorus ogilbyi* (Table 11.1). In the case of the percentage of guts that contained food, these ranged from a low of 26.3% for *Lesueurina platycephala* to 100% for three species (*Spratelloides robustus, Sillago bassensis* and *Sillago vittata*) and lay between 50 and 85% for the remaining four species (*A. ogilbyi, S. schomburgkii, A. elongatus* and *P. jenynsii*). The gut fullness values, which lay between 1 and 10 for all eight species, ranged from between mean values of 3.5 in *L. platycephala* to 7.7 for *S. bassensis* and *S. vittata* and then to 9.6 for *S. robustus* (Table 11.1).

In terms of the major taxa, *i.e.* Foraminifera, Nematoda, Oligochaeta, Polychaeta, Mollusca, Crustacea, Insecta, Arachnidae, Siphonophora and Teleostei, crustaceans were by far the most important prey of seven of the eight species and, in the remaining species (*S. schomburgkii*) they were second in importance only to polychaetes (Table 11.1). The volumetric contributions of crustaceans were also very high, ranging from 51.5% to 95.6% in seven species, while this major taxon comprised 24.9% of the diet of *S. schomburgkii*. Polychaetes, which contributed 51.3% to the overall dietary volume of this sillaginid, also made large contributions to the diets of *S. vittata* (35.9%), *L. platycephala* (23.9%), *A. elongatus* (19.8%), *S. bassensis* (10.5%) and *P. jenynsii* (9.2%). The only other major taxa to make substantial volumetric contributions to the diet of any of the species were insects in the case of *A. ogilbyi* (8.2%), teleosts in the case of *P. jenynsii* (27.1%), *S. bassensis* (12.0%), *L. platycephala* (10.1%) and *S. schomburgkii* (5.3%) and molluscs and oligochaetes for the last sillaginid species, *i.e.* 7.4 and 5.6%, respectively (Table 11.1).

Although crustaceans were overall the most important for the different species, there were considerable differences in the contributions of the different dietary categories within this major taxon. Thus, calanoid copepods contributed 71.2% to the diets of *S. robustus* and made large contributions, *i.e.* ranging between 16.7 and 50.9% in the diets of *A. ogilbyi, S. bassensis* and *S. vittata* (Table 11.1). Amphipods (26.7%) and cladocerans (7.7%) were also important in terms of dietary volume for *A. ogilbyi*, with amphipods being ingested in moderate to large amounts, *i.e.* 8.3-21.5%, by three other species (*L. platycephala, A. elongatus* and *P. jenynsii*) and cladocerans contributing 15.7 and 17.3% to the dietary volume of *S. bassensis* and *S. vittata*, respectively. *Lesueurina platycephala* ingested a wide range of crustacean prey, with mysids comprising 11.9% and cumaceans and isopods each contributing *ca* 5.6% to the diets. Cumaceans, which were also ingested by *S. vittata* (7.8%), were very important in the diets of *A. elongatus* (32.1%) and mysids were similarly important for *P. jenynsii* (19.6%). Harpacticoid copepods made small contributions to the diets of *S. schomburgkii* and *S. vittata, i.e.* 5.3 and 6.1%, respectively, and tanaids, which made only low contributions to the diets of seven of the species, contributed 23.5% to the overall dietary volume of *A. elongatus* (Table 11.1).

When the similarity matrix representing the dietary data collected during the day for the eight species at different habitat types and seasons were subjected to ANOSIM, highly significant differences were recorded between the species (irrespective of habitat type and season), habitat type (irrespective of species and season) and season (irrespective of species and

Table 11.1 Frequency of occurrence (%F) and percentage contributions to the overall gut volume (%V) of the major dietary taxa (boldface) and other dietary categories (marked with an asterisk) in the guts of *Spratelloides robustus, Atherinomorus ogilbyi, Lesueurina platycephala, Sillago bassensis, Sillago schomburgkii, Sillago vittata, Ammotretis elongatus* and *Pseudorhombus jenynsii.*

	Spratelloides robustus		*Atherinomorus ogilbyi*		*Lesueurina platycephala*		*Sillago bassensis*		*Sillago schomburgkii*		*Sillago vittata*		*Ammotretis elongatus*		*Pseudorhombus jenynsii*	
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
***Foraminifera**	**1.2**	**<0.1**	**11.2**	**2.7**	**3.4**	**0.2**	**2.8**	**0.2**	**1.3**	**<0.1**	**3.4**	**<0.1**	**23.7**	**1.3**	**5.7**	**0.1**
***Nematoda**	**-**	**-**	**3.4**	**0.3**	**1.7**	**0.2**	**7.3**	**0.3**	**11.8**	**0.9**	**10.9**	**0.3**	**5.3**	**0.3**	**-**	**-**
***Oligochaeta**	**-**	**-**	**0.5**	**<0.1**	**1.7**	**1.5**	**-**	**-**	**14.5**	**5.6**	**-**	**-**	**2.6**	**0.7**	**-**	**-**
***Polychaeta**	**3.7**	**0.3**	**16.6**	**4.8**	**39.0**	**23.9**	**29.4**	**10.5**	**86.2**	**51.3**	**54.4**	**35.9**	**47.4**	**19.8**	**14.3**	**9.2**
Mollusca	**3.7**	**0.3**	**18.5**	**2.9**	**3.4**	**1.7**	**6.4**	2.1	**11.8**	**7.4**	**6.8**	1.2	5.3	0.3	**-**	**-**
* Bivalvia	3.7	<0.1	-	-	-	-	2.8	2.1	7.2	5.9	5.8	1.2	-	-	-	-
* Cephalopoda	-	-	-	-	-	-	-	-	0.7	0.2	-	-	-	-	-	-
* Gastropoda	2.4	0.3	-	-	1.7	1.5	0.9	<0.1	1.3	0.2	2.0	<0.1	-	-	-	-
* Micromolluscs	1.2	<0.1	18.5	2.9	1.7	0.2	3.7	<0.1	3.3	1.1			5.3	0.3	-	-
Crustacea	**100**	**95.6**	**88.8**	**78.8**	**93.2**	**59.8**	**75.2**	**74.6**	**58.6**	**24.9**	**70.7**	**51.5**	**86.8**	**76.7**	**62.9**	**71.3**
* Notostraca	-	-	0.5	<0.1	-	-	-	-	-	-	-	-	-	-		
* Conchostraca	-	-	5.4	0.4	-	-	-	-	0.7	<0.1	-	-	-	-		
* Cladocera	18.3	1.4	11.2	7.7	-	-	33.0	15.7	0.7	<0.1	19.0	17.3	-	-	-	-
* Copepoda (Calanoida)	97.6	71.2	45.9	24.5	1.7	0.2	63.3	50.9	0.7	0.6	28.6	16.7	-	-	-	-
* Copepoda (Harpacticoida)	30.5	0.2	22.4	1.4	1.7	0.7	10.1	1.6	7.9	5.3	24.5	6.1	2.6	<0.1	-	-
* Copepoda (Cyclopoida)	-	-	3.4	0.3	-	-	0.9	0.2	-	-	1.4	<0.1	-	-	-	-
* Ostracoda	28.0	1.0	2.9	0.1	3.4	0.7	1.8	0.2	-	-	4.1	0.1	5.3	0.5	2.9	<0.1
* Cumacea	-	-	14.1	2.5	11.9	5.7	-	-	11.2	2.1	14.3	7.8	65.8	32.1	-	-
* Tanaidacea	-	-	15.1	3.2	-	-	0.9	-	21.7	4.4	2.7	0.1	42.1	23.5	-	-
* Mysidacea	-	-	11.2	3.3	16.9	11.9	4.6	0.3	5.9	2.2	1.4	0.3	-	-	25.7	19.6
* Amphipoda	-	-	42.0	26.7	35.6	21.5	3.7	0.8	23.7	4.1	6.8	0.9	60.5	17.5	17.1	8.3
* Isopoda	-	-	11.7	1.2	8.5	5.6	-	-	2.0	0.2	2.0	0.6	5.3	0.3	-	-
* Decapoda (Penaeoidea)	-	-	-	-	-	-	-	-	5.9	3.4	-	-	5.3	2.7	-	-
* Decapoda (Caridae)	1.2	<0.1	2.0	0.3	6.8	3.0	7.3	3.9	0.7	0.1	2.7	0.1	-	-	11.4	6.2

Table 11.1 continued

	Spratelloides robustus		*Atherinomorus ogilbyi*		*Lesueurina platycephala*		*Sillago bassensis*		*Sillago schomburgkii*		*Sillago vittata*		*Ammotretis elongatus*		*Pseudorhombus jenynsii*	
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
* Decapoda (Brachyura)	-	-	-	-	1.7	1.4	0.9	<0.1	4.6	1.8	1.4	1.2	-	-	37.1	21.2
* Mysis/Zoea	3.7	<0.1	13.7	4.7	1.7	<0.1	1.8	<0.1	0.7	<0.1	0.7	-	-	-	5.7	0.2
* Megalopae	-	-	2.9	0.3	-	-	-	-	-	-	-	-	-	-	8.6	1.8
Unidentifiable crustaceans	68.3	23.7	4.4	2.1	23.7	9.1	1.8	1.0	3.3	0.5	2.0	0.3	-	-	17.1	8.2
Insecta	**-**	**-**	**20.2**	**8.2**	**-**	**-**	**-**	**-**	**2.0**	**0.2**	**-**	**-**	**-**	**-**	**-**	**-**
* Curculionidae (adult)	-	-	0.5	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
* Dytiscidae (larvae)	-	-	0.5	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
* Staphylinidae (adults)	-	-	0.5	0.2	-	-	-	-	-	-	-	-	-	-	-	-
* Corixidae (adult)	-	-	1.5	0.5	-	-	-	-	-	-	-	-	-	-	-	-
* Notonectidae (adult)	-	-	0.5	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
* Culicidae (adult)	-	-	1.0	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
* Culicidae (larvae)	-	-	1.5	0.1	-	-	-	-	-	-	-	-	-	-	-	-
* Tipulidae (larvae)	-	-	4.4	2.8	-	-	-	-	1.3	0.1	-	-	-	-	-	-
* Dipteran sp. 1	-	-	1.5	0.3	-	-	-	-	0.7	<0.1	-	-	-	-	-	-
* Formicidae (adult)	-	-	9.8	3.8	-	-	-	-	-	-	-	-	-	-	-	-
Unidentifiable insects	-	-	2.9	0.5	-	-	-	-	-	-	-	-	-	-	-	-
***Arachnidae (Terrestrial)**	**-**	**-**	**1.5**	**0.2**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
***Arachnidae (Marine)**	**-**	**-**	**1.0**	**<0.1**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
***Siphonophora**	**40.2**	**0.9**	**1.5**	**0.3**	**-**	**-**	**0.9**	**<0.1**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
***Teleostei**	**-**	**-**	**0.5**	**<0.1**	**10.2**	**10.1**	**11.9**	**12.0**	**7.2**	**5.3**	**4.1**	**6.1**	**-**	**-**	**22.9**	**27.1**
*Eggs	45.1	0.5	2.0	0.3	-	-	7.3	<0.1	-	-	4.1	<0.1	-	-	2.9	0.1
*Plant material	2.4	<0.1	9.3	1.1	5.1	2.5	7.3	0.3	39.5	4.5	7.5	1.0	7.9	0.9	0.1	0.1
Total number of guts	**82**		**244**		**225**		**109**		**233**		**147**		**75**		**35**	
Percentage of guts with food	**100**		**84.0**		**26.2**		**100**		**65.2**		**100**		**50.7**		**94.3**	
Mean gut fullness (± SE)	**9.6 ± 0.1**		**6.4 ± 0.1**		**3.5 ± 0.1**		**7.7 ± 0.3**		**4.2 ± 0.1**		**7.7 ± 0.2**		**4.7 ± 0.2**		**5.6 ± 0.6**	

habitat type), with the R-statistic value being greatest for species (0.471), followed by season (0.287) and then habitat type (0.171). On the MDS ordination plot, it was evident that the samples grouped together strongly according to species (Fig. 11.1). Thus, the points for the dietary samples of *S. robustus* formed a tight group in the upper lefthand corner of the plot, and typically above those for *A. ogilbyi, S. bassensis* and *S. schomburgkii*, for which the points were also mainly on the lefthand side of the plot. The points for both *L. platycephala* and *P. jenynsii* lay in the upper righthand corner of the plot, above those of *A. elongatus*, which lay in the lower righthand corner. The points for *S. vittata* were distributed across the horizontal midline of the plot (Fig. 11.1).

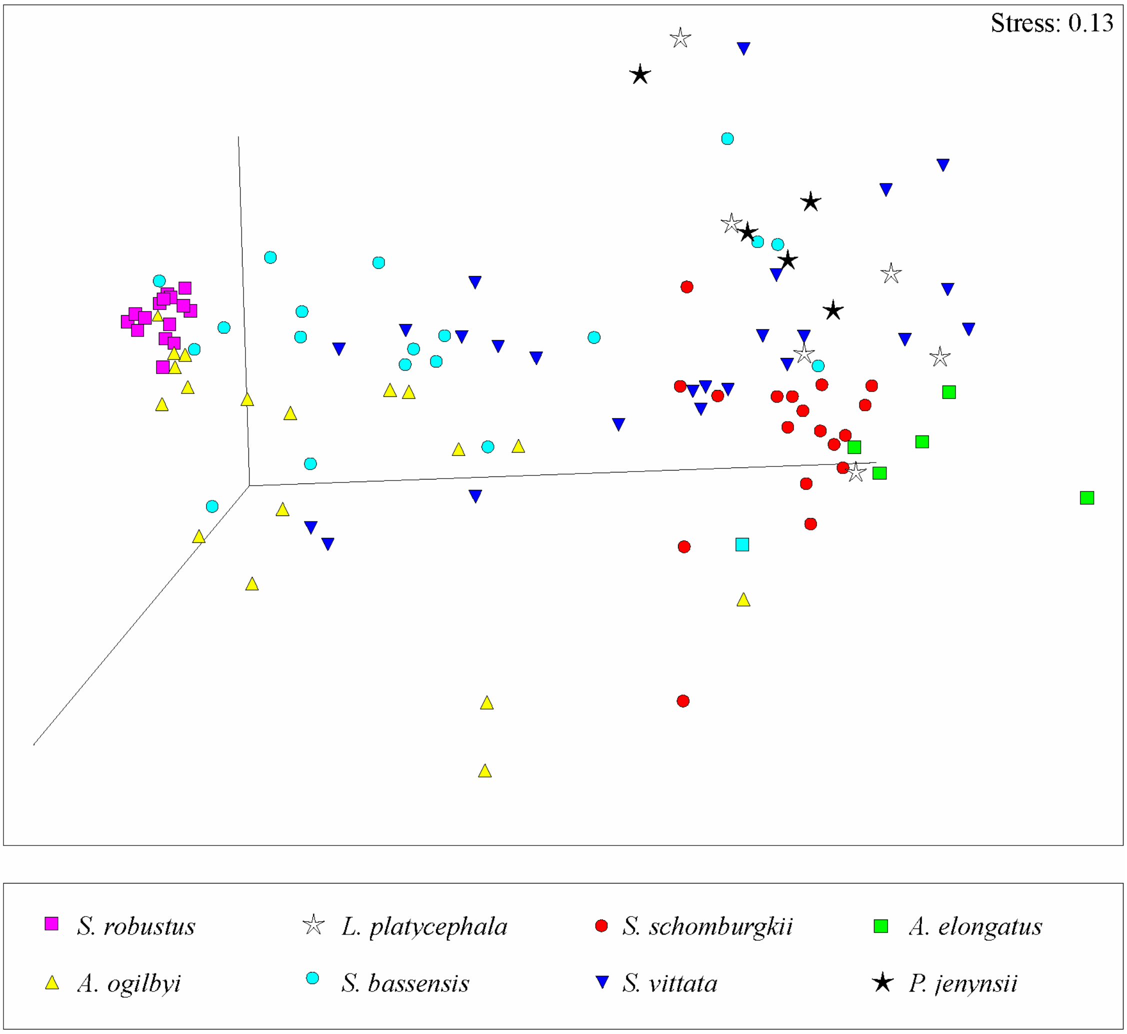


Figure 11.1: Three-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of five individuals, recorded during the day, of each of *Spratelloides robustus, Atherinomorus ogilbyi, Lesueurina platycephala, Sillago bassensis, Sillago schomburgkii, Sillago vittata, Ammotretis elongatus* and *Pseudorhombus jenynsii.*

Pairwise ANOSIM comparisons between the dietary compositions of the eight species demonstrated that, with the exception of *L. platycephala vs P. jenynsiii* (p=15.3%), highly significant differences were recorded (p<2%) between all pairs of species, with the R-statistic values ranging between 0.159 for *S. schomburgkii vs S. vittata* to 0.925 for *S. robustus vs A. elongatus* (Table 11.2).

SIMPER showed that the dietary categories that most typified the diets of each of the eight species were calanoids for both *S. robustus* and *A. ogilbyi*, amphipods, polychaetes and mysids for *L. platycephala,* calanoids and polychaetes for *S. bassensis*, polychaetes and plant material for *S. schomburgkii*, polychaetes for *S. vittata*, tanaids for *A. elongatus* and crabs for *P. jenynsii*. SIMPER also demonstrated that other dietary categories, which sometimes contributed less to the overall diets, were often important in distinguishing the diets of different pairs of species. For example, the consumption of harpacticoids and insects by *A. ogilbyi* helped distinguish the diet of this species from other species and the presence of carids and teleosts helped distinguish the diets of *P. jenynsii* from the other species (Table 11.3).

Following PCA of standardised measurements of the various head and mouth dimensions of the individuals of each species, the points representing the individuals of each of those species formed tight and very discrete groups on the resultant PCA plot (Fig. 11.2). PC1 and PC2 explained 26.7 and 39.0% of the total variation, respectively (Table 11.4). The eigenvectors for PC1 (Table 11.4), in conjunction with the distribution of the points on the PCA plot (Fig. 11.2), demonstrate that a combination of head length and the protrusiveness of the upper jaws were least in *L. platycephala,* moderate and comparable in *S. robustus*, *A. ogilbyi*, *A. elongatus* and *P. jenynsii* and greatest in *S. bassensis, S. schomburgkii* and *S. vittata*, while the reverse was the case for mouth width. The particularly high and negative eigenvectors for premaxilla length, lower jaw extension and mouth height on PC2, coupled with the distribution of the points on the PCA plot, emphasises that *L. platycephala, S. schomburgkii* and *A. elongatus* have the smallest premaxilla, least extensible lower jaw and the least vertical gape of the different species, while *P. jenynsii* has the relatively largest premaxilla, most extensible lower jaw and a relatively high mouth and the other four species are intermediate in terms of these mouth measurements (Fig. 11.2). N.B. When interpreting the results for the above eight species, it should be recognised that, for both the pleuronectid and bothid, the migration of their eyes to either the left or right side of their head and associated flattening of their body during development means that any measurements of the mouth height and width of these flatfish are comparable, when taking into account their orientation to the substrate, to the opposite measurements of the mouth of the other six species.

Table 11.2 Significance levels (p; %) and R-statistic values for the pairwise comparisons in one-way ANOSIM tests of the dietary compositions of the eight fish species. Only data recorded during the day has been used in these analyses. Significant values are highlighted in boldface.

	Spratelloides robustus	*Atherinomorus ogilbyi*	*Lesueurina platycephala*	*Sillago bassensis*	*Sillago schomburgkii*	*Sillago vittata*	*Ammotretis elongatus*
Atherinomorus ogilbyi	**p=0.1%; R=0.238**						
Lesueurina platycephala	**p=0.1%; R=0.862**	**p=0.1%; R=0.666**					
Sillago bassensis	**p=0.4%; R=0.215**	**p=0.1%; R=0.225**	**p=0.1%; R=0.618**				
Sillago schomburgkii	**p=0.1%; R=0.918**	**p=0.1%; R=0.748**	**p=0.1%; R=0.587**	**p=0.1%; R=0.587**			
Sillago vittata	**p=0.1%; R=0.552**	**p=0.1%; R=0.475**	**p=1.1%; R=0.304**	**p=0.2%; R=0.174**	**p=0.3%; R=0.159**		
Ammotretis elongatus	**p=0.1%; R=0.925**	**p=0.1%; R=0.587**	**p=2.2%; R=0.296**	**p=0.1%; R=0.737**	**p=0.4%; R=0.441**	**p=1.0%; R=0.366**	
Pseudorhombus jenynsii	**p=0.2%; R=0.937**	**p=0.1%; R=0.739**	p=17.5%; R=0.152	**p=0.1%; R=0.630**	**p=0.1%; R=0.742**	**p=0.7%; R=0.408**	**p=0.8%; R=0.904**

Table 11.3 Dietary categories detected by SIMPER as those most responsible for distinguishing the diets of each pair of the eight fish species. The species for which each of these categories were more important as a dietary item is also provided (see superscripts; Sr=*Spratelloides robustus,* Ao=*Atherinomorus ogilbyi,* Lp=*Lesueurina platycephala,* Sb=*Sillago bassensis,* Ss=*Sillago schomburgkii,* Sv=*Sillago vittata,* Ae=*Ammotretis elongatus* and Pj=*Pseudorhombus jenynsii*).

	Spratelloides robustus	*Atherinomorus ogilbyi*	*Lesueurina platycephala*	*Sillago bassensis*	*Sillago schomburgkii*	*Sillago vittata*	*Ammotretis elongatus*
Atherinomorus ogilbyi	Calanoids(Sr) Adult formicids(Ao) Micromolluscs(Ao)						
Lesueurina platycephala	Calanoids(Sr) Polychaetes(Lp) Amphipods(Lp) Mysids(Lp) Cumaceans(Lp)	Calanoids(Ao) Harpacticoids(Ao) Amphipods(Lp) Mysids(Lp)					
Sillago bassensis	Calanoids(Sr) Polychaetes(Sb) Cladocerans(Sb)	Harpacticoids(Ao) Calanoids(Sb) Polychaetes(Sb)	Polychaetes(Lp) Amphipods(Lp) Mysids(Lp) Calanoids(Sb) Cladocerans(Sb)				
Sillago schomburgkii	Calanoids(Sr) Plant material(Sr) Polychaetes(Ss)	Calanoids(Ao) Polychaetes(Ss) Plant material(Ss)	Amphipods(Lp) Mysids(Lp) Cumaceans(Lp) Polychaetes(Ss) Plant material(Ss)	Calanoids(Sb) Cladocerans(Sb) Polychaetes(Ss) Plant material(Ss)			
Sillago vittata	Calanoids(Sr) Polychaetes(Sv) Cladocerans (Sv) Harpacticoids (Sv)	Calanoids(Ao) Polychaetes(Sv)	Amphipods(Lp) Mysids(Lp) Polychaetes(Sv) Cumaceans(Sv)	Calanoids(Sb) Polychaetes(Sv)	Plant material(Ss) Polychaetes(Sv) Calanoids(Sv)		
Ammotretis elongatus	Calanoids(Sr) Tanaids(Ae) Polychaetes(Ae) Cumaceans(Ae) Amphipods(Ae)	Calanoids(Ao) Tanaids(Ae) Cumaceans(Ae) Amphipods(Ae)	Polychaetes(Lp) Mysids(Lp) Tanaids(Ae) Amphipods(Ae) Cumaceans(Ae)	Calanoids(Sb) Tanaids(Ae) Polychaetes(Ae) Cumaceans(Ae) Amphipods(Ae)	Polychaetes(Ss) Tanaids(Ae) Cumaceans(Ae) Amphipods(Ae)	Polychaetes(Sv) Tanaids(Ae) Cumaceans(Ae) Amphipods(Ae)	
Pseudorhombus jenynsii	Calanoids(Sr) Crabs(Pj) Amphipods(Pj) Polychaetes(Pj) Carids(Pj)	Calanoids(Ao) Crabs(Pj) Amphipods(Pj) Polychaetes(Pj) Carids(Pj)	Polychaetes(Lp) Mysids(Lp) Crabs(Pj) Amphipods(Pj) Carids(Pj)	Calanoids(Sb) Crabs(Pj) Amphipods(Pj) Polychaetes(Pj)	Polychaetes(Ss) Crabs(Pj) Amphipods(Pj) Carids(Pj) Teleosts(Pj)	Polychaetes(Sv) Crabs(Pj) Amphipods(Pj) Teleosts(Pj)	Tanaids(Ae) Polychaetes(Ae) Cumaceans(Ae) Crabs(Pj) Amphipods(Pj)

Table 11.4 Eigenvalues and cumulative percentage variation explained by five principal components axes, using head and mouth measurements of *Spratelloides robustus, Atherinomorus ogilbyi, Lesueurina platycephala, Sillago bassensis, Sillago vittata, Sillago schomburgkii, Ammotretis elongatus* and *Pseudorhombus jenynsii.* Eigenvectors for each of seven measurements for each of the five principal components are shown, with the most important values for PC1 and PC2 being highlighted in boldface.

	Principal components axis				
	1	2	3	4	5
Eigenvalues	3.27	2.73	0.56	0.22	0.10
Cumulative variation (%)	46.7	85.7	93.7	96.8	98.3
Eigenvectors					
Head length	**0.510**	-0.200	0.061	0.151	-0.008
Premaxilla length	-0.102	**-0.564**	0.066	-0.506	0.531
Dentary length	-0.383	-0.331	0.482	0.598	0.274
Upper extension	**0.465**	-0.268	-0.158	0.513	0.003
Lower extension	0.363	**-0.426**	-0.207	-0.168	-0.014
Mouth width	**-0.405**	-0.155	-0.826	0.252	0.110
Mouth height	-0.265	**-0.505**	0.099	-0.094	-0.794

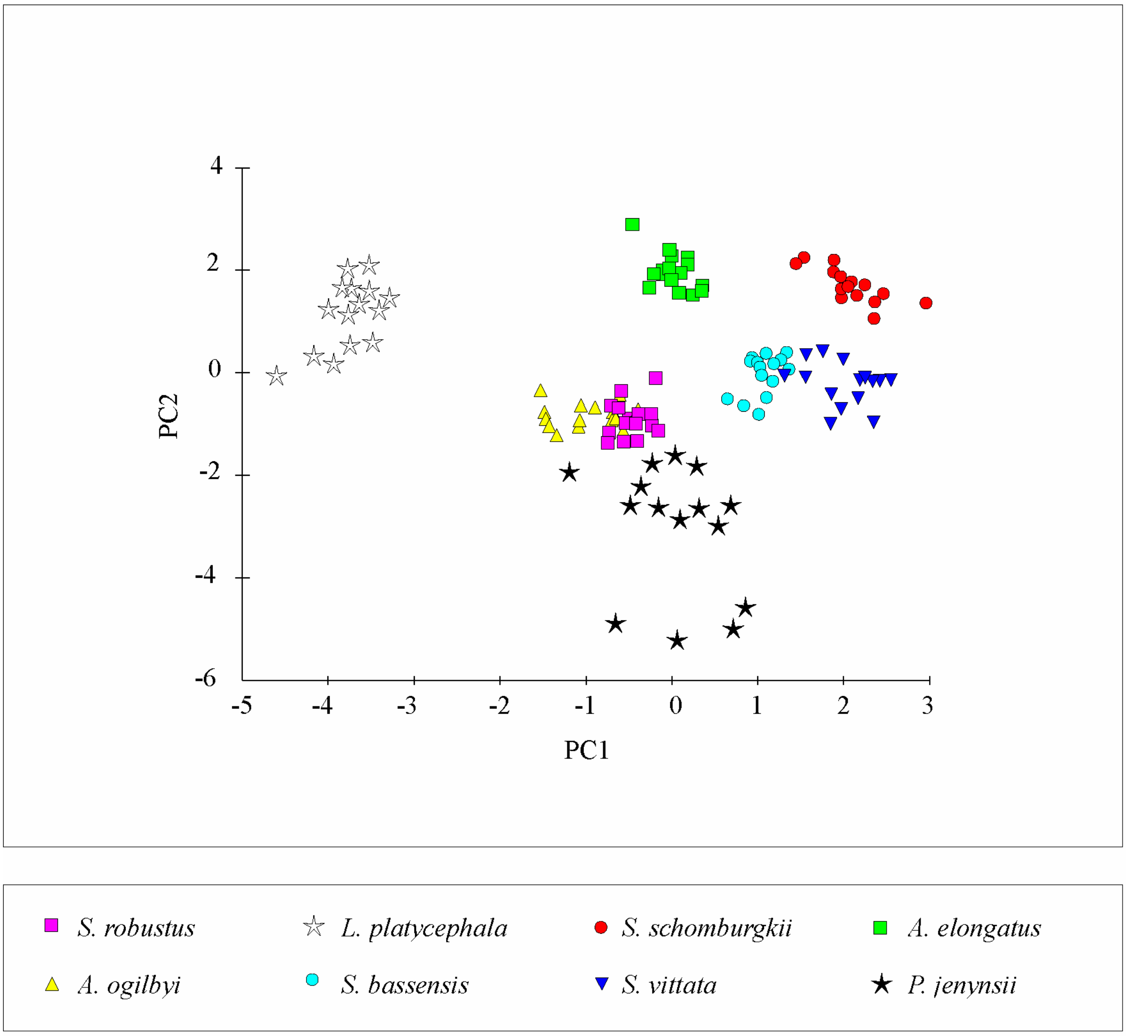


Figure 11.2: Plot of Axis 1 *vs* Axis 2 of the Principal Component Analysis of the head and mouth measurements of *Spratelloides robustus, Atherinomorus ogilbyi, Lesueurina platycephala, Sillago bassensis, Sillago schomburgkii, Sillago vittata, Ammotretis elongatus* and *Pseudorhombus jenynsii.*

Since species exerted the greatest effect on the dietary compositions, the next section presents results for each of the eight species separately to explore the influence of habitat type, season and/or time of day on the dietary compositions of those species.

11.3.2 Dietary composition of Spratelloides robustus

Two-way crossed ANOSIM showed that the dietary compositions of *S. robustus* differed significantly among both habitat types and seasons (p=0.1% in each case), with the global R-statistic value being greater for season than habitat type, *i.e.* 0.929 and 0.766, respectively. When the dietary samples for *S. robustus*, that were collected during the day, were subjected to ordination, all but one of the points for the dietary samples were located on the extreme right-hand side of the plot. The sole exception was a single point which lay to the extreme left and represented that of fish caught at habitat type 1 in winter (see insert box in Fig. 11.3). Thus, the data were re-ordinated without those for this latter sample.

On the resultant ordination plot, eight of the ten samples from habitat type 2 then formed a dispersed group on the right side of the plot that was separate from those of habitat type 6 and habitat type 1 (Fig. 11.3). Within this group of eight dietary samples, there was a small group containing the three autumn samples which was discrete from the group containing the five samples from summer. The points for the dietary samples from habitat type 6, which all came from autumn, formed a discrete and very tight group in the upper left-hand corner of the plot, largely to the left of the five samples from habitat type 1, which also came entirely from autumn, and also the two winter samples from habitat type 2 (Fig. 11.3). Pairwise ANOSIM demonstrated that the dietary compositions of *S. robustus* differed significantly amongst each pair of habitat types (p=0.6-1.8%) and between each pair of seasons (p=0.8-1.8%). Note that because there was only a single sample for winter, it was not included in these later analyses.

SIMPER showed that the single and highly atypical dietary sample, representing the diets of three individuals of *S. robustus* from habitat type 1 in winter (see insert in Fig. 11.3), differed from all other dietary samples in that it consisted exclusively of ostracods, gastropods, polychaetes and harpacticoid copepods, rather than predominantly or exclusively calanoid copepods. The differences between the dietary samples from habitat type 2 and habitat type 6 were due to the relatively greater volumes of cladocerans ingested by *S. robustus* at habitat type 6 and of siphonophores at habitat type 2. Siphonophores and cladocerans were more prevalent in the diets of *S. robustus* in autumn than summer, the two seasons for which there were several samples, whereas the reverse pertained with harpacticoid copepods.

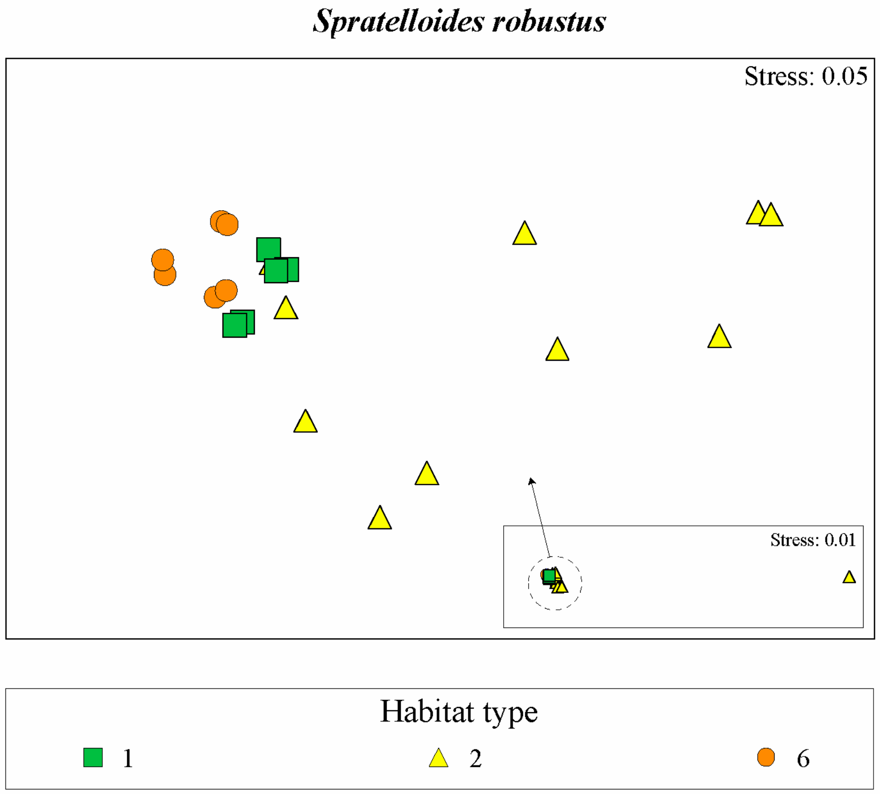


Figure 11.3: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of *Spratelloides robustus* recorded during the day coded for habitat type.

11.3.3 Dietary composition of Atherinomorus ogilbyi

One-way ANOSIM showed that the diets of *A. ogilbyi* were significantly influenced by time of day, *i.e.* day *vs* night (p=0.1%, Global R=0.648), season (p=0.1%, Global R=0.445) and habitat type (p=0.2%, Global R=0.149). Since the R-statistic value was greatest for time of day, the dietary samples on the MDS ordination plot are coded by day and night (Figure 11.4a), with the points for each of day and night lying in two relatively discrete groups on the plot. SIMPER demonstrated that greater volumes of calanoids were consumed during the day than night, while the reverse was true for amphipods. As the diets were influenced most by time of day, focus was then placed on determining the influence of season and habitat type on the diet of *A. ogilbyi* during both the day and night separately.

Ordination of the dietary data for *A. ogilbyi* during the day showed that the dietary samples formed groups according to both season and habitat type (Fig. 11.4b, c). Two-way crossed ANOSIM tests showed that the diets of *A. ogilbyi* during the day differed significantly both amongst seasons (p=0.1%, Global R=0.777) and habitat types (p=0.1%, Global R=0.657), with pairwise tests indicating that the diets in summer 2001 and summer 2002 were significantly different (p=0.1%, R=0.719). SIMPER showed that *A. ogilbyi* consumed relatively more cladocerans and less calanoid copepods in summer 2001 than summer 2002. Although there were insufficient permutations among the other pairwise seasonal comparisons to be confident of the results of ANOSIM, the R-statistic values for each of those comparisons were 1, which implies that the dietary compositions did vary markedly between those seasons. Pairwise ANOSIM comparisons for habitat type showed that the diets of *A. ogilbyi* at habitat type 2 differed significantly from those at both habitat type 1 (p=0.8%, R=0.869) and habitat type 6 (p=0.1%, R=0.739). SIMPER demonstrated that, during the day, the diets of *A. ogilbyi* at habitat type 2 were distinguished from those at the other two habitat types by the predominance of calanoid copepods and cladocerans.

MDS ordination of the dietary data for *A. ogilbyi* at night showed that the dietary samples tended to fall into groups according to both habitat type and season (*cf* Figures 11.4d and e). The diets differed significantly amongst both seasons (p=0.1%, Global R=0.881) and habitat types (p=0.2%, Global R=0.860). Since *A. ogilbyi* was only recorded at two habitat types (habitat type 1 and 2) during the night, the overall significant difference between habitat types means that the dietary compositions of this species differed between those two habitat types. The dietary samples from habitat type 2 contained relatively greater amounts of amphipods and polychaetes and lesser amounts of calanoid copepods and cumaceans than those at habitat type 1. For season, all pairwise ANOSIM comparisons were significant when a sufficient number of permutations could be calculated, *i.e.* in all seasons except summer 2001. However, the R-statistic values for all comparisons involving this season were 1, implying that there were also large differences between the dietary compositions in this season and the other seasons. SIMPER demonstrated that the dietary compositions of *A. ogilbyi* in autumn differed from those in winter, spring and summer 2002 by the consistently lower proportion of amphipods. Furthermore, the diets in winter differed from those in spring and summer 2002 by the relatively greater contributions of mysis larvae and lower contribution of mysids. The diets of *A. ogilbyi* in summer 2002 also contained a relatively greater contribution of polychaetes than in the preceding spring.

Atherinomorus ogilbyi

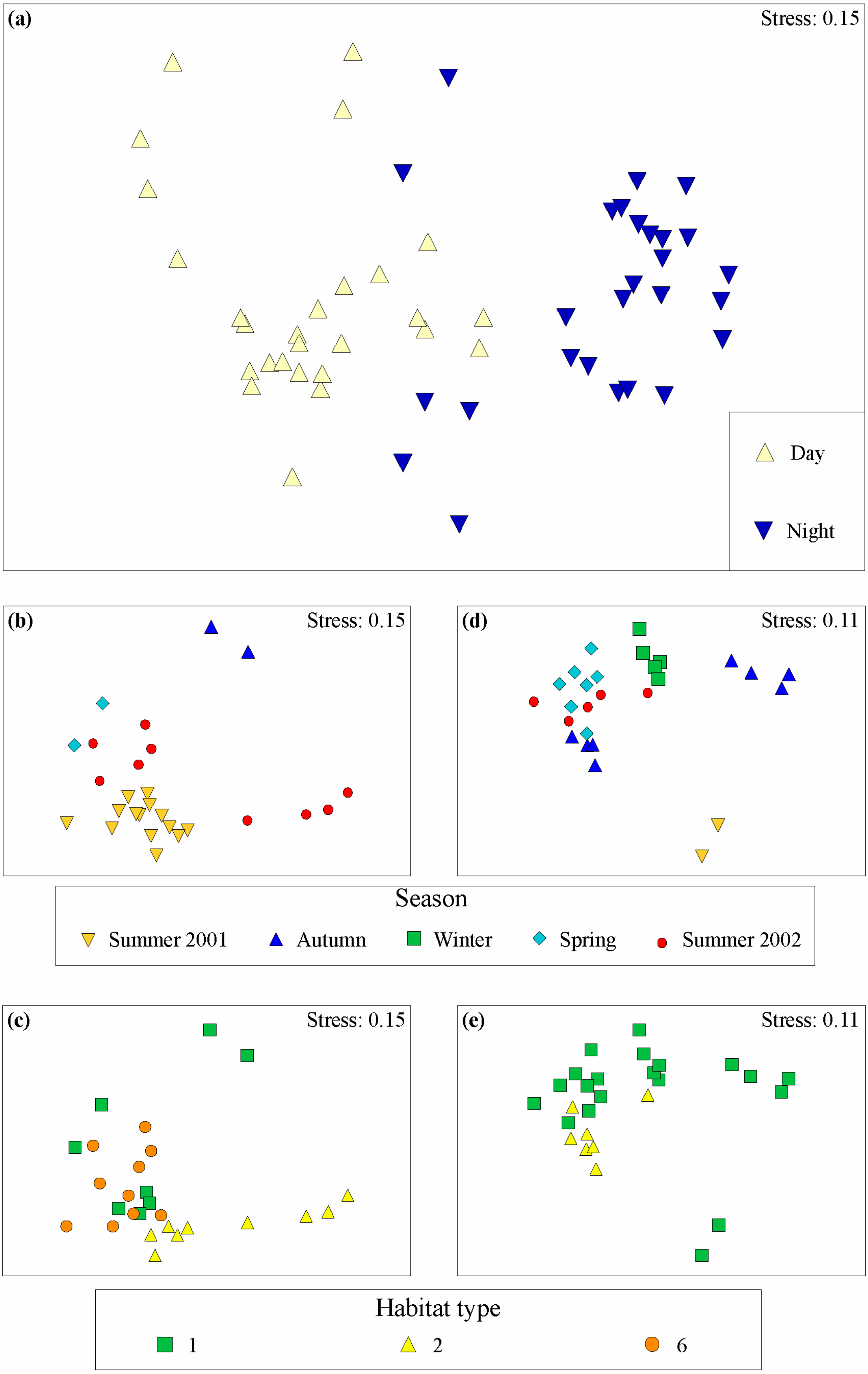


Figure 11.4: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of *Atherinomorus ogilbyi*, recorded during the day and night, coded for (a) time of day. Following separation of the dietary data by time of day, the data were re-ordinated, with the dietary samples during the day coded for each (b) season and (c) habitat type and those during the night coded for each (d) season and (e) habitat type.

11.3.4 Dietary composition of Lesueurina platycephala

One-way ANOSIM demonstrated that the dietary compositions of *Lesueurina platycephala* at the two habitat types at which this species was recorded (habitat types 2 and 6) did not differ significantly among habitat type, season or time of day (p>5%) and the R-statistic value for each of these three factors was low, *i.e.* ranged from -0.090 to 0.141. This is consistent with the lack of any clear separation on the ordination plot between the dietary samples for the different habitat types (Fig. 11.5), seasons and time of day (data not shown).

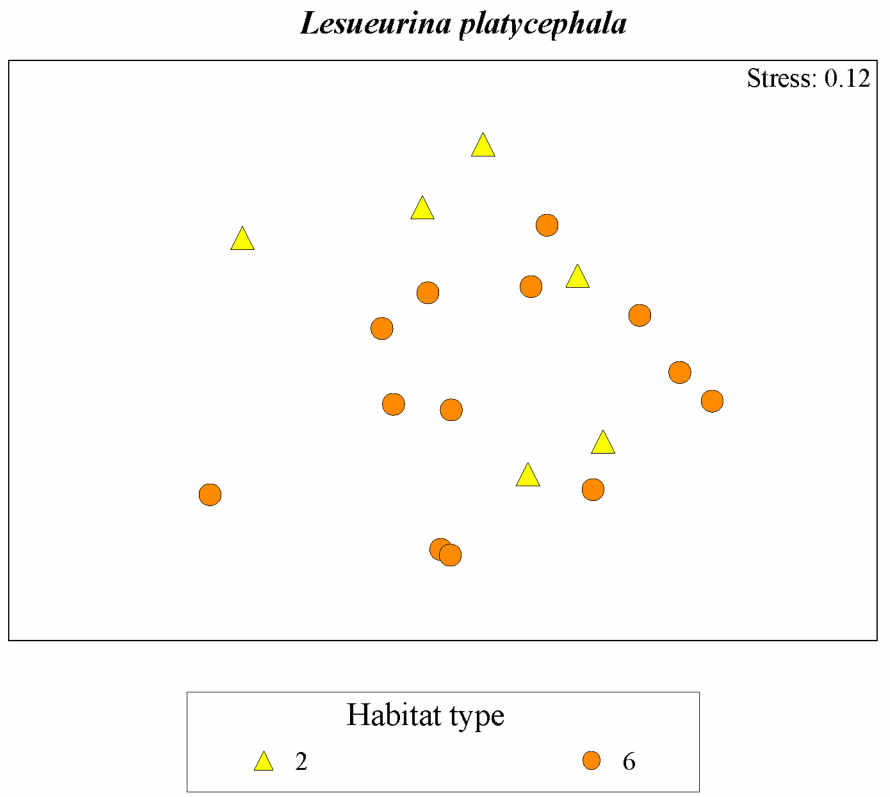


Figure 11.5: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of *Lesueurina platycephala* recorded during both the day and night, coded for habitat type.

11.3.5 Dietary composition of Sillago bassensis

Two-way crossed ANOSIM demonstrated that the dietary compositions of *S. bassensis* differed significantly both with habitat type and season (p=0.1%), with the global R-statistic value being greater for habitat type (0.931) than season (0.796). Following ordination of the volumetric dietary data for *S. bassensis,* the points representing the dietary samples for fish collected at habitat type 2 formed a discrete band that lay horizontally in the upper half of the plot (Fig. 11.6a). The points representing samples from habitat type 6 mainly lay in a tight group along the vertical midline of the plot while the single point for the sample from habitat type 1 lay to the right of all points but one of those for habitat type 2. When the dietary data was re-ordinated separately for habitat types 2 and 6 and the dietary samples were coded for season, it was evident that, for habitat type 2, the points for the samples collected during winter formed a very discrete group to the left of those for summer and autumn (Fig. 11.6b). On the right half of the plot, the points for summer lay mostly above those for autumn. In the case of habitat type 6, the points for the summer samples formed a group that lay to the left of those for autumn, which lay above those for spring (Fig. 11.6c). Pairwise ANOSIM comparisons demonstrated that the dietary compositions of *S. bassensis* at habitat type 2 and 6 were significantly different (p=0.1%) and that they differed significantly between summer, autumn and spring (p=0.1%) at habitat types 2 and 6.

Although *S. bassensis* consumed relatively large volumes of calanoid copepods at both habitat type 2 and habitat type 6, SIMPER emphasised that this species also ingested relatively greater volumes of teleosts and relatively lower volumes of cladocerans at the former than latter habitat type. SIMPER also revealed that the seasonal changes in the diet of this species at habitat type 2 were due to the greater volumes of teleosts and lower volumes of calanoid copepods ingested in spring than in summer and autumn, and the greater volumes of bivalves and lower volumes of calanoid copepods that were ingested in autumn than in summer. The seasonal changes in the diet of *S. bassensis* at habitat type 6 were attributable to the consumption of relatively greater volumes of cladocerans in summer, carid decapods in autumn and teleosts in spring.

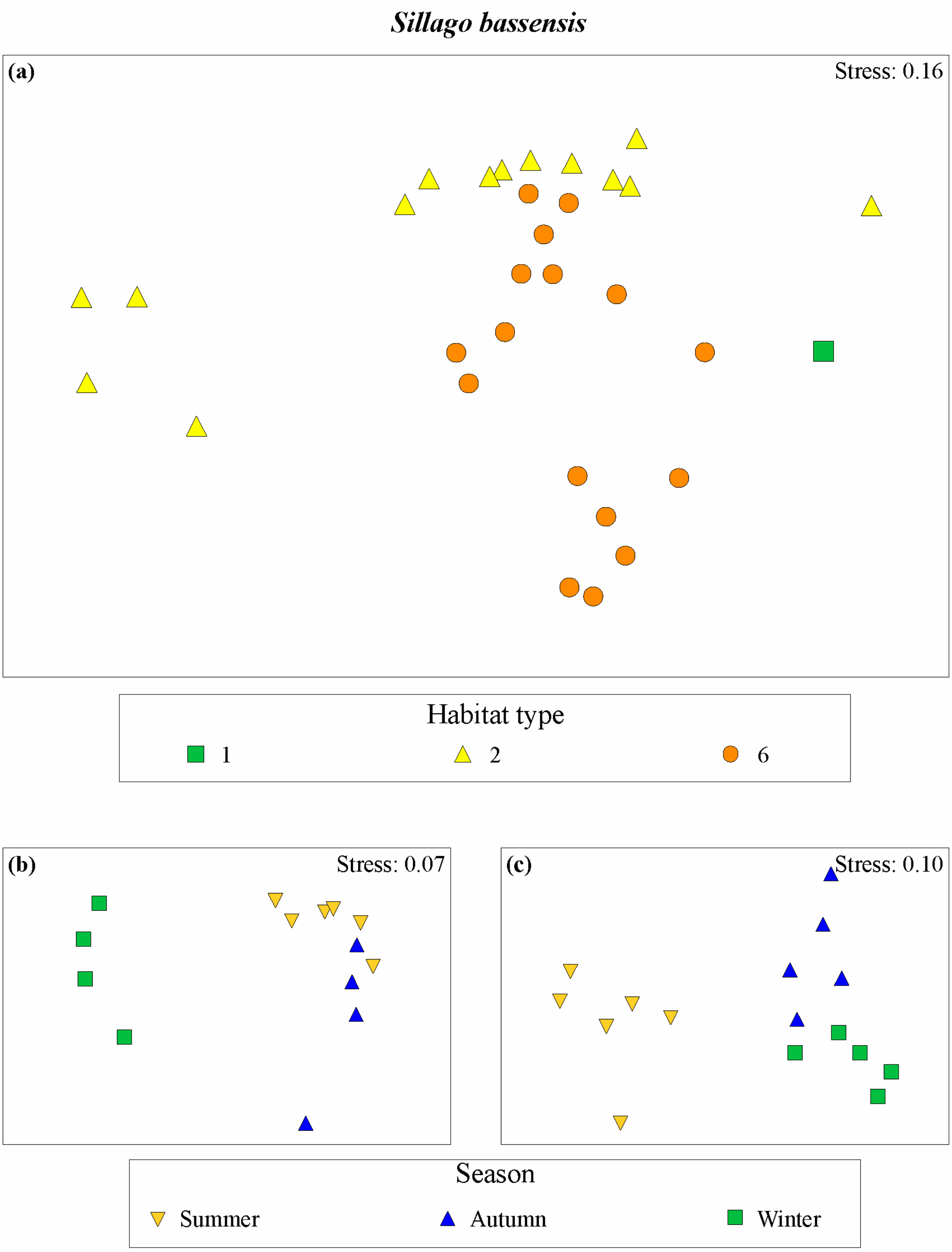


Figure 11.6: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of *Sillago bassensis* recorded during the day and coded for (a) habitat type. Following separation of the dietary data by habitat type, the data were re-ordinated, with the dietary samples at (b) habitat type 2 and (b) habitat type 6 being coded for season.

11.3.6 Dietary composition of Sillago schomburgkii

One-way ANOSIM demonstrated that the dietary composition of *S. schomburgkii* was influenced more by habitat type (p=0.1%, Global R=0.350) than by season (p=0.1%, Global R=0.226) or day *vs* night (p=3.5%, Global R=0.093). Thus, when the dietary data for *S. schomburgkii* were ordinated and the dietary samples coded for habitat type, the vast majority of the samples for habitat type 1 formed a group that was discrete from the two samples of habitat type 6, while the points for habitat type 2 were far more widely distributed over the plot (Fig. 11.7a). Pairwise ANOSIM showed that the dietary compositions at habitat type 1 differed significantly from those at both habitat type 2 and habitat type 6 (p=0.1%, R=0.344 and p=2.9%, R=0.534, respectively). SIMPER showed that the diets at habitat type 1 contained relatively greater volumes of polychaetes and relatively lower amounts of bivalves and plant material than those at habitat type 2, while greater amounts of teleosts and oligochaetes were present in the diet at habitat type 6.

The dietary samples for *S. schomburgkii* at the two habitat types for which there were sufficient data, *i.e.* habitat types 1 and 2, were subjected to analysis separately to assess the relative influence of season and time of day at those two habitat types on the diets of this sillaginid. The dietary samples for *S. schomburgkii* at habitat type 1 showed no tendency to separate by time of day (data not shown) but, when those samples were coded for season, the samples for three of the four seasons formed relatively tight groups on the ordination plot (Fig. 11.7b). Two-way crossed ANOSIM showed that, while the dietary composition of *S. schomburgkii* at habitat type 1 did not vary between day and night (p=10.0%), it did differ amongst seasons (p=1.8%, Global R=0.382). For the pairwise seasonal comparisons, sufficient dietary samples were present to compare only one pair of seasons, *i.e.* spring and summer 2002, which were shown to significantly differ (p=1.4%, R=0.652), SIMPER showed that greater amounts of plant material were present in the diets during spring, while bivalves were more important in the diets of this sillaginid during summer 2002.

The samples for day and night on the ordination plot for the dietary compositions of *S. schomburgkii* at habitat type 2 were both widely distributed (data not shown). However, when the samples were coded for season, the samples for some of the seasons formed relatively discrete groups on the plot (Fig. 11.7c). Two-way crossed ANOSIM showed that the diets of *S. schomburgkii* at habitat type 2 differed significantly overall with season (p=0.1%, Global R=0.666), but not between day and night (p=17.5%). Pairwise comparisons showed that the diets significantly differed between each pair of seasons (p=0.1–2.9%, R=0.512–1.000),

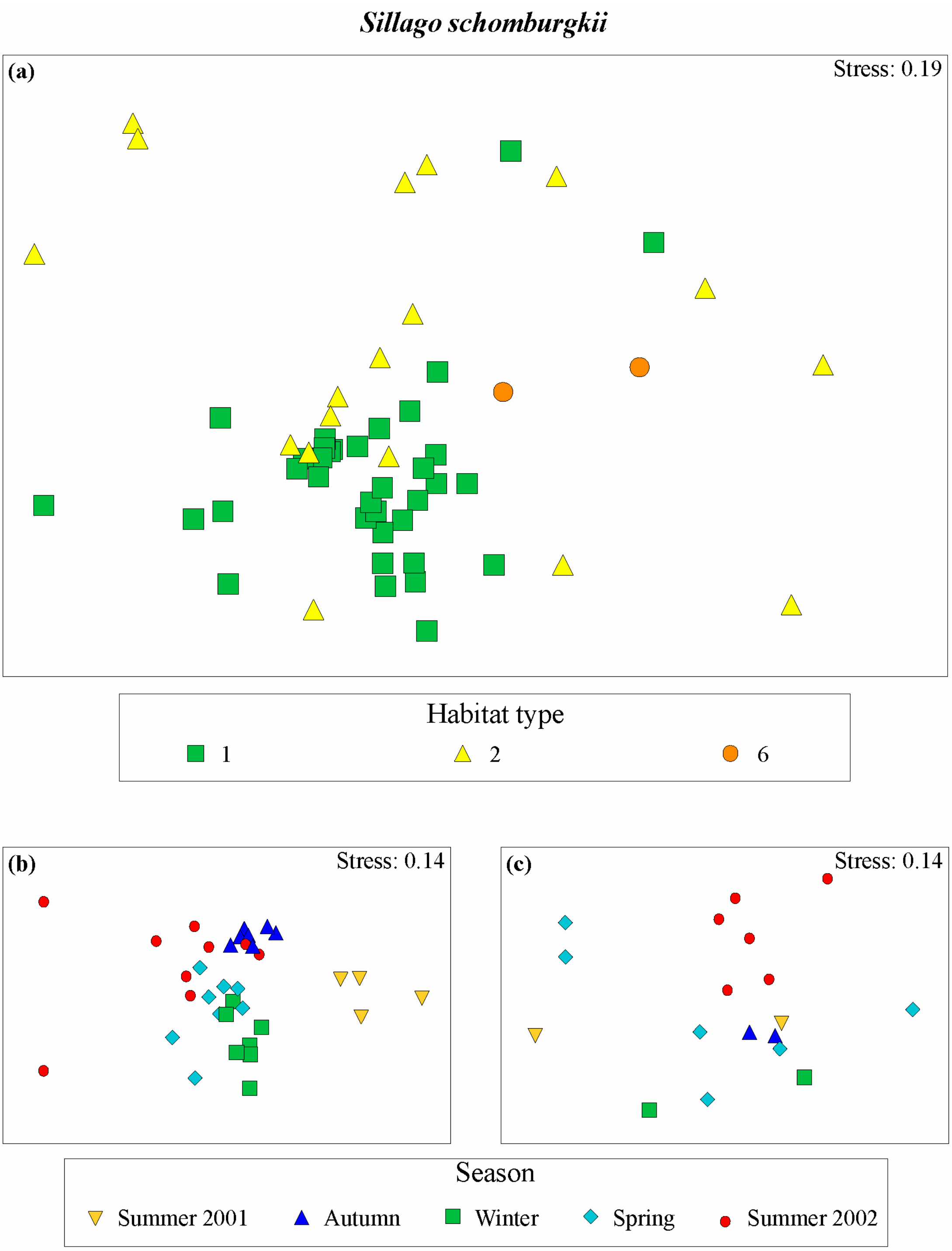


Figure 11.7: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of *Sillago schomburgkii* recorded during the day and night coded for (a) habitat type. Following separation of the dietary data by habitat type, the data were re-ordinated, with the dietary samples at (b) habitat type 1 and (c) habitat type 2 being coded for season.

except for spring *vs* winter and spring *vs* summer 2002. The diets of *S. schomburgkii* in summer 2001, autumn, winter, spring and summer 2002 were shown by SIMPER to be characterised by harpacticoid copepods, polychaetes, tanaids, amphipods and oligochaetes, respectively.

11.3.7 Dietary composition of Sillago vittata

Two-way crossed ANOSIM showed that the dietary compositions of *S. vittata* differed significantly among both habitat types and seasons (p=0.1% in each case), and the global R-statistic values of 0.771 and 0.662, respectively, showed that there was good separation amongst both of these factors. Ordination of the dietary data for *S. vittata* resulted in a complete separation of the points for the dietary samples from the three habitat types, with those for habitat type 6 lying at the extreme left-hand side of the plot and those for habitat type 1 lying largely above those for habitat type 2 (Fig. 11.8d). When the data was ordinated separately for those *S. vittata* at habitat types 1 and 2, the points for the different seasons formed discrete groups on the ordination plot, with those for summer, autumn and spring lying on the left side of the plot, and to the right of the group of winter samples (Fig. 11.8b,c). ANOSIM also demonstrated that the dietary compositions of *S. vittata* differed significantly amongst each pair of habitat types (p=0.1-0.2%) and between fish from each pair of seasons (p=0.1-2.9%) at habitat types 1 and 2.

SIMPER revealed that *S. vittata* typically consumed relatively greater volumes of polychaetes at habitat type 1, calanoid copepods and teleosts at habitat type 2 and cladocerans at habitat type 6. Although the diets were typified by teleosts and cumaceans in spring, at habitat type 1, the diets were typified by polychaetes in summer, autumn and winter, while at habitat type 2, the diets of *S. vittata* were typified mainly by both calanoid copepods and cladocerans in summer, and calanoids and polychaetes.

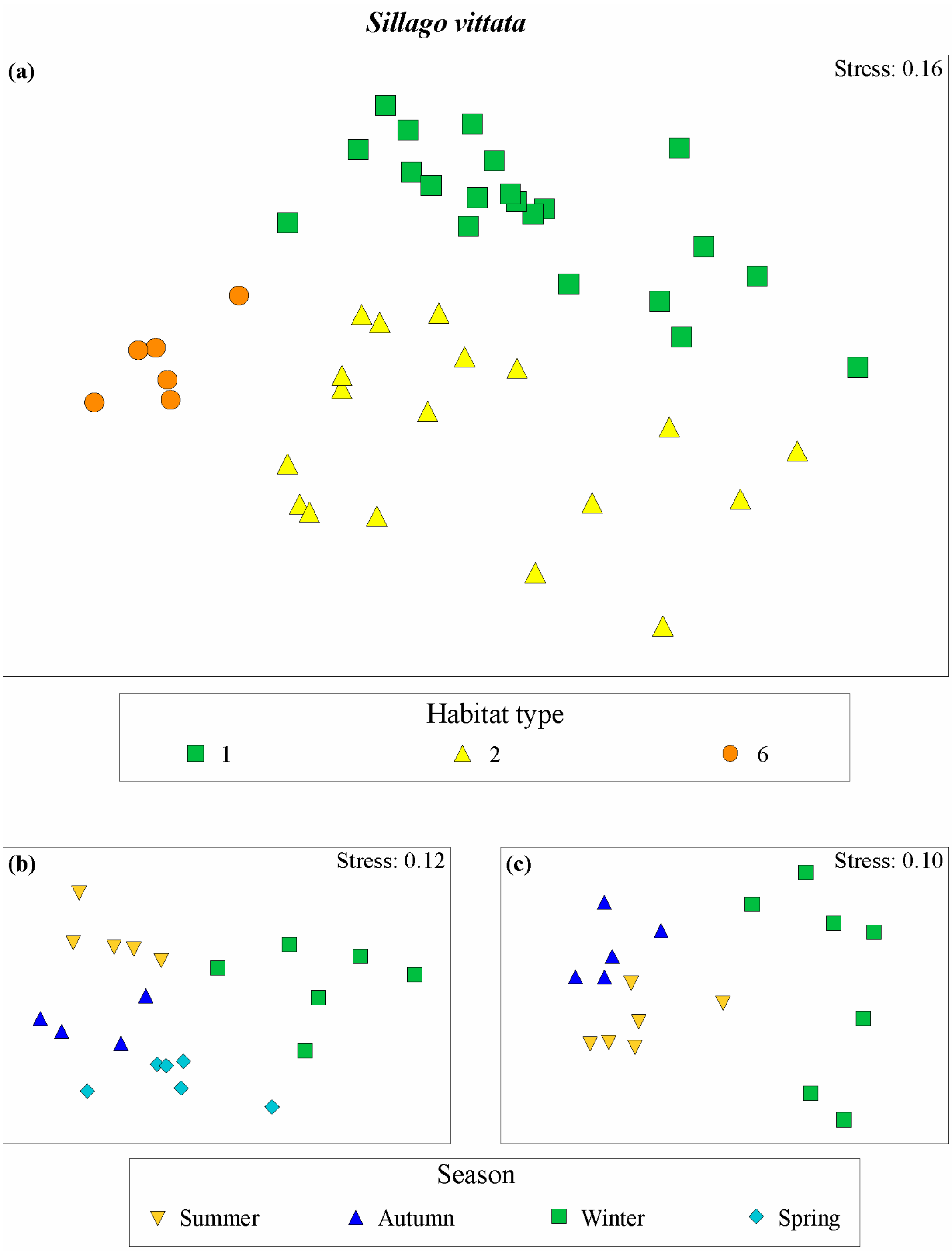


Figure 11.8: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of *Sillago vittata* coded for (a) habitat type. Following separation of the dietary data by habitat type, the data were re-ordinated, with the dietary samples at (b) habitat type 1 and (c) habitat type 2 being coded for season.

11.3.8 Dietary composition of Ammotretis elongatus

The dietary samples of the pleuronectid *A. elongatus*, which was only well represented in two seasons at habitat type 1, were insufficient to conduct ANOSIM analysis. MDS ordination of the dietary samples, with the points being coded for both season and time of day, demonstrated that the three points for spring lay to the right of those for summer 2002 and that that the two nighttime samples lay close together on the upper left part of the plot and away from the large aggregation of daytime samples (Fig. 11.9a). SIMPER showed that cumaceans were more important than tanaids in the diets of *A. elongatus* in spring while the reverse was true for summer 2002.

11.3.9 Dietary composition of Pseudorhombus jenynsii

This bothid, which was only recorded in abundance at habitat type 1 and whose diets were examined during the day, was collected in insufficient numbers in each of the different seasons to justify analysis using ANOSIM. However, all of the six points for the dietary samples for *P. jenynsii* in summer lay in the centre of the plot, to the left of the point for the single spring sample and to the right and/or below the two dietary samples for autumn (Fig. 11.9b). SIMPER showed that mysids were more important in the diets of *P. jenynsii* in summer than autumn, while the reverse was the case with crabs and polychaetes.

11.3.10 Size-related changes in the diets of the eight species at different habitat types

In the case of *S. robustus*, calanoid copepods constituted at least 94% by volume to the gut contents of each size class at habitat type 6, each of the four size classes between 30 and 70 mm at habitat type 2, and the group of fish >60 mm in length at habitat type 1 (Fig. 11.10). Cladocerans were found in the diets of all four size classes at habitat type 6 and contributed as much as 17% to those of the largest fish at habitat type 2. Although siphonophores (coded as other taxa in Fig. 11.10) were found in the diets of two of the four size classes at habitat type 6 and three of those at habitat type 2, their contribution only exceeded 5% in the case of the largest fish at the latter habitat type. In marked contrast to the situation described for all size classes at habitat type 6 and habitat type 2 and the two largest size classes at habitat type 1, the diets of the 40-49 and 50-59 mm size classes of *S. robustus* at habitat type 1 contained substantial volumes of ostracods, *i.e.* 89 and 32%, respectively, and gastropods, *i.e.* 11% in both cases (Fig. 11.10).

During the daytime, the smaller representatives of *A. ogilbyi, i.e.* <40 and 40-59 mm, ingested large volumes of calanoid copepods at habitat type 1, with the contribution of this prey undergoing a substantial decline in fish of greater than this size (Fig. 11.11). In the larger *A. ogilbyi* (>60 mm), their diet comprised large amounts of other taxa (mainly plant material and terrestrial arachnids) and insects, with smaller contributions being made by tanaids and

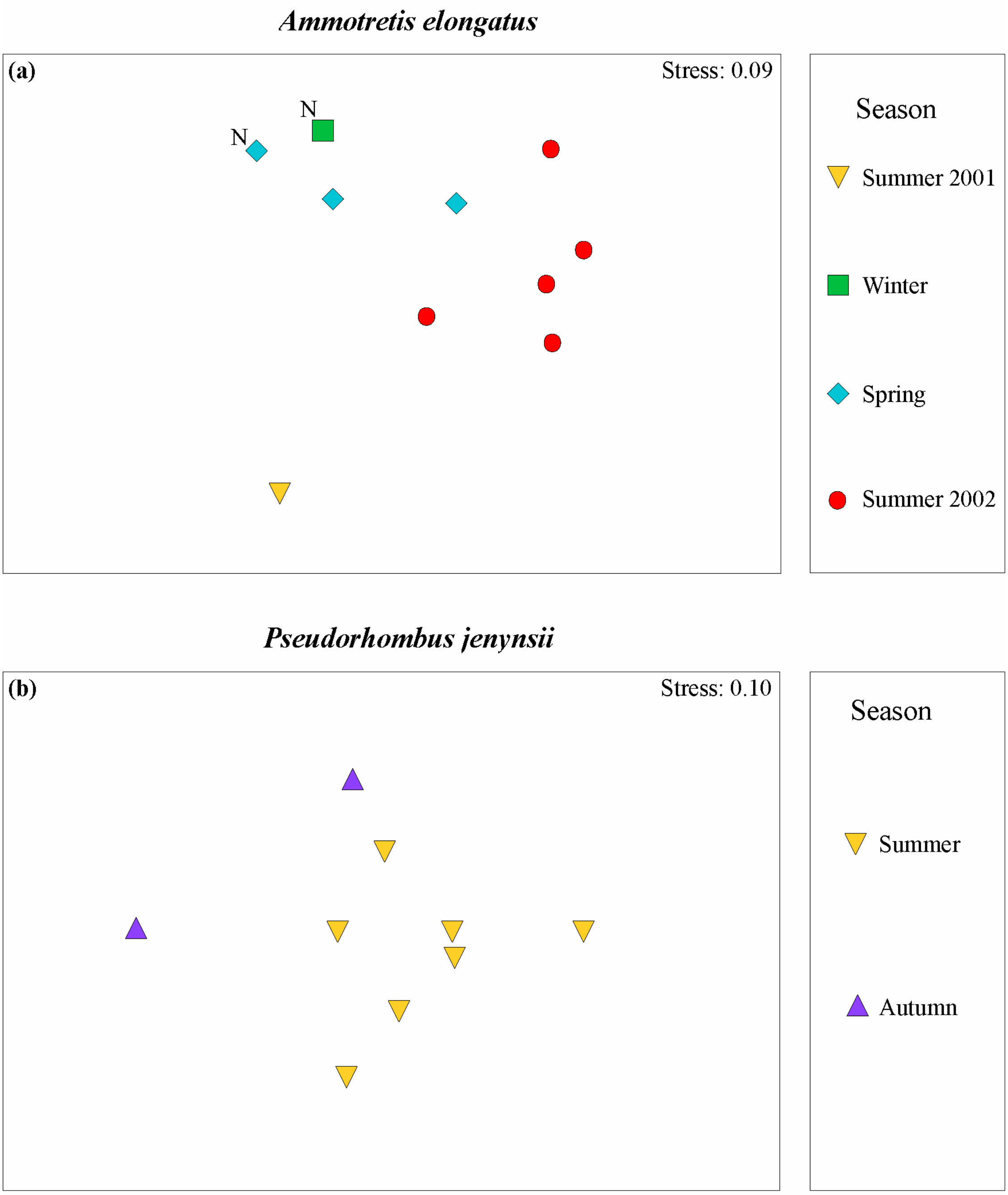


Figure 11.9: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of groups of three individuals of (a) *Ammotretis elongatus* and (b) *Pseudorhombus jenynsii*, coded for season. "N" denotes that dietary samples were recorded during the night.

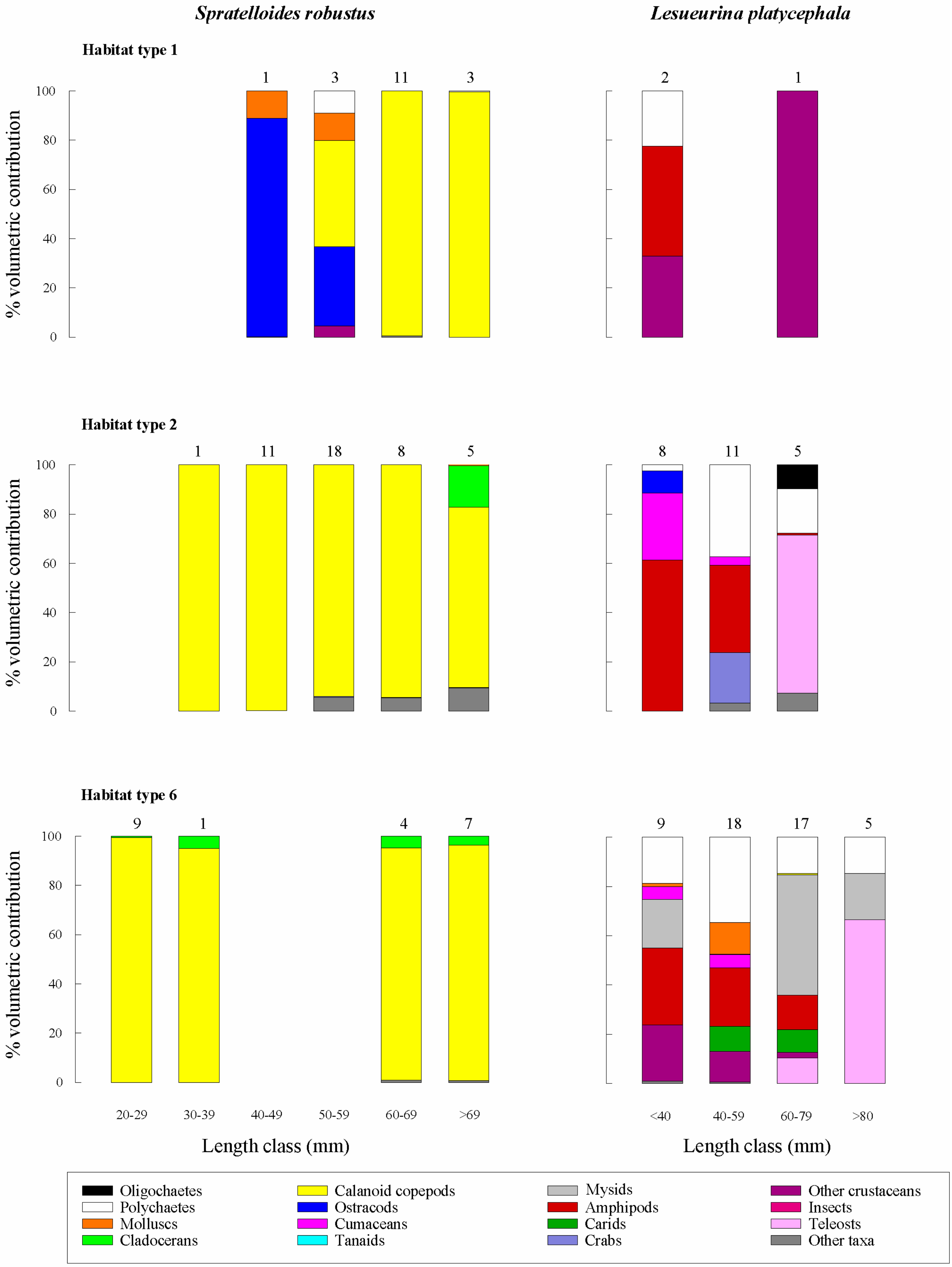


Figure 11.10: Mean percentage volumetric contributions of the 16 broad prey groups to the diets of sequential length classes of *Spratelloides robustus* and *Lesueurina platycephala* during the day and night collectively. Note that, in this Figure and Figs 11.10 - Fig. 11.12, the number of individuals of each size class that contained identifiable food in their guts is shown above each histogram.

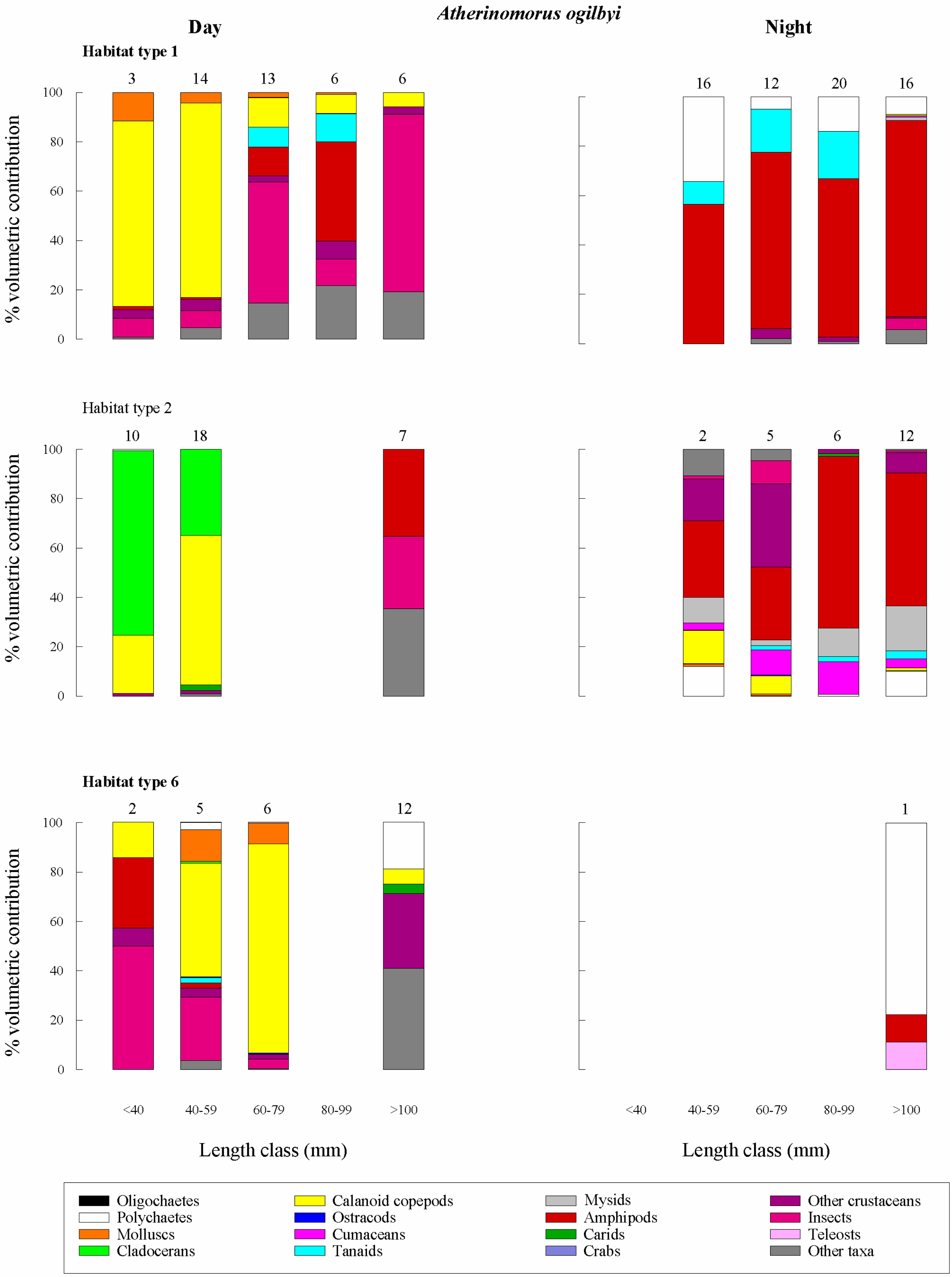


Figure 11.11: Mean percentage volumetric contributions of the 16 broad prey groups to the diets of sequential length classes of *Atherinomorus ogilbyi* during both the day and night separately.

amphipods. Although small *A. ogilbyi* likewise ingested calanoids at habitat types 2 and 6 during the day, the contribution of this prey initially increased with increasing body size, *i.e.* from *ca* 17% in fish of <40 mm to nearly 90% in fish of 60-79 mm at habitat type 6, and declined thereafter (Fig. 11.11). The larger fish at habitat types 2 and 6 also ingested large amounts of other taxa (plant material and terrestrial arachnids) and insects and polychaetes also each contributed *ca* 15% to the diet of the largest individuals, *i.e.* >100 mm, at habitat type 6. During the night, the different size classes of *A. ogilbyi* at habitat types 1 and 2 each ingested amphipods to at least a moderate extent, while taxa such as mysids, calanoids, tanaids and polychaetes made small contributions to the diets of most of these size classes (Fig. 11.11).

The diets of *L. platycephala* of less than 40 mm in length at habitat types 2 and 6 comprised varying amounts of polychaetes, cumaceans and amphipods, and this species also consumed ostracods at habitat type 2, while at habitat type 6 it also ingested mysids (Fig. 11.10). As the fish increased in size, the contributions of polychaetes showed no tendency to increase or decrease with increasing fish size at both habitat types. However, the contributions of amphipods declined as fish grew larger and only the larger fish consumed teleosts, with this dietary category contributing *ca* 70% to the largest size class at the two habitat types (Fig. 11.10).

The diet of small *S. bassensis* at habitat type 6, *i.e.* those <50 mm in length, consisted almost exclusively of small planktonic prey, *i.e.* calanoid copepods and cladocerans, whereas that of the largest fish, *i.e.* 100-169 mm, was dominated by more benthic prey, such as polychaetes and carid shrimps (Fig. 11.12). In contrast, although the type and size of prey ingested by *S. bassensis* also changed with increasing fish size at habitat type 2, the gut contents of the smallest fish at this habitat type consisted exclusively of calanoid copepods, and those of the largest fish contained a substantial volume of teleosts as well as polychaetes. The decline in the contribution of calanoid copepods to the diet of this species with increasing body size was particularly pronounced at habitat type 2, where it declined progressively from 99.8% in the smallest fish to 19.4% in the largest fish (Fig. 11.12).

The smallest *S. schomburgkii, i.e.* <100 mm, consumed other crustaceans (mainly harpacticoid copepods), polychaetes and tanaids at habitat type 1 while, at habitat type 2, the diets of this sillaginid were instead dominated by mysids, calanoid copepods and polychaetes (Fig. 11.12). As *S. schomburgkii* increased in size at habitat type 1, the contribution of polychaetes increased markedly to *ca* 90% and then gradually declined to *ca* 60% in the largest fish at this habitat type. Although a similar trend was present for polychaetes at habitat type 2, their overall contributions were much less and the diets of the largest fish were dominated by teleosts. The two large size classes of fish at habitat type 6 mainly ingested polychaetes, oligochaetes and teleosts (Fig. 11.12).

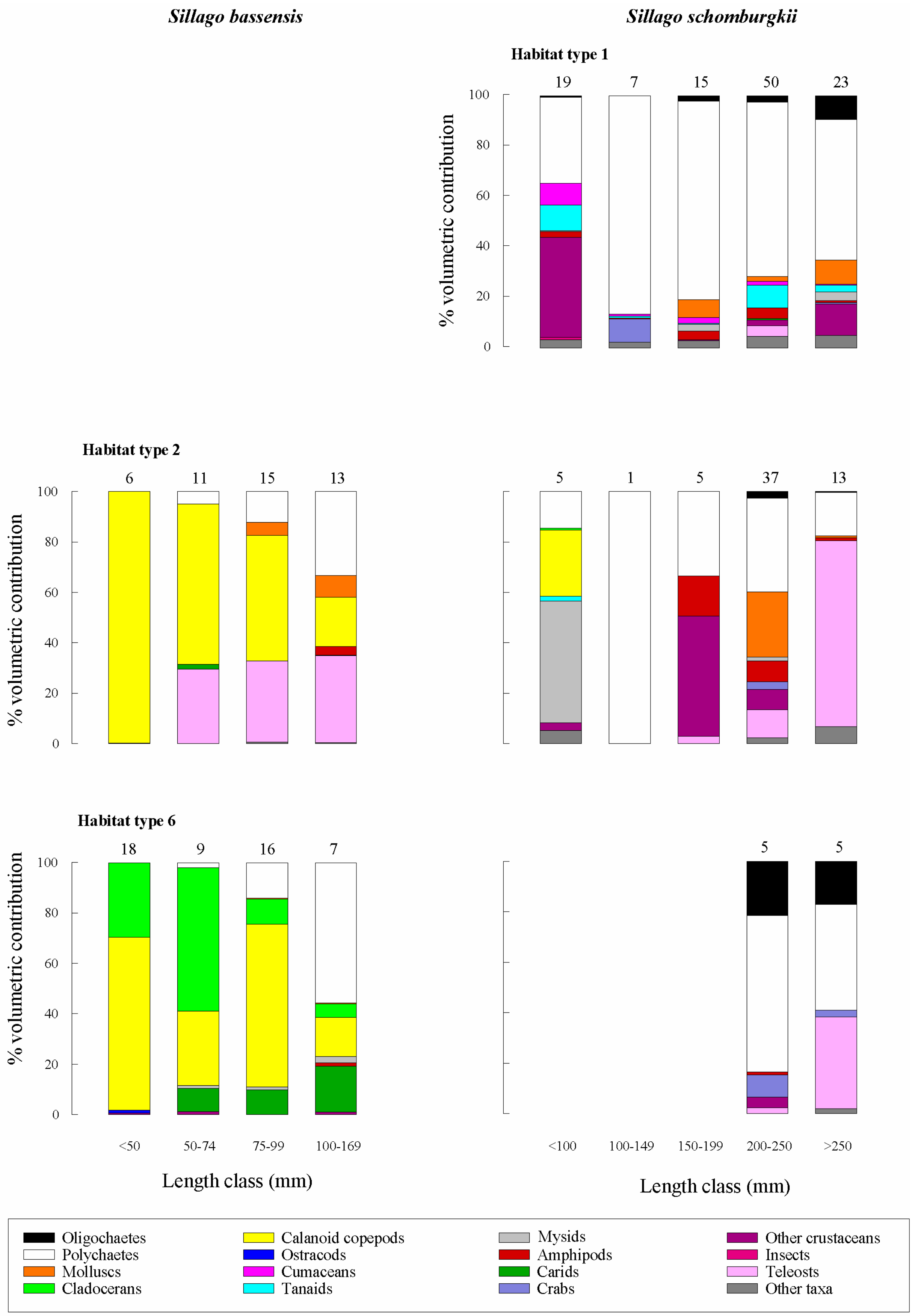


Figure 11.12: Mean percentage volumetric contributions of the 16 broad prey groups to the diets of sequential length classes of *Sillago bassensis* and *Sillago schomburgkii* during the day and night collectively.

The compositions of the diets of the *S. vittata* <50 mm differed markedly among habitat types, with that at habitat type 1 comprising almost exclusively polychaetes (50%), harpacticoid copepods (30%) and cladocerans (17%), and those at habitat type 6 and habitat type 2 consisting predominantly of cladocerans (87%) and calanoid copepods (95%), respectively (Fig. 11.13). At habitat type 2, the contribution of calanoid copepods to the diets of *S. vittata* declined from 95% in fish <50 mm in length to less than 1% in the 100-169 mm size class and this dietary category was not found in the diets of the largest fish, whereas teleosts were not found in the diets of small fish and contributed as much as 24% in the 100-169 mm size class and 70% in fish >169 mm. In contrast to the situation with *S. vittata* that are greater than 50 mm in length at habitat type 2, the comparable-sized individuals of this species at habitat type 1 ingested substantial amounts of polychaetes and the contribution made by cumaceans to the diet of fish in the 100-169 mm size class at this habitat type was greater (Fig. 11.13).

The diets of nearly all size classes of *A. elongatus* at habitat type 1 contained cumaceans, with the contributions of this taxa being relatively high, *i.e. ca* 60% in fish of <40 mm, and which then gradually declined to *ca* 14% in fish of 80-99 mm (Fig. 11.13). Polychaetes, tanaids and amphipods were also ingested by the different size classes of this pleuronectid, but showed no conspicuous tendency to either increase or decrease with increasing fish size.

The gut contents of all size classes of *P. jenynsii* at habitat type 1 contained substantial volumes of crabs, *i.e.* 19-36% (Fig. 11.13), comprising zoea, megalopae and juveniles. However, those of length classes <75 mm were otherwise dominated by mysids (36-49%) and polychaetes (17-19%), whereas those of larger fish contained substantial volumes of teleosts (33-78%).

11.3.11 Ordinations of size-related changes in the diets of the eight species at different habitat types

The mean volumetric data for the different size classes of the four species that were captured at each of the three habitat types (*S. robustus, A. ogilbyi* during the day*, S. schomburgkii* and *S. vittata)*, keeping the data separate for each species, were first subjected to MDS ordination, on which the dietary samples on the resultant plots were coded for habitat type and size class of fish. Thus, when the data was ordinated for *S. robustus*, the points for the 40-49 and 50-59 mm size classes of this species from habitat type 1 lay on the left of the plot and were particularly discrete from the remaining samples, which formed a very tight group on the other side of the plot (insert on Fig. 11.14a). When the data were re-ordinated, this time excluding the data for those two points, the largest *S. robustus* from habitat type 1, representing the 60-69 and >69 mm size classes of this species, lay on the far left of the plot, close to those of the smallest size classes of fish at habitat types 2 and (Fig. 11.14a). As this species increased in size, the

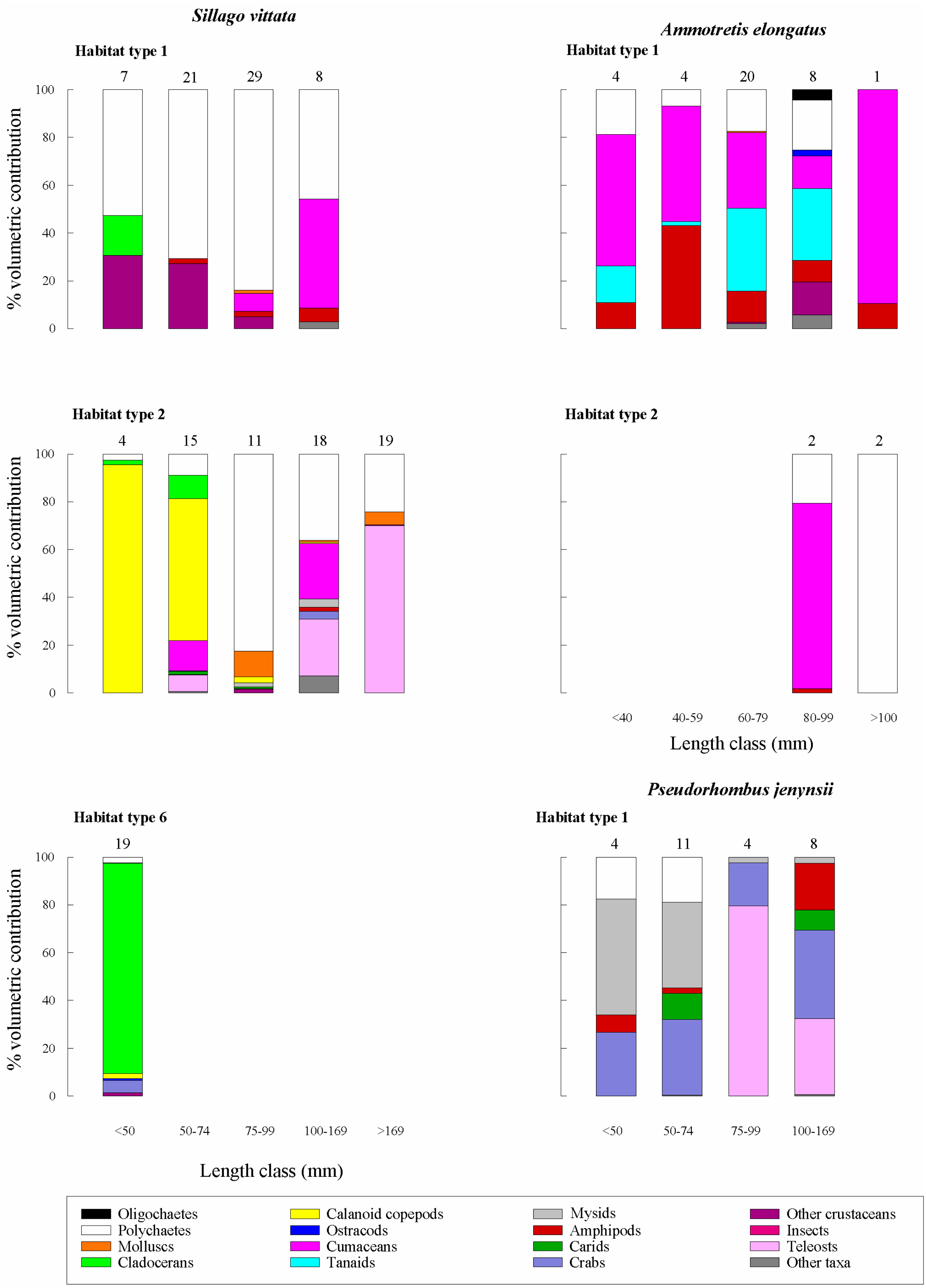
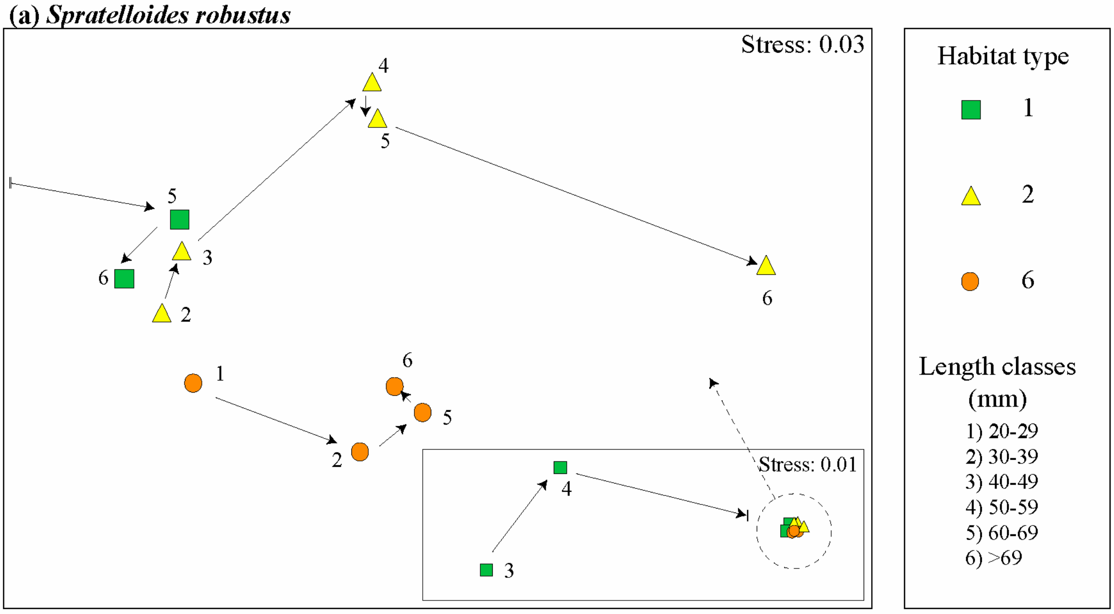


Figure 11.13: Mean percentage volumetric contributions of the 16 broad prey groups to the diets of sequential length classes of *Sillago vittata, Ammotretis elongatus* and *Pseudorhombus jenynsii* during the day and night collectively.

(a) *Spratelloides robustus*



(b) *Atherinomorus ogilbyi*

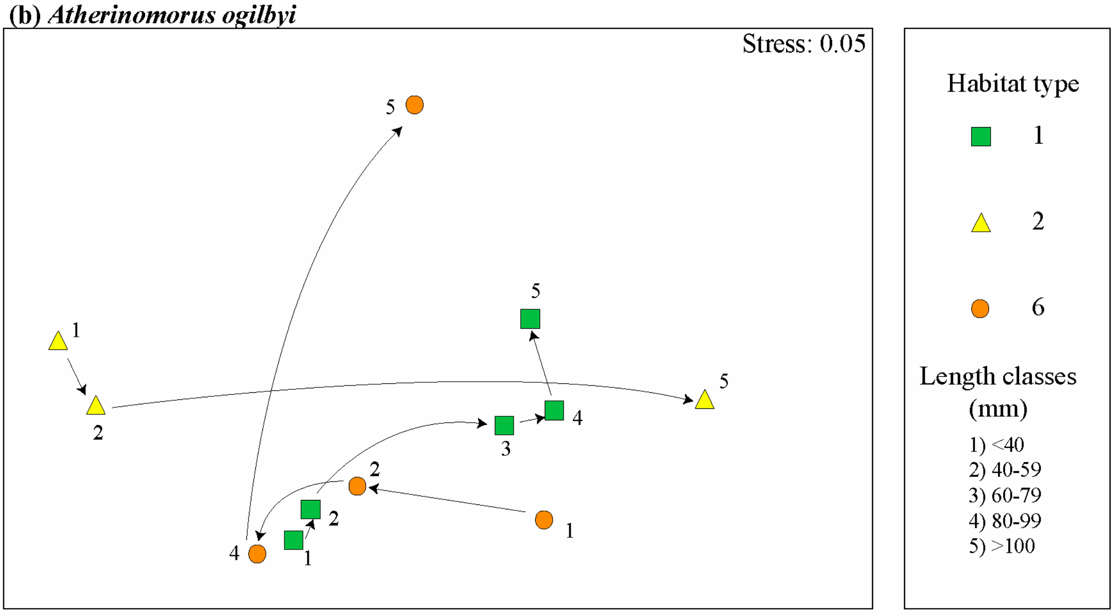


Figure 11.14: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories recorded for sequential length classes of (a) *Spratelloides robustus*, during the day, and (b) *Atherinomorus ogilbyi* during the day, coded for both habitat type and length class.

points progressed from left to right on the plot, with the extent of change being greater at habitat type 2 than 6 and the points for the former habitat type always lying above the latter habitat type.

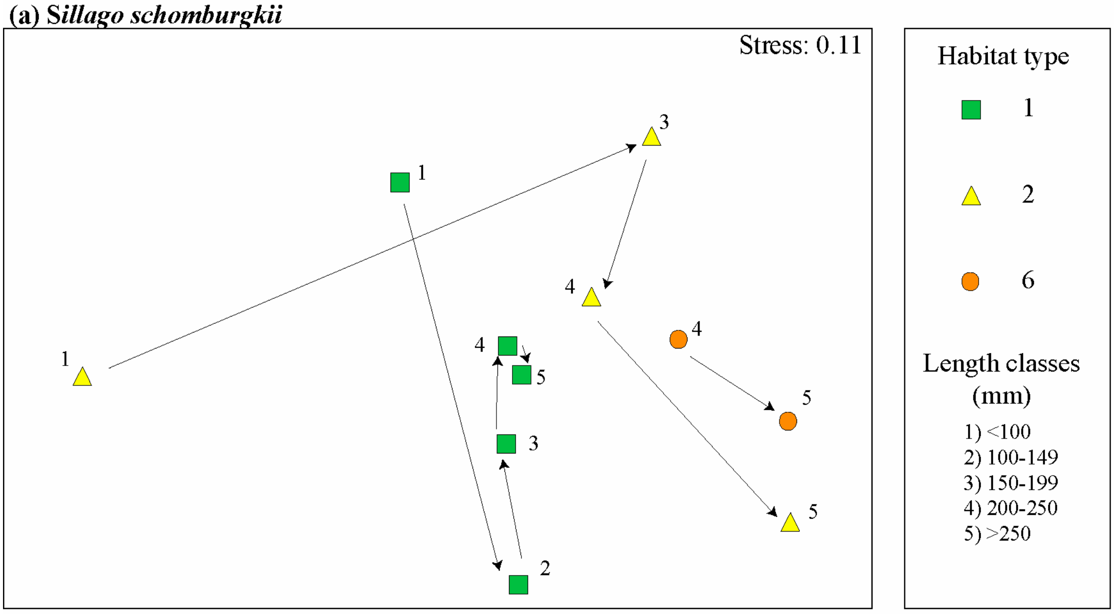
The smaller size classes of *A. ogilbyi* at habitat types 1 and 2 during the day were found on the left side of the plot, and those for the largest size classes lay on the right, the opposite was true for those size classes from habitat type 6 (Fig. 11.14b). However, as for *S. robustus*, the distance between the smallest and largest size classes of *A. ogilbyi* was greatest for habitat type 2. The points for *A. ogilbyi* for the different habitat types were more interspersed on the plot than those of *S. robustus* (*cf* Figs 11.14a and b).

When the points for the different size classes of *S. schomburgkii* at the three habitat types were ordinated, the points for habitat type 1 lay on the vertical midline of the plot, with the smallest fish at the top and the other size classes of fish lying near the bottom of the plot (Fig. 11.15a). The points for the 200-250 mm size class of *S. schomburgkii* at habitat type 6 lay on the far right of the plot, just to the left of the point for the >250 mm size classes of this sillaginid at the same habitat type. In the case of habitat type 2, the smallest fish, *i.e.* <100 mm, lay on the far left of the plot, while those of the largest *S. schomburgkii* lay on the furthermost right part of the plot, and thus showed the greatest extent of size-related changes in the diets (Fig. 11.15a). For *S. vittata*, the sole point for fish from habitat type 6, *i.e.* <50 mm, lay on the left side of the plot, well above that for the same size class from habitat type 2 (Fig. 11.15b). In the case of the latter habitat type, the points progressed to the right of the plot with increasing body size. Although a similar trend was observed for habitat type 1 as for habitat type 2, the extent of change in the dietary compositions with increasing body size was less for habitat type 1 (Fig. 11.15b).

The mean volumetric data for the different size classes of the different species that were captured at each of the three habitat types were also subjected to ordination, but this time keeping the data separate for habitat type, and coding the dietary samples for both species and size class. On the ordination plot for the six of the eight fish species that were abundant at habitat type 1, *i.e. S. robustus, A. ogilbyi* during the day and night*, S. schomburgkii, S. vittata, A. elongatus* and *P. jenynsii*, the points for each species, with the exception of the two sillaginid species, formed groups that were entirely separate from one another (Fig. 11.16). Furthermore, the dietary samples for each of *S. robustus*, *A. ogilbyi* during the day, *S. vittata* and *P. jenynsii* clearly progressed upwards on the plot, with the greatest change occurring in the diets of *S. robustus*, which lay on the left of the plot.

For the seven fish species at habitat type 2, *i.e. S. robustus, A. ogilbyi* during the day and night, *L. platycephala, S. bassensis, S. schomburgkii, S. vittata* and *A. elongatus*, the points for the first two and last species formed discrete groups, while the points for *L. platycephala* and the three sillaginid species were interspersed (Fig. 11.17). There was a clear upwards progression on the plot for *A. ogilbyi* during the day, and to the left for *S. bassensis* and *S. vittata* while, for those of *L. platycephala, S. schomburgkii* and *A. elongatus*, the points progressed in a downwards direction on the plot. The extent of size-related changes was by far the greatest in *A. ogilbyi* during the day and particularly small for *S. robustus*, given the large number of size classes for that clupeid (Fig. 11.17). In the case of habitat type 6, at which the fewest species

(a) *Sillago schomburgkii*



(b) *Sillago vittata*

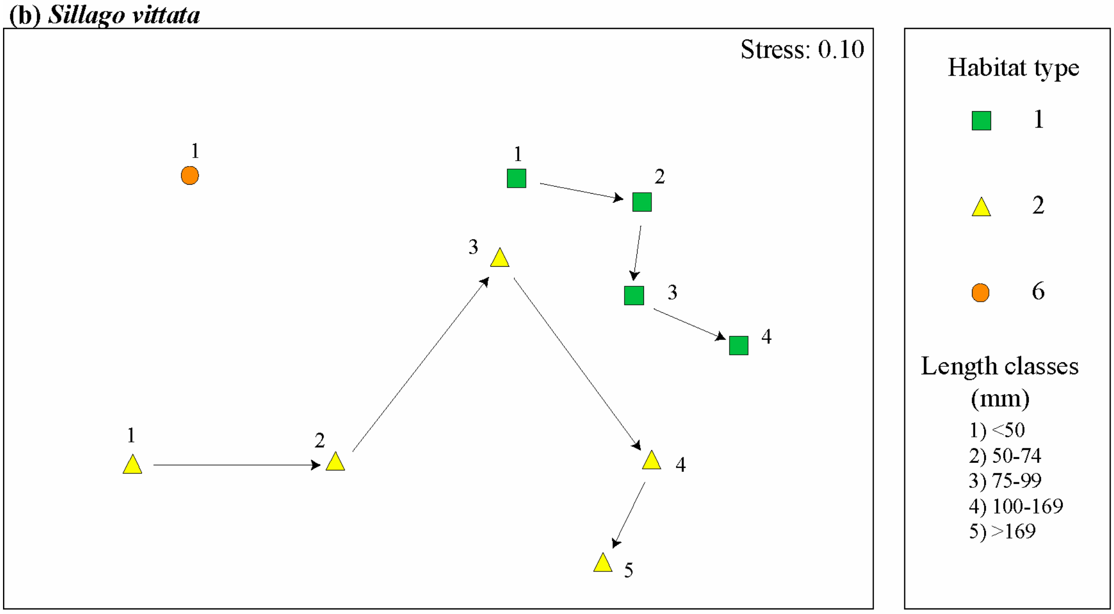


Figure 11.15: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories recorded for sequential length classes of (a) *Sillago schomburgkii*, during the day, and (b) *Sillago vittata*, during the day, coded for both habitat type and length class.

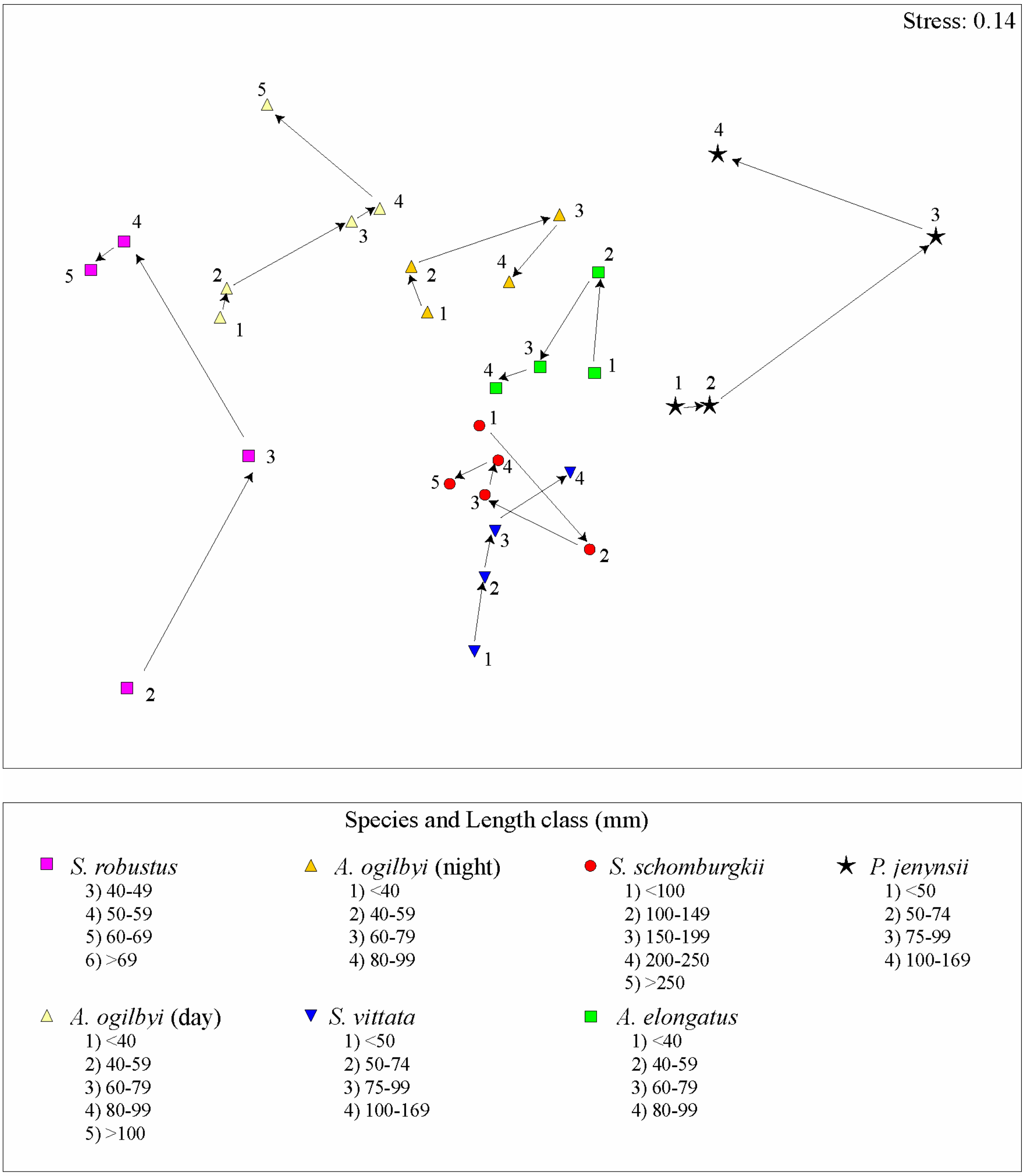


Figure 11.16: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of the different length classes of *Spratelloides robustus, Atherinomorus ogilbyi* during the day and night, *Sillago schomburgkii, Sillago vittata, Ammotretis elongatus* and *Pseudorhombus jenynsii* at habitat type 1.

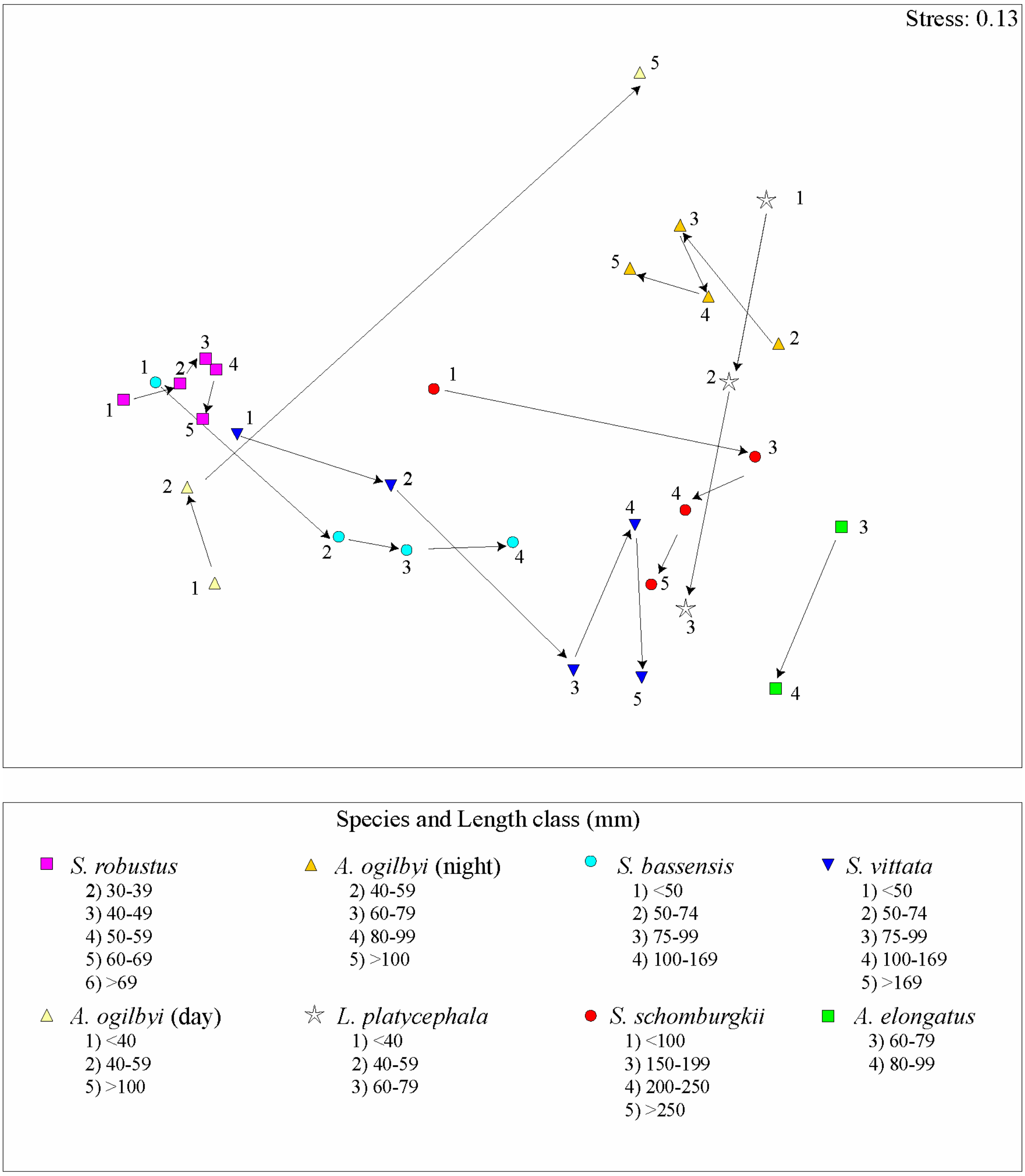


Figure 11.17: Two-dimensional MDS ordination of the mean volumetric contributions of the various dietary categories to the diets of the different length classes of *Spratelloides robustus, Atherinomorus ogilbyi* during the day and night, *Lesueurina platycephala, Sillago bassensis, Sillago schomburgkii, Sillago vittata* and *Ammotretis elongatus* at habitat type 2.

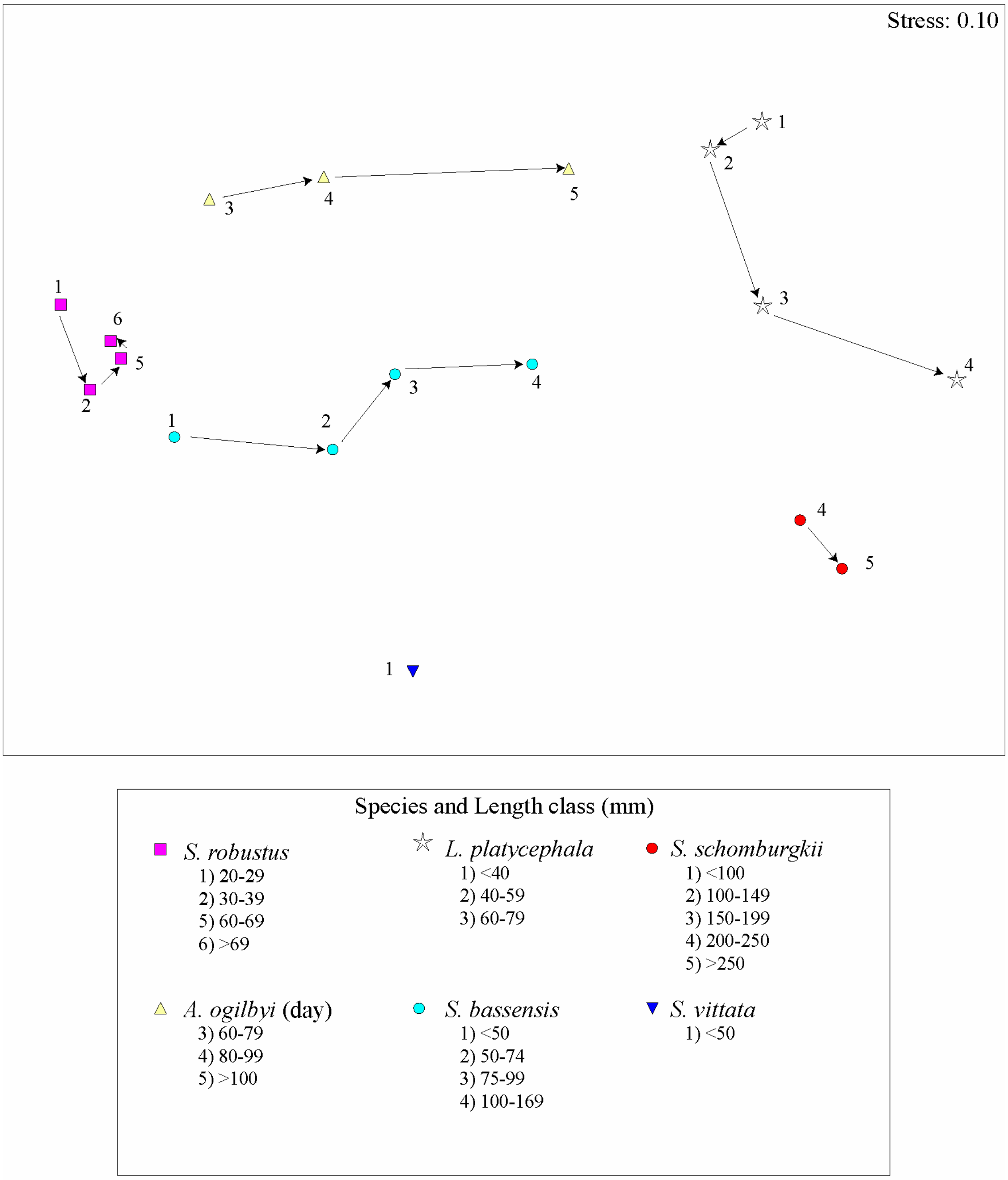


Figure 11.18: Two-dimensional MDS ordination of the mean volumetric contribution of the dietary categories to the diets of the different size classes of *Spratelliodes robustus, Atherinomorus ogilbyi, Sillago bassensis, Sillago schomburgkii, Sillago vittata* and *Lesueurina platycephala* at habitat type 6.

were abundant, *i.e. S. robustus, A. ogilbyi* during the day, *L. platycephala, S. bassensis, S. schomburgkii* and *S. vittata*, the points for each species formed groups that were very discrete from those of the other species (Fig. 11.18). The points for most species typically progressed to the right on the plot, and in the case of *S. robustus, S. schomburgkii* and *L. platycephala*, also downwards on that plot (Fig. 11.18).

11.4 Discussion

11.4.1 Overall dietary compositions and relationships to morphology

This study has demonstrated that, when Spratelloides robustus, *Atherinomorus ogilbyi*, *Lesueurina platycephala*, *Sillago bassensis*, *Sillago vittata*, *Sillago schomburgkii*, *Ammotretis elongatus* and *Pseudorhombus jenynsii* are abundant in the nearshore marine waters on the lower west coast of Australia, they ingest different suites of prey. Thus, although the clupeid *S. robustus* and the atherinid *A. ogilbyi* consume the greatest amounts of zooplankton, the former species mainly focuses on calanoid copepods while the latter species ingests a combination of amphipods, calanoids and insects. This would also imply that these relatively mobile species feed predominantly within the water column, with the latter species probably feeding slightly higher in the water column, including at its surface. In the case of the relatively mobile sillaginids, the juveniles of *S. bassensis* and *S. vittata* also feed to a large extent on the zooplankton, and particularly calanoids and cladocerans, while *S. vittata* also ingests more benthic prey such as cumaceans and harpacticoid copepods. The third species of sillaginid, *S. schomburgkii*, feeds mainly on prey, such as polychaetes and bivalves, which are found within the substrate. Two of the three least mobile species, *i.e. A. elongatus* and *L. platycephala*, also ingest substantial amounts of polychaetes, which shows that, like S. schomburgkii, they feed to a large extent on prey that live within the benthos. However, unlike *S. schomburgkii*, *L. platycephala* also consumes considerable volumes of mysids and, in the case of its larger individuals, also members of its own species while A. elongatus also ingests small epibenthic crustaceans, such as cumaceans and tanaids. This implies that these two species also feed on prey on the substrate surface. In the case of the last species, P. jenynsii, the domination of its diets by fish, crabs and mysids demonstrates that this species feeds mainly on prey that resides on or just above the substrate surface. The marked differences in the diets of the above eight species, which incorporated dietary data from the different sites and seasons during the day, were invariably shown to be significantly different using ANOSIM, with the sole exception being a lack of a significant difference in the dietary compositions of *L. platycephala vs P. jenynsii*. Such differences in dietary compositions would imply that the food resources of nearshore marine waters in south-western Australia are partitioned overall amongst these species. In the case of *L. platycephala vs P. jenynsii*, for which a significant difference was not detected in their dietary compositions, it is very relevant that the former species is restricted to habitat types 2 and 6 while the latter is only abundant in habitat type 1, which means that their dietary resources are thus spatially partitioned.

The above differences in the dietary compositions of the eight fish species in the same region of the coast can be related to differences in their mouth morphology, mobility, location within the water column and mode of feeding. Thus, the possession by both *S. robustus* and *A. ogilbyi* of a relatively large vertical gape (Figs. 11.4, 11.19), accounts for the ability of these mobile species to target aggregations of calanoid copepods and cladocerans in the water column (Ritz 1994). Members of the Pempherididae also possess a combination of a large vertical gape and mobility and likewise feed on prey in the water column (Platell and Potter 1999). In the case of *A. ogilbyi,* its relatively wide mouth in comparison to *S. robustus*, could partly account for its ability to feed on larger prey such as amphipods and insects.

Similar to the above clupeid and atherinid species, both *S. bassensis* and *S. vittata* possess a mouth which is relatively high and exhibits a greater lower jaw extension, which would help account for the ability of these two species to target zooplankton, typically feeding upwards within the water column. The additional ingestion of more benthic prey by *S. vittata* is partly explained by its greater degree of upper jaw extension, which would be more effective at feeding on prey beneath the body of the fish. The mouth of *S. schomburgkii* is less high and tends to be more downward protruding than the other two species of sillaginid, which would obviously facilitate this bottom-living species to target and extract its polychaete prey from the substrate. The gerreids *Parequula melbournensis* and *Gerres subfasciatus*, which likewise possess highly protrusible and downwards-pointing mouths and large eyes, also ingest substantial amounts of polychaetes (Platell *et al.* 1997, Linke *et al.* 2001).

Although *A. elongatus* possesses a protrusible and downwards-pointing mouth, this mouth is not as relatively large or robust as that of *S. schomburgkii* (Fig. 11.19). Furthermore, this pleuronectid is also morphologically far more adapted to living on the substrate surface and thus to a less active mode of life and, in nearshore waters, is represented only by smaller individuals. The possession of a small mouth that is adapted for removing food from the substrate is consistent with their feeding on small benthic crustaceans, such as cumaceans and tanaids, which are both smaller and burrow less deeply in the substrate than the polychaete prey of *S. schomburgkii*. Similarly, the closely-related species *Ammotretis rostratus*, which has similar mouth morphology, also consumes mainly benthic prey such as crustaceans, polychaetes and molluscs (Edgar and Shaw 1995a).

In contrast to the previous six species, *L. platycephala* is an ambush predator and shows a greater tendency to burrow than *A. elongatus*, the only one of those first six species that does not typically remain above the substrate surface. Furthermore, unlike the mouths of the previous six species, that of *L. platycephala* has only limited protrusibility, contains rows of numerous sharp teeth on the upper and lower surfaces of the mouth and possesses a particularly wide gape (Fig. 11.19). A combination of a mottled beige dorsal surface, ability to conceal itself just below the substrate surface and the possession of a particularly wide mouth that is armed internally

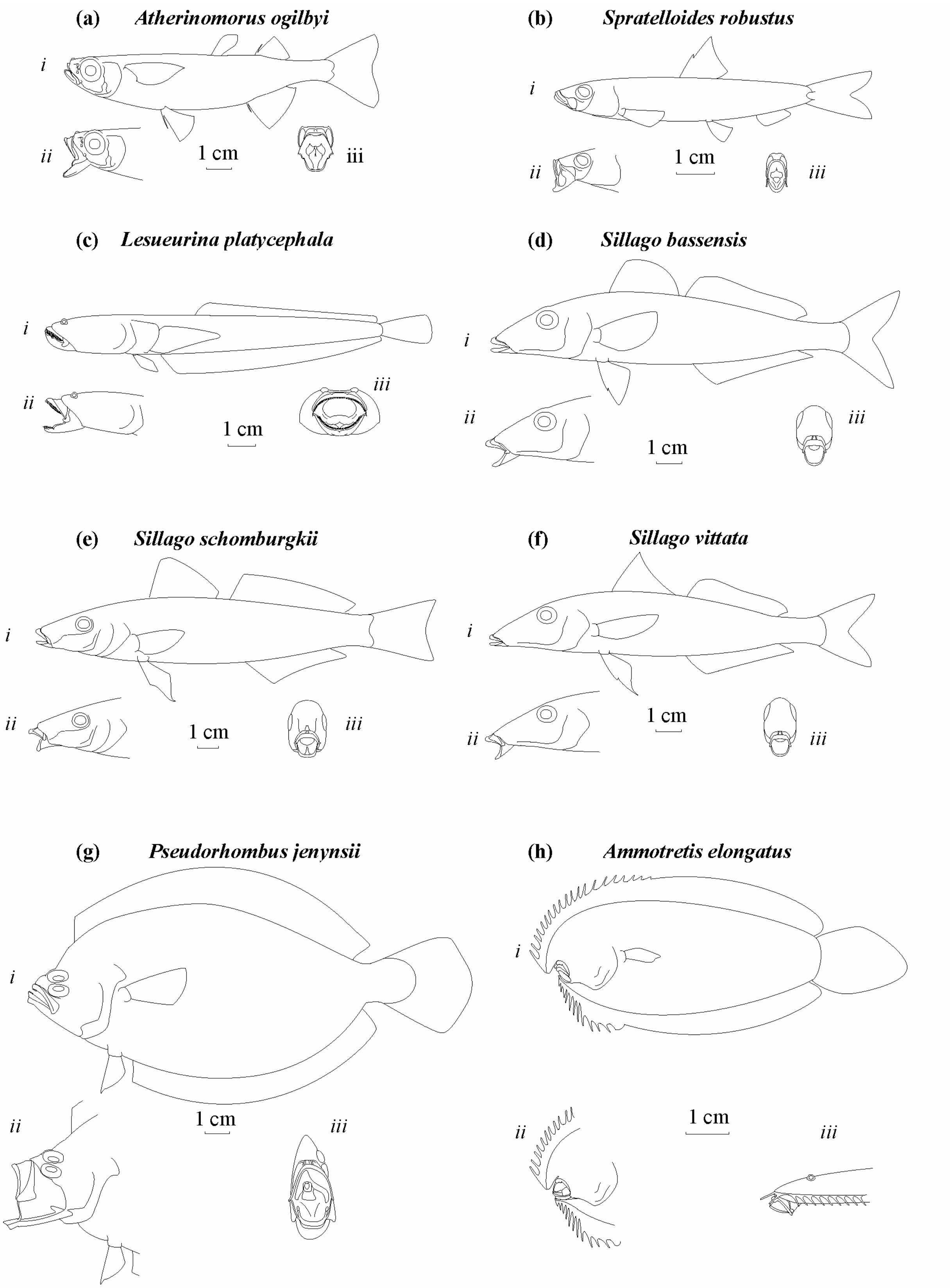


Figure 11.18: Illustrations of the salient features of the body, head and mouth morphology for (a) *Atherinomorus ogilbyi,* (b) *Spratelloides robustus,* (c) *Lesueurina platycephala,* (d) *Sillago bassensis,* (e) *Sillago schomburgkii,* (f) *Sillago vittata,* (g) *Pseudorhombus jenynsii* and (h) *Ammotretis elongatus*, showing (i) lateral view of the entire animal, (ii) lateral view of head with mouth extended and (iii) "en face" view, or, in the case of *A. elongatus,* dorsal view of the head.

with an array of small pointed teeth clearly represent ideal adaptations for facilitating the ambush of both its small prey (amphipods and mysids) and large prey (teleosts and polychaetes), which are either mobile or possess rapid escape responses. The bothid *P. jenynsii*, which is the only one of the eight species to feed extensively on crabs and mysids, but like *L. platycephala*, ingests large amounts of fish, was shown by PCA to have a relatively high and wide mouth and considerable extension of particularly its lower jaw. This ambush predator is thus well suited to capture and ingest relatively large prey such as crabs or other sedentary crustaceans and fish.

11.4.2 Diel and size-related changes in dietary compositions at different habitat types

Of the four species for which the dietary compositions were analysed for differences between day and night (*A. ogilbyi, L. platycephala, S. schomburgkii* and *A. elongatus*), there was a marked difference in the dietary compositions between day and night only in the case of *A. ogilbyi*. Thus, in particular, this species fed far more extensively on calanoid copepods in the plankton and insects on the water surface during the day, whereas it consumed mainly gammarid amphipods at night. Concomitant sampling of the potential prey communities during the same times and at the same locations when this species was abundant demonstrated that calanoid copepods were present in very high densities during both the day and night, whereas amphipods were only abundant in the water column at night (Chapters 8 and 10). Thus, *A. ogilbyi* either prefers to feed on amphipods, rather than calanoids, if they are present, or because, through their larger size, they are easier to target at night.

The progressive changes that occurred during the day in the suite of prey ingested by *A. ogilbyi* as it increased in size reflected a sequential decrease in the consumption of very small prey, such as cladocerans and calanoids, and a concurrent increase in the ingestion of larger and more mobile invertebrate prey, such as amphipods and insects. Although the ability of *A. ogilbyi* to ingest increasingly larger and more active prey as it increases in size, reflects, in part, a progressive increase in actual mouth size, it would be enhanced by the concomitant increase that occurs in the relative extent to which the mouth can be protruded and which thereby increases even further the strike range of larger individuals. The observation that, at night, all size classes of this atherinid consumed substantial volumes of amphipods is clearly related to the migration of large numbers of these crustaceans into the water column at night (Chapter 10) and thus to a greatly increased accessibility to capture by a species that is well adapted to feeding throughout the water column (Prince *et al.* 1982).

Since the gut contents of even the larger individuals of *S. robustus* consisted predominantly or exclusively of calanoid copepods, the diet of this species does not undergo marked size-related changes. Indeed, calanoids dominate in the diets of all size classes of this species in all seasons and at all sites, except for in winter at habitat type 1 when calanoids were not present in samples taken from the water column (Chapter 8). This could account for the fact that the most marked differences in dietary composition with increasing fish size were present in this habitat type.

The consumption by individuals of *L. platycephala* <40 mm in length of large volumes of medium-sized crustaceans, such as amphipods and isopods, is attributable, in particular, to its possession of a relatively large mouth. However, the relative width of the mouth of fish >80 mm in length becomes even greater, which accounts for the ability of the larger individuals of this species to ingest substantial volumes of teleosts, despite the fact that the length of those individuals were generally <100 mm.

The size-related changes in the diets of both *S. bassensis* and *S. vittata* broadly involved a shift from the ingestion of predominantly small zooplankters, *i.e.* calanoid copepods and/or cladocerans by small fish, to larger and often benthic prey, such as polychaetes and teleosts, by larger fish. A shift from ingesting crustaceans to teleosts with increasing body size has been recorded for a number of other fish species in Australian waters (*e.g.* Blaber and Bulman 1987, Linke *et al.* 2001, Platell and Potter 2001). It should be recognised that, although seasonal differences in the dietary composition will be related to seasonal variations in the composition of the available prey, the fact that the size of the juveniles of the *Sillago* species increases during the year means that the seasonal changes in the diet of these species also partly reflects size-related changes in the type of prey ingested.

The diet of the smallest *S. schomburgkii*, *i.e.* <100 mm length, differed from that of the larger individuals of this species, in that it contained large volumes of small crustaceans such as harpacticoid and calanoid copepods, tanaids and cumaceans. Although the relative volume of polychaetes ingested by fish >100 mm in length were greater than that by smaller fish, their contributions to the diets of those fish declined progressively with increasing body size, while those of teleosts and oligochaetes increased. Thus, as with *A. ogilbyi* during the day, the changes in the diet of *S. schomburgkii* with body size reflected an increasing ability of this species to ingest larger prey as it increases in size. However, the extent of the size-related changes in dietary compositions was less in *S. schomburgkii* than of *A. ogilbyi* during the day.

The relatively small mouth possessed by *A. elongatus* throughout its life in the nearshore region is reflected in the fact that the individuals of all size classes of this species consumed small prey, such as cumaceans, tanaids, amphipods and small polychaetes. Although the diet of *P. jenynsii* changed with increasing body size, this occurred far more abruptly than with either of the two *Sillago* species. This was attributable to the fact that the diets of the two smallest size classes were dominated by mysids, crabs and polychaetes, whereas those of the two larger size classes contained considerable volumes of teleosts.

The diets of different size classes of fish at different habitat types, which were first subjected to intraspecific comparisons for each of the four species that were abundant at all three habitat types, *i.e. S. robustus, A. ogilbyi* during the day*, S. schomburgkii* and *S. vittata*, showed that the diets of each of the species showed similar types of intraspecific size-related changes at each habitat type. Thus, the tendency of the points on the ordination plot to progress from left to right implies that similar size-related changes occurred in the diet of each species, which in turn implies that similar factors must be governing such change in the different fish species. It is thus relevant that larger prey, such as teleosts and oligochaetes, only ever appear in the diets of larger size classes of fish and that contributions of smaller prey, such as calanoids, amphipods and tanaids, are typically greater in the smallest size classes of fish.

The above comparisons also demonstrated that the extent of change occasionally varied among habitat types, being greatest for *S. robustus* at habitat type 1 and also high at habitat type 2, while for the other three species, the extent of change was greatest at habitat type 2. This would be consistent with the observation that the prey at this site was reasonably diverse, but not particularly abundant (Chapters 7, 8 and 10), and is likely thus to be well partitioned by its fish predators (see Gerking 1994).

When the species that were abundant at each of three habitat types were collectively ordinated for each of the three habitat types separately, the groups for the different species were similarly, or even more discrete, than in the first series of ordinations, which did not take into account body size. This implies that, due to morphological and other feeding constraints, each of the eight species is adapted to feeding on a different suite of prey during all stages of its life cycle in nearshore waters. The wide distribution of points on the ordination plots, when taken into consideration with the fact that the points for the different species or size classes are almost never super-imposed, also suggests that the prey resources of these nearshore waters are widely utilised by these species, which would reduce the potential for competition for food resources in these waters.

11.4.3 Influence of habitat and season on the diets of the different fish species

All of the *Spratelloides robustus* caught at habitat type 2 and 6 fed either exclusively or predominantly on a single prey type, namely calanoid copepods, and the same was true for the two larger size classes at habitat type 1. Since this taxon was not found in zooplankton samples in winter at habitat type 1, it is highly relevant that the only exception to the above generalisation was provided by the individuals of *S. robustus* that were caught at this site in winter. Thus, while *S. robustus* exhibited a far stronger tendency than either of the sillaginid species or *Pseudorhombus jenynsii* to focus on an individual prey type (see later), this clupeid feeds opportunistically on other invertebrates when its usual prey is not available. Indeed, the fact that, in winter at habitat type 1, *S. robustus* was able to consume large volumes of fauna that is typically benthic (ostracods, gastropods, polychaetes and harpacticoid copepods) demonstrates that, when the need arises, this clupeid is able to forage for different invertebrate taxa in or on the substrate rather than feed on zooplankters. This suggests that clupeids, such as *S. robustus*, which are typically filter feeders (Gerking 1994), are also able to feed on more benthic prey by using suction feeding. Although the diets of *S. robustus* were almost invariably dominated by calanoid copepods, the differences amongst the less abundant taxa in the diets from the different sites and seasons were still sufficient to produce a significant difference in the dietary composition of fish at the three sites and between those of fish caught in summer, autumn and winter.

Although *Sillago bassensis*, which was found predominantly at the moderately sheltered and relatively exposed sites (*i.e.* habitat type 2 and 6, respectively), ingested substantial volumes of calanoids at both of these sites, its dietary composition in these two habitat types differed markedly in some respects. Thus, cladocerans and carids were ingested only at habitat type 6 and teleosts were consumed only at habitat type 2. The greater prevalence of cladocerans in the diets of fish from habitat type 6 reflects the relatively greater densities of these zooplankters at this site (Chapter 7).

The results of ordination demonstrated very clearly that the dietary composition of *S. bassensis* was also influenced by time of year. However, while the points for the dietary samples for summer, autumn and spring at both habitat type 2 and 6 formed discrete groups, those for the corresponding seasons at the two habitat types were not closely apposed. This emphasises that, in any given season, the compositions of the prey ingested by this species at the two habitat types differed. For example, in spring, *S. bassensis* ingested relatively greater volumes of polychaetes at habitat type 2 than at habitat type 6, whereas the reverse was true for calanoid copepods and teleosts, and in summer it consumed relatively greater volumes of calanoids and teleosts at habitat type 2 and cladocerans and polychaetes at habitat type 6. It is thus concluded that, while the dietary composition of *S. bassensis* is influenced by time of year, this influence is not as great as that of habitat type.

The dietary composition of *S. vittata* was profoundly influenced by habitat type. The differences among the dietary compositions of this species at the three habitat types are very clearly illustrated by comparing the prey ingested by the smallest individuals at these habitat types. These individuals ingested predominantly polychaetes and harpacticoid copepods at habitat type 1, calanoids at habitat type 2 and cladocerans at habitat type 6. Dietary differences between sites were also found among larger *S. vittata*, with those at habitat type 1 consuming considerable volumes of polychaetes and those at habitat type 2 ingesting substantial amounts of teleosts. Although season also had a substantial effect on the dietary composition of *S. vittata*, with the points for the dietary samples for the corresponding seasons at the different sites forming discrete groups on the ordination plot, the extent of their separation was not as great as with *S. bassensis*.

A previous study found that *S. vittata*, and even more particularly *S. bassensis*, consumed considerable volumes of amphipods in nearshore waters (Hyndes *et al.* 1997) and thereby differed from the results of the present study. This difference is almost certainly due to the greater abundance of macrophytes, which often contain high densities of amphipods in south-western Australian coastal waters (Robertson and Lenanton 1984), in the sites sampled by Hyndes *et al.* (1997). The above differences further emphasise the opportunistic nature of the feeding of the two *Sillago* species. These two sillaginid species have also been shown to feed opportunistically by ingesting large amounts of *Acetes australis*, when this carid decapod became seasonally abundant (Gunn and Milward 1985).

Although the dietary data for *P. jenynsii* at the single site (habitat type 1) at which this species was caught were derived largely from summer samples, the distribution of the points for the dietary samples for summer, autumn and spring on the ordination plot strongly indicate that the diet of this species changes during the year.

11.4.4 Assessment of opportunism in the diets of fish

The marked differences that occur in the dietary compositions of the eight species which are abundant in nearshore marine waters of the lower west coast of Australia most likely reflect substantial differences in morphological and other feeding constraints that govern the types of food ingested by each fish species (see first part of Discussion). However, the differences that are apparent in the diets of each of these fish species with location and season of capture, and even for a variety of corresponding size classes of those fish species, would imply that different-sized individuals of all eight species are capable of at least a small degree of opportunism in the types of food that are ingested in the study area. In the case of *S. robustus*, whose individuals feed mainly on zooplanktonic calanoids at all habitat types and in all seasons, the focusing of their small individuals on very small and benthic prey at habitat type 1 during the winter shows that this apparently specialised feeder is capable of a large degree of dietary opportunism, presumably in response to a decline in their usual prey source. Such a broadening of the prey ingested by this clupeid is typical of that of a specialist feeder when faced with a shortage of its usual prey (Gerking 1994). Although it is obviously more difficult to detect opportunism in those fish species which are more generalist feeders, such as each of the three species of sillaginid, the habitat type differences recorded for *S. vittata* were substantial, implying that this species is also capable of a large degree of opportunism in its diet. Such differences in the diets of fish species, when they occur in more than one of the habitat types and season, may well have an influence on the determination of the extent of resource partitioning among those members of the fish community. It is obviously crucial, when undertaking any dietary study, to understand the relative extents to which each of the species of interest is capable of dietary opportunism.

11.4.5 Conclusions

The diets of the eight species, which collectively contributed 30.9, 69.7 and 88.5% to the total numbers of fish during the day at habitat type 1, 2 and 6, respectively (Chapter 4), also made large contributions to the biomass of each of those habitat types in the nearshore marine waters of the lower west coast of Australia (data not shown). The dietary comparisons shown in this chapter represent the first attempt to determine the extent of partitioning of the dietary resources by the abundant teleosts in the nearshore waters of this region. Our analyses demonstrated that the diets of all but one pair of species, *i.e. L. platycephala* and *P. jenynsii*, were significantly different from each other. This provides strong evidence that a range of intrinsic and extrinsic mechanisms facilitate partitioning of food resources amongst these species. The intrinsic mechanisms include differences in the dimensions and orientation of their feeding apparatus, location in the water column, swimming ability and mode of feeding, whereas the main extrinsic factor is prey availability. The two species whose diets were not significantly different, *i.e. L. platycephala* and *P. jenynsii,* rarely co-occurred, with the former species being found mainly at habitat types 2 and 6, and the latter predominantly at habitat type 1. These differences in distribution mean that the dietary resources of the region are still partitioned by those two species.

At the commencement of this project, it was envisaged that dietary data that had been previously collected for other species in similar environments could be used in conjunction with the current data to produce a preliminary food web for the nearshore marine waters on the lower west coast of Australia. Although such data is available for comparison, the marked differences in the diets of the various fish species among the different habitat types, would imply that previously collected data, which has been collected in other areas, such as in nearby estuaries, will only have limited applicability in such a situation. Therefore, in the case of the other species which made large contributions to the abundance and/or biomass of the different habitat types in the study area (*e.g. Rhabdosargus sarba, Aldrichetta forsteri, Sillago burrus, Pelates sexlineatus* and *Leptatherina presybteroides*), data should also be determined for those species in each of the different habitat types in which they are abundant.

Chapter 12. Relationships between different components of invertebrate faunas and dietary compositions of selected teleost species

12.1 Introduction

The results presented in Chapter 3 demonstrate that, on the basis of values for a suite of seven enduring environmental characteristics, six habitat types were identified in nearshore marine waters along the lower west coast of Australia. Accompanying studies showed that the characteristics of both the relatively mobile teleost faunas and the more sessile benthic macroinvertebrate in most of those habitat types are different (Chapters 5 and 7). The characteristics of other components of the invertebrate faunas, *e.g.* zooplankton, meiofauna and hyperbenthic invertebrates, have also been shown to vary markedly among a subset of those six habitat types, *i.e.* 1, 2 and 6 (Chapters 8-10). The invertebrates that comprise the benthic macroinvertebrate, hyperbenthic and zooplanktonic faunas in the three habitat types constitute the main prey of the juveniles and adults of fish species that were chosen for dietary analyses on the basis that they represented a range of feeding modes (Chapters 7, 8, 10 and 11). The diets of six of those fish species, that were abundant in more than one habitat type, also differed significantly among habitat types (Chapter 11).

The development of particular multivariate techniques for analysing faunal communities now enables the following to be determined quantitatively:

1) The extent to which the compositions of the benthic macroinvertebrate, hyperbenthic invertebrate and zooplankton assemblages are different.
2) The extent to which the differences in the dietary compositions of seven abundant fish species among the various habitat types are correlated with differences in the compositions of invertebrate faunas among those habitat types.
3) The precise mode of feeding of those abundant fish species, *i.e.* the location in the water column where they feed and the extent to which they target particular prey.

12.2 Materials and methods

The regimes for sampling benthic macroinvertebrate, hyperbenthic and zooplanktonic fauna during the day were described in sections 7.2, 10.2 and 8.2, respectively. The regimes employed for sampling the fish species (*Spratelloides robustus, Atherinomorus ogilbyi, Lesueurina platycephala, Sillago bassensis, Sillago schomburgkii, Sillago vittata* and *Pseudorhombus jenynsii*), and for processing and analysing the dietary data for these species was provided in section 4.2. Note that the eighth species for which dietary data were obtained

(*Ammotretis elongatus*) was not included in this part of the study because it was not caught in sufficiently large numbers.

12.2.1 Comparison of the compositions of different components of the invertebrate faunas

To compare the overall compositions of the benthic macroinvertebrate, hyperbenthic and zooplankton faunas at sites that represented habitat types 1, 2 and 6, the data were recalculated so that they could be used to construct a single similarity matrix that could be subjected to the various subroutines in the PRIMER v5.2 package (Clarke and Gorley 2001). This involved firstly producing, to as low a taxonomic level as possible, a list of taxa for each of the above three components of the invertebrate faunas. In the case of benthic macroinvertebrates, the data were restricted to those in the subtidal area (zone C), since that was the area in which the hyperbenthic and zooplankton faunas were sampled.

The number of each taxon of each of the components of the invertebrate faunas in each sample was firstly expressed as a density, *i.e.* number of individuals of each taxon m^{-2}. Since the benthic macroinvertebrates and the zooplankton fauna were collected over two years, while the hyperbenthic invertebrates were sampled only over the second of those years, the replicate data for the benthic macroinvertebrates and zooplankton in the corresponding seasons of the two years were both averaged.

The densities derived for each taxon from each replicate sample of the benthic macroinvertebrate, hyperbenthic and zooplankton faunas in each of the three habitat types in the four seasons were $\log_{10}(n+1)$ transformed, the transformation previously shown to be the most appropriate for these data (Chapters 7, 8 and 10). The Bray-Curtis similarity coefficient was applied to the data to produce a similarity matrix that could then be subjected to non-metric multi-dimensional scaling (MDS) ordination and associated subroutines (Clarke and Gorley 2001). Analysis of similarities (ANOSIM) was used to identify whether there were any significant differences in the composition of the three faunal communities in the three habitat types and, if so, the extent of these differences (Clarke 1993). Wherever significant differences were detected, Similarity Percentages (SIMPER) was used to identify which taxa typified the different components of the invertebrate faunas and were thus mainly responsible for those significant differences.

12.2.2 Comparison between prey communities and dietary compositions of fish species

In order to ascertain the extent to which the teleost species fed on different components of the invertebrate fauna and thus be able to infer their modes of feeding, the matrices constructed from the dietary compositions of these fish species at the various habitat types and seasons were correlated, separately, with each of the matrices constructed from the densities of the taxa of each of the potential prey communities, *i.e.* benthic macroinvertebrates, hyperbenthos and zooplankton. These correlations were undertaken using the RELATE routine in the PRIMER 5.2 package (Clarke and Gorley 2001), which compares the patterns of the rank orders between the various samples in the dietary and invertebrate similarity matrices. A major advantage of this routine is that, because only the arrangement of the ranks orders are compared, the data in the separate matrices only need to contain matching sample labels and thus do not all need to be of the same "type". The resultant sample statistic, *i.e.* ρ value, ranges from 0 (no correlation) to +1 (complete correlation) and, in combination with a significance level (p) of <5%, demonstrates which patterns in each of the three invertebrate communities correlated best to the patterns of dietary compositions for each of the seven fish species.

The mean percentage volumetric contributions of the different dietary categories in groups of three randomly-selected individuals of each fish species from the different habitat types in each of the four seasons were calculated (see Platell and Potter (2001) for rationale for pooling dietary data and randomisation procedure). A randomisation procedure was then employed to ensure that the number of samples for an invertebrate group in a particular habitat type in a given season matched that of the dietary composition of a particular species in that habitat type and season. Note that for these dietary/invertebrate prey comparisons, the data for the benthic macroinvertebrates incorporated those from zones A-C, since the invertebrates in all of those zones would be potential prey for fish during at least part of a tidal cycle.

The dietary data for each of the seven species were square root-transformed, as is appropriate for percentage data (Platell and Potter 2001), while the replicate data for the three potential prey communities were $\log_{10}(n+1)$ transformed, as is appropriate (see earlier). The Bray-Curtis similarity coefficient was then used to produce similarity matrices from these data. The RELATE procedure was then used to compare the similarity matrices of the dietary compositions of each of the seven fish species to each of the replicate data for the benthic macroinvertebrate, hyperbenthic and zooplankton fauna.

12.3 Results

12.3.1 Comparisons of the different components of the invertebrate faunas

When the replicate densities for the various taxa in the benthic macroinvertebrate, hyperbenthic and zooplankton faunas in each season and in each habitat type were subjected to MDS ordination, the samples for the benthic macroinvertebrates lay predominantly in the bottom left hand side of the plot and discrete from those of the zooplanktonic fauna on the lower right of the plot (Fig. 12.1). The samples of the hyperbenthic invertebrates lay to the right of those for the benthic macroinvertebrates and largely above those for the zooplankton.

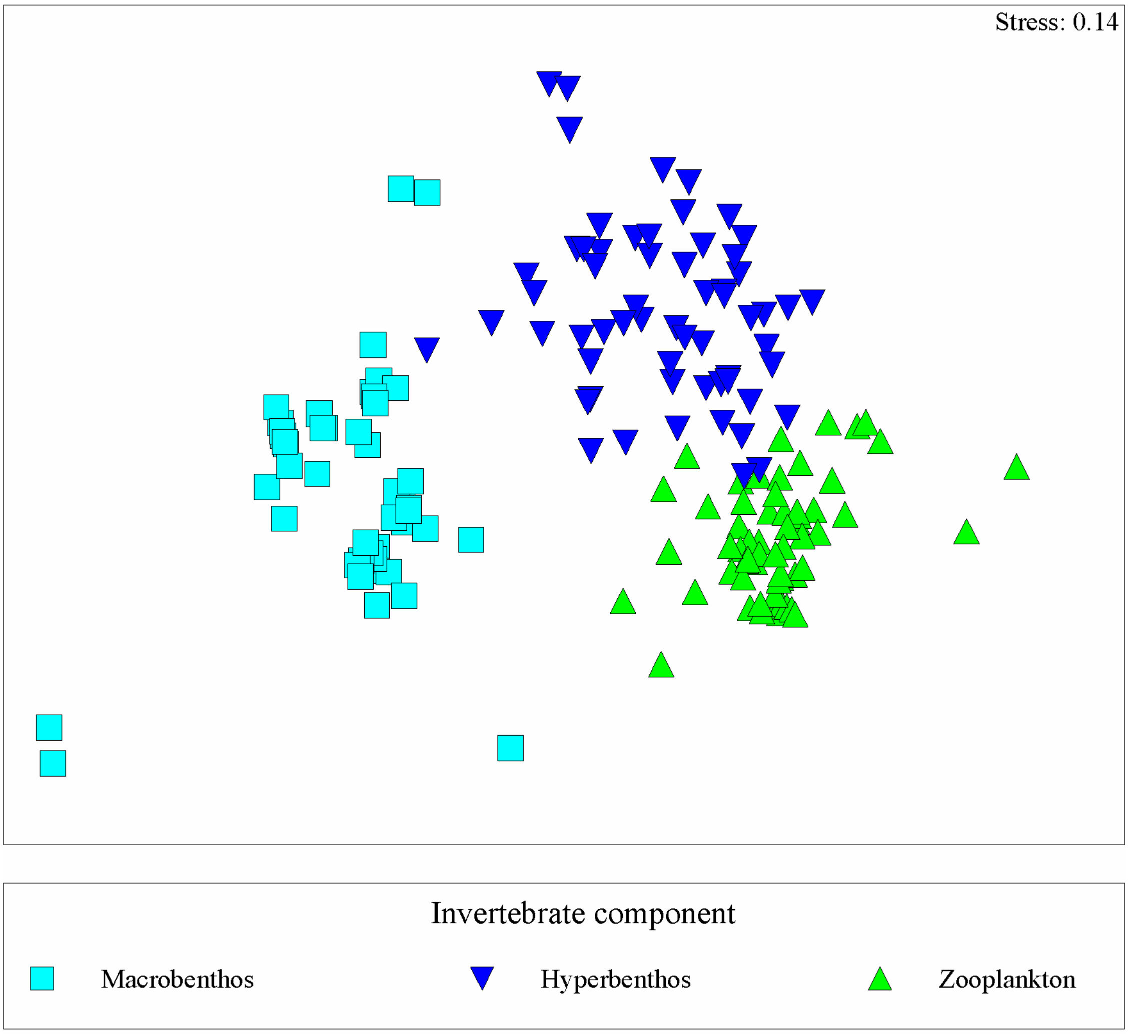


Figure 12.1: Two-dimensional MDS ordination of the densities of the various faunal constituents comprising the macrobenthic, hyperbenthic and zooplanktonic assemblages in habitats 1, 2 and 6.

One-way ANOSIM showed that the compositions of the benthic macroinvertebrate, hyperbenthic and zooplankton communities were significantly different overall (p=0.1%, Global R=0.793). Pairwise tests demonstrated that the compositions of each of these communities were significantly different from each other (p=0.1%), with the R-statistic value being greatest for benthic macroinvertebrates *vs* zooplankton (0.901) and least, but still very high, for the hyperbenthic *vs* zooplanktonic fauna (0.678). SIMPER demonstrated that the taxa which typified these communities best were polychaetes, gammarid amphipods and bivalves for benthic macroinvertebrates, calanoid and cyclopoid copepods and gammarids for the hyperbenthic fauna and calanoid, harpacticoid and cyclopoid copepods for the zooplanktonic fauna (Table 12.1). Relatively greater densities of polychaetes and gammarids and relatively lower densities of calanoids helped distinguished the benthic macroinvertebrates from the hyperbenthic invertebrates and relatively greater densities of polychaetes and relatively lower densities of calanoids, harpacticoids and gastropods helped distinguish the benthic macroinvertebrates from the zooplanktonic fauna (Table 12.1). The hyperbenthic fauna was distinguished from the zooplanktonic fauna by relatively greater densities of cumaceans and polychaetes and relatively lower densities of calanoids, harpacticoids and gastropods.

Table 12.1 Taxa detected by SIMPER as those most responsible for typifying the main groups of invertebrate faunas (*i.e.* benthic macroinvertebrates, hyperbenthic fauna and zooplankton) recorded in nearshore waters along the lower west coast of Australia (see taxa arranged along diagonal cells), and distinguishing each pair of those main invertebrate groups (see taxa arranged along vertical cells). The invertebrate assemblage in which each taxa is most important is also provided (see superscripts; BM=benthic macroinvertebrates, H=hyperbenthos and Z=zooplankton).

	Benthic macroinvertebrates	**Hyperbenthos**	**Zooplankton**
Benthic macroinvertebrates	Polychaetes Gammarids Bivalves		
Hyperbenthos	Polychaetes$^{(BM)}$ Gammarids$^{(BM)}$ Calanoids$^{(H)}$	Calanoids Cyclopoids Gammarids	
Zooplankton	Polychaetes$^{(BM)}$ Calanoids$^{(Z)}$ Harpacticoids$^{(Z)}$ Gastropods$^{(Z)}$ Cyclopoids$^{(Z)}$ *P. avirostris*$^{(Z)}$ Bivalves$^{(BM)}$	Calanoids$^{(Z)}$ Harpacticoids$^{(Z)}$ Gastropods$^{(Z)}$ Cumaceans$^{(H)}$ Polychaetes$^{(H)}$	Calanoids Harpacticoids Cyclopoids Gastropods

12.3.2 Relating fish dietary matrices and invertebrate community matrices

RELATE showed that the diets of all but *L. platycephala* were significantly correlated with the compositions of the benthic macroinvertebrates, with ρ values for species with significant correlations ranging from 0.232 for *S. robustus* to 0.452 with *P. jenynsii* (Table 12.2). The diets of the three species of sillaginid (*S. bassensis, S. schomburgkii* and *S. vittata*) and of *P. jenynsii* were significantly correlated with the compositions of the hyperbenthic faunas, with the ρ value being highest for *S. schomburgkii* (0.472), followed by that for *P. jenynsii* (0.351). The diets of *A. ogilbyi, S. schomburgkii* and *S. vittata* were significantly correlated with the zooplankton communities, with the ρ values ranging from 0.435 for *S. vittata* to 0.668 for *A. ogilbyi* (Table 12.2).

Table 12.2 Significance levels (p; %) and associated rho (ρ) values reflecting the extent of the correlation between similarity matrices constructed from the dietary composition data of seven fish species and similarity matrices constructed from each of the main groups of nearshore invertebrate assemblages, *i.e.* benthic macroinvertebrates, hyperbenthos and zooplankton. Significant values are highlighted in boldface.

	Benthic macroinvertebrates	**Hyperbenthos**	**Zooplankton**
Spratelloides robustus	**p=1.3%; ρ= 0.232**	p=11.8%; ρ=0.141	p=16.1%; ρ=0.102
Atherinomorus ogilbyi	**p=0.1%; ρ= 0.381**	p=70.3%; ρ=0.058	**p=0.1%; ρ=0.668**
Lesueurina platycephala	p=8.0%; ρ= 0.244	p=31.4%; ρ=0.046	p=39.7%; ρ=0.034
Sillago bassensis	**p=0.1%; ρ= 0.272**	**p=3.6%; ρ=0.158**	p=7.7%; ρ=0.153
Sillago schomburgkii	**p=1.4%; ρ= 0.262**	**p=0.1%; ρ=0.472**	**p=0.1%; ρ=0.511**
Sillago vittata	**p=0.1%; ρ= 0.312**	**p=2.7%; ρ=0.098**	**p=0.1%; ρ=0.435**
Pseudorhombus jenynsii	**p=1.3%; ρ= 0.452**	**p=4.1%; ρ=0.351**	p=11.6%; ρ=0.224

12.4 Discussion

12.4.1 Invertebrate communities

During this part of the study, the compositions of the taxa that comprised the benthic macroinvertebrate, hyperbenthic and zooplankton communities at three habitat types in nearshore, marine waters were compared, after adjusting the densities of those three components to the same unit, *i.e.* numbers m^{-2}. These comparisons demonstrated that the composition of the benthic macroinvertebrate community, which was sampled using a substrate corer, differed markedly from that of the zooplankton community, which was sampled using a plankton net in the middle of the water column. The fauna that typified the benthic macroinvertebrate community were polychaetes, gammarid amphipods and bivalves, while three orders of copepods (Harpacticoida, Calanoida and Cyclopoida) and planktonic gastropods typified the zooplankton community.

Although, on the ordination plot (Fig. 12.1), the samples of the hyperbenthic community were largely discrete from those of the zooplankton and, to an even greater extent, those of the benthic macroinvertebrates, they showed a marked tendency to occupy an intermediate position between those for the latter two components of the invertebrate fauna. This accounts for the fact that the hyperbenthic fauna, which was collected from just above the substrate using a modified small sled, contained some taxa that typified both this fauna and either the benthic macroinvertebrate or zooplankton assemblages. Thus, gammarid amphipods also typified the benthic macroinvertebrate fauna and calanoid and cyclopoid copepods also typified the zooplankton. However, the hyperbenthic fauna was distinguished from those of the benthic macroinvertebrates and zooplankton by the presence, in particular, of cumaceans. The members of this order of crustaceans, which are typically small, with a rounded and often ornate cephalothorax, small thoracic appendages and a relatively slender abdomen, live partially within and slightly above the substrate surface (Fage 1951). Likewise, the presence of polychaetes in samples from the hyperbenthos, as well as the benthos, reflects the fact that some members of this taxa, such as spionids, also extend from the upper part of the substrate into the water column. Since gammarids live on the substrate surface, and were thus susceptible to capture by both the small sled and substrate corer, it is not surprising that this taxon typifies both the hyperbenthic and benthic macroinvertebrate communities.

12.4.2 Relationships between dietary compositions of fish species and invertebrate communities

When using the RELATE subroutine in PRIMER and mean data for each habitat type and season to determine the extent to which the dietary compositions of the selected teleost species are correlated with those of the benthic macroinvertebrate, hyperbenthic and zooplankton assemblages, it must be recognised that a low correlation between the dietary compositions of a fish species and a particular invertebrate community implies that the fish species either does not feed on the members of that community or feeds only on certain members of that community. Thus, appropriate interpretation of the results of the RELATE procedure relies on direct knowledge of the composition of the prey ingested.

Although the diet of *Spratelloides robustus* was not correlated with the compositions of either the zooplankton or hyperbenthic communities, this clupeid fed very largely on calanoid copepods, which were abundant within the water column. This lack of correlation thus further emphasises that *S. robustus* either selectively fed on these small crustaceans and/or that the other members of the invertebrate community within the water column are unsuitable prey. Although the diet of *S. robustus* was correlated with the composition of the benthic macroinvertebrate fauna, the correlation was low. This finding is consistent with this typically planktivorous species switching to feeding non-selectively on prey within the benthos in winter, when the densities of calanoids were particularly low (see Chapter 8).

The high and moderate correlations between the dietary compositions of *Atherinomorus ogilbyi* and the zooplankton and benthic macroinvertebrate faunas, respectively, demonstrate that, while this atherinid feeds to a large extent in the water column, it also targets prey within the substrate (see also Prince *et al.* 1982). However, the lack of correlation between the diet of *A. ogilbyi* and the composition of the hyperbenthic fauna implies that, when this species switches from a planktonic to a more benthic mode of feeding, it does not browse along the substrate surface.

Lesueurina platycephala was the only species for which the diet was not significantly correlated with the compositions of any of the three main invertebrate communities. This was despite the fact that this species ingested large amounts of polychaetes and gammarid amphipods, which are both abundant in the benthos and the latter of which is abundant in the hyperbenthos. The implication that *L. platycephala* has a highly specialised mode of feeding is consistent with our conclusion that this leptoscopid is an ambush predator and, despite its small size, feeds on fish as well as the above invertebrates (Chapter 11). Although the other ambush predator, *Pseudorhombus jenynsii*, also fed on teleosts, it otherwise ingested, in particular, prey that were less common in the environment, such as mysids and brachyuran crabs (Chapters 10, 11). However, the significant correlations found between the diets of this pleuronectid and the composition of the benthic macroinvertebrate fauna, and even more particularly the hyperbenthic fauna, imply that the taxa within these communities are ingested in a relatively non-selective manner.

Uniquely, the diets of *Sillago schomburgkii* and *Sillago vittata* were both significantly correlated with the compositions of each of the benthic macroinvertebrate, hyperbenthic and zooplanktonic communities. Furthermore, the diet of the third sillaginid, *Sillago bassensis*, was correlated with the composition of the first two of those invertebrate communities. These results imply that these sillaginids feed on invertebrates over a wide vertical range in their environment and in a relatively non-selective manner. However, the ρ values for the correlations between the diets of these fish species and the invertebrate communities indicate that *S. bassensis* feeds to the greatest extent on benthic macroinvertebrates, while *S. schomburgkii* feeds to a considerable extent on members of both the hyperbenthic and zooplankton communities and *S. vittata* feeds mainly on benthic macroinvertebrates and zooplankon. These results, in turn, suggest that the food resources in nearshore, marine waters on the lower west coast of Australia are partitioned, to a certain extent, amongst these three morphologically similar congeneric species.

Benefits and adoption

The commercial and recreational fishers in Western Australia will benefit from the results of this study because it will enable better management of the fish resources in nearshore marine waters. In particular, the results of this project will enable managers to identify the key habitats of the most valuable fish species in these waters and thus devise plans for maintaining those habitats. These benefits and beneficiaries are as anticipated in the original project application. Prior to our study, there were no reliable and quantitative data on the ways in which key fish species were distributed among different habitat types in the nearshore coastal waters on the lower west coast of Australia. We have provided regular updates of the results of our research to the Department of Fisheries Western Australia and the Marine Branch of the Department of Conservation and Land Management, and will provide both of these agencies, and others which have expressed interest in the results of this study, with a copy of our Final Report once it has been approved by the FRDC. The application of the results of this research will be discussed with fisheries and natural resource managers to facilitate their adoption for the benefit of recreational and commercial fishers.

Further development

The results of this research will be disseminated further by discussing the potential uses of the approach with scientists and managers at the Department of Fisheries Western Australia and the Marine Branch of the Department of Conservation and Land Management. Seminars will also be delivered to other interested parties such as Recfishwest, WAFIC or the Royal Society of WA. In addition to those papers that have already been published or accepted for publication in international scientific journals, further results of the relationships between nearshore marine fauna and the various habitat types will be submitted for publication. An application has also recently been submitted to the FRDC for extending the current approach for identifying habitat types and their likely faunal compositions to the environments found in estuaries in south-western Australia.

Planned outcomes

The readily usable and quantitative method that has been developed during this study enables any site along the lower west coast of Australia to be assigned to its appropriate habitat type. The statistically significant associations that were identified between particular suites of the fish and invertebrate fauna and each of the various habitat types then enable the types of fauna that are likely to characterise any nearshore site to be predicted. Such reliable information was previously unavailable to environmental and fisheries managers along this coastline. The ability to readily make predictions of the likely faunal composition at any nearshore site will enable managers to devise more appropriate plans for protecting those nearshore areas that provide crucial habitats for key commercial and/or recreational fish species or contain a particularly diverse suite of fauna. The planned outcomes of the project will be realised increasingly as current management plans are revised and new coastal developments are proposed.

Conclusion

- This study has demonstrated that measurements for a suite of seven statistically-selected enduring environmental characteristics can be used, readily and reliably, to distinguish the different types of habitats found in nearshore marine waters along the lower west coast of Australia.
- The advantages of identifying habitat types using enduring environmental characteristics, rather than environmental variables that are subject to short-term temporal changes or the biota, reside in the fact that accurate measurements for these characteristics over large spatial scales can be obtained readily from remote sources, such as maps, and thus do not require measurements or sampling in the field.
- It is also considered disadvantageous to use biotic data to identify habitat types, as the acquisition of reliable biotic information would be very demanding in terms of resources and time and the resultant habitat types can only be used to explain the distribution of the type(s) of biota used for identifying those habitat types.
- The number of species, density, diversity and composition of the nearshore fish faunas differed significantly among habitat types along the lower west coast of Australia, irrespective of the time of day, season or year. Moreover, the extent of the ichthyofaunal differences among the various habitat types matches statistically those for the environmental characteristics that distinguish those habitat types.
- Some species characterised the ichthyofauna of only one habitat type. For example, *Silliginodes punctata* and *Pseudorhombus jenynsii* in the highly sheltered habitat type 1, *Arripis georgiana* and *Enoplosus armatus* in the moderately sheltered habitat type 2, *Pelsartia humeralis* and *Schuettea woodwardi* in the moderately exposed habitat type 4. Although several other species characterised more than one habitat type, they still exhibited a marked affinity for a particular habitat type. For example, while *Spratelloides robustus* characterised the faunas at habitat types 2-5, it occurred most consistently and was most abundant by far at habitat type 2, and *Sillago bassensis*, which characterised the faunas at habitat types 2-6, was far more prevalent at habitat type 4 than any of those other habitat types.
- The characteristics of the fish fauna at several of the habitat types differed significantly between day and night and/or among seasons. The diel differences were attributable mainly to onshore/offshore migrations of the small juveniles of certain fish species, such as *Spratelloides robustus* and *Hyperlophus vittatus*, and larger piscivorous species, *e.g. Arripis georgiana*, *Pseudocaranx dentex* and *Sphyraena novaehollandiae.* Seasonal differences were due largely to

time-staggered recruitments into the shallows of certain habitat types of large numbers of small 0+ juveniles of species such as *Sillago vittata, Sillago bassensis* and *Aldrichetta forsteri*.

- The compositions of the benthic macroinvertebrates, zooplankton, meiofauna (and particularly nematodes) and hyperbenthic fauna, which constitute the main prey of fish in nearshore waters, differed significantly among habitat types. In general, the spatial distinctions were least among the benthic macroinvertebrates.
- The dietary composition of abundant fish species in nearshore waters varied among habitat types, seasons and/or day and night, which could be related to differences in the densities and availability of their preferred prey. The order of importance of these spatial and temporal factors on dietary composition differed among species.
- Statistical comparison between the compositions of the diets of abundant fish species and those of the benthic macroinvertebrate, zooplankton and hyperbenthic assemblages in the various samples facilitated a precise identification of the location in the water column in which those fish species fed and the extent to which they targeted particular prey.
- From the above, it follows that managers are able to use values for the seven enduring environmental variables at any site of interest along the lower west coast of Australia to identify quantitatively the habitat type to which that site belongs and thus the fish species that are likely to be found at that site. The results of this study also provide a sound basis for scientists to test hypotheses regarding ecological inter-relationships in those waters in the future. Thus, managers are now in a far better position to be reactive and proactive in managing the environmental resources along the lower west coast of Australia, that are crucial for sustaining the stocks of recreational and commercial fish species that occupy those waters.

References

Abou-Seedo, F., Clayton, D. A. and Wright, J. M. (1990). Tidal and turbidity effects on the shallow-water fish assemblages of Kuwait Bay. *Marine Ecology Progress Series* **65**, 213-223.

Alldredge, A. L. and King, J. M. (1980). Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology* **44**, 133-156.

Alldredge, A. L. and King, J. M. (1985). The distance demersal zooplankton migrate above the benthos: implications for predation. *Marine Biology* **84**, 253-260.

Allee, R. J., Dethier, M. N., Brown, D., Deegan, L., Ford, R. G., Hourigan, T. F., Maragos, J., Schoch, G. C., Sealey, K., Twilley, R., Weinstein, M. P. and Yoklavich, M. (2000). *Marine and estuarine ecosystem and habitat classification*. NOAA Technical Memorandum NMFS-F/SPO-43 (America: U.S Department of Commerce). pp. 43.

Allen, L. G. and Horn, M. H. (1975). Abundance, diversity and seasonality of fishes in Colorado lagoon, Alamitos bay, California. *Estuarine and Coastal Marine Science* **3**, 371-380.

Allison, H. and Grassia, A. (1979). Sporadic sea-level oscillations along the Western Australian coastline. *Australian Journal of Marine and Freshwater Research* **30**, 723-730.

Alongi, D. M. (1986). Population structure and trophic composition of the free-living nematodes inhabiting carbonate sands of Davies Reef, Great Barrier Reef, Australia. *Australian Journal of Marine and Freshwater Research* **37**, 609-619.

Ambrose, R. F. and Anderson, T. W. (1990). Influence of artificial reef on the surrounding infaunal community. *Marine Biology* **107**, 41-52.

Andrew, N. L. and O'Neill, A. L. (2000). Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales. *Marine and Freshwater Research* **51**, 255-263.

Archambault, P. and Bourget, E. (1999). Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* **241**, 309-333.

Archambault, P., Roff, J., Bourget, E., Bang, B. and Ingram, G. (1998). Nearshore abundance of zooplankton in relation to shoreline configuration and mechanisms involved. *Journal of Plankton Research* **20**, 671-690.

Armonies, W. and Reise, K. (2000). Faunal diversity across a sandy shore. *Marine Ecology Progress Series* **196**, 49-57.

Arrivillaga, A. and Baltz, D. M. (1999). Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. *Bulletin of Marine Science* **65**, 301-319.

Arvanitidis, C., Bellan, G., Drakopoulos, P., Valavanis, V., Dounas, C., Koukouras, A. and Eleftheriou, A. (2002). Seascape biodiversity patterns along the Mediterranean and Black Sea: lessons from the biogeography of benthic polychaetes.. *Marine Ecology Progress Series* **244**, 139-152.

Australian Bureau of Statistics. (2001). *2001 Census of population and housing*. 4th August 2003. http://www.abs.gov.au/websitedbs/D3310114.NSF/4a256353001af3ed4b2562bb00121

Ayvazian, S. G. and Hyndes, G. A. (1995). Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Marine Biology* **122**, 527-536.

Azeiteiro, U. M. M. and Marques, J. C. (1999). Temporal and spatial structure in the suprabenthic community of a shallow estuary (western Portugal: Mondego river estuary). *Acta Oecologica* **20**, 333-342.

Bally, R. (1981). *The ecology of three sandy beaches on the west coast of South Africa*. PhD Thesis. (South Africa: University of Cape Town).

Banks, S. A. and Skilleter, G. A. (2002). Mapping intertidal habitats and an evaluation of their conservation status in Queensland, Australia. *Ocean and Coastal Management* **45**, 485-509.

Barnes, R. D. (1987). *Invertebrate Zoology*. USA: CBS College Publishing.

Barnes, R. S. K. and Hughes, R. N. (1998). *An Introduction to Marine Ecology*. Oxford: Blackwell Scientific Publications.

Barrett, N., Sanderson, J. C., Lawler, M., Halley, V. and Jordan, A. (2001). *Mapping of Inshore Marine Habitats in South-Eastern Tasmania for Marine Protected Area Planning and Marine Management*. Technical Report Series no. 7 (Tasmania: Tasmanian Aquaculture and Fisheries Institute). pp. 1-74.

Barros, F., Underwood, A. J. and Lindergarth, M. (2001). The influence of rocky reefs on the structure of bethic macrofauna in nearby soft sediments. *Estuarine, Coastal and Shelf Science* **52**, 191-199.

Barros, F., Underwood, A. J. and Lindergarth, M. (2002). A preliminary analysis of the structure of benthic assemblages of surf zones on two morphodynamic types of beach. *Journal of the Marine Biological Association of the United Kingdom* **82**, 353-357.

Batchelder, H. P., Edwards, C. A. and Powell, T. M. (2002). Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Progress in Oceanography* **53**, 307-333.

Bell, S. S. and Sherman, K. M. (1980). A field investigation of meiofaunal dispersal: tidal resuspension and implications. *Marine Ecology Progress Series* **3**, 245-249.

Bennett, B. A. (1989). The fish community of a moderately exposed beach on the southwestern cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Estuarine, Coastal and Shelf Science* **28**, 293-305.

Bennett, J. (1992). *Australian Seashores; adapted from W.J. Dakin's Australian Seashores.* New South Wales: Collins/Angus & Robertson.

Beyst, B., Hostens, K. and Mees, J. (2001a). Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. *Journal of Sea Research* **46**, 281-294.

Beyst, B., Buysse, D., Dewicke, A. and Mees, J. (2001b). Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns. *Estuarine, Coastal and Shelf Science* **53**, 877-895.

Beyst, B., Hostens, K. and Mees, J. (2002). Factors influencing the spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium. *Journal of the Marine Biological Association of the United Kingdom* **82**, 181-187.

Bird, E. (2000). *Coastal Morphology. An Introduction*. Chichester, England: John Wiley and Sons, Ltd.

Blaber, S. J. M. and Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* **17**, 143-162.

Blaber, S. J. M. and Bulman, S. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific value, dietary overlap and trophic relationships. *Marine Biology* **95**, 345-356.

Blaber, S. J. M., Brewer, D. T. and Salini, J. P. (1995). Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. *Estuarine, Coastal and Shelf Science* **40**, 177-193.

Blome, D., Schleier, U. and Bernem, K.-H. v. (1999). Analysis of the small-scale spatial patterns of free-living marine nematodes from tidal flats in the East Frisian Wadden Sea. *Marine Biology* **133**, 717-726.

Blomgren, S. and Hanson, H. (2000). Coastal geomorphology at the Falsterbo Peninsula, southern Sweden. *Journal of Coastal Research* **16**, 15-25.

Bowman Bishaw Gorham. (1994). *Characterization of study areas: Habitat mapping / Bowman Bishaw Gorham*. (Western Australia: Water Authority of Western Australia).

Bouillon, S., Raman, A. V., Dauby, P. and Dehairs, F. (2002). Carbon and Nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). *Estuarine, Coastal and Shelf Science* **54**, 901-913.

Brazeiro, A. (2001). Relationship between species richness and morphodynamics in sandy beaches: what are the underlying factors?. *Marine Ecology Progress Series* **224**, 35-44.

Brazner, J. C. and Beals, E. W. (1997). Patterns in fish assemblages from coastal wetland and beach habitats in Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors. *Canadian Journal of Fish and Aquatic Science* **54**, 1743-1761.

Brown, A. C. and McLachlan, A. (1990). *Ecology of Sandy Shores*. Amsterdam: Elsevier Science Publishers B.V.

Burrows, M. T., Gibson, R. N., Robb, L. and Comely, C. A. (1994). Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *Journal of Experimental Marine Biology and Ecology* **177**, 251-268.

Cahoon, L. B. and Tronzo, C. R. (1992). Quantitative estimates of demersal zooplankton abundance in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series* **87**, 197-200.

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M. and Duarte, C. M. (2001). Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *Journal of Plankton Research* **23**, 319-331.

Calliari, L. J. (1994). Cross-shore and longshore sediment size distribution on southern currituck spit, North Carolina: implications for beach differentiation. *Journal of Coastal Research* **10**, 360-373.

Cambridge, M. L. and McComb, A. J. (1984). The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* **20**, 229-243.

Cambridge, M. L., Chiffings, A. W., Brittan, C., Moore, L. and McComb, A. J. (1986). The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquatic Botany* **24**, 269-285.

Cappo, M., Alongi, D. M., Williams, D. and Duke, N. (1998). *A Review and Synthesis of Australian Fisheries Habitat Research: Major threats, issues and gaps in knowledge of coastal and marine fisheries habitats - a prospectus of opportunities for the FRDC "ecosystem protection program" Volume 2: Scoping Review*. FRDC 95/055 (Australia: Australian Institute of Marine Science *for* Fisheries Research and Development Corporation). pp. 1-319.

Caputi, N., Fletcher, W. J., Pearce, A. and Chubb, C. F. (1996). Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research* **47**, 147-155.

Carranza-Edwards, A. and Rosales-Hoz, L. (1995). Grain-size trends and provenance of southwestern Gulf of Mexico beach sands. *Canadian Journal of Earth Sciences* **32**, 2009-2014.

Carranza-Edwards, A., Bocanegra-García, G., Rosales-Hoz, L. and de Pablo Galán, L. (1998). Beach sands from Baja California peninsula, Mexico. *Sedimentary Geology* **119**, 263-274.

Carter, R. W. G. (1988). *Coastal Environments: An introduction to the physical, ecological and cultural systems of coastlines*. London: Harcourt Brace Jovanovich.

Chamberlain, R. H. and Barnhart, R. A. (1993). Early use by fish of a mitigation salt marsh, Humboldt Bay, California. *Estuaries* **16**, 769-783.

Chesney, E. J., Baltz, D. M. and Thomas, R. G. (2000). Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecological Applications* **10**, 350-366.

Chubb, C. F., Potter, I. C., Grant, C. J., Lenanton, R. C. J. and Wallace, J. (1981). Age structure, growth rates and movements of Sea Mullet, *Mugil cephalus* L., and Yellow-eye Mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon river system, Western Australia. *Australian Journal of Marine and Freshwater Research* **32**, 605-628.

Clark, B. M., Bennett, B. A. and Lamberth, S. J. (1996a). Factors affecting spatial variability in seine net catches of fish in the surf zone of False Bay, South Africa. *Marine Ecology Progress Series* **131**, 17-34.

Clark, B. M., Bennett, B. A. and Lamberth, S. J. (1996b). Temporal variations in surf zone fish assemblages from False Bay, South Africa. *Marine Ecology Progress Series* **131**, 35-47.

Clarke, D. J. and Eliot, I. G. (1983). Mean sea-level and beach-width variation at Scarborough, Western Australia. *Marine Geology* **51**, 251-267.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143.

Clarke, K. R. and Gorley, R. N. (2001). *PRIMER v5: User Manual/Tutorial.* Plymouth: PRIMER-E.

Clarke, K. R. and Green, R. H. (1988). Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series* **46**, 213-226.

Clarke, K. R. and Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* **35**, 523-531.

Clarke, K. R. and Warwick, R. M. (2001a). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. PRIMER-E Ltd: Plymouth Marine Laboratory, U.K.

Clarke, K. R. and Warwick, R. M. (2001b). A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* **216**, 265-278.

Clarke, K. R., Chapman, M. G. and Somerfield, P. J. (in prep). Modified Bray-Curtis similarity calculations for vanishingly sparse and highly clustered species assemblages.

Cloern, J. E. (2001). Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* **210**, 223-253.

Colebrook, J. M. (1977). Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955-59. *Fisheries Bulletin* **75**, 357-368.

Connelly, D. P., Readman, J. W., Knap, A. H. and Davies, J. (2001). Contamination of the coastal waters of Bermuda by organotins and the triazine herbicide Itgarol 1051. *Marine Pollution Bulletin* **42**, 409-414.

Connor, D. W. (1997). *Marine Biotope Classification for Britain and Ireland.* (Peterborough, U.K.: Joint Nature Conservation Review).

Constable , A. J. (1999). Ecology of benthic macroinvertebrates in soft-sediment environments: A review of progress towards quantitative models and predictions. *Australian Journal of Ecology* **24**, 452-476.

Coogee Coastal Action Coalition. (2002). *Metropolitan Region Scheme Amendment.* No. 1010/33 (Perth: Coogee Coastal Action Coalition).

Coull, B. C. (1988). Ecology of marine meiofauna. In *Introduction to Marine Meiofauna*, (eds. R. P. Higgins and H. Thiel), pp. 18-38.

Coull, B. C. (1999). Role of meiofauna in estuarine soft-bottom habitats. *Australian Journal of Ecology* **24**, 327-343.

Coull, B. C. and Bell, S. S. (1979). Perspectives of marine meiofaunal ecology. In *Ecological Processes in Coastal and Marine Ecosystems*, (ed. R. J. Livingstone), pp. 189-216.

Coull, B. C., Greenwood, J. G., Fielder, D. R. and Coull, B. A. (1995). Subtropical Australian juvenile fish eat mieofauna: experiments with winter whiting *Sillago maculata* and observations on other species. *Marine Ecology Progress Series* **125**, 13-19.

Creach, V., Schricke, M. T., Bertru, G. and Mariotti, A. (1997). Stable isotopes and gut analyses to determine feeding relationships in saltmarsh macroconsumers. *Estuarine, Coastal and Shelf Science* **44**, 599-611.

Cresswell, G. R. and Golding, T. J. (1980). Observations of a south-flowing current in the southeastern Indian Ocean. *Deep Sea Research* **27A**, 449-466.

Cunha, M. R., Sorbe, J. C. and Bernardes, C. (1997). On the stucture of the neritic suprabenthic communities from the Portuguese continental margin. *Marine Ecology Progress Series* **157**, 119-137.

D'Adamo, N. (1992). *Hydrodynamics and recommendations for further studies in Cockburn Sound and adjacent waters.* (Perth: Environmental Protection Authority of Western Australia).

Dahl, E. (1952). Some aspects of the ecology and zonation of the fauna on sandy beaches. *OIKOS* **4**, 1-27.

Danovaro, R. (2002). Biodiversity and trophic structure of nematode assemblages in sea grass systems: evidence for a coupling with changes in food availability. *Marine Biology* **141**, 667-677.

Dauvin, J. C. and Zouhiri, S. (1996). Suprabenthic crustacean fauna of a dense *Ampelisca* community from the English Channel. *Journal of the Marine Biology Association of the United Kingdom* **76**, 909-929.

Dauvin, J. C., Iglesias, A. and Lorgeré, J. C. (1994). Circalittoral suprabenthic coarse sand community from the western English Channel. *Journal of the Marine Biology Association of the United Kingdom* **74**, 543-562.

Dauvin, J. C., Vallet, C., Mouny, P. and Zouhiri, S. (2000). Main characteristics of the boundary layer macrofauna in the English Channel. *Hydrobiologia* **426**, 139-156.

Davies, J. L. (1964). A morphogenic approach to world shorelines. *Zeitschrift für Geomorphologie* **8**, 127-142.

Davis, C. S., Gallager, S. M. and Solow, A. R. (1992). Microaggregations of oceanic plankton observed by towed video microscopy. *Science* **257**, 230-232.

Day, J. C. and Roff, J. C. (2000). *Planning for Representative Marine Protected Areas: A framework for Canada's Oceans*. Report prepared for World Wildlife Fund Canada: Toronto.

Dean, T. A., Haldorson, L., Laur, D. R., Jewett, S. C. and Blanchard, A. (2000). The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: associations with vegetation and physical habitat characteristics. *Environmental Biology of Fishes* **57**, 271-287.

Defeo, O. (1993). *The Effect of Spatial Scales in Population Dynamics and Modelling of Sedentary Fisheries: the Yellow Clam Mesodesma mactroides of an Uruguyan Exposed Sandy Beach.* Ph.D. Thesis. (Unidad Mérida, Mexico: CINVESTAV-IPN

Defeo, O. (1996). Experimental management of an exploited sandy beach bivalve population. *Revista Chilena de Historia Natural* **69**, 605-614.

Defeo, O., Jaramillo, E. and Lyonnet, A. (1992). Community and intertidal zonation of the macroinfauna on the Atlantic Coast of Uruguay. *Journal of Coastal Research* **8**, 830-839.

Defeo, O., Brazeiro, A., de Alva, A. and Riestra, G. (1997). Is sandy beach macrofauna only physically controlled? Role of substrate and competition in isopods. *Estuarine, Coastal and Shelf Science* **45**, 453-462.

Department of Defence. (1998). *Australian National Tide Tables , 1998.* (Australian Oceanographic Publication 11: Department of Defence). pp. 372.

Department of Environmental Protection. (1996). *Southern Metropolitan Coastal Waters Study (1991-1994). Final Report*. (Perth, Western Australia: Department of Environmental Protection). pp. 288.

Department of Planning and Infrastructure. (2003). *Coastal data centre: Tide predictions, Fremantle*. 4th August 2003. http://www.coastaldata.transport.wa.gov.au/tides/predictions.html

Department of Primary Industries, Water and Environment, Tasmania. (2000). *Tasmanian Marine Protected Areas Strategy: Background Report*. (Tasmania: Department of Primary Industries, Water and Environment). pp. 109.

Dethier, M. N. (1992). Classifying marine and estuarine natural communities: an alternative to the cowardin system. *Natural Areas Journal* **12**, 90-100.

Dexter, D. M. (1979). Community structure and seasonal variation in intertidal Panamanian sandy beaches. *Estuarine and Coastal Marine Science* **9**, 543-558.

Dexter, D. M. (1983). Community structure of intertidal sandy beaches in New South Wales, Australia. In *Sandy Beaches as Ecosystems*, (eds. A. McLachlan and T. Erasmus), pp. 461-472. The Hague: W. Junk Publishers.

Dexter, D. M. (1984). Temporal and spatial variability in the community structure of the fauna of four sandy beaches in south-eastern New South Wales. *Australian Journal of Marine and Freshwater Research.* **35**, 663-672.

Dexter, D. M. (1985). Distribution and life-histories of abundant crustaceans of four sandy beaches of south-eastern New South Wales. *Australian Journal of Marine and Freshwater Research* **36**, 281-289.

Dexter, D. M. (1989). Sandy beach fauna of Egypt. *Estuarine, Coastal and Shelf Science* **29**, 261-271.

Dexter, D. M. (1992). Sandy beach community structure: the role of exposure and latitude. *Journal of Biogeography* **19**, 59-66.

Diggle, P. J. (1983). *Statistical Analysis of Spatial Point Patterns*. London: Academic Press.

Dittmann, S. (2000). Zonation of benthic communities in a tropical tidal flat of north-east Australia. *Journal of Sea Research* **43**, 33-51.

Doucette, J. S. (2000). The distribution of nearshore bedforms and effects on sand suspension on low-energy, micro-tidal beaches in southwestern Australia. *Marine Geology* **165**, 41-61.

Du Preez, H. H., McLachlan, A., Marais, J. F. K. and Cockcroft, A. C. (1990). Bioenergetics of fishes in a high-energy surf-zone. *Marine Biology* **106**, 1-12.

Duffy, J. E. and Hay, M. E. (2000). Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* **70**, 237-263.

Dugan, J. E., Hubbard, D. M., Engle, J. M., Martin, D. L., Richards, D. M., Davies, G. E., Lafferty, K. E. and Ambrose, R. F. (2000). Macrofauna communities of exposed sandy beaches on the southern California mainland and Channel Islands. In *Fifth California Islands Symposium, OCS Study*. pp. 339-346.

Edgar, G. J. (1990). The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. *Journal of Experimental Marine Biology and Ecology* **137**, 215-240.

Edgar, G. J. (2001). *Australian Marine Habitats in Temperate Waters*. Australia: Reed New Holland.

Edgar, G. J. and Shaw, C. (1995a). The production and trophic ecology of shallow water assemblages in southern Australia: II Diets of fishes and the trophic relationships between fishes and benthos at Western Point, Victoria. *Journal of Experimental Marine Biology and Ecology* **194**, 83-106.

Edgar, G. J. and Shaw, C. (1995b). The production and trophic ecology of shallow water fish assemblages in southern Australia III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* **194**, 107-131.

Edgar, G. J., Shaw, C., Watson, G. F. and Hammond, L. S. (1994). Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **176**, 201-226.

Edyvane, K. S. (1999). *Conserving Marine Biodiversity in South Australia - Part 1 - Background, Status and Review of Approach to Marine Biodiversity Conservation in South Australia*. (South Australia: South Australian Research and Development Institute).

Eliot, I. and Clarke, D. J. (1986). Minor storm impact on the beach face of a sheltered sandy beach. *Marine Geology* **73**, 61-83.

Eliot, I., Clarke, D. J. and Rhodes, A. (1982). Beach-width variation at Scarborough, Western Australia. *Journal of the Royal Society of Western Australia* **65**, 153-158.

Ellis, M. J. and Coull, B. C. (1989). Fish predation on meiobenthos: field experiments with juvenile spot *Leiostomus xanthurus* Lacépède. *Journal of Experimental Marine Biology and Ecology* **130**, 19-32.

Environmental Protection Authority. (2000). *Managing Perth's Coastal Waters: Towards a Cockburn Sound Environmental Protection Policy (EEP). A public explanatory document.* (Perth: Environmental Protection Authority). pp. 1-11.

Environmental Resources of Australia. (1971a). *The Ecology of Cockburn Sound, Summer 1970-71.* (Western Australia: Fremantle Port Authority).

Environmental Resources of Australia. (1971b). *The Cockburn Sound Ecosystem, Autumn 1972.* (Western Australia: Fremantle Port Authority).

Emery, A. R. (1968). Preliminary observations on coral reef plankton. *Limnology and Oceanography* **13**, 293-303.

Erwin, D. G. (1983). The community concept. In *Sublittoral Ecology: The Ecology of the Shallow Sublittoral Benthos*, (eds. R. Earll and D. G. Erwin), pp. 145-207. Oxford: Clarendon Press.

European Environmental Agency. (2002). *EUNIS Habitat classification. Version 2.3.* 4th August 2003. http://mrw.wallonie.be/dgrne/sibw/EUNIS/home.html

Fage, L. (1951). Faune de France: 54 Cumacés, pp. 1-136. Paris: Muséum National d'Histoire Naturelle.

Fairclough, D. V., Dimmlich, W. F. and Potter, I. C. (2000). Reproductive biology of the Australian herring *Arripis georgiana*. *Marine and Freshwater Research* **51**, 619-630.

Faubel, A. (1976). Population dynamics and life cycles of interstitial Acoela and Macrostomida (Turbellaria). Investigations of a middle lotic sandy beach of the Island of Sylt. *Microfauna Meeresbodens* **56**, 1-107.

Fauchald, K. and Jumars, P. A. (1979). The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology: an Annual Review* **17**, 193-284.

Ferns, L. W. and Hough, D. (2002). *High Resolution Marine Habitat Mapping of the Bunurong Coast (Victoria) - Including the Bunurong Marine and Coastal Park.* Melbourne: Parks, Flora and Fauna Division, Department of Natural Resources and Environment.

Ferns, L. W., Hough, D. and Catlin, J. (1999). *Environmental Inventory of Victoria's Marine Ecosystems Stage 3 (2nd Edition) - Understanding Biodiversity Representativeness of Victoria's Rocky Reefs*. Melbourne.

Field, J. G., Clarke, K. R. and Warwick, R. M. (1982). A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* **8**, 37-52.

Fisher, R. (2003). Spatial and temporal variations in nematode assemblages in tropical seagrass sediments. *Hydrobiologia* **493**, 49-63.

Fleischack, P. C. and de Freitas, A. J. (1989). Physical parameters influencing the zonation of surf zone benthos. *Estuarine, Coastal and Shelf Science* **28**, 517-530.

Fonseca, M. S. and Cahalan, J. A. (1992). A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine, Coastal and Shelf Science* **35**, 565-576.

Friedlander, A. M. and Parrish, J. D. (1998). Temporal dynamics of fish communities on an exposed shoreline in Hawaii. *Environmental Biology of Fishes* **53**, 1-18.

Frost, M. T., Rowden, A. A. and Attrill, M. J. (1999). Effect of habit fragmentation on the macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**, 255-263.

Frouin, P., Hily, C. and Hutchings, P. (1998). Ecology of spionid polychaetes in the swash zone of exposed beaches in Tahiti (French Polynesia). *Ecology* **321**, 47-54.

Gaughan, D. J. (1992). Feeding by estuarine and marine fish larvae. In *Larval Biology: Proceedings No. 15*, (ed. D. A. Hancock). Canberra: Australian Government Publishing Service.

Gaughan, D. J. and Fletcher, W. J. (1997). Effects of the Leeuwin Current on the distribution of carnivorous macrozooplankton in the shelf waters off Southern Western Australia. *Estuarine, Coastal and Shelf Science* **45**, 89-97.

Gaughan, D. J. and Potter, I. C. (1994). Relative abundance and seasonal changes in the macrozooplankton of the lower Swan Estuary in south-western Australia. *Records of the Western Australian Museum Supplement* **16**, 461-474.

Gaughan, D. J. and Potter, I. C. (1995). Composition, distribution and seasonal abundance of zooplankton in a shallow, seasonally closed estuary in temperate Australia. *Estuarine, Coastal and Shelf Science* **41**, 117-135.

Gaughan, D. J., Fletcher, W. J. and Tregonning, R. J. (1996). Spatial and seasonal distribution of eggs and larvae of sandy sprat, *Hyperlophus vittatus* (Clupeidae), off South-western Australia. *Marine and Freshwater Research* **47**, 971-979.

Gaus, C., Papke, O., Dennison, N., Haynes, D., Shaw, G. R., Connell, D. W. and Muller, J. F. (2001). Evidence for the presence of a widespread PCDD source in coastal sediments and soils from Queensland, Australia. *Chemosphere* **43**, 549-558.

Gee, J. M. (1989). An ecological and economic review of meiofauna as food for fish. *Zoological Journal of the Linnean Society* **96**, 243-261.

Gentilli, J., (ed)**.** (1971). *World Survey of Climatology. Volume 13. Climate of Australia and New Zealand.* Amsterdam: Elsevier Publishing Company.

Gerking, S. D. (1994). *Feeding ecology of fish*. San Diego: Academic Press.

Gerlach, S. A. and Riemann, F. (1973/1974). The Bremehavenchecklist of aquatic nematodes. A cataloge of Nematoda Adenophera excluding the Dorylaimida. *Veroffentlichungen des Instituts fuer Meersforschung in Bremerhaven* **Suppl. 4, part 1(1973) and part 2 (1974)**, 1-736.

Gibson, R. N., Ansell, A. D. and Robb, L. (1993). Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. *Marine Ecology Progress Series* **98**, 89-105.

Gibson, R. N., Robb, L., Burrows, M. T. and Ansell, A. D. (1996). Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. *Marine Ecology Progress Series* **130**, 1-17.

Gibson, R. N., Pihl, L., Burrows, M. T., Modin, J., Wennhage, H. and Nickell, L. A. (1998). Diel movements of juvenile plaice *Pleuronecies platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* **165**, 145-159.

Gierre, O. (1993). *Meiobenthology: The Microscopic Fauna in Aquatic Sediments*. Berlin: Springer-Verlag.

Gierre, O. and Pfannkuche, O. (1992). Biology and ecology of marine oligochaeta, a review. *Oceanography and Marine Biology: an Annual Review* **20**, 173-308.

Gilligan, M. R. (1980). Beta diversity of a Gulf of California rocky-shore fish community. *Environmental Biology of Fishes* **5**, 109-116.

Glasby, C., Hutchings, P., Fauchald, K., Paxton, H., Rouse, G. W., Watson, R. C. and Wilson, R. S. (2000). Class Polychaeta. In *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol.4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*, (eds. P. L. Beesley G. J. B. Ross and C. Glasby). Melbourne: CSIRO Publishing.

Goh, J. (1992). *The biology of the sandy sprat Hyperlophus vittatus in coastal waters along the west coast of Australia*. BSc (Hons) Thesis. (Perth: Murdoch University).

Gomman, M. F., Glover, J. C. M. and Kuiter, R. H., (eds). (1994). *The Fishes of Australia's South Coast*. Adelaide: State Print.

Gotceitas, V., Fraser, S. and Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Canadian Journal of Fish and Aquatic Science* **54**, 1306-1319.

Greenslade, P. (1989). Checklist of free-living marine nematodes from Australia, Macquarie Island and Heard Island. *Records of the South Australia Museum* **23**, 7-19.

Grémare, A., Medernach, L., deBovée, F., Amouroux, J. M., Vétion, G. and Albert, P. (2002). Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). *Marine Ecology Progress Series* **234**, 85-94.

Guidetti, P. (2000). Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuarine, Coastal and Shelf Science* **50**, 515-529.

Guillén, J. and Hoekstra, P. (1997). Sediment distribution in the nearshore zone: grain size evolution in response to the shoreface nourishment (island of Terschelling, The Netherlands). *Estuarine, Coastal and Shelf Science* **45**, 639-652.

Gunn, J. S. and Milward, N. E. (1985). The food, feeding habits and feeding structures of the whiting species *Sillago sihama* Forsskål and *Sillago analis* Whitley from Townsville, North Queensland, Australia. *Journal of Fish Biology* **26**, 411-427.

Hakala, T., Viitasalo, M., Rita, H., Aro, E., Flinkman, J. and Vuorinen, I. (2003). Temporal and spatial variation in the growth rates of Baltic herring (*Clupea harengus membras* L.) larvae during summer. *Marine Biology* **142**, 25-33.

Hamner, W. M. and Carlton, J. H. (1979). Copepod swarms: attributes and roles in coral reef ecosystems. *Limnology and Oceanography* **24**, 1-14.

Hansen, J. A. (1984). *Accumulate's of macrophyte wrack along sandy beaches in Western Australia*. PhD Thesis. (Perth: University of Western Australia).

Harkantra, S. and Parulekar, A. (1984). Intertidal benthic community ecology of sand-dwelling macroinvertebrates of Goa beaches. In *Biology of Benthic Organisms*, (eds. M. F. Thompson R. Seijorni and R. Nayabhushanam). Delhi: Oxford & IBH Publishing Co.

Harris, S. A. and Cyrus, D. P. (1996). Larval and juvenile fishes in the surf zone Adjacent to the St Lucia estuary mouth, KwaZulu-Natal, South Africa`. *Marine and Freshwater Research* **47**, 465-482.

Harvey, C. J. (1998). Use of sandy beach habitat by *Fundulus majalis*, a surf-zone fish. *Marine Ecology Progress Series* **164**, 307-310.

Hatcher, B. G. (1991). Coral reefs in the Leeuwin current - an ecological perspective. *Journal of the Royal Society of Western Australia* **74**, 115-127.

Havens, K. E. (1998). Size structure and energetics in a plankton food web. *OIKOS* **81**, 346-358.

Haynes, D. and Quinn, G. P. (1995). Temporal and spatial variability in community structure of a sandy intertidal beach, Cape Paterson, Victoria, Australia. *Marine and Freshwater Research* **46**, 931-942.

Heath, M. R., Henderson, E. W. and Baird, D. L. (1988). Vertical distribution of herring larvae in relation to physical mixing and illumination. *Marine Ecology Progress Series* **47**, 211-228.

Heck, K. L., Jr, Hays, G. and Orth, R. J. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* **253**, 123-136.

Hegge, B. (1994). *Low energy sandy beaches of southwestern Australia: 2D morphology, sediments and dynamics*. PhD Thesis. (Perth: University of Western Australia).

Hegge, B., Eliot, I. and Hsu, J. (1996). Sheltered sandy beaches of southwestern Australia. *Journal of Coastal Research* **12**, 748-760.

Heip, C., Vincx, M. and Vranken, G. (1985). The ecology of marine nematodes. *Oceanography and Marine Biology: an Annual Review* **23**, 399-489.

Helleren, S. K. R. and John, J. (1997). *Phytoplankton and Zooplankton Dynamics in the Southern Metropolitan Coastal Waters, Perth*. (Western Australia: Curtain University of Technology).

Henry, G. W. and Lyle, J. M. (Eds). (2003). *The National Recreational and Indigenous Fishing Survey*. FRDC Project No. 99/158 (Canberra: Fisheries Research and Development Corporation).

Hicks, G. and Coull, B. C. (1983). The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology: an Annual Review* **21**, 67-175.

Hodgkin, E. P. and di Lollo, V. (1958). The tides of south-western Australia. *Journal of the Royal Society of Western Australia* **41**, 42-54.

Holmes, R. A. and Gibson, R. N. (1983). A comparison of predatory behaviour in flatfish. *Animal Behaviour* **31**, 1244-1255.

Horner Rosser, S. M. J. and Thompson, P. A. (2001). Phytoplankton of the Swan-Canning Estuary: a comparison of nitrogen uptake by different bloom assemblages. *Hydrological Processes* **15**, 2579-2594.

Hourston, M., Platell, M. E., Valesini, F. J. and Potter, I. C. (submitted). Factors influencing the diets of four morphologically divergent fish species in nearshore marine waters. *Journal of the Marine Biological Association of the United Kingdom.*

Howard, R. K. (1989). The structure of a nearshore fish community of Western Australia: diel patterns and the habitat role of limestone reefs. *Environmental Biology of Fishes* **24**, 93-104.

Howard, R. K., Edgar, G. J. and Hutchings, P. (1989). Faunal assemblages of seagrass beds. In *Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australasian Region*, (eds. A. W. D. Larkum A. J. McComb and S. A. Shepherd), pp. 536-564. North Holland: Elsevier.

Howes, D., Harper, J. and Owens, E. (1994). *Physical shore-zone mapping system for British Columbia*. (British Columbia: Resource Inventory Committee).

Humphries, P. and Potter, I. C. (1993). Relationship between the habitat and diet of three species of atherinids and three species of gobies in a temperate Australian estuary. *Marine Biology* **116**, 193-204.

Huntley, M. (1985). Experimental approaches to the study of vertical migration of zooplankton. In *Migration, mechanisms and adaptive significance - contributions in marine science*, vol. 37 (ed. M. A. Rankin), pp. 71-90. Austin: Marine Science Institute University of Texas.

Hutchings, P. A. (1981). The fauna of Australian seagrass beds In *Proceedings of the Linnean Society of New South Wales*. pp. 181-200.

Hutchings, P. and Jacoby, C. A. (1994). Temporal and spatial patterns in the distribution of infaunal polychaetes in Jervis Bay, New South Wales, Australia. In *Actes de la 4ème Conférence internationale des Polychètes.*, vol. 162 (eds. J. C. Dauvin L. Laubier and D. J. Reish), pp. 441-452. Paris: *Mém. Mus. natn. Hist. nat.*

Hutchins, B. and Swainston, R. (1986). *Sea Fishes of Southern Australia*. Perth: Swainston Publishing.

Hutchins, J. B. (1991). Dispersal of tropical fishes to temperate seas in the southern hemisphere. *Journal of the Royal Society of Western Australia* **74**, 79-84.

Hutchins, J. B. and Pearce, A. F. (1994). Influence of the Leeuwin current on recruitment of tropical reef fishes at Rottnest Island, Western Australia. *Bulletin of Marine Science* **54**, 245-255.

Huys, R., Herman, P. M. J., Heip, C. and Soetaert, K. (1992). The meiobenthos of the North Sea: density, biomass trends and distribution of copepods communities. *ICES Journal of Marine Science* **49**.

Hyndes, G. A. and Potter, I. C. (1996). Comparisons between the age structures, growth and reproductive biology of two co-occuring sillaginids, *Sillago robusta* and *S. bassensis*, in temperate coastal waters of Australia. *Journal of Fish Biology* **49**, 14-32.

Hyndes, G. A., Potter, I. C. and Lenanton, R. C. J. (1996a). Habitat partitioning by whiting species (*Sillaginidae*) in coastal waters. *Environmental Biology of Fishes* **45**, 21-40.

Hyndes, G. A., Potter, I. C. and Hesp, S. A. (1996b). Relationships between the movements, growth, age structures, and reproductive biology of the teleosts *Sillago burrus* and *S. vittata* in temperate marine waters. *Marine Biology* **126**, 549-558.

Hyndes, G. A., Platell, M. E. and Potter, I. C. (1997). Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. *Marine Biology* **128**, 585-598.

Hyndes, G. A., Platell, M. E., Potter, I. C. and Lenanton, R. C. J. (1998). Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia. *Fishery Bulletin* **96**, 258-270.

Hynes, H. B. N. (1950). The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* **19**, 36-58.

Hyslop, E. J. (1980). Stomach content analysis - a review of methods and their application. *Journal of Fish Biology* **17**, 411-429.

Interim Marine and Coastal Regionalisation of Australia Technical Group. (1998). *An ecosystem-based classification for marine and coastal environments.* Version 3.3 (Canberra: Australian and New Zealand Environment and Conservation Council).

Jackson, N. L., Nordstrom, K. F., Eliot, I. and Masselink, G. (2002). 'Low energy' sandy beaches in marine and estuarine environments: a review. *Geomorphology* **48**, 147-162.

Jacoby, C. A. and Greenwood, J. G. (1989). Emergent zooplankton in Moreton Bay, Queensland, Australia: seasonal, lunar, and diel patterns in emergence and distribution with respect to substrata. *Marine Ecology Progress Series* **51**, 131-154.

James, R. J. and Fairweather, P. G. (1996). Spatial variation of intertidal macrofauna on a sandy ocean beach in Australia. *Estuarine, Coastal and Shelf Science* **43**, 81-107.

Jaramillo, E. and McLachlan, A. (1993). Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. *Estuarine, Coastal and Shelf Science* **37**, 615-624.

Jaramillo, E., Contreras, H., Duarte, C. and Quijon, P. (2001). Relationships between community structure of the intertidal macroinfauna and sandy beach characteristics along the Chilean coast. *Marine Ecology* **22**, 323-342.

Jenkins, G. P., Black, K. P., Wheatley, M. J. and Hatton, D. N. (1997a). Temporal and spatial variability in recruitment of a temperate, seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. *Marine Ecology Progress Series* **148**, 23-35.

Jenkins, G. P., May, H. M. A., Wheatley, M. J. and Holloway, M. G. (1997b). Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. *Estuarine, Coastal and Shelf Science* **44**, 569-588.

Jenkins, G. P., Welsford, D. C., Heough, M. J. and Hamer, P. A. (1998). Diurnal and tidal vertical migration of pre-settlement King George whiting *Sillaginodes punctata* in relation to feeding and vertical distribution of prey in a temperate bay. *Marine Ecology Progress Series* **170**, 239-248.

John, J. (2000). *Diatom prediction and classification system for urban streams. A model from Perth, Western Australia.* (Canberra: Land and Water Resources Research and Development Corporation).

Jones, A. R. (1986). Spatial and temporal variations in a community of nektobenthic invertebrates from Moreton Bay, Queensland. *Estuarine, Coastal and Shelf Science* **23**, 131-146.

Jones, A. R. and Short, A. D. (1995). Sandy Beaches. In *Coastal Marine Ecology of Temperate Australia*, (eds. A. J. Underwood and M. G. Chapman), pp. 137-151. Sydney: Institute of Marine Ecology.

Jorgensen, B. B. and Revsbech, N. P. (1983). Photosynthesis and the structure of benthic microbial mats: Microelectrode and SEM studies of four cyanobacterial communities. *Limnology and Oceanography* **28**, 1075-1093.

Karjalainen, J., Rahkola, M., Viljanen, M., Andronikova, I. N. and Avinskii, V. A. (1996). Comparison of methods used in zooplankton sampling and counting in the joint Russian-Finnish evaluation of the trophic state of Lake Ladoga. *Hydrobiologia* **322**, 249-253.

Kempin, E. T. (1952). Beach sand movements at Cottesloe, Western Australia. *Journal of the Royal Society of Western Australia* **37**, 35-58.

Kendrick, G. A., Hegge, B. J., Wyllie, A., Davidson, A. and Lord, D. A. (2000). Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. *Estuarine, Coastal and Shelf Science* **50**, 341-353.

Kendrick, G. A., Aylward, M. J., Hegge, B. J., Cambridge, M. L., Hillman, K., Wyllie, A. and Lord, D. A. (2002). Changes in seagrass coverage in Cockburn Sound, Western Australia between 1967 and 1999. *Aquatic Botany* **73**, 75-87.

Kennedy, A. D. and Jacoby, C. A. (1997). Biological indicators of marine environmental health: meiofauna - a neglected benthic component. *Environmental Monitoring and Assessment* **54**, 47-68.

Kennish, M. J. (1990). *Ecology of Estuaries: Volume II Biological Aspects*. Florida: CRC Press Inc.

Kerr, S. R. and Ryder, R. A. (1989). Current approaches to multispecies analyses of marine fisheries. *Canadian Journal of Fish and Aquatic Science* **46**, 528-535.

Kikuchi, T. (1980). Faunal relationships in temperate seagrass beds. In *Handbook of Seagrass Biology: An Ecosystem Perspective*, (eds. R. C. Phillips and C. P. McRoy), pp. 153-167. New York: Garland STM Press.

Kimmera, W. J., McKinnon, A. D., Atkinson, M. J. and Kessell, J. A. (1985). Spatial distributions of plankton in Shark Bay, Western Australia. *Journal of Marine and freshwater Research* **36**, 421-432.

King, C. A. M. (1972). *Beaches and Coasts*. London: Edward Arnold Ltd.

Kingsford, M. J. (1992). Drift algae and small fish in coastal waters of northeastern New Zealand. *Marine Ecology Progress Series* **80**, 41-55.

Kingsford, M. J. (1995). Planktonic Processes. In *Coastal Marine Ecology of Temperate Australia*, (eds. A. J. Underwood and M. G. Chapman), pp. 28-41. Sydney: University of New South Wales Press Ltd.

Kirkman, H. (1985). Community structure in seagrasses in southern Western Australia. *Aquatic Botany* **21**, 363-375.

Kirkman, H. and Walker, D. I. (1989). Regional studies - Western Australian seagrasses. In *Biology of seagrasses; a treatise on the biology of seagrasses with special reference to the Australian region*, (eds. A. W. D. Larkum A. J. McComb and S. A. Shepard), pp. 157-181. Amsterdam: Elsevier.

Klein, M. and Zviely, D. (2001). The environmental impact of marina development of adjacent beaches: a case study of the Herzliya marina, Israel. *Applied Geography* **21**, 145-156.

Knott, D. M., Calder, D. R. and Van Dolah, R. F. (1983). Macrobenthos of sandy beach and nearshore environments at Murrells Inlet, South Carolina, U.S.A.. *Estuarine, Coastal and Shelf Science* **16**, 573-590.

Knox, G. A. (1994). *The Biology of the Southern Ocean*. Cambridge: Cambridge University Press.

Kobayashi, T., Shiel, R. J., Gibbs, P. and Dixon, P. I. (1998). Freshwater zooplankton in the Hawkesbury-Nepean River: comparison of community structure with other rivers. *Hydrobiologia* **377**, 133-145.

Kokita, T. and Nakazono, A. (2000). Seasonal variation in the diel spawning time of the coral reef fish *Oxymonacanthus longirostris* (Monacanthidae): parental control of progeny development. *Marine Ecology Progress Series* **199**, 263-270.

Kuo, S. R., Lin, H. J. and Shao, K. T. (2001). Seasonal changes in abundance and composition of the fish assemblage in Chiku lagoon, southwestern Taiwan. *Bulletin of Marine Science* **68**, 85-99.

Labropoulou, M. and Eleftheriou, A. (1997). The foraging strategy of two pairs of congeneric demersal fish species: the importance of morphological characteristics in prey selection. *Journal of Fish Biology* **50**, 324-340.

Labropoulou, M., Tserpes, G. and Tsimenides, N. (1998). Age, growth and feeding habits of the brown comber *Serranus hepatus* (Linnaeus, 1758) on the Cretan Shelf. *Estuarine, Coastal and Shelf Science* **46**, 723-732.

Lasiak, T. A. (1981). Nursery grounds of juvenile teleosts: evidence from the surf zone of king's beach, Port Elizabeth. *South African Journal of Science* **77**, 388-390.

Lasiak, T. A. (1984). Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: long-term fluctuations. *Estuarine, Coastal and Shelf Science* **18**, 459-483.

Lasiak, T. A. (1986). Juveniles, food and the surf zone habitat: implications for teleost nursery areas. *south African Journal of Zoology* **21**, 51-56.

Layman, C. A. (2000). Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia barrier Islands. *Estuarine, Coastal and Shelf Science* **51**, 201-213.

Lazzari, M. A. and Tupper, B. (2002). Importance of shallow water habitats for demersal fishes and decapod crustaceans in Penobscot Bay, Maine. *Environmental Biology of Fishes* **63**, 57-66.

Leber, K. M. (1982). Seasonality of macroinvertebrates on a temperate, high wave energy sandy beach. *Bulletin of Marine Science* **32**, 86-98.

Lemm, A. J., Hegge, B. J. and Masselink, G. (1999). Offshore wave climate, Perth (Western Australia), 1994-96. *Marine and Freshwater Research* **50**, 95-102.

Lenanton, R. C. J. (1982). Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Australian Journal of Marine and Freshwater Research* **33**, 881-900.

Lenanton, R. C. J. and Caputi, N. (1989). The roles of food supply and shelter in the relationship between fishes, in particular *Cnidoglanis macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. *Journal of Experimental Marine Biology and Ecology* **128**, 165-176.

Lenanton, R. C. J., Robertson, A. I. and Hansen, J. A. (1982). Nearshore accumulations of detached macrophytes as nursery areas for fish. *Marine Ecology Progress Series* **9**, 51-57.

Lenanton, R. C. J., Joll, L., Penn, J. and Jones, K. (1991). The influence of the Leeuwin Current on coastal fisheries of Western Australia. *Journal of the Proceedings of the Royal Society of Western Australia* **74**, 101-114.

Levinton, J. S. (1979). Deposit-feeders, their resources, and the study of resource limitation. In *Ecological Processes in Coastal and Marine Systems*, (ed. R. J. Livingston). New York: Plenum Press.

Lindeman, K. C. and Snyder, D. B. (1999). Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging. *Fishery Bulletin* **97**, 508-525.

Linke, T. E., Platell, M. E. and Potter, I. C. (2001). Factors affecting the partitioning of food resources among six fish species in a large embayment with juxtaposing bare sand and seagrass habitats. *Journal of Experimental Marine Biology and Ecology* **266**, 193-217.

Lippman, T. C. and Holman, R. A. (1990). The spatial and temporal variability of sand bar morphology. *Journal of Geophysical Research* **95**, 11,575-11,590.

Lock, K. and Mees, J. (1999). The winter hyperbenthos of the Ria Formosa - a lagoon in southern Portugal - and adjacent waters. *Cahiers de Biologie Marine* **40**, 47-56.

Lund, M. A. and Davis, J. A. (2000). Seasonal dynamics of plankton communities and water chemistry in a eutrophic wetland (Lake Monger, Western Australia): implications for biomanipulation. *Marine and Freshwater Research* **51**, 321-332.

M.P. Rogers & Associates Pty Ltd. (1995). *Owen Anchorage wave study - model set-up, calibration and verification. Prepared for Cockburn Cement Limited*. report R008 Rev 1 (Perth).

MacKenzie, B. R., Miller, T. J., Cyr, S. and Leggett, W. C. (1994). Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography* **39**, 1790-1799.

Macquart-Moulin, C. (1999). Diel vertical migration and endogenous swimming rhythm in *Asterpe mariae* (Baird) and *Philomedes interpuncta* (Baird) (Crustacea Ostracoda Cypridinidae). *Journal of Plankton Research* **21**, 1891-1910.

Maloney, C. L., Field, J. G. and Lucas, M. I. (1991). The size-based dynamics of plankton food webs II, simulations of three contrasting southern Benguela food webs. *Journal of Plankton Research* **13**, 1039-1092.

Marcotte, B. M. (1983). The imperatives of copepod diversity: perception, cognition, competition and predation. In *Crustacean Phylogeny*, (ed. F. R. Schram), pp. 47-72.

Masselink, G. (1996). Sea-breeze activity and its effect on coastal processes near Perth, Western Australia. *Journal of the Royal Society of Western Australia* **79**, 199-205.

Masselink, G. and Pattiaratchi, C. (1998). Morphodynamic impact of sea breeze activity on a beach with beach cusp morphology. *Journal of Coastal Research* **14**, 393-406.

Masselink, G. and Pattiaratchi, C. B. (2001a). Characteristics of the sea breeze system in Perth, Western Australia, and its effect on the nearshore wave climate. *Journal of Coastal Research* **17**, 173-187.

Masselink, G. and Pattiaratchi, C. B. (2001b). Seasonal changes in beach morphology along the sheltered coastline of Perth, Western Australia. *Marine Geology* **172**, 243-263.

Masselink, G. and Short, A. D. (1993). The effect of tide range on beach morphodynamics and morphology: a conceptual beach model. *Journal of Coastal Research* **9**, 785-800.

Mattila, J., Chaplin, G., Eilers, M. R., Heck, K. L. J., O'Neal, J. P. and Valentine, J. F. (1999). Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). *Journal of Sea Research* **41**, 321-332.

Mauchline, J. (1998). *The Biology of Calanoid Copepods. (Advances in Marine Biology vol. 33).* London: Academic Press.

Maxwell, J. G. H. and Cresswell, G. R. (1981). Dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. *Australian Journal of Marine and Freshwater Research* **32**, 493-500.

McArdle, S. B. and McLachlan, A. (1992). Dynamics of the swash zone and effluent line on sandy beaches. *Marine Ecology Progress Series* **76**, 91-99.

McIntyre, A. D. and Murison, D. J. (1973). The meiofauna of a flatfish nursery ground. *Journal of the Marine Biological Association of the United Kingdom* **53**, 93-118.

McLachlan, A. (1977). Composition, distribution, abundance and biomass of the macrofauna and meiofauna of four sandy beaches. *Zoologica Africana* **12**, 279-306.

McLachlan, A. (1978). A quantitative analysis of the meiofauna and the chemistry of the redox potential discontinuity zone in a sheltered sandy beach. *Estuarine, Coastal and Shelf Science* **7**, 275-290.

McLachlan, A. (1983). Sandy beach ecology - a review. In *Sandy Beaches as Ecosystems*, (eds. A. McLachlan and T. Erasmus), pp. 321-379. Netherlands: Dr W. Junk Publishers.

McLachlan, A. (1985). The biomass of macro-and interstitial fauna on clean and wrack covered beaches in Western Australia. *Estuarine, Coastal and Shelf Science* **21**, 587-599.

McLachlan, A. (1990). Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research* **6**, 57-71.

McLachlan, A. and Jaramillo, E. (1995). Zonation on sandy beaches. *Oceanography and Marine Biology: an Annual Review* **33**, 305-335.

McLachlan, A. and Hesp, P. (1984). Faunal response to morphology and water circulation of a sandy beach with cusps. *Marine Ecology Progress Series* **19**, 133-144.

McLachlan, A., Wooldridge, T. and Dye, A. H. (1981). The ecology of sandy beaches in southern Africa. *South African Journal of Zoology* **16**, 219-231.

McLachlan, A., Cockcroft, A. C. and Malan, D. E. (1984). Benthic faunal response to a high energy gradient. *Marine Ecology Progress Series* **16**, 51-63.

McLachlan, A., Jaramillo, E., Donn, T. E. and Wessels, F. (1993). Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *Journal of Coastal Research* **15** (special issue), 27-38.

McLachlan, A., Fisher, M., Al-Habsi, H., Al-Shukairi, S. and Al-Habsi, A. (1998). Ecology of sandy beaches in Oman. *Journal of Coastal Conservation* **4**, 181-190.

McLusky, D. S. and Elliot, M. (1981). The feeding and survival of estuarine mollusks. In *Feeding and Survival Strategies of Estuarine Organisms*, (eds. N. V. Jones and W. J. Wolff), pp. 36-51. New York: Plenum Press.

Mees, J. and Jones, M. B. (1997). The hyperbenthos. *Oceanography and Marine Biology: an Annual Review* **35**, 221-255.

Mees, J., Dewicke, A. and Hammerlynk, O. (1993). Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. *Netherlands Journal of Aquatic Ecology* **27**, 359-376.

Menge, B. A. and Farrell, T. M. (1989). Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Advances in Ecological Research* **19**, 189-262.

Menge, B. A. and Sutherland, J. P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**, 730-757.

Menn, I. (2002). Beach morphology and food web structure: comparison of an eroding and an accreting sandy shore in the North Sea. *Helgoland Marine Research* **56**, 177–189.

Mileikovsky, S. A. (1973). Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Marine Biology* **23**, 11-17.

Mills, D. A. and D'Adamo, N. (1995). *The application of a three-dimensional baroclinic model to the hydrodynamics and transport of coastal waters between Fremantle and Mandurah, Western Australia: the interconnectedness of the coastal zone*. (Perth: Department of Environmental Protection).

Modde, T. and Ross, S. T. (1981). Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. *Fishery Bulletin* **78**, 911-922.

Modde, T. and Ross, S. T. (1983). Trophic relationships of fishes occurring within a surf zone habitat in the northern gulf of Mexico. *Northeast Gulf Science* **6**, 109-120.

Moens, T. and Vincx, M. (1997). Observations on the feeding ecology of estuarine nematodes. *Journal of the Marine Biological Association of the United Kingdom* **77**, 211-227.

Moens, T., Van Gansbeke, D. and Vincx, M. (1999). Linking estuarine nematodes to their suspected food. A case study from the Westerschelde Estuary (south -west Netherlands). *Journal of the Marine Biological Association of the United Kingdom* **79**, 1017-1027.

Möller, P., Pihl, L. and Rosenberg, R. (1985). Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. *Marine Ecology Progress Series* **27**, 109-121.

Möller, I., Spencer, T., French, J. R., Leggett, D. J. and Dixon, M. (1999). Wave transformation over salt marshes: a field and numerical modelling study from north Norfolk, England. *Estuarine, Coastal and Shelf Science* **49**, 411-426.

Morin, J. G., Kastendiek, J. E., Harrington, A. and Davis, N. (1985). Organization and patterns of interactions in a subtidal sand community on an exposed coast. *Marine Ecology Progress Series* **27**, 163-185.

Morrisey, D. J., Underwood, A. J., Howitt, H. and Stark, J. S. (1992). Temporal variation in soft-sediment benthos. *Journal of Experimental Marine Biology and Ecology* **164**, 233-245.

Mueter, F. J. and Norcross, B. L. (1999). Linking community structure of small demersal fishes around Kodiak Island, Alaska, to environmental variables. *Marine Ecology Progress Series* **190**, 37-51.

Mullin, M. M. and Onbé, T. (1991). Diel reproduction and vertical distributions of the marine cladocerans, *Evadne tergestina* and *Penilia avirostris*, in contrasting coastal environments. *Journal of Plankton Research* **14**, 41-59.

Mumby, P. J. and Harborne, A. R. (1999). Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. *Biological Conservation* **88**, 155-163.

Muniz, P. and Pires, A. M. S. (1999). Trophic structure of polychaetes in the Sao Sebastiao Channel (southeastern Brazil). *Marine Biology* **134**, 517-528.

National Oceans Office and Fisheries Research and Development Corporation. (2002). *Marine Classification System Workshop*. 23 - 24 September 2002 pp. 1-84.

Nash, R. D. M., Santos, R. S., Geffen, A. J., Hughes, G. and Ellis, T. R. (1994). Diel variability in catch rate of juvenile flatfish on two small nursery grounds (Port Erin Bay, Isle of Man and Porto Pim Bay, Faial, Azores). *Journal of Fish Biology* **44**, 35-45.

Netto, S. A., Atrill, M. J. and Warwick, R. M. (1999). The effect of a natural water-movement related disturbance on the structure of meiofauna and macrofauna communities in the intertidal sand flat of Rocas Atoll (NE, Brazil). *Journal of Sea Research* **42**, 291-302.

Newell, G. E. and Newell, R. C. (1963). *Marine Plankton: A Practical Guide*. London: Hutchinson Educational.

Nicholas, W. L. (2001). Seasonal variations in nematode assemblages on an Australian temperate ocean beach; the effect of heavy seas and unusually high tides. *Hydrobiologia* **464**, 17-26.

Nicholas, W. L. and Hodda, M. (1999). The free living nematodes of a temperate, high energy, sandy beach: faunal composition and variation over time. *Hydrobiologia* **394**, 113-127.

Noda, M., Ikeda, I., Shunshiroh, U., Hashimoto, H. and Gushima, K. (1998). Enrichment of coastal zooplankton communities by drifting zooplankton patches from the Kuroshio front. *Marine Ecology Progress Series* **170**, 55-65.

Nordstrom, K. F. (1994). Beaches and dunes of human-altered coasts. *Physical Geography* **18**, 497-516.

Ochieng, C. A. and Erftemeijer, P. L. A. (1999). Accumulation of seagrass beach cast along the Kenyan coast: a quantitative assessment. *Aquatic Botany* **65**, 221-238.

O'Hara, T. D. (2001). Consistency of faunal and floral assemblages within temperate subtidal rocky reef habitats. *Marine and Freshwater Research* **52**, 853-863.

Onbé, T. and Ikea, T. (1995). Marine cladocerans in Toyama Bay, southern Japan Sea: seasonal occurrence and day-night vertical distributions. *Journal of Plankton Research* **7**, 595-609.

Ornellas, A. B. and Coutinho, R. (1998). Spatial and temporal patterns of distribution and abundance of a tropical fish assemblage in a seasonal *Sargassum* bed, Cabo Frio Island, Brazil. *Journal of Fish Biology* **53** (Supplement A), 198-208.

Orth, R. J. and Heck, K. L., Jr. (1980). Structural components of eelgrass (*Zostera marina*) meadows in the lower chesapeake bay - fishes. *Estuaries* **3**, 278-288.

Pagès, F. and Gili, J. M. (1991). Effects of large-scale advective processes on the gelatinous zooplankton population in the northern Benguela ecosystem. *Marine Ecology Progress Series* **75**, 205-215.

Palmer, M. A. (1986). Hydrodynamics and structure: interactive effects on meiofauna dispersal. *Journal of Experimental Marine Biology and Ecology* **104**, 53-68.

Pattiaratchi, C. B. and Buchan, S. J. (1991). Implications of long-term climate change for the Leeuwin Current. *Journal of the Royal Society of Western Australia* **74**, 133-140.

Pattiaratchi, C., Hegge, B., Gould, J. and Eliot, I. (1997). Impact of sea-breeze activity on nearshore and foreshore processes in southwestern Australia. *Continental Shelf Research* **17**, 1539-1560.

Pearce, R. J. (1991a). Management of the marine environment in Western Australia: an ecosystem approach. *Marine Pollution Bulletin* **23**, 567-572.

Pearce, A. F. (1991b). Eastern boundary currents of the southern hemisphere. *Journal of the Royal Society of Western Australia* **74**, 35-45.

Pearse, A. S., Humm, H. J. and Wharton, G. W. (1942). Ecology of Sand Beaches at Beaufort, N.C. *Ecological Monographs* **12**, 137-181.

Penn, J. W. (2002). *State of the Fisheries Report, 2001/2002.* (Perth: Department of Fisheries).

Perissinotto, R. and McQuaid, C. (1990). Role of the sub-antarctic shrimp *Nauticaris marionis* in coupling benthic and pelagic food webs. *Marine Ecology Progress Series* **64**, 81-87.

Phillips, F. E. and Fleeger, J. W. (1985). Meiofauna meso-scale variability in two estuarine habitats. *Estuarine, Coastal and Shelf Science* **21**, 745-756.

Phillips, J. C., Kendrick, G. A. and Lavery, P. S. (1997). A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. *Marine Ecology Progress Series* **153**, 124-138.

Pihl, L. (1985). Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Marine Ecology Progress Series* **22**, 169-179.

Pihl, L. (1986). Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research* **20**, 75-83.

Pihl, L. and Wennhage, H. (2002). Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. *Journal of Fish Biology* **61**, 1-19.

Platell, M. E. and Potter, I. C. (1999). Partitioning of habitat and prey by abundant and similar sized species of the Triglidae and Pempherididae (Teleostei) in coastal waters. *Estuarine, Coastal and Shelf Science* **48**, 235-252.

Platell, M. E. and Potter, I. C. (2001). Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. *Journal of Experimental Marine Biology and Ecology* **261**, 31-54.

Platell, M. E., Sarre, G. A. and Potter, I. C. (1997). The diets of two co-occurring marine teleosts *Parequula melbournensis* and *Pseudocaranx wrighti*, and their relationships to body size and mouth morphology, and the season and location of capture. *Environmental Biology of Fishes* **49**, 361-376.

Platell, M. E., Potter, I. C. and Clarke, K. R. (1998). Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. *Marine Biology* **131**, 719-734.

Platt, H. M. and Warwick, R. M. (1988). *Free-Living Marine Nematodes: Part II. British Chromadorids*. Shrewsbury: Field Studies Council.

Posey, M. H. and Ambrose, W. G., Jr**.** (1994). Effects of proximity to an off-shore hard-bottom reef on infaunal abundances. *Marine Biology* **118**, 745-753.

Prince, J. D., Potter, I. C., Lenanton, R. C. J. and Loneragan, N. R. (1982). Segregation and feeding of Atherinid species (Telestei) in south-western Australian estuaries. *Australian Journal of Marine and Freshwater Research* **33**, 865-880.

Pyökäri, M. and Lehtovaara, J. J. (1993). Beach material and its transport in accordance with the predominant and prevailing wave directions on some shores in northern Greece. *Journal of Coastal Research* **9**, 609-627.

Ray, C. G. (1991). Coastal-zone Biodiversity patterns: principles of landscape ecology may help explain the processes underlying coastal diversity. *Bioscience* **41**, 490-499.

Rios-Jara, E. (1998). Spatial and temporal variations in the zooplankton community of Phosphorescent Bay, Puerto Rico. *Estuarine, Coastal and Shelf Science* **46**, 797-809.

Ritz, D. A. (1994). Social aggregation in pelagic invertebrates. *Advances in Marine Biology* **30**, 155-216.

Robblee, M. B. and Zieman, J. C. (1984). Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bulletin of Marine Science* **34**, 335-345.

Robertson, A. I. (1980). The structure and organization of an eelgrass fish fauna. *Oecologia* **47**, 76-82.

Robertson, A. I. and Lenanton, R. C. J. (1984). Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. *Journal of Experimental Marine Biology and Ecology* **84**, 265-283.

Robinson, C. L. K. and Levings, C. D. (1995). *An overview of habitat classification systems, ecological models, and geographic information systems applied to shallow foreshore marine habitats. Canadian manuscript report of fisheries and aquatic sciences 2322*. British Columbia: Department of Fisheries and Oceans Science Branch.

Roff, J. C. and Evans, S. M. J. (2002). Frameworks for marine conservation - non-hierarchial approaches and distinctive habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* **12**, 635-648.

Roff, J. C. and Taylor, M. E. (2000). National frameworks for marine conservation - a hierarchial geophysical approach. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**, 209-223.

Roff, J. C., Taylor, M. E. and Laughren, J. (2003). Geophysical approaches to the classification, delineation and monitoring of marine habitats and their communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**, 77-90.

Rose, K. A. (2000). Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecological Applications* **10**, 367-385.

Ross, S. T. (1986). Resource partitioning in fish assemblages: a review of field studies. *Copeia* **2**, 352-388.

Ross, S. T., McMichael, R. H., Jr and Ruple, D. L. (1987). Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. *Estuarine, Coastal and Shelf Science* **25**, 391-412.

Rossi, R. and Underwood, A. J. (2002). Small-scale disturbance and increased nutrients as influences on intertidal macrobenthic assemblages: experimental burial of wrack in different intertidal environments. *Marine Ecology Progress Series* **241**, 29-39.

Rowe, P. M. and Epifanio, C. E. (1994). Tidal stream transport of weakfish larvae in Delaware Bay, USA. *Marine Ecology Progress Series* **110**, 105-114.

Salvat, B. (1964). Les conditions hydrodynamiques interstitielles des sédiment meubles intertidaux et la repartition verticale de la jemme endogée. *Academie des Sciences (Paris), Comptes Rendus* **259**, 1576-1579.

San Vicente, C. and Sorbe, J. C. (1999). Spatio-temporal structure of the suprabenthic community from Creixell beach (western Mediterranean). *Acta Oecologica* **20**, 377-389.

Sanchez-Jerez, P., Barbera-Cebrian, C. and Ramos-Espla, A. A. (2000). Influence of the structure of *Posidonia oceanica* meadows modified by bottom trawling on crustacean assemblages: comparison of amphipods and decapods. *Scientia Marina* **64**, 319-326.

Sanders, H. L. (1958). Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnology and Oceanography* **3**, 245-258.

Sanders, H. L. (1968). Marine benthic diversity: a comparative study. *The American Naturalist* **102**, 243-282.

Sanderson, P. G. (1997). *Cuspate forelands on the west coast of Western Australia*. PhD Thesis. (Perth: University of Western Australia).

Sanderson, P. G. (2000). A comparison of reef-protected environments in Western Australia: the central west and ningaloo coasts. *Earth Surface Processes and Landforms* **25**, 397-419.

Sanderson, P. G. and Eliot, I. (1996). Shoreline salients, cuspate forelands and tombolos on the coast of Western Australia. *Journal of Coastal Research* **12**, 761-773.

Sanderson, P. G., Eliot, I., Hegge, B. and Maxwell, S. (2000). Regional variation of coastal morphology in southwestern Australia: a synthesis. *Geomorphology* **34**, 73-88.

Schafer, L. N., Platell, M. E., Valesini, F. J. and Potter, I. C. (2002). Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *Journal of Experimental Marine Biology and Ecology* **278**, 67-92.

Schoch, G. C. and Dethier, M. N. (1996). Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. *Journal of Experimental Marine Biology and Ecology* **201**, 37-72.

Schratzberger, M., Rees, H. L. and Boyd, S. E. (2000). Effects of simulated deposition of dredged material on structure of nematode assemblages - the role of contamination. *Marine Biology* **137**, 613-622.

Schreider, M. J., Glasby, T. M. and Underwood, A. J. (2003). Effects of height on the shore and complexity of habitat on abundances of amphipods on rocky shores in New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology* **293**, 57-71.

Scott, J. K. (1981). The seagrass fish fauna of Geographe Bay, Western Australia. *Journal of the Royal Society of Western Australia* **63**, 97-102.

Searle, D. J. (1984). *Sediment transport system, Perth sector Rottnest shelf, W.A.* PhD Thesis. (Perth: University of Western Australia).

Searle, D. J. and Semeniuk, V. (1985). The natural sectors of the inner Rottnest shelf coast adjoining the swan coastal plain. *Journal of the Royal Society of Western Australia* **67**, 116-136.

Searle, D. J. and Semeniuk, V. (1988). Pertology and origin of beach sand along the Rottnest shelf coast, southwestern Australia. *Journal of the Royal Society of Western Australia* **70**, 119-128.

Semeniuk, V. and Searle, D. J. (1986). The whitfords cusp - its geomorphology, stratigraphy and age structure. *Journal of the Royal Society of Western Australia* **68**, 29-36.

Shaghude, Y. W. and Wannäs, K. O. (1998). Morphology and sediment distribution of the Zanzibar channel. *Ambio* **27**, 729-733.

Shanks, A. L., McCulloch, A. and Miller, J. (2003). Topographically generated fronts, very nearshore oceanography and the distribution of larval invertebrates and holoplankters. *Journal of Plankton Research* **25**, 1251-1277.

Shaw, M. and Jenkins, G. P. (1992). Spatial variation in feeding, prey distribution and food limitation of juvenile flounder *Rhombosolea tapirina* Günther. *Journal of Experimental Marine Biology and Ecology* **165**, 1-21.

Shaw, W. and Robinson, C. L. K. (1998). Night versus day abundance estimates of zooplankton at two coastal stations in British Columbia, Canada. *Marine Ecology Progress Series* **175**, 143-153.

Shepherd, R. A., Knott, B. and Eliot, I. G. (1988). The relationship of juvenile southern mole crabs *Hippa australis* Hale (Crustacea: Anamura: Hippidae) to surficial swash water-circulation over several diurnal spring-tide cycles during winter conditions on a micro-tidal sandy beach. *Journal of Experimental Marine Biology and Ecology* **121**, 209-225.

Shih, S. and Komar, P. D. (1994). Sediments, beach morphology and sea cliff erosion within an Oregon coast littoral cell. *Journal of Coastal Research* **10**, 144-157.

Short, A. D. (1999). *Handbook of Beach and Shoreface Morphodynamics*. Chichester, England: John Wiley and Sons, Ltd.

Short, A. D. and Wright, L. D. (1983). Physical variability of sandy beaches. In *Sandy Beaches as Ecosystems*, (eds. A. McLachlan and T. Erasmus), pp. 133-144. Netherlands: Dr W. Junk Publishers.

Silberstein, K., Chiffings, A. W. and McComb, A. J. (1986). The loss of seagrass in Cockburn Sound, Western Australia. III. the effect of epiphytes on productivity of *Posidonia australis* Hook. F. *Aquatic Botany* **24**, 355-371.

Skilleter, G. A. and Loneragan, N. R. (in press). Assessing the importance of coastal habitats for fisheries, biodiversity and marine reserves: a new approach taking into account "habitat mosaics" In *Proceedings of the World Congress of Aquatic Protected Areas*. (Cairns, Queensland)

Somerfield, P. J. and Clarke, K. R. (1995). Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* **127**, 113-119.

Sorbe, J. C. (1981). Rôle du benthos dans la régime alimentaire des poissons démer-saux du secteur Sud Gascogne. *Kieler Meeresforschungen sonderheft* **5**, 479-489.

Suchanek, T. H. (1994). Temperate coastal marine communities: biodiversity and threats. *American Zoology* **34**, 100-114.

Sundbäck, K., Miles, A. and Göransson, E. (2000). Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: an annual study. *Marine Ecology Progress Series* **200**, 59-76.

Takahashi, K. and Kawaguchi, K. (1995). Inter- and intraspecific zonation in three species of sand-burrowing mysids, *Archaeomysis kokubi, A. grebnitzkii* and *Iiella ohshimai*, in Otsuchi Bay, northeastern Japan. *Marine Ecology Progress Series* **116**, 75-84.

Takahashi, K. and Kawaguchi, K. (1997). Diel and tidal migrations of the sand-burrowing mysids, *Archaeomysis kokubi, A. japonica* and *Iiella ohshimai*, in Otsuchi Bay, northeastern Japan. *Marine Ecology Progress Series* **148**, 95-107.

Tararam, A. S., Wakabara, Y. and Flynn, M. N. (1996). Suprabenthic community of the Cananeia lagoon estuarine region, southeastern Brazil. *Cahiers de Biologie Marine* **37**, 295-308.

The Planning Group. (2002). *South Beach Structure Plan Report*. 702.164 (Perth: The Planning Group). pp. 1-49.

Tita, G., Desrosiers, G., Vincx, M. and Clement, M. (2002). Intertidal meiofauna of the St Lawrence estuary (Quebec, Canada): diversity, biomass and feeding structure of nematode assemblages. *Journal of the Marine Biological Association of the United Kingdom* **82**, 779-791.

Tolosa, I., Readman, J. W., Blaevoet, A., Ghilini, S., Bartocci, J. and Horvat, M. (1996). Contamination of Mediterranean (Cote d'azur) coastal waters by organotins and Irgarol 1051 used in antifouling paints. *Marine Pollution Bulletin* **32**, 335-341.

Travers, M. J. and Potter, I. C. (2002). Factors influencing the characteristics of fish assemblages in a large subtropical marine embayment. *Journal of Fish Biology* **61**, 764-784.

Valesini, F. J., Potter, I. C., Hyndes, G. A. and Platell, M. E. (1998). *The fish faunas in the vicinity of the proposed Port Kennedy Marina development, with particular reference to the sandy sprat (Hyperlophus vittatus) and the blue sprat (Spratelloides robustus).* (Perth: Murdoch University). pp. 17.

Valesini, F. J., Clarke, K. R., Eliot, I. and Potter, I. C. (2003). A user friendly quantitative approach to classifying nearshore marine habitats along a heterogeneous coast. *Journal of Experimental Marine Biology and Ecology* **56**, 1-15.

Vallet, C. and Dauvin, J. C. (1998). Composition and diversity of the benthic boundary layer macrofauna from the English Channel. *Journal of the Marine Biology Association of the United Kingdom* **78**, 387-409.

Vallet, C. and Dauvin, J. C. (1999). Seasonal changes of macrozooplankton and benthic boundary layer macrofauna from the Bay of Saint-Brieuc (western English Channel). *Journal of Plankton Research* **21**, 35-49.

van der Spoel, S. and Heyman, R. P. (1983). *A Comparative Atlas of Zooplankton: Biological Patterns in the Ocean*. Berlin: Springer-Verlag.

Vanderklift, M. A. (1996). *Influence of adjacent seagrass on the fish assemblages off sandy beaches*. Masters Thesis. (Perth: Edith Cowan University).

Vanderklift, M. A. and Jacoby, C. A. (2003). Patterns in fish assemblages 25 years after major seagrass loss. *Marine Ecology Progress Series* **247**, 225-235.

Vizzini, S. and Mazzola, A., 2003. Seasonal variation in the stable carbon and nitrogen isotope ratios (C-13/C-12 and N-15/N-14) of primary producers and consumers in a western Mediterranean coastal lagoon. *Marine Biology*, **142**, 1009-1018.

Wang, Z. and Dauvin, J. C. (1994). The suprabenthic crustacean fauna of the infralittoral fine sand community from the Bay of Seine (eastern English Channel): composition, swimming activity and diurnal variation. *Cahiers de Biologie Marine* **35**, 135-155.

Ward, T. J., Vanderklift, M. A., Nicholls, A. O. and Kenchington, R. A. (1999). Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* **9**, 691-698.

Warwick, R. M. (1971). Nematode associations in the Exe Estuary. *Journal of the Marine Biological Association of the United Kingdom* **51**, 439-454.

Warwick, R. M. and Clarke, K. R. (1995). New "biodiversity" measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* **129**, 301-305.

Warwick, R. M. and Clarke, K. R. (1998). Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology* **35**, 532-543.

Warwick, R. M. and Clarke, K. R. (2001). Practical measures of marine biodiversity based on relatedness of species. *Oceanography and Marine Biology: an Annual Review* **39**, 207-231.

Warwick, R. M., Clarke, K. R. and Gee, J. M. (1990). The effect of disturbance by soldier crabs, *Mictyrus platychelas* H. Milne Edwards, on meiobenthic community structure. *Journal of Experimental Marine Biology and Ecology* **135**, 19-33.

Warwick, R. M., Platt, H. M. and Somerfield, P. J. (1998). *Free-Living Marine Nematodes: Part III. Monhysterids*. Shrewsbury: Field Studies Council.

Warwick, R. M., Ashman, C. M., Brown, A. R., Clarke, K. R., Dowell, B., Hart, B., Lewis, R. E., Shillabeer, N., Somerfield, P. J. and Tapp, J. F. (2002). Interannual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. *Marine Ecology Progress Series* **234**, 1-13.

Webber, M. K., Roff, J. C., Chisholm, L. A. and Clarke, C. (1996). Zooplankton distribution and community structure in an area of the south coast shelf of Jamaica. *Bulletin of Marine Science* **59**, 259-270.

Werner, E. E. and Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**, 393-425.

Whitlatch, R. B. (1981). Animal-sediment relationships in intertidal marine habitats: some determinants of deposit-feeding species diversity. *Journal of Experimental Marine Biology and Ecology* **53**, 31-45.

Wickstead, J. H. (1976). *Marine Zooplankton*. London: Arnold.

Wieser, W. (1959a). Reports of the Lund University Chile expedition 1948-49. 10. Free-living marine nematodes. IV. General part. *Acta Universitatis Lundensis, Series 2.* **55**, 1-111.

Wieser, W. (1959b). Free living marine nematodes and other small invertebrates of Puget Sound beaches. *University of Washington Publication of Biology* **19**, 1-17.

Wong, C. K., Chan, A. L. C. and Tang, K. W. (1992). Natural ingestion rates and grazing impact of the marine cladoceran *Penilia avirostris* Dana in Tolo Harbour, Hong Kong. *Journal of Plankton Research* **14**, 1757-1765.

Woolridge, T. (1983). The ecology of beach and surf zone mysids in the Eastern Cape, South Africa. In *Sandy Beaches as Ecosystems*, (eds. A. McLachlan and T. Erasmus). Netherlands: Dr W. Junk Publishers.

Wright, J. M. (1988). Seasonal and spatial differences in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. *Marine Biology* **100**, 13-20.

Wright, J. M. (1989). Diel variation and seasonal consistency in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. *Marine Biology* **102**, 135-142.

Wright, L. D. and Short, A. D. (1983). Morphodynamics of beaches and surfzones in Australia. In *CRC Handbook of Coastal Processes and Erosion*, (ed. P. D. Komar), pp. 35-64. Boca Raton, Florida: CRC Press.

Wright, L. D. and Short, A. D. (1984). Morphodynamic variability of surfzones and beaches: a synthesis. *Marine Geology* **56**, 93-118.

Young, P. C. and Wadley, V. A. (1979). Distribution of shallow-water epibenthic macrofauna in Moreton Bay, Queensland, Australia. *Marine Biology* **53**, 83-97.

Zacharias, M. A. and Roff, J. C. (2000). A hierarchial ecological approach to conserving marine biodiversity. *Conservation Biology* **14**, 1327-1334.

Zacharias, M. A. and Roff, J. C. (2001a). Explanations of patterns of intertidal diversity at regional scales. *Journal of Biogeography* **28**, 471-483.

Zacharias, M. A. and Roff, J. C. (2001b). Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**, 59-76.

Zacharias, M. A., Howes, D. E., Harper, J. R. and Wainwright, P. (1998). The British Columbia marine ecosystem classification: rationale, development and verification. *Coastal Management* **26**, 105-124.

Zacharias, M. A., Morris, M. C. and Howes, D. E. (1999). Large scale characterization of intertidal communities using a predictive model. *Journal of Experimental Marine Biology and Ecology* **239**, 223-242.

Zouhiri, S. and Dauvin, J. C. (1995). Diel changes of the benthic boundary layer macrofauna over coarse sand sediment in the western English Channel. *Oceanologica Acta* **19**, 141-153.

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The following staff were employed, either full-time or part-time, to undertake work on a component of this project for some or all of its duration.

- **Fiona Valesini**; Research Assistant.
- **Michelle Wildsmith**; Research Assistant.
- **Margaret Platell**; Professional Officer.
- **Sandra Seidel**; Research Assistant.
- **Linda Schafer**; Research Assistant.
- **Mathew Hourston**; Research Assistant.
- **Natasha Coen**; Research Assistant.
- **Aeysha Whitehead**; Research Assistant.

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- **Ian Potter**; Director of the Centre for Fish and Fisheries Research, Murdoch University.
- **Dr Bob Clarke**; Director of PRIMER, Plymouth Marine Laboratory, United Kingdom.
- **Dr Ian Eliot**; Department of Geography, University of Western Australia.
- **Dr Margaret Platell**; Research Fellow, Murdoch University Centre for Fish and Fisheries Research.
- **Colleen Hubbard**; Secretary, Murdoch University Centre for Fish and Fisheries Research.