THE INFLUENCE OF MID-OCEAN RIDGES ON EUPHAUSIID AND PELAGIC ECOLOGY

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The Influence of Mid-Ocean Ridges on Euphausiid and Pelagic Ecology

By

Tom Bech Letessier

Thesis submitted to The University of St Andrews for the degree of

Doctor of Philosophy (Marine Ecology)

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Abstract

1 & 2. Euphausiids comprise a major component of ecosystems in the pelagic realm, the world's largest habitat, but basin scale drivers of euphausiids diversity and abundance are poorly understood. Mid-Ocean Ridges are the largest topographical feature in the pelagic realm and their benthic and pelagic fauna have only just recently become the focus of research. This thesis present new analyses on the drivers of euphausiids species richness in the Atlantic and the Pacific, giving specific attention to the influence of Mid-Ocean Ridges. New information is given on the biogeography of euphausiids and pelagic food-web trophology of the Mid-Atlantic Ridge, and on the biogeography of pelagic decapods on the South-West Indian Ocean ridge.

3. A Generalized Additive Model framework was used to explore spatial patterns of variability in euphausiid species richness (from recognized areas of occurrence) and in numerical abundance (from the Continuous Plankton Recorder survey) in conjunction with variability in a suite of biological, physical and environmental parameters on, and at either side of, the Mid-Atlantic Ridge. Euphausiid species richness peaked in mid-latitudes and was significantly higher on the ridge than in adjacent waters, but the ridge did not influence numerical abundance in the top 10 m significantly. Sea surface temperature (SST) was the most important single factor influencing both euphausiid numerical abundance (-76.7%) and species richness (34.44%). Dissolved silicate concentration, a proxy for diatom abundance, significantly increased species richness (29.46%). Increases in sea surface height variance, a proxy for mixing, increased the numerical abundance of euphausiids. GAM predictions of variability in species richness as a function of SST and depth of the mixed layer were consistent with present theories, which suggest that pelagic niche-availability is related to the thermal structure of the near surface water.

4. Using a Generalized Additive Model in the Pacific, the main drivers of species richness, in order of decreasing importance, were found to be sea surface temperature (explaining 29.53% in species variability), salinity (20.29%), longitude (-15.01%, species richness decreased from West to East), distance to coast (10.99%), and dissolved silicate concentration (9.03%). An additional linear model poorly predicted numerical abundance. The practical differences in drivers of species richness in the Atlantic and Pacific Ocean were compared. Predictions of future species richness changes in the Pacific and Atlantic were made using projected environmental change from the IPCC A1B climate scenario, suggesting an increase in species richness in temperature latitudes (30° to 60° N and S) and little to no change in low latitudes (20° N to 20° S).

5. New baseline information is presented on biogeography, abundance and vertical distribution of euphausiids along the Mid-Atlantic Ridge (40° to 62° N). 18 species were recorded, with *Euphausia krohni* and *Thysanoessa longicaudata* being most abundant. Eight species had not been recorded in the area previously. The Subpolar Front is a northern boundary to some southern species, but not a southern boundary to northern ubiquitous species that show submergence. Four major species assemblages were identified and characterised in terms of spatial distribution and species composition. Numerical abundance was highly variable but decreased by orders of magnitude with depth. The Mid-Atlantic Ridge showed only a marginal effect on euphausiid distribution and abundance patterns.

Abstract

6. Zooplankton and micronektic invertebrate epi- and mesopelagic (0-200 and 200-800m) vertical distribution (e.g. Euphausiacea, Decapoda, Amphipoda, Thecosomata, Lophogastrida) on either side of the Subpolar Front of the Mid-Atlantic Ridge is described. Dietary relationships are explored, using stable isotope ratios and fatty acid trophic marker (FATM) composition. An increase in trophic level with size was observed. Individuals from southern stations were higher in dinoflagellate Fatty Acid Trophic Markers (FATM) (22:6(n-3)) and individuals from northern stations were higher in *Calanus* spp and storage FATMs (20:1(n-9) and 22:1(n-9)) reflecting primary production patterns in the two survey sectors. Observations on the geographical and vertical variability in trophodynamics are discussed.

7. New baseline information is presented on the biogeography, abundance, and vertical distribution of mesopelagic (200-1000 m), crustacean micronekton on- and off-seamounts of the South-West Indian Ocean Ridge (26° to 42° S). Species richness and numerical abundance were typically higher near seamounts and lower over the abyssal plains, with several species being caught uniquely on seamounts. Observations suggest that the ‘oasis effect’ of seamounts conventionally associated with higher trophic levels is also applicable to pelagic micronektic crustaceans at lower trophic levels. Biophysical coupling of micronekton to seamounts may be an important factor controlling benthopelagic coupling in seamount food-webs.

8. Euphausiid and pelagic diversity is driven primarily by geographical variability in temperature, by longitudinal patterns in upwellings, and by variability in nutrient concentration. Mid-Ocean Ridges modify pelagic ecology, by raising the seafloor and by bringing in proximity true pelagic and bathypelagic predators associated with the seabed. The increase in specialized fauna and biomass associated with ridges and seamounts serves to deplete zooplankton in the near bottom layer (0-200 m) and affect systems in and above the benthic boundary layer (<200 m from the seafloor), and the benthopelagic faunal layer. Mid-Ocean Ridges may serve to structure pelagic faunal distribution, and increase the overall diversity of the world ocean. The influence of ridges in the ocean basin may be comparable to that of hedges in a farmland; whilst delimiting the extent of crops (or zooplankton assemblages), hedges serve as local hotspots of mammal and avian diversity.

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It doesn’t matter how beautiful your theory is,

it doesn’t matter how smart you are,

if it doesn’t agree with experiment, it’s wrong.

Richard P. Feynman, American Physicist (1918-1988)

Chapter 1

General Introduction

The primary aim of the work described in this thesis was to investigate the influence of underwater Mid-Ocean Ridges (MORs) on the distribution and abundance of zooplankton. A secondary aim was to explore drivers of pelagic euphausiid species diversity on the scale of ocean basins, and to explore potential impacts upon species richness of anthropogenically induced climate change. These two aims were met through five independent ecological investigations, primarily on the zooplankton order Euphausiacea, on three scales:

1. Two ecological modelling approaches, using low-resolution (~ 1° x 1°) data on euphausiid species distribution, euphausiid numerical abundance, and environmental data, spanning the entire basins of the Atlantic and Pacific oceans, in order to explore global drivers of species richness and numerical abundance (Ch. 3 and 4).
2. Two descriptive, mesoscale (10s to 100s of km), biogeographical analyses of net-caught euphausiid from the northern Mid-Atlantic Ridge (MAR, Ch. 5), and pelagic decapod shrimps and lophogastrids (>20 mm) from seamounts of the South West Indian Ocean Ridge (SWIOR, Ch. 7), in order to explore faunal distribution patterns. Both

analyses sought to contribute to debates on the degrees of connection between discrete elements of MORs in a foodweb and genetic sense.

3. An analysis of the pelagic trophic spectrum towards the lower end of the oceanic food web, utilizing biochemical techniques to establish dietary relationships between zooplankton and micronekton, and to explore energy transfer to the bathypelagic (>1000 m) of the MAR (Ch. 6).

This first chapter introduces the concepts of plankton and the order Euphausiacea, and theories of mechanisms driving patterns in pelagic faunal diversity and abundance. Potential ecological influences of MORs are discussed and gaps in knowledge on current understanding in basin scale drivers of diversity are identified (section 1.1.1). Study areas on the MAR are identified and described with focus on known ecology, biogeography, and oceanography (section 1.2.2, 1.2.3). Finally, the aims of this thesis are outlined (section 1.3). The next chapter (Ch. 2) presents the methods used in order to meet these aims.

1.1 Plankton, euphausiids and pelagic diversity

Plankton, derived from the Greek word ‘planktos’ for drifter, is a general term used to describe plants and animals that drift passively in the horizontal plane of lakes, seas and oceans, and that do not have the ability to swim against horizontal currents (ocean current velocities are typically around 1 $m.s^{-1}$). The term is taxonomically broad and includes immobile phytoplankton and active zooplankton swimmers such as euphausiids and pteropods. Organism size ranges considered in this thesis are defined as mesozooplankton (0.2-2 mm), macrozooplankton (2-20 mm), and micronekton (>20 mm; Harris et al., 2000). Although zooplankton are typically poor swimmers, evidence exists that many taxa are capable of horizontal migrations, to remain in proximity with, or migrate to, feeding grounds (Smyth et al., 2006; Benoit-Bird and Au, 2006). Moreover, while many euphausiid species are in the macrozooplankton size range, they are often called micronekton because of their great capacity for vertical and even horizontal migration (Huntley and Niiler, 1995). Since euphausiids possess characteristics of both the plankton and nekton, this group are considered good model organisms with which to investigate large-scale patterns of pelagic faunal distribution (Mauchline and Fisher, 1969). Macrozooplankton/ micronekton are not biological concepts with sharp boundaries and either term may be appropriate in certain circumstances.

There are 85 described species of the order Euphausiacea (Brinton et al., 2000), and the majority are shallow living and marine. They are pelagic and ubiquitous in the world’s oceans. Their ecological importance is reflected by a large body of literature (Nicol, 2003; Nicol and Brierley, 2010), and is particularly evident where food chains are short (such as at latitudes of >60°; Saunders et al., 2007a), as there they provide a direct link between the primary producers and top predators. In oceanic and neritic (coastal) ecosystems in general they exert control both upwards, as an important source of food for birds, whales and commercially important species of fish (Haberman et al., 2003; Verity et al., 2002), and downwards, by grazing on phytoplankton, and preying upon other zooplankton such as copepods (Beyer, 1992). Their biological importance is partly due to their high lipid content, especially in females (Cuzin-roudy and Buchholz, 1999; Mayzaud et al., 2003), which makes them attractive food items.

Zooplankton in general and euphausiids specifically are capable of large vertical migrations, and contribute to the transport of carbon to the deep sea (Schnack-Schiel and Isla, 2005; Tarling and Johnson, 2006) through Diurnal Vertical Migration (DVM). DVM in the plankton community is normally characterised by movement of biota to shallow water at dusk and deeper water (>200 m) at dawn, and constitutes the largest animal migration on earth (Ringelberg, 2010). The subject of DVM has been extensively researched over the last century and proximal reasons for it are relatively well understood, as a beneficial foraging behaviour (Hays et al., 2001) and as a predation avoidance strategy (Liu et al., 2006). This behaviour is flexible and can be modified in response to various predator pressures (Ohman, 1990) and satiation (Tarling and Johnson, 2006).

The habitat of plankton and euphausiids is the pelagic realm, which is the Earth's largest habitat (Horn, 1972) and measures approximately 1,368,000,000 km^3 (Angel, 1993). The pelagic realm overlays the continental shelves and the abyssal plains, which are interrupted by deep trenches, seamounts, volcanic islands and ridges. Since many benthic animals have pelagic larval stages, the pelagic is generally considered to be a more diverse marine habitat than the benthic, temporally at least, because it includes all major benthic animal Phyla as well as the true pelagics. Diversity patterns in the pelagic have sometimes been described as paradoxical (Ayala et al., 1979) due to the presence of a large number of species in an environment that appears homogeneous. However, both physical structure (e.g temperature, mixing, salinity, proximity to seafloor) and biological mechanisms (primary production, predation) interact over a variety of scales causing environmental heterogeneity and niche diversity (Haury et al., 1978). In plankton, high diversity, abundance and patchiness is supported by consistently changing environmental conditions, and is thus not really a paradox at al (Hutchinson 1961).

1.1.1 Pelagic diversity

Species diversity is a measure that incorporates the number of species in an area (species richness) and their relative abundance. The most conspicuous pattern of marine species richness across all taxa is an increase in species numbers with decreasing latitude, or increasing sea surface temperature (Fig. 1.1, Tittensor et al., 2010).

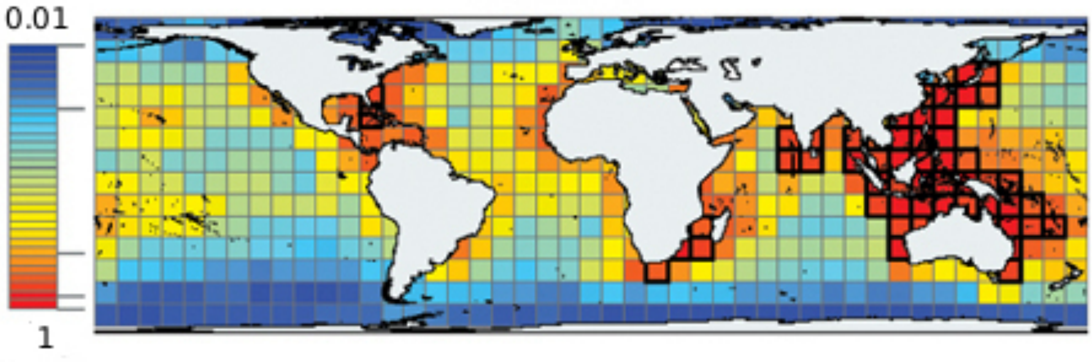

Fig. 1.1 Global species richness for all marine taxa modified from Tittensor et al., (2010). Values for each taxon have been normalized by rescaling from zero to one, and averaged across taxa by cell.

While this pattern also pertains to the pelagic realm, high biodiversity in the pelagic realm has also been related to primary production (global patterns of microzooplankton <0.2 mm diversity is unimodaly correlated with phytoplankton biomass, i.e highest at intermediate productivity; see Irigoien et al., 2004), to low seasonality and little year-to-year temperature variation (for zooplanktic ostracods, see Angel, 1993), and even, perhaps unexpectedly, to high productivity (for some nekton, see Rosa et al., 2008). Moreover, the productivity/diversity relationship is confounded by strong negative spatial correlations between seasonality (yearly environmental variability), and temperature (there is little seasonality at low latitudes/higher temperature, whereas high latitudes typically experience high seasonality; Kicklighter et al., 1999).

Presently, the best-supported unifying theory explaining global marine diversity patterns is the kinetic-energy (K-E) hypothesis. Support most recently arises from an analysis of a global marine taxonomic data set averaged over 660,000 km^2 cells (n = ~ 400; Tittensor et al., 2010). The K-E hypothesis states that high temperatures promote greater speciation rates because higher metabolic rates are supported (Allen et al., 2002; Allen and Gillooly, 2006). While this probably pertains to pelagic fauna as well (the study of Tittensor et al. did incorporate variability in distribution several pelagic taxa), studies on pelagic taxa have revealed that highest species richness in the pelagic realm is found at intermediate latitudes (20° to 40°; Rutherford et al., 1999; Angel, 1993), as opposed to in the tropics. The reasons for this are not well understood, but may be related to the sub-surface temperature structure of the ocean: less steep thermoclines at intermediate latitudes apparently provide larger number of niches, and thus harbour greater species richness (Angel, 1993).

Although the broad pattern of zooplankton diversity and abundance are related in part to latitudes, local distribution is susceptible to multiple variables and physical controls (Huntley and Niiler, 1995). On a local scale, distributions are subject to broad seasonal fluctuations, frontal changes, and bathymetric features such as seamounts (Haury et al., 2000; Haury et al., 1978), and possibly Mid-Ocean Ridges (MORs, Pitcher, 2008).

Amongst these, ridges are the only features that can have potential ecological implications on a basin scale, because of their surface area (some 31% of the global oceanic surface; Marshall, 1979), and physical continuity across large distances. The MORs' extends horizontally for more than 60,000 km, (Kious and Tilling, 1996), through many latitudes (60° S to 80° N) and spanning many biomes (Longhurst, 1998).

Studies have examined mesoscale drivers of euphausiid distribution (in the Antarctic, see Trathan et al., 1993) and have provided biogeographical information on the basin scale (in the South and North Atlantic Ocean; Gibbons, 1997; and Lindley, 1977 respectively). Understanding the contribution of euphausiids to marine ecosystem processes globally, and the responses that the group may have to global change, could be improved by exploring drivers of species richness and numerical abundance patterns on the global ocean-basin scales. Moreover, exploring the influence of variables shown to be predictive on the meso-scale, on the global scale may prove more informative than assuming a direct temperature/richness relationship (e.g see Tittensor et al., 2010). Bridging the gap in knowledge between drivers of local and global patterns of euphausiid species richness and numerical abundance in the Atlantic and Pacific Ocean will be the focus of work described in Ch.3 and Ch.4 of this thesis respectively. Understanding of pelagic diversity in general and euphausiids in particular would be well served by further investigations in biogeographical patterns, in particularly that of the sub-surface ocean and will form the focus of Ch. 5.

1.2 Underwater ridges, and study sites considered in this thesis

1.2.1 The Mid-Ocean Ridges

Amongst the bathymetric features of the open ocean basin such as trenches, seamounts and fracture zones, Mid-Ocean Ridges (MORs) have by far the largest area, some 22% of the planet's surface (for comparison, dry land constitutes 29% of the planet's surface; Fairbridge, 1966; Garrisson, 2002; Marshall, 1979), and extend horizontally for more than 60, 000 km in the Atlantic, Indian, Southern, and Pacific Oceans combined, at depths typically around ~2000 m and deeper (Kious and Tilling, 1996; Fig. 1.2A). Here MORs are defined as continuous mountain chains that are typically deeper than 1500 m. The term seamounts here will be used for features >1000 m in elevation (typical in ecological contexts, see Pitcher et al., 2010) but only when those feature penetrates at least into the mesopelagic (1000 m from the surface).

Ridges form at divergence zones, where tectonic plates are forced apart by volcanic activity, causing the formation of new sea floor, and serving to increase the distance between bordering continents (Kay, 1969). The tops of ridges usually have a valley running along their axes. Fracture zones punctuate ridges, running orthoghonal to the main ridge axis. Ridges may accommodate elevated benthic macrofaunal diversity compared to surrounding plains (Gebruk, 2008), and are the sites of expanding benthic and bentho-pelagic fisheries (Lorance et al., 2008).

It is possible that ridges, as with seamounts (Dower et al., 1992), harbour elevated pelagic biomass. Ridges are shallow in parts and although they are generally deeper (>2000 m), they often form seamounts. While ridges are continuous features, seamounts rise abruptly, at least 1000 m from the surrounding seafloor (Kitchingman and Lai, 2004), and are typically clustered along side the ridge axis, perhaps with the exception of the East Pacific Rise (Fig. 1.2B). Like seamounts, ridges have no terrigenous input of nutrients, so are nutrient poor compared with habitats on the continental shelves and margins (with the exception of coastal ridges). Ridges are the sites of rare chemosynthetic hydrothermal vent communities (Glowka, 2003).

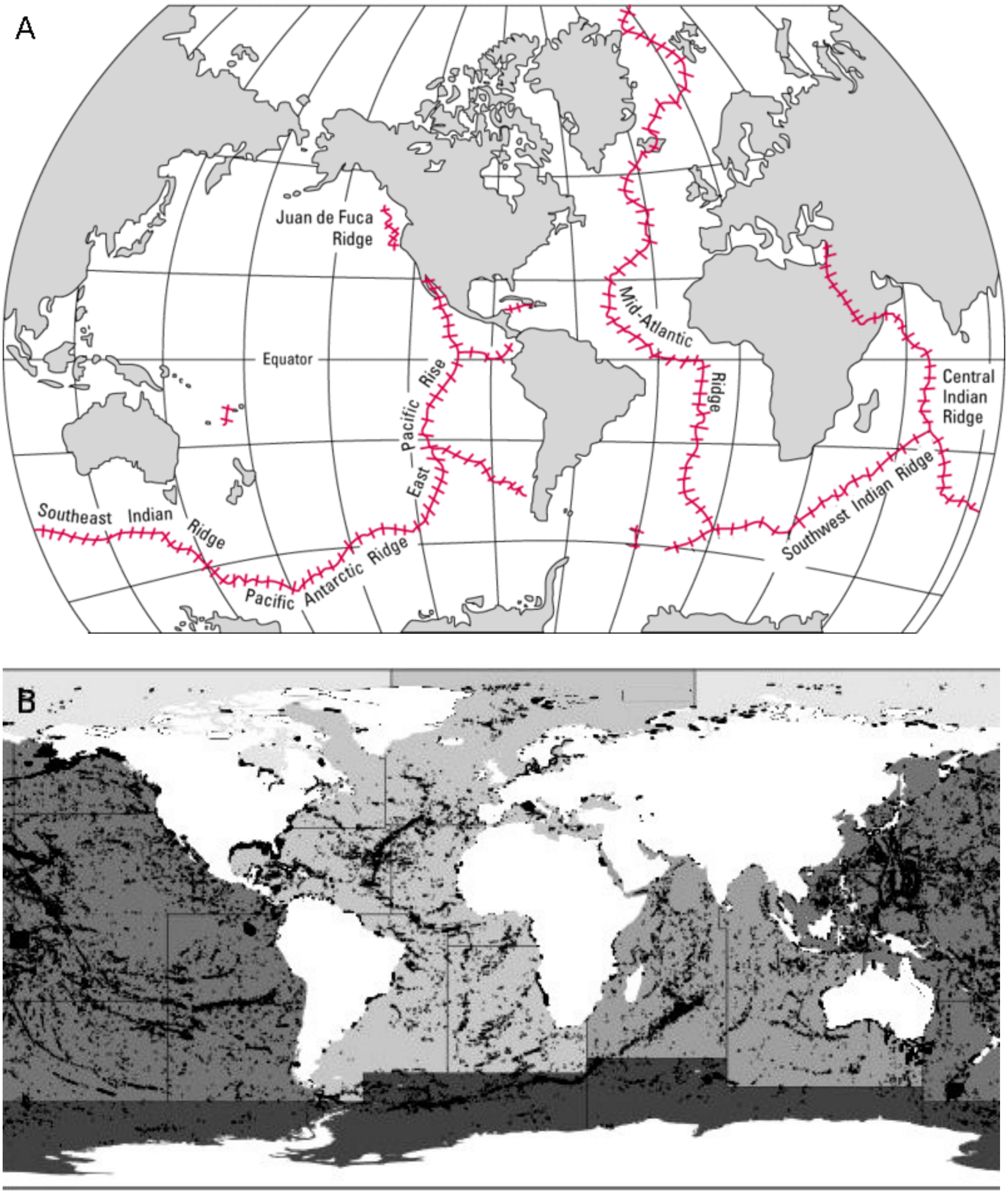

Fig. 1.2 World Distribution of Mid-Ocean Ridges (A), from the U.S. Geological Survey (Watson, 1999), and predicted seamount locations (B, number of seamounts = 33,452) from Yesson et al., (2011). The latter study used gridded bathymetry data at 2 arc-min resolution and identifying local peaks in elevation on the seafloor, and classified these by examining the surrounding neighbourhood bathymetry.

Although the contribution of these ecosystems to total marine primary production is minor (~10^{12} g C yr^{-1}; Bach and Edwards, 2003) compared with surface photosynthetic production (5 10^{16} g C yr^{-1}; Field et al., 1998), they are hotspots of deep-sea species diversity (Tittensor et al., 2009), and their contribution to the nutrient pool in the Worlds' Ocean is disproportionally high (Adams et al., 2011). Moreover, such deep-sea ecosystems have commercial value for genetic and mineral mining, for conservation (Mossop, 2005), and as nursery habitats (King and Beazley, 2005).

As a consequence of the overexploitation of fish resources on the continental shelves, MORs are increasingly becoming the focus of developing international deep-sea fisheries for, amongst other things, orange roughy (*Hoplostethus atlanticus*), a fish whose management has failed (Fulton et al., 2010). Other important catches include red fish (*Sebastes mentella*), and roundnose grenadier (*Coryphaenoides rupestris*; Bergstad et al., 2008; Lorance et al., 2008). In the Indian Ocean, many seamounts associated with the South West Indian Ocean Ridge have experienced boom and bust fisheries. Little regulation exists on these seamounts and this region is the sector of the world with the highest proportion of exploited fish stocks with uncertain status (Kimani et al., 2009). Understanding energy fluxes to these ridges and seamounts is a crucial component of any ecosystem based fishery management strategy.

Interactions between demersal fish species and mesopelagic fauna increase on seamounts (Fock et al., 2002) where diurnally migrating zooplankton are preyed upon by resident nekton. Vertically migrating zooplankton layers may interact with MORs, perhaps through the mechanism described by Rogers (Fig. 1.3; 1994).

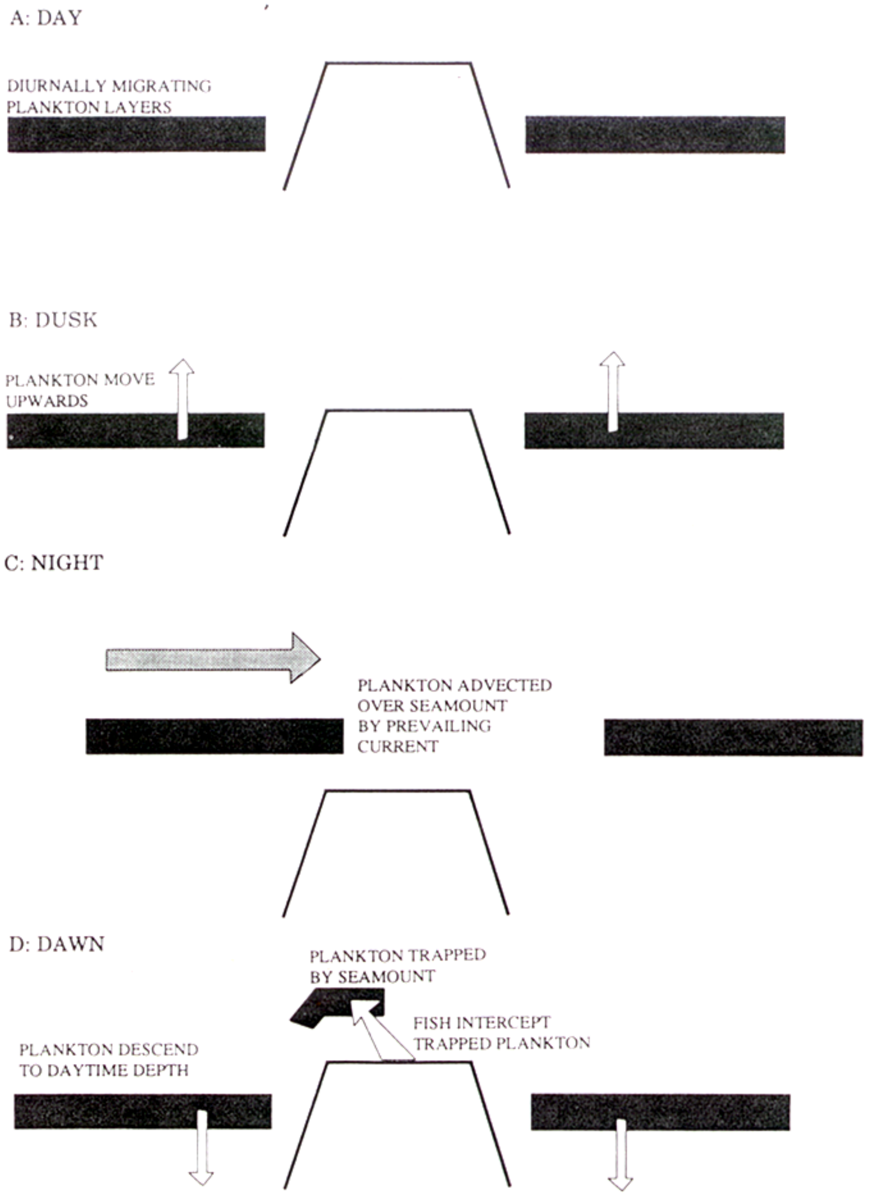

Fig. 1.3 Model depicting modification of DVM as a result of interception by zooplanktivorous predators on seamounts (from Rogers, 1994).

Although MORs represent a shallow sub-area of the seabed, the majority of DVM takes place in the epi- (0-200 m) and mesopelagic (200-1000 m; Angel and Pugh, 2000). Moreover, DVM trapping might not be relevant for the majority of the MORs, which are defined here as deeper than 1500 m.

In the pelagic realm, biomass decreases logarithmically with depth (see Fig. 1.4, Angel, 1982). To the greater depths common place amongst ridges (~2500 m, Kious and Tilling, 1996), vertical export of organic material from the epipelagic productive layer

(0-200 m) is by far the greatest contributor to the benthic and benthopelagic food-web (Wei et al., 2010; Wassmann et al., 2006), This material may pass through several pelagic organisms en-route (Barnes et al., 2010).

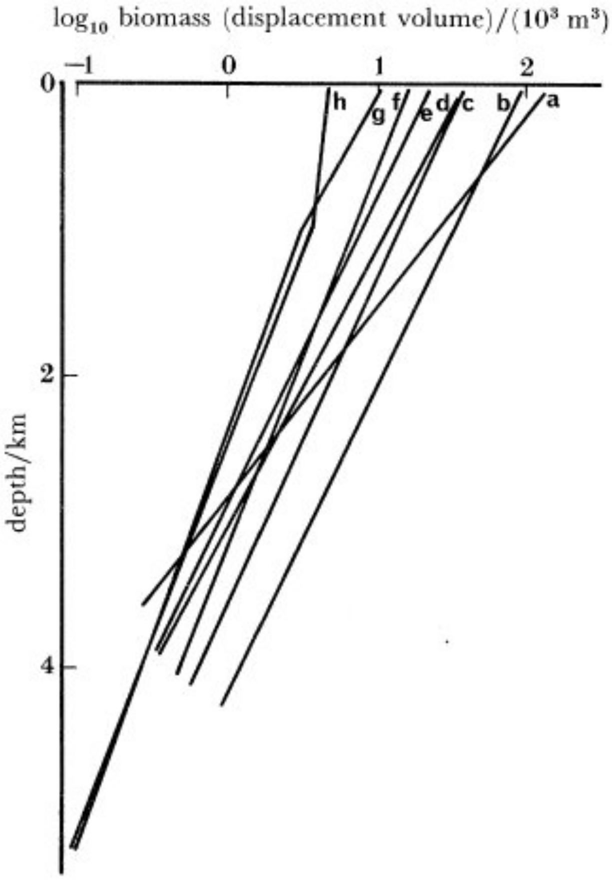

Fig. 1.4 Biomass (displacement volume, 10^{-3} m^{-3}) decrease with depth (km) in the North-East Atlantic, from Angel and Boxshall (1990).

Trophic positions and size for a given individual typically increase with depth (Ramirez-Llodra et al., 2010). The bulk of carbon input to the deep-sea is in the form of ‘marine snow’, which is phytoplanktic and zooplanktic in origin (Billett et al., 1983). Marine snow-fall is further mediated by macrozooplankton (Dilling and Alldredge, 2000). Particle size is fragmented through zooplankic swimming activity (Goldthwait et al., 2004), and material is transported to deeper waters in faecal pellets, if the zooplanktic gut clearance time is shorter than the length of their migratory phase, (Angel et al., 2000), and by sinking dead plankton carcases.

Energy fluxes to deep-sea habitats such as ridges stem from and are mediated by zooplanktic processes, which are dependent upon physical and biological processes and interactions in the pelagic realm. Moreover understanding planktic patterns and their drivers on a variety of scales is necessary for the investigation of MORs ecology. The poor knowledge of open-ocean trophic interactions and their potential modifications by MORs (only 0.0001% of the sea floor has been explored; Gjerde, 2006) is a major shortcoming for conservation of rare deep-sea habitats, managements of fish stocks (Gjerde and Breide, 2003), and for pelagic ecology in general.

1.2.2 The North Atlantic

The Atlantic is the world's second largest ocean (106,400,000 km^2). It is longitudinally narrow and latitudinal broad (60°N to 60 °S), and has an elongated 'S' shape contained by the Americas in the west, and Europe and Africa in the east. The main topographical feature of the Atlantic Ocean is the Mid-Atlantic Ridge (MAR, Fig. 1.5), an underwater mountain chain that rise from the abyss at 4000 m, forming a rough central terrain that includes sea-mounts (up to 500 m deep), gulleys, fracture zones, and surface islands. In the North-Atlantic (40° to 60°N) the MAR is shallow in parts and forms islands, including Iceland in the north, and the Azores in the south (Fig. 1.5) and covers ~ 46 % of the bathyal benthic habitat (800-3500 m).

While Soviet scientists conducted exploratory studies on the MAR benthos in the 1950s (Coyle et al., 2007), the MAR has only just recently become the focus of targeted study (plans initially emerged in the 1990s; Bergstad et al., 2008). MAR-ECO (Patterns and processes of the Northern Mid-Atlantic Ridge, www.mar-eco.no, 2000-2010), a project under the Census of Marine Life (CoML), investigated the deep-sea of the mid-North Atlantic by a targeted series of cruises, in order to explore the effect of the MAR on the biota. This thesis work was conducted as a component of ECOMAR (Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone www.oceanlab.abdn.ac.uk/ecomar/), a National Environmental Research Council (NERC) funded consortium effort that was a UK contribution to CoML targeting the fauna of the MAR, on a series of cruises from 2007 to 2010.

Because of the proximity to nations with historical marine research programmes, the physical oceanography of the North Atlantic is well understood. In the mid-North Atlantic, the main factor determining nutrient distribution and as such, primary productivity and pelagic faunal distribution, is likely to be the stratification of cold nutrient-rich waters of the Subpolar Front, as revealed by studies on zooplankton patterns: in the northern mid-Atlantic zooplankton biovolume (110 $mm^3. m^{-3}$) and abundances (~225 ind. m^{-3}) peak near the Subpolar Front (SPF; Clark et al., 2001; Hays et al., 2001). The dominant flow of water over the MAR is an eastward current, the North Atlantic Current, which crosses the ridge between 45º and 48 º degrees N. The current then continues northeast over the Wyville Thompson ridge, fuelling the Irminger Current (IC). The MAR itself may promote ocean mixing, by the generation of energetic internal tide (Holloway and Merrifield, 1999) and by channelling deeper waters between the two halves of the basins via fracture zones (Read et al., 2010).

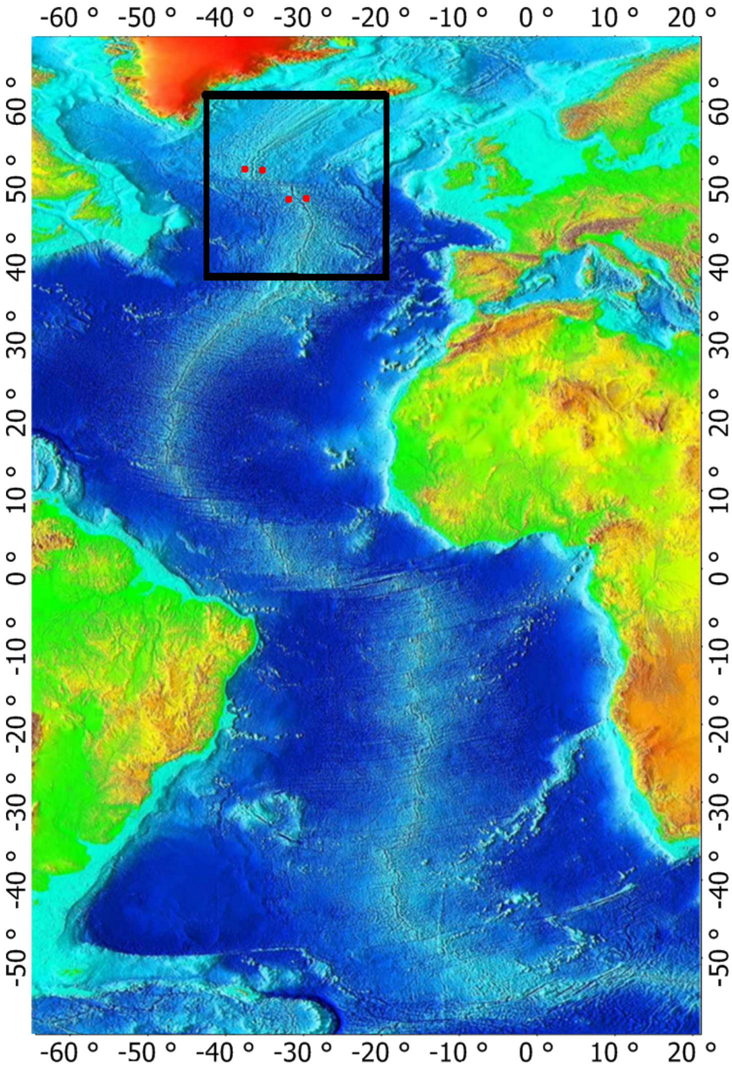

Fig. 1.5 Seabed bathymetry of the Atlantic Ocean, and the Mid-Atlantic Ridge, from NOAA (http://en.wikipedia.org/wiki/Atlantic_Ocean). The basin scale distribution of euphausiid species in the Atlantic, and surface numerical abundance in the North Atlantic is the focus of Ch. 3. Square indicates area of study of the MAR-ECO project of the Census of marine life, the focus of Ch. 5; and red dots indicates the ECOMAR cruise stations and the focus of Ch. 6.

The North Atlantic (35° to 65° N) is probably the world's most intensively sampled ocean, at least with respect to surface (0-10 m) plankton. Because of the efforts of the Continuous Plankton Recorder (CPR, Fig. 1.6 and Fig. 1.7), which has been deployed from ships of opportunity (non research ships) since the 1930s, over 380 000 samples had been collected by 2009 in the North Atlantic and North Sea combined (Batten and Burkill, 2010), providing information on phytoplankton and zooplankton taxa, including euphausiids. The use of the CPR has enabled the collation of time series, and the study of yearly and seasonal variability over large areas (Beaugrand et al., 2002; Beaugrand and Ibañez, 2002), and has revealed changes in mesozooplankton distribution in response to climate change (Beaugrand and Ibañez, 2004). While the CPR is not primarily designed for the sampling of euphausiids, because of small aperture (1.62 cm^2), quantitative information can be gained from time series (Batten et al. 2003).

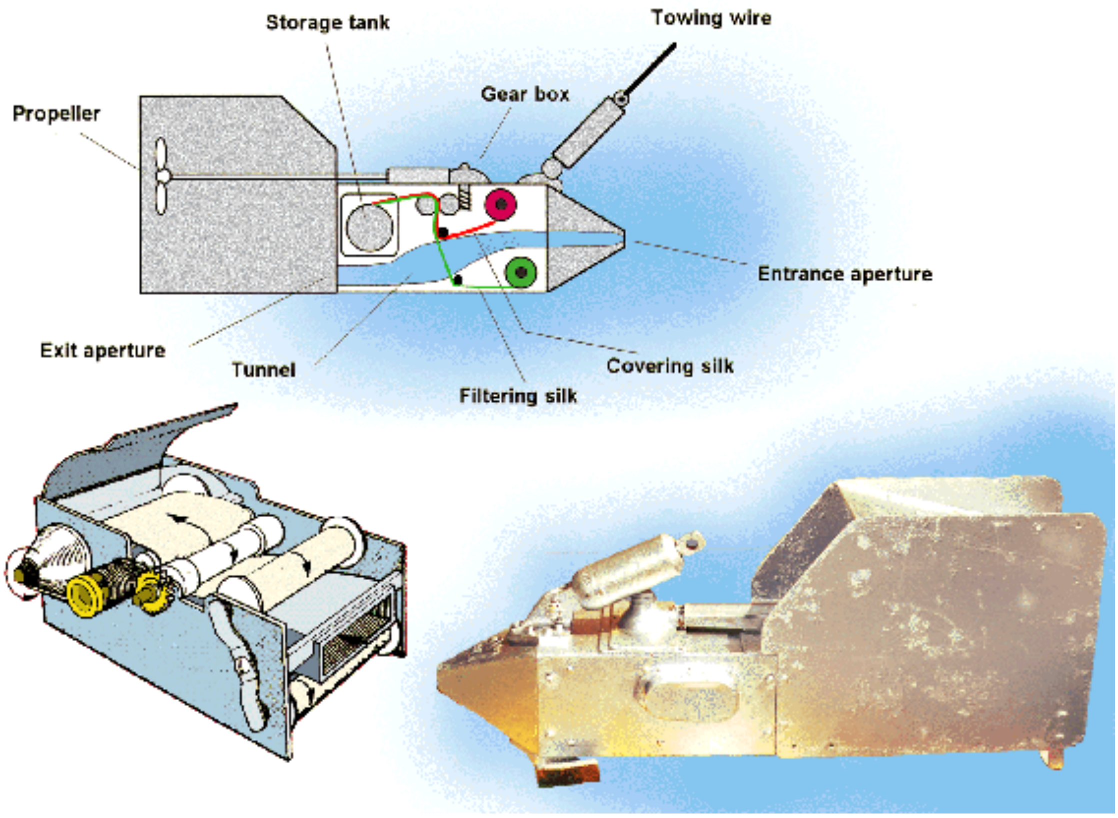

Fig. 1.6 Diagram and picture of the continuous plankton recorder from of SAHFOS (http://en.wikipedia.org/wiki/File:Sahfos_cpr.gif)

The CPR data set is restricted to the top 10 m of the water column, so that no data are collected on deeper species/communities such as those associated with the MAR. The CPR survey has yielded biogeographical information on euphausiids (Lindley, 1977) and has revealed that within the survey area (40º to 60º N) the euphausiid community in the top 10 m is dominated by the species *Thysanoessa longicaudata*. While Lindley et al. (1977) did not detect any biogeographical signature of the MAR, the studies of

Beaugrand et al. (2002, 2003) have revealed, perhaps coincidentally, that the MAR axis north of 50º N serves as a boundary between two apparently different shifts in community responses to changing sea surface temperature. While communities to the west are shifting south, to the east they are shifting north (Beaugrand et al., 2002).

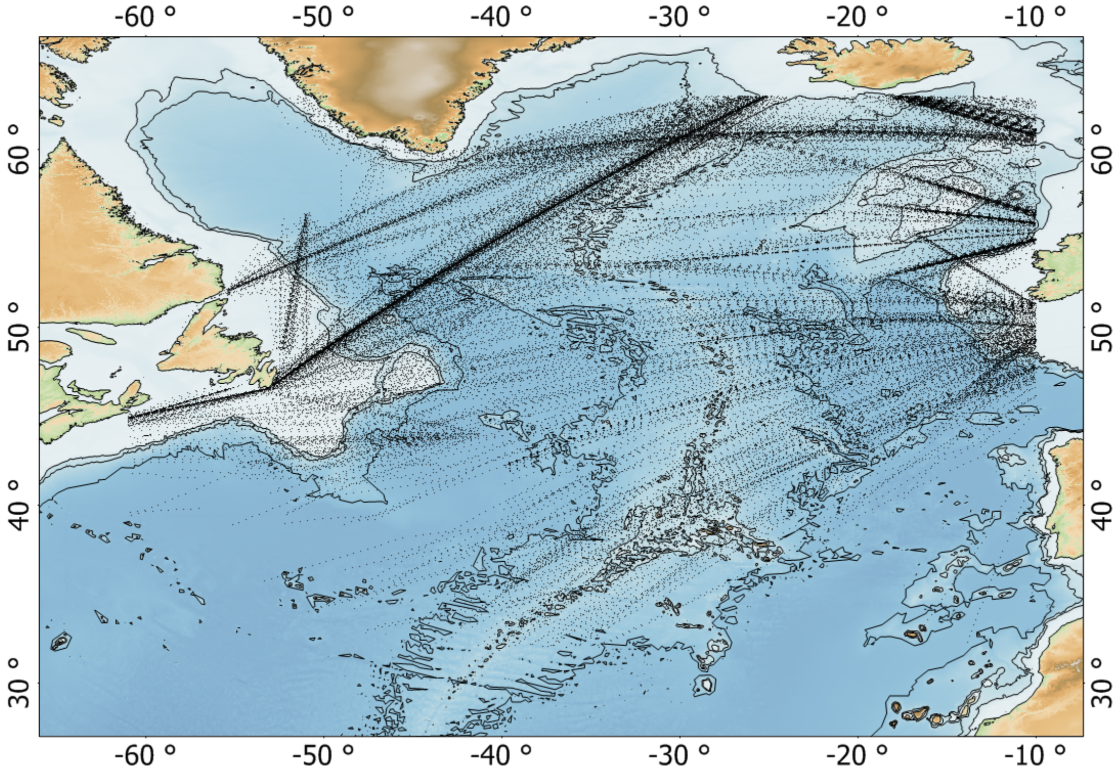

Fig. 1.7 Survey effort of the Continuous Plankton Recorder in the North Atlantic (87314 samples collected from 1958 to 2006). The 1000, 2000 and 4000 m isobaths are shown.

In this thesis, the CPR data will form the basis for a study of potential basin scale drivers of euphausiid numerical abundance in the North Atlantic, whilst simultaneously enabling the investigations into surface signature (if any) of the MAR (Ch. 3). In the Pacific, a sister CPR survey has been collecting data since 2000 (Batten and Mackas, 2007) and arising data there will form the basis of a similar investigation in Ch. 4.

Baseline data on euphausiid species distribution arrising from the CPR survey studies (Lindley, 1977) will act as a baseline for comparison with the investigation in to the horizontal and vertical distribution of euphausiids over the MAR in the mid-North Atlantic (in Ch. 5).

1.2.2.1 The deep–sea of the North Atlantic

Initial pilot studies as part of the MAR-ECO consortium were conducted on sections of the MAR by the Russian R/V *Akademik Mstislav Keldysh* in July 2003 using manned submersible (Vinogradov, 2005) and by the Iceland R/V *Arni Fridrikkson* using pelagic nets. Recent multidisciplinary biological and oceanographic work on the ridge commenced in 2004, with the study by the Norwegian R/V *G.O. Sars* (Bergstad et al., 2008; Wenneck et al., 2008).

The MAR has a major influence on the tidal regimes of the overlaying water column (Egbert and Ray, 2001; Read et al., 2010) and on the gross circulation between the eastern and western basin of the North Atlantic (Harvey, 1980), yet no biogeographical study has identified the MAR as a faunal barrier (Boltovskoy, 1988; Gibbons, 1997). Furthermore, whilst seamounts have a number of potential effects on pelagic ecology, ranging for example from increased biodiversity/biomass to increased patchiness caused by predatory fish species intersecting vertically migrating zooplankton (Pitcher, 2008; Rogers, 1994), it is unclear to what extent this mechanism is effecting systems over the the MAR.

Studies under the umbrella of MAR-ECO consortium have described horizontal and vertical patterns of distribution for a range of taxa on the MAR (Chaetognatha, bioluminescent organisms, and Copepoda, (Pierrot-bults, 2008, Heger et al., 2008 and Gaard et al., 2008 respectively) using scientific techniques such as video cameras, nets, and trawls. Studies arising from MAR-ECO (Sutton et al., 2008; Bergstad et al., 2008), and previous studies (Fock et al., 2004; Anderson et al., 2004), have revealed that the

MAR may increase the abundance of deep-sea pelagic and demersal fish in by mechanisms as yet unknown: remote sensing from satellites (SeaWifs) has revealed no major pattern of increased productivity on the MAR itself (Tilstone et al., 2009). Petursdottir et al. (2008) investigated the dominant pelagic species over the northern MAR using lipid analysis (Falk-Petersen et al., 1990; Falk-Petersen et al., 2000), and stable isotopes analysis (SI, Schmidt et al., 2003) and identified two main energy pathways to the deep-sea: 1) the copepod *Calanus finmarchicus* is an important part of the diet of pearlside *Maurolicus muelleri*, the myctophid *Benthosema glaciale* and the shrimp *S. arcticus*, and 2) the euphausiid *M. norvegica* is more important than *Calanus* sp. in the diet of the red fish *Sebastes mentella*.

Subsequent studies on the MAR, including this thesis, have been conducted under the umbrella of the ECOMAR project. Euphausiids were collected as part of the MAR-ECO consortium and ECOMAR project along with the other taxa, and are analysed in this thesis. Zooplankton and nektic interactions between the surface layers and the deeper MAR nekton remain a gap in knowledge, and would be better understood through the investigation of euphausiid horizontal and vertical distribution patterns (presented in this thesis in Ch. 5). The influence of the MAR on biogeography may be more evident for the distribution of zooplankton from greater depths than those typically sampled by the CPR (<10 m). For example, a marked influence by the MAR on the teleost assemblages has previously been detected near the seabed only (0-200 m, Sutton et al., 2008) and not in shallower regions. Sampling has been conducted down to the near seabed (0-200 m) as part of the MAR-ECO consortium, and the potential proximity to the MAR and any resident nekton will be a further explored as part of this thesis.

1.2.3 The Charlie Gibbs Fracture Zone at the Subpolar Front

The SPF overlays the Charlie Gibbs Fracture Zone (CGFZ), two 4500 m deep rifts that intersect the MAR at 52º N and act as a boundary between the warm (>12° C) nutrient-poor water of the North Atlantic Current, and the cold, nutrient-rich water of the Eastern Greenland Current (<8 °C). Fauna on either side of the SPF and the CGFZ has been the focus of ECOMAR, the experimental design of which targeted the fauna of the MAR at four different locations, either side of the MAR and north and south of the CGFZ (Fig. 1.8).

The SPF marks the intersection between three different biogeographic biomes (Atlantic, Arctic, and North Atlantic Drift; Longhurst, 1998), which are distinct in oceanographic patterns and dominant phytoplankton flora. Faunal biogeographical studies have shown marked differences in the copepod community composition on either side of the SPF (Falkenhaug, 2007; Gaard et al., 2008). The sub-polar waters north of the SPF on the MAR are characteristic of high latitude waters and have low temperature (<8 °C), low salinity (<35) and oxygen content, and are highly productive during the spring and summer months (80 g $C.m^{-2}.month^{-1}$; Longhurst, 1998).

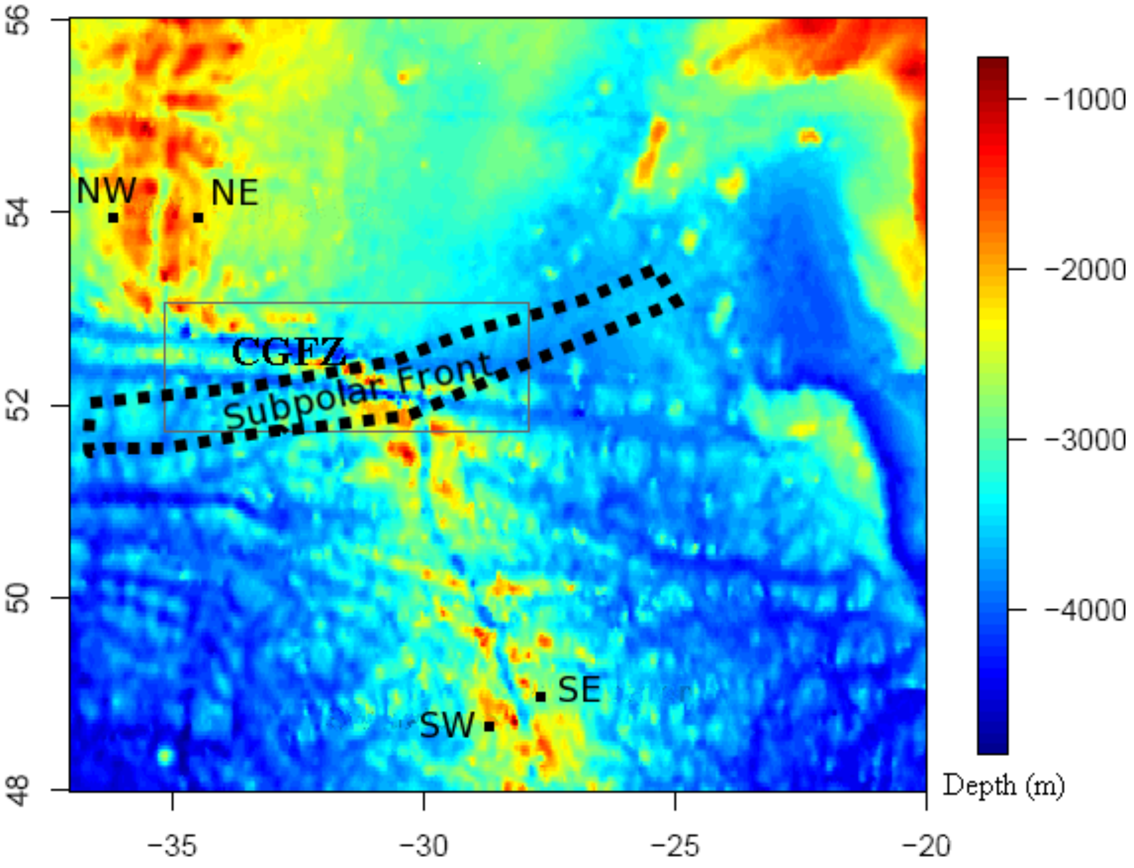

Fig. 1.8 Survey stations of ECOMAR (Patterns and Processes of the Northern Mid-Atlantic), the Charlie-Gibbs Fracture Zone, and the Subpolar Front, the survey sites of Ch. 5 (in parts), and Ch. 6.

To the south of the SPF, waters are more typical of temperate waters, with a somewhat lower production peak (<50 g $C.m^{-2}.month^{-1}$; Longhurst, 1998) and sustained production throughout the summer months. The SPF presents an unusual environment in pelagic terms in being highly productive, yet with no terrigenous input of nutrient (for comparison, mid-oceanic gyres in the Pacific have production rates typically ~ 5 of $gC.m^{-2}.month^{-1}$).

1.2.3.1 The pelagic food-web of the SPF

Present knowledge on how the different production regimes to the north and south of the SPF influence energy transfer to the deep sea and the MAR is still limited. Trophic studies to date have either focused on a narrow faunal group (Bergstad et al., 2010; Petursdottir et al., 2010) or to geographically narrow sites like the Reykjanes ridge (Petursdottir et al., 2008). Oceanic food webs in general are poorly understood. A better understanding of benthopelagic energy coupling would be well served by further exploring dietary relationships between epi- and mesopelagic organisms from areas of marked differences in primary productivity to the north and south of the SPF (Longhurst, 1998).

The trophic level of the key components of a zooplanktic pelagic ecosystem, indeed of any ecosystem, can be described using different techniques, such as stomach content analysis (Kaartvedt et al., 2002), SI, and FA. SI uses the increase in heavier isotopes between the consumer and its energy source as a proxy for the relative trophic level of a species in its ecosystem (Jardine et al., 2003). The ratios are identified through isotopic ratio mass spectrometry (IRMS), and the results are reported as δX (X being either ^{13}C, ^{15}N, or ^{34}S, equation [1.1]), the difference of the heavier isotope from the given standard (Vienna Peedee Belemmite formation of South Carolina):

Equation [1.1]: $\delta X = [R_{sample}/R_{standard}-1] \times 10^3$

$\delta^{13}C$ vs $\delta^{15}N$ plots provide a means of visualizing energy transfers through the food web, and can be useful tools when exploring trophic relationships in the deep sea (Rau et al., 1989). Typically, depleted $\delta^{13}C$ indicates a pelagic source of diet, whilst enriched

$\delta^{13}C$ indicates benthic diet sources (Jardine et al., 2003). Because geographical baseline variability in $\delta^{13}C$ and $\delta^{15}N$ is often echoed throughout the foodweb (Lara et al., 2010), energy sources should often be ground truthed by investigating Particulate Organic Matter isotopic values. POM samples can be collected by filtering seawaters on ashed GF/F filters.

FA analysis is more discriminative than SI analysis, enabling the identification of the exact source of the lipid, and hence, the prey, to a more precise taxonomic level. Fatty acid trophic markers (FATMs) provide qualitative information on the source of primary productivity in the food web, and can be used to trace the transfer of energy in the web. For example, the FATM 20:5 (n-3), 16:1(n-7), and C16 polyunsaturated fatty acids 9 (PUFA) for diatoms, C18 PUFAs for dinoflagellates; and the FATMs, 20:1 (n-9) and 22:1(n-11) for *Calanus* copepods (Dalsgaard et al., 2003).

Using the platform of ECOMAR cruises to the CGFZ, this thesis describes the macrozooplankton and micronekton community and investigated assimilated diets and trophic interactions in dominant invertebrates, on either side of the SPF, using biochemical techniques, (SI and FA; in Ch. 6). The overall results will link to on-going studies of the benthic and demersal food web.

1.3 Aims of study

The 5 specific aims of this thesis were:

1) To investigate basin scale drivers of euphausiid species richness in the Atlantic, and numerical abundance in the North Atlantic, whilst considering the particular effect of the MAR (Ch. 3).
2) To investigate basin scale drivers of euphausiid species richness in the Pacific, compare results with the Atlantic (1), and make predictions of species abundance changes in response to projected environmental variability using the A1B IPCC scenario (Ch. 4).
3) To describe the vertical and horizontal biogeography of euphausiids over the Mid-Atlantic Ridge, and the potential influence of bottom topography and oceanographic fronts (Ch. 5).
4) To describe the vertical distribution of macrozooplankton and micronekton on either side of the Subpolar Front, to investigate dietary niches and variability in trophodynamics with respect to depth, and to examine the role of different primary production regimes on energy transfer to the different zones of the MAR (Ch. 6).
5) To describe the mesopelagic (200-1000 m) micronekton crustacean community associated with seamounts of the South-West Indian Ocean Ridge Ch. 7), and discuss the wider influence of seamounts and MORs on pelagic fauna globally (Ch. 8).

Chapter 2

Methods

This section outlines the methods applied within this thesis. Basin scale analyses of euphausiid species richness were conducted using GIS and Generalized Additive Models (Ch. 3 and 4). Zooplankton samples were collected using nets (Ch. 5, 6 and 7). Biogeographical data were analysed using multivariate techniques and non-metric multi-dimensional scaling (NMDS, Ch. 5 and 7). This chapter presents a general introduction to these methods, but specific treatments are described in greater detail in each chapter.

2.1 Data analysis

2.1.1 Mapping and Geographical Information Systems

This thesis considered biological variability over numerous scales of influence, and thus required the construction of maps and the manipulation and overlaying of environmental data on bathymetry plots. Without exception, maps in this thesis were constructed using the Geographical Information Systems Manifold (CDA-International L, 1993-2008). Compared to traditional language-based GIS packages such as ARC-GIS Manifold has a more direct visual interface, and a more gradual learning curve.

2.1.2 Generalized Additive Modelling

Regression analysis is the statistical method of relating variability in one or more independent variables to one dependent variable. Basin scale analyses of euphausiid distribution (Ch. 3 and 4) were conducted using habitat modelling. Habitat modelling is the prediction of patterns in a continuous biological variable, often the number of individuals of a given species, from a score of environmental variables; see Wintle et al., 2005). Species richness and numerical abundance were predicted using Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990). GAMs are recognised tools for the detection of the influence of environmental variables (environmental data can be either physical or biological) on the variability in a single dependent variable (often a biological term requiring ecological insight). GAMs are generally considered superior to Generalized Linear Models, because they can accommodate non-linear relationships, and thus make fewer assumptions than GLMs (which only accommodate linear relationships; Wood, 2006). However, model selection is generally considered more difficult. GAMs require a link function (e.g logarithmic, inverse) and a distribution (e.g normal, binomial) to be specified for the dependent variable. GAMs may overfit data (constructing overly complicated smooth terms) by suggesting relationships that are not biologically meaningful, if allowed full freedom to choose the shape of the non-parametric function of the independent variable (Steyerberg et al., 2001). It is thus sensible to restrict models to low degrees of freedom, at least below those offered by the data alone. The full model takes the form of equation [2.1] where E is the model function, Y the dependent variable, g the link function between the dependent variable x, and the f smooth function of the *m* predictor:

Equation [2.1]: $g(E(Y))) = B + f_1(x_1) + f_2(x_2) + \ldots + f_m(x_m)$

2.1.3 Multivariate analysis

All multivariate analyses within this thesis were conducted using the statistical software PRIMER (Plymouth Routines In Multivariate Ecological Research; Clarke and Gorley, 2006). Multivariate analysis is a statistical method for comparing different sets of data matrices of environmental or biological data, and provides powerful tools for identifying patterns and trends in ecological communities.

Non-Metric Multidimensional Scaling (Kruskal and Wish, 1978) is a method of comparing the species composition across various samples. Information on individual species density (or biomass) is retained and used for cluster analysis. The analysis is considered non-metric because the multidimensional distance between samples is calculated on a Bray-Curtis similarity matrix (BC; Bray and Curtis, 1957), as opposed to a Euclidian similarity matrix (using standard Pythagoras derivations). The analysis is considered multidimensional because each species conveys an additional dimension. When comparing sample composition, a Euclidian similarity matrix is deemed inadequate, because species universally absent would convey greater similarity. BC similarity Index (S) between two communities (A and B) is derived from equation [2.2] where A_x and B_x is the density of the xth variable (species) in sample A and B.

Equation [2.2]: $(S) = 100 \times (1 - ((\Sigma |A_x - B_x|) / (\Sigma (A_x + B_x)))$

ANOSIM (Analysis Of Similarity) provides a way of testing the significance of *a priori* defined groups of samples in a BC Similarity Matrix. The average differences in similarity between *a priori* groups of samples (R) is derived from equation [2.3] where

n is the total number of samples, A is the average BC similarity between each sample in different groups, and B the average BC similarity of samples in each group.

Equation [2.3]: $R=(A - B)/ (0.5 \times (n(n-1) / 2))$

The R-value always is considered in reference to a p value, which is calculated through permutation tests. In these tests, R is calculated multiple times (usually 999) but using sample groups drawn at random from the full data set. The distribution of these R values provides the null hypothesis of no grouping amongst the samples. The derived R value of the *a priori* defined group is then compared to this distribution. ANOSIM tests provide a means of testing two-way crossed and nested designs, and may thus be conducted on samples in several groups.

2.2 Net sampling

Since the late 1800s, plankton data have been collected with opening-closing nets and trawls (Wiebe and Benfield, 2003). Scientific nets enable quantitative and qualitative investigations of the taxonomic composition in pelagic ecosystems, but are not bias free. The choice of mesh size is a trade-off between quantitatively catching the smallest animals of interest, whilst reducing bucket effects (Tseng et al., 2011). Bucket effects occurs when high trawl speeds or fine mesh sizes causes water to be pushed out and in front of the net, rather than allowing it to filter through the mesh. Moreover, several taxa including jellyfish, salps, pelagic holothurians, and gelatinous pteropods, are too fragile to be retained intact in nets and break apart, making them ill-suited for net-based collection. In contrast, larger nektic species like cephalopods and some fish move probably too rapidly to be caught whilst trawling at conventional pelagic sampling speeds (~2 knts; Heino et al., 2010).

New data presented in this thesis (in Ch. 5, 6 and 7) were collected using either opening and closing nets, such as the RMT1+8 (Roe and Shale, 1979) and the macrozooplankton trawl (Wenneck et al., 2008), or non-closing nets such as the Åkratrawl. The use of opening-and-closing nets minimizes net contamination by shallow or deep fauna. When non-opening-and-closing nets were used, nets were fished by collapsing the trawl and reducing vessel speed during deployment to nominal depths. Data stemming from non-opening-and-closing nets were treated in similar fashion to opening-closing nets; however the potential of shallow water contamination on the statistical analysis is discussed in greater detail in the relevant chapter (Ch 5 and 7). All samples collected at sea for taxonomic purposes were preserved in borax-buffered formaldehyde (4%; Steedman, 1976), with a fraction (usually 1/2) preserved in ethanol (96 %) for molecular purposes (such as for DNA bar coding). Samples collected for stable isotope (SI) analysis (Ch. 6) were frozen at -80 °C upon recovery from the cod-end, and then transferred to -20 °C for long-term storage. Samples collected for fatty acid (FA) analysis were flash frozen and preserved at -80 °C to avoid oxidation of lipids (Ohman, 1996).

Chapter 3

Drivers of variability in euphausiid species richness and numerical abundance in the Atlantic Ocean[1]

3.1 Abstract

Data on euphausiid distribution and abundance arising from recognised ranges of species occurrence and from the Continuous Plankton Recorder survey were analysed in a Generalized Additive Model (GAM) framework. Spatial patterns of variability in euphausiid distribution on, and at either side of, the Mid-Atlantic Ridge from 60° N to 55 S° were investigated in conjunction with variability in a suite of biological, physical and environmental parameters. Euphausiid species richness peaked in mid-latitudes and was significantly higher on the ridge than in adjacent waters, but the ridge did not influence numerical abundance significantly. Sea surface temperature (SST) was the most important single factor influencing both euphausiid numerical abundance and species richness. Increases in sea surface height variance, a proxy for mixing, increased the numerical abundance of euphausiids. GAM predictions of variability in species richness as a function of SST and depth of the mixed layer were consistent with present theories suggesting that pelagic niche-availability is related to the thermal structure of the near surface water: more deeply-mixed water contained higher euphausiid biodiversity.

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[1] The work described in this chapter was published as: **Letessier, T. B.,** Cox, M. J. and Brierley, A. S. (2009) Drivers of euphausiid species abundance and numerical abundance in the Atlantic Ocean. *Mar. Biol.,* 156, 2539–2553.

3.2 Introduction

The MAR extends from Iceland (64ºN) in the north to the Southern Ocean (57ºS) (Fig. 3.1). Knowledge of the fauna of the MAR is presently limited largely to species that live directly on the MAR (e.g. benthic macrofauna, see Gebruk 2008), and pelagic nektic species that live in proximity to the MAR (see Bergstad et al. 2008; Felley et al. 2008; Sutton et al. 2008). Studies investigating the drifting planktic animals living in the water column above the MAR are historically few, although a recent flurry of activity has begun to improve the picture (Stemmann et al. 2007; Gaard et al. 2008; Gislason et al. 2008; Heger et al. 2008; Hosia et al. 2008; Klimpel et al. 2008; Petursdottir 2008; Pierrot-Bults 2008; Youngbluth et al. 2008). It remains unclear whether planktic species are affected by the presence of ridges at all.

In this chapter the potential influence of a suite of environmental variables on the number of species and catch per unit effort (CPUE, a proxy for abundance) of euphausiids are investigated. A grid of cells spanning the majority of the latitudinal extent of the Atlantic Ocean was designed (Fig. 3.1), with particular focus on the MAR and its associated fracture zones. Each cell was populated with historical data on euphausiid species presence/absence and euphausiid CPUE when available, and with environmental data. A Generalized Additive Model (GAM) approach (Wood 2006) was then taken to examine the influence of these environmental variables on euphausiid species richness and CPUE.

3.3 Materials and methods

3.3.1 Grid cell design

The MAR runs broadly north to south but is intersected by fracture zones that result in numerous step-wise offsets along the ridge. A grid of sample cells was designed to cover the ridge and neighbouring open water. The grid comprised a total of 280 cells (370 km east to west × 222 km north to south, 5 columns by 59 rows Fig. 3.1). The east-west topography of the MAR determined the east/west extent of the cells, such that three cells spanned the width of the MAR: the central cell lay over the ridge crest and mid-axial valley, and the two adjacent cells covered the eastern and western MAR slopes. The north/south cell extent was set with consideration of the distance between the major fracture zones, such that multiple cells fitted entirely between fracture zones without any individual cells spanning them. Additional cells were positioned off ridge, midway between the ridge and the east and west coasts. These off-ridge cells served as latitudinally-varying 'controls', being representative of non-ridge open ocean basin environment. All cells were populated, where possible, with euphausiid and environmental data (e.g sea surface temperature, Fig. 3.2) using the Geographical Information System Manifold ® System 8.0 (CDA-International 1993-2008).

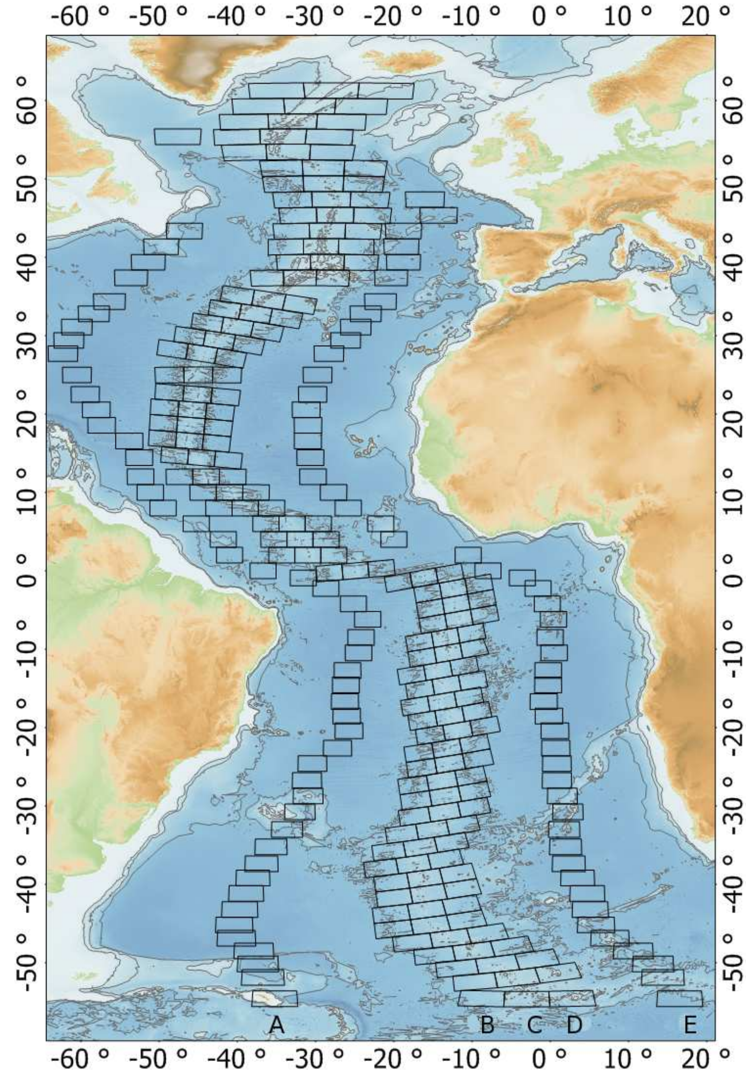

Fig. 3.1 Sampling cells (n=280) on the Mid-Atlantic Ridge on a Latitude-Longitude projection (latitudes and longitudes plotted as if they were X and Y coordinates). Each box is 370 km east to west and 222 km north to south, and is aligned with regionally dominant fracture zones and faults. The three central columns (B, C and D) covered the MAR. Whenever distance from the ridge centre to the coastline enabled, Columns A and E were halfway between the central box and the coastline. The 1000, 2000 and 4000 m isobaths are shown.

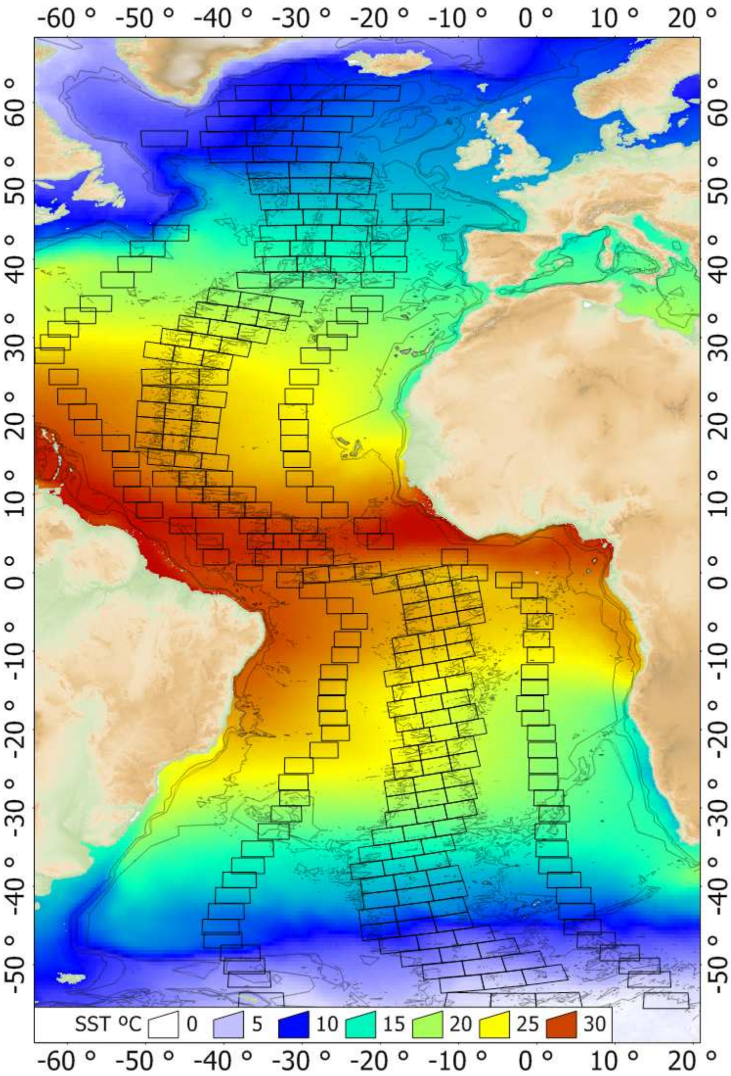

Fig. 3.2 Sea-surface temperature from SeaWiFS with grid cells overlayed. The 1000, 2000 and 4000 m isobaths are shown.

3.3.2 Euphausiid numerical abundance and species richness data sources

3.3.2.1 Species distributions and areas of occurrence

Data on Atlantic euphausiid species distribution ranges (Mauchline and Fisher 1969; Mauchline 1980; Brinton 2000) were used to populate cells with species presence/absence data. Additional searches were conducted in the Global Biodiversity Information Facility for most up-to-date species distributions (updated to 2008), but the majority of records within that Facility stem from well-surveyed areas such as coastal waters, and no species records where found there outside the ranges proposed by Brinton (2000). Additionally, searches were conducted in the primary literature, including recent publications from research programmes that have sampled the MAR, for example the UK Natural Environmental Research Council's (NERC) Marine Productivity programme (e.g. Saunders et al. 2007b), The Census of Marine Life's MAR-ECO (Patterns and processes of the ecosystem of the northern Mid-Atlantic, Wenneck et al. 2008), and NERC's ECOMAR (Ecosystem of the Mid-Atlantic ridge at the sub-polar front and Charlie-Gibbs fracture zone, Read et al. 2009). These records were added to the database whenever they served to extend the historical range of a species' distribution. Together all searches located a total of 54 species throughout the range of the sampling grid, with the species count per cell ranging from 5 to 30 (Fig. 3.3). The full data set can be accessed in supplementary spreadsheet 1 (cell labels is shown in supplement 2).

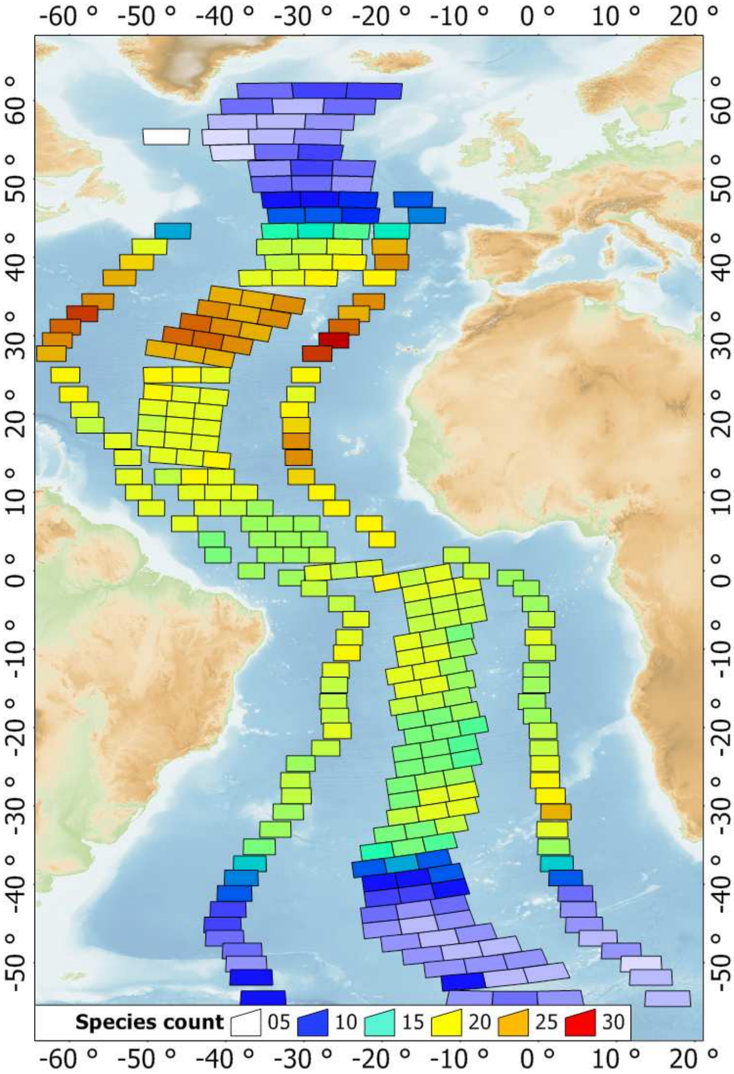

Fig. 3.3 Number of euphausiid species (range 5 to 30)

3.3.2.2 Continuous Plankton Recorder data

The Continuous Plankton Recorder (CPR) has been deployed from ships of opportunity in the Atlantic (and North Sea) since 1931, taking underway samples from the top 10 m (Stevens et al. 2006). Euphausiids have been counted throughout that period, but have not routinely been identified to species level. The exception was in 1966-1967 when euphausiids were identified to species (Lindley 1977). CPR data from 1958-2006 (n=34903 samples falling within the grid of cells) were used to populate the cells with euphausiid numerical abundance. One CPR sample corresponds to a 10 nautical mile haul, along which approximately 3 m^3 of water were filtered. Samples were available between 30º N to 63º N on the MAR (Fig. 3.4) but sampling effort was not distributed evenly. To account for the uneven spatial nature of CPR sampling (Fig. 3.4), euphausiid numerical abundance was scaled by effort (*n* the number of samples per grid cell number) to give catch per unit effort (CPUE, euphausiids per $3m^3$) in cell *j* and.where:

Equation [3.1]: $CPUE_J = \frac{1}{n}\sum_{i=1}^{n} numerical\_density_i$

The full data set can be accessed through supplementary spreadsheet 2.

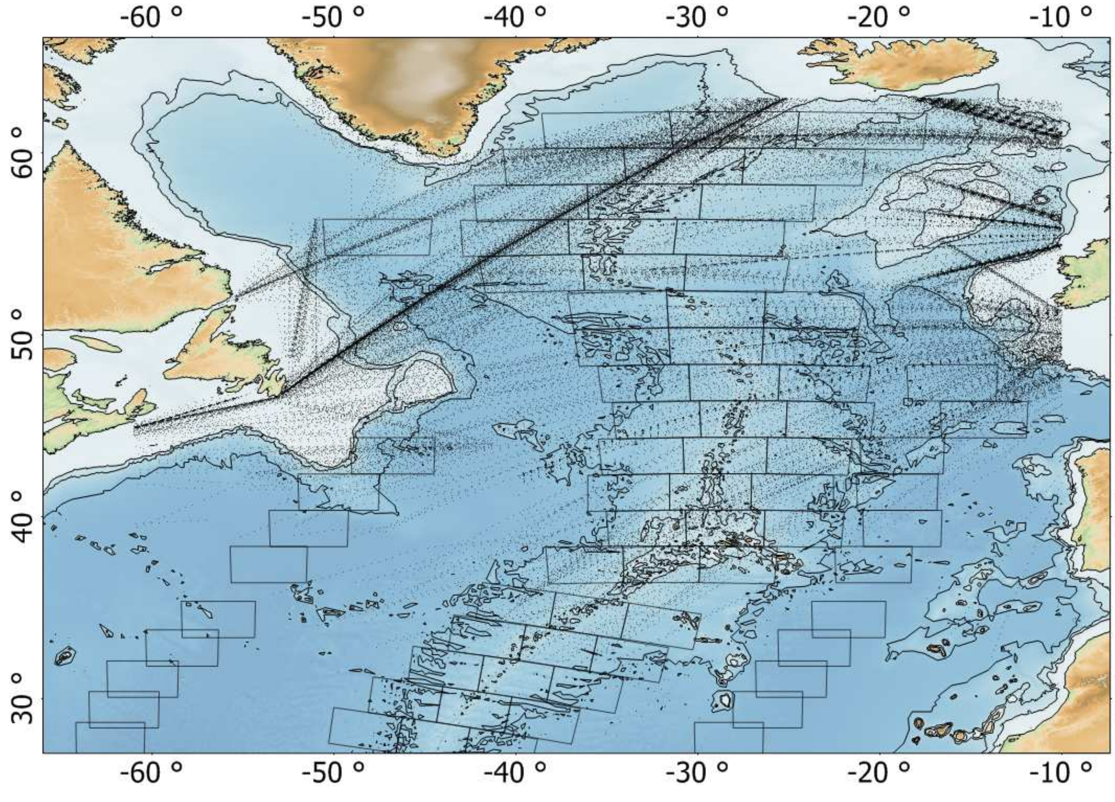

Fig. 3.4 Sampling cell grid and survey stations of the Continuous Plankton Recorder in the north Atlantic (n=87314). Observations span from 1958 to 2006

3.3.3 Statistical modelling

A Generalized Additive Model (GAM) approach was adopted to investigate the influence of various environmental variables on euphausiid species richness and numerical abundance (Table 3.1). The GAM approach was chosen because it enabled both the identification of the statistically significant environmental characteristics (amongst the entire suite of candidate variables) and the scales of influence of the identified variables (magnitude of model parameter estimates) to be determined. Statistical analyses and GAM fitting were carried out using the R language (R v2.5.1 Core development team, 2007). Separate models were fitted to predict species richness and numerical abundance (from CPUE).

3.3.3.1 Explanatory variables

Candidate explanatory environmental variables were obtained from a variety of sources (see Table 3.1 for a list of the 51 variables and their abbreviations as used from here on). Following Austin (2007) the candidate explanatory variables were split into two types: (i) proximal or direct variables, such as SST that may influence euphausiid species distribution directly (Gibbons 1997; Rutherford et al. 1999), and (ii) distal or indirect variables, such as latitude, that have no direct biological affect but are correlated with proximal variables and may be used as surrogates, e.g. latitude is a surrogate for the light intensity and seasonality at a given location.

Table 3.1 Explanatory variables used in the Generalized Additive Models, sources, and rational for including them. Unless otherwise stated data resolution is a 1º latitude-longitude grid. NA = Not applicable

Environmental variables	Abbreviation	unit	Online source	Time range	Resolution/average over	Reference and rational
Rossby radius of deformation	Rossby	km	Global Atlas of the First-Baroclinic Rossby Radius: http://www.coas.oregonstate.edu/research/po/research/chelton/index.html	NA	1º /NA	Chelton et al (2008) define Rossby radius as “the length scale of baroclinic variability longer than which internal vortex stretching is more important than relative vorticity”. The large Rossby radius at high latitudes has been shown to increase the dispersal of euphausiid populations (Huntley & Niiler 1995)
Chlorophyll a concentration	Chl-a	mg m^{-3}	OceanColor: http://oceancolor.gsfc.nasa.gov/	2002-2008	1º/monthly	NASA Ocean Biology Processing Group (OPBG) Moderate Resolution Imaging Spectroradiometer(MODIS) -Aqua Monthly Global 9-km Products. Euphausiid populations are often bottom-up controlled, and are linked to primary production (Kim et al., 2010)
Sea surface temperature	SST	ºC	OceanColor: http://oceancolor.gsfc.nasa.gov/	2002-2008	1º/monthly	NASA OBPG MODIS-Aqua Monthly Global 9-km Products. Sea surface temperature has been shown to be a strong predictor of species richness in marine systems (Tittensor et al., 2010). The data is average over 6 years in this study.The short-wave SST algorithm make use of MODIS bands 22 and 23 at 3.959 and 4.050 um. The brightness temperatures are derived from the observed radiances by inversion (in log space) of the radiance versis blackbody temperature relationships (from the SeaWIFS website).
Dissolved and detrital organic matter absorption coefficient	Domac	m^{-1}	OceanColor: http://oceancolor.gsfc.nasa.gov/	2002-2008	1º/monthly	NASAGarver-Siegel-Maritorena (GSM) SeaWiFS Optical Monthly Global 9-km Products. A satellite product that may be a proxy for the availability of dissolved detritus for euphausiid consumption.
Particulate backscatter coefficient	Pac	m^{-1}	OceanColor: http://oceancolor.gsfc.nasa.gov/	2002-2008	1º/monthly	NASA GSM SeaWiFS Optical Monthly Global 9-km Products. See above.
Salinity	Sal		OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), zooplankton diversity has been linked to salinity in estuaries (Primo et al., 2009)
Dissolved O_2 concentration	O_2	ml l^{-1}	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), euphausiid swarm formation is linked to access to dissolved Oxygen concentration (Brierley & Cox, 2010)
Dissolved SiO_3 concentration	SiO_3	µmol l^{-1}	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), silicate concentration can act as control for zooplankton diversity (Roy, 2008)
Dissolved NO_3 concentration	NO_3	µmol l^{-1}	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), a nutrient that is important for primary production

Dissolved PO_4 concentration	PO_4	µmol l^{-1}	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), a nutrient that is important for primary production
Temperature at 50 m	T-50	ºC	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), see SST for rational
Temperature at 100 m	T-100	ºC	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), see SST for rational
Temperature at 150 m	T-150	ºC	OceanAtlas: http://odf.ucsd.edu/joa/	1990-1998	2º/NA	Osborne and Flinchem (1994), see SST for rational
Mixed layer depth values for May and June	MLD-may and june	m	U.S. Naval Research Laboratory, Stennis Space Center: http://www7320.nrlssc.navy.mil/nmld/nmld.html	1900-1992	1º/NA	Kara et al. (2002), MLD is the depth to which surface waters have been homogenized by turbulence. Values were cubed to reflect the volume of water affected. MLD has implication for the seasonal production patterns of marine systems, and thus for the growth and diversity of krill populations.
Mixed layer depth values for November and December	MLD-november and december	m	U.S. Naval Research Laboratory, Stennis Space Center: http://www7320.nrlssc.navy.mil/nmld/nmld.html	1900-1992	1º/NA	
Sea level anomaly (height) mean	SSH-m	cm	AVISO: http://www.aviso.oceanobs.com/	2001-2008	0.33º/7 days	Ducet et al. (2000), the altimeter products were produced by Ssalto/Duacs and distributed by *Aviso*, with support from *Cnes*. Zooplankton population can be correlated with coastal sea level anomalies *(Clarke & Dottori 2008)*
Sea level anomaly (height) variance	SSH-var	cm^2	AVISO http://www.aviso.oceanobs.com/	2001-2008	0.33º/7 days	Ducet et al. (2000), sea level variance was used as a proxy for water dynamics, which is known to be linked to zooplankton biomass heterogeneity (Piontkovski and Williams 1995).
Surface current velocity	Vector V and Vector U	m s^{-1}	OSCAR http://www.oscar.noaa.gov/	1992-2008	2º /5º/NA	Bonjean and Lagerhoed (2002), currents can transport krill species to waters outside their traditional range (Saunders et al., 2007b). V and U denote the vertical and horizontal magnitude of the current.
Box coordinates	Latitude and Longitude	Decimal degrees		NA	NA	Latitude and longitude of the cell centre.
Distance to Pacific Ridge	DR	km	The ridge was defined by points located over 2º of latitude/longitude			Distances to the following ridges were calculated: Juan de Fuca, Chile, Galapogos spreading centre, East Pacific Rise, Pacific-Antarctic Rise. Seamounts and ridges can enhance local population and species diversity of plankton and nekton (Pitcher et al., 2008)
Distance to coast	DC	km	The coast was defined by points located ever 5º of latitude/longitude			
Depth	Depth	m	Depth	NA	NA	Average seabed depth within each cell

As proposed by Harrell et al. (1996), the rule of thumb of limiting the degrees of freedom (q) of the explanatory variables offered for model selection to $q = m/10$ was followed, where m is the minimum number of observations in the response for each of the explanatory variables. Using this rule, the maximum degrees of freedom for explanatory variables entering the model selection procedure was $q = 28$ for the euphausiid species richness and $q = 6$ for the euphausiid numerical abundances.

Of the 51 candidate explanatory variables (including distances to fracture zones), 20 were considered potential proximal and 31 distal environmental drivers (Table 3.1). Even for conventional linear modelling, where each explanatory variable 'costs' one parameter, the number of candidate variables exceeded the recommended number of degrees of freedom, m. Consequently the number of candidate variables was initially reduced using the following rationale before the more formal model selection procedure was used.

1) Candidate explanatory variables that were considered to have no effect on euphausiid numerical abundance or species richness were removed following the recommendations of Harrell (2001). For example, distance to the Conrad fracture zone, located in the southern hemisphere, would probably not influence euphausiid numerical abundance in the northern hemisphere.

2) A correlation matrix between environmental variables was constructed and, following Wintle et al. (2005), one of each pair of explanatory variables with correlation $R > 0.7$ was discarded, keeping the variable that was deemed most likely to have a biologically-founded impact. Since any potential influence of proximal explanatory variables could be interpreted directly, e.g. +1°C increases euphausiid species richness by x, whenever possible proximal variables were retained in preference to distal variables.

Following this process, 11 potential candidate explanatory variables remained for model selection (Table 3.2).

Table 3.2 An example of the backwards model selection algorithm applied to the euphausiid species richness generalized additive model. See table 3.1 for abbreviations. A subset of the candidate models based on cross-validation scores (GCV) is given. Terms preceded by an "s" are smooths with "k" the dimension of the basis the smooth terms

Model number	Model structure	GCV	Dropped term
1	Species richness ~ Longitude + Rossby + Depth + Chl + s(SST, k = 3) + s(SiO_3, k = 3) + MLD_nd + MLD_mj + DR + SSH_var +factor (ridge side)	0.3059	Rossby
2	Species richness ~ Longitude + Depth + Chl_a + s(SST, k = 3) + s(SiO_3, k = 3) + MLD_nd + MLD_mj + DR + SSH_var + factor (ridge side)	0.3038	SSH_var
3	Species richness ~ Longitude + Depth + Chl_a + s(SST, k = 3) + s(SiO_3, k = 3) + MLD_nd + MLD_mj + DR + factor (ridge side)	0.3032	Factor (ridge side)
4	Species richness ~ Longitude + Depth + Chl_a + s(SST, k = 3) + s(SiO_3,k = 3) + MLD_nd + MLD_mj + DR	0.3031	

3.3.3.2 Functional form of environmental variables

A log-link function was used within the selected GAM framework to accommodate potential non-linear relationships between euphausiid response variables (either species richness or numerical abundance) and explanatory variables (see Fox 2002 for a full list of assumptions). Incorporating smooth functions within the GAM framework enabled accommodation of non-linear continuous explanatory variables (Wood 2006). Non-linear explanatory variable forms may have been quadratic, cubic, or of a more complex shape. Fully automated model selection would allow the model full freedom to select a non-linear form that balanced variance with complexity. However, Steyerberg et al. (2001) demonstrated that this approach may generate relationships that have no sensible biological basis. Consequently, using the approach of Wintle et al. (2005) univariate GAMs were inspected visually, with 5 df (Austin and Meyers 1996), between each continuous candidate explanatory variable and the response variable. The models were restricted to 5 df, thus avoiding the generation of relationships that were biologically too complex, whilst permitting the models sufficient freedom to reveal underlying biological patterns. Knowledge of the biological processes, and visual inspection of the resultant relationships, was used to guide manual selection of the non-linear shape of candidate explanatory variable models (e.g. species diversity was set as a smooth function of sea surface temperature, as per Rutherford et al. (1999)). Where non-linear candidate explanatory variables were found to exist it was the manually selected, non-linear forms that were used as candidate explanatory variables during final automated model selection.

3.3.3.3 Species richness model selection

The bimodal nature of the euphausiid species richness data (Fig. 3.5) required that the modelling framework should estimate the dispersion parameter (i.e. mean≠variance). Therefore a quasi-Poisson error distribution (to estimate dispersion) and a log-link function (to account for the bimodal frequency distribution) were opted for. The selection of a quasi-likelihood error distribution meant that, for the euphausiid species richness investigation, model selection had to be carried out using the model generalized cross validation score (GCV, Wood 2006). The GCV score was employed because more conventional likelihood based model selection approaches, such as Akaike information criteria (AIC, Akaike 1973; Burnham and Anderson 2002) are not possible with quasi-distributions since likelihoods cannot be calculated. The GCV score can be thought of as a scaled AIC, in that the model with the lowest GCV score offers the optimum combination of fit and parsimony. A GCV score-based backwards model selection algorithm (Table 3.2) was used because this generally performs better than AIC in the presence of collinear variables (Harrell 2001), and also includes all possible explanatory variables in the first candidate model.

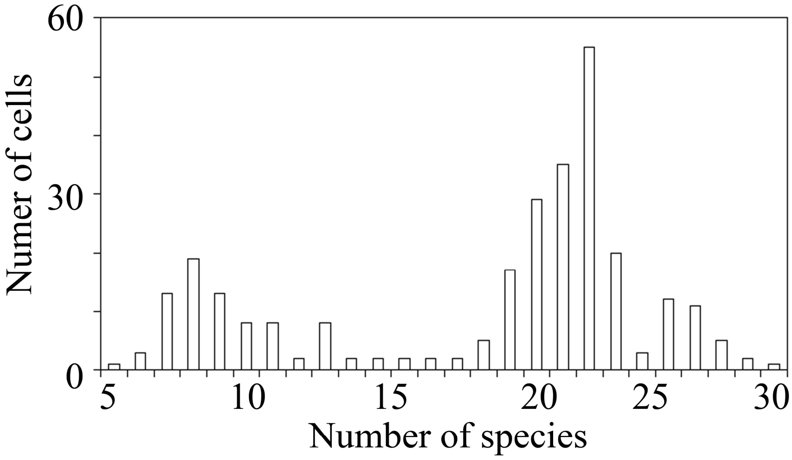

Fig. 3.5 Number of cells containing a given number of euphausiid species. The lowest species richness was located at high latitude and the highest at mid-latitude in the northern hemisphere (see Fig. 3.4)

3.3.3.4 Numerical abundance model selection

Numerical abundances were modelled using CPR CPUE data as the response variable, and a log-link function with a Gamma error distribution since CPUE was a continuous variable. Following the recommendations of Burnham and Anderson (2002), competing hypotheses for the biological drivers of numerical abundance were set up, and model selection was based on a subset of the explanatory variables. Within these explanatory variable subsets, backwards selection using the GCV was carried out.

3.3.3.5 Model evaluation

Model performance was evaluated based on three of the four metrics used by Potts and Elith (2006): (1) Pearson's correlation coefficient, r, was used as an indication of the relative agreement of the observed and predicted values. (2) Model calibration was assessed by linear regression between the predicted and observed values; the intercept of the linear regression c provided an indication of bias, and the gradient m (3) provided a comparison between the spreads of the data and model predictions. A perfectly calibrated model would have $c = m = 1$.

3.3.3.6 Explanatory variable practical influence

The biological, or practical, influence of statistically significant explanatory variables for the selected euphausiid species richness and numerical abundance models was investigated as follows. All explanatory variables were set to their mean observed value. Model predictions then were made for each explanatory variable in turn, with the value of the explanatory variable under investigation adjusted first to the 2.5% then the 97.5% quantile of the explanatory variable observed values. The percentage change was calculated by standardizing the change of the response variable between the quantiles of each explanatory variable (species richness and CPR CPUE) by the difference in the response variables from this respective 2.5% and 97.5% quantiles. For the smooth functions (SST and SiO_3) the change between the quantiles was assumed to be linear.

3.3 Results

3.3.1 Spatial patterns of distribution and abundance

3.3.1.1 Species richness

The species richness was typically high in mid-latitude and tropical regions, and low in higher latitudes (Fig. 3.3). The highest species richness per cell (30) was found in the mid-latitude in the northern hemisphere, in the eastern mid-ocean cell (29.3854 ºN 26 ºS). A peak in abundance was located off the coast of southeast Africa. The lowest species richness (5) was located in the Labrador Sea (Fig. 3.3).

3.3.1.2 Numerical abundance

The general pattern of euphausiid numerical abundance was a southward decrease in abundance in the northern hemisphere (Fig. 3.6). The highest abundance of euphausiids was located in the Labrador Sea. High abundance was located in the area immediately north of the Charlie-Gibbs fracture zone and in the cell south of Iceland on the Reykjanes ridge. Low abundances were recorded predominantly south of the North Atlantic Current.

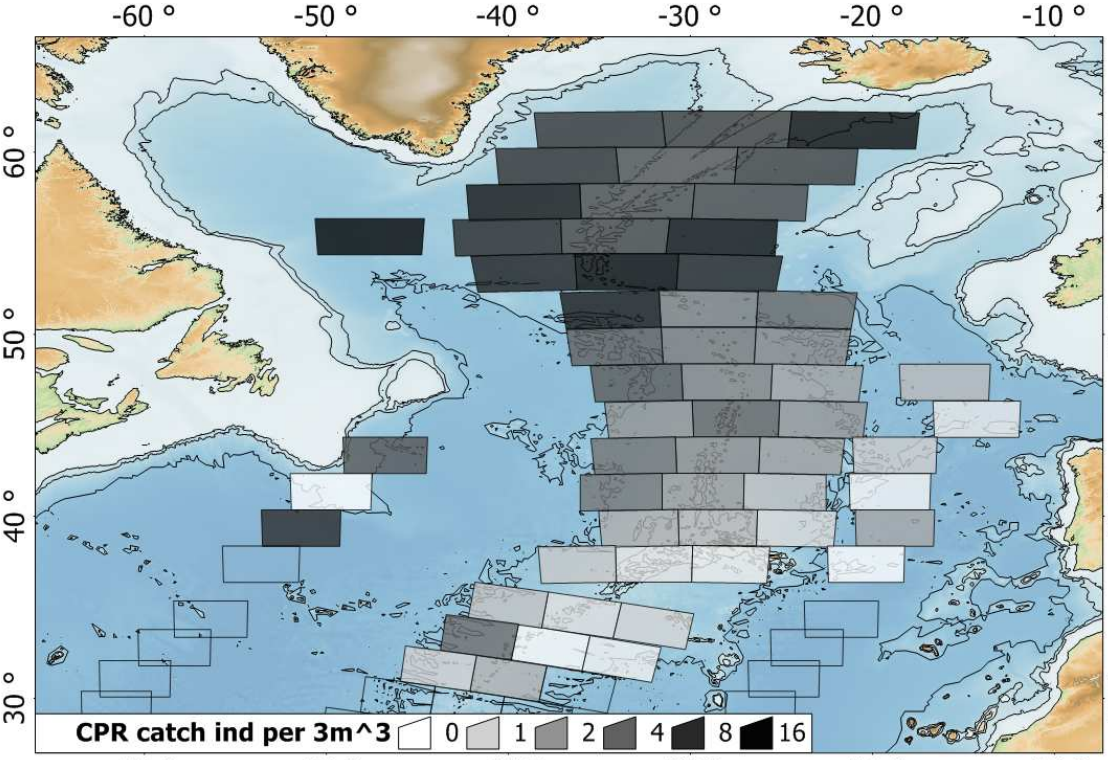

Fig. 3.6 Euphausiid density (individuals. 3m^{-3}) in the North Atlantic as collected by the Continuous Plankton Recorder

3.3.2 Statistical modelling

The modelling objective was to determine the influences of environmental variability on species- and numerical-abundance of euphausiids. Models for both performed well in this regard, with the species richness and numerical abundance GAMs explaining 86.9% and 83.3% of the variability (R^2) respectively (Table 3.3).

Table 3.3 Model performance metrics for the assessment of the performance of the euphausiid numerical and species richness models

Model performance metric	Numerical abundance	Species abundance
correlation r	0.92	0.93
calibration intercept (b)	0.49	2.47
calibration slope (m)	0.88	0.87
R^2	0.83	0.87

3.3.3 Model selection

3.3.3.1 Species richness model

The selected explanatory variables for the species richness model were SST, SiO_3, Chl-a, Longitude, MLD-nd, MLD-mj, depth and DR (see Table 3.1 for abbreviations, Tables 3.2 and 3.4). The differences between the predicted species richness values at the 2.5% and 97.5% quantiles showed that the greatest change in numerical abundance was caused by changes in SST, followed by changes in SiO_3 (Table 3.5). An increase in the numerical value of these explanatory variables lead to an increase in species richness. These terms were both fitted as smooths (Fig. 3.7).

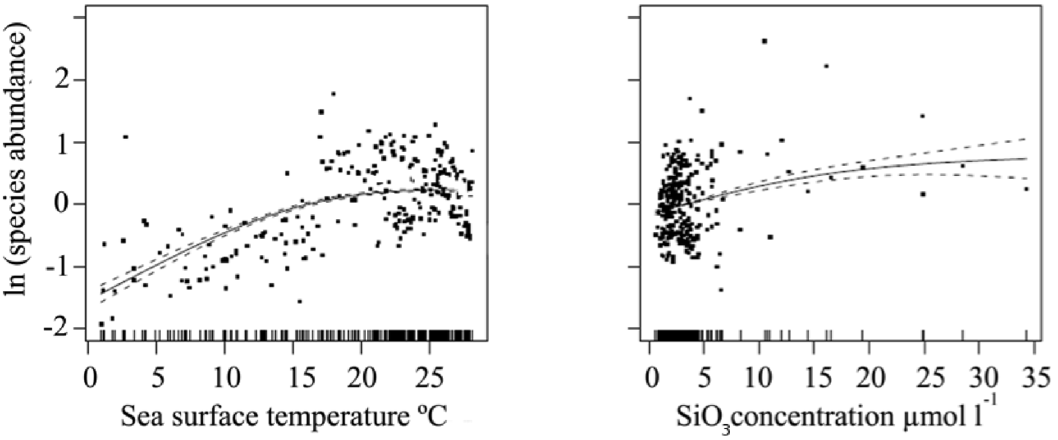

Fig. 3.7 Partial plots of the relationships between euphausiid species richness and smooth terms of SST and SiO_3 concentration. Partial plots investigate the influence of the variable in question only. The euphausiid species richness counts on the y-axes are presented in the log domain so can be interpreted in the same way as linear regressions. The dashed lines represent the 95% confidence intervals for curves.

Other important proximate variables were chlorophyll-a (Chl-a), Mixe-layer depth (MLD) and depth. Increase in depth and distance to ridge (DR) lead to a decrease in species richness, although the impact of distance to the MAR was minor (percentage change credited to DR<-0.0001). Longitude was the only distal variable selected, and it appeared that there was an eastward decrease in species richness. The species richness predictions were consistent with the general pattern of species richness (Fig. 3.4) as demonstrated by the residuals plot (predicted minus observed values; Fig. 3.8). Areas of under-prediction occurred in the north (50ºN, 30ºW), the western tropics (5ºN, 30ºW), and the southwest (20ºS, 15ºW; and 30ºS, 30ºW). Over-prediction occurred in the central north (30ºN, 40ºW) and eastern north Atlantic (40ºN, 15ºW), and along the western coast of South Africa.

Table 3.4 Statistical significance of retained p-values for explanatory variables retained in the GAM species count and numerical abundance models. Variables that were not selected in the final model are denoted by NA

Environmental variables	Numerical abundance model	Species richness model
	p-value	p-value
Longitude	NA	$5.71e^{-08}$
Depth	NA	0.035
Chl_a	NA	$5.41e^{-12}$
MLD_nd	NA	$8.93e^{-05}$
MLD_mj	NA	0.036
DR	NA	$1.57e^{-05}$
SST	$<2e^{-16}$	$<2e^{-16}$
SiO_3	0.00324	$<2e^{-16}$
SSH_var	$4.19e^{-16}$	NA

Table 3.5 Euphausiid species richness model parameter estimates and associated confidence intervals. The influence of each explanatory variable on euphausiid species richness is shown by predictions made at the 2.5% and 97.5% quantiles of the explanatory variable data values on the scale of the response variable. During the prediction all other explanatory variables were fixed at their mean value. S.E. is the standard error of the prediction and estimated change is the number of species prediction, made at the 2.5% and the 97.5% explanatory variable quantiles. Negative percentage change indicate a decrease in species between the quantiles. See ”Explanatory variable practical influence” for the calculation of estimated change and the percentage change

Explanatory variable	Explanatory variable value at the 2.5% quantile	2.50% Estimate	S.E	Explanatory variable value at the 97.5% quantile	97.50% Estimate	S.E	Estimated change (n species)	Percentage change
SST	2.613	5.18	0.32	27.88	22.98	0.46	17.80	34.44
SIO_3	1.05	20.32	0.45	14.74	35.56	1.96	15.23	29.46
Chl_a	0.043	23.13	0.37	0.55	16.81	0.63	-6.32	-12.23
Longitude	-57.20	23.27	0.53	3.76	19.56	0.35	-3.71	-7.18
MLD_nd	20102	21.89	0.36	2420529	18.44	0.67	-3.44	-6.65
MLD_mj	12608	21.90	0.36	2063857	18.92	0.58	-2.98	-4.28
Depth	-5540.40	20.24	0.58	-2312.80	22.45	0.61	2.21	-4.28
DR	0.000	21.39	0.29	1761.95	21.39	0.29	-0.00051	-0.00

3.3.3.2 Numerical abundance model

For the numerical abundance model, the use of the full suite of candidate variables was not possible because only 6 candidate degrees of freedom were available. Following Burnham & Anderson (2002) competing hypotheses for the biological drivers of numerical abundance (section 3.3.2) were set up. The model selection was based on a subset of 6 of the 51 explanatory variables (see the first row of Table 3.2). Within these explanatory variable subsets, backwards selection using the GCV score was carried out. The selected explanatory variables were a non-parametric smooth of the relationship with SST, and linear relationships with SiO_3 and SSH-var (Fig. 3.9, Table 3.6). The difference in numerical abundance at the 2.5% and 97.5% quantiles indicate that increased SST and increased SiO_3 led to decreases in the numerical abundance of euphausiids (Table 3.6), whereas increased SSH-var led to increased numerical abundance of euphausiids. SST was the most important driver of variation in euphausiid numerical abundance.

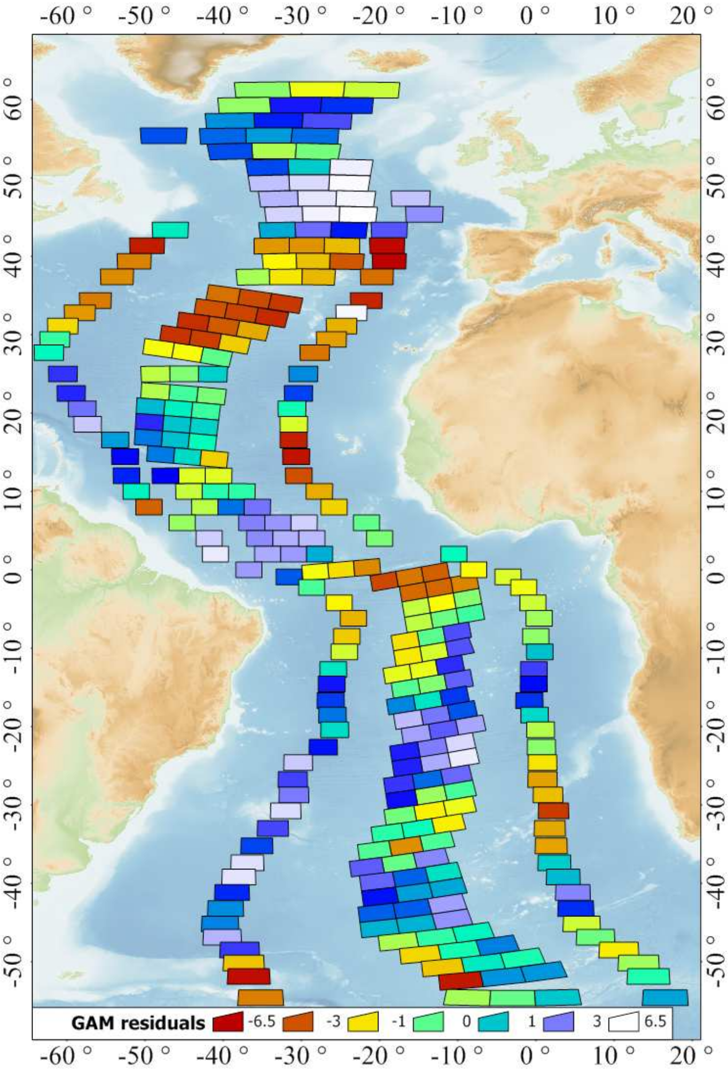

Fig. 3.8 Species richness model residuals (predicted minus observed values).

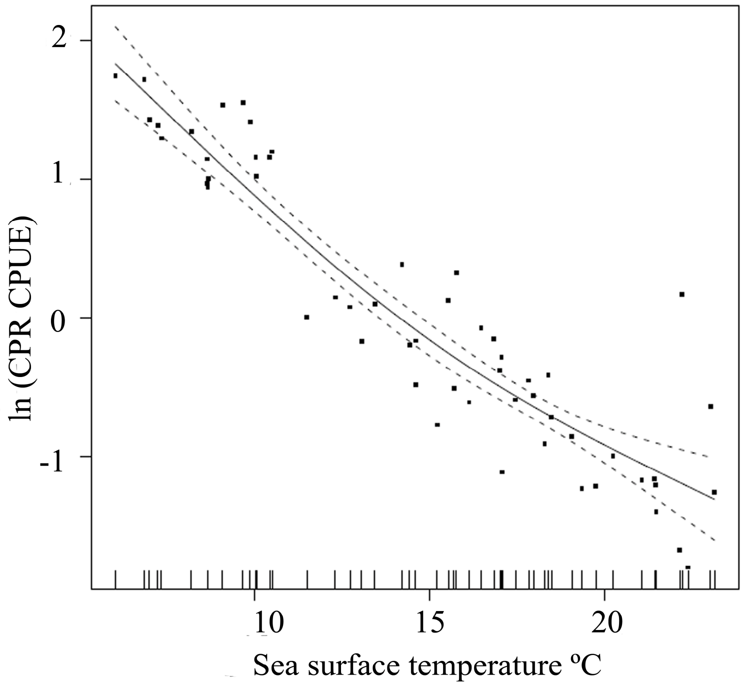

Fig. 3.9 Partial plot of the relationship between catch per unit effort (CPUE) of euphausiid numerical densities obtained from Continuous Plankton Recorder (CPR) observations and smooth terms of SST. The fitted curve shows the relationship between SST and CPR CPUE. The dashed lines represent the 95% confidence intervals for the curve. SSTs are annual means per sampling cell between 2002 and 2008

3.3.4 Model performance

Under the model assessment criteria proposed by Potts and Elith (2006), both species richness and numerical abundance models performed adequately, as demonstrated by the high correlation between predicted and observed values (Table 3.3). The calibrations revealed some evidence of bias in the model predictions, particularly for the numerical abundance model that had a low intercept parameter. There was some under-dispersion in the species richness data, as indicated by the high dispersion parameter (0.291), thus validating the choice of quasi-Poisson distribution.

Table 3.6 Euphausiid numerical abundance model parameter estimates and associated confidence intervals. The influence of each parameter on euphausiid numerical abundance is shown by predictions made at the 2.5% and 97.5% quantiles of the explanatory variable data values on the scale of the response variable. During the prediction all other explanatory variables were fixed at their mean value. S.E. is the standard error of the prediction and estimated change in numerical abundance is the prediction made at the 2.5% and the 97.5% explanatory variable quantile. See section ”Explanatory variable practical influence” for the calculation of estimated change and the percentage change

Explanatory variable	Explanatory variable value at the 2.5% quantile	2.5 % Estimate	S.E.	Explanatory variable value at the 97.5% quantile	97.5 % Estimate	S.E.	Estimated change (n euphausiids)	Percentage change
SST	6.91	14.77	1.82	22.774	0.8289	0.121	-13.94	-76.7
SSH_var	17.87	2.212	0.189	316.7	4.606	0.591	2.394	13.2
SiO_3	2.100	3.58	0.521	6.914	1.737	0.232	-1.843	-10.1

3.4 Discussion

The aim of this investigation was to determine what factors, if any, influenced the distribution and abundance of euphausiids in the Atlantic, giving special consideration to the Mid-Atlantic Ridge. Two ridge proxies, total depth and distance to ridge, were significant variables in the final species richness model, and thus provide evidence that the ridge itself has a minor influence on the species richness of euphausiids. These ridge proxies did not influence the numerical abundance of euphausiids. Euphausiid species richness was driven primarily by SST, and the results are consistent in this regard with present understanding of diversity patterns of euphausiids (Reid et al. 1978; Gibbons 1997) and other zooplankton groups (McGowan and Walker 1985).

3.4.1 Drivers of species richness

Across latitudes and taxa, and all else being equal, species richness is traditionally believed to increase towards in the tropics, (Fuhrman et al. 2008). Several hypotheses, such as the species-energy hypothesis (Rohde 1992; Allen et al. 2002; Cardillo et al. 2005; Clarke and Gaston 2006), the species-area hypothesis (Currie et al. 2004), and the historical perturbation hypothesis (Stevens 2006) have been proposed to explain this latitudinal gradient. The euphausiid species richness data showed, by contrast, that the greatest number of species within this taxon was located in the mid-latitudes, and not in the tropics. Moreover, the results indicate that the greatest change, some 34.44%, in euphausiid species richness may be explained by variation in SST.

The primary productivity proxy (Chl-a) was included in the final model, although this was as an annual mean, and did not encompass a proxy for seasonal patterns. The influence of seasonality on euphausiid species/numerical abundance was initially considered by assigning a categorical value to each cell using Longhurst's biomes and re-running the model. Some biomes were statistically significant, but General Variance Inflation factor was very high for the categorical biome variable (>1000). This suggested strong multicolinearity between biomes and other variables in this model. Therefore, the original model was retained.

The exposure of Chl-a as a negative driver of euphausiid species richness by the model is consistent with present understanding regarding the relationship between phytoplankton biomass and planktic diversity (Agard et al. 1996). Maximum micro-zooplanktic diversity levels have been found typically at intermediate levels of phytoplankton biomass (zooplanktic diversity is a bimodal function of phytoplankton biomass, see Irigoien et al. 2004), however few studies have investigated the link between primary productivity and larger pelagic taxa (but see Rosa et al., 2008).

Increases in the winter and summer averages for the volume of the mixed layer significantly decreased species richness. The mixed layer depth (MLD) is the depth to which active turbulence has homogenized the water (Levitus 1982). Throughout the cell grid the highest species richness values corresponded to intermediate levels of MLD (e.g. 100 to 150 m), as located at mid-latitudes (Floder and Sommer 1999). The link detected by the model is probably related to the influence of the MLD on primary productivity patterns: a basin-wide and decadal study in the Pacific has shown that deepening of the MLD may increase local primary productivity by up to 50% by supplying deeper waters with nutrients (Polovina et al. 1995) in subtropical regions. Furthermore, climate-driven deepening of the mixed layer is now driving down overall total production in the Pacific (Behrenfeld et al. 2006). As previously stated, Chl-a was significant in predicting some of the decreases in species richness. Here evidence is presented for a mechanism by which the depth of the mixed layer can affect patterns of pelagic species richness, potentially through influencing primary productivity.

A larger percentage of the increase in species richness was driven by the increase in SiO_3 concentration, although this relationship was biased by a few high SiO_3 concentration observations. The scale of the observations here means that these results only pertain to average relationships, across seasonal patterns. On a smaller, seasonal, scale high SiO_3 concentration usually indicates that the silicate has not been used up by siliceous phytoplankton, and phytoplankton blooms may typically be associated with low SiO_3 concentration because the phytoplankton had already utilized the SiO_3. On a yearly scale, SiO_3 concentration has an effect on the species richness ratio of phytoplankton, and diatom growth rate is correlated with silicate concentrations (increases in SiO_3 may shift a flagellate dominated system to a diatom dominated system, see Escaravage and Prins 2002). SiO_3 availability can limit phytoplankton growth in many systems (Hashioka and Yamanaka 2007). Larger diatom species often are inaccessible to higher trophic level in planktic systems (such as some euphausiids) (see section 4.3), so silicate availability can influence community composition amongst primary grazers and beyond. Moreover, a high silicate concentration may inhibit competitive exclusion of certain mesozooplanktic species typical of high productivity regimes, thus increasing species richness (Roy 2008).

3.4.2 Model residuals

There is some consistency and predictability in the species richness model residuals. Under-prediction (positive residuals) occurs predominantly in the North Atlantic, and is associated geographically with the sub-polar front. This discrepancy might be due to the mixing of different water masses (Iceland Current and North Atlantic Current) over the Charlie-Gibbs Fracture Zone (CGFZ). The CGFZ has been identified as a boundary between biomes (Longhurst 1998) and a faunal divide for zooplankton (Gaard et al. 2008), and is likely to harbour a mix of species arising from different water masses. Although this area is high in productivity, which should decrease the number of species, the localized biogeographical properties of this region may counter this effect.

Over-prediction (negative residuals) occurred near the east coast of Africa and along the fringe of the Benguela upwelling system. The cold, nutrient-rich upwelling water drives the high productivity of this area (Loncaric et al. 2007), and may serve to reduce the species richness, as per the model results.

Over-prediction in the North Atlantic gyre might be linked to the formation of 18ºC Mode Water (Goldthwait and Steinberg 2008) in the Sargasso Sea. Mode Water is characterised by uniform properties over an extensive depth range. and its formation in the Sargasso Sea is likely to impact vertical niche availability, and may subsequently affect pelagic diversity (Michaels and Knap 1996).

Some over-prediction also occurs in the western sector of the Atlantic and may, in some cases, be linked to coastal plankton blooms associated with river run-off (Livingston 2007). River run-off enhances nutrient input and can stimulate enhanced primary productivity. Moreover river run-off can, according to Huston’s dynamic equilibrium model, increase disturbance and subsequently reduce species diversity (see Huston 1979, highest species diversity is located in systems with intermediate disturbance) of a pelagic system through competitive exclusion (Agard et al. 1996). In this context, disturbance is defined as rate of mortality of individuals caused by biotic or abiotic factors (Agard et al. 1996).

The species richness data have several limitations, the most troublesome of which is the inconsistency of effort between cells. Species richness by cell was compiled with reference to maps of species distributions, and these maps are themselves subject to sampling limitations: some regions of the Atlantic have been repeatedly sampled (such as the coastal regions of the British Isles), yet others have seldom been visited. Moreover the sampling is further complicated by the use of different sampling gears, and different sampling depths between trawls. This is potentially problematic as the vertical distribution of euphausiids varies on a temporally (Endo and Wiebe 2007) and there is considerable temporal variation in euphausiid horizontal distribution on an annual (Saunders et al. 2007a) and monthly scale (Trathan et al. 1993). It is likely that the estimates of species numbers in poorly surveyed areas, such as the central mid Atlantic, are low (certain sectors of the MAR have only been sampled once (see Gibbons 1997)). This lack of effort could help explain the grouping of negative residuals in certain sectors of the tropical and south Atlantic. The most recent description of a previously unknown euphausiid species was in 1987 in the Pacific (Brinton 1987). Nevertheless, I contend that euphausiid distribution is adequately known for the present purpose, and that for euphausiids generally the hypothetical species discovery curve is close to the asymptote (Bebber et al. 2007), and that further sampling is unlikely to markedly influence our results. Thus although sampling might be biased, the broad conclusions drawn are probably not compromised by sampling effort limitations.

3.4.3 Drivers of numerical abundance

Several studies address the capacity of the CPR to quantitatively sample zooplankton and euphausiids (Batten et al., 2003; Batten et al., 2007). Although the CPR under samples zooplankton compared with traditional vertical nets, seasonal and geographical patterns are reflected by the data (Batten et al., 2003) and the data are considered adequate for purposes here. The most influential predictors of numerical abundance (in terms of percentage species change per interquantile range) were, in decreasing importance, SST, SSH-var, and SIO_3. The influence of SST on zooplankton abundance is well known, and instances of decreases in zooplankton abundance due to increases in SST have been recorded previously (McGowan et al. 2003; Wiafe et al. 2008). The average effect of SST between the 2.5 and 97.5 % quantiles is estimated as a decrease of 0.29 euphausiids m^{-3} ºC $^{-1}$ assuming a linear change. It is important to emphasize however, that the modelled relationship is smoothed and hence not strictly linear.

Elevated zooplankton biomass often is found in frontal sectors and their areas of influence (Hense et al. 2003), where SSH-var is typically high. The observed effect of SSH-var on the numerical abundance may be due to increased productivity often associated with frontal features (Heath and Beare 2008; Sambrotto et al. 2008): indeed the highest numerical abundance was located at the sub-polar front, an area that harbours high phytoplankton biomass (Tilstone et al. 2009). This observation supports the theory that copepod grazing on phytoplankton is reduced by predation from larger zooplankton (see Gaard et al. 2008).

Many euphausiids are grazers and their distribution is expected to be related to primary production. The proxy for productivity (Chl-a), was not selected in the final numerical abundance model. Moreover, this result is counter to the observation that zooplankton populations are limited by bottom-up regulation (Edwards and Richardson 2004).

The influence of SiO_3 concentration suggested by the model is consistent with present understanding of impacts of nutrient limitation on trophic interactions between primary productivity and primary consumers (see section 4.1). As previously stated, high SiO_3 concentration is correlated with diatom growth rate. Moreover a high diatom biomass can lead to a trophic mismatch, where the elevated phytoplankton biomass is inaccessible to higher levels (Escaravage and Prins 2002). The effect of SiO_3, assuming linear change between the 2.5 and 97.5% quantiles, is estimated to be -0.18 euphausiids

m^{-3} µmol^{-1} l^{-1}. The influence of silicate concentration may also be synergistic with ocean mixing patterns, high concentration is typically correlated with low temperature and high SSH variability.

The overall sample size (n=34903) and the broad seasonal span of the CPR data (sampling is conducted year round) means that the numerical abundance values are unlikely to be influenced by the high temporal frequency and mesoscale variability that is a feature of marine systems (Brierley et al. 2006; Sherwin et al. 2006). However, when inferring upon broad scale patterns of numerical abundance, the CPR data have many limitations. The CPR samples are geographically limited to a sector of the North Altantic and the small size of the sampling device aperture (1.62 cm^2) means that not all species are sampled equally (Kane 2009). Deeper living species will not be sampled at all due to the shallow depth (c. 10 m) of the tows. As a consequence larger species may evade the net and, abundance estimates for areas dominated by larger and deeper living species (such as *Meganyctiphanes norvegica*) are likely to be low. Moreover, the samples are composites from multiple ship tracks so cannot be considered strictly independent.

3.4.4 Effect of the Mid-Atlantic Ridge

The study has revealed a decrease in euphausiid species richness with increasing ocean depth and distance from the Mid-Atlantic Ridge, although the change brought about by the latter was minor (<-0.0001 %). At the present stage the mechanisms for these observations are necessarily speculative. The perceived increase in euphausiid species over the ridge is may be the result of the combined effect of biotic and abiotic factors. Biotic factors might include ontogenic horizontal and vertical migrations of euphausiids from neighbouring areas and greater depth horizons. Theoretically, the modification of surface currents by the ridge may lead to localized increases of species on and in the vicinity of the ridge. The model suggests that this effect would diminish with increasing distance to the ridge. There is evidence of a modification of acoustic deep-sea scattering layers over the ridge (Sutton et al. 2008), which may be representative of increases in pelagic biomass and/or diversity.

In this study, an increase in the abundance of euphausiid species over the ridge was detected. This result is not reflected by the numerical abundance model. Although it is unlikely that differences in ocean depth would be reflected in the numerical abundance of the top 10 m (depth sampled by the CPR) it is possible that an increase in available "habitat" (here represented by volume of water) could lead to a larger numerical abundance, and hence be reflected in the CPR data. As stated the numerical abundance model did not detect the ridge as significant in predicting euphausiid abundance, leading to one of three explanations:

- The CPR euphausiid data are inadequate for the detection of a ridge effect, as the effect of the ridge on euphausiids is not apparent in the numerical abundance in the top 10 m.
- The CPR euphausiid data are adequate for the detection of a ridge effect but need to be analysed to species level: numerical abundances are not affected by the ridge, but the species richness is.
- The ridge does not affect numerical abundance of euphausiids.

With the data available these explanations cannot be distinguished.

3.4.5 Conclusion and suggestions for further work

The results suggest that the distribution and abundance of euphausiids is driven strongly by SST. The work is of ecological relevance because euphausiids are among the most important links in coastal and oceanic food webs. Given the sensitivity of many additional predatory species to changes in euphausiid abundance (such as whales, see Konishi et al. 2008) there is an increasing need for understanding how abundance and distribution of euphausiids has and will change with ocean warming (Walther et al. 2002), and how euphausiids are affected by environmental variability. Large distributional changes in copepod assemblages have been reported due to increased SST (Beaugrand et al. 2002b), and similar processes could be relevant to euphausiid communities.

Through the use of the GAM framework this study has detected an effect of distance from the ridge and of depth on the euphausiids. Since presence/absence data were used to compile the number of euphausiid species per cell, and not diversity indices (due to lack of numerical abundance coverage), the model is not as informative as it could be. Further sampling would increase rather than diminish the perception of the importance of the ridge. Further investigation is required to determine whether the observed responses relative to the MAR pertain to ocean ridges generally. To that end the next chapter will explore patterns of euphausiids in the Pacific Ocean in order to enable a comparison between ocean basins.

Chapter 4

Drivers of variability in euphausiid species richness and numerical abundance in the Pacific Ocean[2]

4.1 Abstract

A Generalized Additive Model was used to investigate the influence of a suite of physical, chemical and biological variables upon euphausiid species richness and numerical abundance throughout the Pacific. The main drivers of species richness, in order of decreasing importance, were sea surface temperature (explaining 29.53% in species variability), salinity (20.29%), longitude (-15.01%, species richness decreased from West to East), proximity to coast (10.99%), and dissolved silicate concentration (9.03%). Variability in dissolved oxygen concentration was responsible for some 20% of numerical abundance variability, but numerical abundance was poorly predicted by the model overall (R^2=0.12). The influence of these variables is discussed within the context of known ecology and biology of euphausiids. With reference to a previously published model in the Atlantic, the differences in the Atlantic and Pacific Ocean are compared. Projected environmental change from the IPCC A1B climate scenario is used to make predictions of future species richness changes in the Pacific and Atlantic. Results suggests that species richness in both oceans between latitudes 30-60° N and 30-60°S will increase due to the temperature rise predicted over the next 200 years, whereas at low latitudes responses are likely to differ between the oceans, with little change predicted for the Atlantic, but species depletion predicted for the Pacific.

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[2] Part of the work described in this chapter was published as: **Letessier, T B**, Cox, M. J. Brierley, A. S.(2011) Drivers of variability in Euphausiid species abundance throughout the Pacific Ocean *Journal of Plankton Research* 10.1093/plankt/fbr033

4.2 Introduction

The Pacific Ocean is the world's largest, and covers approximately 32% of the Earth's surface (Barkley 1968). The bathymetry is complex, more so than in the Atlantic, with the basin containing many deep trenches, seamounts, and submerged and semi-submerged volcanic islands. The bathymetry of the southern Pacific is dominated by the presence of oceanic ridges, which can best be described as underwater mountain chains that are offset by several fracture zones. Several studies have investigated euphausiid distribution in the Pacific (Brinton 1962, Murase et al., 2009) and studies have investigated euphausiid biogeography on a meso- (20-200 km) and basin-scale (Lindley 1977, Gibbons 1997, Letessier et al. 2009 in the Atlantic; and Trathan et al. 1993 in the Southern Ocean), but there is a gap in knowledge with respect to basin-scale processes in the Pacific Ocean.

The most striking global pattern in species richness across all marine taxa is a latitudinal decrease in species richness from low latitudes to high latitudes (Fuhrman et al. 2008), a pattern that is most readily described as a polynomial function of sea surface temperature (Rutherford et al. 1999). Several hypotheses have been proposed to explain the apparent relationship between high temperature/low latitude and high biodiversity. The species-area hypothesis states that species richness increases as area available for habitat increases. The Kinetic Energy hypothesis suggests that high temperature supports elevated metabolic and mutation rates, causing increased speciation (see Tittensor et al. 2010 for the most comprehensive multi-taxon study to date). The species-energy or potential energy hypothesis suggests that high energy input and productivity supports greater species richness (Rohde 1992; Huston et al. 2003; Cardillo et al. 2005; Allen and Gillooly 2006; Jetz et al. 2009). The historical perturbation hypothesis states that low species richness at high latitude is due to lack of time for recolonization and time for speciation, following perturbations events such as glaciations (Stevens 2006). Tittensor et al. (2010) conducted a global analysis of multiple marine taxa, and concluded that the species-energy hypothesis or kinetic energy hypothesis, which states that high temperature supports higher metabolic rates and promotes speciation, is best supported.

Marine species richness has been associated with sea surface temperatures and other variables, such as dissolved silicate concentration (Roy 2008) and river outputs (Rutherford et al., 1999) but many taxa, including euphausiids, deviate from the high temperature/diversity trend and show increasing species numbers at intermediate latitudes (Gibbons 1997; Rutherford et al. 1999; Letessier et al. 2009). This has been attributed to the increase in pelagic niches in mid-latitudes, associated with the thermal structure of the surface layer (Rutherford et al. 1999) and, in the Atlantic, the depth of the mixed layer (deepening of the mixed layer depth serves to decrease the number of species, Letessier et al. 2009).

Present understanding of pelagic diversity variability is complex and includes poorly understood relationships (such as the effect of mid-ocean ridges and seamounts, see Pitcher 2008). Moreover, global marine datasets for non-commercial species richness are rare, and where these data sets exist they are of low resolution (either spatially or temporally). Quantitative, long-term data are rare and are by and large limited to the Continuous Plankton Recorded Surveys (CPR) in the North Atlantic and North Sea, although a CPR Survey has been running in the Pacific since 1997 (Batten and Mackas, 2007).

Here, a Generalized Additive Statistical modelling approach was used to examine patterns and drivers of euphausiid species richness and numerical abundance in the

Pacific Ocean, in relation to a suite of environmental and physical variables. A similar exercise conducted in Ch. 3 (Letessier et al. 2009), provided a useful insight into pelagic processes driving species richness in the Atlantic Ocean basin. The additional aim was to compare the Pacific model arising here with a previously published model for the Atlantic and to gain insight into similarities and differences between planktic processes of the two oceans. Finally future species richness was predicted in both the Atlantic and the Pacific within the context of projected environmental conditions over the next two hundred years to examine the resilience of the two oceans to anthropogenic climate change.

4.3 Materials and method

4.3.1 Grid design

In order to investigate the potential effect of environmental variables on species richness and numerical abundance of euphausiids throughout the Pacific Ocean, a sampling grid with cells of uniform area was designed, spanning the ocean basin (Fig. 4.1). The cell dimensions were 300 km east to west, by 200 km north to south, with cell corner coordinates calculated using the Geographic Information System Manifold (CDA-International 1993-2008). Cell dimensions were chosen based upon previous experience with an Atlantic model (Ch. 3; Letessier et al. 2009): this size provided a biologically meaningful resolution that also spanned dominant underwater features such as mid-ocean ridges and fracture zones. The sampling grid extended between latitudes of 61˚N to 61˚S and longitudes of 119.08˚E to 70.94 ˚W. Continental coastal cells that included major landmasses (including Japan and New Zealand) were omitted, leaving a grid of

3,051 cells. The final grid included only 11 cells deemed to be ‘on shelf’ (average sea-bed depth <500m).

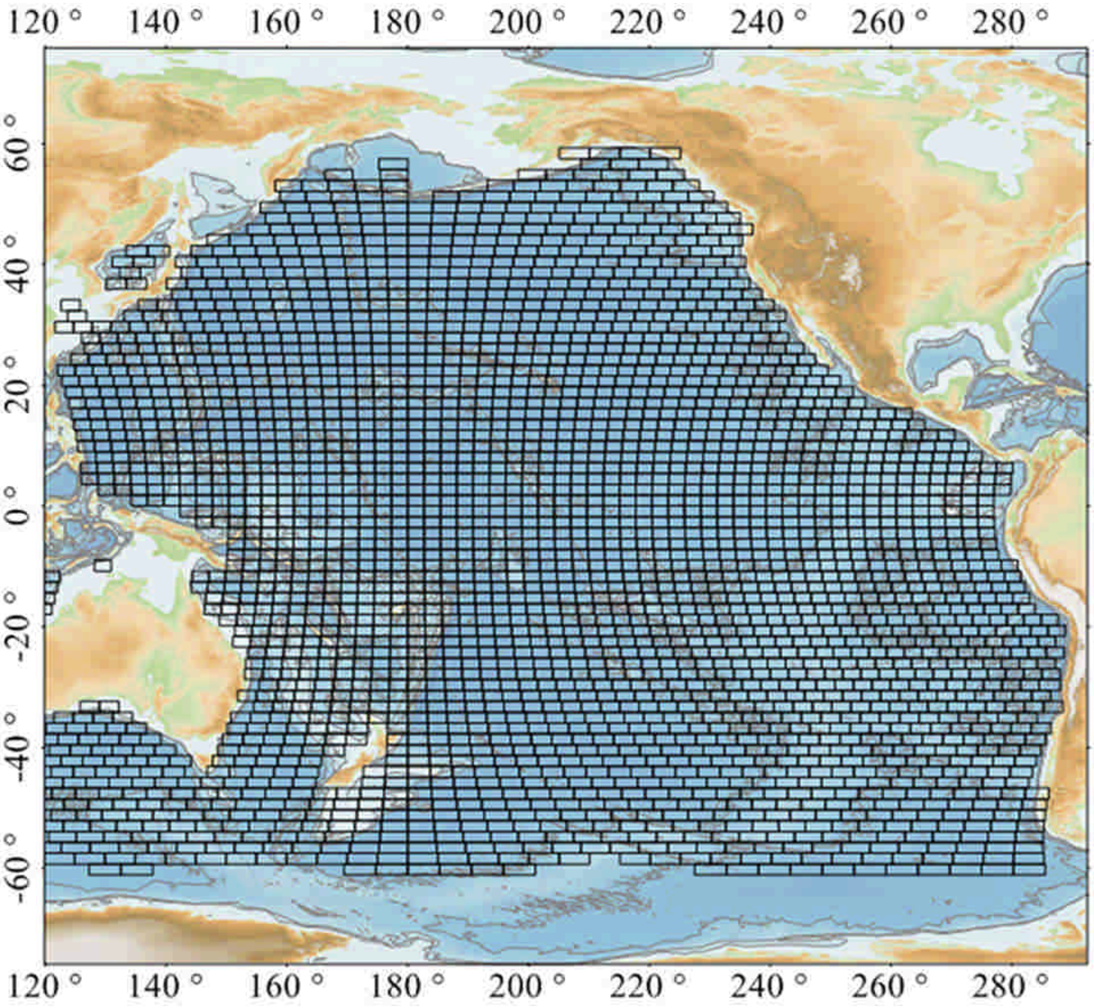

Fig. 4.1 Sampling cells (n=2658) in the Pacific Ocean for the investigation of the drivers of euphausiids species and numerical abundance. The cell dimensions were 300km east to west, by 200km north to south. Cells including continental land mass were omitted. The 1000, 2000 and 4000 m isobaths are shown

4.3.2 Euphausiid species richness and numerical abundance data

Published Pacific euphausiid species distribution ranges (Brinton 2000) were used to populate the grid cells with occurrence data (Fig. 4.2 and Fig. 4.3, see Appendix 2 for species richness data per grid cell).

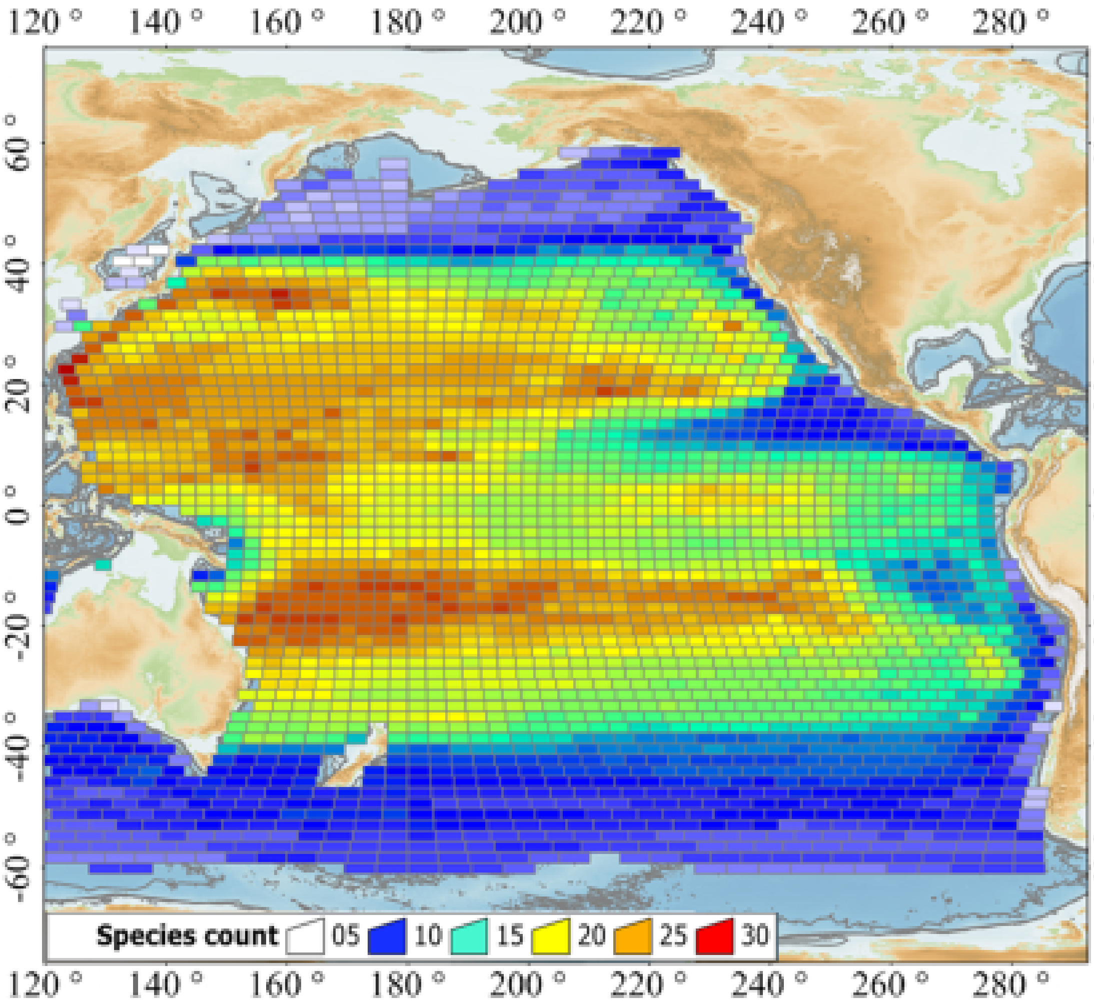

Fig. 4.2 Sampling cell grid populated with the number of euphausiid species per cell (range 0 to 32). Areas of high species count are situated in the centre of the North and South pacific sub-tropical gyres. Low species richness predominated along the western coast of the American continent and at high latitudes

Additionally, more recent data on the occurrence of Pacific species were sought from the Global Biodiversity Information Facility (GBIF; www.gbif.com). However, no occurrences were reported outside the distribution maps provided by Brinton (2000), and thus the Brinton data were considered indicative of euphausiid distribution for the purpose of detecting broad-scale patterns and drivers.

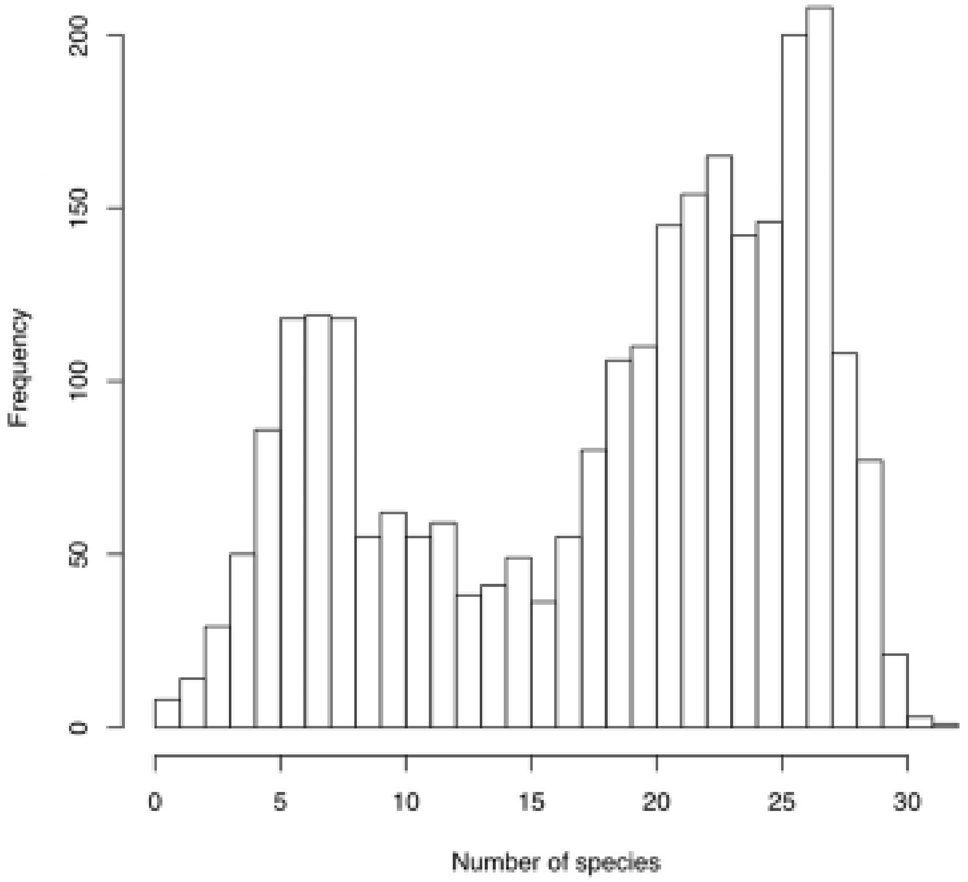

Fig. 4.3 Species richness histogram in the Pacific

Euphausiid abundance data were obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) CPR survey in the Pacific. The CPR data are limited to the north Pacific, spanning a latitudinal range from 33^{o} to 61^{o} N (Fig. 4.4). The Pacific CPR surveys began in July 1997, and ran 52 times (i.e. 52 separate voyages) during an initial annual pilot study. They then ran sporadically throughout 2000 to 2007 (frequency approximately 400 to 500 samples per year) yielding a total of 3,645 CPR samples. CPR samples are taken from within the top 10 m of the ocean and are analysed to the level of Family, giving a count of euphausiids by Family at sample locations (Batten and Crawford 2005).

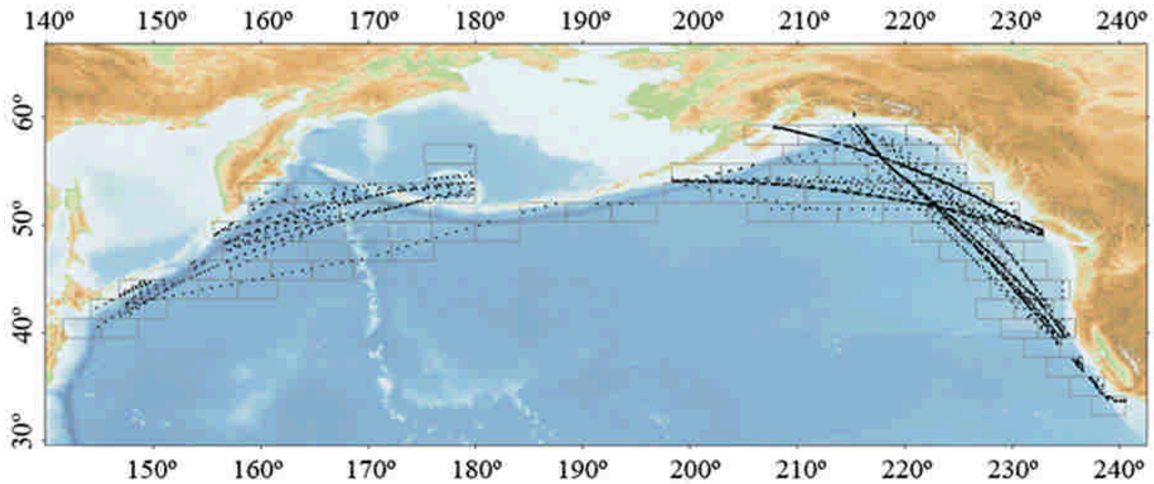

Fig. 4.4 Sampling cell grid with North Pacific CPR Catch Per Unit Effort (CPUE) (n=3645) overlaid

CPR sampling effort is not distributed evenly throughout the north Pacific. Most survey lines are coastal and over shelf areas, and are centred in just 20 of the 79 grid cells in the north Pacific latitudinal range (30°- 60° N, Fig. 4.4). In order to account for the uneven spatial nature of CPR sampling, euphausiid numerical abundance was scaled by effort following CPUE derivations in Ch.3 (Equation [3.1], Fig. 4.5)

4.3.3 Explanatory variables

For each cell, five explanatory variables were obtained, or derived, using the Manifold GIS system (centre latitude, centre longitude, average of seabed depth, distance to coast, and distance to nearest ridge). Distance to ridge was a variable of interest following on from motivation of the Atlantic study, which examined the hypothesis that the Mid-Atlantic Ridge influenced diversity (Ch. 3; Letessier et al. 2009). Nineteen further variables were obtained from various sources (see Table 3.1, Ch. 3 for a description of the 19 explanatory variables, the rationale for including them, their sources, and the abbreviations used for them from henceforth in this paper. Also see Fig. 4.5). The spatial resolution for three of the datasets from which variables were drawn (Osborne and Flinchem 1994; Chelton et al. 2008, see Table 3.1) was such that some cells had missing data values.

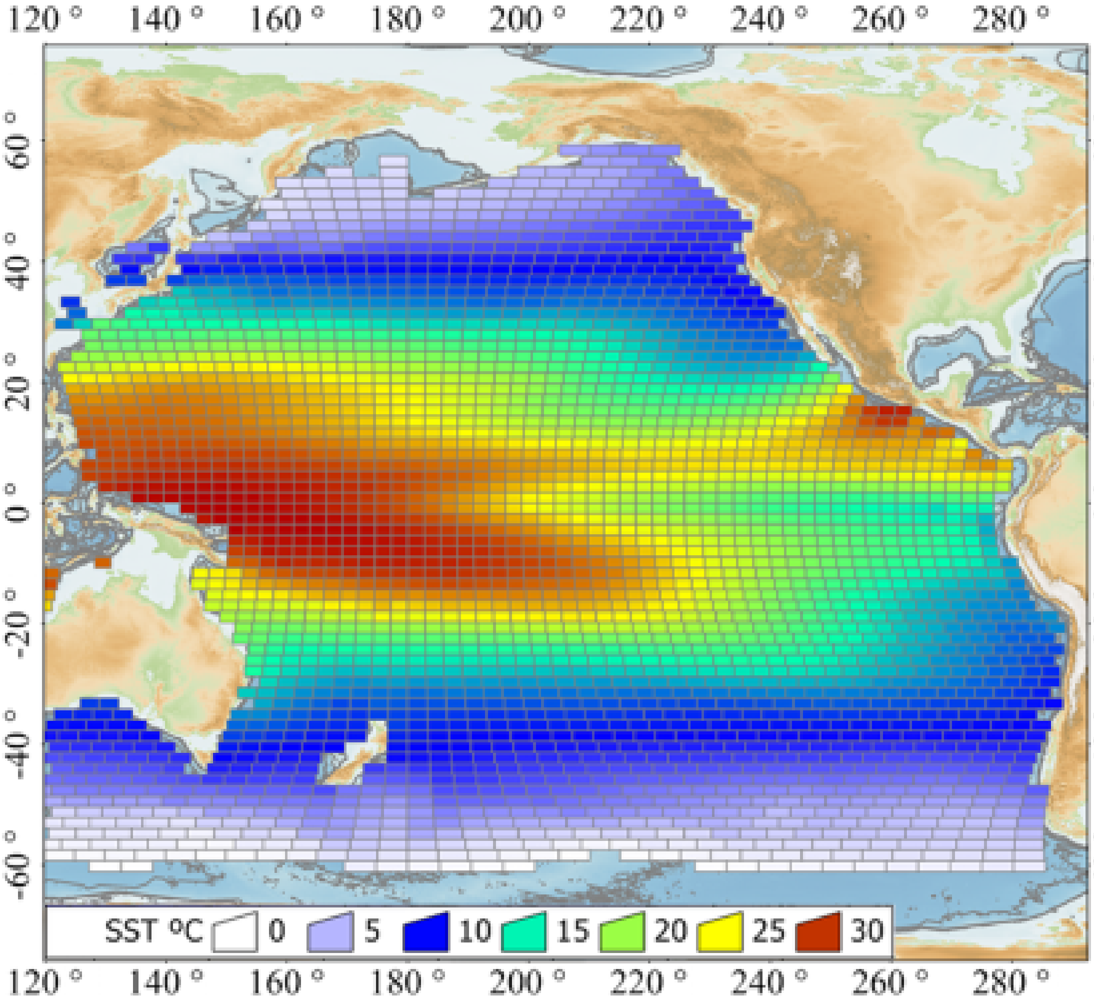

Fig. 4.5 Sea Surface Temperature (in □C) from SeaWiFS (Table 3.1) extracted to each sampling cell.

To obtain variables at a finer spatial resolution, published data were interpolated on a 1° x 1° latitude x longitude grid using universal Kriging (Chiles and Delpiner 1999). Current vectors (Bonjean and Lagerhoed 2002) were available only within the 60° N to 60° S latitudinal range, so cells outside this range were disregarded, thus leaving 2,658 cells for subsequent analysis.

4.3.4 Statistical modelling

The influences of the selected environmental variables (Table 3.1, Ch. 3) on euphausiid species richness (Fig. 4.2) and numerical abundance (CPUE derivations from the CPR data Fig. 4.4) were investigated using Generalized Additive Models (GAMs), and a linear model, both with a spatial correlation structure. Statistical analyses and GAM fitting were carried out using the R-project for statistical computing language (R v2.0.1 Core Development Team 2007) with the mgcv (Wood 2006) and nlme (Pinheiro and Bates 2000) packages.

4.3.4.1 Selection of explanatory variables and model selection

For selection of the explanatory variables and the form (i.e. linear or smooth on the scale of the log-link function) the approach documented in Ch. 3 and Letessier et al. (2009) was followed. The species richness model selection procedure was divided into two parts: (i) selection of spatial correlation structure, and (ii) selection of explanatory variables. Intercept only models were used to select the spatial correlation form (intercept models give us a benchmark value of the deviance, the degree of model misfit, see Hox 2002). Candidate spatial correlation models were: none, Gaussian, spherical, linear, and rational quadratic (see Cressie 1991 for correlation model description). Model selection was carried out using the Akaike information criterion (AIC; Akaike 1973), with candidate spatial correlation structures being compared using the difference in AIC (Table 4.1, Burnham and Anderson 2002). The selected spatial correlation structure was then used in a Generalized Additive Model (GAM) with a Poisson distribution structure and log-link function. The model was allowed to estimate the dispersion parameter (relationship between mean and variance). AIC was also used to determine the optimum subset of candidate explanatory variables from the initial

GAM formulation, which contained all the candidate explanatory variables (full model) to describe the number of euphausiid species.

Numerical abundance was modelled using CPR CPUE data as the response variable, within a linear model framework with a spatial correlation structure. Selection of spatial correlation form was carried using the same procedure as for the species richness model. Since only eight variables were available for candidate explanatory variables selection (following the rule of Harrell et al., 1996) and limiting the degrees of freedom (q) of the explanatory variables offered for model selection to $q = m/10$, where m is the minimum number of observations in the response for each of the explanatory variables), I set up competing hypotheses for the biological drivers of numerical abundance, and based the model selection on a subset of the explanatory variables (Burnham and Anderson 2002). Within these competing explanatory variable subsets, model selection using AIC was carried out.

Model performance evaluation was carried out with reference to three of the metrics used by Potts and Elith (2006) and the explanatory variable practical influence (see Letessier et al., 2009). The practical influences of the explanatory variables were described by setting the value of explanatory variables in question at the 2.5 and 97.5% quantiles while fixing all other explanatory variables at their mean value (see Ch. 3, Letessier et al., 2009).

Table 4.1 An example of the backwards model selection algorithm applied to the euphausiid species richness generalized additive model with spatial correlation structure. A subset of the candidate models based on the difference in AIC (dAIC) is given. Terms preceded by an "s" are smooths with "k" the dimension of the basis the smooth terms

Term dropped	Model structure	dAIC
	Species richness ~ Longitude+DC+s(SST,k=3)+Sal+SiO_3+Chl_a+MLD-may-june+Rossby+vector_U+DR	9.803
Rossby	Species richness ~ Longitude+DC+s(SST,k=3)+Sal+SiO_3+Chl_a+MLD-may-june+vector_U+DR	0
DR	Species richness ~ Longitude+DC+s(SST,k=3)+Sal+SiO_3+Chl_a+MLD-may-june+vector_U	11.314

4.3.4.2 Response to predicted climate change

The impacts of predicted environmental change on euphausiid species richness were evaluated (in the Atlantic and Pacific) under the Intergovernmental Panel on Climate Change (IPCC) A1B scenario, which predicts an atmospheric temperature rise of 2.8 ºC, with a likely range of 1.7 to 4.4 ºC in the 21^{st} century (IPCC 2007a). The impact of oceanic temperature change in the Atlantic was evaluated using the species richness model in Ch. 3. Binary SST prediction data under the A1B scenario from the Hadley Centre for Climate Prediction and Research (data reference 'UKMO_HadCM3_SRMESA1B_1') were extracted from the World Data Centre for Climate, Hamburg. The Hadley Centre provides SST predictions corresponding to the SST satellite observations, such as those derived from SeaWIFS. Predictions of species richness were made along two latitudinal bands of grid cells covering areas of interest (See section 4.2.3, data averaged over six years intervals from 2010 to 2046, and over a single year in 2100 and 2199) and along a 5° N and 5 S° latitudinal band around the equator.

4.4 Results

4.4.1 Spatial pattern of species richness and numerical abundance

4.4.1.1 Species richness

Species richness of euphausiids in the Pacific was low at high latitudes (40° to 60° N and S), intermediate in the tropics, and high at mid-latitude (20° to 40°, Fig. 4.2 and Fig. 4.4). Species richness was highest (>25) in the centre of the North-Pacific subtropical gyre and South-Pacific subtropical gyre. The overall species count was higher (>20) in the western Pacific than in the east. The species count was low along the shelf margin off the west coast of the American continent, with a particularly impoverished area extending longitudinally with the North Equatorial Current.

4.4.1.2 Numerical abundance

The majority of CPR samples were taken along shipping lines from Vancouver to Alaska. Within this zone the numerical abundance of euphausiids as described by CPUE was higher (>9) off the coast of California, around and west of the Aleutians Islands, and south of the Kamchatka Peninsula (Fig. 4.6).

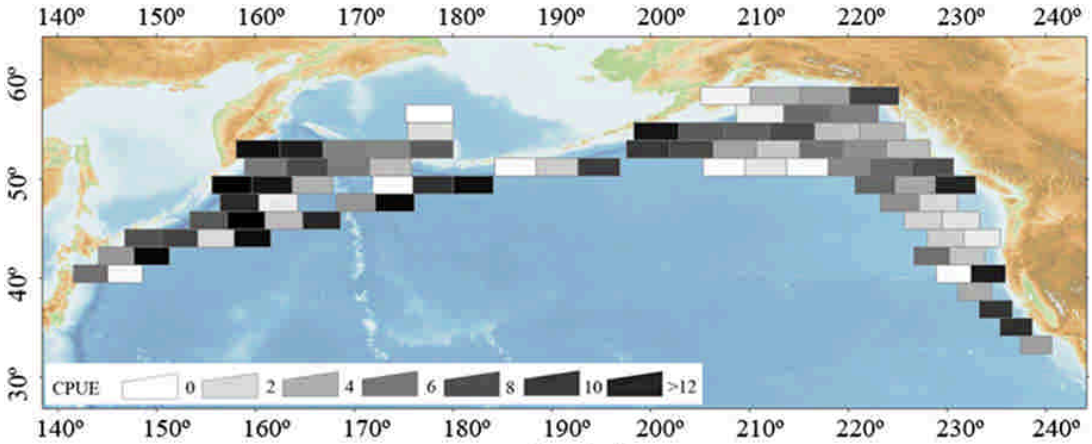

Fig. 4.6 Sampling cell grid with North Pacific CPR Catch Per Unit Effort (CPUE) (n=3645) overlaid

4.4.2 Statistical modelling

4.4.2.1 Model performance

The primary aim of the statistical modelling was to investigate the effect of environmental variability on the species richness and numerical abundance of euphausiids. Under the model assessment criteria proposed by Potts and Elith (2006), the species richness model performed well, as shown by the high correlation between predicted and observed values (r=0.91, Table 4.2). The numerical abundance model performed poorly however, as demonstrated by the poor model calibration statistics and a low coefficient of correlation (r=0.35).

Table 4.2 Model performance metrics for the assessment of the performance of the euphausiid numerical and species richness models

Model performance metric	Numerical abundance	Species abundance
correlation r	0.35	0.91
calibration intercept (b)	6.17	3.49
calibration slope (m)	0.11	0.79
R^2	0.12	0.82

4.4.2.2 Model variables

The selected variables and forms for the species richness model were linear terms on the scale of the log-link function of longitude, distance to coast, salinity, mixed layer depth (May and June), vector U, distance to ridge, salinity, SiO_3 concentration, Chl-a concentration and a smooth of SST (see Table 4.1 for model selection, and Table 4.3 practical influence of variables).

The factors having the greatest influence on species richness, in decreasing order, were smooth term of SST, linear terms of Salinity, Longitude and Silicate concentration (responsible for 29.53%, 20.29%, -15.01% and 9.63% of the change in the response variable between the 2.5% and 97.5% quantiles respectively, see Table 4.3 and see Fig. 4.7 for a partial plot of the SST smooth function). The remaining significant terms were, in decreasing order: distance to coast, distance to ridge, Chl-a, vector U, Mixed Layer Depth (May and June).

Species richness underprediction occurred off the southern and south-eastern coast of Australia (40ºS, 120 to 150º E, Fig. 4.8), around the Aleutian Islands (50ºN, 160E to 140ºW), off the west coast of Chile (5 to 40º S, 120º E), and along the shelf area off the west coast of the South-American continent, with a particularly impoverished area extending longitudinally with the North Equatorial Current.

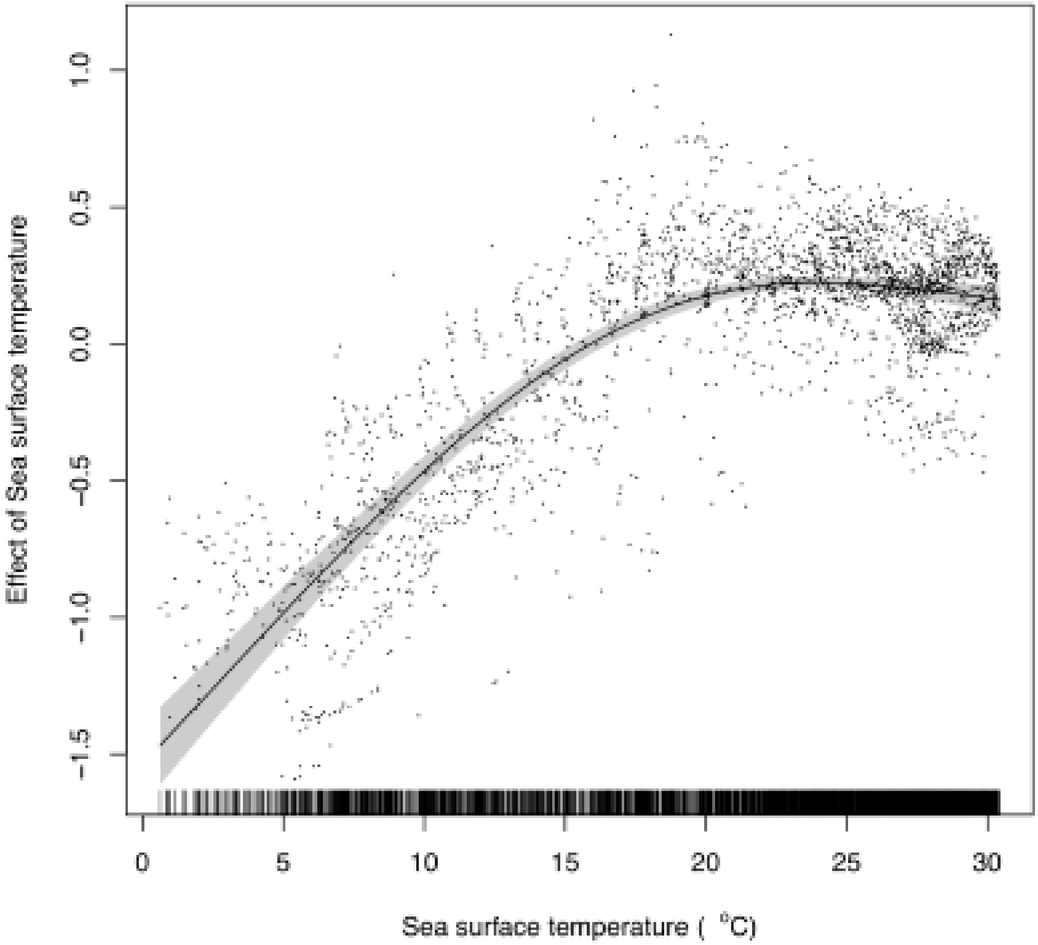

Fig. 4.7 Partial plot of the relationship between euphausiid species richness and the smooth term of Sea surface Temperature

Overprediction in species richness occurred predominantly along the Californian coast (20 to 40º N, 160º to 120º W), extending into the north Pacific Gyre, off the North-eastern Australian coast (20ºS 170ºE) and extending longitudinally into the South Pacific Gyre, and around the Cocos plate (15ºN 255ºE).

Table 4.3 Pacific Euphausiid species richness model parameter estimates and associated confidence intervals. The influence of each explanatory variables on euphausiid species richness is shown by predictions made at the 2.5% and 97.5% quantiles of the explanatory variable. During the prediction all other explanatory variables were fixed at their mean value. S.E. is the standard error of the prediction and estimated change is the number of species predicted between the 2.5% and 97.5% explanatory variable quantiles. See section 3.4 for description of the calculation of estimated change and percentage change for a particular variable.

Explanatory variable name	Explanatory variable value at the 2.5% quantile	2.5% estimate	S.E.	Explanatory variable value at the 97.5 % quantile	97.5% estimate	S.E.	Estimate change (n species)	Estimated change (%)
SST	4.37	5.64	0.31	29.98	19.10	0.52	13.46	29.53
Salinity	33.97	15.00	0.51	35.12	24.26	0.64	9.25	20.29
Longitude	129.42	23.40	0.90	277.94	16.56	0.62	-6.84	-15.01
Distance to coast	277.43	17.79	0.41	4893.69	22.81	0.68	5.01	10.99
SiO3	27.00	17.87	0.47	103.87	22.26	0.71	4.39	9.63
Distance to ridge	127.33	18.25	0.57	7286.35	22.17	1.02	3.92	8.60
Chl-a	0.03	20.02	0.35	0.49	18.81	0.37	-1.21	-2.65
Vector U	-0.25	19.15	0.37	0.17	20.14	0.37	0.99	2.17
MLD (May-June)	8770.57	19.61	0.33	5847647.07	20.13	0.39	0.51	1.12

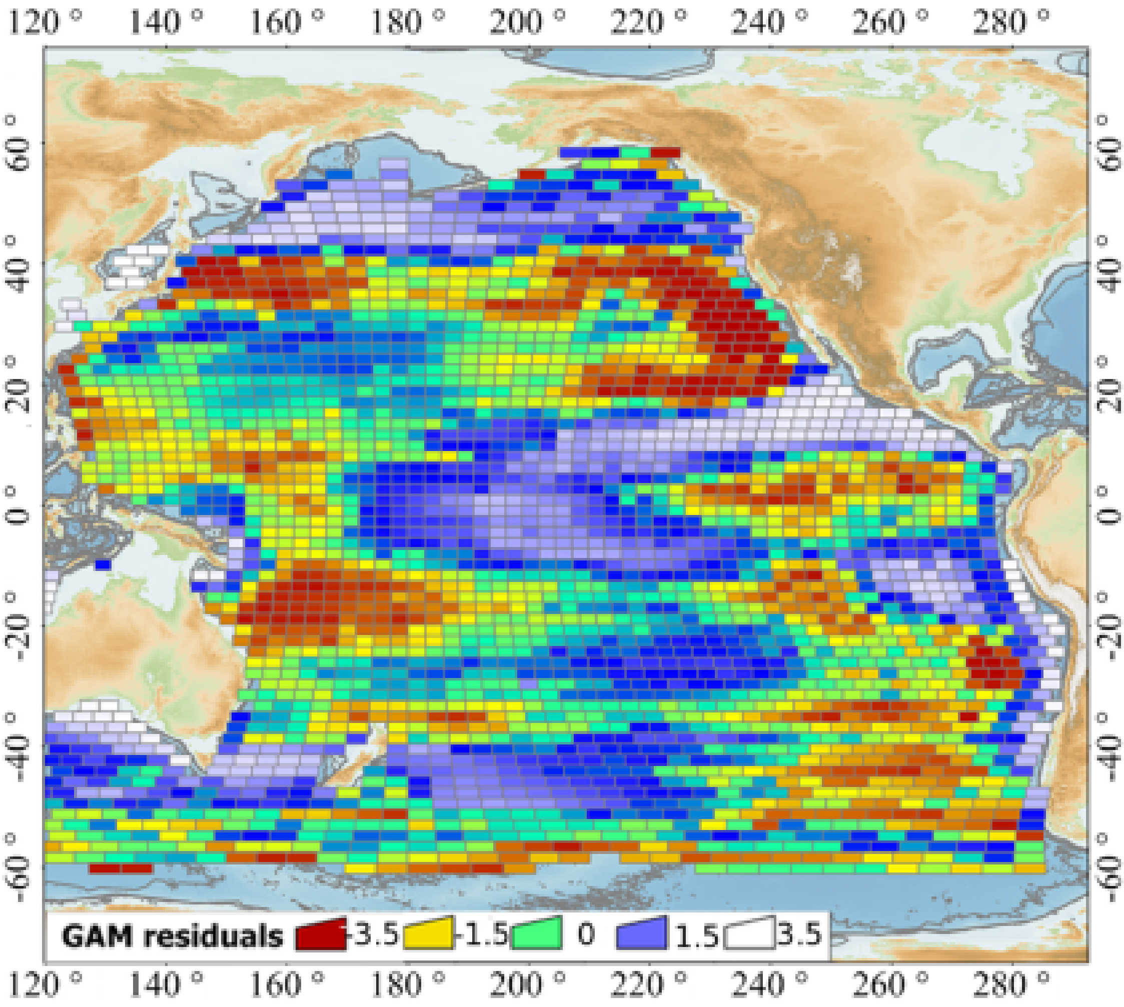

Fig. 4.8 Residuals (Predicted minus observed values) of the statistical model prediction of species richness. Species richness underprediction occurred off the southern and south-eastern coast of Australia (40°S, 120 to 150° E), the on shelf area of the west coast of Japan (40ºN,138ºE), around the Alucians islands (50ºN, 160ºE to 140ºW), off the west coast of Chile around the Humboldt current (5 to 40° S, 80° W) and along the shelf area off the west coast of the South-American continent, with a particularly impoverished area extending latitudinally with the North Equatorial Current. Overpredictions were largely restricted to the open ocean, and to the West coast of North America

4.4.2.3 Species richness changes associated with climate change

The differences in species richness predicted from the models to arise under the IPCC A1B climate change scenario were plotted against latitude along transect lines for the Pacific and Atlantic oceans (Fig. 4.9 and Fig. 4.10). The Pacific transect average shows an average increase in +0.75 species per cell whereas the Atlantic shows a change of +1.1 species per cell by the year 2199.

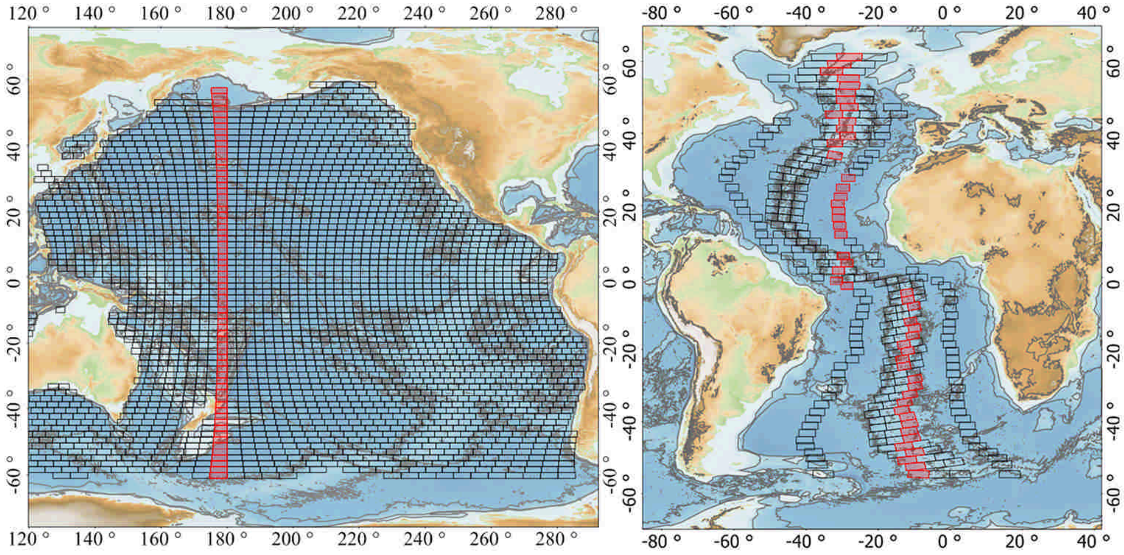

Fig. 4.9 Transect lines along which potential species richness changes were investigated in the Pacific and the Atlantic

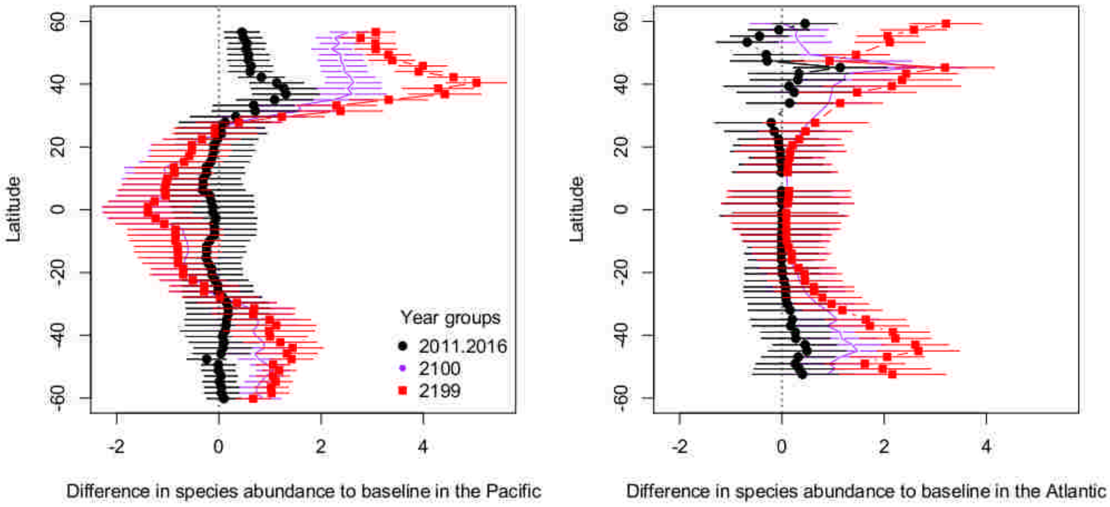

Fig. 4.10 Predicted species richness difference to projected environmental change vs. latitude in the Pacific and the Atlantic. Species richness is plotted as difference to baseline predictions (2002-2008) along the lines of interest (Fig. 4.9). Error bars are one standard error from the mean. Legend applies to both oceans

The greatest response to environmental change in the Pacific and the Atlantic was predicted to occur at intermediate latitudes (30° to 60°, Fig. 4.10). The response in the northern Pacific (max change ~4.5 euphausiid species per cell) was more extreme than in the south (max change ~1.8 euphausiid species per cell), showing a unidirectional, positive increase outside the 30° latitudinal band around the equator (30° to 60°). Within this +/-30° latitudinal band, the species richness showed progressive decrease, with the greatest decrease set to occur around the equator. The greatest change in species per cell in the Atlantic was predicted in the northern hemisphere (+3.2). Little change was predicted for the +/-20° latitudinal band around the equator in the Atlantic.

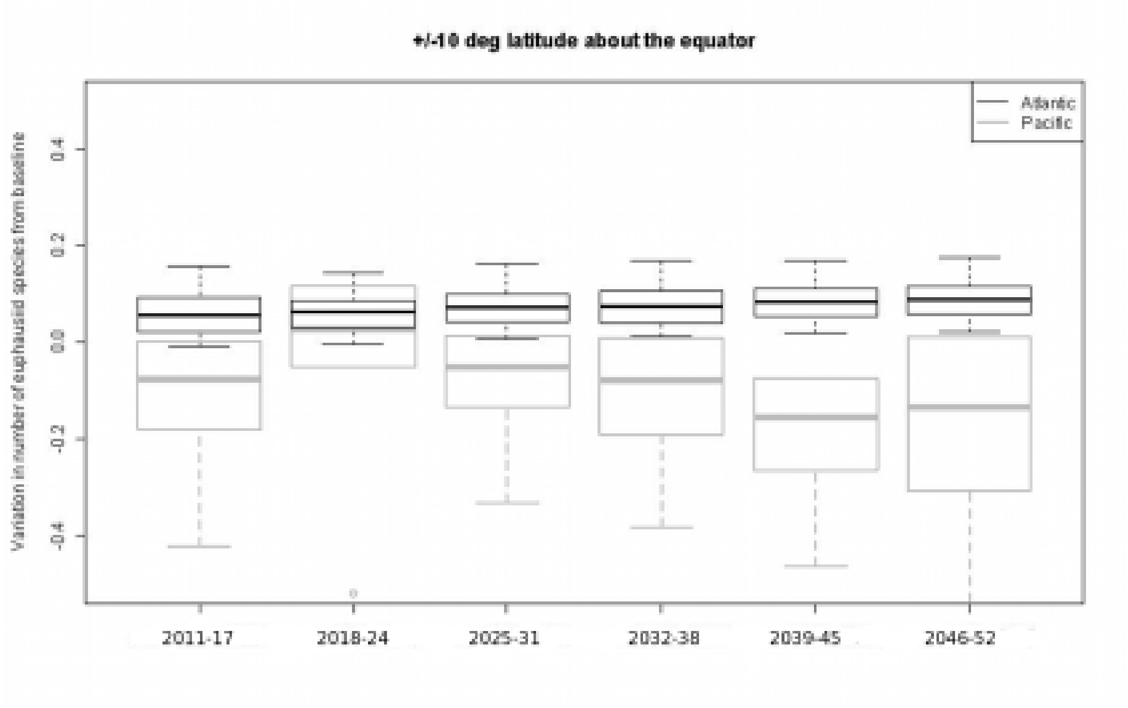

Fig. 4.11 Box and whisker plots of changes predicted in numbers of euphausiid species in 10 degree latitude bands about the equator in 5 year bins to 2045 under the SST-changes expected according to the IPCC scenario A1B.

The change in the +/-10° latitudinal band around the equator is expected to be a slight increase in species richness in the Atlantic and a decrease in the Pacific (Fig. 4.11). The initial (2011-2016) response in the Northern Atlantic shows an oscillating change in species richness, followed by a progressive increase in abundance that is still climbing by 2199. The south Atlantic will experience a more linear increase in species richness.

4.4.2.4 Numerical abundance model

From the candidate explanatory variables, only oxygen concentration was retained during AIC-based model selection. An increase in dissolved O_2 concentration was associated with an increase in euphausiid numerical abundance (Table 4.4).

Table 4.4 Euphausiid numerical abundance model parameter estimates and associated confidence intervals. The influence of each parameter on euphausiid numerical abundance is shown by predictions made at the 2.5% and 97.5% quantiles of the explanatory variable data values on the scale of the response variable.

Explanatory variable	Explanatory variable value	2.5% estimate	Explanatory variable value	97.5% estimate	Estimate change (n euphausiid)	Estimated percentage change
O_2	2.54	4.17	3.85	11.77	7.61	100

4.5 Discussion

4.5.1 Drivers of species richness

4.5.1.1 Explanatory variables

The most important driver of species richness included in the model was sea surface temperature (explaining 29% of variance). The apparent influence of SST on euphausiid species richness in the Pacific is consistent with previous modelling (34% in the Atlantic, Letessier et al. 2009, also see Table 4.5) and observational work on Atlantic euphausiids (Gibbons 1997). SST can be considered a proxy for energy input and was derived using SeaWIFS satellite data (Table 3.1).

Table 4.5 Percentage change between the 2.5% and 97.5% quantiles of the explanatory variables retained in the GAM species count and numerical abundance models for the Pacific Ocean and Atlantic Ocean model (see Ch.3 and Letessier et al., 2009 for Atlantic modelling) NA denotes variables that were not selected in the final model.

	Species richness model	
Environmental variable	Pacific % change	Atlantic % change
Longitude	-15.01	-7.18
MLD_mj	1.12	-5.77
MLD_nd	NA	-6.65
Depth	NA	-4.28
Vector U	2.17	NA
Distance to Ridge	8.60	-0.00
SST	29.53	34.44
Salinity	20.29	NA
O_2	NA	NA
SiO3_umol_l	9.63	29.46
SSH_var	NA	NA
Chl-a	-2.65	-12.23
Distance to Coast	10.99	NA

Considering that the SST values were averaged over 6 years, and that the species richness data were collected using recognised areas of distribution, this model probably does not capture the dynamism of quasiperiodic climate patterns such as El Niño in the Pacific, even though there has been two recent minor El Niño events, and one La Niña event during this period (2002-2008). Out of the few general hypotheses explaining patterns in latitudinal scale (section 4.2), the influence of temperature in the model best support the Kinetic Energy hypothesis. Moreover, the lack of positive influence of Chl-a concentration suggests that direct energy input, in the form of sun light and SST, increases speciation by supporting higher rates of metabolisms, and is consistent with the Kinetic Energy hypothesis.

Variation in salinity explained some 20.29% of the variation in euphausiid abundance in the Pacific (Table 4.3). Although the majority of euphausiids species are oceanic some species are considered coastal/neritic (e.g. *Euphausia crystallorophias*), and are expected in low salinity environments such as in coastal and fjordic systems (Mauchline, 1969), where river outfalls can markedly lower salinity. Moreover, systems where ice melt have a strong influence upon salinity, such as in polar regions, are typically species-poor, but can support large quantities of euphausiid biomass (Saunders et al., 2007). Variation in salinity can be an important factor in structuring coastal and estuarine zooplankton communities (Calliari et al. 2008), and different zooplankton species have varying tolerances to changes in salinity (Holste et al. 2009; Primo et al. 2009). Moreover salinity can act as a dominant control of water stability in polar and coastal regions, because it can vary strongly as a function of river run-off and ice melt (Bouman et al. 2003). Waters with fluctuating patterns of salinity, and thus fluctuating water-column stability, are expected to harbour reduced species richness, following the Huston equilibrium model (Huston 1979, highest species diversity is located in systems with intermediate disturbance). Highest species richness was typically found in centres of the subtropical gyres in both hemispheres, where salinity is high. Euphausiid species richness is apparently driven higher in stable high salinity waters and lower in unstable polar waters, although further consideration is required to determine whether this is due to the direct influence of salinity, or of some other co-variate, presently unknown.

The explanatory variable in the model exerting the fifth greatest influence on euphausiid species richness was SiO_3 concentration. Although the mechanism behind the SiO_3 /species richness relationship is presently unclear, it is likely to involve a combination of silicate concentration control of phytoplankton growth and diatom growth (Hashioka and Yamanaka 2007) mediation of zooplankton diversity by non-toxic phytoplankton (Roy 2008). Euphausiid grazing rates are known to vary depending upon diatom species (McClatchie et al., 1991). The sensitivity of euphausiid species richness to phytoplankton species composition may be mediated through bottom-up control and tight trophic coupling between phytoplankton, primary grazers (such as most copepod species, and many euphausiid species e.g. *Thysanoessa longicaudata, Euphausia superba*), and primary/secondary consumers (such as some euphausiid species, i.e. *Meganyctiphanes norvegica* and *Nematobrachion boopis,* Richardson and Schoeman 2004).

4.5.1.2 Statistical model residuals

The Pacific model residuals (predicted minus observed values) of the species richness GAM are consistent with present understanding of oceanographic systems. Zones of underprediction in the Pacific model coincide geographically with two of Longhurst's provinces: the Costa Rican Dome in the North Pacific Equatorial Countercurrent province, and the Tasmanian Sea province (CRD, PNEC and TASM respectively, see Longhurst 1998). The TASM province is a very dynamic and turbulent part of the Pacific (Harris et al. 1988; Harris et al. 1991), with primary productivity patterns typical for provinces at similar latitudes (enhanced spring blooms) and with deep winter mixed layer depths. The underprediction by the model here can be explained, at least partly, by the specific geographical and environmental properties of this area. The retroflection of the East Australia Current forms a northward front across the TASM and Tasman Sea that separates bodies of water with very distinct properties: to the north lies the warm Coral Sea and to the south lies the cool Tasman Sea water. It is likely that this frontal zone combines species typical of either area and, in conjunction an with enhanced production in the northward flow (Gibbs et al. 1991), causes a localized increase in niche availability and species richness, which the model fails to predict.

The PNEC province is defined more on ecological criteria than being based upon oceanographic features (Longhurst 1998) and is, to a large extent, influenced by the productivity patterns of the Costa Rican Dome. This area has been identified as hotspot of coastal zooplanktic diversity (Morales-Ramirez 2008). The isolated nature of the islands of the eastern tropical Pacific has led to the evolution of many endemic species and the extension of the range of many coastal species (such as *Euphausia lamelligera*), which may explain the underprediction of the model (Brinton et al., 2000).

Underprediction of species richness in the Humboldt Current may be a consequence of localized upwelling and associated mixing of different water masses in this area (Chavez et al. 2003; Ayon et al. 2008). Local euphaussiids is highly adapted to the characteristic salinity/high seasonal heterogeneity and enhanced productivity, where endemic zooplankton species proliferate (e.g. *Euphausia mucronata* accounts for 50% of the mesozooplankton wet weight in winter, and is highly specialized for preying on anchovetta eggs, see Antezana 2010; Krautz 2003).

Overprediction coincided with the Pacific Equatorial Divergence Province (PEQD, Longhurst 1998); the dominant characteristic of this biome is the High Nitrate, Low Chlorophyll (HNLC) content of the water. Moreover, this province has a low productivity regime, typical of HNLC biomes. The area has been described as an iron-limited, grazer-controlled ecosystem (Price et al. 1994). The overprediction in this province may simply be because local production regimes do not sustain high species richness otherwise typical of similar latitudes.

4.5.1.3 Inter-Basin comparison

The statistical method utilised here is deliberately similar to that employed in the previous study, focusing on drivers of variability in Atlantic euphausiid abundance and diversity (Letessier et al. 2009). The environmental and biological data considered in both were retrieved from the same online and published sources. Overall the directions of the responses to the important variables (sea surface temperature, longitude, silicate concentration) were similar in the Pacific and the Atlantic (Table 4.5).

In both ocean models, an eastwards decrease in species richness was observed (longitude was responsible for 15% and 7% species richness reduction in the Pacific and Atlantic respectively). On the eastern side of the two oceans the major currents transport cool water toward the tropics, meaning the warm tropical seas will span a broad latitudinal range in the west but not in the east (see Fig. 4.3), and communities will be typical of higher latitudes in the east. The observed patterns probably are a function of the predominance of upwelling on the east coast of the Atlantic and the Pacific Oceans (Brown et al. 1989).

A total of 81 euphausiid species were located within the Pacific survey grid, a greater number than in the Atlantic (54 species). Moreover, the Pacific modelling has revealed several variables to be significant there that were not significant in the Atlantic study (e.g current vector U, distance to coast, distance to ridge; Table 4.5). The Pacific Ocean is, by some estimates, close to a billion years old (The Open University 1998) and is, much older than the Atlantic (150 million years). The last common ancestor of the Euphausiidea lived ~130 mya and most modern genera were present before 23 mya (Jarman 2001). Since then, the Pacific has undergone relatively few geological changes compared to the Atlantic. Furthermore, the Atlantic has become separated from the Indopacific (in the late Miocene, some 7 mya), a source of radiative diversity. That combined with the large area of the Pacific (32% of surface of the Earth), is a potential explanation for the greater overall abundance of marine species observed in the Pacific Ocean (Briggs 1999; Williams 2007) and, in this case, the increased model complexity compared to the Atlantic. The large size of the Pacific makes the distribution of its fauna susceptible to a greater number of external factors and environmental variables. The Atlantic study was largely restricted to the mid-ocean, as the sampling grid specifically omitted continental shelves and margin sectors and was constructed with the specific objective of enabling testing of hypotheses relating to the influences of bathymetric features (such as ridges and fracture zones) on diversity and abundance. This might explain the influence of proximity to coast in the Pacific. The comparison between oceans will not be bias-free because of the different grids used in each. However, the two oceans have fundamentally different characteristics in terms of basin dimension, and any completely uniform grid will hold some inherent bias. The number of cells covering shelf sectors in the Pacific (average seabed depth < 500 m, n=11) only amounted to some 0.4% of the total grid, and had they not been included the conclusions of the study would probably not have changed. The differences exposed here between the Atlantic and the Pacific (Table 4.5) are at odds with of the results of Tittensor et al. (2010). Tittensor et al. (2010) suggested, following analysis of a global data set of diversity, that ocean basin variability (i.e. Pacific, Atlantic, Indian) was not a factors influencing global diversity.

4.5.1.4 Species richness changes with temperature rise

The data show that the species richness of euphausiids in the Pacific is influenced less by SST variability (some ~5% difference in between the quantiles) than in the Atlantic (Table 4.5). Moreover, the higher richness of Pacific euphausiid species (81 from the dataset) means that every degree change in SST will increase the average euphausiid species richness by 0.52 due to increase in species ranges, as opposed to 0.70 in the Atlantic (assuming linear change between the quantiles). All else remaining equal, the model predicts that the distributions of Pacific euphausiid species richness will be more resistant to climate change than the Atlantic.

The functions of marine and terrestrial biological processes are predicted to change as a consequence of present and future anthropogenic climate change. Whereas environmental changes might be quantifiable, the biological responses are harder to predict and are typically speculative (see Brierley and Kingsford 2009, and Walther 2010 for a review of potential marine and terrestrial changes respectively). This model is no exception to this. The functions have been extrapolated assuming a consistent response to temperature, and by holding all other variables equal.

Both oceans will on average see an increase in species richness per cell. This is due to a redistribution of species due to thermal habitat change, and not does consider the evolution of inclusion of ‘new’ species. Although the greatest increase in species richness is predicted to take place in the Pacific (maximum increase +4.5 species in Pacific vs +3 species per cell the Atlantic) the Pacific will, on average, experience less change than in the Atlantic (+0.75 species per cell vs +1.1) by the year 2199, thus confirming the earlier predictions regarding the difference in sensitivity between the two basins (see first paragraph this section). The results suggest that the present broad patterns apparent in species richness will become less pronounced in a warming ocean; eventually species richness will be enhanced within intermediate-to-high latitude regions (30ºN to 60ºN and 30ºS to 60ºS) and diminished in the tropics (20ºN to 20ºS). Moreover, species with polar ranges (e.g. *E. superba*, *T. enermis*) are likely to suffer a greater risk of extinction in a warmer ocean, as their distribution ranges will likely be restricted. The predicted change of species richness (less marked in the tropics, more pronounced at intermediate to high latitude) is consistent with changes already observed in terrestrial systems in Europe and America (species ranges moving north, see

Rosenzweig et al. 2008). However, recent evidence points to increased vulnerability in tropical ectotherms (Dilling and Alldredge 2000). The changes predicted in intermediate latitude (30° to 60°) are consistent with already-observed changes in zooplankton assemblages in the North Atlantic (species communities shifting north in the northern hemisphere, see Beaugrand and Ibanez 2004; Beaugrand et al. 2002; Richardson and Schoeman 2004). This study provides some evidence that shifts in species richness may not be restricted to the North Atlantic zooplankton community.

The particular pattern in species change closely follows predicted SST changes: the difference in species change between the north and the south Pacific reflect real differences in the magnitude of the decadal SST changes between the two hemispheres (~0.75 C° at 40°S and ~1.20 C° at 40° N, Xie et al., 2009). Moreover, actual reduction in species richness in the tropical Pacific is due to stronger predicted decadal SST increase in the equatorial Pacific compared with the Atlantic (~1.40 C° in the Pacific; 1 C° in the Atlantic). Such asymmetric differences between hemispheres and between oceans are due to coupling and feedback mechanisms between atmospheric features, such as trade winds, and SST, which will differ in intensity between ocean sectors (Xie et al., 2009).

This study opted to consider variability modes for the A1B scenario from the Intergovernmental Panel on Climate Change (IPCC), which provides environmental variables predictions under assumptions regarding anthropogenic impact on climate deemed to be ‘intermediate’ (O'Neill and Oppenheimer 2002). However, annual CO_2 emission increases (>2 parts per millions, Goodwin & Lenton 2009) are surpassing the worst-case scenario by the IPCC (scenario A2, IPCC 2007b), and it is likely that this choice is conservative. Changes in euphausiid distribution, as with other ecosystem changes (Jackson, 2008), may be more pronounced than expected.

4.5.2 Drivers of numerical abundance

The only variable with a significant predictive influence on the distribution of euphausiid numerical abundance in the Pacific was dissolved O_2 concentration. Although the model poorly predicted numerical abundance of euphausiids derived from CPR CPUE, it appears that increasing oxygen concentration may serve to increase euphausiid numerical abundance by +1.93 euphausiids m^{-3} per ml l^{-1} O_2, assuming that the relationship does not mask a co-variate. These results may have relevance to 'dead zones' in the World Ocean: dead zones are coastal waters that are too low in oxygen to sustain life (<2.00 O_2 ml l^1, Diaz 2001, but see Vaquer-Sunyer and Duarte 2008). Recent studies have linked the increase of dead zone occurrences in the World Ocean to increases in human agriculture activity (see Dybas 2005; Diaz and Rosenberg 2008) and present trends in changing ocean temperature as de-oxygenation is likely to follow rising ocean temperature and increased surface water stratification (see Stramma et al. 2008 and Keeling et al. 2010).

Overall, the numerical abundance model fared poorly compared to the similar study in the Atlantic (Table 4.4). Although most euphausiid species are slightly larger than the target species of the CPR survey (<2mm; Batten et al. 2003), modelling efforts in Ch.3 suggest that meaningful abundance patterns can be extracted from these data. As the design of the sampling grid in this chapter did not differ in any important manner from this previous study, these differences in model performance can almost entirely be attributed to the quantity of the data available (~3000 samples in the Pacific vs ~50000 in the Atlantic). The CPR survey effort in certain sectors of the Pacific sampling grid was extremely low. Twelve of the cells were sampled by a single ship track only. The difficulty in gathering any meaningful abundance patterns from low efforts confirms the high temporal variability and heterogeneity of zooplankton distribution and abundance, partly caused by diel and seasonal patterns of zooplankton migration. Further sampling in the Pacific is likely to increase the predictive power of habitat modelling of euphausiid abundance, and the present analysis suggests that continuous sampling by the CPR survey will likely increase the predictive power of models.

4.5.3 Conclusion

The Pacific species richness model confirms the importance of sea surface temperature as a species richness driver, but also elucidates other predictors. The model study does not integrate effects such as overfishing, pollution, and the migration/transportation of species between oceans (Reid et al. 2007; Greene et al. 2008). Relationships arising out of this modelling effort suffer from being mostly predictive, as opposed to descriptive, and there is always a possibly that the independent variables are masking some unknown covariate. This chapter has shown that there are substantial residuals in the species richness/temperature model in some locations, and that other variables such as silicate concentration, salinity and longitude also are significant predictors of euphausiid species richness in the Atlantic and Pacific. The model framework is relevant for predicting the effects of future climate changes, and this study has described different potential responses to climate change in each basin. The GAM approach in the Atlantic (Ch.3) and in the Pacific Ocean did not detect any conclusive evidence pertaining to the influence of Mid-Ocean Ridges on the distribution of pelagic diversity. Ch. 5 will explore the influence of Mid-Ocean Ridges in greater details, by investigating the subsurface distribution of euphausiids throughout the water column to the seabed, using net collected samples; an approach which is probably more suited for the detection of such influences.

Chapter 5

Abundance patterns and species assemblages of euphausiids associated with the Mid-Atlantic Ridge, North Atlantic[3]

5.1 Abstract

New baseline information is presented on the biogeography, abundance and distribution of euphausiids from discrete depth samples collected in the entire water column to 3000 m at 42 locations along the Mid-Atlantic Ridge (MAR) between Iceland and the Azores. Eighteen species were recorded, with *Euphausia krohni* and *Thysanoessa longicaudata* being most abundant. Eight species had not been recorded previously in the area. The Subpolar Front is a northern boundary to some southern species, but not a southern boundary to northern ubiquitous species that show submergence. Four major species assemblages were identified and characterised in terms of spatial distribution and species composition. Numerical abundance was highly variable but decreased logarithmically with depth. The greatest average abundance and the greatest spatial variation in abundance occurred in northern waters, over the Reykjanes ridge. Abundance declined less with depth in the sub-Arctic Intermediate Water/North Atlantic Current Water than in other areas and watermasses. The near bottom layer (0-200 m from the seabed) typically had low density of euphausiids. The MAR is generally deeper than the typical depth distribution of euphausiids (0-300 m), but many species undergo vertical migrations to ridge crest depths. Euphausiid distribution and abundance patterns appeared only weakly affected by the MAR.

[3] The work described in this chapter has been published as **Letessier, T B**, Falkenhaug T, Høgni D, Bergstad O. A., Brierley, A. S. (2011) Abundance patterns and species assemblages of euphausiids associated with the Mid-Atlantic Ridge, North Atlantic[3]. *Journal of Plankton Research* 10.1093/plankt/fbr033

5.2 Introduction

Partly because of the basin-wide and consistent sampling with the Continuous Plankton Recorder (Stevens et al*.,* 2006) the zooplankton, including euphausiids, of the North Atlantic is probably the most extensively surveyed basin in the world ocean. Since 1946, using ships of opportunity, the CPR has been used to sample the top 10 m, and has provided basin scale data on total euphausiid abundance and species composition (Lindley, 1977; Lindley, 1978; Letessier et al*.,* 2009). However, studies to full ocean depth remain comparatively rare. In the North Atlantic, epi- (0-200m) and mesopelagic (200-1000m) studies were conducted by Angel and Pugh (2000), who described vertical migrations. Endo and Wiebe (2005; 2007) showed the influence of cold-core ring systems on euphausiid species composition, and Saunders et al. (2007b) analysed distribution and population structures of two euphausiid species in the Irminger Sea. The present study was motivated by a shortage of information on bathypelagic species composition and distribution in mid-ocean North Atlantic. The objective was to analyse euphausiid occurrence and abundance in relation to water masses and the major benthic topographic feature, the Mid-Atlantic Ridge (MAR). This study analyses data collected on five summer cruises to the MAR in the years 2003, 2004, 2007 and 2009 (2 cruises in 2009), that sampled waters between Iceland and the Azores, across the depth range 0-3000 m on either side of the mid-ocean ridge.

The MAR represents a major shallow subarea of the mid-Atlantic with axial depths probably sufficiently shallow to affect distribution patterns of at least meso- and bathypelagic organisms. The ridge topography influences circulation features and water mass distributions (e.g. Søiland et al., 2008; Read et al., 2009 and references therein). A major hydrographic feature structuring distributions of marine organisms (e.g.

Longhurst 1998; Dinter 2001; Vierros et al*.,* 2009) is the Subpolar Frontal Zone (SPF) crossing the MAR at 48-52°N (Fig. 5.1). The SPF creates the division between the North Atlantic Drift Province and the Atlantic Subarctic Province (NADR and SARC defined by Longhurst, 1998). To the north of the SPF waters are typical of high latitudes, with low temperature (<8 °C), low salinity (<35 PSU) and oxygen content, and high production during the spring and summer months (80 g $C.m^{-2}.month^{-1}$; Longhurst, 1998). Further to the north still (>57º N), waters are typical of Modified North Atlantic Waters (MNAW, 6.6º < SST <9º C; Søiland et al., 2008). To the south of the SPF, temperate waters predominate (North Atlantic Central Waters, NACW) with a somewhat lower production peak (<50 g $C.m^{-2}.month^{-1}$; Longhurst, 1998) and sustained production throughout the summer months. Recent comprehensive studies associated with the MAR elucidated distribution patterns of nekton (Opdal et al*.,* 2008, Sutton et al*.,* 2008), mesozooplankton and phytoplankton (Gaard et al*.,* 2008, Gislason, et al*.,* 2008, Heger et al*.,* 2008, Pierrot-Bults, 2008, Hosia et al*.,* 2008, Petursdottir et al*.,* 2008) and their association with hydrographic conditions and water masses (Søiland et al*.,* 2008). Some apparent influence of the MAR topography has been observed on deep scattering layers (Opdal et al*.,* 2008), and net sampling of pelagic fish revealed bathypelagic maxima in abundance and biomass, and concentration in the benthic boundary layer along the MAR (Sutton et al*.,* 2008). The MAR also has a demersal fish community similar to that found on adjacent continental slopes (Bergstad et al*.,* 2008; Fossen et al. 2008), which feeds in part on euphausiids (*Coryphaenoidis rupestris*, a dominant demersal fish on the MAR, see Bergstad et al*.,* 2010). How these communities are sustained in a deep mid-ocean area that has conventionally been considered less productive compared with coastal waters is not fully understood.

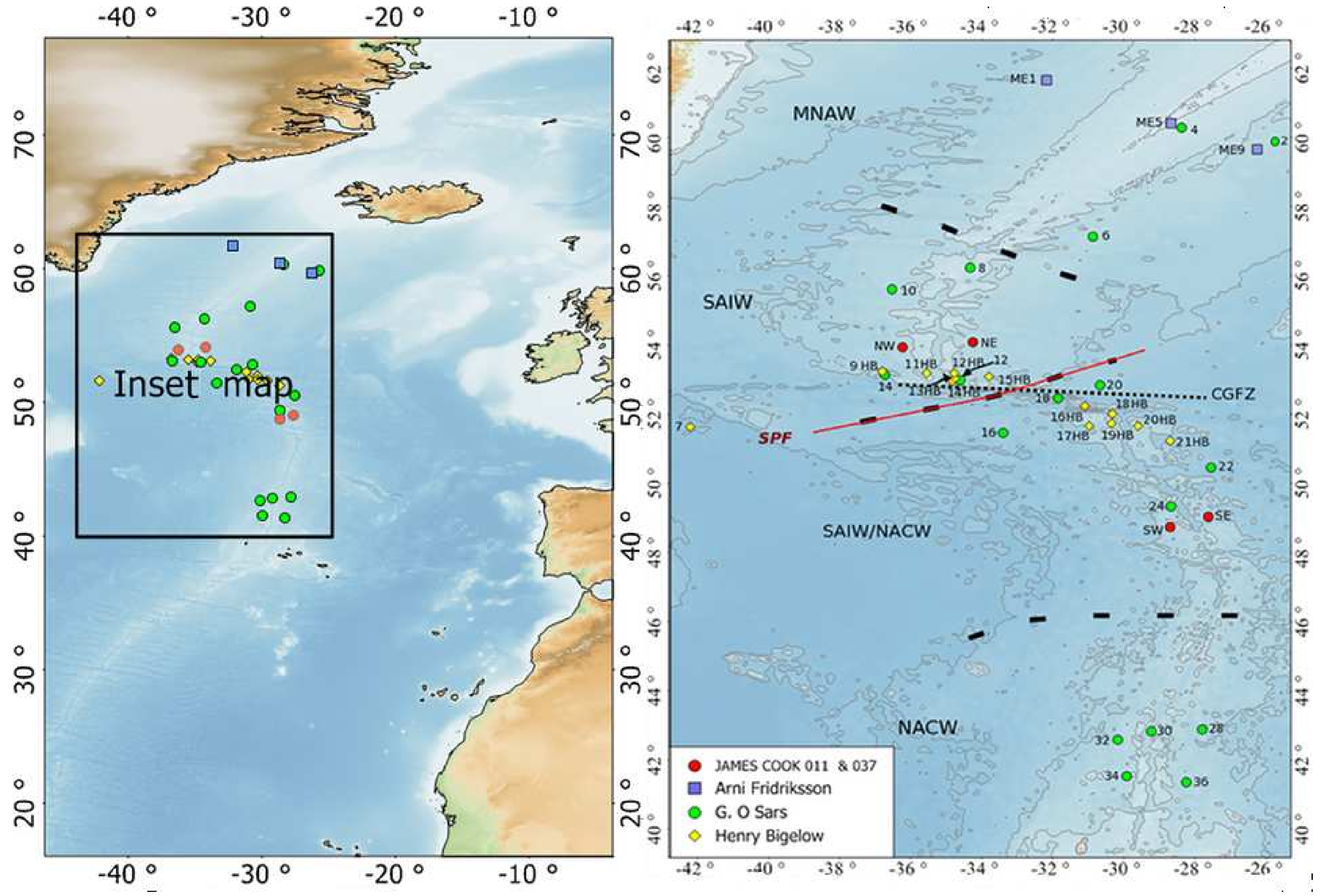

Fig. 5.1 Locations where euphausiids were sampled on research vessel cruises to the Mid-Atlantic Ridge in 2003, 2004, 2007 and 2009, and subareas of the sampling area characterised by dominant water masses (after Søiland et al. 2008): MNAW - Modified North Atlantic Water (MNAW), SAIW- Sub-Arctic Intermediate Water, NACW - North Atlantic Central Water. In the Subpolar Frontal Zone (SPF) either SAIW or NACW were observed. The 500, 1000, 2000, 3000, and 4000m isobaths are indicated.

Distribution and abundance of euphausiids in relation to any mid-ocean ridge, i.e. MAR, has so far not been considered. Since euphausiids possess characteristics of both the plankton and nekton, this group may be good model organism with which to investigate the potential large-scale influence of the ridge on the pelagic fauna (Mauchline and Fisher, 1969). Euphausiids are capable of major vertical and horizontal migration, to the extent that they can be classified as micronekton (Raymont, 1983). These characteristics have implications for nutrient transfer to the deep sea, because of the potential of euphausiids to contribute to the dissolved/particulate organic carbon and nitrogen pools through respiration and excretion (Schnack-Schiel and Isla, 2005; Schnetzer and Steinberg, 2002). In this study, the vertical and horizontal distribution of euphausiid species and abundance was investigated, from the surface to 3000 m. In addition to characterising the euphausiid fauna in the area, the results are of more general relevance to deepwater systems ecology.

5.3 Materials and methods

5.3.1 Sampling and sample analysis

Pelagic net sampling was conducted along the Mid-Atlantic Ridge between Iceland and the Azores on a series of summer cruises on the research vessels *Arni Fridriksson, G.O.Sars, Henry Bigelow,* and *James Cook* (Table 5.1, and Fig. 5.1 for a summary of activities, gears, stations, and acronyms used in this study). The midwater trawling process, and gears used, on one of the major cruises on the Norwegian RV *G.O.Sars* in 2004 was described in detail by Wenneck et al. (2008) and Sutton et al. (2008). A mainstay of trawling was the macrozooplankton trawl, a double-warp otter trawl with 6x6 m mouth opening and 3x3 mm mesh (6 mm, stretched) from the mouth to the cod end. On the *G.O. Sars* (2004) and the *Henry Bigelow* (2009) cruises, the trawl was equipped with a multisampler and five cod-ends, opening and closing by a pre-programmed timer, allowing depth stratified sampling (Wenneck et al. 2008). On the Icelandic vessel (2003) a smaller (4x4m mouth opening) single-cod end version of this trawl was used. The RMT1+8M (Roe and Shale, 1979) used on *James Cook* consists of two nets with mouth openings of 1 m^2 and 8 m^2, and mesh width of 330 µm and 4.5 mm respectively. In this study, only samples from the 8 m^2 net were included in the analyses. Both a single (one pair of nets, JC011) and multiple (three pairs of nets, JC037) versions of the RMT were used.

Table 5.1 Pelagic sampling efforts and station coordinates on the mid-Atlantic ridge during research cruises from 2003 to 2009, in chronological order. All gears had a mesh size of 4.5 mm under nominal deployment-speed conditions (2knts).

Cruise	Cruise date	Station name	Latitude	Longitude	Depth sampled (m)	Gear	Trawl opening (m^2)
Arni Fridriksson	04/06/2003-30/06/2003	ME1	61.65	-32.15	0-350, 350-700, 700-1000	Small macrozooplankton trawl (SMZT)	16
		ME5	60.43	-28.71	0-350, 350-700, 700-900		16
		ME9	59.7	-26.22	0-350, 350-700, 700-1000[2,3]		16
G.O Sars Leg 1	05/06/2004-03/07/2004	2	60	25.75	0-200, 200-850, 850-1500, 1500-1800,1800-2150[2,3]	Large macrozooplankton trawl with multisampler (LMZT)	36
		4	60.3	-28.43	0-200, 200-500, 500-750, 750-1300, 1300-1350[2,3]		
		6	57.2	-31.12	0-200, 200-850, 850-1500, 1500-2100, 2100-2150[2,3]		
		8	56.32	-34.27	0-200, 200-800, 800-1250, 1250-1350[3], 1350[2,3]		
		10	55.62	-36.57	0-200, 200-750, 200-750, 750-1500[2], 1500-2000, 2000-1900[2,3]		
		12	53.1	-34.58	0-200, 200-700, 700-1200, 1200-1500, 1500-1450[2,3]		
		14	53.1	-36.72	0-200, 200-700, 700-1500, 1500-2300, 2300-2500		
		16	51.45	-33.45	0-200, 200-700, 700-1500, 1500-2300, 2300-3000		
		18	52.4	-31.82	0-200, 200-700, 700-1500, 1500-2300, 2300-2700		
		20	53.05	-30.87	0-200, 200-700, 700-1500, 1500-2300, 2300-2500		
		22	50.6	-27.5	0-200[2], 200-700[2], 700-1500, 1500-2300, 2300-2700		
		24	49.58	-28.48	0-200, 200-700, 700-1700, 1500-2300, 2300-2700		
		28	42.9	-27.75	0-200, 200-700, 700-1500, 1500-2300, 2200-2300		
		30	42.88	-29.3	0-200, 200-600, 600-1500, 1500-2300[2,], 2300-2400[2]		
		32	42.52	-30.15	0-200, 200-700, 700-1500, 1500-2000, 2000-1800[3]		
		34	41.76	-30	0-200, 200-700, 700-1500, 1500-1900, 1900-2000		
		36	41.5	-28.45	0-200. 200-700, 700-1500, 1500-2050, 2050-2000		
James Cook 011	13/07/2007-18/08/2007	SWJC011	48.9	-28.45	50-300, 400-500	Single RMT1+8	8
		NEJC011	54.09	-34.13	100-150, 400-500, 300-400, 0-100, 450-550, 0-200		8
Henry Bigelow	8/06/2009-12/07/2009	7HB	51.5	-42.12	0-200, 200-900, 900-1800, 1800-2500, 2500-2450[3]	Large macrozooplankton trawl with multisampler	36

		9HB	53.28	-36.76	0-100, 100-700, 700-1900, 1900-2700[2], 2700-2800[3]		
		11HB	53.27	-35.51	0-200, 200-700, 700-1400		
		12HB	53	-34.82	0-200, 200-900, 900-1600, 1550-1600[2,3]		
		13HB	53.13	-34.82	0-600, 600-1500		
		14HB	53.13	-34.77	100-300, 300-900, 900-1500, 1500-1400		
		15HB	53.02	-34.77	0-200, 200-900, 900-1900, 1900-2800[2, 3]		
		16HB	52.27	-33.6	0-200, 200-400, 400-500[3]		
		17HB	51.53	-31	250-550, 550-1300, 1300-1800, 1800-2500, 2500-2720		
		18HB	51.91	-30.41	250-450[1], 450-1100, 1100-1500, 1500-1200[3]		
		19HB	51.55	-30.3	0-200, 200-800, 800-1200, 1200-1100[1, 3]		
		20HB	51.75	-29.55	300-550, 550-1200, 1200-1400, 1300-1400		
		21HB	51.31	-28.87	400-600, 600-1150, 1150-1900, 1900-2550, 2550-2650[2, 3]		
James Cook 037	1/08/2009-09/09/2009	23SEJC037	49.05	-27.63	0-200[1], 200-500, 500-800,	Multiple RMT1+8	8
		38SWJC037	48.73	-28.7	0-200, 200-500, 500-800		
		40SWJC037	48.73	-28.7	0-200, 200-500, 500-800		
		47SWJC037	48.73	-28.7	200-500, 500-800, 800-1000[2]		
		64NWJC037	53.93	-36.21	200-500, 500-550, 550-700		
		89NEJC037	54.08	-34.25	0-200, 200-500, 500-800		
		90NEJC037	54.08	-34.25	0-200, 200-350, 350-500		

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[1] Sample lost
[2] No euphausiids caught
[3] Near bottom trawl

Sampling at pre-determined discrete depths was achieved with all nets. The RMT1+8M and macrozooplankton trawl were fished by lowering the closed trawl to the maximum depth of sampling. The trawl then was towed obliquely while closing and opening successive cod-ends to sample discrete depths (nominal depth ranges different throughout and in-between cruises, see Table 5.1). On the *Arni Fridriksson* the trawl was lowered rapidly to the minimum depth to be sampled and then fished and slowly lowered through to the maximum depth layer, after which the trawl was collapsed, so as to not fish anymore, and rapidly heaved to the surface, in order to minimise net contamination from shallower waters.

The material was fixed in 4% borax-buffered seawater solution of formaldehyde and transferred to ethanol upon arrival on shore. Sub-samples preserved in ethanol or frozen for molecular analysis were included in the abundance estimates. Specimens were in most instances identified to species, otherwise to a species-group, following Brinton et al. (2000) and Baker et al. (1990). When catches numbered more than 100 individuals, a subsample was extracted using a Folsom splitter, usually to an aliquot of 1/8 or 1/16.

Abundance was expressed as numbers per unit volume (individuals 10^{-3} m^{-3}) and surface area (individuals m^{-2}). Volumes filtered per individual cod-end were estimated by multiplying the mouth area of the trawl or net (16 m^2, 36 m^2, and 8 m^2 for the small and large macrozooplankton trawl, and the RMT 8, respectively) by the oblique towing distance. Depth integrated density (individuals m^{-2}) was derived by summing numerical net catches from all depth layers sampled at a site and dividing the total catch by the total volume sampled at the site, and finally multiplying by the maximum sampling depth (i.e. height of water column sampled).

5.3.2 Environmental data

Published summaries on hydrographical observations in 2004 and 2007 are available (Søiland et al. 2008; Read et al. 2009), and Fig. 5.1 shows the sampling area divided into hydrographical regions in accordance with Søiland et al. (2008). This spatial pattern is strictly valid only for 2004, but the major patterns may be assumed to be similar in all years.

5.3.3 Data analysis

In order to explore patterns of species diversity, vertically integrated species richness data were grouped in 5° latitudinal bands. Groups were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using the Cochran's test. Differences between normally distributed homogeneous bands were explored using one-way ANOVA in the programme R (R v2.9.1 Development Core Team 2007). Tukey's honestly significant difference (HSD) *post hoc* test was used to identify specific differences between groups.

Distribution and species composition patterns were explored with multivariate ordination and classification techniques using PRIMER software v6 (Clarke and Gorley, 2006). Non-metric multidimensional scaling (MDS) and cluster analysis were adopted. Input density data were fourth-root transformed (ind. 10^{-3} m^3) to reduce the weight of dominant species. The similarity measure applied was the Bray-Curtis similarity index (Bray and Curtis, 1957). Because of identification difficulties *Thysanopoda acutifrons* and *Thysanopoda microphthalma* were pooled. Nets with no euphausiid catch were omitted from the MDS analysis, since these would show up as outliers. Analysis of individual net samples was carried out, where each cod-end collected was considered an individual sample. Each cod-end was characterised by its standardized species-specific abundances and sampling depth (Table 5.1).

Associated with cluster analysis, permutation tests (Analysis of similarity ANOSIM, 999 iterations, p< 5%) were carried out to determine association of groups of samples with five *a priori*-defined factors: affinity with hydrographic regions (from Søiland et al*.,* 2008); depth-stratum (nominal depth strata: 0-300, 350-900, 950-1350, 1400-2200, >2250 m; trawls that came within 200 m off the seabed were considered a unique depth stratum called the near bottom layer, n=17); position with respect to ridge axis (east, west, or directly on top); solar cycle (day, night, or dusk/dawn); and sampling gear (Table 5.1).

The appropriate discrimination level for determining clusters was decided by running similarity profile permutation tests (SIMPROF, 1000 permutations, p < 5% to test at which similarity the clusters significantly differed in structure). Species contribution to similarity (SIMPER) was applied to determine the characteristic species contribution to each significant cluster.

Euphausiids exhibit diel vertical migration (DVM), but since net sampling was conducted throughout the diurnal cycle this behaviour could potentially inflict a source of bias in the multivariate analysis. In order to explore possible effects of euphausiid vertical distribution in relation to actual light levels linear models were fitted (using R) between depth (m) of maximum density (the dependent variable) and Photosynthetically Active Radiation (the independent variable and a proxy for time of day, recorded at the time of opening of each net). The PAR sensor (PAR *LITE* Lipp and Zonen, recording light intensity every 20 min) was placed on deck of the ship, but the surface light can be assumed to correlate with the *in situ* light intensity. A model was fitted for each of the five most abundant species, using data from samples collected by the RV *G.O Sars*.

Mean species accumulation curves (over all permutations, see Ugland et al., 2003) were plotted for the different gears (LMZT, SMZT, and mRMT1+8, see Table 5.1) using the 'species accumulation' routine in PRIMER. Catchability of nets were compared from proximate stations (Stations 2, 4, 6 and ME1, ME5, ME9 for the LMZT/SMZT comparison; and stations 8, 10, 12 and NEJC011, NEJC037 for the LMZT/mRMT1+8 comparison) and from samples restricted to the top 1000 m.

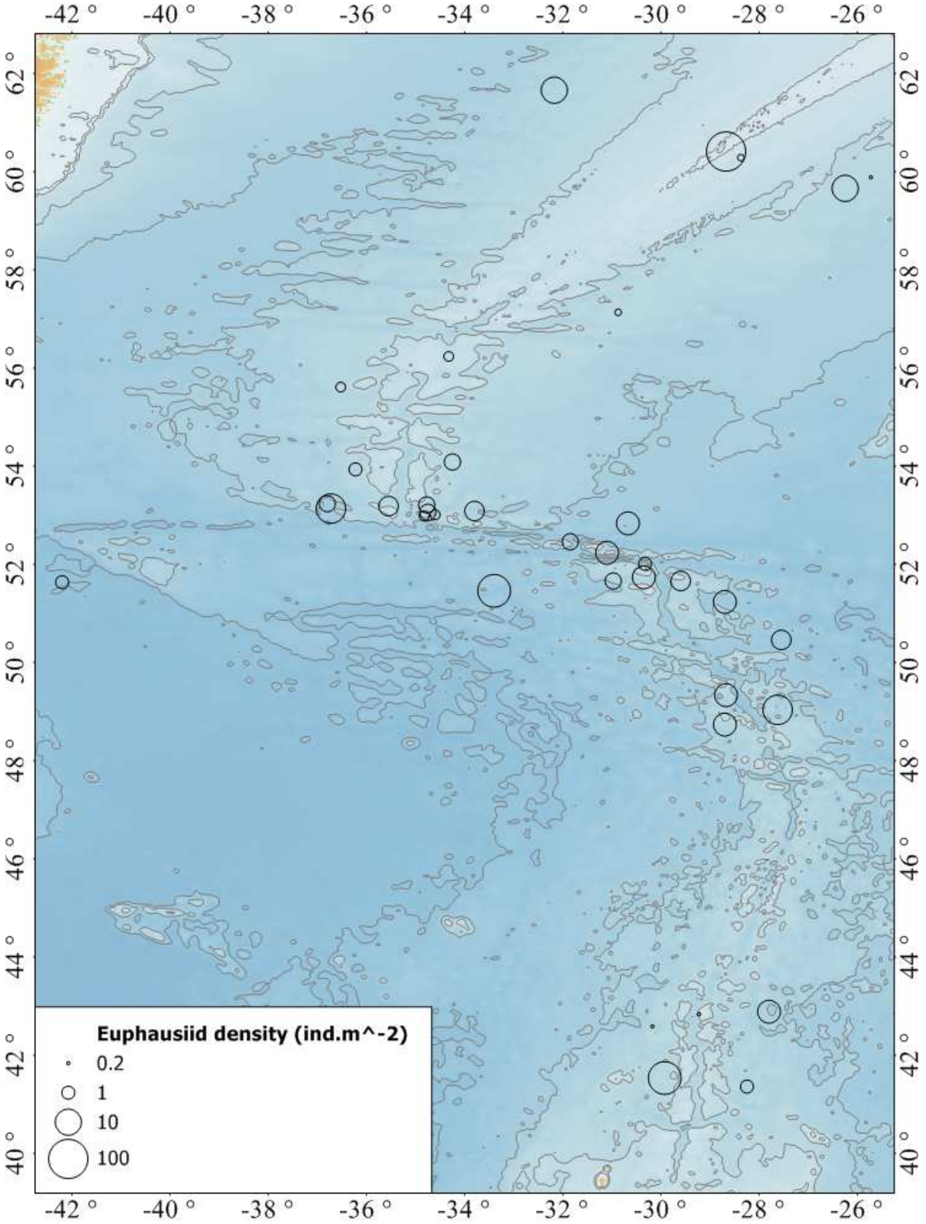

Fig. 5.2 Euphausiid density (ind. m^{-2}) by location. At locations sampled repeatedly, (i.e. on the James Cook 037 in 2009), the density shown is an average of estimates from several visits.

5.4 Results

5.4.1 Euphausiid abundance

The average euphausiid abundance (all species pooled) was highly variable throughout the study area, ranging from 0.08 to 112 ind. m^{-2} (Fig. 5.2), and the abundance varied without an obvious geographical pattern. Densities were greatest in the top 300 m and decreased by orders of magnitude with depth (Fig. 5.3). This pattern was observed in all hydrographic regions (Fig. 5.1), but the rate of decline with depth varied between regions. Abundance at depth (>350 m) appeared highest at sites within the SAIW/NACW region. Density was either low or zero in near-bottom tows: of the 17 cod-ends fished within 200 m of the seabed, 10 caught no euphausiids i.e. 58%. By comparison, amongst open-water trawls at similar depths (500 m and beyond, n=120), only 6% caught no euphausiids.

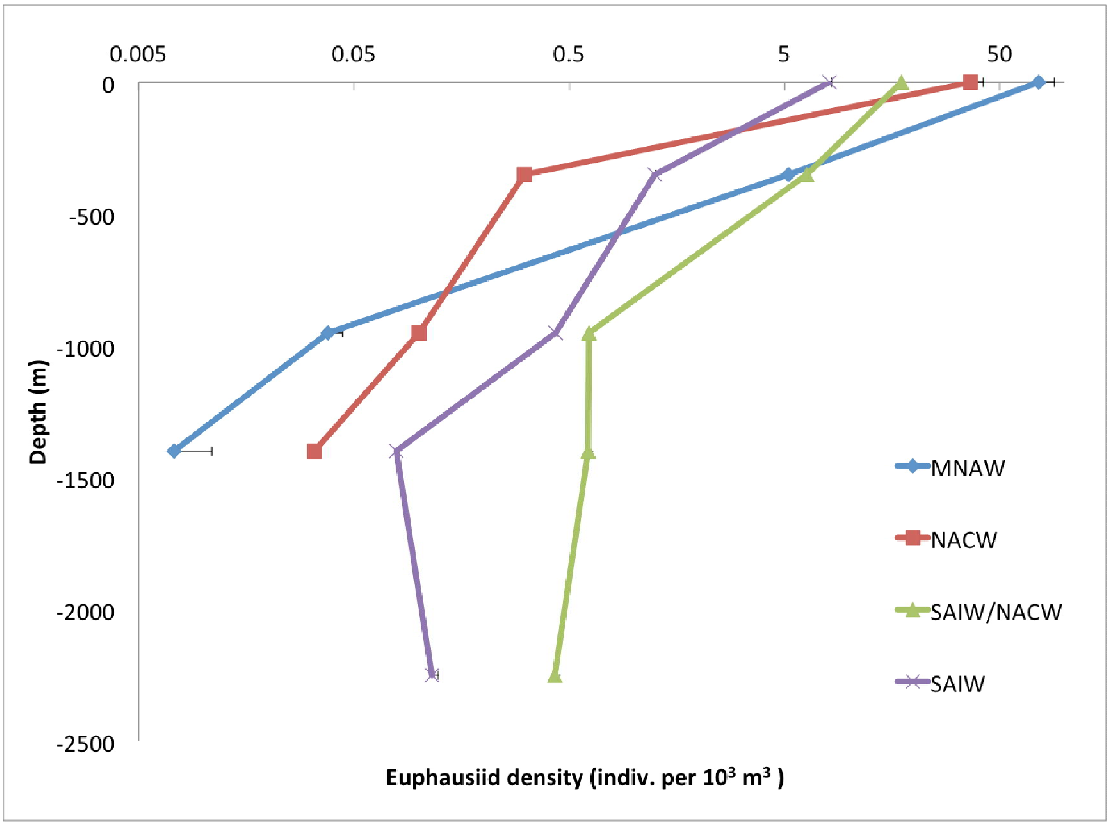

Fig. 5.3 Mean euphausiid density (ind.10^{-3}m^{-3} mean±S.E.) within depth strata, in each hydrographical regions as defined by Søiland et al., 2008 (Fig. 5.1).

The average euphausiid density of near bottom nets deeper than 1000 m (0.025 ind.10^{-3} m^{-3}) was an order of magnitude lower than the equivalent depth in the open water (0.37 ind.10^{-3} m^{-3}), and abundance was significantly less (Student's t-test, p=0.032).

5.4.2 Species recorded

It total, 18 euphausiid species from 6 genera occurred in the 159 samples from the 42 sites sampled (Fig. 5.1, Table 5.2). The majority of species had broad vertical depth ranges, e.g. *Meganyctiphanes norvegica* and *Thysanopoda acutifrons* were both found from 0 to 2800 m. The deepest recorded species was *Thysanopoda cornuta* at 3000m. An increase in species richness was found south of the SPF, but species richness did not change with latitude between 48º N and 55º N, (Fig. 5.4). There was a significant heterogeneity amongst the 5° bands (Fig. 5.4; ANOVA, $F=_{3,38}$ 19.9, p<0.0001). Pairwise comparisons showed highly significant differences between the southernmost band (45-50° N) and all three northern bands (60-55°, 55-50°, and 50-45° N; Tukey's HSD, p <0.000). No differences were found between 60-55° and 55-50° (p = 0.043), 55-50° and 50-45° (p = 0.95), and 60-55° and 50-45 (p = 0.36). Species were found exclusively (*Nematoscelis microps, Stylocheiron abbreviatum),* or predominantly (*Thysanopoda pectinata, Nematobrachion flexipes)* in waters immediately north of the Azores. These species had their apparent northern distribution limits within the study area. Only one species, *Thysanopoda longicaudata,* had a southern distribution boundary within the study area and was not observed south of the 48°N (Table 5.2). The most abundant species were *Euphausia krohni* and *T. longicaudata.* Compared with previous records (see Brinton et al., 2000), greater maximum depths were observed for all species except for *Thysanoessa gregaria*, *Thysanopoda cristata*, *Thysanopoda cornuta* and *Thysanopoda egregia* and *Thysanopoda aequalis.*

Table 5.2 Euphausiid species sampled in 2003, 2004, 2007 and 2009 on the mid-Atlantic Ridge and in adjacent waters of the North Atlantic (41-62° N). Station locations given in Table 5.1 and Fig. 5.1.

Species	Authority	Year	Number of specimens collected	Latitudinal range (deg N)	Depth range	Stations at which species was recorded
Euphausia krohni	Brandt	1851	15168	60-41.5	0-2700	2, 6, 12, 14, 16, 18, 20, 22, 24, 28, 30, 34, 36, SW-JC011, NE-JC011, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Thysanoessa longicaudata	Krøyer	1846	13587	62-49	0-2300	ME1, ME5, ME9, 8, 12, 14, 18, 20, 22, SWJC011, NEJC011, 16HB, 90JC037
Nematoscelis megalops	Sars	1883	6799	60-41.5	0-2720	ME5, 2, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 34, 36, SWJC011, NE-JC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Thysanopoda acutifrons/microphthalma	Holt & Tattersall	1905	3100	62-41.5	0-2800	ME1, ME5, ME9, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 34, 36, NE-JC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Meganyctiphanes norvegica	Sars	1857	2138	62-41.5	0-2800	ME1, ME5, ME9, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 34, 36, SW-JC011, NE-JC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 47JC037, 64JC037, 89JC037, 90JC037
Stylocheiron maximum	Sars	1883	529	62-41.5	0-2700	ME1, ME9, 2, 4, 8, 10, 14, 22, 28, 34, 36, SWJC011, NEJC011, 9HB, 14HB, 15HB, 17HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 89JC037, 90JC037
Nematobrachion boopis[1]	Calman	1905	411	62-41.5	0-2500	ME1, ME5, 4, 8, 10, 12, 14, 20, 22, 28, 30, 34, 36, SWJC011, NEJC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 20HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Thysanopoda cornuta[1]	Illig	1905	61	54-41.5	0-3000	14, 16, 18, 20, 22, 24, 30, 32, 34, 36, NE-JC011, 7HB, 9HB, 16HB, 17HB
Thysanopoda pectinata[1]	Sars	1883	31	49-41.5	0-1500	28, 30, 32, 34, 36, 23JC037
Stylocheiron abbreviatum[1]	Sars	1883	29	42.5-41.5	0-1500	32, 34, 36
Nematobrachion flexipes	Ortman	1905	24	53-41.5	0-2000	20, 28, 30, 34, 36
Nematoscelis microps[1]	Sars	1893	11	42.5-41.5	0-1500	32, 34, 36

Thysanopoda egregia[1]	Hansen	1905	8	51.5-41.5	200-2300	16, 24, 28, 30, 36, 18HB, 20HB
Thysanopoda cristata[1]	Sars	1883	3	41.5	0-700	36
Stylocheiron sp	*(c.f. robustus)*[1]		3	42.5-41.5	200-700	32
Thysanopoda aequalis	Hansen	1905	2	41.5	0-200	34
Thysanoessa gregaria	Sars	1883	1	43	200-600	30

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[1] Species not recorded by Lindley (1977)

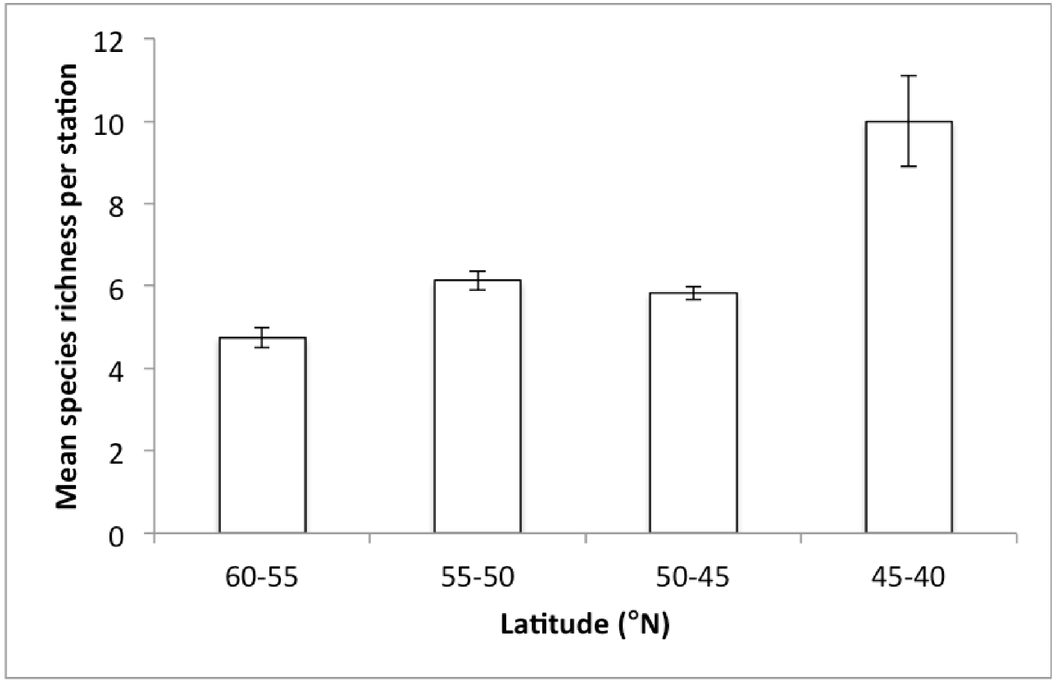


Fig. 5.4 Species richness (number of species observed at individual locations ± SE) of euphausiids per stations against latitude along the Mid-Atlantic-Ridge. Values were not standardised by effort as species accumulation curves for the different gears approaches an asymptote at ~10 tows (see section on MDS and Cluster analysis) and each of the 5º bands comprised > 25 tows.

Linear models on depth of maximum density against PAR (of the five most abundant species: *E. krohni*, *T. longicaudata*, *N.megalops*, *T. acutifrons microphthalma*, *M. norvegica,* see Table 5.2) were not significant ($p>0.05$ for all species).

5.4.3 MDS and Cluster analysis

The MDS (stress=0.17, Fig. 5.5A) suggested a wide dispersion rather than grouping of samples. Horizontal dispersion appeared related to latitude as samples to the extreme left in the plot were mostly northern stations, those to the right were southern stations. Superimposed on the MDS plot (Fig. 5.5B) are clusters resulting from the classification of depth-specific samples (see Fig. 5.6 for station names and species contribution to dissimilarity). There was substantial overlap between clusters in the middle of the plot, indicating basic similarity between samples in mid-latitudes, i.e. geographically located within the Subpolar Frontal Zone.

Similarity profile tests (SIMPROF) of clusters identified two major clusters at 20% similarity ($\pi=2.44$, $p<0.1$), and one of these (Group F) did not show significant clustering at higher similarity values (>20%). The other group showed significant clustering into 5 groups by 39% similarity (SIMPROF, $\pi=1.65$, $p< 1.5$, Fig. 5.6).

The six groups (A, B, C, D and E defined at 39%, and F defined at 20% similarity) had the following geographical and vertical characteristics:

Group A had just the one sample, and was omitted from comparative multivariate descriptions. Group B was restricted to north of 50° N, and included all samples from 2003, mainly from MNAW, and was constituted predominantly of *T. longicaudata* (80%) and *M. norvegica* (7%, Fig 5.7 B)

Group C (70 samples) spanned the broadest latitudinal range and was dominated by samples from the entire water column from MNAW (in 2004 only) and SAIW; samples were from >500m for the Subpolar Frontal Zone (SPF), and SAIW/NACW. Samples from the North Atlantic Central Water were deeper still (>1000m). Dominant species where *T. microphthalma*/*acutifrons* (63%), *E. krohni* (13%), and *M. norvegica* (10.5%, see Figure 5.7C).

Group D was restricted to two epipelagic samples from the NACW regions and was composed mainly of *N. flexipes* (13.5%) and *S. abbreviatum* (13.5%).

Group E (69 samples) comprised mostly samples from the RSS *James Cook* and the *Henry Bigelow* cruises (2007 and 2009; Subpolar Frontal Zone). This group of samples was shallow, for the most part (n=5 for samples deeper than 1500m, Fig. 5.7E) and was dominated by *E. krohni* (52%) and *N. megalops* (32%).

Group F, defined at 20% similarity comprised mostly southerly samples collected across a wide depth range of 0-2000m. Northernmost samples (latitude > 48°N) clustering with these southern samples were deep, i.e. from 1000-3000 m. This group was characterised by high proportions of *N. megalops* (24%), *T. pectinata* (13%), *E. krohni* (12%), and the deep-sea species *T. cornuta* (16.5%, see Figure 7F).

ANOSIM tests revealed that hydrographic region was the most important factor (Søiland et al. 2008, global R=0.287, p<0.1%) followed by depth strata (global R=0.229, p<0.2%). An effect of gear type was also detected (global R=0.201, p<0.2%), and the greatest differences were observed between the small macrozooplankton trawl and the single RMT1+8 (R=0.613, p<0.1%). Position relative to ridge axis and solar cycle were not significant (global R=-0.012 and -0.025, p<91.4% and p<16.7% respectively).

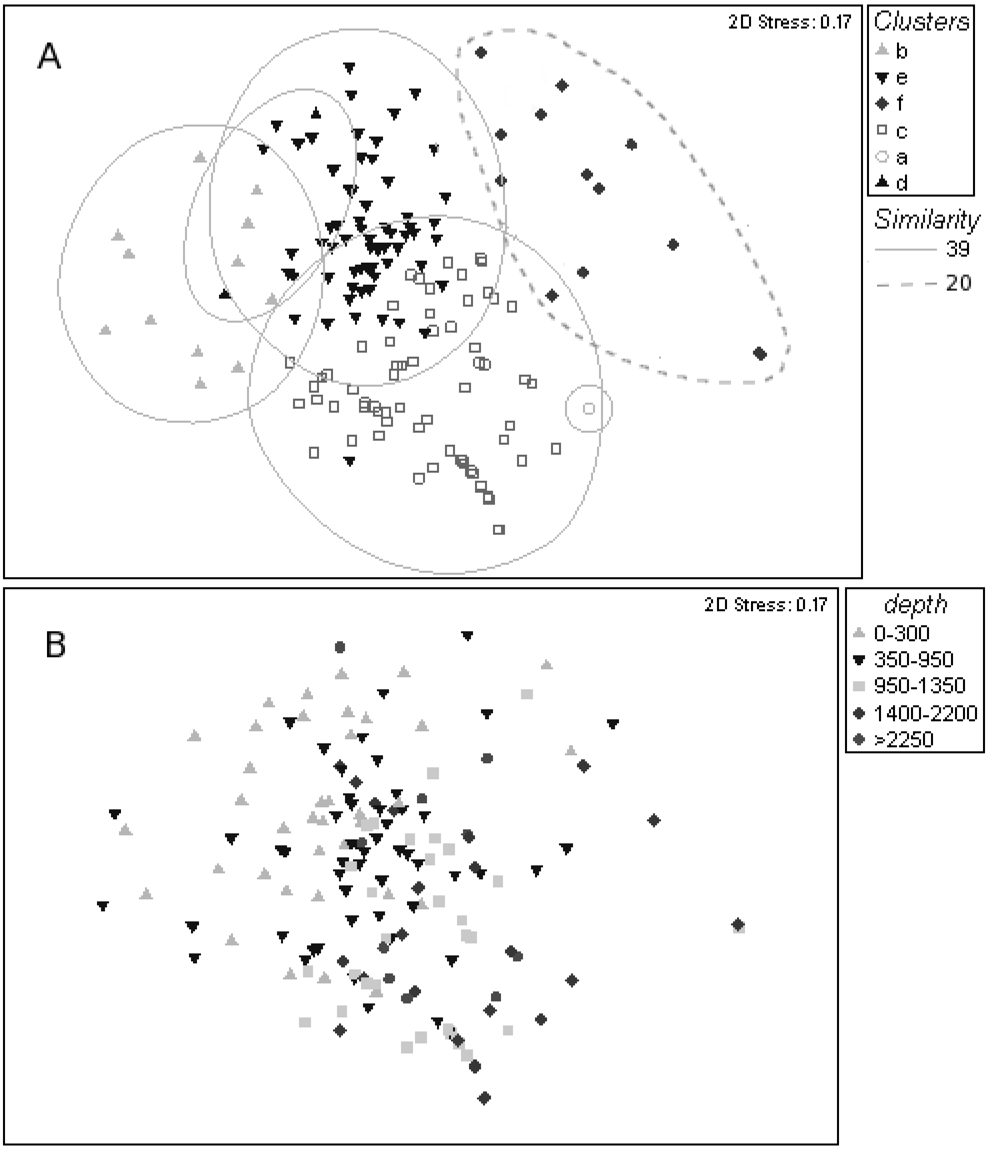
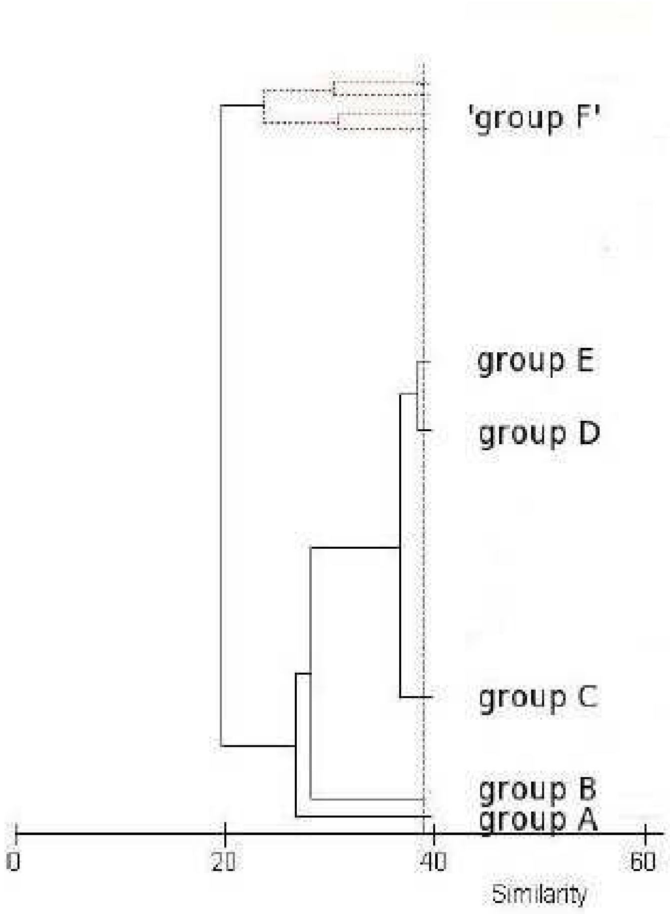


Fig. 5.5 Non-metric multidimensional scaling ordination (MDS) of fourth root transformed density estimates in individual net samples (cod ends). Overlayed are A) Significant clusters A-F resulting from the classification analysis (see text for explanation), and B) depth-strata from which individual samples originated.

Mean species-accumulation curves showed that an asymptotic species number was approached for all gears with the sampling effort applied in this study (Fig. 5.8), and suggested similar catchability between the LMZT and the mRMT1+8. The SMZT approached an asymptotic species richness maximum somewhat more rapidly than the LMZT.



Group characteristic		
Depth	Stations	Species contribution
0-2720	N=13: 18, 30, 32, 34, 36, 17, 20, 40	*N. megalops*: 51.11% *T. cornuta*: 32.66%
0-2300. Shallow north of CGFZ (0-1500) and deepening across the SPF. Becomes shallower again (0-700) south of 49°	n=69: 12, 16, 22, 24, 28,90JC037 SWJC011, NEJC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 20HB, 21HB, 23JC037, 40JC037, 47JC037, 64JC037	*N. megalops*: 34.23% *T. microphthalma* and *acutifrons*: 21.23%
0-200	n=2: 34, 36	*N. flexipes*: 13.50% *S. abbreviatum*: 13.50%
0-2300 in MNAW and SAIW, 900-1800 North of CGFZ, deepening south of the CGFZ, and exclusively deeper than 700 m in NACW	n=70: 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 34, 36, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 17HB, 18HB, 19HB, 20HB, 21HB, 64JC037, 89JC037	*T. microphthalma* and *acutifrons*: 79.98% *M. norvegica*: 10.23%
0-200, 0-1000	n=12: ME, 8, 14, 20, NE	*T. longicaudata* 36.90% *M. norvegica* 33.74%
2050-2000	n=1: 36	NA: less than 2 samples

Fig. 5.6 Cluster analysis dendrogram and group characteristics of samples, based on fourth-root transformed species density data (at 20 and 39 percent similarity). Station composition, and species contribution to similarity of samples within clusters, derived by SIMPER analysis.

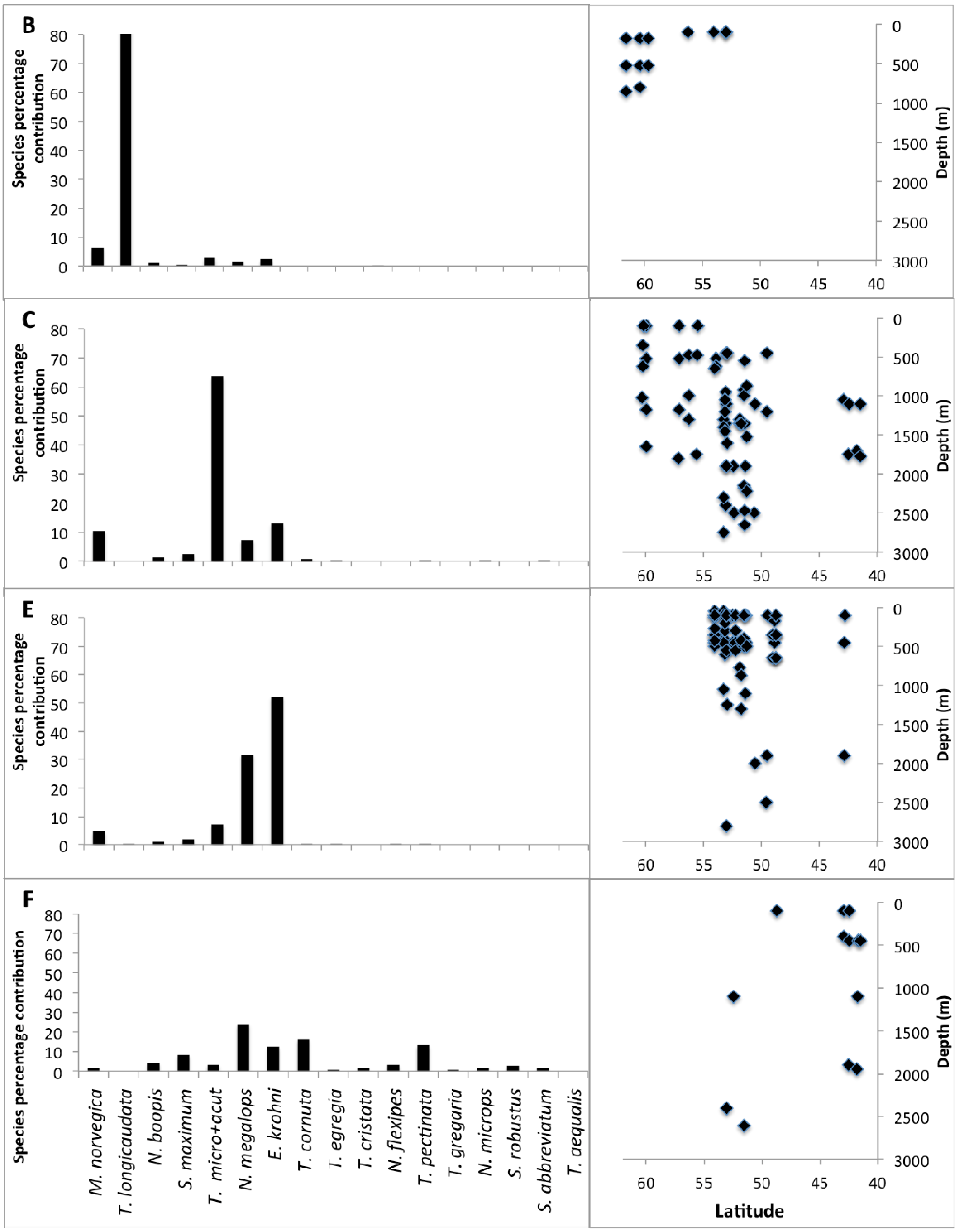


Fig. 5.7 Total species composition (proportion of each species in the summed standardized catches from all cod-ends in a cluster), and latitudinal and mean sampling depth of net hauls belonging to each sample clusters (B, C, E, F).

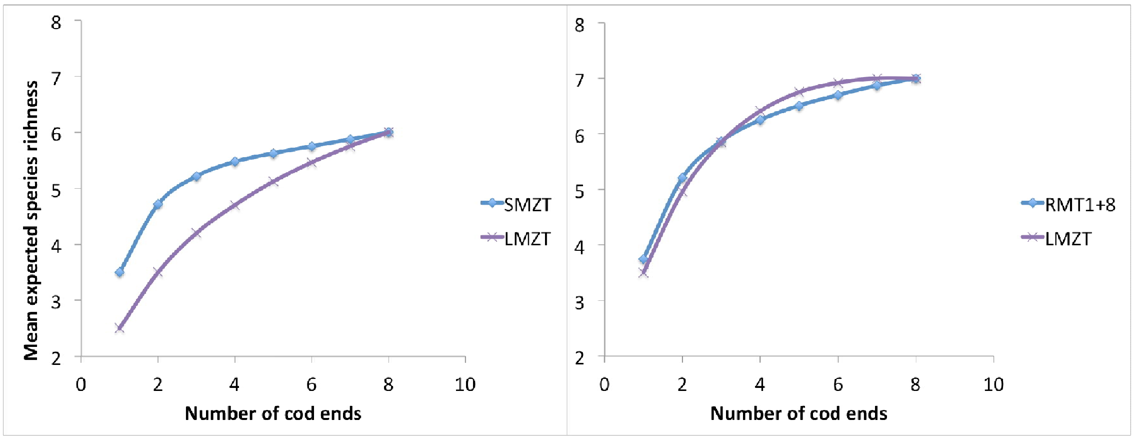


Fig. 5.8 Mean species accumulation curves (over all permutations, see Ugland et al., 2003) for different gears (0-1000m) in subareas where all gears were used, i.e. the MNAW (A) and SAIW regions (B) (Fig 1). SMZT and LMZT– small and large macrozooplankton trawls, respectively. mRMT1+8- multiple Rectangular Mid-water Trawl 1+8

5.5 Discussion

5.5.1 Euphausiid abundance patterns

Hydrographically, the Mid-Atlantic Ridge (MAR) region of the North Atlantic is heterogeneous, as shown in previous studies and in oceanographic papers summarising results from cruises considered in the present investigation (Søiland et al. 2008; Read et al. 2009). A prominent feature is the Subpolar Front (SPF) detected at approximately 52°N, near the Charlie-Gibbs Fracture Zone, but actually forming a frontal zone between 48° and 52°N. Enhanced Chl-a values observed in stations overlaying the CGFZ in the SPF during the *G.O Sars* cruise (e.g. 2.0 mg. m^{-3} at station 18, Gaard et al., 2008) suggest this area may have somewhat elevated production. Past studies have shown that the main production bloom in the Irminger Sea and neighbouring regions (MNAW) takes place from April to June (Holliday et al., 2006; Clark et al., 2001) which would mean that all of the sampling in this study (from the 1st of June to 9th of September) was conducted during declining bloom or in a post-bloom conditions. Euphausiids occurred throughout the entire study area and depth range sampled. While previous studies have shown increased zooplankton biomass and abundance at 49º- 52º and 53º, possibly linked to high productivity around the SPF (Hays et al., 2001; Hosia et al., 2008, Stemmann, et al., 2008), other studies have not (Gaard et al., 2008). Total water column abundance (ind.m^{-2}) per station showed great variability without any obvious spatial pattern. Such variability, and patchiness, is typical of euphausiids, and long-term monitoring often is required to certain general abundance patterns (such as from the CPR, see Lindley, 1978). As studies considering greater temporal scales (Lindley, 1977; 1978; Letessier et al., 2009) typically see the SPF as an area of high euphausiid abundance, the perceived low and heterogeneous abundance of euphausiids within the SPF area here may reflect high yearly variability in this sector.

Highest euphausiid abundances in all regions were detected in the 0-300 m depth-stratum. The expected decline in abundance with depth was found in all hydrographical regions, but abundance at depth was higher in the SAIW/NACW zone. The mean and dispersion of the euphausiid abundance in the top 300 m of the MNAW region are similar in magnitude to previous records from the Irminger Sea (Saunders et al., 2007b). Logarithmic reduction in abundance with depth is consistent with previous studies and is associated with the increasing distance between euphausiids and their primary source of food (Angel, 1989; Angel and Boxshall, 1990; Wei et al., 2010). The steep slope of the regression of abundance against depth found in the SAIW/NACW region suggests that abundance at depth is relatively high compared with other subareas. This may suggest that higher surface production near frontal zones results in greater abundance at depth. The same area has elevated concentration of marine snow (Vinogradov 2005) potentially supporting larger abundances of facultative detritus-feeding euphausiids (such as *M. norvegica* and *T. acutifrons*; Schmidt et al., 2010).

Observation on depth distribution patterns may be biased by diel vertical migration (DVM, sampling here was inconsistently conducted throughout the daily cycle). Euphausiids are capable of extensive DVM and their presence at considerable depth is not uncommon, even if most feeding takes place in shallow water (Kaartvedt, 2010; but see Clarke and Tyler 2008). However, the majority of DVM takes place in the top 700m, (Angel and Pugh, 2000), and thus any DVM-related bias in euphausiids vertical distribution would be mostly restricted to the top two depth strata of sampling (0-300 and 350-900m). The broad patterns in vertical distribution (1000-2500 m) are probably still valid.

5.5.2 Species diversity and distribution

Several species of euphausiids were observed at almost every station and appeared ubiquitous: *M. norvegica, N. megalops, T. acutifrons, N. boopis.* The overall pattern in the study area is an increase in total recorded species with decreasing latitude (Fig. 5.4). This trend is maintained at depth, and reflects basin scale patterns in the Atlantic (Angel, 1993; Angel et al., 2007).

Species contributing most to the clusters present in the northernmost section B and C (*T. longicaudata, M. norvegica, T. microphathalma/acutifrons, E. krohni, N. megalops*) generally were found at all stations (see Fig. 5.7) whereas many southern species showed a northern boundary (*N. flexipes, S. abbreviatum*), usually south of the SPF at 48º. In this study the SPF marks the northernmost extent of a “transitional area” in agreement with the results of previous studies on other planktonic taxa (Pierrot-Bults, 2008, Gaard et al., 2008). This ‘transitional area’ is placed between 42° and 48° N, a sector which was not sampled in this study (Fig. 5.4).

Highest richness was found in the southernmost subarea of the MAR, in waters just north of the Azores. Several species were found exclusively in this sector: *N. microps S. abbreviatum, T. aequalis, T. cristata* and *T. gregaria* (and with one exception: *N. flexipes*). Distribution maps place the northernmost boundary of these species at ~40º N (Brinton et al., 2000) which also coincided with the southernmost extent of the sampling. Previous studies have suggested that this subarea is next to an area of high diversity. Here, the observation of the exclusive presence of so many species suggests a faunal shift, to an area of high diversity, centred around the North Atlantic gyre and the Sargasso Sea (Endo and Wiebe, 2005; Letessier et al., 2009).

The total number of euphausiid species found in this study, i.e. 18, is the same as the number reported from the Continuous Plankton Recorder (CPR) surveys in the central North Atlantic (Lindley, 1977). However, 8 of the species found in this study were not previously recorded by the CPR. This is presumably due to the greater sampling depth here (3000 m) compared with the CPR sampling restricted to the near-surface 10 m; many species caught here are considered mesopelagic (*N. boopis*) and even abyssal (*T. cornuta*, Brinton, 2000) and thus would not be adequately sampled by the CPR. On the other hand Lindley (1977) listed 8 species not recorded in the present study, three of which are neritic and thus not expected in the mid-ocean Atlantic. Lindley’s study also identified furcilias to species and some discrepancy in species caught with this study is perhaps not surprising. Conventional distribution maps (Brinton, 2000) placed 28 species of euphausiids on the Mid-Atlantic Ridge between 40º and 60º N, i.e. considerably more species than observed in the present study. In the poorly sampled mid-ocean area these generalised distribution maps most likely illustrate assumed distributions rather than actual records. It can be argued that the lower number reflects the relatively short sampling period, limited to the summer season. Although the distribution of krill species is variable on weekly and interannual time scales (Endo and Wiebe, 2007b; Saunders et al., 2007b), no previous studies have conducted sampling across such a wide area and depth range with gears probably suitable for capturing euphausiids of most size classes.

Amongst all euphausiid species, Lindley (1977) found *T. longicaudata* to be the most abundant in the top 10 m north of 40º N. In this study this species was dominant north of the Charlie-Gibbs Fracture Zone, but only in 2003, as reflected by its contribution to Cluster B. Moreover, this study found a southern limit for the distribution of *T. longicaudata* at 48º N, compared to 40º N as reported by Lindley (1977). The most abundant and widespread species was *E. krohni*. A large swarm of *E. krohni* was detected at station 32 (42º N). While the vertical distribution of the two species (*T. longicaudata* and *E. krohni*) overlap at the surface during the night (Brinton et al., 2000), *E. krohni* is generally considered a deeper species during the day and might be undersampled by the CPR. This probably explains the discrepancy between these results and those of Lindley (1977), who found *E. krohni* less abundant than *T. longicaudata.* Since sampling only was conducted during the summer, distinction cannot at this point be made between seasonal and interannual variability in community composition as other possible explanations for the discrepancy between Lindleys' results (1977) and those presented here. Further bias may arguably be attributed to the sampling: the macrozooplankton trawl and RMT 8 likely under-sample some species of euphausiids due to the 4.5 mm mesh size, and probably are suboptimal for estimating abundances of small species and juveniles. However, these species should have been sampled by the mesozooplankton gears used on some of the same cruises, i.e. Multinet (Gaard et al.,

2008) and RMT1, and they were not prominent in these catches. Therefore, the results here probably reflect differences in the relative abundance of these species (*E. krohni* and *T. longicaudata*). Species accumulation curves suggested that the sampling effort was sufficient to describe the euphausiid fauna and also revealed similarity in species catchability between the mRMT1+8 and the LMZT. Moreover, the differences in catchability between the gears within this study probably are not significant.

5.5.3 Vertical and horizontal structures of euphausiid assemblages

Longhurst (1998) regarded the SPF as a boundary between the Atlantic-Arctic Province (ARCT) and the North Atlantic Drift Province (NADR). Moreover the northern sections of the Azorean waters are considered the boundary of the NADR and the East North Atlantic Subtropical Gyre Province (NAST). Observations of euphausiid assemblage structure and species patterns are not inconsistent with Longhurst's biomes (1998). However complete correspondence is not expected, given that Longhurst's biomes are principally based on phytoplankton abundance data and linked to surface water properties, while the present results pertain to euphausiid communities to full ocean depth.

The northernmost cluster (B) showed little depth differentiation but was restricted to the epipelagic zone south of 58°, and was dominated by *T. longicaudata* and *M. norvegica,* typical of the northern North Atlantic (Papetti et al., 2005; Tarling et al., 2010; Lindley, 1978). The predominance of these species in systems adjacent to the Irminger Sea is consistent with past studies west of the Reykjanes ridge (Saunders et al., 2007b). High year-to-year variability in MNAW also is reflected in the community clustering. Sites visited one year apart do not necessarily cluster within the same group. The detected year-to-year variability in the area was attributed to high net catches of *T. longicaudata,* which dominated the catches in 2003 at ME5 and ME9, whilst being almost completely absent in 2004. Because of the identical mesh sizes between the two trawls, it is highly unlikely that sampling bias between the large and small macrozooplankton trawl caused these different observations. More likely, the results reflect actual biological differences between years, making the assemblage structure of MNAW euphausiids highly heterogeneous.

To the south of the SPF *T. longicaudata* is replaced with greater abundances of *N. megalops* and *E. krohni* in the epi- and mesopelagic zones (0-500 m, see Fig. 5.7) and with *T. microphthalma/acutifrons* at depth. Cluster C spanned the broadest depth and latitudinal range, and showed deepening at 54° and tropical submergence (Pearse and Lockhart, 2004) south of the CGFZ. This probably reflects the spatial distribution of the watermasses. In the SAIW/NACW region, NACW was often observed to overlay the SAIW (Søiland et al., 2008). Group E was typical of the SPF regions and was characterized by a sharp northern border, much less so than in the south (Fig. 5.7E). Group F did not show any conspicuous vertical partitioning, but was perhaps deeper and less conspicuous in the northern section of its range (>48°N, >1000 m, Fig. 5.7F) and was even in terms of species composition.

In the MDS, distances between samples from deeper layers are typically shorter in two-dimensional space than distances between shallower samples (Fig. 5.5B). This shows that highest similarity was typically found between deep samples (>1000 m), whereas shallow samples were likely to diverge, presumably reflecting greater spatial hydrographic heterogeneity in the upper layer. This is consistent with present understanding of deep-sea community structuring, i.e. little diurnal and seasonal environmental variation is found at depths deeper than the twilight zone and associated thermocline (>1000 m, Angel, 2003), and the bathypelagic is generally considered a highly homogeneous habitat compared to shallower depth (Robinson, 2009). Linear models suggest that no detectable bias had been inflicted upon the vertical distribution of euphausiids by sampling at different times of day.

The similarity analysis probably is not as sensitive as it could have been to geographical patterns, given the pooling of *T. microphthalma* and *T. acutifrons*. *T. microphthalma* were positively identified in the CGFZ (A. Lindley and N. Copley, personal communications), based on adult males, although DNA barcoding will be required for confirmation (for discussion on taxonomy see Guglielmo and Costanzo, 1977). The ecology and vertical distributions of these species are similar, although *T. microphthalma* is generally found deeper and at lower latitudes than *T. acutifrons*. *T. microphthalma* has not been previously recorded north of the West of Ireland (Brinton, 2000). Differentiation of these two species may have enabled the detection of significant clusters within cluster C.

5.5.5 Effect of the MAR

As originally proposed by Isaacs and Schwarzlose (1965) advection of zooplankton over seamounts by prevailing currents may cause diurnally migrating zooplankton to be trapped on seamounts summits where they can be preyed upon in daylight by seamount fish. Whether this mechanism is at all relevant on the rather deep MAR cannot be determined from the data. Given that the dominant residual surface current is eastwards across the MAR, it is conceivable that the shallowest parts of the ridge and shallowest hills might influence euphausiid distribution and abundance by a similar trapping effect. If so, perhaps higher heterogeneity and fewer deep-sea species and individuals might be expected to the east of the MAR. However, evidence presented to date, including in this study, does not suggest relations between assemblage structure or abundance and position of samples in relation to the ridge-axis or horizontal proximity to the ridge crest. The same was found for meso- and bathypelagic fishes (Sutton et al., 2008) and near-surface euphausiids (Letessier et al., 2009).

Abundance was low near the seabed over the ridge, however. Within the study area, the Reykjanes Ridge in the north, essentially the MNAW region, has the shallowest seabed, and effects of shallow topography might be expected to be more pronounced in this area than elsewhere. The less steep slope of the abundance regression with depth could be due to the influence of the seabed on the density of deep euphausiids. Of the six deepest trawls in MNAW, four were near-bottom trawls, three of which contained no euphausiids. Studies have shown that the standing stock of nekton can be high in the near bottom layer (Angel and Baker 1982), and also on the MAR (Sutton et al., 2008). Bottom trends in plankton abundance are less clear; some studies report increases in near-bottom standing stocks (Angel and Baker, 1982) whereas some show decreased abundances compared to open water at similar depth (Vereshchaka, 1995). The evidence presented here supports the conclusion in the latter study. Recent studies suggest some euphausiid species (*E. superba* and *M. norvegica*) regularly conduct large and deep (>1000 m) migration for feeding on the sea-bed, and that krill at depth reflects an important aspect of the life of adult krill rather than an ecological outlier (Schmidt et al., 2011). An explanation for the low near-bottom abundance of euphausiids may be tight trophic coupling with enhanced populations of bottom-associated nektonic predators (Sutton et al., 2008, Mauchline and Gordon, 1991), an issue that would have to be further explored through fish and micronektic diet analysis. Benthic boundary layer sampling is challenging and was not conducted in a satisfactory manner on any of the cruises.

Chapter 6

Trophic interaction of invertebrate micronekton on either side of the Charlie Gibbs Fracture Zone / Subpolar Front of the Mid-Atlantic Ridge[4]

6.1 Abstract

This study investigates trophic relationships amongst epi- and meso-pelagic (0-200 and 200-800 m) macrozooplankton (2-20 mm) and micronekton (>20 mm) north (54° N) and south (49° N) of the Subpolar Front (SPF) on the Mid-Atlantic Ridge (MAR). Vertical distribution patterns of dominant Euphausiacea, Copepoda, Decapoda, Amphipoda, Thecosomata and Lophogastrida are described from net collected samples. Dietary relationships were explored using fatty acid trophic marker (FATM) composition, and stable isotope ratios of nitrogen and carbon. Pteropods, euphausiids and the hyperiid *Themisto compressa* had broad dietary ranges, showing evidence of both predation and grazing. Bathypelagic species (> 1000 m, *Acanthephyra pelagica, Sergia japonica, Gennadas elegans*) and benthopelagic species (*Gnathophausia zoea*) exhibited evidence of a carnivorous diet. Diet composition, as inferred from δ^{15}N values were inconsistent with FATM composition at low trophic levels. Carbon and nitrogen stable isotope analyses showed ^{15}N enrichment with species average size and lipid levels, and with depth. Individuals from the southern stations (~ 49° N) had a higher concentration of the dinoflagellate FATM (22:6(n-3)), and individuals from northern stations had a higher concentration of *Calanus* spp and storage FATM (20:1(n-9) and 22:1(n-9) concentrations. Observations of FATM levels and numerical abundance patterns are consistent with present understanding pertaining to primary production patterns at the base of the food chain, which is higher in the northern sector than in the south.

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[4] The work presented in this chapter is currently in preparation for publication as **Letessier T. B**., Pond D. A., McGill R A R, Reid W. D. K, Brierley A. S (in prep) Trophic interaction of invertebrate micronekton on either side of the Charlie Gibbs Fracture Zone / Subpolar Front of the Mid-Atlantic Ridge. *Journal of Marine Systems*

6.2 Introduction

Open water zooplankton play a key role in the transfer of energy to the deep-sea, forming a trophic and migratory link between the surface productivity and deeper predatory fauna. Energy is transferred to the deep-sea food webs indirectly, in the form of detritus, faecal pellets and dead organisms sinking (Schnack-Schiel and Isla, 2005), but also directly through the consumption of prey by predators. Diely migrating zooplankton drift into close proximity of predatory demersal nekton, particularly at seamounts and ridges (Pitcher, 2008; Rogers, 1994). Some taxa such as copepods and euphausiids form key links in oceanic pelagic food webs, exerting both top-down and bottom-up control. In oceanic and pelagic systems, interactions between zooplankton and demersal fish stocks are mediated by the trophic links of organisms in the micronekton size range (>20 mm). Some seamounts and ridges have experienced boom and bust exploitation (Pitcher, 2008) and, therefore, broad ecosystem knowledge is becoming increasingly important in order to undertake ecosystem-based fishery management. There is a need to understand and describe the trophodynamics of the primary and secondary consumers of oceanic food chains.

The Mid-Atlantic Ridge (MAR) has recently become of the focus of several studies stemming from a series of cruises under the umbrella of the Census of Marine Life. The ridge is a major shallow subarea of the central Atlantic with peak depths probably sufficiently shallow to affect distribution patterns of at least meso- and bathypelagic organisms. Studies have revealed horizontal and vertical patterns in pelagic (Anderson et al., 2005; Falkenhaug et al., 2007; Petursdottir et al., 2010; Sigurdsson et al., 2002; Petursdottir et al., 2008; Letessier et al., 2011) and nektic/demersal species (Bergstad et al., 2008; Sutton et al., 2008).

Previous studies suggest that even though there is no increased productivity associated with the ridge, there is an increase in demersal and pelagic biomass (Anderson et al., 2005, Sutton et al., 2008) in the benthic boundary layer (BBL, 0-200 m from the sea bed). In this thesis, it has already reported that the density of euphausiids is low near the seabed (<200 m, Ch. 5), perhaps because of competition with, or predation by, ridge-specialist nekton (Bergstad et al., 2010).

Potential interactions between fauna associated with the bottom topography and ‘true pelagics’ (animals that do not interact with the benthos) can be investigated using a combination of techniques, such as stomach content analysis (Kaartvedt et al., 2002), lipid analysis (Falk-Petersen et al., 1990; Falk-Petersen et al., 2000), and carbon and nitrogen stable isotope analysis (SI, Schmidt et al., 2003). Several studies utilising different combinations of these techniques have focused on the higher trophic levels (pelagic and demersal fish, see Hoffman and Sutton, 2010), and lower trophic levels (mesozooplankton, Petursdottir et al., 2010) of the MAR. Studies restricted to the shallow Reykjanes ridge-section to the north suggest that the enhanced BBL nektic biomass may be transferred through trophic levels by at least two pathways (Petursdottir et al., 2008). In one pathway *Calanus* spp, is an important component in the diet of *Sergestes* sp and the myctophiid *Benthosema glaciale*, and in the other pathway *Meganyctiphanes norvegica* is the dominant source of food of the red fish *Sebastes mentella*. Mechanisms serving to maintain this enhanced biomass across the latitudinal extend of the MAR, compared to open water habitats, remain largely unknown.

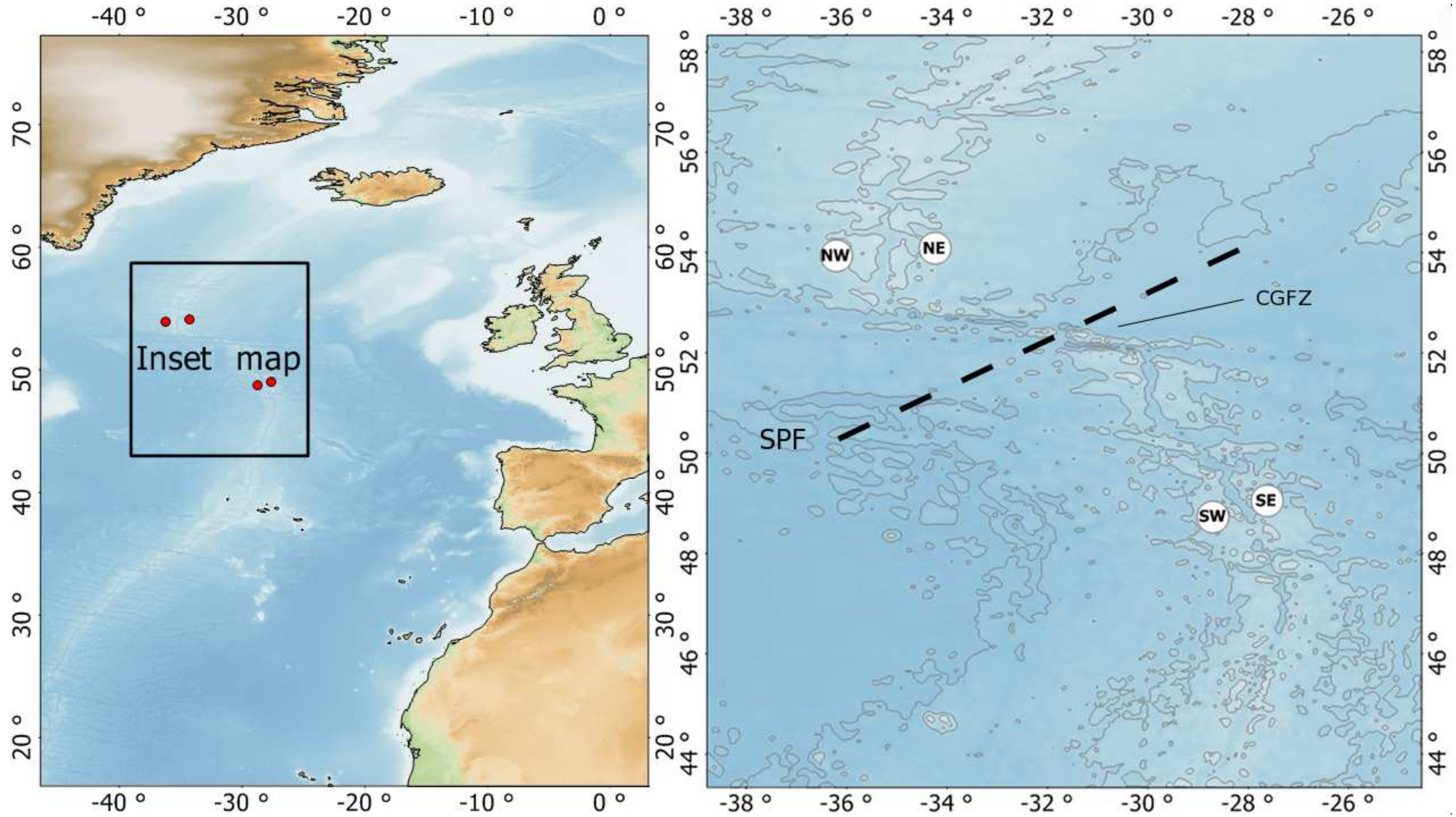

Fig. 6.1 Sampling locations on the Mid-Atlantic-Ridge during the JC011 (2007) and JC037 cruise (2009), the Subpolar Front (SPF) and the Charlie Gibbs Fracture Zone (CGFZ). Only the SW and NE stations were sampled in 2007 (see Table 6.1). Seabed depth at all stations was 2500m. The 500, 1000, 2000, 3000, and 4000m isobaths are shown.

The Charlie-Gibbs Fracture Zone (CGFZ) at the Subpolar Front (SPF, Fig. 6.1) intersects the MAR at 52° N and lies at the junction of three different oceanic provinces (North Atlantic Drift Province, and Atlantic Subarctic, NADR and ARCT see Longhurst, 1998) and between two sectors of different patterns of primary productivity. The Subarctic waters north of the SPF over the Reykjanes ridge are characteristic of high latitude waters and have low temperature (<8 °C), high salinity (>35), and are highly productive during the spring and summer months (80 g C.m^{-2}.month^{-1}; Longhurst, 1998). To the south of the SPF, waters are more typical of temperate latitudes, with a somewhat lower production peak (<50 g C.m^{-2}.month^{-1}; Longhurst, 1998) and sustained production throughout the summer months. These two sectors support different communities of primary consumers (Falkenhaug et al., 2007), but the influences of these production patterns on higher trophic levels residing at greater depths, and the extent to which primary production regimes influence benthopelagic communities is currently unknown.

Fatty Acid (FA) analyses provide qualitative information on the source of primary productivity in the food web and can be used to trace the transfer of energy in the web. Not many species synthesise *de-novo* fatty acids, and Fatty Acid Trophic Markers (FATMs) accumulate in grazers and predators over time. Tracing FATMs is one means of investigating energy transfer and predator-prey relationships. For example, the FATM 20:5 (n-3), 16:1(n-7), and the C16 polyunsaturated fatty acids 9 (PUFA) indicates consumption of diatoms. C18 PUFAs indicates consumption of dinoflagellates, and the FATMs 20:1 (n-9) and 22:1(n-11) indicates consumption of *Calanus* spp copepods (Dalsgaard et al., 2003). The FA composition of the diet is quantitatively assimilated in the tissues of the individual. Their relative ratios provide an indication of long-term trophic exchange and can provide information on ontogenetic and seasonal differences in diet, as well as inter- and intraspecific differences (Kattner et al., 1994) The method is more discriminatory than carbon and nitrogen stable isotope analyses, enabling the identification of the exact source of the lipid, and hence, the prey. $\delta^{15}N$ provides an integrated picture of the average trophic level of diet. Stable nitrogen isotope values compositions in organisms are different to the composition of their diet as consumers show a stepwise enrichment of the heavier isotope ^{13}C and ^{15}N as a result of isotopic fractionation or discrimination during metabolic processes (in contrast to the lighter isotope ^{14}N). This relative increase in nitrogen isotope values, approximately 3-5 ‰ (Hobson et al., 1995; Hobson and Welch, 1992) between the consumer and its energy source is used as a proxy to determine the relative trophic level of a species or individual in its ecosystem (Jardine et al., 2003). Stable carbon isotopes give indications to the source of the primary productivity (pelagic CO_2 sources are depleted in ^{13}C relative to ^{12}C, see France (1995) and Hecky and Hesslein (1995). Both $\delta^{13}C$ and $\delta^{15}N$ ‰ values obtained from particulate organic matter (POM) provide a baseline, which varies geographically (Waser et al., 2000) and is transmitted through the food web. This variation needs to be accounted for when comparing patterns in trophodynamics between regions.

The combination of carbon and nitrogen stable isotope (SI) and FA analysis combined provide powerful tools in determining the major dietary inputs to assimilated tissues, thus providing a time-integrated image of diet assimilation. By contrast, traditional stomach content analysis provides only a short-term image of ingested prey over a limited time period.

The objectives of this study were twofold:

1) To describe vertical patterns of the invertebrate macrozooplanktic (drifters) and micronektic (swimmers) distribution in the epi-and mesopelagic (0-800 m) over the MAR.
2) Using FA and SI analysis, to investigate dietary niches and their variability in trophodynamics with respect to depth and locations, and examine the implications of different primary production on energy transfer to the different zones of the MAR.

6.3 Materials and methods

6.3.1 Field sampling

6.3.1.1 Zooplankton community and Particulate Organic Matter

Invertebrate macrozooplankton (2-20 mm) and micronekton (>20mm) were collected at sea from two stations on either side of the SPF (Fig. 6.1), using a multiple Rectangular Mid-Water trawl (RMT1+8M, Roe and Shale 1979), during NERC (National Environmental Research Council)-funded ECOMAR (Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone) consortium cruises on board the R.R.S *James Cook* cruises to the MAR in 2007 and 2009 (see Fig. 6.1 for survey stations and dates, and Table 6.1 for station activities and depth strata sampled).

Table 6.1 Sampling conducted and environmental variables on either side of the Sub-Polar Front and the CGFZ during the RSS James Cook cruises in 2007 and 2009 (JC011 and JC037), Sampling in 2007 and 2011 was done using a single and multiples RMT1+8 respectively.

Cruise	Date	Station	Latitude	Longitude	Depth sampled and time of day (Night=N, Day=D, Dawn=DW	Temperature (°C average over top 200 m)	Chl.a max (mg. m^{-3})
James Cook 011	13/07/2007-18/08/2007	SWJC011	48.9	-28.45	50-300(N), 400-500(N)	13.82	0.46
		NEJC011	54.09	-34.13	100-150(D), 400-500(N), 300-400(N), 0-100(N), 450-550(D), 0-200(N)	8.19	0.64
James Cook 037	1/08/2009-09/09/2009	23SEJC037	49.05	-27.63	0-200*(D), 200-500(D), 500-800(D),	12.94	1.09
		39SWJC037	48.73	-28.7	0-200(N), 200-500(N), 500-800(N)	14.33	0.51
		40SWJC037	48.73	-28.7	0-200(D), 200-500(D), 500-800(D)	14.33	0.51
		47SWJC037	48.73	-28.7	200-500(N), 500-800(N), 800-1000(N)**	14.33	0.51
		64NWJC037	53.93	-36.21	200-500(D), 500-550(D), 550-700(D)	8.27	0.74
		89NEJC037	54.08	-34.25	0-200(D), 200-500(D), 500-800(D)	8.54	0.88
		90NEJC037	54.08	-34.25	0-200(D), 200-350(D), 350-500(D)	8.54	0.88

* Net lined with salp and catch deemed non-quantitative

** included in the 500-800 m depth stratum for the purpose of calculating densities

Only the catches from the RMT8 net were considered in this study (4.5 mm mesh size). For the estimation of faunal abundance, the bulk of the material was sorted to genera or species at sea, and preserved in borax-buffered 4% formaldehyde (Steedman, 1976). Upon return to the laboratory, samples were transferred to 70% ethanol for preservation and further taxonomic analysis. Dominant zooplankton taxa were identified to the lowest taxonomic category using morphology based taxonomical guides and keys, and numerical abundance was recorded. The ten most abundant zooplankton taxa in an individual net were targeted for food web analysis (See Table 6.2 for taxa retained and preserved for subsequent analysis here).

In order to explore general vertical patterns in zooplankton density over the MAR, densities from all stations were averaged. Vertical density Catch per Unit Effort (CPUE) was expressed as ind. m^{-3}. For comparison between the two theoretically distinct regions, areal density was recorded as CPUE = ind.10^{-3}.m^{-2} and was integrated over the water column (800 m), with the two northern, and the two southern stations being respectively combined.

Samples for fatty acid analysis were flash-frozen as soon as possible in liquid nitrogen and transferred to -80 °C in glass vials for long-term storage. Samples for SI analysis were preserved in glass vials, frozen at -80 °C, then transferred to -20°C for long-term storage. The number of individuals preserved per net varied between taxa, but for the smaller taxa (<4 mm, Euchaetidea, *D. trispinoza* and *C. pyramidata*), >10 were preserved and for the bigger species (>4mm, euphausiids, decapoda, amphipoda) four, in order to collect at least 1 g of dry material (see Table 6.2 for total individuals analysed across stations and number of pools).

For $\delta^{13}C$ and $\delta^{15}N$ SI analysis, all species were processed whole, with the exception of decapods (excluding the genus *Gennadas*) and pteropods, which were de-shelled. For FA analysis, all species were processed whole. Baseline variability in $\delta^{13}C$ and in $\delta^{15}N$ values was determined by examining seawater particulate organic matter (POM). The POM samples were collected by filtering seawater (collected using Niskin bottles) on ashed GF/F Whatman filters (25 mm). Seawater (1L) was initially sieved through a 125 μm sieve to remove zooplankton prior to filtration. After filtration samples were folded in half and preserved on hexane-wiped aluminium foil. Next, POM samples were flash-frozen in liquid nitrogen and preserved at -80 °C. Replicates were kept from all surface stations (n=4 for SE and n=6 for NW, NE, SE of the CGFZ/MAR intersect). In addition, the SE station was sampled opportunistically at depth through the productive/mixed layer (n=6 at 15 m and 30 m, and n=4 at 45 m) to explore vertical variability in POM isotope values.

6.3.1.2 Environmental variables

Fluorometrically derived chlorophyll-a concentrations and sea surface temperatures were collected at all stations from optical casts using a Seabird 19 Conductivitity-Temperature-Density (CTD) Profiler.

6.3.2 Lipid Analysis

Whole individual macrozooplankton and micronekton (see Table 6.2 for species and total number of individuals processed) were freeze-dried and weighed at the British Antarctic Survey, then transferred to chloroform-methanol (2:1 vol/vol) solution. Individuals were pooled for analysis (see Table 6.2 for number per pools and number of pools). Samples were homogenized and filtered on a Whatman No. 1 paper filter. Total lipids were extracted and dry weights recorded following the method of Folch et al., (1957). Lipids were then trans-esterified in methanol containing 1% sulphuric acid at 50°C for 16 hours, generating fatty acid methyl esters (FAME, see Christie, 1982). FAMEs were purified by thin layer chromatography in a hexane/diethyl-ether/acetic acid (90:10:1, vol/vol/vol) solvent. FAMEs were subsequently dissolved in hexane to a concentration of 1μm/μg. Samples were analyzed in a trace gas chromatograph (GC) using hydrogen as the carrier gas. A standard of known composition was used as a reference to identify FAMEs.

6.3.3 Stable isotope analysis

Carbon and Nitrogen stable isotope ratios were measured at the NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre (SUERC), at East Kilbride, UK (n=428). Samples were freeze-dried for 24 hours and homogenized using a ball mill.

Subsamples of 800 μg to 1200 μg ground material were transferred to tin capsules and analysed by a Costech ECS4010 elemental analyser coupled to a Thermo Finnigan DELTA plus XP mass spectrometer for $\delta^{13}C$ and $\delta^{15}N$. POM residue extracted from filters and placed into silver capsules. Two internal laboratory standards were run every 10 samples to enable corrections of possible instrumental drift. Measurement precision was estimated (n=18; 0.07 for $\delta^{13}C$; 0.17 for $\delta^{15}N$) using the fish *Antimora rostrata* as the internal standard.

Replicates of zooplanktic samples across taxa (n=39) and all POM material (n=34) were acid treated in order to detect potential bias from inorganic carbonates, following a protocol modified from Harris et al., (2001): 2 M HCL were added to the samples in silver capsules and left to incubate at 60 ºC for 12 hours. Zooplankton samples did not bubble after acidification, and no significant difference in $\delta^{13}C$ was detected after acidification (one tailed student t-test p=0.34). Thus, the use of non-acidified samples was deemed appropriate for sensible interpretation of trophic relationships. POM samples did, upon acidification, release bubbles, and as such were likely to contain inorganic carbonates. POM δ^{13}C values presented here are derived from the acidified replicates.

Carbon and nitrogen isotope ratios were compared to a known reference and expressed in parts per thousand (‰) as δX (X being either ^{13}C, or ^{15}N), the difference in the ratio of the heavier to the lighter isotope in the sample compared to the same ratio in the given standard (Vienna Peedee Belemnite for carbon or atmospheric AIR for nitrogen) see equation [6.1]).

Equation [6.1]: $\delta X = [(R_{sample}/R_{standard})-1] \times 10^3$

Samples were not lipid extracted prior to isotopic analysis. Regression of δ^{13}C versus C:N molar ratio detected a significant but weak relationship (least-square regression, $R^2 = 0.35$ $p<0.001$), and as a consequence no lipid correction transformation was applied to the raw δ^{13}C values, using empirical lipid normalization models (Smyntek et al., 2007).

6.3.4 Data analysis

δ^{13}C, δ^{15}N and FA composition data were tested for normality using the Shapiro-Wilk test. Normal and non-normal data were tested for homogeneity of variance using the Levene's test, which is considered less sensitive to departure for normality than Cochran's test. Analysis of variance (ANOVA) was carried out to investigate intraspecific and interspecific carbon and nitrogen isotopic differences and FA composition between taxa. One-way ANOVAs were conducted $\delta^{13}C$, $\delta^{15}N$ and FA composition data with equal variance and was followed by Tukey's Honesty Significant Difference test (HSD) for pairwise comparisons, using R project (R v2.9.1 Development Core Team, 2007).

Draftmans' plots of zooplankton FA composition were visually inspected and Principal component analysis (PCA) was conducted on log transformed Fatty acid compositions (%) using PRIMER (Plymouth Routines in Multivariate Ecological Research) Version 6 (Clarke and Gorley, 2006) to explore interspecific patterns in FA variability.

In order to detect patterns in energy pathways and variability in energy sources, Pearson's correlations analysis was utilized to detect association between $\delta^{13}C$ and $\delta^{15}N$ variability in each survey sector. To explore relationships between average sizes, lipid content and trophic position, Pearson's correlations analyses were utilized to detect association between $\delta^{15}N$ and $\log_{10}$ mean dry weight or $\log_{10}$ lipid levels per zooplankton and micronekton species.

6.4 Results

6.4.1 Environmental variables

Environmental conditions varied considerably between years and stations. Maximum chlorophyll-a values ranged between 0.46 (SW, 2007, see Table 6.1) and 1.09 mg m^{-3} (SE, 2011) and temperature (average to 200 m) between 8.19 (NW 2011) and 14.33 °C (SW, 2011). In 2007, the southern stations had greater amounts of detrital material than phytoplankton, and lower levels of Chl-a values (Tilstone, personal communication). The same pattern was not observed in 2009.

6.4.2 Faunal composition of study area

Two vertical patterns of faunal abundance were detected. Most taxa decreased in abundance with depth, such as *Meganyctiphanes norvegica*, *Nematoscelis megalops*, *Themisto compressa, Carinaria lamarcki,* Euchaetida*,* and *Clio pyramidata* (Fig. 6.2). Abundances of *Gnathophausia zoea, Acanthephyra pelagica, Parapasiphae sulcatifrons, Gennadas elegans,* and *Sergia japonica* (Decapoda) however, increased with depth. Amongst these, *G. zoea* was the most abundant. No clear vertical patterns were detected for *Nematobrachion boopis*, *Clione limacina, Stylocheiron maximum, Euphausia krohni, Diacra spinosa, Sergestes arcticus, Thysanopoda acutifrons,* or *Sagitta* sp.

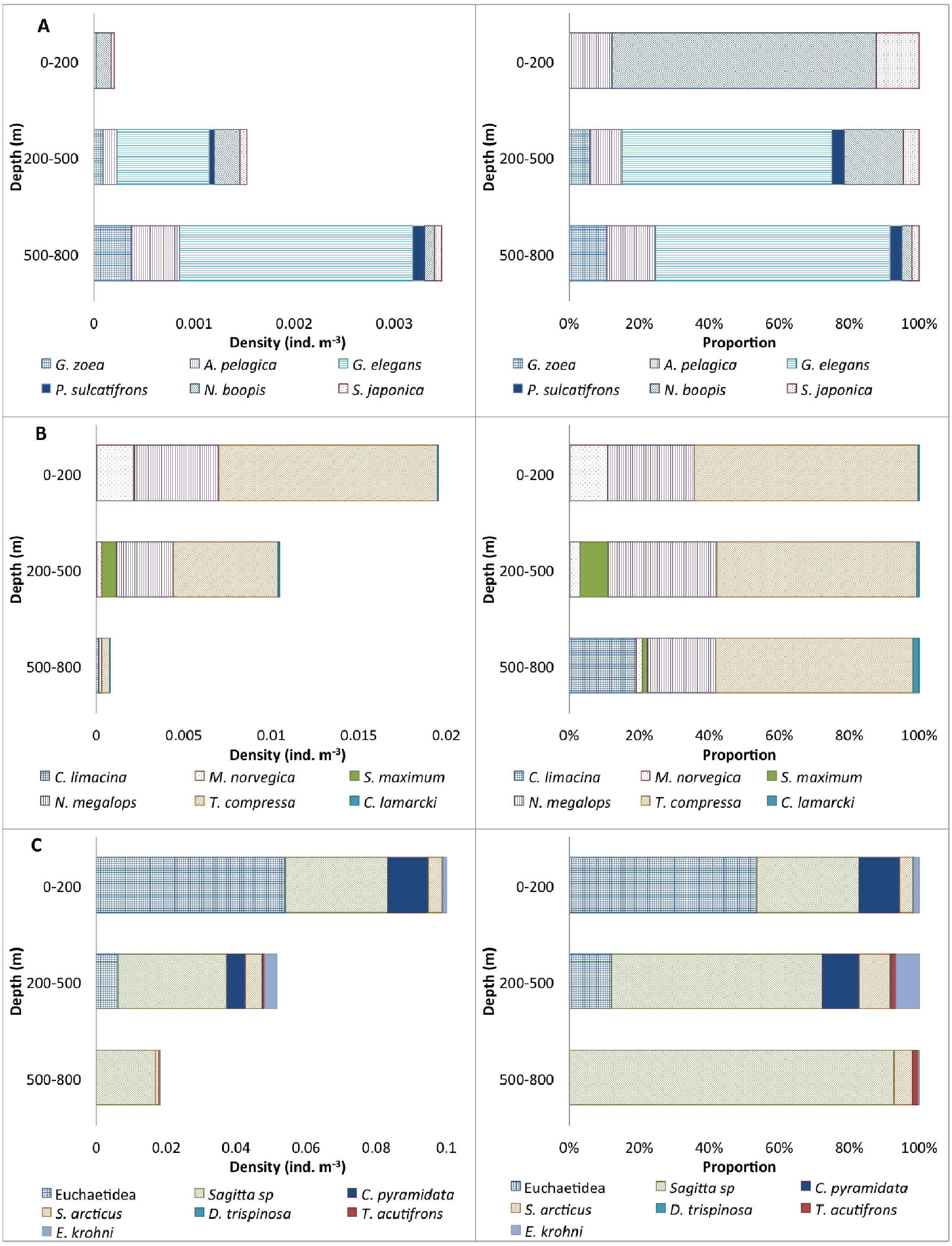

Fig. 6.2 Mean vertical distribution of target species (ind. m^{-3}) for all stations combined (north and south). Figures on left side show abundance, and right side shows proportion of species. Plot row A reflects bathypelagic species (increase abundance with depth) and row B and C epi- and mesopelagic species (decrease abundance with depth, or no clear pattern). The scale of abundance axis varies between plots, reflecting difference density in groups of species.

Individuals of the species *S. japonica, A. pelagica,* and *G. elegans* were more abundant in the southern than in the northern stations (Fig. 6.3). Amongst the decapods species, the most abundant was *S. arcticus* (610-4850 ind.$10^{-3}m^{-2}$). The hyperiid amphipod *T. compressa* was highly abundant at all stations (300-8600 ind.10^{-3} m^{-2}) particularly in the north. The species *E. krohni* was the most abundant euphausiid across all stations (280-2320 ind.$10^{-3}m^{-2}$). The pteropod *C. pyramidata* was the most abundant pteropod, with densities spanning three orders of magnitude between the two stations (2-6000 ind.10^{-3} m^{-2} in the northern and the southern stations respectively). *D. trispinosa* was found uniquely in the southern stations (150 ind.$10^{-3}m^{-2}$). *C. limacina* was found uniquely in the north (120 ind.$10^{-3}m^{-2}$). *Sagitta* sp was the most abundant taxon present overall (11000-30100 ind.$10^{-3}m^{-2}$) and was most abundant in the north.

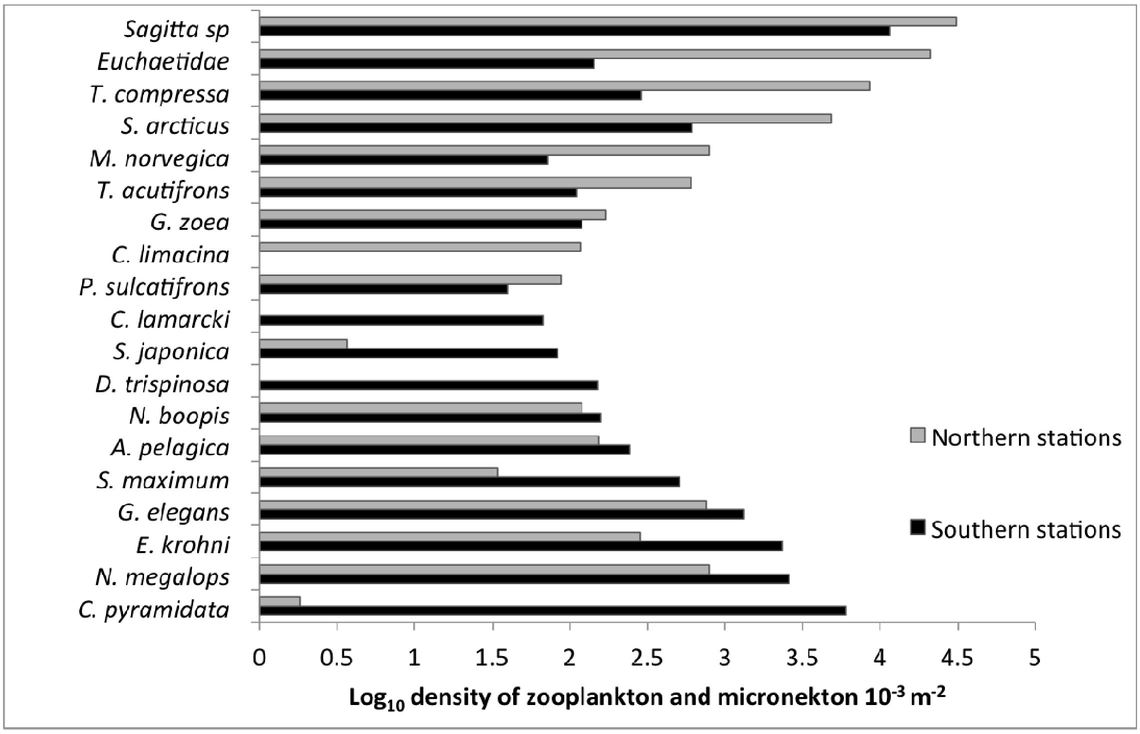

Fig. 6.3 Average target species density ($\log_{10}$ abundance. ind. 10^{-3} m^{-2}), pooled between all northern, and all southern stations respectively, integrated over the sampled water column (800 m). Taxa are listed vertically according to the location where they are most abundan i.e. *Parapasiphae sulcatifrons* and taxa ranked above were most abundant in the northern sector.

6.4.3 Lipid levels, dry weights, and fatty acids

6.4.3.1 Dry weight and lipid levels

Individual dry weight values spanned three orders of magnitude (0.003-0.26 g, Table 6.3). The deep-sea shrimps *S. japonica* and *A. pelagica* had the greatest individual mass (average dry weights 0.26±0.07 and 0.24±0.03 g respectively, Table 6.2) and heavier animals were generally found to increase in abundance with depth. The amphipod *T. compressa* and the euchaetids had the smallest dry weights (0.003±0.001 and 0.003±0.00 g respectively). The taxa *G. elegans,* Euchaetidea, *M. norvegica* and *P. sulcatifrons* were the most lipid rich (~ 26, 22, 22 and 21 % of DW respectively) and *E. krohni* was the most lipid poor (8 % of DW, Table 6.2).

6.4.3.2 Fatty Acids

32 Fatty acids were identified (Table 6.2) with both intra and interspecific variability in FA being apparent (Fig. 6.4 and Fig 6.5). Lipid composition across all species was dominated by the fatty acids 14:0, 16:0, 16:1(n-7), 18:1(n-9), 20:5(n-3), 22:6(n-3), 18:0. Mono-unsaturated fatty acids (MUFAs) usually were present in higher concentrations than poly-unsaturated fatty acids (PUFAs). The major FATM component was 18:1(n-9) (with the exception of the euphausiids *M. norvegica, E. krohni* and *N. megalops* which had greater concentrations of 16:0).

Principal component analysis suggested separation in the FA signature of several zooplankton species, although overlap did occur in many cases (Fig. 6.4A). PC 1 and 2 accounted for 57.3 and 22.4 % of the total variation respectively (total of 79.7%). Differences in FA composition were predominantly attributed to differences in relative concentrations of the MUFAs 18:1(n-9)(eigenvectors 0.656 and 0.663 for PC1 and 2 respectively) 20:1(n-9) (eigenvectors 0.207 and -0.503 for PC1 and 2), 16:0 (-0.325 and 0.131 for PC1 and 2), 20:5(n-3) (eigenvectors -0.241 and 0.056 for PC1 and 2), and the PUFAs 22:6(n-3) (eigenvectors -0.538 and 0.333 for PC1 and 2).

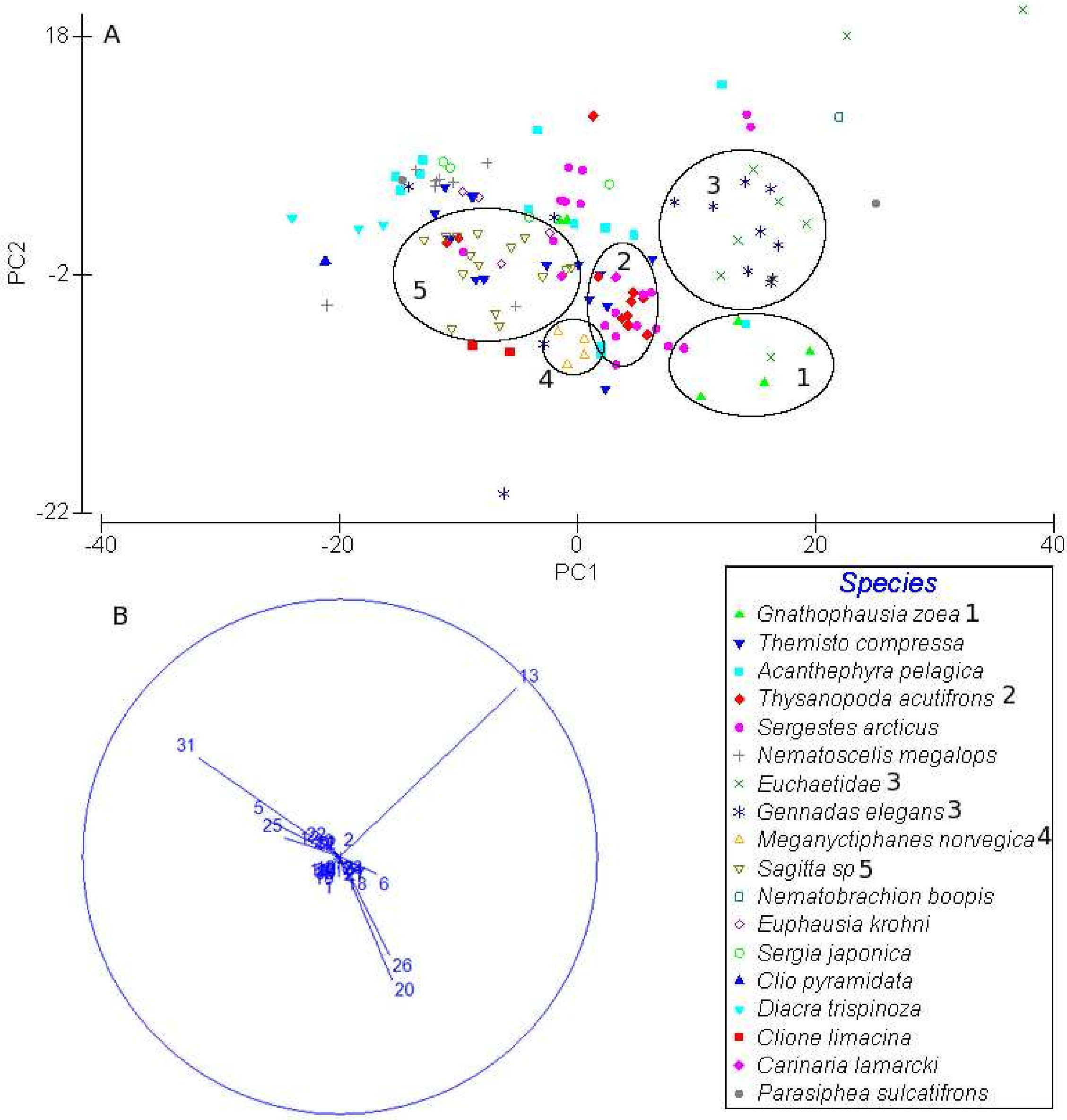

Fig. 6.4 Principal component analysis of Fatty Acid composition for all species (A) and key fatty acid scores (vector length proportional to fatty acid vector, see table 6.2 for numerical code interpretation B). PC 1 and 2 accounted for 57.3 and 22.4 % of the total variation respectively. Analysis is based on 132 zooplankton samples (see Table 6.2 for numbers of individual in each pool).

FA analysis of Euchaetidea revealed large concentrations of 18:1(n-9) and low concentrations of 22:6(n-3) (Table 6.2). FAs from individual *G. zoea* had high concentrations of the MUFAs 22:1(n-11) and 20:1(n-9) (11.5±2.0% and 13±2.8% respectively). *Sagitta* sp. and the euphausiid *M norvegica* were characterised by relatively low concentrations of the MUFA 18:1(n-9) (<15%). 18:1(n-9) levels were high (> 18%) in all bathypelagic species: ie *G. zoea, A. pelagica, P. sulcatifrons, G. elegans,* and *S. japonica.*

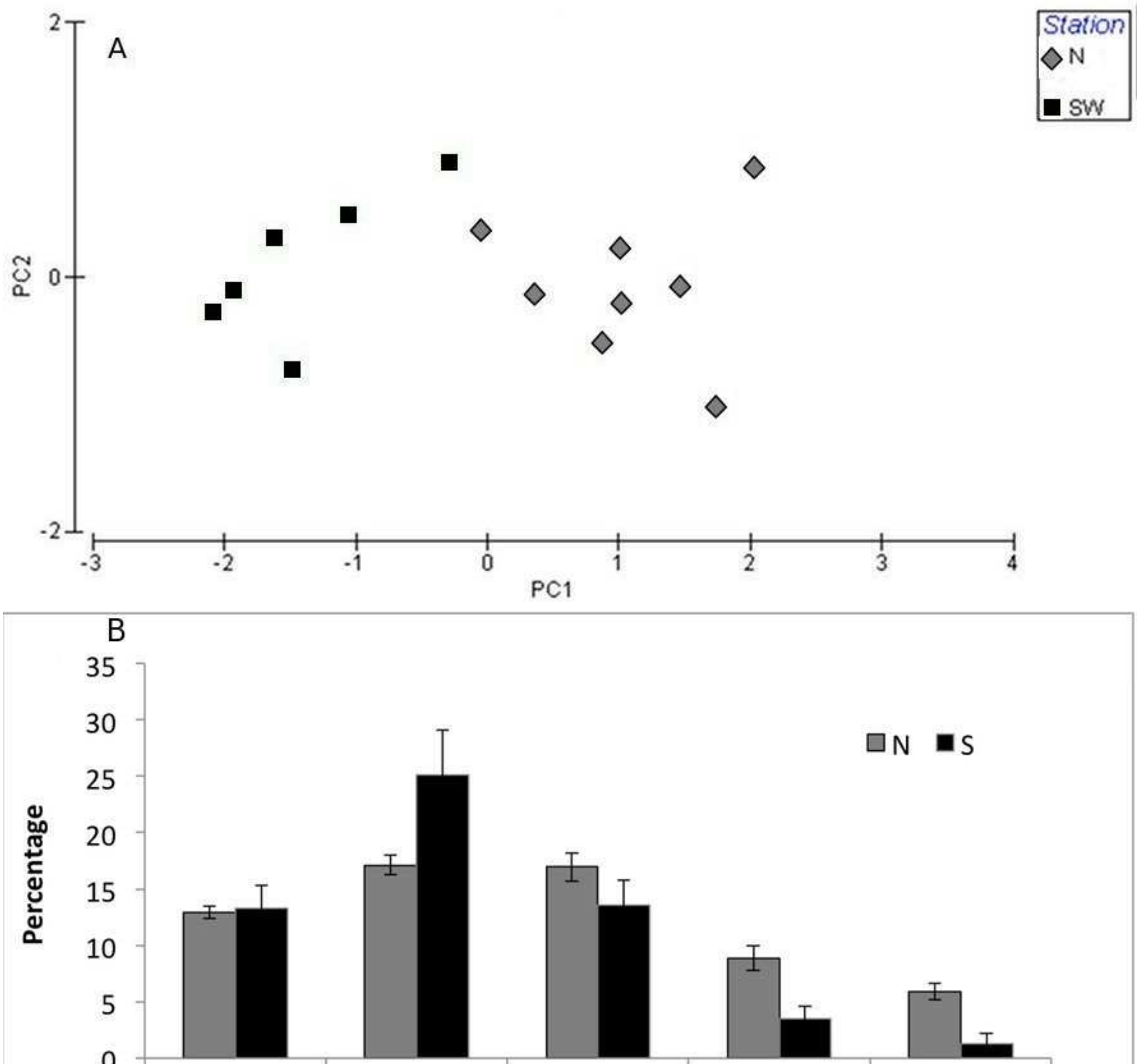

Fig. 6.5 Principal Component Analysis of Fatty Acid composition of *Themisto compressa* across stations (A) and average proportion of FATM from the northern and southern sectors (B). Highest eigenvector coefficients were 22:1(n-11)(-0.593), 20:1(n-9)(-0.473) and 22:6(n-3)(0.331).

The main differences between the northern and southern stations were attributed to concentrations of the MUFAs 20:1(n-9) and 22:1(n-11), and the C_{22} PUFA 22:6(n-3) (see Fig. 6.5A and B for *T. compressa*). In cosmopolitan species, concentrations of 20:1(n-9) and 22:1(n-11) were significantly higher in individuals caught at the northern stations (ANOVA, $F_{10,22}$=4.41 p<0.000, and $F_{10,22}$=3.66, p<0.000 respectively) and the concentration of PUFA 22:6(n-3) was higher in the southern sectors ($F_{10,22}$=2.3, p=0.016).

Table 6.2 Target taxa for lipid analysis, lipid concentration (%) and Fatty Acid composition of macrozooplankton, species and number of individual analysed for SI.and FA. The first column indicates the numerical code of each fatty acid (see Fig. 6.4)

		Gnathophausia zoea	*Acanthephyra pelagica*	*Sergia japonica*	*Parapasiphae sulcatifrons*	*Sergestes arcticus*	*Gennadas elegans*	*Themisto compressa*	*Nematoscelis megalops*	*Meganyctiphanes norvegica*
	Authorities, and common name	Willemoes-Suhm, 1873 Lophogastrid	Risso, 1816 Decapod shrimp	Bate, 1881 Euphausiid	Smith, 1884 Decapod shrimp	Kroyer, 1855 Decapod shrimp	Smith, 1882 Decapod shrimp	Goës, 1866 Hyperiid amphipod	G.O. Sars, 1883 Euphausiid	M. Sars, 1857 Euphausiid
	Number analysed for FA and number of pools in bracket	6(6)	13(13)	4(4)	4(2)	50(19)	54(13)	72(14)	30(8)	8(4)
	Number analysed for SI Acidified replicates in brackets	15	30(3)	12(3)	4(1)	20(3)	18	53(3)	42(1)	12(3)
	Dry weight(g)	0.09±0.02	0.24±0.03	0.26±0.07	0.18±0.001	0.08±0.007	0.06±0.009	0.003±0.0	0.05±0.03	0.13±0.04
	Lipid %	12.6±3.5	9.2±1.3	NA	20.8±0.7	17.7±6.8	26.1±4.1	10.6±0.7	9.1±0.8	22.1±1.6
1	14:0	1.3±0.2	1.9±0.3	1.3±0.3	1.0±0.1	2.6±0.2	2.1±0.2	3.2±0.3	2.3±0.4	5.2±0.6
2	I IS:0	0.2±0.1	0.7±0.6	0.1±0.0	0.1±0.1	0.2±0.0	0.1±0.0	0.3±0.0	0.2±0.0	0.3±0.0
3	a IS:0	0.1±0.0	0.1±0.0	0.1±0.0	0.0±0.0	0.2±0.0	0.1±0.0	0.2±0.0	0.1±0.0	0.1±0.0
4	15:0	0.3±0.1	0.4±0.1	0.4±0.1	0.3±0.1	0.5±0.1	0.4±0.0	0.8±0.1	0.6±0.0	0.7±0.0
5	16:0	9.2±1.0	15.2±1	14.5±1.4	11.6±4.9	9.9±0.7	11.2±0.6	13.8±0.9	18.5±1	16.5±0.6
6	16:1(n-7)	6.3±1.0	3.5±0.5	5.3±1.3	5.6±3.9	6.6±0.3	5±0.5	4.0±0.3	2.7±0.2	4.0±0.4
7	16:1(n-5)	0.2±0.0	0.2±0.1	0.3±0.1	0.4±0.4	0.4±0.1	0.2±0.0	0.3±0.0	0.2±0.0	0.4±0.0
8	16:2(n-4)	0.5±0.0	0.4±0.1	0.5±0.0	0.6±0.1	0.6±0.0	0.7±0.1	0.7±0.0	0.4±0.0	0.6±0.1
9	17:0	0.2±0.0	0.3±0.1	0.7±0.1	0.0±0.0	0.4±0.1	0.4±0.1	1.0±0.2	0.8±0.1	0.3±0.0
10	16:3(n-4)	0.7±0.1	0.6±0.1	0.7±0.1	0.3±0.3	0.7±0.1	0.7±0.0	0.6±0.1	0.9±0.2	0.5±0.0
11	16:4(n-1)	0.2±0.1	0.1±0.0	0.1±0.1	0.2±0.2	0.0±0.0	0.0±0.0	0.3±0.1	0.1±0.0	0.1±0.1
12	18:0	1.4±0.2	2.4±0.2	3.1±0.5	1.9±1.3	1.7±0.1	2.4±0.4	2.4±0.2	1.7±0.3	2.1±0.1
13	18:1(n-9)	22.4±1.4	19.4±1.8	18.7±1.8	25.8±12.6	20.3±1.4	24±2.8	15.5±0.9	15.1±0.6	13.2±0.4
14	18:1(n-7)	2.0±0.1	5.2±0.5	2.6±0.2	6±0.0	4.1±0.3	4.1±0.5	1.8±0.1	3.0±0.3	5.4±0.2
15	18:1(n-5)	0.5±0.0	0.4±0.1	0.4±0.0	0.4±0.0	0.4±0.0	0.4±0.1	0.4±0.1	0.2±0.1	0.4±0.0
16	18:2(n-6)	1.2±0.1	1.0±0.1	1.2±0.1	0.9±0.3	1.9±0.1	1.2±0.1	1.9±0.1	2.0±0.2	1.5±0.1
17	18:3(n-3)	0.5±0.1	0.4±0.1	0.5±0.1	0.3±0.1	1.0±0.1	0.5±0.0	0.9±0.1	1.1±0.1	0.8±0.1
18	18:4(n-3)	0.9±0.2	0.5±0.2	0.4±0.2	0.1±0.1	2.6±0.3	1.1±0.1	2.3±0.2	1.0±0.2	1.8±0.1
19	20:0	0.4±0.2	0.1±0.0	0.2±0.0	0.0±0.0	0.1±0.0	0.1±0.0	0.2±0.0	0.1±0.0	0.2±0.0

		Gnathophausia zoea	*Acanthephyra pelagica*	*Sergia japonica*	*Parapasiphae sulcatifrons*	*Sergestes arcticus*	*Gennadas elegans*	*Themisto compressa*	*Nematoscelis megalops*	*Meganyctiphanes norvegica*
20	20:1(n-9)	13±2.8	5.6±1.2	4.4±1	6.9±4.5	7.7±0.9	10.2±1.1	6.6±1.0	2.6±0.7	9.6±0.5
21	20:1(n-7)	0.8±0.3	0.4±0.1	0.2±0.1	0.1±0.1	0.4±0.1	1.4±0.2	0.4±0.0	0.0±0.0	0.1±0.0
22	20:4(n-6)	1.0±0.3	1.3±0.1	1.6±0.2	1.0±0.5	1.3±0.1	1.1±0.1	1.9±0.2	2.4±0.3	0.7±0.0
23	20:3(n-3)	0.2±0.1	0.2±0.0	0.3±0.0	0.2±0.0	0.2±0.0	0.4±0.1	0.2±0.0	0.1±0.0	0.4±0.0
24	20:4(n-3)	0.4±0.0	0.5±0.1	0.6±0.1	0.4±0.0	1.0±0.1	0.8±0.1	0.8±0.0	0.6±0.1	0.7±0.0
25	20:5(n-3)	8.2±2.2	12.9±1.2	10.6±0.6	11.5±6.3	12.1±0.3	9.1±1.1	13.1±0.3	14.4±0.8	9.9±0.4
26	22:1(n-11)	11.5±2.0	4.0±1.2	2.2±0.8	3.6±3.0	4.8±0.6	4.9±0.8	3.9±0.8	1.4±0.8	8.2±0.7
27	22:1(n-9)	1.0±0.2	0.6±0.2	0.6±0.1	1.0±0.7	0.5±0.0	1.0±0.1	0.8±0.1	0.3±0.1	1.2±0.1
28	22:1(n-7)	0.1±0.0	0.1±0.0	0.1±0	0.3±0.1	0.0±0.0	0.2±0.0	0.1±0.0	0.0±0.0	0.1±0.0
29	22:5(n-6)	0.0±0.0	0.2±0.1	0.6±0.1	0.2±0.2	0.4±0.1	0.5±0.1	0.6±0.1	0.6±0.0	0.3±0.0
30	22:5(n-3)	0.6±0.2	0.6±0.0	0.6±0.0	0.4±0.1	0.6±0.0	1.7±0.9	0.6±0.0	0.5±0.0	0.8±0.0
31	22:6(n-3)	14.7±2.5	20.8±1.9	27.3±2.2	18.9±11.6	16.7±0.9	14.1±1.6	20.6±1.2	25.8±1.0	13.5±0.6
32	24:1(n-9)	0.0±0.0	0.1±0.0	0.2±0.1	0.1±0.1	0.1±0.0	0.1±0.0	0.0±0.0	0.2±0.0	0.0±0.0

Values are mean ±SE.

Table 6.2 cont.

		Nematobrachion boopis	*Stylocheiron maximum*	*Euphausia krohni*	*Thysanopoda acutifrons*	*Sagitta* sp.	Euchaetidae
	Authorities, and common name	Calman, 1896 Euphausiid	G. O. Sars, 1883 Euphausiid	(Brandt, 1851) Euphausiid	Holt and Tattersall, 1905. Euphausiid	Quoy and Gaimard, 1827 Arrow worm	Giesbrecht, 1893 Copepod
	Number analysed for FA and number of pools in bracket	2(2)	NA	19(4)	20(11)	48(16)	42(8)
	Number analysed for SI Acidified replicates in brackets	4	4(2)	16(2)	33(3)	74(4)	82(6)
	Dry weight(g)	0.03	NA	0.01±0.005	0.1±0.008	0.02±0.003	0.003±0.001
	Lipid %	1.0	NA	7.9±1.0	12.9±1.0	8±0.7	22.3±2.7
1	14:0	0.0	NA	3.4±0.4	3.6±0.5	1.3±0.2	1.4±0.3
2	I IS:0	0.0	NA	0.3±0.0	0.4±0.1	0.1±0.0	0.1±0.0
3	a IS:0	0.1	NA	0.2±0.0	0.3±0.1	0.1±0.0	0.1±0.0
4	15:0	5.7	NA	0.7±0.0	0.5±0.1	0.3±0.0	0.1±0.0
5	16:0	9.7	NA	16.9±1.0	11.8±1	11.2±0.5	3.7±0.6
6	16:1(n-7)	0.0	NA	3.3±0.3	6.6±0.6	7.8±0.6	10.8±0.4
7	16:1(n-5)	0.9	NA	0.3±0.0	0.4±0.1	0.3±0.0	0.4±0.1
8	16:2(n-4)	0.1	NA	0.6±0.1	0.8±0.1	0.8±0.0	1.1±0.2
9	17:0	1.0	NA	0.9±0.1	0.3±0.1	0.5±0.0	0.1±0.0
10	16:3(n-4)	0.0	NA	0.8±0.0	0.7±0.1	0.7±0.1	0.9±0.0
11	16:4(n-1)	0.5	NA	0.1±0.1	0.0±0.0	0.1±0.0	0.1±0.1
12	18:0	41.1	NA	2.3±0.2	1.1±01	2.9±0.2	0.8±0.1
13	18:1(n-9)	3.2	NA	15.7±0.9	18±1.1	15.3±1.8	34.8±3.9
14	18:1(n-7)	0.0	NA	3.7±0.1	3.7±0.1	3.3±0.2	1.7±0.3
15	18:1(n-5)	1.7	NA	0.2±0.1	0.4±0.0	1.5±0.2	0.2±0.1
16	18:2(n-6)	1.2	NA	1.9±0.1	2.0±0.1	1.5±0.1	1.5±0.2
17	18:3(n-3)	1.2	NA	0.9±0.0	1.3±0.1	0.7±0.1	1.0±0.2
18	18:4(n-3)	0.0	NA	1.0±0.2	2.6±0.4	0.6±0.1	2.7±0.7
19	20:0	7.1	NA	0.1±0.0	0.0±0.0	0.1±0.1	0.0±0.0
20	20:1(n-9)	0.0	NA	2.7±0.7	8.0±0.7	8.0±0.7	6.7±1.5

		Nematobrachion boopis	*Stylocheiron maximum*	*Euphausia krohni*	*Thysanopoda acutifrons*	*Sagitta* sp.	Euchaetidae
21	20:1(n-7)	0.5	NA	0.2±0.1	0.1±0.1	0.5±0.1	0.4±0.2
22	20:4(n-6)	0.0	NA	2.7±0.3	1.0±0.1	0.9±0.0	0.4±0.1
23	20:3(n-3)	0.0	NA	0.3±0.0	0.2±0.1	0.1±0.0	0.0±0.0
24	20:4(n-3)	8.1	NA	1.0±0.0	0.7±0.0	0.5±0.0	0.6±0.1
25	20:5(n-3)	3.7	NA	15.7±0.5	10.2±0.5	11.1±0.7	8.6±0.9
26	22:1(n-11)	0.0	NA	2.3±0.1	5.8±0.7	4.2±0.5	7.7±1.6
27	22:1(n-9)	0.0	NA	0.2±0.1	0.4±0.1	0.8±0.1	0.6±0.2
28	22:1(n-7)	0.0	NA	0.0±0.0	0.0±0.0	0.2±0.0	0.0±0.0
29	22:5(n-6)	0.0	NA	0.5±0.1	0.3±0.1	0.3±0.0	0.1±0.1
30	22:5(n-3)	13.2	NA	0.6±0.0	0.6±0.0	0.6±0.0	0.5±0.0
31	22:6(n-3)	0.0	NA	20.7±1.1	18.1±1.6	23.7±1.6	12.9±1.1
32	24:1(n-9)	1.0	NA	0.1±0.0	0.0±0.0	0.1±0.0	0.0±0.0

Table 6.2 cont

		Clio pyramidata	*Carinaria lamarcki*	*Diacra trispinosa*	*Clione limacina*
	Authorities, and common name	Lesueur, 1813 Pteropod	Péron and Lesueur, 1810 Heteropod	Lesueur, 1821 Pteropod	Phipps, 1774 Pteropod
	Number analysed for FA and number of pools in bracket	20(2)	2(2)	13(3)	6(2)
	Number analysed for SI Acidified replicates in brackets	18	5(2)	12	4(1)
	Dryweight(g)	0.015±0.002	0.06±0.01	0.017±0.006	0.009±0.0006
	Lipid %	4.7±0.2	3.7±0.5	3.4±0.4	NA
1	14:0	4.8±0.1	2.7±0.1	2.9±0.1	1.9±0.0
2	I IS:0	0.4±0.0	0.1±0.0	0.5±0.0	0.1±0.0
3	a IS:0	0.3±0.0	0.1±0.0	0.3±0.0	0.1±0.1
4	15:0	1.8±0.1	0.3±0.3	0.8±0.1	7.8±0.4
5	16:0	13.3±0.1	13.0±0.1	14.0±0.7	10.9±1.1
6	16:1(n-7)	2.4±0.0	3.8±0.2	2.6±0.3	10.9±
7	16:1(n-5)	0.5±0.1	0.4±0.1	0.4±0.1	0.4±0.1

		Clio pyramidata	*Carinaria lamarcki*	*Diacra trispinosa*	*Clione limacina*
8	16:2(n-4)	0.6±0.0	0.8±0.0	0.5±0.1	0.2±0.2
9	17:0	1.5±0.0	1.1±0.2	1.1±0.1	3.6±0.5
10	16:3(n-4)	0.3±0.0	0.7±0.0	0.7±0.3	16.1±0.2
11	16:4(n-1)	1.0±0.0	0.0±0.0	0.6±0.3	0.0±0.0
12	18:0	4.7±0.1	5.0±1.1	4.0±1.2	1.6±0.3
13	18:1(n-9)	3.1±0.1	17.9±1.7	6.7±1.5	5.5±0.9
14	18:1(n-7)	1.1±0.0	2.7±0.0	2.4±0.9	4.5±0.1
15	18:1(n-5)	0.2±0.0	0.5±0.0	0.6±0.3	0.7±0.1
16	18:2(n-6)	1.2±0.0	2.0±0.1	1.2±0.2	0.4±0.4
17	18:3(n-3)	0.9±0.0	0.7±0.0	0.9±0.2	1.0±0.1
18	18:4(n-3)	2.7±0.4	0.9±0.1	1.9±0.7	1.0±0.1
19	20:0	0.3±0.0	0.1±0.0	0.2±0.2	0.2±0.1
20	20:1(n-9)	2.1±0.2	8.4±1.4	2.5±1	3.3±0.5
21	20:1(n-7)	1.5±0.0	1.3±0.1	1.8±0.2	1.2±0.1
22	20:4(n-6)	1.9±0.0	1.6±0.2	2.2±0.3	0.7±0.1
23	20:3(n-3)	1.9±0.0	0.5±0.1	0.3±0.1	0.5±0.0
24	20:4(n-3)	0.8±0.1	0.6±0.0	1.2±0.4	0.5±0.0
25	20:5(n-3)	15.8±0.3	10.8±1.0	10.3±0.6	9.0±0.8
26	22:1(n-11)	0.2±0.0	4.7±0.0	1.0±0.5	0.9±0.6
27	22:1(n-9)	0.3±0.0	0.8±0.0	0.2±0.1	0.2±0.1
28	22:1(n-7)	0.0±0.0	0.1±0.0	0.0±0.1	0.1±0.0
29	22:5(n-6)	1.2±0.0	0.8±0.0	1.1±0.0	0.1±0.1
30	22:5(n-3)	1.1±0.0	1.5±0.1	1.3±0.1	0.5±0.0
31	22:6(n-3)	31.9±0.2	16.4±1.0	35.7±1.6	16.1±0.3
32	24:1(n-9)	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0

6.4.4 Stable isotopes

Pearson's correlation between $\delta^{15}N$ and $\delta^{13}C$ values in the northern and southern sector was 0.48 and 0.55 respectively (Fig. 6.6). The correlation was significant at the in the south only ($p<0.05$).

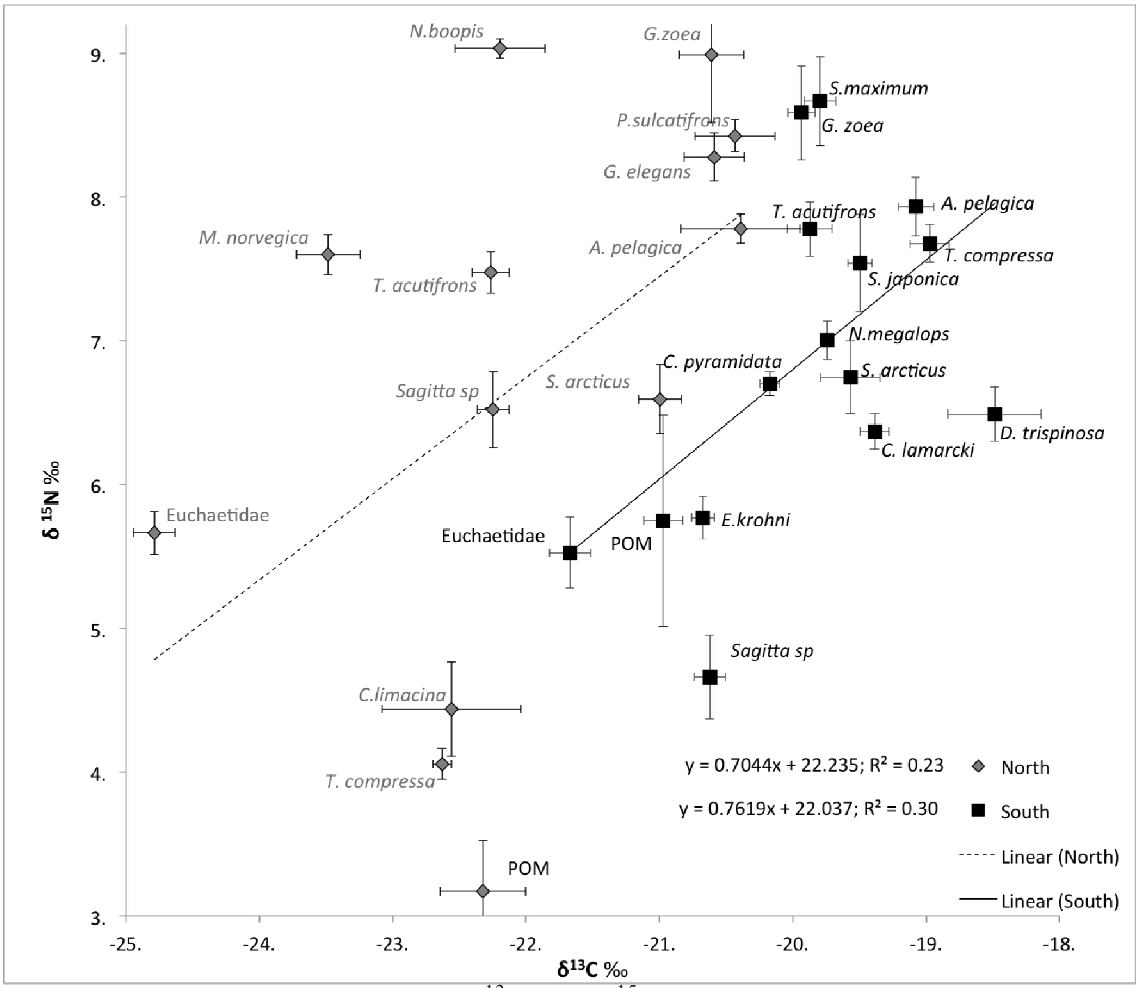

Fig. 6.6 Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ for invertebrate zooplankton and micronekton taxa and POM at the northern and southern sector. $\delta^{13}C$ values for POM are acidified values. Values are mean±SE.

6.4.4.1 $\delta^{15}N$ values

$\delta^{15}N$ values were significantly different between taxa (ANOVA, $F_{18,25,}$=25.2 p<0.000). Euphausiid $\delta^{15}N$ values ranged from 9.03‰, (*N. boopis* and the highest $\delta^{15}N$ ‰ values found in organisms analysed here) and 4.77‰ (*E. krohni*). *G. zoea* had the second highest $\delta^{15}N$ (~9 ‰; in the North). The five species that showed increased abundance with depth (all large crustaceans: *G. zoea, Acanthephyra pelagica, P. sulcatifrons, Gennadas elegans,* and *Sergia japonica*) all had $\delta^{15}N$ >7.5‰. Pteropods $\delta^{15}N$ values ranged between 4.43‰ (*C. limacina*) and 6.7‰ (*C. pyramidata*).

$\delta^{15}N$ values spanned a greater range in the north than in the south (9.03-3.08‰ vs 7.9-4.6‰ respectively). Within-species $\delta^{15}N$ values were significantly different between northern and southern sectors ($F_{6,25}$=28.56, p<0.000): *Themisto compressa* $\delta^{15}N$ values were significantly higher in the south than in the north ($\delta^{15}N$ ~7.8‰ and 4‰ in southern and northern sectors respectively; Tukey's HSD, p<0.001). *Sagitta* sp $\delta^{15}N$ values were significantly higher in the north than in the south ($\delta^{15}N$ = 4.6‰, Tukey's HSD, p<0.000).

Surface POM $\delta^{15}N$ values were significantly different between stations and at depth (F_4 = 8.8, p<0.000). Values were lower in the north compared to the south (mean ±SE were 3.0 ± 0.35‰ and 5.74 ± 0.74‰ in the northern and southern sectors respectively, Fig. 6.6, Tukey's HSD p<0.005).

Mean $\delta^{15}N$ values per species were significantly correlated with the natural logarithm of average individual total lipid weight (Pearson's correlation r=0.68 p=0.0016), and with the natural logarithm of average individual dry weight (r=073. p=0.00067, see Fig. 6.7).

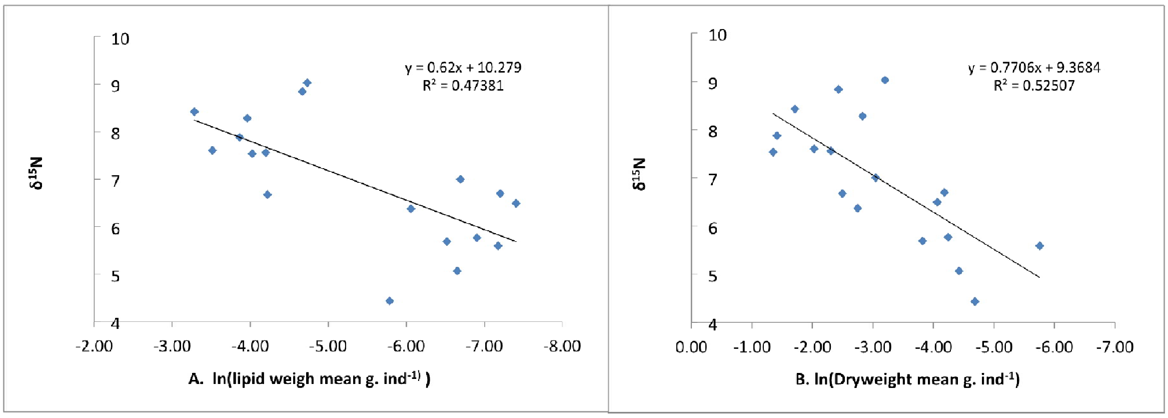

Fig. 6.7 Natural logarithm of lipid weight (A, mean g. ind^{-1}) and dry weight (B, mean g. ind^{-1}) against mean δ^{15}N ‰ values per species.

6.4.4.2 δ^{13}C values

δ^{13}C values were significantly different between taxa ($F_{19,25,}$=81.6; $p<0.0001$) and between northern and southern sites (n=9; $F_{1,25}$=777.6, $p<0.000$). δ^{13}C were higher in the south (Tukey's HSD $p<0.000$, Fig. 6.6). No differences were detected between each side of the ridge, nor with respect to different depth strata. δ^{13}C values regressed marginally better with δ^{15}N values in northern stations than southern stations (r=0.53 and r=0.5 respectively), although the correlation was significant in the south only (p=0.036 and p= 0.09 in the south and north respectively).

Surface POM δ^{13}C values were not significantly different between the northern and southern stations, but values were higher in the North (mean ±SE; -20.90 ± 0.41‰ and -19.47 ± 0.25‰ in the northern and southern stations respectively, Fig. 6.8). Differences were significant between the SW and NE sites (F=9, $p<0.000$, Tukey's HSD, p=0.03). POM values decreased with depth, and variability increased with depth through the productive layer (see Fig. 6.8).

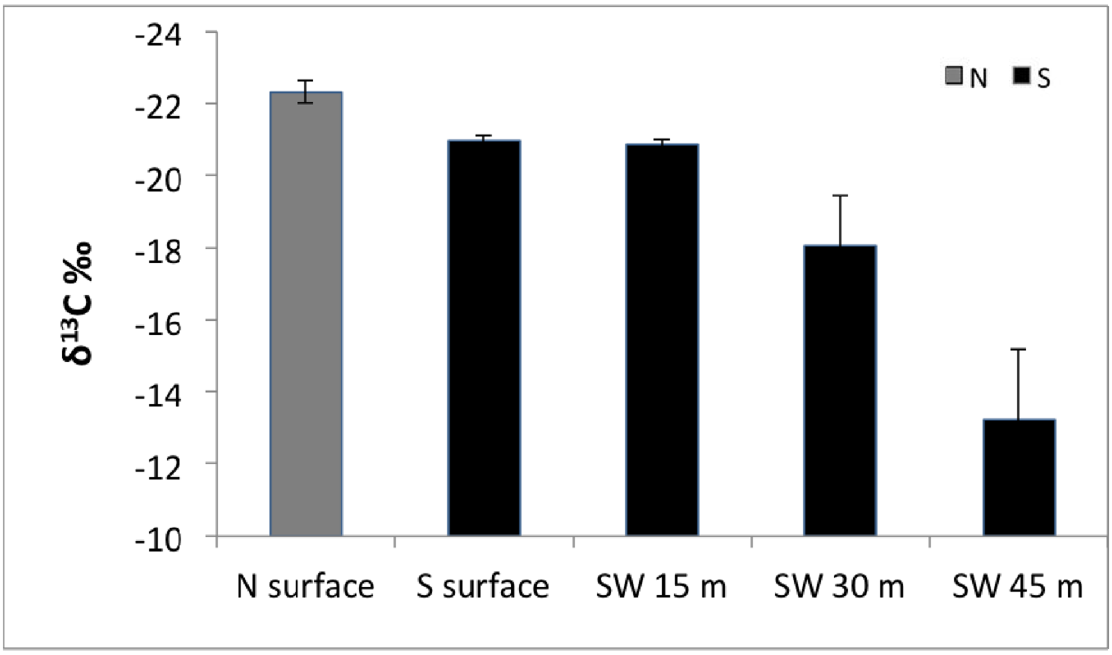

Fig. 6.8 Acidified particulate organic matter $\delta^{13}C$ ‰ values average across the northern and southern stations. Sampling at depth was conducted at the SW station only. Values are mean±SE.

6.5 Discussion

6.5.1 Environmental conditions

Recent studies of the mid-Atlantic hydrography have provided overviews of the general oceanographic conditions on the MAR (in 2004, see Soiland et al., 2008), and of the different hydrographic properties of waters on either side of the SPF (in 2007, Read et al., 2010). Surface temperature in 2007 was 15-16 °C at the southern sites, and 9-10 °C at the northern sites (Read et al., 2010). In the southern sector, water at depth was characteristic (temperature and salinity) of the northern site, suggesting submergence of northern watermasses at the SPF. Cold and warm water intrusions are typical in both the northern and southern sectors, and the characteristics of surface waters in the two sectors are variable on yearly and monthly scales (Table 6.1). Previous studies have detected high Chl-a levels at locations in between the two sectors (in 2004; Soiland et al., 2008). Previous studies have shown that, at the time of sampling, both sectors were in a post spring bloom state (Holliday et al., 2006), although this bloom is considered more intense in the northern sectors (Clark et al., 2001; Longhurst 1998).

6.5.2 Vertical and horizontal patterns in faunal distribution

The two patterns observed in species vertical abundance (either increase, or decrease in densities with depth) define two types of fauna, which are either true epi-pelagics (negatively correlated with depth), or bathypelagic (positively correlated with depth). Animals that did not show any clear pattern are most probably meso- pelagics. In the southern sectors, the decapods *Sergia japonica*, *Parapasiphae sulcatifrons, Acanthephyra pelagica* and *Gennadas elegans* were most abundant. Day/night sampling was not balanced between northern and southern sectors (8 night hauls were conducted in the southern sector compared to only 4 in the northern sector) and the higher abundance of bathypelagic species observed in the south might arguably be because of this. High abundances of the benthopelagic *Gnathophausia zoea* were found at all stations. Studies show that abundances of *G. zoea* typically increase with proximity to continental shelves (Hargreaves, 1989), and this species is ubiquitous on the MAR between 40° and 60° (K. Meland personal communications).

Overall the study area was dominated by *Sagitta* sp*,* Euchaetidae*, Themisto compressa* and *Sergestes arcticus.* These were most abundant in the northern sector, and these observations are probably indicative of the greater primary production spring bloom (Longhurst, 1998), which would support larger populations of grazers and consumers there. Observations of high abundance of *Sergestes arcticus*, *Meganyctiphanes norvegica* and *Thysanopoda acutifrons* in the northern sites are consistent with the findings of Petursdottir et al. (2008) and Saunders et al. (2007b). In Ch. 5, it was shown that *T. acutifrons* was ubiquitous on the MAR between Iceland and the Azores, but showed submergence south of the SPF. *T. compressa* is common throughout the north Atlantic but is generally considered sub-arctic (Dalpadado et al., 2001), and although it was ubiquitous in stations sampled here, abundance was several orders of magnitude greater in the north. In general, pteropods were more abundant in the southern sectors (with the exception of the species *Clione limacina*, which is also considered sub-arctic; Gannefors et al., 2005).

6.5.3 Trophic niches

6.5.3.1 Interspecific differences in FA

This study elucidates interspecific patterns in FA composition and carbon and nitrogen stable isotope values in target organisms. Similarity in FA composition suggests strong dietary overlap between crustacean groups, such as between Euchaetidae and *G. elegans,* between *E. krohni* and *N. megalops*, and between the largest target decapod species. The differences in depth distribution between *Gennadas elegans* and Euchaetidae in this study may reduce interspecific competition enabling these organisms to exploit similar prey and diet in a non-competitive way. The euphausiids *E. krohni* and *N. megalops* have similar vertical and horizontal ranges (Brinton et al., 2000), however higher concentrations of the diatom 22:6(n-3) FA in *N. megalops* (~ 26%) suggest a higher grazing component than in *E. krohni*. This is inconsistent with the δ^{15}N values, which were higher (7‰) in *N. megalops*, thus indicating a greater prey component in the diet. The euphausiids *T. acutifrons* and *M. norvegica* had the highest δ^{15}N values (7.3‰ to 7.7‰), and showed differentiation in principal component by variability in 18:1(n-9) concentration, which was higher in the former. *M. norvegica* is generally considered omnivorous whilst retaining a potential to switch to carnivory in the presence of available prey (Beyer, 1992). The observed difference in FA composition suggests a greater predatory component in the diet of *T. acutifrons*.

The only amphipod species investigated (*T. compressa)* showed broad dietary variability in terms of FA PCA spread, and in terms of the difference in δ^{15}N values between the north (7.7‰) and the south (4.0‰). This species is considered a zooplankton predator (Angel and Pugh, 2000) with raptorial feeding behaviour (Dalpadado et al., 2008). *T. compressa* provided the only record of net feeding in this study, and was observed browsing upon floating fish in the net buckets (and which potentially created a source of experimental bias).

The high concentration of FATM 18:1(n-9) (>15%) in all target decapods (*S. arcticus*, *G. elegans, A. pelagica, P. sulcatifrons,* and *S. japonica*) and in the lophogastrid *G. zoea* is evidence of a carnivorous diet (Falk-Petersen et al., 2000). Moreover, the high proportion of *Calanus* spp FATM (22:1(n-11), 20:1(n-9) is indicative of a large dietary component of *Calanus* spp (Dalsgaard et al., 2003). These organisms are primarily lower meso- and bathypelagic predators and, with the exception of *G. zoea*, undergo large vertical migrations (approximately 500 to 1500 m: Auel, 1999; Hargreaves, 1989; Mauchline and Gordon, 1991). Indeed, observed increases in δ^{13}C values with δ^{15}N (more typically characteristic of bathypelagic animals) suggest a shifting pelagic baseline with depth. The individuals collected were probably from the shallowest depth range of these species (hence the perceived increase in abundance with depth). Predatory diet is further supported by high δ^{15}N values (with the exception of *Sergestes arcticus*). The δ^{15}N values for *S. japonica* and *A. pelagica* (7.54‰ and 7.89‰) are consistent with a diet consisting mostly of primary grazers and secondary consumers, such as ostracods, copepods, euphausiids and chaetognaths (Cartes et al. 2007; Vereshchaka, 1995). High 18:1(n-9) concentrations (20%) of *S. arcticus* here suggest a highly carnivorous diet, which is consistent with the observations of Petursdottir et al. (2008).

Pteropods had generally low 18:1(n-9) FATM concentration, suggesting little carnivory. *C. limacina* is specialist predator, which feeds almost entirely on the herbivorous pteropod *Limacina helicina*. The almost complete absence of *L. helicina* in the RMT1 nets suggests that either *C. limacina* is not an important part in the diet in this particular location, or that *C. limacina* may have almost completely depleted the *L. helicina* population. Contrary to Falk-Petersen et al. (2001), *Calanus* spp FATMs were not in high concentration in *C. limacina*, when *L. helicina* prey was absent. Moreover, the $\delta^{15}N$ values ~4.5 are inconsistent with the conventional view that *C. limacina* is an obligate predator. Although *C. limacina* has been found to have a varied diet (Falk-Petersen et al., 2001) and a broad range of $\delta^{15}N$ values is expected, these values are surprising and may suggest analytical errors rather than difference in relative trophic level. Similarly, $\delta^{15}N$ values for *C. pyramidata* were surprisingly high (~6.7) for a species that is considered herbivorous. Furthermore, isotopic values were not supported by the *C. pyramidata* FA composition, because high 20:5(n-3) (~15%) and 22:6(n-3) FATMs are representative of a diet high in diatom and marine algae in general (Dalsgaard et al., 2003).

An increase in $\delta^{15}N$ and trophic position was correlated with size (dry weight). This observation is common for organisms from marine ecosystems (Kerr and Dickie, 2001). Trophic interactions usually are size dependent, because bigger animals have the potential to consumer a wider size range of prey as they grow (Jennings et al., 2001; France et al., 1998). Here, increased $\delta^{15}N$ values also correlate with lipid concentration, because consumers usually have greater lipid concentrations than their prey. Species at higher trophic levels typically increase in abundance with depth, at least within the macrozooplankton/micronekton size range.

Many species of crustacean showed intraspecific differences in lipid levels between the northern and southern sector. Individuals of *A. pelagica, S. arcticus*, and *T. compressa* typically had greater concentrations of the dinoflagellate FATM 22:6(n-3) in the south (Fig. 6.5, Dalsgaard et al., 2003). This lipid is important in membrane structure and is typical of lipids with high polarity. Moreover, greater *Calanus* spp/storage FATMs MUFA (20:1(n-9) and 22:1(n-11) were found in the north, typically across a broad range of taxa. Such differences may reflect patterns in primary production in the two sectors. The greater magnitude of the spring bloom in the north (Longhurst, 1998) may sustain greater feeding rates in primary grazers, thus increasing the availability of prey to higher predators. The copepod community in the south is known to harbour relatively lower abundances of *Calanus* spp copepods, and greater abundances of *Oithona* spp (Gaard et al., 2008), which have a less pronounced FATM signature. Petursdottir et al. (2010) suggest that frontal area copepod populations (situated approximately at 50°N) surface from diapause later than populations further north and maybe at a more advanced stages of development than on the Reykjanes ridge. The delay in vertical ascent of SPF copepod populations compared to those in the northern sectors is counter to that expected given the latitudinal progress of spring and summer (Gislason et al., 2008). In this study, large numbers of immature copepods were detected in the southern sector (analysis of 200 μm meshsize ring-net zooplankton revealed that 65% of copepods were immature in the southern sector, S. Evans, personal communication), suggesting a similar delay in ascent to stations in the SPF. These results are not surprising, and although the SPF is traditionally placed at ~50°N and has a sharp boundary to the north, it is less defined to the south and its influence might be extending further in that direction.

6.5.3.2 Intraspecific differences in δ^{13}C and FA

The pattern observed of δ^{13}C values (being less negative in the south) suggests local geographical differences in carbon isotope baseline, rather than differences in trophic interactions. Potentially, this could be due to differences in temperature and dissolved CO_2 concentration variability (Rau et al., 1989), and interspecific differences in metabolic pathways of phytoplankton CO_2 uptake (Gearin et al., 1984). The POM δ^{13} values observed in the northern sectors (-22.5‰ ± 0.3‰) are somewhat lower than typical Arctic values (-27 to -23 ‰; Guo et al., 2004), but are similar to values from these latitudes (mean = - 21 ‰, Lara et al., 2009). POM from diatom-rich waters typically has elevated $\delta^{13}C$ values (Miller et al., 2010). The values observed here, and the high concentration of dinoflagellate FATMs, suggests a more diverse phytoplankton flora in the southern sector. This is not inconsistent with the present paradigm of more sustained and intermediate production regimes in the southern region compared with the northern region (Irigoien et al., 2004). In an oceanic system with little or no terrigenous input, $\delta^{13}C$ values typically increase with depth (Druffel et al., 1998). The expected increase in $\delta^{13}C$ was observed in the SW stations where POM was sampled at depth. Although terrigenous nutrients sources are more enriched in $\delta^{13}C$ than oceanic sources, these sources are unlikely to be influential on the MAR compared to continental waters, and the assumption of a single energy source in the two sectors is probably valid.

As expected in food webs with single energy sources, the energy pathways (as indicated by $\delta^{13}C$/ $\delta^{15}N$ plots, Fig 6.6) at the northern and southern sectored converged at higher trophic level, although both pathways preserve geographical baseline differences in $\delta^{13}C$ (less negative in the south, and more negative in the north). These differences are apparent in epi- (*T. compressa*), meso- (*T. acutifrons*), bathy- (*A. pelagica*, *G. elegans*) and bentho-pelagic (*G. zoea*) species, and are likely retained in greater depth (> 800 m) and thus, in higher trophic levels than those investigated here.

In this study, zooplankton samples were not lipid extracted prior to SI analysis, and the $\delta^{13}C$ values presented are from non-acidified samples. Acidification can significantly affect $\delta^{13}C$ values when samples contain inorganic carbon (Jardine et al 2003). Upon acidification, the zooplankton samples did not release bubbles, and the assumption of little-to-no inorganic carbon content is probably valid. High lipid content in zooplankton can leave $\delta^{13}C$ values depleted. Here, the correlation between C:N (a proxy for lipid content) and $\delta^{13}C$ values was low (R^2=0.35), suggesting that lipid related bias was low, and did not warrant lipid extractions of samples prior to analysis. Furthermore, applying lipid correction models to zooplankton with high C:N values can leave $\delta^{13}C$ vs $\delta^{15}N$ plots more vertical, and impose difficulties in interpretation (William D Reid, personal communication). Lipid transformation should not be applied unless there is strong evidence of lipid-related bias.

6.5.4 Conclusion

This study has detected and described patterns in vertical and horizontal heterogeneity in species composition and trophic positions of mesopelagic invertebrates over the MAR. Relative abundance of FATM has revealed trophic niches and interactions between mesopelagic zooplankton (euphausiid, pteropod) and bathypelagic (such as *A. pelagica*) or benthopelagic consumers (such as *G. zoea*) over the ridge. Geographical variability in FATM, SI ratios, and faunal abundance are not inconsistent with theoretical primary production patterns north and south of the SPF in the North Atlantic.

Retention of baseline $\delta^{13}C$ differences as expressed by POM in demersal and benthic fauna would suggest geographical fidelity in the linkage between the surface layers and the benthos of the MAR sectors. Energy transfer fluxes in the northern and southern sectors from surface layers to the deep-sea demersal and benthic communities may be regulated by differences in micronektic communities and tropho-dynamic; however, the differences in production and in abundance between the two regions were only conspicuous at low trophic levels ($\delta^{15}N < \sim 8‰$). At higher levels, differences in abundance are less pronounced, which suggests that at the depth typical of the MAR (> ~2500 m) differences in bloom seasonality might not be as important as yearly production rates.

Overall, there were several inconsistencies between the $\delta^{15}N$ values and the FA composition data, particularly for taxa with low trophic position. In marine systems, baseline isotopes naturally vary geographically, and high variability between sectors is not necessarily an indication of analytical error ($\delta^{13}C$ values were consistently less negative in the south). However, no such consistent geographical pattern was found in the $\delta^{15}N$ values, suggesting the presence of additional factors, which are still unknown. While the general patterns observed between DW, TL and average $\delta^{15}N$ per species may be valid, the inconsistencies between the $\delta^{15}N$ and FA data indicate that the $\delta^{15}N$ data are too variable for investigations of intraspecific variability and geographical variability in diet.

Chapter 7

The biogeography of pelagic shrimps (Decapoda) and gnathophausiids (Lophogastridea) on seamounts of the South-West Indian Ocean Ridge[5].

7.1 Abstract

New baseline information is presented on the distribution of epi- (0-200 m) and meso-pelagic (200-1000 m) micronektic crustaceans (> 15 mm; order Lophogastridea, family Gnathophausiidea; and order Decapoda) on and off seamounts of the South West Indian Ocean Ridge (SIOR, 27° to 42° S) and on a seamount off the Madagascar Ridge (31.6° S, 42.8° E). 31 species of micronektic crustacean were found within the study area. No latitudinal pattern in species richness was observed. Species richness and numerical abundance was highest in the vicinity of seamounts (species richness: 13 to 20; abundance: 10 ± 2 to 20 ± 1 ind.10^{-3} m^{-1}) compared with over the abyssal plains and ridge slopes (species richness: 9; abundance: 24 ± 2 to 79 ± 8 ind.10^{-3} m^{-1}). Multivariate analysis of community composition revealed significant groupings of individual net samples with respect to seamounts position (on/off) and hydrographic region, but not with respect to diel cycle (day/night or dawn) or depth (0-500, 500-800, > 800 m). The dominant species assemblage was composed of *Systellaspis debilis* (28.8 %) and *Sergia prehensilis* (31 %), and was restricted to seamounts on the subtropical SIOR. Results are discussed with respect to present theories pertaining to the maintenance of high biomass of pelagic nekton on seamounts. Observations suggest that the ‘oasis effect’ of seamounts conventionally associated with higher trophic levels also is applicable to pelagic micronektic crustaceans at lower trophic levels. The biophysical coupling of micronekton on seamounts may be an important factor controlling benthopelagic coupling in seamount food-webs.

[5] The work presented in this paper is currently in preparation for publication as: **Letessier T. B.,** De Grave S., Boersch-Supan P H, Kemp K, Brierley A S, Rogers A D (in prep). The biogeography of pelagic shrimps (Decapoda) and gnathophausiids (Lophogastridea) on seamounts of the South-West Indian Ocean Ridge (*Deep Sea Research II: Topical studies in oceanography*)

7.2 Introduction

Seamounts are underwater mountains that rise at least 1000 m above the adjacent ocean floor. They number more than 33,000 in the world ocean (Yesson et al., 2011). The biomass of commercially important species of fishes (e.g orange roughy and billfish) and that of other large nekton is often enhanced on seamounts (Morato et al., 2008; Hirch and Christiansen, 2010). The ecological mechanisms leading to enhancement are, however, poorly understood, making seamounts an important subject of scientific research and fisheries management. This enhanced biomass is theoretically sustained through trophic interactions of fish with diurnally migrating layers (DVM) of epi- (0-200 m) and mesopelagic (200-1000 m) zooplankton (Rogers, 1994) and micronekton drifting over the seamount summit and slopes at night. Upon descent, at dawn, zooplankton layers are trapped in the shallower waters over the seamount and preyed upon by predators. This is known as the sound-scattering layer interception hypothesis, or the trophic blockage hypothesis (Isaac and Schwarzlose, 1965; Hirch and Christiansen, 2010). Predation causes a reduction in the abundance of zooplankton and micronekton leading to heterogeneity in their distribution downstream of the seamount (Haury et al., 2000; Genin, 2004)

In oceanic systems, interactions between mesozooplankton and demersal fish populations are mediated by trophic links between organisms in the micronekton size range (>15 mm), which will form the focus of this study. Pelagic shrimps and Gnathophausiidae serve as a link, often direct, between zooplankton (0.2-20 mm), and higher trophic levels, including fish, mammals, and birds. On seamounts, micronekton can actively resist advection away from the seamount (Wilson and Boehlert, 2004), although the reasons for this behaviour and its prevalence are poorly understood.

Possibly the behaviour is related to local increases in primary production and the trophic enrichment (Genin, 2004), itself a result of topographically-induced nutrient upwelling (Uda and Ishino, 1958). Gnathophausiids and decapod shrimps are an important component in the diet of demersal and benthopelagic fish on ridges (Horn et al., 2010; Bergstad et al., 2010), abyssal plains (Stowasser et al., 2009), and seamounts (Hirch and Christiansen, 2010). The importance of shrimps in the diet of fish stocks on seamounts may be independent of DVM trapping (Hirch and Christiansen, 2010, but see Horn et al., 2010), and although DVM has been observed both in shrimps and gnathophausiids, the behaviour is not universal within either (sergestoids, see Flock and Hopkins, 1992; and *Gnathophausia ingens* see Hargreaves, 1985). The faunal community composition of seamount micronekton, their overlap with true pelagic communities, and their potential role in the trophic blockage hypothesis are poorly understood, yet relevant for the ecosystem-based management of seamount fish stocks.

The seamounts of the southwestern Indian Ocean have been exploited for nearly forty years. Exploratory fishing on the South West Indian Ocean Ridge, the Mozambique Ridge and the Madagascar Ridge began in the 1970s by the Soviet fleet, and associated research institutions, with commercial trawling beginning in the early 1980s (Romanov, 2003; Clark et al., 2007). These fisheries targeted redbait (*Emmelichthys nitidus*) and rubyfish (*Plagiogeneion rubiginosus*) with catches peaking about 1980 and then decreasing to the mid 1980s (Clark et al., 2007). Fishing then switched to alfonsino (*Beryx splendens*) in the 1990s as new seamounts were exploited. Some exploratory trawling was also carried out on the Madagascar Ridge and South West Indian Ocean Ridge (SWIOR) by French vessels in the 1970s and 1980s, particularly targeting Walter's Shoals and Sapmer Bank (Collette and Paring, 1991). In the late 1990s, a new fishery developed on the South West Indian Ocean Ridge with trawlers targeting deep-water species such as orange roughy (*Hoplostethus atlanticus*), black cardinal fish (*Epigonus telescopus*), southern boarfish (*Pseudopentaceros richardsoni*), oreo (Oreosomatidae) and alfonsino (Clark et al., 2007). These species are generally slow to reproduce and typically form breeding aggregations on seamounts, rendering them particularly susceptible to overexploitation (Koslow et al., 2000). This fishery rapidly expanded, with estimated catches of orange roughy being in the region of 10,000t, but then rapidly collapsed. Fishing then shifted to the Madagascar Plateau, Mozambique Ridge and Mid-Indian Ocean Ridge, targeting alfonsino and rubyfish (Clark et al., 2007). Most of these areas have therefore been significantly impacted by deep-sea bottom fisheries and exploitation of these stocks, as well as new targets, such as the lobster fishery (*Palinurus barbarae*) on Walter's Shoal, continue (Bensch et al., 2008).

The SWIOR (Fig. 7.1) extends from northeast to southwest in the west of the Indian Ocean basin, extending over 1,800 km and varies from 300 to 450 km in width (Romanov, 2003). The result is an axial valley with ridge terraces on either side, with several areas rising from the abyssal plains to within <1000 m of the surface. To the north of the SIOR lies the Island of Madagascar with its associated shelf and the Mascarene plateau, and Walters' shoal, a productive fishing ground that has recently had a small area voluntarily closed by some of the fishing industry (bottom trawl) for conservation (Coyle et al., 2007). Oceanographically, the SWIOR is influenced by several fronts with the combined effect of the retroflection of the Aghulas Current and the sub-Antarctic Front creating one of the most productive areas in the ocean (Read et al., 2000). The SWIOR is also characterised by two biomes deemed ecologically distinct in primary production pattern: the Indian South Subtropical Gyre Province

(ISSG), and the South Subtropical Convergence Province (Longhurst, 1998; see also Vierros et al., 2009). Kostianoy (2004) defined oceanographic regions further by deriving frontal features from satellite sea surface temperature patterns: the Tropical region (TR, ~25° to 40° S; 25° to 17° C), Subtropical convergence (STC, ~40° to 43° S; 17° to 13° C), sub-Antarctic convergence (SAC, ~43° to 46° S; 13 to 10 °C).

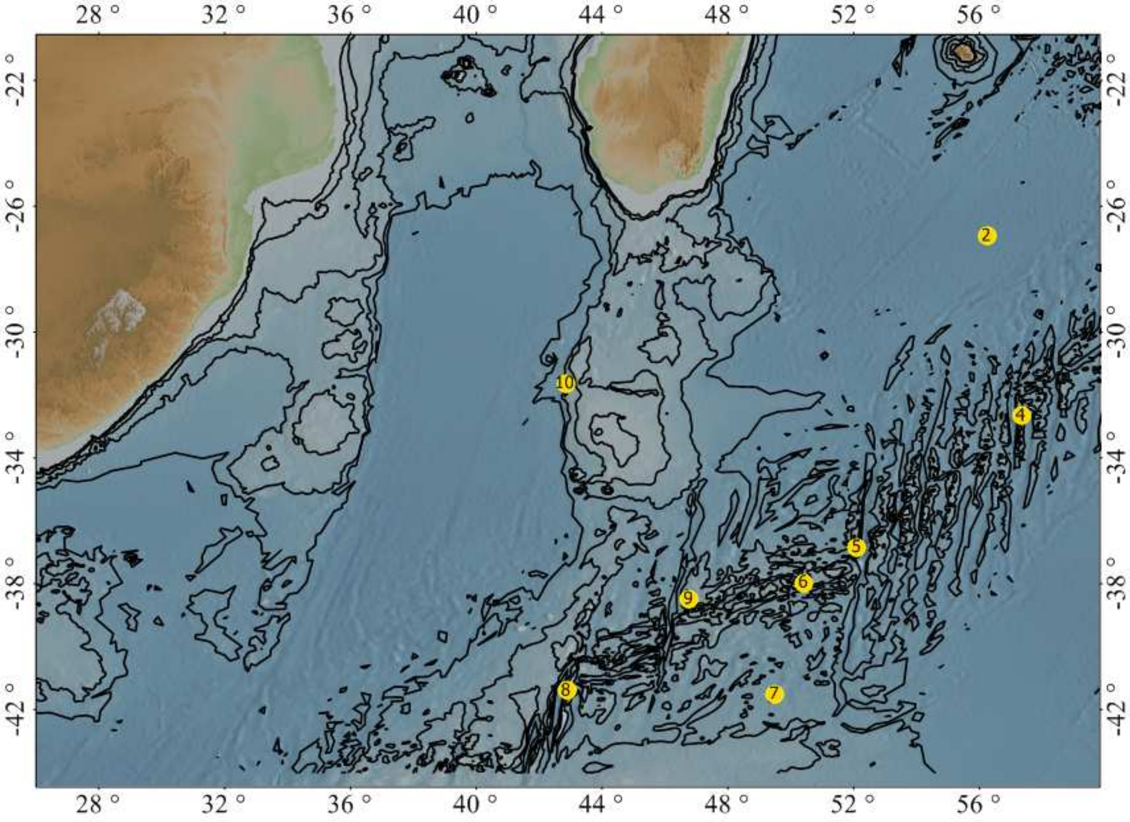

Fig. 7.1 Map of survey area and stations. See Table 7.1 for station activity. The 500, 1000, 2000, 3000, 4000 m isobaths are shown.

In spite of a series of concerted efforts in the 1960s (Zeitzschel, 1973), the basin scale ecology of the Indian Ocean and the SWIOR is poorly known, in part because of the ocean's remoteness to nations with large-scale historical, oceanographic research programmes. Most basin-scale studies arising from those intensive efforts were on epipelagic mesozooplankton (0.2-2 mm), and few baseline data exist for deeper depth horizons, or on specific energy pathways in oceanic food webs (Sestak, 1974).

Moreover, recent deep-sea studies on the SWIOR are limited to a series of geological surveys of the Atlantis Bank (Dick, 1998), and to the hydrothermal vents in the vicinity of Melville Banks (Tao et al., 2007). Some previous work stemming from a series of Russian cruises in the 1990s provides baseline species records for zooplankton and micronekton from Walter’s Shoal (Vereshchaka, 1995). Knowledge of food web dynamics and faunal composition is a crucial component in ecosystem based fishery management and is presently lacking from the SWIOR and associated fishing grounds. Here, new records are presented of epi- and mesopelagic crustaceans along the SWIOR and on a seamount on the Madagascar Ridge, north of Walters’ shoal.

The aims of this study were threefold:

1) To describe epi- (0 – 200 m) and mesopelagic (200-1000 m) micronektic crustacean community composition on and off seamounts of the SWIOR.

2) To explore the influence of seamounts and hydrographical regions on the abundance and diversity of micronektic crustaceans, and to elucidate biogeographical patterns.

3) To determine whether micronektic crustacean seamount communities are distinct from pelagic communities over the abyssal plains and ridge slopes.

Work was conducted as part of the UNDP/IUCN project, which aims to provide ecosystem-based management of fisheries of the South West Indian Ocean.

7.3 Materials and methods

7.3.1 Net sampling

Pelagic sampling was conducted using scientific nets at eight stations along the South-West Indian Ocean Ridge (SIOR, Fig. 7.1) from the R/V *Fridtjof Nansen* Cruise 2009-410. 40 depth targeted hauls were conducted on five seamounts along the ridge, a single seamount of Walter's Shoal, and on two 'off-seamount' sites considered as control stations (station 2 on the abyssal plains between the Reunion and Atlantis seamount, and station 7 in the sub-Antarctic convergence, see Table 7.1, Fig.7.1). Nominal trawl sampling at all stations generally consisted of two day-time hauls (400-600 m and 720-1100 m) and two night-time replicates, using a medium-sized pelagic fish trawl (a Norwegian 'Åkratrawl', cod-end mesh size 4 mm stretched). Finally, on three occasions, a 'benthic' trawl rigged without rollers or bobbins was hauled at high speed as close to the seamount peak as possible, without touching the seabed, in order to catch larger/benthopelagic species, usually shoals identified by ship-mounted echosounders. In all cases, the trawl was lowered rapidly to the minimum depth to be sampled, and then fished and slowly lowered through to the maximum depth layer, after which the trawl was collapsed and heaved quickly to the surface, in order to minimise net contaminations from shallower waters.

Upon recovery of the cod-end on deck, the material was retrieved, sorted to nearest taxa, and fixed in 4% buffered formaldehyde (Steedman, 1976). Subsamples (usually ~50 individuals) of dominant species were fixed in 96 % ethanol for molecular studies. The portion of the catch kept in formaldehyde was transferred to 70% ethanol, usually within 48 hours of fixation. All samples were analysed to lowest taxonomic level in the Oxford Museum of Natural History.

7.3.2 Data analysis

7.3.2.1 Net catchability

Abundance (numerical count) and species richness (total number of species recorded) were determined for each station. Because of the poor catchability of large crustaceans by the ‘benthic’ trawl (the ‘benthic’ trawl was fished at high speed and the net bag mesh size was coarser than the Åkratrawl) crustacean densities were derived using the Åkratrawl catches only. The benthic trawl catches only were considered when deriving species richness. Catch per Unit Effort (CPUE) densities were derived by standardizing the catch by the horizontal distance trawled (m) CPUE = ind 10. ^{3} m^{-1}.

Table 7.1 Trawl activity on the R/V *Fridtjof Nansen* Cruise 2009-410

Station	Latitude (deg S)	Longitude	Depth (m), Day, Night, Dawn (D,N, DWN)	Hydrographic region (Kostianov, et al. 2004): Tropical (TR), Subtropical convergence (STC), sub-Antarctic convergence (SAC)	Target location	Seamount summit depth or seabed depth (m)
2	26.94	56.23	50D, 300D, 600D, 800D	TR	Off-Ridge 1	5000
4	32.72	57.29	700D, 400D^{+}, 700N, 400N, 740DW*	TR	Atlantic Bank	700
5	36.86	52.05	750D, 400D, 720N, 400N, 500N*, 750DW*	STC	Sapmer Bank	300
6	37.95	50.37	700N, 400N, 930N, 700D, 420D	STC	Middle of What	970
7	41.48	49.53	700N, 400N, 700D, 400D^{+}	SA	Off-Ridge 2	3500
8	41.42	42.9	900D, 600D, 900N, 600N, 270DW*	SA	Coral Seamount	120
9	38.5	46.75	860N, 480N, 320DW*, 850D, 430D^{+}, 560D*	STC	Melville Bank	90
10	31.64	42.83	700N, 1100N, 300DW, 1100D, 700D	TR	Walters Shoal	1300

*'Benthic' trawl

$^{+}$Negative trawls

Studies have shown that the catchability of invertebrate micronekton by the Åkratrawl can be very taxon specific, probably because of taxon specific size differences, 'herding' effects of the trawl doors, and the large mesh size at the mouth of the trawl (Heino et al., 2010; Wenneck et al., 2008). Although any gear would hold some inherent bias, the data derived directly from the raw Åkratrawl catches probably are unfit for comparison of relative abundance between the target taxa, or for community analysis (of other than the species presence/absence data). As a consequence the selectivity of the Åkratrawl, derived from Heino et al., (2010) and from personal communications (Heino, M), was considered for further analysis. This is aimed at making this study more comparable to other macrozooplankton/micronekton studies, as these commonly use smaller gear types (e.g. Letessier et al., in press; Deforest and Drazen, 2009; Pakhomov et al., 1994). The selectivity of the Åkratrawl ('y') relative to the reference trawl ('x'; a Norwegian macrozooplankton trawl, mouth area 36 m^2, Wenneck et al., 2008) can be expressed by equation [1] where p is the relative catchability coefficient and C is the catch standardized by the trawled distance (CPUE here). The Norwegian macrozooplankton reference trawl is assumed to carry 100% catchability for the fauna in the size-range targeted here (<100 mm):

Equation [1]: $C_y = \rho C_x$

True catches (C_x) were derived by dividing the raw catches (C_y) by the taxon specific catchability coefficients (‘ρ’) using parameters from Heino et al. (2010; equation [2]) and ‘*a_y*’ a taxon specific model parameter (see Table 7.2 for the selected model taxon and model parameter).

Equation [2]: $\rho = e^{a\_y}$

Exploratory analyses revealed that these catchability modifications could substantially change the similarity analysis between the samples. The Åkratrawl coefficients were derived with inherent error estimates (Heino et al., 2010), which cannot be adequately expressed in multidimensional space, and thus could not be explored to satisfaction within the framework of this study. However, previous studies have shown that, in the context of multidimensional community analysis, the transformation applied here reduces the gear effect to a weakly significant grouping term, when analysed together with replicates from a standard macrozooplankton trawl (ANOSIM, global R= 0.094, p<2.2%; see Sutton et al., 2008), which was deemed an acceptable bias for purposes here.

The coefficients from Heino et al (2008) were calculated with respect to an Åkratrawl with a net bag mesh of 22 mm, and this is likely to infer some bias compared to the trawl used here (net bag mesh 4 mm). However, net bags typically becomes clogged rapidly during hauls, and the difference in mesh size in the net bags would probably not influence the results, especially as the majority of species considered were larger than 22 mm.

7.3.2.2 Statistical analysis

Pearson’s correlation analyses were conducted on abundance and species richness to detect patterns with respect to seabed depth. Distribution and species composition patterns were explored with multivariate statistics and classification techniques using Primer software v6 (Clarke and Gorley, 2006), namely non-metric multidimensional scaling (NMDS) ordination and cluster analysis. Input density data were root-transformed (ind. 10^{-3} m^{-1}) to reduce the weight of dominant species. The similarity measure applied was the Bray-Curtis similarity index (Bray and Curtis, 1957). Analysis of individual net samples was carried out, where each cod-end collected was considered a distinct sample. Each cod-end was characterised by its standardized species-specific abundances and sample depth (Table 7.2). Nets with no micronektic catch were omitted from the multivariate analysis.

Associated with cluster analysis, permutation tests (Analysis of similarity ANOSIM, 999 iterations, p< 5%) were carried out to determine association of groups of samples with five *a priori*-defined factors: proximity to seamount (on or off), affinity with hydrographic regions (as defined by Kostianoy et al., 2004; Table 7.1), depth-stratum (nominal depth strata were 0-500, 500-800, > 800 m), and diel cycle (Night, Day and Dawn; Table 7.1).The appropriate discrimination level for determining clusters was decided by running similarity profile permutation tests (SIMPROF, 1000 permutations, p < 5% to test at which similarity the clusters significantly differed in structure). Species contribution to similarity (SIMPER) was applied to determine the characteristic species contribution to each significant cluster.

7.4 Results

7.4.1 Crustacean micronekton abundance and diversity distribution patterns

This study caught 4936 individual micronektic crustaceans in the size range 15 mm to 60 mm. Mean numerical abundance per station ranged from 10 to 79 ind.10^{-3} m^{-1} within the survey area. Highest numerical abundance was observed over seamounts (Fig. 7.2 A). No significant numerical abundance pattern was detected with respect to seabed depth (Pearson's correlation $r=0.4$; $p>0.05$). Species richness was highest in the vicinity of seamounts (Fig. 7.2) and a significant negative relationship was detected between seabed depth and species richness (Pearson's correlation $r = 0.81$; $p = 0.05$). Highest species richness was detected over Coral seamount (20 species, station 8), Walter's Shoal (17 species, station 10), and Melville bank (16 species, station 9). No clear latitudinal pattern was observed within in the survey area.

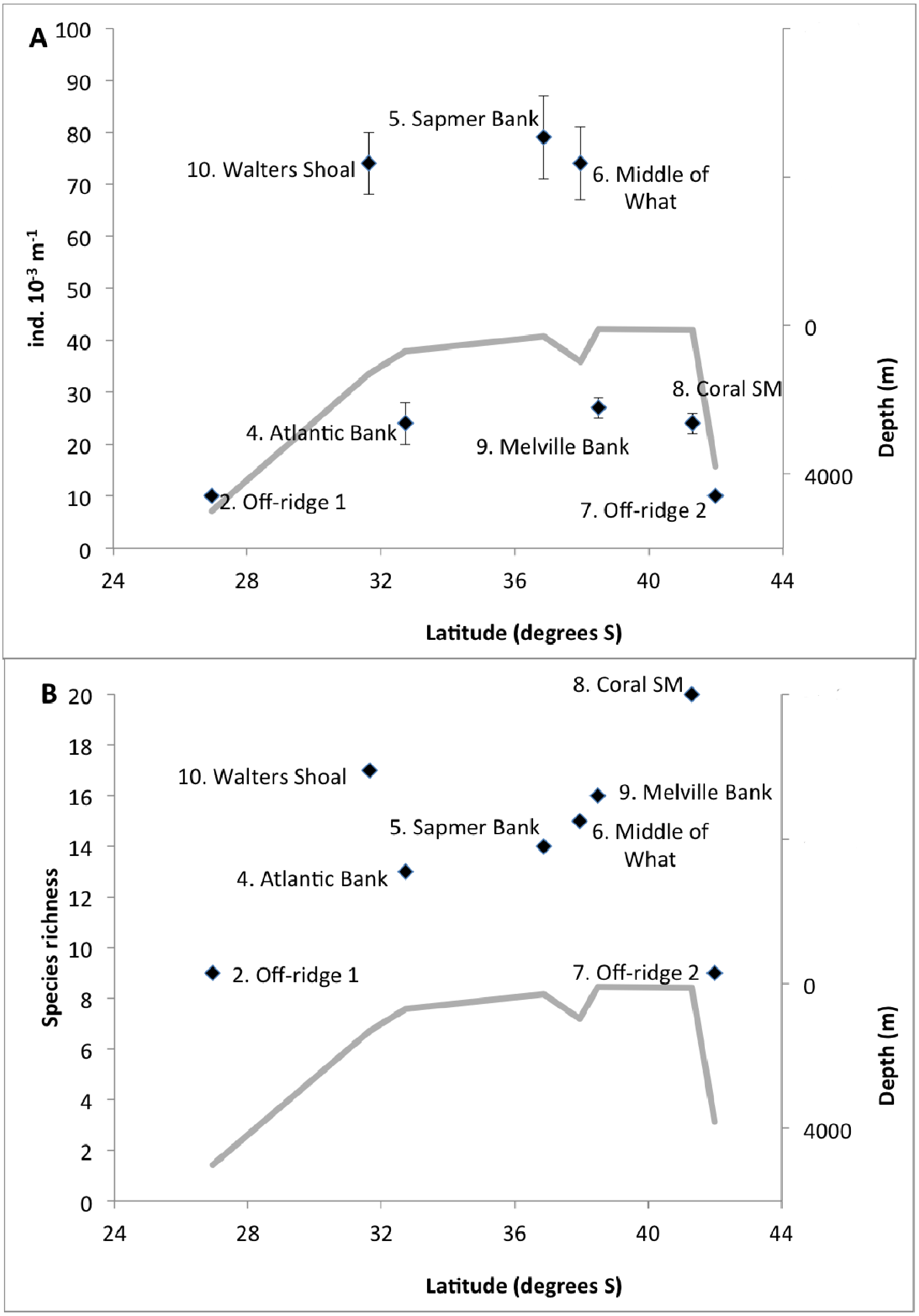

Fig 7.2 Micronekton crustacean density (A. mean ± SE ind.10^3 m^{-1}) and species richness (B. total number of species recorded) and seabed depth (gray line, in m) per stations.

Table 7.2 Micronektic crustacean species sampled in association with the South West Indian Ocean Ridge (26-42 °S). Station locations given in Table 7.1 and Fig. 7.1.

Species	Authority	Number of specimens collected (C_y)	e^{a_y}	Closest taxon to which relative catchability coefficient exists (from Heino et al 2011)	True catches (C_x)	Latitudinal range (deg S)	Longitudinal range (deg E)	Stations at which species was recorded
Sergia prehensilis	(Bate, 1881)	2092	0.90	*Sergia* sp	2306	27-38.5	57-42	2.800D, 4.700N, 4.400, 4.740DW, 5.750D, 5.400D, 5.720N, 5.400N, 5.500N, 5.750DW, 6.700N, 6.400N, 6.930N, 6.700D, 8.900D, 8.600D, 8.643N, 9.860N, 9.480N, 9.850D, 10.700N, 10.1100N, 10.1100D, 10.700D
Systellaspis debilis	(A. Milne-Edwards, 1881)	1392	0.75	*S. debilis*	1834	27-38.5	57-42	2.600D, 2.300D, 2.50D, 2.800D, 4.700N, 4.400N, 4.740DW, 5.750D, 5.400D, 5.720N, 5.400N, 5.500N, 5.750DW, 6.700N, 6.400N, 6.930N, 6.700N, 9.860N, 9.480N, 9.850D, 10.700N, 10.1100N, 10.300N, 10.1100D, 10.700D
Parasergestes armatus	(Krøyer, 1855)	96	0.20	*Sergestes* sp	457	27-38.5	57-42	2.600D, 4.700D, 5.400D, 5.400N, 5.750DW, 6.400N, 6.700D, 7.400N, 8.900N, 9.860N, 9.850D,10.700N
Acanthephyra quadrispinosa	Kemp, 1939	118	0.57	*Acanthephyra* sp	205	32.8-41.5	57.3-42.8	4.700N, 4.740DW, 5.400N, 5.500DW, 5.750N, 6.400N, 6.700N, 6.930DW, 8.600D, 10.700N,10.1100D
Oplophorus novaezelandiae	(De Man, 1931)	208	1.60	*Oplophorus* sp	129	27-38.5	57-42	2.300D, 4.700N, 4.400N, 4.740DW, 6.700N, 6.400N, 6.930N, 6.700D, 6.420D, 7.700D, 7.700N, 8.900D, 9.860N, 9.480N, 9.850D
Eusergestes cf antarctica	(Vereschaka, 2009)	25	0.20	*Sergestes* sp	119	41.5	43	8.600D

Funchalia villosa	(Bouvier, 1905)	93	NA(1)	NA	93	27-38.5	57-42	2.800D, 2.50D, 4.400N, 4.400N, 4.700N, 4.740DW, 6.700N, 6.400N, 6.420D, 9.480N, 10.700N, 10.300N, 10.1100D, 10.700D
Petalidium folicea	Bate, 1881	19	0.20	*Sergestes* sp	90	38-42	50-43	7.700N, 8.900D, 8.900N,9.860N
Acanthephyra sica	Bate, 1888	40	0.57	*Acanthephyra* sp	70	31-41	43-49	7.700N, 8.900D, 8.900N, 10.1100D
Gennadas gilchristi	Calman, 1925	43	0.75	*Gennadas* sp	57	31-42	50-43	6.700D, 8.900D, 8.900N, 9.860N, 9.850D, 10.700N
Deosergestes corniculum	(Krøyer, 1855)	384	8.40	*S. corniculum*	46	27-38.5	57-42	2.600D, 2.300D, 2.300D,4.700D, 4.740DW, 5.400D, 5.720N, 5.400N, 5.750DW, 6.700N, 6.400N, 6.930N, 6.700D, 7.700N, 8.900D, 9.860N, 9.480N, 9.850D,10.700N,10.1100N, 10.1100D,10.700D
Pasiphaea diaphana	Burukovsky and Romensky, 1980	99	2.51	*Pasiphaea* sp	39	27-38.5	57-42	6.700N, 6.930N(c.f), 8.900N, 9.850D, 5.720D(c.f), 5.400N(c.f), 5.750DW(c.f) 9.480N(c.f), 10.700N (c.f), 4.700N (c.f), 6.700N, 9.860N, 10.300N, 10.1100D, 4.740DW, 5.750DW
Gnathophausia ingens	(Dohrn, 1870)	39	NA(1)	NA	39	27-38.5	57-42	4.740DW, 5.750DW, 6.700N, 6.930N, 8.900D, 8.900N, 9.860N, 9.850D, 10.1100N, 10.300N, 10.1100D, 10.700N
Pasiphaea romenskyi	Burukovsky, 1995	73	2.51	*Pasiphae* sp	29	33-42	58-50	7.700N(c.f), 4.400N, 5.400N, 4.700N, 4.400D
Oplophorus spinosus	(Brullé, 1839)	37	1.66	*O. spinosus*	22	27-38.5	57-42	2.50D, 2.300D, 2.800D, 4.700N, 4.400N, 4.740DW, 9.480N, 10.700N, 10.300N, 10.700D
Pasiphaea rathbunae	(Stebbing, 1914)	50	2.51	*Pasiphaea* sp	20	42	50-43	7.400N, 7.700N, 8.900D, 8.900N,
Gennadas kempi	Stebbing, 1914	11	0.75	*Gennadas* sp	14	41.5	43	8.900D, 8.900N
Sergia potens	(Burkenroad,	12	0.90	*Sergia* sp	13	38-42	47.5-43	8.900D, 8.900N, 9.850D

	1940)							
Pasiphaea gelasinus	Hayashi and Yaldwyn, 1998	27	2.51	*Pasiphaea* sp	11	38.5	46.75	9.480N(c.f)
Gennadas propinquus	Rathbun, 1906	8	0.75	*Gennadas* sp	11	37-38.5	47-52	5.400N, 6.400N, 9.480N
Notostomus auriculatus	Barnard, 1950	7	0.66	*Notostomus* sp	11	38-41.5	50-43	6.700N, 6.930N, 8.900N, 9.850D
Eupasiphae gilesii	(Wood-Mason, 1892)	11	NA(1)	NA	11	31-42	50-43	6.930N, 10.700N, 8.900D, 8.900N, 10.1100D
Stylopandalus richardi	(Coutière, 1905)	9	NA	NA	9	27-37	57-43.5	5.400D, 5.400N, 2.300D, 10.700D, 4.700N
Pasiphaea barnardi	Yaldwyn, 1971	21	2.51	*Pasiphae* sp	8	41.5	43	8.900N, 8.643N
Meningodora vesca	(Smith, 1886)	4	0.52	*M. vesca*	8	38-32	50-43	6.700N, 6.930N, 10.1100N, 10.1100D
Parapasiphae sulcatifrons	Smith, 1884	6	0.89	*P. sulcatifrons*	7	38-41.5	50-43	6.930N(c.f), 8.900N(c.f), 10.1100N, 1100D
Funchalia danae	Burkenroad, 1940	4	NA(1)	NA	4	41.5	43	8.900D, 8.600D, 8.900N
Gennadas capensis	Calman, 1925	3	0.75	*Gennadas* sp	4	32-33	57.5-43	4.700N, 10.1100D
Gnathophausia zoea	Willemoes-Suhm, 1875	3	NA(1)	NA	3	32.8-41.5	57.3-42.8	4.700N, 8.900D, 8.900N
Gennadas brevirostris	Bouvier, 1905	1	0.75	*Gennadas* sp	1	37	52	5.400N
Gnathophausia gracilis	Willemoes-Suhm, 1875	1	NA(1)	NA	1	32	43	10.1100D

Thirty-one species of decapod and lophogastrids were recorded within the survey area (Table 7.2). Several decapod species were caught at nearly every station and appeared ubiquitous (*Oplophorus novaezelandiae, Systellaspis debilis, Funchalis villosa*, *Sergia prehensilis, Deosergestes corniculum*, Table 7.2) but *S. debilis* and *F. villosa* appeared absent from many stations in the sub-Antarctic convergence. Amongst these, the most abundant were *S. prehensilis* and *S. debilis.* Several species were caught uniquely in the vicinity of seamounts (all lophogastrids and *Gennadas* spp, *Acanthephyra sica, Eupasiphae gilesii, Funchalia danae, Acanthephyra quadrispinosa, Meningodora vesca, Notostomus auriculatus. Parapasiphae sulcatifrons, Pasiphaea barnardi, Pasiphae gelasinus*, Table 7.2). Several species were caught uniquely in the sub-Antarctic convergence (*Pasiphaea rathbunae, Pasiphaea barnardi, Eusergestes* cf. *antarcticus, Petalidium foliceum, Gennadas kempi*). No species were caught uniquely on off-seamount stations, although *Sergestes armatus* was most abundant on off-seamount stations.

7.4.1 MDS and assemblage composition

ANOSIM tests revealed that amongst the five *a priori* groups investigated, proximity to seamount was by far the most important (Global R=0.52; p<0.1%), followed by hydrographic region (Global R=0.212; p<0.1%), gear (Global R=-0.148; p<74.5%), diel cycle (Global R=-0.037, p<67.7%), and depth stratum (Global R=-0.011; p<53%). The greatest pairwise difference was found between the sub-Antarctic convergence and the Subtropical convergence (STC; R = 0.278, p < 0.1), and the Tropical region (TR; R = 0.311, p < 0.1).

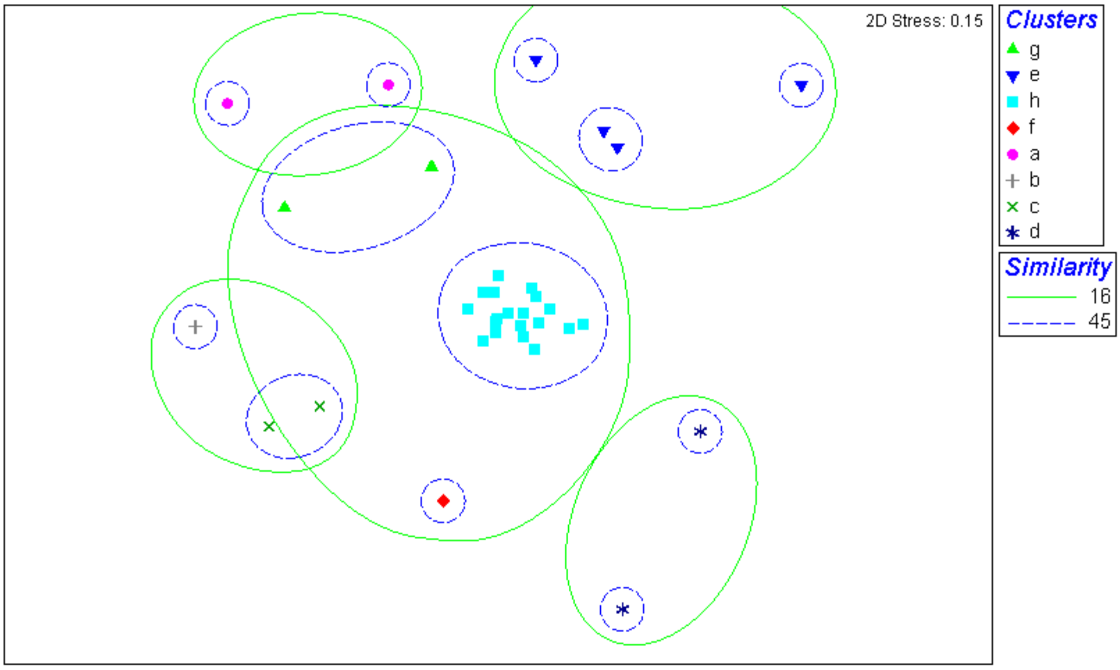

Fig. 7.3 Non-metric multidimensional scaling ordination (MDS) of root transformed density estimates in individual net samples. Overlayed are significant clusters ‘a-h’ t 16 and 45 % similarity, resulting from the SIMPROF classification analysis (see text for explanation).

The two dimensional MDS ordination was under a stress index of 0.15, which is acceptable for meaningful interpretations of ecological patterns (Fig. 7.3). Horizontal dispersion in multidimensional space appears related to latitude, as samples to the top right of the plot were mostly from northern stations and those to the bottom left were southern stations. SIMPROF identified 8 significant clusters (Fig. 7.4) at 55% similarity ($\pi=8.64$, $p<1.1\%$). The largest of these clusters (h) contained 19 samples from seamounts between 31.5° and 40°S, and all but two stations from the Subtropical Convergence region (STC) region (Table 7.1, Fig. 7.5). Cluster ‘h’ contained 70 % of seamounts stations overall and was composed mostly of *Sergia prehensilis* and *Systellaspis debilis* (31 and 28.8 % respectively, see Fig. 7.5). Cluster ‘e’ consisted of four samples from the TR regions (station 2, 4 and 10) and was composed of *S. debilis*, *Funchalia villosa* and *Oplophorus spinosus* (29.2, 34, and 24 % respectively, Fig. 7.5).

Cluster 'a', 'b', were from the sub-Antarctic convergence (SAC) zone.

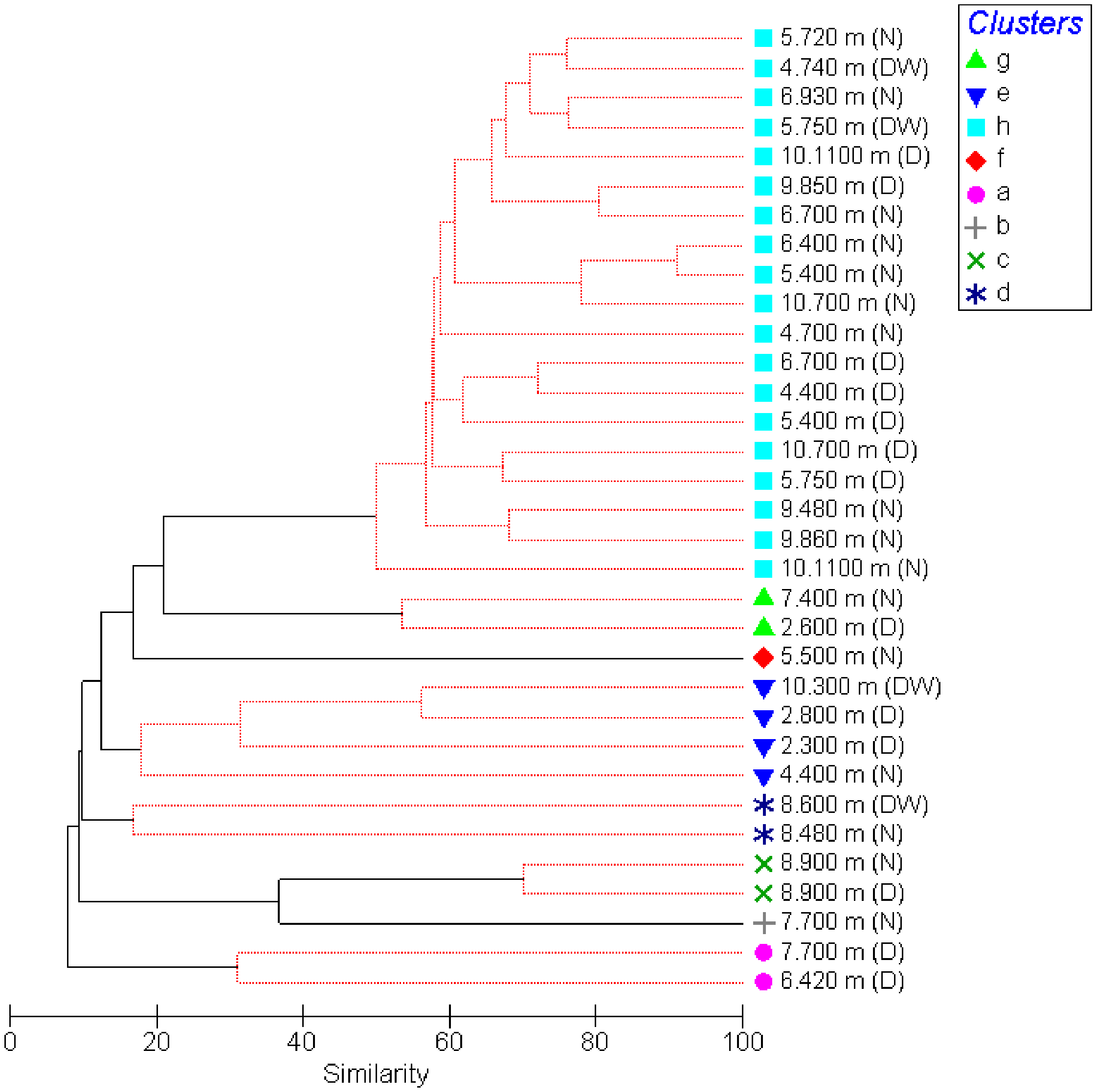

Fig. 7.4 Cluster analysis dendrogramme based on root transformed species density data, and characteristics of samples in significant clusters (SIMPROF): depth (m), Diel cycle (D/N/DW).

Clusters 'c' and 'd' contained all samples from Coral seamount (station 8). Cluster 'c' was composed mostly of *Sergia potens* and *Acanthephyra sica* (see Fig. 7.5). Cluster 'd' was composed entirely of *S. prehensilis*. Cluster 'g' was composed uniquely of off-seamount stations, and was composed of *Sergestes armatus* and *Oplophorus novaezelandiae* (91 and 6.9 % respectively).

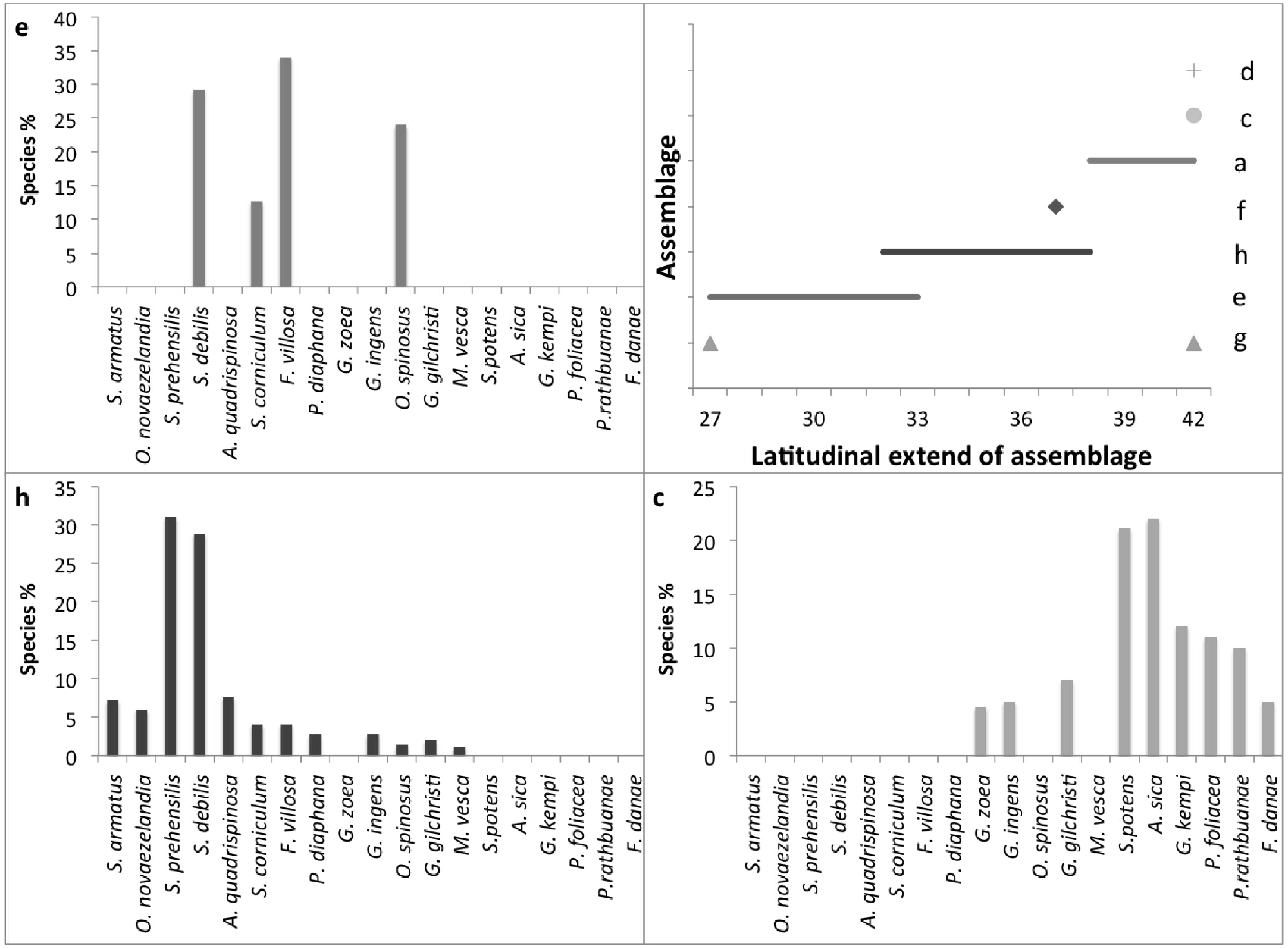

Fig. 7.5 Species abundance composition (proportion of each species in the summed standardized catches from all cod-ends in a cluster) in clusters ‘e’, ‘h’, ‘e’; and latitudinal extent of assemblages.

7.5 Discussion

Very little information exists on the deep-sea ecosystems of the Indian Ocean outside the Arabian Sea (Ingole and Koslow, 2005) and the majority of species caught in this study represent new records of occurrence. As the ANOSIM results suggest that both the numerical abundance and species composition of the target taxon are strongly influenced by the proximity to seabed (or to seamounts) and, to a lesser extent, the properties of the water mass, this discussion will be focused on these two factors. The low grouping of clusters according to depth strata (0-500, 500-800, > 800 m. R = -0.011) and solar cycle (day/night/dawn, R = -0.037) may be due to the lack of opening/closing mechanisms utilised on the Åkratrawl on this cruise. Arguably, although the trawl was collapsed during deployments, the efforts were probably not sufficient to avoid shallow water contamination. Typically, shallow-living species are more abundant than deeper living species (pelagic biomass decreases logarithmically with depth, (Angel and Pugh, 2000)), thus the Bray Curtis similarity measures could potentially be highly sensitive to biases imposed by this shortcoming. Nevertheless, previous studies on DVM taxa, which utilize opening/closing gears, have not detected such effects (Sutton et al., 2008; Ch. 5), and it appears that the Bray Curtis index is poorly suited to identifying patterns in DVM over geographical scales, and DVM patterns are best investigated on smaller scales (< mesoscale, 10-100 km).

7.5.1 Biogeography

High abundances of *Systellaspis debilis* and *Sergia prehensilis* were found throughout the survey area outside the sub-Antarctic convergence, and these species were dominant in the seamount cluster (h) and the tropical cluster (e). This is not consistent with the findings of Vereshchaka (1995) who observed that both species showed decreased abundance with proximity to the seabed. While *S. debilis* is pan-temperate (Poupin, 1998), this species is typically less abundant over continental slopes than over seamounts (Vereshchaka, 1995). Here, this species was caught in all the nets over the tropical abyssal plains (i.e. station 2), albeit in fewer numbers than over the seamounts. This species has been shown to have a high benthic component to its diet compared to other shrimps (Rau et al., 1989), thus potentially explaining its affinity with seamounts.

Previous records of *Acanthephyra sica* have been restricted to the Antarctic convergence (Burukovsky and Romensky, 1982) and this study presents a first record of this species north of 40º S (station 10, 32 ºS, north of Walter's Shoal). Several species were caught uniquely in the sub-Antarctic convergence, although they were not ubiquitous south of 40º S. Three species, were found uniquely on Coral Seamount, *Pasiphae barnardi, Gennadas kempi, Funchalia danae* but the SAC region was not sampled sufficiently to distinguish whether these were endemic to the seamount or rather inhabitants of the SAC region.

Observations of greater dissimilarity amongst samples south of 37ºS (of seven significant clusters, four were restricted to > 37º S, Fig. 7.5) suggest that this area is highly heterogeneous, as expected from this frontal zone where there is substantial mesoscale eddy formation and mixing of water masses (37 - 38 º S; Read et al., 2000), as indicated by high sea surface height variance (Babu et al., 2011). Decapod abundance was at it highest in this section (~75 ind 10. ^{3} m^{-1}, station 5 and 6), which is consistent with the findings of Pakhomov (1999) and Pakhomov et al. (1994). Southern stations (station 6 to 9) also harboured several species not observed elsewhere (such as *Pasiphae rathbunae, Pasiphae gelasinus, Notostomus auriculatus, Pasiphae barnardi,* *Eusergestes cf antarctica*, see Table 7.2), and thus indicating the influence of Antarctic faunas (Burukovsky and Romensky, 1982; Clarke and Holmes, 1987).

7.5.2 Seamount effect

The most important factor in determining species composition and numerical abundance was proximity to seamount. This is not surprising, considering that less than 200 of the world's ~4000 shrimp species are true pelagics (De Grave and Fransen, in press), and the probability of catching a species is expected to increase with increased proximity to the seabed. However, the absence of any apparent latitude/species richness trend is contrary to observations on other pelagic taxa such as euphausiids or decapod shrimps on similar scales (20° of latitude, Letessier et al., in press; Falkenhaug T., personal communications), or on basin scales (Letessier et al., 2011), as species richness typically decreases with increased latitude. The increased numerical abundance and species richness of micronekton on seamounts here is similar to patterns observed of higher trophic levels such as marine mammals and commercially important species of fish (Rogers, 1994; Genin, 2004; Haney et al., 1995; Pitcher and Bulman, 2007).

Observations of relatively high biomass and species richness on seamounts have been linked to localized upwelling (Uda and Ishino, 1958) and increased productivity (Samadi et al., 2006), and trapping by Taylor cones (Pitcher and Bulman, 2007). However, as these features are not universal to seamounts (Verlaan, 1992; Dower and Mackas, 1996 and Genin, 2004), the increase in numerical abundance and richness on seamounts here are unlikely to be caused by increased localized primary productivity alone (Genin, 2004). Moreover, since the seamounts surveyed here spanned a great range in the minimum peak depth (1300 m to 90 m), oceanography and patterns of primary production are likely to vary amongst them. As the increase in numerical abundance and species richness was observed universally, such mechanisms are unlikely to be key drivers here.

Highest species richness was observed near seamounts compared to over the abyssal plains and ridge slopes. This does not support the ‘island’ hypothesis of seamounts (i.e. seamounts are reproductively isolated, thus promoting endemism, see Koslow and Poore, 2000, and see McClain, 2007 for a review), at the scale of the present study, as species were typically present on several seamounts (Table 7.2). Moreover, for benthic decapods at least, localized oceanographic properties of seamounts that may restrict dispersal (such as Taylor columns) are not predictive of community structuring (whereas the depth of the seamount is; see Brewin et al., 2009). As 70% of the seamount station clustered within one group, spanning almost 10° of latitude (with no apparent influence of diel cycle or depth strata), the statement of Gjerde and Breide (2003) does not pertain to pelagic micronekton: ‘Seamounts are areas of high endemic biodiversity with little overlap in community composition between seamounts’.

The findings here supports the hypothesis of the ‘oasis’ effect of seamounts, and are in agreement with the hypothesis of Genin (2004): that the increased numerical abundance and richness on seamounts is related to biophysical coupling between seamounts characteristics and faunal behaviour, which is traditionally applied to explain elevated fish biomass (and, in some cases, to micronekton; see Wilson and Boehlert 1993, 2004 and Genin, 2004). This explanation is consistent with the apparent lack of correlation between abundance/ species richness and seamount depth (as opposed to seabed depth per se; r = 0.41, $p = 0.48$; and r = -0.55, $p = 0.52$, Pearson’s correlation): for the ‘seamount effect’ to be observable on pelagic shrimps, it is seemingly sufficient for the peak of the seamount within ~1300 m of the surface. Abundance/species richness is not affected in a predictable manner in seamounts that reach closer to the surface, in contrast to observations of Brewin et al., on the influence of depth on the structuring of benthic decapods (Brewin et al., 2009). This boundary is presumably linked to the same mechanisms that restrict DVM to the upper 1000 m of the water column, where the majority of DVM takes place for zooplankton in general (Angel and Pugh, 2000) and pelagic shrimps specifically (Flock and Hopkins, 1992).

Biophysical coupling was most apparent in the species of the benthopelagic lophogastrids *Gnathophausia* spp, which were only observed in the vicinity of seamounts, and *Acanthephyra quadrispinosa*, which was ubiquitous and found only on seamounts. The proximity to the seafloor, which by definition is reduced on seamounts, increases food and, perhaps habitat availability for these organisms. While most decapod shrimps sampled here were 'pelagic' (i.e. they were caught in the water column), only one species (*Sergestes armatus*) showed increased abundance on the off-seamount stations, consistent with the findings of Vereshchaka, (1995). Some *Gnathophausia* species are considered seamount specialist (e.g *Gnathophausia longispina*, see Wilson and Boehlert, 1993) and have been observed to actively resist advection away from seamounts (Wilson and Boehlert, 2004). Moreover most Gnathophausiids show some fidelity with respect to distance to the seabed (Hargreaves, 1989, K. Meland personal communication). Previous studies have considered differences in faunal assemblages between slope and summit sections of the seamount, and have detected that the summit can harbour lower abundances compared with the slope, presumably because of avoidance of the summit by micronekton (as the summit are predator rich; Deforest and Drazen, 2009). Because of the scale considered here, this study is not able to provide information on differences in micronekton abundance between disparate sections of seamounts. Evidence presented here suggests that in the mesopelagic, most pelagic decapod species populations become enhanced on seamounts slopes.

7.5.3 Conclusion

This study shows that the distribution of *Gnathophausia* spp. and decapod shrimps on high-seas fishing grounds in the SWIOR are greatly influenced by the presence of seamounts. Enhanced numerical abundance and species richness probably is linked to active migration to maintain proximity to the seabed on seamounts, which theoretically provides food and habitat. The target taxa are an important component of demersal fish diet (Mauchline and Gordon, 1991; Bergstad et al,. 2010), perhaps more so than diurnally migrating zooplankton, even on seamounts (Hirch and Christiansen, 2010). Thus this work suggests that these decapod shrimp may provide an important trophic link between pelagic and/or benthic ecosystems and the demersal / pelagic fish fauna and other predators in the vicinity of seamounts (Haney et al., 1995). Ubiquitous mesopelagic crustaceans with a benthic component to their diet (such as *S. debilis*, and maybe gnathophausiids) may hold key trophic positions in seamount food webs, perhaps more so than previously assumed (Pitcher and Bulman, 2007) and make benthic energy sources available to larger pelagic predators observed on seamounts. Moreover, these results suggest that biophysical coupling is an important factor in the distribution patterns of most of the species studied here. Future work should explore micronektic interspecific differences in pelagic and benthic trophic energy input, and dietary relationships to higher trophic levels, in order to elucidate seamount energy pathways. The, as yet uncertain, energy input from specialized deep-sea communities such as hydrothermal vents and cold-water coral reefs on the SWIOR seamounts to the pelagic realm should be a further consideration; the former could be explored using isotopic ratios in sulphur (Jardine et al., 2003). Conservation and holistic fishery management efforts on seamounts require good understanding of open ocean energy pathways and food webs, and should consider micronekton distribution patterns on the micro- to mesoscale (1 to 100 km). The consideration of potential influences of different seamount substrates on associated resident micronekton community structure should be an important aspect of fishery management and conservation, particularly when mitigating against anthropogenic impacts such as bottom trawling and mining operations with potential impacts on the water column through suspension of sediment.

Chapter 8

General Discussion

8.1 Introduction

The pelagic realm is the worlds' largest habitat by volume (Horn, 1972; ~1,368,000,000 km^3 (Atkinson et al., 2010). Like mountains in the troposphere, Mid-Ocean Ridges (MORs) protrude into the water column, and are the longest continuous geological features on the Earth's crust, extending geographically more than 60,000 km (Fig. 1.2 A, Kious and Tilling, 1996). MORs are ecologically important because they support many rare and fragile ecosystems, such as deep-sea coral reefs, cold seeps, and vents, yet are also targets of fisheries. The rarity/fishery conflict and the fact that they are on the high seas, out of national jurisdiction, make them important sites for scientific study and conservation (Tyler et al., 2005). Resident fish populations on ridges and seamounts have become the target of trawlers and long-liners, following the collapse of coastal and continental shelf stocks (Pitcher, 2008). With the exception of a few studies on hydrothermal vents and seeps, the fauna of ridges such the Mid-Atlantic Ridge (MAR) and the South-West Indian Ocean ridge (SWIOR) have only just recently become the subject of multidisciplinary studies, mostly because of the difficulties and expense associated with sampling remote deep-sea habitats. Only an estimated 0.0001% of the deep-sea floor has been the subject of studies (Gjerde, 2006) ‘less than the area of a football field’ (quote: Tony Rice in Billett, 2001).

Mechanisms controlling energy links between the pelagic realm and the seabeds of ridges, seamounts, and continental shelves (benthopelagic coupling), are of fundamental interest in pelagic ecology, since these mechanisms will have implications for holistic, eco-system based fishery management and marine conservation (Salomon et al., 2011). At the start of the work reported in this thesis, few studies had attempted to investigate the basin scale influences of MORs, although there had been studies on seamounts. Isaac and Schwarzlose (1965) originally proposed an explanatory mechanism for enhanced benthic and benthopelagic biomass on seamounts: resident nektic predators consume trapped diurnally migrating plankton, causing increased heterogeneity downstream of the seamount (see Haury, 2000 for observations to that effect). To date this remains the dominant paradigm (see Ch. 1; Fig.1.3 from Rogers, 1994, and see Pitcher, 2008). The mechanism is applicable to ridges only in the sense that many ridge-sections extend into the top 1000 m of the water column, where more than 90% of the DVM by biomass takes place (Angel and Pugh, 2000). Residual DVM effects probably are present down to 1500 m (such as in the diurnal pulses of marine-snow fall; Tittensor et al., 2009). Indeed observations and predictions of seamount (rising >1000 m above the surrounding sea floor) locations are prominent in proximity to ridges, perhaps with the exception of the East Pacific Rise (see Fig. 1.2 B, Yesson, et al., 2011). The average MOR depth is deep (~2500 m), and ecological interactions between migrating layers and enhanced nekton biomass observed on ridge crests and slopes (Sutton et al., 2008; Bergstad et al., 2008) remain poorly understood.

8.2 Summary of results in this thesis

This thesis has explored the effect of mid-ocean ridges on the distribution of macrozooplankton and micronekton, and has explored drivers of euphausid diversity and abundance, and pelagic diversity in general, in the Atlantic and the Pacific Oceans.

In Ch. 3 and 4, using euphausiids as model organisms to explore global drivers of species richness, I have shown that the effects of MORs are difficult to detect on a global scale. An expansive set of potential parameters that may influence the distribution of euphausiids was considered in a Generalized Additive Model framework, in the Atlantic and Pacific. The limits imposed by poor spatial data resolution presently available for this type of basin-scale analysis restricted the ability to detect any influence of topography in the open ocean on euphausiid species richness.

The analysis of CPR data revealed that the abundance of euphausiids in the top 10 m of the North-Atlantic is not influenced by the presence of the Mid-Atlantic Ridge (MAR), but is driven primarily by geographical variability in SST (from CPR data, a decrease in 0.29 euphausiids m^{-3} $°C^{-1}$), sea surface height variance (near frontal zones = ~ 300 cm^2) and SiO_3 concentration (-0.18 euphausiids m^{-3} μmol^{-1} l^{-1}). Hypothetically, SSH variance and SiO_3 influences euphausiid abundance through bottom-up mechanisms, by modifying primary production. Although the study did not include proxies for predation (e.g. data on fish abundance), and thus did not to investigate the influence of top-down control mechanisms, the model's high rate of correlation ($r=0.92$) between the predicted and observed values suggests that ecology of euphausiid in the North-Atlantic is strongly bottom-up driven. The CPR survey data from the Pacific were not sufficient to enable prediction of euphausiid abundances throughout the areal extent of the survey, using Generalized Additive Models in this model framework. The general lack of appropriate data for the Pacific compared to the Atlantic means that the study suffered too much from spatial and temporal variability in euphausiid abundance.

Species richness in both oceans increases with sea surface temperature and by dissolved SiO_3 concentration (up to 30% increase over the range of temperature and between 9 and 30% over the range of dissolved SiO_3). The results support the kinetic energy-biodiversity hypothesis (high temperature facilitates high metabolisms, which in turn promotes speciation; see Allen et al., 2002), and provide some support for the potential energy hypothesis (bottom up mechanisms and increased energy supply support higher species richness; Jetz et al., 2009). In the subtropical gyres of the Atlantic and Pacific Ocean, where species richness is higher than that predicted by temperature alone, salinity and less steep thermoclines than in the tropics potentially serve to stabilize the water column and increase niche availability, although exact mechanisms remain conjectural at this point. Species richness is lower in the east of the world's ocean, in seas including the Benguela upwelling (in the Atlantic) and the Humboldt current (in the Pacific), where localized upwelling narrows the latitudinal range of warm, species-rich, tropical water, and instead sustains cold, species poor, and highly productive regimes (which typically harbor specialist fauna; Antezana, 2010). This thesis has revealed notable differences in the drivers of diversity in the Pacific and Atlantic Oceans, for example dissolved silicate concentration was responsible only for some 10 % variability in species richness in the Pacific compared to 30 % in the Atlantic (Table 4.5). The study enabled the prediction of future climate-related species distribution patterns in the Pacific and Atlantic Oceans and the detection of latitudinal heterogeneity in species richness, and differences in the response of the fauna distribution in the two oceans to climate change.

In Ch. 5, I explored the vertical and horizontal distribution patterns of euphausiid species in the North Atlantic (40° to 60° N), in the water column over the Mid-Atlantic Ridge, in relation to dominant hydrographic regions and oceanic fronts. The abundance of euphausiids in the northern mid-Atlantic ocean above the MAR was highly variable on a yearly and spatial scale (Ch. 5), particularly in watermasses north of the Subpolar Front (SPF). There, Arctic currents and coastal retroflection influence community composition, and bring neritic species such as the *Thysanoessa longicaudata* (80%) (and the pteropod *Clione limacina,* see Ch. 5) over the Reykjanes Ridge, where their presence is subject to year-to-year variability. Euphausiid abundance in the SPF also is highly variable (high abundances are not observed throughout the year; Ch. 3 and Ch. 5); the SPF apparently supports enhanced abundance of euphausiids at depth. Sampling at previously unexplored depths (3000 m) revealed a contrasting biogeographic status to that at the near surface. The most latitudinally-extended assemblage of euphausiids showed submergence at the SPF, and is dominated by the epi- and mesopelagic species *Thysanopoda acutifrons* (65%). The SPF epipelagic is dominated by an assemblage composed of *E. krohni* (52%) and *N. megalops* (32%). Assemblages further south (<45°) were not dominated by a single species and overall were more species rich.

Three explanations were originally proposed as potential explanations for the lack of ridge influence on the abundance of surface (10 m) euphausiids caught by the CPR (Ch. 3).

1) The CPR euphausiid data are inadequate for the detection of a ridge effect, as the effect of the ridge on euphausiids is not apparent in the numerical abundance in the top 10 m.

2) The CPR euphausiid data are adequate for the detection of a ridge effect but need to be analysed to species level: numerical abundances are not affected by the ridge, but the species richness is.
3) The ridge does not affect numerical abundance of euphausiids.

The perceived influence detected in Ch. 5 is evidence in support of the first explanations: Near bottom sampling (200 m from the seabed) showed that the abundance of euphausiids in close proximity to the Mid-Atlantic Ridge may be lower than at similar depths in the water column away from the ridges (0.025 ind.10^3 m^{-3} compared with 0.37 ind.$10^3 m^{-3}$ in the open water column). The most geographically-extensive assemblage shows tropical submergence at the Subpolar Front (SPF).

In Ch. 6 I described in greater detail the epi- and mesopelagic invertebrate micronekton community surmounting the MAR, at two locations of distinct primary production patterns. I explored dietary relationships and energy pathways in these two locations and discussed mechanisms by which ecological processes on MOR might serve to deplete the abundance of euphausiids (and potentially mesozooplankton) by harbouring specialized benthopelagic fauna like the decapod *Parapasiphae sulcatifrons* (T. Falkenhaug, personal communications) and the lophogastrid *Gnathophausia* sp (Hargreaves, 1989), and by depleting bathypelagic plankton (Cartes et al., 1994; Hargreaves, 1984) in the benthic boundary layer. Finally, in Ch. 7, I investigated the distribution of crustacean micronekton, and their association with seamounts, on the South-West Indian Ocean Ridge (25° to 42°S). The increase in diversity and abundance of lophogastrid and decapod (both bentho- and bathypelagic) species in association with seamounts are consistent with some of the observations made in Ch. 5 and 6, and was expected, given that only a small percentage of decapod shrimps are entirely pelagic (~10%, Bracken et al., 2010).

8.3 Trophic depletion and nektic biomass enhancement

Evidence presented in this thesis suggests that the influence of MORs on euphausiid abundance is only immediately apparent within 200 m directly of the sea-bed. Euphausiids are mostly epi- and mesopelagic (Brinton et al., 2000), and their abundance decreases logarithmically with depth (see Ch. 5 for evidence to that effect). This makes them unsuited for the investigation of deep-sea topographic signatures. Nevertheless, I contend that mechanisms explored in Ch. 6 and 7, such as the increase in abundance and species richness of benthopelagic and bathypelagic micronekton, may be apparent in even shallower waters above the ridge crest. These mechanisms presently are detectable in the potential changes in abundance of benthopelagic fauna only. As yet unpublished data (on decapod shrimp and lophogastrids; T. Falkenhaug; and K. Meland, personal communication) may provide further support for this.

I propose a modified version of Rogers' explanation (1994; Fig. 8.1) for the influence to underwater ridges of >1500 m depth in the pelagic realm. This new modified version assumes ridges, at depth deeper than those influenced by epipelagic DVM (> 1500 m), have an intrinsic population of micronekton, in the bathypelagic layer (BPL, such as *Gnathophausia* sp), in addition to the benthopelagic boundary layer (ie enhanced fish biomass in the top 200 m above the sea bed, see Sutton et al., 2008)). The BPL is composed of animals that increase in abundance in proximity to the seabed, and interact with it in some way, yet still are caught several hundred meters above, usually in conjunction with benthopelagic DVM ascension from the seabed (i.e DVM plankters being preyed upon directly by nekton). The model does not incorporate ‘seamount’ effects, such as the trapping of the DVM, and does not predict the large nekton stocks on ridges typically observed on seamounts (although the biomass of the BBL may be higher than at similar depth in the watercolumn).

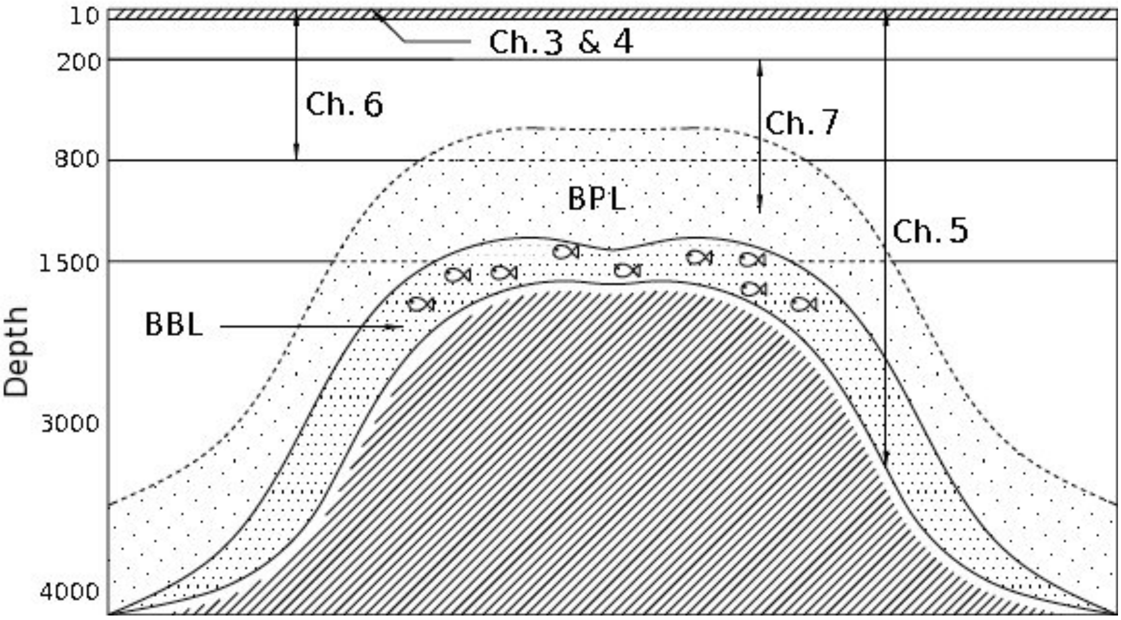

Fig. 8.1 The cross-section of a hypothetical Mid-Ocean Ridge (MOR) deeper than the influence of DVM (> 1500 m). Contribution of each thesis chapter to knowledge on various faunal categories is shown. The biomass of the benthopelagic boundary layer (BBL, mostly fish) is enhanced on ridges (see Sutton et al., 2008), and depletes zooplankton abundance there (Ch. 5). The bathypelagic layer (BPL) of the MOR extends into the mesopelagic, and competes with 'true' pelagic zooplankton and crustacean micronekton in the mesopelagic (200-1000 m, see Vereshchaka, 1995, Ch. 6). Combination of BPL species and mesopelagic crustacean micronekton leads to the increase in species richness in the mesopelagic over ridges (some evidence to that effect presented in Ch. 6) and in seamounts (Ch.7). Little to no ridge signature is detected in the top 10 m, as sampled by the Continuous Plankton Recorder (Ch.3 and 4).

However, the BPL penetrates into the mesopelagic, and thus interacts with epi- and mesopelagic diel migrators. Consequently, biomass in the BBL may be enhanced and maintained via a trophic 'detour' in the BPL. I propose a hypothesis with regard to this model: all else being equal, trophic level (using $\delta^{15}N$ for proxy) of resident demersal fish on seamounts/ridges will typically be positively correlated with depth (i.e the greater the depth, the higher the trophic level). Some evidence not inconsistent with this hypothesis stems from ingested diet studies on the MAR, which suggest that demersal fish (like roundnose grenadier) feed predominantly on micronekton such as cephalopods, decapod shrimps and small teleosts, rather than on more planktic species such as euphausiids (Bergstad et al., 2010). Moreover, the proportion of planktic animals in the diet shows little ontogenetic variation; in fact other studies indicated that depth could be a better predictor of diet than size (Stowasser et al., 2009). Species with broad vertical ranges (such as the demersal fish *Antimora rostrata*) are best suited for testing this hypothesis.

While interactions between fish and DVM zooplankton typically leave zooplankton populations (such as euphausiids) depleted and heterogeneous downstream of seamount (Haury et al., 2000), no observation to that effect on ridges has been made as part of this thesis. However, given the depletions observed in the BBL, it is not inconceivable that similar mechanisms could deplete deep zooplankton population downstream of ridges.

The total area of oceanic ridge accounts for some 22% of the planet's surface, and is similar in size to the total area covered by dry land (29%, Fairbridge, 1966; Marshall, 1979; Garrisson, 2002). The total area of ridges is 115,200,000 km^2, and the volume of the near-bottom layer (200 m) on ridges is therefore 230,400,000 km^3. The total volume of the pelagic habitat is 1,368,000,000 km^3 (Angel, 1993), which means that mechanisms explained here serve to deplete euphausiids from some 2% of the total volume of the pelagic realm. Assuming an average ridge depth of 2500 m, residual effects may be detectable throughout the entire water column, and involving some 20% of the pelagic realm (=115,200,000 km^2 * 2500 m*100/1,368,000,000 km^3). As some euphausiid assemblages are restricted to specific depths at varying latitudes (because of tropical submergences, Ch. 5), MORs that run east to west (e.g such as the SWIOR, and the East Pacific rise) may serve to restrict their horizontal distribution. The influence of ridges in the ocean basin may be comparable to that of hedges in a farmland (Pulido-Santacruz and Renjifo, 2010): whilst delimiting the extent of crops (or zooplankton assemblages), hedges serve as local hotspots of mammal and avian diversity (or Gnathophausiids and decapod shrimps, and hydrothermal vents).

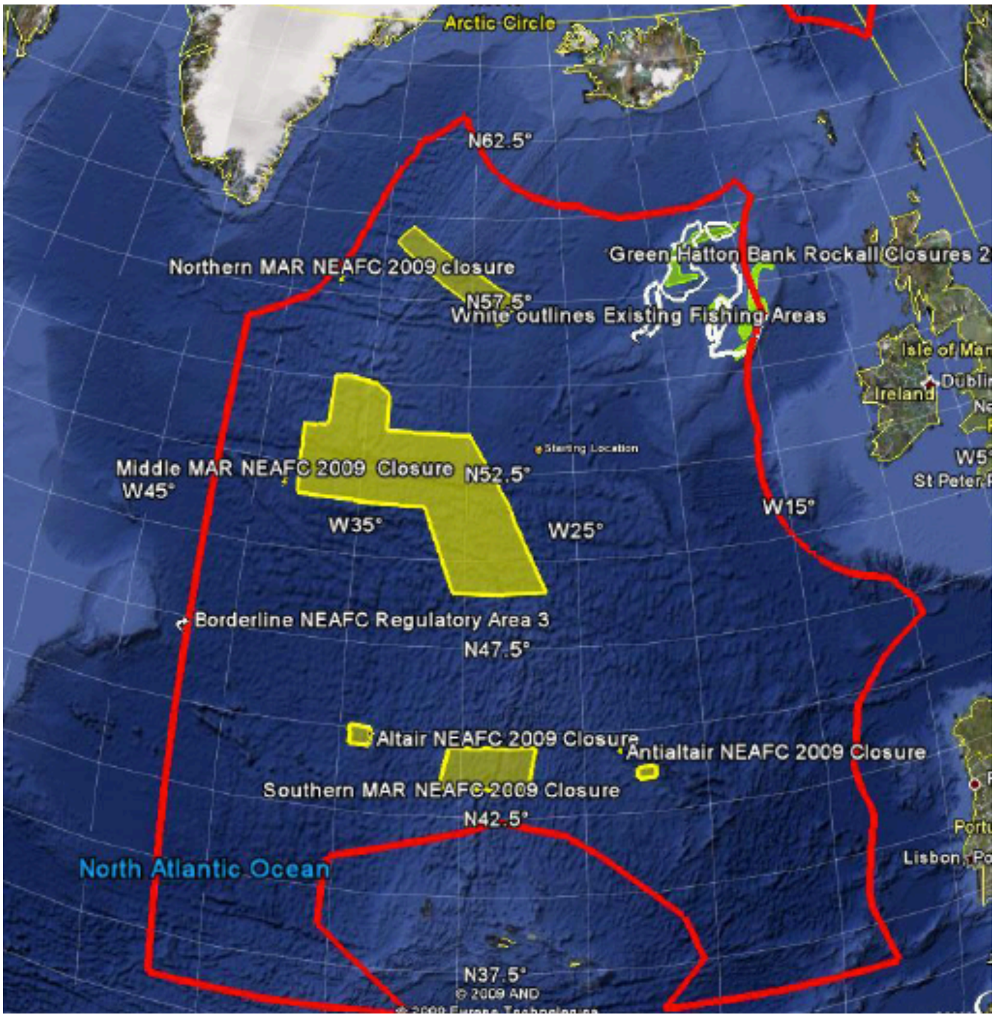

Fig. 8.2 The five yellow areas on the Mid-Atlantic ridge are closed to bottom trawling by the NEAFC in April 2009. The red line is the boundary of the high sea areas in the North East Atlantic. From NEAFC (2009).

In the pelagic realm, MORs increases heterogeneity, by limiting the spatial extent of zooplankton assemblages at depth, and diversity, in the BPL. MORs also served to increase benthic diversity (see Gebruk, 2008). In the Atlantic, recognition of this by the North-East Atlantic Fisheries Commission has led to several areas of the high-sea sector of the MAR being closed to bottom trawling (NEAFC, 2009; see Fig 8.2).

8.4 Future research and recommendations

8.4.1 Species distribution and biogeography

This thesis has shown that some 30% of variability in euphausiid species richness on a basin scale can be explained by variability in temperature alone. The remaining 70 % is explained by different combinations of longitudinal patterns in upwelling, and geographical variability in nutrients and salinity. Recent work (Tittensor et al., 2010) has shown that averaging over greater grid resolution (774400 km^2, compared to 82140 and 60000 in the Atlantic and Pacific here) can mask such differences (the term ‘ocean’, e.g. Atlantic or Pacific, was not a significant predictors of species richness in the Tittensor study). Moreover, when predicting biological responses to environmental change, and when devising mitigations to potentially detrimental ecological effects, attention to different processes in either ocean may prove essential. For example, high productivity due to river output in the tropical Indian Ocean means pelagic diversity there is markedly lower than at similar latitude in the Atlantic or Pacific (Zeitzschel, 1973).

Whilst the basin scale modeling approach is informative for the detection of ecological patterns, the physiological basis underlying the environmental relationships remains unclear. When considering the potential responses of zooplankton distribution to environmental change (Beaugrand et al., 2002; Lynam et al., 2010), little empirical evidence exists on the physiological mechanisms responsible for the variable-diversity patterns (Roy, 2008). Such evidence often is extrapolated from *in vitro* experiments on model organisms, or derived from high-resolution data and direct observations over a limited spatio-temporal scale (Brierley and Cox, 2010). Expanding the scope of such studies is crucial, considering the potential global biological impact to predicted environmental change (Brierley and Kingsford, 2009). As the amount of data on the distribution of marine (and terrestrial) species increases, so should the predictive power of models such as those explored in Ch. 3 and 4. While the global scope of marine environmental data will enable more studies such as those presented here (Ch. 3 and 4, where no assumption are made regarding the hypothetical drivers of diversity), the relationships established between the individual predictive terms and species, should leave several avenues open for further study. For example:

1) What is the nature of the dissolved SiO_3 concentration/plankton diversity relationship?
2) By what mechanisms do the specific characteristics of the sub-tropical gyres in the world's ocean increase planktic species diversity?
3) What are the specific ecological consequences of species assemblages moving poleward in each hemisphere?

8.4.2 The influence of Mid-Ocean Ridges

In this thesis, studies on remote MORs have provided a framework and outlines for mechanisms that may explain observations of ridge-associated fauna, by exploring the influences of ridges on a variety of scales. However, there is a need to understand the fine scale interactions between the pelagic mesozooplankton, micronekton, and nekton, in the bentho-pelagic and the benthic boundary layer. This kind of high-resolution deep-sea research is notoriously expensive and time consuming, and requires specialized sledges (Vereshchaka, 1995; Cartes et al., 1994) and remotely operated vehicles and manned submersibles (Vinogradov, 2005).

A complete understanding of the oceanic trophic spectrum, away from coastal shelves and margins, is still a distant prospect, and several questions remain open for future study. Meta-analysis of high- to low-end trophic interactions, and full food-webs are beginning to emerge, combining data from trophic studies on ingested (e.g stomach content) and integrated (e.g from Fatty acid and Stable isotope analyses) diets of fauna across the trophic spectrum (Atkinson et al., 2010). For example, on the MAR in the North Atlantic, studies are emerging on the benthic macrofauna and nekton, pelagic nekton, and macrozooplankton (presented in Ch. 6 in this thesis), and may provide overview of broad energy pathways there. The improved understanding of integrated diets, following the increased use of biochemical techniques, can elucidate benthopelagic coupling (using Nitrogen and Carbon isotopes) and hydrothermal energy sources in the deep-sea (using Sulphur; Hügler, et al., 2011). Sulphur isotopes may provide useful insight in the potential energy input of vents and seeps to the pelagic realm, traditionally considered minor (some 1 ‰ of the global marine primary production; Bach and Edwards, 2003 and Field et al., 1998; but see Adams et al., 2011). Further and ongoing work on the MAR includes the analysis of decapod shrimps and lophogastrids collected on the R/V *G.O Sars* cruise (T. Falkenhaug and K. Meland personal communications), and the analysis of the bathypelatic nektic food web on the ridge (V. Carmo, T. Sutton personal communications). The final ECOMAR cruise conducted several Remotely Operating Vehicle (ROV) transects on the ridge. While this thesis includes a pilot study from the SWIOR, subsequent cruises are planned to seamounts there, equipped with an ROV in order to survey prevalence of deep-sea coral reefs, and hydrothermal vents. Information on the distribution of these habitats at or over the mesoscale would enable the exploration of regional effects of hydrothermal vents and deep-sea coral reefs on pelagic processes, a further consideration in the management of high-sea fish stocks. Further efforts are planned for the southern MAR, between South-America and Africa. Pilot studies were conducted in October 2009 onboard the Russian RV *Akademik Ioffe* on the southern MAR in order to replicate efforts from the North Atlantic there. While research programs targeting MORs in the

South Atlantic and in the Indian Ocean are still at an early stage, it is the ultimate aim that ongoing survey efforts will lead to closure of areas of special biological interests to bottom fishing, in order to provide better managed and sustained fish stocks overall.

9 References

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Appendix A

This section contains electronic copies of published papers resulting from the work described in this thesis, and data used in the analysis presented in chapter 3 and 4. The papers and associated disclaimers of contribution are given in chronological order of article publication.

(Note: Owing to copyright restrictions, the electronic version of this thesis does not contain the texts of these articles.)

-Letessier, T. B., Cox, M. J., and Brierley, A. S. (2009). Drivers of euphausiid species abundance and numerical abundance in the Atlantic Ocean. *Marine Biology*, *156*(12), 2539-2553.

I estimate I contributed 60 % of the total effort towards this paper. Grid construction and data mining/generation was conducted by myself under the directions of ASB. GAM modelling and writing of method section was conduct mostly by MJC. The paper was mostly written by myself with help from ASB and MJC

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-Letessier, T. B., Cox, M. J., and Brierley, A. S. (2011). Drivers of variability in Euphausiid species abundance throughout the Pacific Ocean. *Journal of Plankton Research*. doi: 10.1093/plankt/fbr033

I estimated I contributed 65% to the total efforts toward this paper. Grid construction and data mining/generation was conducted by undergraduate students under my supervision. GAM modelling was conduct mostly by MJC. The paper was written by myself with input from ASB and MJC.

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-Letessier, T B, Falkenhaug, T, Debes, H, Bergstad, O A, and Brierley, A S (2011). Abundance patterns and species assemblages of euphausiids associated with the Mid-Atlantic Ridge, North Atlantic. *Journal of Plankton Research*.

I estimate I contributed 70% to the total efforts towards this paper. Euphausiid samples on the RV *Arni Fridrikkson* were sorted and identified by HD. Samples from the RV *G.O Sars* were initially analysed by myself, but needed revisions from TF. Samples on the RV *Henry Bigelow* and RV *James Cook* were sorted and identified by myself. The data analysis and write-up was done by myself, with inputs from all authors.

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-Letessier, T. B., Pond D. A., McGill R. A. R., Reid W. D. K., Brierley, A S (in prep) Trophic interaction of invertebrate micronekton on either side of the Charlie Gibbs Fracture Zone / Subpolar Front of the Mid-Atlantic Ridge. *Journal of Marine Systems*

I estimate I contributed 85 % to the total efforts toward this paper. Net sampling, sample preparation, data analysis and writing was conducted by myself with guidance on the biochemical aspects from DAP, RARM, WDKR. The paper was written by me with input from DAP, WDKR and ASB.

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-Letessier T. B, De Grave S., Boersch-Supan P., Rogers A. D., Kemp K., Brierley A. S. (in prep) The biogeography of pelagic shrimps (Decapoda) and gnathophausiids (Lophogastridea) on seamounts of the South-West Indian Ocean Ridge. *Deep-Sea Research Part II-Topical Studies in Oceanography*

I estimate I contributed 80% to the total efforts toward this paper. Net sampling and catch sorting was conducted by myself with assistance from PBS, KK, and ADR. Samples identification was conducted by myself and SDG. Data analysis was conducted by myself. The paper was written by me, with inputs from all authors.