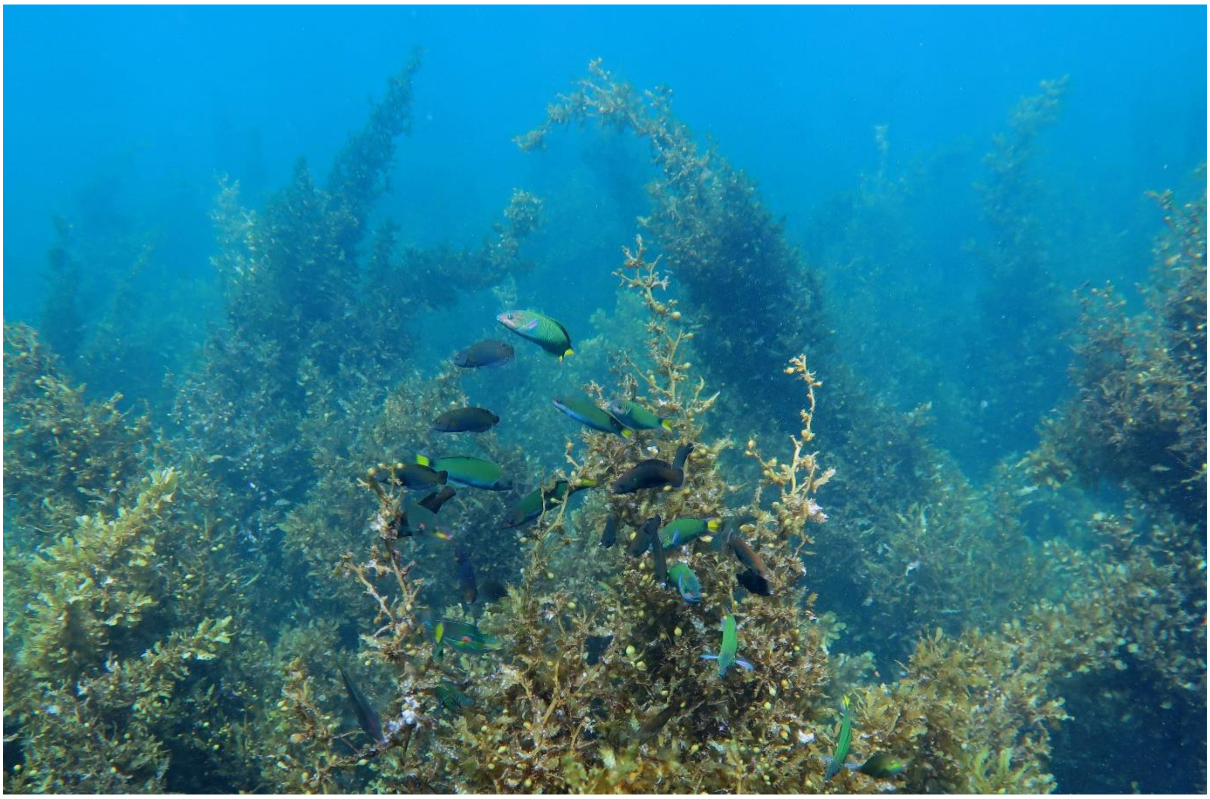
THE NATURE AND SIGNIFICANCE OF 'MACROALGAE – EPIFAUNA – INVERTIVOROUS FISH' TROPHIC LINKS WITHIN A MACROALGAL-DOMINATED REEF ECOSYSTEM



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A thesis submitted for the degree of Doctor of
Philosophy of The Australian National University

October 2021

Declaration

This thesis is my original work, containing no materials which have been accepted for a degree by any other university or institution. This thesis is for the degree of Doctor of Philosophy at The Australian National University. I am the chief author on all the chapters presented in this thesis, with my role being to lead the development of ideas, experimental design, data collection in the field, sample processing in the lab, statistical analysis and publication writing.

Rebecca Fox (primary supervisor), Michael Jennions (chair of supervisory panel), Paul Cooper (co-supervisor), Graham Edgar and Chris Fulton are co-authors who contributed helpful assistance and constructive suggestions either on the published chapters or on the thesis chapters that will be forthcoming as peer-reviewed publications. Given the collaborative nature of these chapters, I use the pronoun ‘we’ to represent all the co-authors in these chapters. Of the chapters that have been published or accepted by peer-reviewed journal (Chapters 2, 3 and 4), the text including figures and tables that are presented in this thesis is the publication version. Of the chapters that are for forthcoming publication (Chapters 5 and 6), the submitted, pre-publication version of the manuscripts is presented in this thesis. Adjustments have been made in each chapter as necessary for formatting purpose only for those which The Australian National University requires.

This thesis followed the instructions of *Animal Ethics Protocol* (protocol number: A2018/01, A2019/01), *Animal Welfare Act 2002 and Animal Welfare (Scientific Purposes) Regulations 2003* (licence number: U41/2019-2021), *Licence to Take Fauna for Scientific Purposes* (licence number: 08-001706-1) and *Fauna Taking (Scientific and Other Purposes) Licence* (licence number: FO25000059), to conduct any relevant data collection and sample process. All fieldwork and lab work were supervised by *The Australian National University Animal Experimentation Ethics Committee*, *The Australian National University* and *Government of Western Australia (The Department of Park and Wildlife*, *The Department of Primary Industries and Regional Development*, and *The Department of Biodiversity, Conservation and Attractions)*.

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Thesis abstract

Canopy-forming seaweeds, generally brown macroalgae, are important primary producers and habitat constructors within marine environments worldwide. In tropical regions, macroalgae have been much maligned because of their negative competitive interactions with corals. However, macroalgal habitats are themselves extremely valuable. They provide food, shelter and nursery for associated invertebrates and fishes, including economically important species, thereby supporting high biodiversity and productivity. However, compared to other marine habitats such as coral reefs and mangroves, our understanding of the productivity and ecosystem functioning of macroalgal habitats is much more limited.

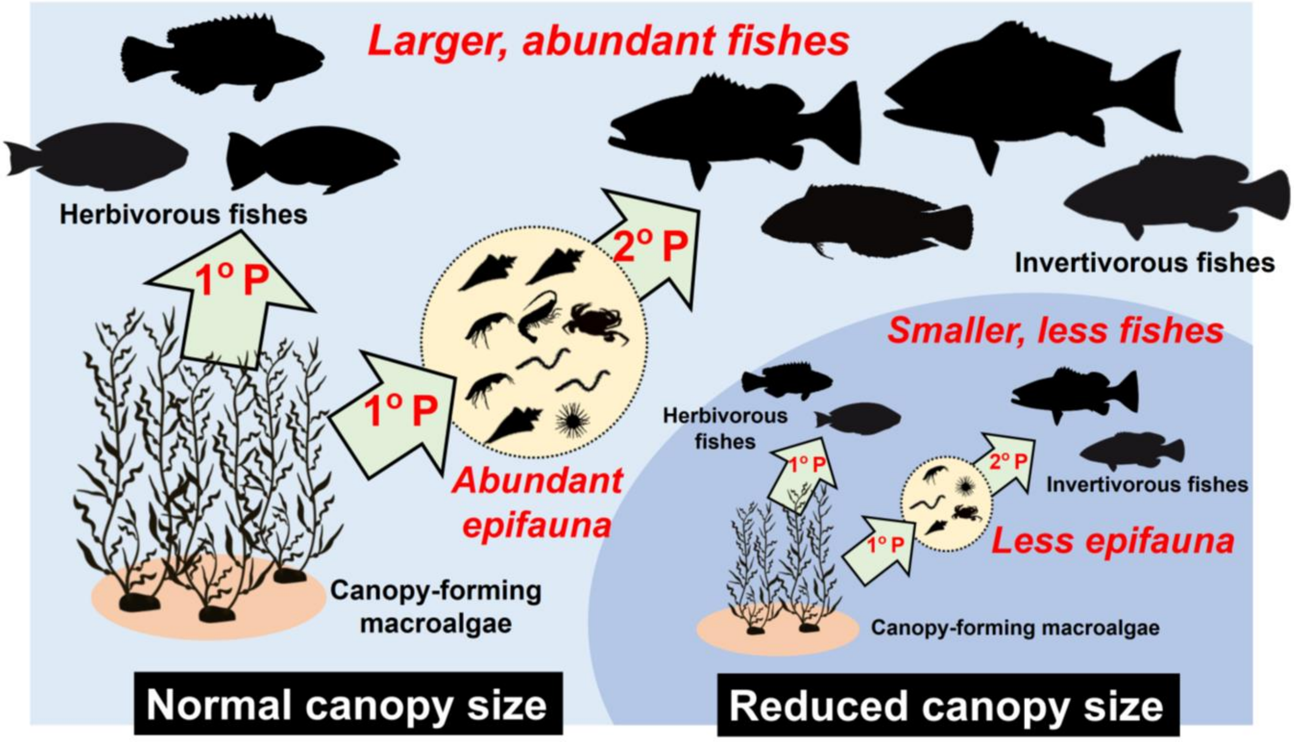
Using field data collected from meadows of the fucoid *Sargassum* in Ningaloo Marine Park, Western Australia, my thesis examines key aspects of the way in which these habitats function including: (1) a general introduction based on a comprehensive review of the role of epifaunal invertebrates as links in the food chain between primary producers (macroalgae) and secondary consumers (invertivorous fishes); (2) the response of epifaunal community structure to primary producers, predators and habitat settings across seascapes; (3) the effect of seasonal fluctuations in macroalgal canopy structure on epifaunal production and the wider implications of changes in meadow size that could occur due to ocean warming; (4) the foraging preferences of key secondary consumers (invertivorous fishes) of epifauna with a discussion of the potential and the importance of niche partitioning within shifting environments; and (5) the impacts of predation by invertivorous fishes on epifaunal biomass associated with these macroalgal habitats based on experimental estimates of the transfer of epifaunal production to the next trophic level.

As the rate of global changes increases, the structure and functioning of marine ecosystem will alter radically. Despite being a pivotal component in marine food webs connecting primary producers and higher-order consumers, epifauna are rarely studied and are ambiguously defined. In chapter 2 I build a systematic framework for the study of epifaunal communities within marine habitats, which offers a consensus-based definition of epifauna as an aid to unify different research areas. In chapters 3 and 4 I examine the community structure and quantify the secondary productivity of epifauna within a macroalgal-dominated marine ecosystem in Ningaloo, and assess how these variables relate to biotic and abiotic environmental factors. Macroalgal canopy size, canopy cover, predator biomass and seascape setting are shown to be key drivers of spatial and temporal fluctuations in epifaunal community structure and productivity, and sensitivity analysis also indicated that even small reductions in canopy size and/or canopy cover could lead to dramatic drop in epifaunal production. In Chapters 5 and 6 of the thesis I move on to examine elements of the trophic linkages between canopy-associated epifauna and higher-order consumers (invertivorous fishes). Invertivorous fishes in Ningaloo were chiefly represented by species belonging to the Labridae, Lethrinidae and Mullidae. Individual species demonstrated strong foraging microhabitat preferences and could be grouped into three foraging categories: ‘canopy forager’, ‘generalist’ and ‘abiotic forager’. Using classic predator exclusion caging experiments, I show that predation by invertivorous fishes has a significant influence on epifaunal density within macroalgal canopy, and I am also able to quantify productivity transfer from epifauna to invertivorous fishes.

My research highlights the importance of trophic links between canopy-forming macroalgae, epifaunal invertebrates and invertivorous fishes within tropical seascapes, as well as the vulnerability of these links to changes in habitat structure that are forecast to occur under global change. The results of my research will enhance our understanding of the functional impacts of macroalgae-associated species, as well as our understanding of trophic flows in marine food webs and assist with the development of appropriate management and conservation planning.

CHAPTER 1

GENERAL INTRODUCTION



The importance of canopy-forming macroalgae in tropical seascapes

Macroalgae are one of the most important macrophytes found worldwide in marine environments, where they are key components of global carbon and oxygen cycles (Chung et al. 2011, Titlyanov & Titlyanova 2012, Fulton et al. 2019). In tropical seascapes, a great diversity of macroalgae can be dominant species, ranging from small-sized algal turfs (1 mm – 2 cm) and medium-sized foliose understory macroalgae (5 cm – 20 cm) to fleshy canopy-forming fucoids and kelps which can reach up to several metres in height (Steneck & Dethier 1994, Titlyanov & Titlyanova 2012, Aued et al. 2018, Assis et al. 2020). Canopy-forming macroalgae have been documented as the major type of macroalgal communities in both tropical and temperate marine environments (Fulton et al. 2019, 2020, Assis et al. 2020). These multicellular autotrophs have highly differentiated tissues which form leaf-like (thallus/blade), stem-like (stipe) and root-like (holdfast) structures, allowing them to attain a complex structure, creating a large-sized leathery canopies which provide an extensive surface for colonisation and residence of associated marine assemblages (Steneck & Dethier 1994, Carvalho et al. 2018, Fulton et al. 2019).

Along tropical coastlines, canopy-forming macroalgae often form dense meadows that are interspersed with other habitat-forming organisms such as corals, sponges and seagrasses. Together these organisms generate an interconnecting mosaic of habitat type which support numerous marine species (Kobryn et al. 2011, Fulton et al. 2019, Hall & Kingsford 2021). Studies have found that canopy-forming macroalgal meadows can support a higher abundance and biomass of marine species than other marine macrophytal habitats such as seagrass and understory macroalgae (Taylor 1998a, Tano et al. 2016, Wenger et al. 2018); and many studies have further documented that canopy-forming macroalgal meadows act as key food resources, foraging grounds, shelters against predators and/or nurseries for associated invertebrates and fishes, including those that are fishery and recreational targets (Wilson et al. 2010, Tano et al. 2017, Chen et al. 2020 (see Chapter 3)).

As key primary producers in tropical seascapes, canopy-forming macroalgae convert solar power into organic matters via photosynthesis to construct the trophic base of marine food webs, which therefore provide a range of ecosystem service across higher trophic levels. Not surprisingly, canopy-forming fucoids such as *Sargassum* have been identified as being as productive as reef building corals in terms of their high rate of net areal primary productivity in tropical marine ecosystems worldwide (studies reviewed in Fulton et al. 2019). Previous studies have also indicated that canopy-forming macroalgae contribute higher net areal primary productivity than other common benthic producers such as seagrasses and corallines (Schaffelke & Klumpp 1997, Eidens et al. 2014). The products of this high rate of primary production are directly used by herbivorous invertebrates and fishes (Lim et al. 2016, Chen et al. 2021 (see Chapter 2), Froese & Pauly 2021), then indirectly utilised by higher-order consumers such as invertivorous and piscivorous fishes which target macroalgae associated herbivores (van Lier et al. 2018, Wenger et al. 2018, Froese & Pauly 2021). In addition, the primary production generated by canopy-forming macroalgae is not only used by local biome but also exported as subsidies into adjacent marine ecosystems (Hyndes et al. 2014, Zubia et al. 2015, Fulton et al. 2019). Canopy-forming macroalgae therefore underpin a wealth of marine biodiversity and important outputs such as productive fisheries. Interestingly, the primary production generated by tropical canopy-forming macroalgae often demonstrates prominent temporal patterns, chiefly due to strong seasonal fluctuations in macroalgal canopy size (e.g., changes in volume, thallus length or biomass) as well as total meadow area. Two opposite patterns of seasonal fluctuations have been well documented: (1) In some regions, canopy-forming macroalgae start their growth in early spring, then reach a maximum of canopy size in late summer when there are higher sea temperature, followed by the detachment of canopies in autumn, with short stipes and spare holdfasts left in winter (Leite & Turra 2003 (Flamengo Bay, Brazil), Lefevre & Bellwood 2010 (The Great Barrier Reef, Australia), Fulton et al. 2014 (Ningaloo Reef, Australia)); and (2) in other regions, canopy-forming macroalgae sprout and reproduce during months with cooler sea temperature, but massively loss their canopies in the summer as water temperatures rise (Trono & Lluisma 1990 (Santiago Island, Philippines), Ang 2006 (Tung Ping Chau Marine Park, Hong Kong), Ateweberhan et al. 2009 (Massawa, Red Sea)). These seasonal fluctuations associated with shifts in sea temperature can impact on associated trophic groups that rely on the primary production generated by canopy-forming macroalgae.

Despite canopy-forming macroalgae playing an important role in our marine ecosystems, tropical macroalgal habitats are far less well studied than their relatives in temperate regions (see studies reviewed in Fulton et al. 2019). Moreover, in most tropical seascapes, macroalgae have been much maligned because of their negative competitive interactions with corals, also known as ‘coral – algal phase shifts’. Phase shifts occur when the cover of scleractinian corals is reduced in favour of macroalgal dominance, gradually switching the ‘coral dominant phase’ to the ‘macroalgae dominant phase’. While this has increased the awareness of the importance of macroalgae in tropical marine management, studies have often been skewed towards documenting the negative effects of macroalgae on reef-building corals (McCook et al. 2001, Bellwood et al. 2004, McManus et al. 2004, Hughes et al. 2017). However, macroalgae, especially canopy-forming species, can be indigenous, occur naturally in some areas, and be the dominant habitat generators and energy providers. They deserve more attention as natural ecosystems.

Key trophic mediator: macroalgal canopy-associated epifaunal invertebrates

Epifauna is a collective term that refers to the small-sized (typically 0.5 – 10 mm), mobile or sessile invertebrates living at the interface between a microhabitat surface and sea water. Epifauna are abundant and common to all marine habitats including the canopies of other organisms such as macroalgae and seagrasses (Edgar 1990a, Fraser et al. 2020a, Chen et al. 2021 (Chapter 2)). Epifauna are important mediators that contribute to key ecosystem processes in marine environments. Firstly, they interact with microbes through multiple processes, including ecosystem engineering, grazing and symbiosis, facilitating the cycling of carbon, nitrogen and other nutrients between the water column and microbes in the benthos (Robertson & Lenanton 1984, Fenchel 2008, Hepburn et al. 2012). Second, epifauna are essential secondary producers which provide the trophic links between primary producers and higher-order consumers (Taylor 1998a, Cowles et al. 2009, Fraser et al. 2020c). The high levels of secondary production generated by epifauna has been suggested to be one of the most productive trophic guilds across seascapes. For example, previous studies have documented that epifaunal communities can produce up to 75% of the total annual secondary production within a habitat, which is sufficient to support large populations of macroinvertebrates and fishes that consume them (Edgar & Aoki 1993, Taylor 1998a, Kramer et al. 2015).

In tropical canopy-forming macroalgal meadows, abundant and diverse epifauna are a key food resource for higher-order consumers, making canopy-forming macroalgal meadows important foraging grounds for a large variety of associated consumers, especially predatory reef fishes (Wilson et al. 2014, Tano et al. 2016, van Lier et al. 2018). Epifauna contribute to the quality and quantity of food resources provided by canopy-forming macroalgal meadows, which have been identified as important nurseries for reef fishes. Consequently, epifauna are themselves likely to be one of the key enhancing factors that integrate the development of appealing fish nurseries with high nutritional load and food availability (see studies reviewed in Chen et al. 2021). Epifaunal secondary production in tropical canopy-forming macroalgal meadows also shows a pattern of seasonality, which chiefly correlate with the previously described temporal fluctuations in the canopies of their macroalgal hosts (Chen et al. *in press* (Chapter 4), Leite & Turra 2003, Ba-Akdah et al. 2016). These periodical shifts in epifaunal secondary production can alter food supply, change the strength of biological interactions such as predation and competition and affect the rate of energy flows across trophic levels (see studies reviewed in Chen et al. 2021). All these factors influence the biodiversity and ecosystem functioning of canopy-forming macroagal habitats. However, despite their ubiquity and their importance in underpinning marine food webs across many global seascapes, epifauna remain a relatively understudied component of marine ecosystems, especially in tropical seascapes such as macroalgal meadows, compared to other visible and gregarious marine organisms such as corals and megafaunal invertebrates.

To date, our understanding of how epifaunal communities and their secondary productivity response to changing environments is still far from complete.

The significant roles of invertivorous fishes in tropical macroalgal meadows

Invertivorous fishes are species that primarily forage on invertebrates, representing one of the most dominant trophic guilds in most marine environments across the world (Randall et al. 1997, Longo et al. 2019, Froese & Pauly 2021). Overall they comprise a varied range of species in numerous diverse families, including the families Labridae (excluding Scarinae), Lethrinidae, Mullidae and Serranidae, many of which are common targets of commercial and recreational fisheries (Sumner et al. 2002, Fulton et al. 2020, Froese and Pauly 2021). In tropical macroalgal meadows, a great abundance and diversity of invertivorous fish communities can often be found using the macroalgal canopies as their foraging grounds where they prey upon epifauna (Tano et al. 2016, Chen et al. 2020, Fulton et al. 2020). Previous studies have shown that macroaglae-associated invertivorous fishes are able to shape the community structure and affect the production of lower trophic levels in the food webs, such as the epifauna (Martin-smith 1994, Wenger et al. 2018, Chen et al. 2020). By consuming macroaglae-associated epifauna, invertivorous fishes which are themselves the prey of mesopredatory piscivores and apex predators, are able to transfer energy to the next trophic level, facilitating the widely perceived important trophic links between primary producers and higher-order consumers that underpin marine biodiversity and ecosystem functioning. Trophic links connected by invertivorous fishes occurs across all trophic levels in marine food webs, and they are bi-direction with both top-down and bottom-up effects. According to recent studies, major shifts in the abundance and/or taxonomic composition of tropical invertivorous fish have been linked to temporal fluctuations in macroalgal canopy size and meadow area (Wilson et al. 2014, 2017, Wenger et al. 2018). Understanding how the density and productivity of invertivorous fishes' response to periodical fluctuations in macroalgal habitats and/or their associated epifaunal community structure can help to improve our knowledge of how natural and anthropogenic disturbances affect fishery production and ecosystem functioning over both space and time. However, attempts to quantify the productivity and influences of invertivorous fishes as middle level consumers of epifauna are still rare and mainly limited to temperate reefs (Edgar & Aoki 1993, Taylor 1998a). To date, the relevant empirical data about factors that would allow us to estimate fish production in tropical seascapes such as foraging rate and dietary details are still limited

(Morais & Bellwood 2018, 2020). These data are necessary to assess how trophic links underpinned by invertivorous fishes affect ecosystem functioning and trophic dynamic, especially if we can then link global changes in sea temperatures to shifts in food availability.

Ningaloo Reef as an excellent ecosystem for studies of marine functionality

Ningaloo Reef (-21°42' – -24°1', 113°25' – 114°15') is a 290 km long fringing coral reef situated in the northwest coastal region of Western Australia. It is a World Heritage site which is also identified as the world’s largest fringing coral reef. Here, shallow water is enclosed to form a large lagoon dominated by brown macroalgae, chiefly belonging to the canopy-forming genus *Sargassum* which produce dense canopies to generate massive meadows that harbour numerous marine species including epifauna and reef fishes (Wilson et al. 2010, Kobryn et al. 2013, van Lier et al. 2018). Terrestrial runoff into the Ningaloo lagoon is minimal, due to the aridity of the adjacent coastline, the lack of major river catchment and the low seasonal rainfall. In addition, the low density of human settlement and non-destructive fishing methods of local recreational fisheries create relatively low pressure on Ningaloo habitats from anthropogenic activities (Cassata and Collins 2008, Wilson et al. 2012, Fulton et al. 2014). As a result, Ningaloo Reef provides a unique ecosystem to assess the interactions and energy flows that occur between each trophic levels, starting with the primary production of macroalgae. It also an ideal location to allow researchers to explore the influences of changing natural environments on marine macrophytes and their associated animal communities.

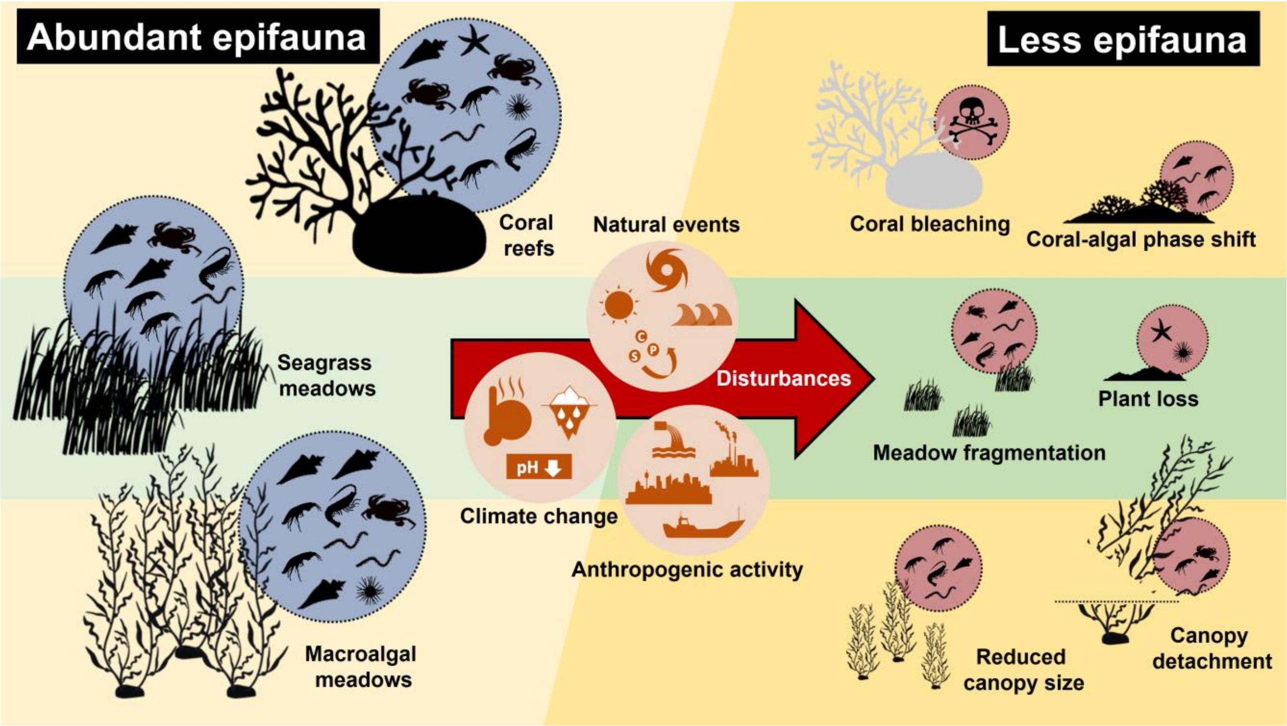
Thesis aims & outline

In this thesis, I introduce the classic ‘*canopy-forming macroalgae – epifaunal invertebrate – invertivorous fish*’ food chain, using a tropical fringing coral reef ecosystem of Ningaloo Marine Park in Western Australia as an example. I then describe the use of *in situ* underwater survey techniques: to inspect the functional nature of macroaglae-associated epifauna and fish; to explore the key aspects of the energy flows happening across different trophic levels; and to examine how primary and higher-order consumers response to shifts in primary production and resource availability. The aims and outline of this thesis follow the order of the links in a typical food chain building from the bottom up to answer specific questions. Investigations relevant to each achieved aim are presented in five chapters. In Chapter 2 '*The nature and ecological significance of epifaunal communities within marine ecosystems*' I examine the definition and functional roles of epifaunal invertebrates as links in the food chain between primary producers (canopy-forming macroalgae) and secondary consumers (invertivorous fishes). This chapter then sets the scene for the empirical chapters that follow. In Chapter 3 '*Sargassum epifaunal communities vary with canopy size, predator biomass and seascape setting within a fringing coral reef ecosystem*' I investigate the response of epifaunal community structure to primary producer *Sargassum*, invertivorous fishes and habitat settings across tropical seascapes in Ningaloo. In Chapter 4 '*Quantifying epifaunal secondary production within tropical macroalgal meadows: seasonality and sensitivity to canopy structure*' I further quantify the secondary production generated by tropical epifauna and explores the effect of seasonal fluctuations in macroalgal canopy structure on epifaunal production in Ningaloo. I then discuss the implications of changes in meadow area that could occur under conditions of global warming. In Chapter 5 '*Foraging microhabitat preferences of invertivorous fishes within tropical macroalgal meadows: identification of canopy specialists*' I highlight the community composition and foraging microhabitat preferences of key secondary consumers (invertivorous fishes) of epifauna in tropical macroalgal meadows in Ningaloo. I also refine the description of the trophic guilds of 'invertivores', and point to the potential importance of niche partitioning among species within shifting environments. In Chapter 6 '*Estimates of trophic linkages between epifauna and invertivorous fishes within a macroalgal-dominated reef habitat: an experimental approach*' I explore the impacts of predation by invertivorous fishes on epifaunal biomass associated with canopy-forming macroalgal habitats. I do so by taking an experimental approach to estimate the transfer of secondary production from epifauna to the next trophic level. Finally, in Chapter 7 I summarise my main findings, synthesis the key discoveries that I have made and suggest productive lines of future research.

Overall, in my thesis I address five important gaps in our knowledge of the functional roles of macroaglae-associated species. I demonstrate the importance of taking a holistic view to understand the energy flows and ecosystem functioning among and across trophic levels in tropical macroalgal meadows. The results of my thesis can be used by stakeholders to benefit our marine conservation and management programs.

CHAPTER 2

THE NATURE AND ECOLOGICAL SIGNIFICANCE OF EPIFAUNAL COMMUNITIES WITHIN MARINE ECOSYSTEMS



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Abstract

As the rate of global change increases, the structure and functioning of marine ecosystems, including the food webs that underpin them, will radically alter. Forecasting the consequences of these changes requires a sound understanding of the fundamental components of marine food webs: their community composition, baseline biomass and productivity. Epifauna, a term restricted here to small invertebrates (both mobile and sessile) that inhabit living and non-living surfaces within marine ecosystems, are a ubiquitous and pivotal component of marine food webs, supporting the flow of energy through marine ecosystems and providing a critical trophic link between benthic primary producers and higher-order consumers. Yet, despite their importance, epifauna are rarely studied compared to the more visible and gregarious components of marine ecosystems. They are also typically neglected in management strategies for the protection of marine habitats. In addition, the plethora of alternative terms used within this research field (macrobenthos, cryptofauna, epibiont, mesograzer) can be a barrier to understanding and assimilating existing research knowledge. This review provides an assessment of epifaunal communities studied within tropical, subtropical and temperate marine ecosystems globally. We first review alternative terms used to describe marine epifaunal communities, with the aim of offering a consensus-based definition of epifauna as an aid for unifying different research areas. We then review the primary literature on epifauna, including the scarce information on tropical marine habitats. We outline how a detailed understanding of epifaunal communities within individual habitats is needed to predict how benthic food webs will alter under global change. While epifauna can persist under degraded habitat conditions, changes to taxonomic composition can fundamentally affect secondary productivity, and impact higher-order consumers through changes in prey size-spectra and foraging habitats. Finally, we issue a 'call-to-arms' for increased focus on the study of epifauna, given their potential to underpin critical aspects of marine ecosystem functioning. We highlight the potential for eDNA sampling, other new technologies, and monitoring by citizen scientists to facilitate the use of epifaunal community metrics, including incorporation into marine ecosystem planning.

Keywords: Climate Change, Epibiota, Epifauna, Ecosystem Functioning, Marine Food Web, Mobile Invertebrates, Sessile Invertebrates

Introduction

Marine ecosystems are facing severe disruption through habitat and biodiversity loss caused by human activities, including interactions with climate (Ives & Carpenter 2007, Wernberg et al. 2013, Tuya et al. 2016, Miloslavich et al. 2018, Smale et al. 2019). The fundamental knowledge required to best support and manage ecosystems includes accurate information on trophic flows – the processes by which energy is transferred through the food web. Yet detailed examination of several critical trophic flows has been neglected in literature on marine ecosystem functioning (Bellwood et al. 2004, Mouillot et al. 2014, Brandl et al. 2016, although see Nagelkerken et al. 2020 for an exception). The biomass and secondary productivity of the direct consumers of primary production represent important metrics of ecosystem health and can be used to evaluate various aspects of ecosystem dynamics, the impacts of environmental change, and relationships between biodiversity and ecosystem functioning (Taylor 1998a, Burkepile & Hay 2008, Dolbeth et al. 2012).

In many marine ecosystems, these critical secondary consumers are dominated by epifaunal communities (Edgar 1994, Taylor 1998a, Cowles et al. 2009). Epifauna is a collective term given to the small, mobile or sessile invertebrates, here defined as <10 mm in body length, which are common to all marine habitats, especially within the living canopy of other organisms such as macroalgae, corals and seagrasses (Edgar & Klumpp 2003, Witman et al. 2004, Fraser et al. 2020a). Their extreme abundances and rapid turnover rates mean that they play a key role in supporting the flow of energy through marine ecosystems (Newcombe & Taylor 2010, Wenger et al. 2018, Fulton et al. 2019). As an essential element in the marine food web, epifauna are therefore a critical trophic link between benthic primary producers and higher-order consumers such as carnivorous invertebrates and fish species, many of which are the targets of fisheries. Epifauna have high levels of secondary production that can represent up to 75% of the total annual secondary production within a habitat – sufficient to support large populations of macroinvertebrates and fishes that consume them (Edgar & Aoki 1993, Taylor 1998a, Kramer et al. 2015). Yet despite their ubiquity and their importance in underpinning marine food webs and ecosystem functioning, epifauna are a relatively poorly studied component of marine habitats (Gan et al. 2019, Chen et al. 2020, Fraser et al. 2020a). Three main reasons account for this: (1) their inconspicuousness compared to vertebrate and invertebrate macro- and mega-fauna (i.e., individuals >10 mm long); (2) the difficulty of quantitatively sampling epifaunal communities within structurally diverse habitats, and associated processing challenges related to their tiny body size and cryptic behaviour (Edgar 1990b, Taylor 1998a, Kramer et al. 2012); (3)

the difficulty of providing high taxonomic resolution when quantifying and describing the constituent organisms within epifaunal samples, due to a lack of taxonomic specialists (Edgar 1990b, Edgar 1994, Taylor 1998a, Cowles et al. 2009). As a result, our understanding of the ecological importance of epifaunal communities in marine ecosystems is far from complete. As potentially one of the largest contributors to production of higher-order consumers, we are therefore unable to accurately estimate the bottom-up consequences of changes in primary productivity for overall structure and function of many marine ecosystems. Moreover, to our knowledge, the nature and role of epifaunal communities in marine ecosystems has not been systematically mapped in the past 20 years.

Here we summarise investigations of marine epifaunal communities to date. We begin with a seemingly trivial question: what are epifauna? Answering this question, however, proves to be a non-trivial task due to a Pandora’s Box of definitional issues and challenges. In order to resolve these challenges, we argue that rationalisation of nomenclature is needed within the field, and that researchers should provide key details of the organisms studied to facilitate future comparative analyses. We set out some minimum definitional criteria that would aid in this regard. Based on a systematic mapping of the literature, we then summarise geographic and habitat trends among investigations of epifaunal communities (as opposed to studies on single species of epifauna) to date and highlight major gaps in our understanding. We then present some of the existing knowledge of temporal and spatial fluctuations in epifaunal community structure, with a focus on tropical ecosystems, and discuss the potential responses of epifaunal communities to disturbance events, including those associated with anthropogenically driven climate change. Finally, our review issues a ‘call-to-arms’ for an increased focus within the scientific community on the ecology of epifaunal communities: their composition, size-structure, productivity, population dynamics, and interactions with other biota and environmental stressors, given their critical contribution to the integrity of trophic flows under conditions of global change.

What are epifauna – a taxonomic definition?

On one level, defining marine epifauna as a list of taxonomic components that are typically studied – orders, classes, subclasses, and genera of organisms – is straightforward (Figure 2.1). Nevertheless, the taxonomic range within epifaunal communities is bewildering. Mobile epifauna contain groups of Arthropoda, especially Crustacea (e.g., isopods, amphipods, tanaidaceans, cumaceans and other peracarids, as well as copepods, ostracods and small decapods), Mollusca (chiefly gastropods, bivalves and chitons), and also Polychaeta, Echinodermata (ophiuroids, echinoids, asteroids, crinoids, holothurioids), Platyhelminthes, Nematoda, Nemertea and Foraminifera. Sessile epifauna contain groups within the Arthropoda (e.g., barnacles), Polychaeta (e.g., serpulids), Cnidaria, Porifera, Tunicata and Bryozoa. The purpose of this review is not to present the taxonomic details or listings of all organisms classified as marine epifauna, rather our focus is at the collective level of the community and its functional role.

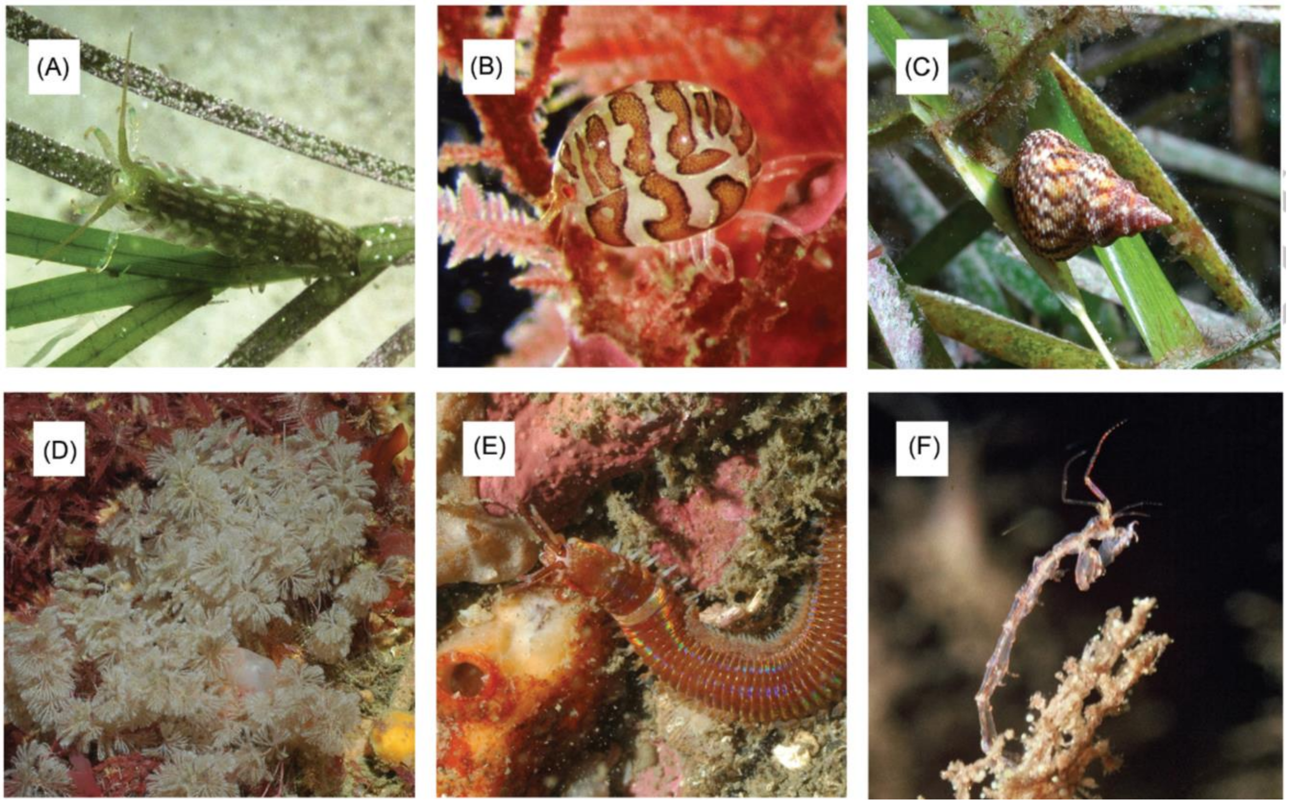

Figure 2.1 Representative taxa commonly found within samples of marine epifauna. (A) Isopod (*Euidotea* sp.). (B) Amphipod (*Cyproidea* sp.). (C) Gastropod (*Prothalotia lehmanni*). (D) Bryozoan. (E) Polychaete (*Eunice* sp.). (F) Caprellid amphipod (*Caprella* sp.).

Community-level nomenclature challenges

Moving on from a taxonomic view of epifauna, challenges arise when defining the community at the collective level. The term 'epifauna' is perhaps best defined by etymology:

‘epi’ from the Ancient Greek ‘on top of’, and ‘fauna’ from the Late Latin for ‘collection of animal life present in a particular place or time’. The Oxford English Dictionary thus defines epifauna as, ‘animals living on the surface of the seabed or a riverbed, or attached to submerged objects or aquatic animals or plants’. Marine benthic communities essentially divide into two categories based on whether those organisms are found ‘on’ (epifauna) or ‘within’ (infauna and endofauna) substrates. Infauna live buried in seafloor sediments or riverbeds, while endofauna bore into solid structures such as coral reefs or the skeletons of marine organisms (Figure 2.2A).

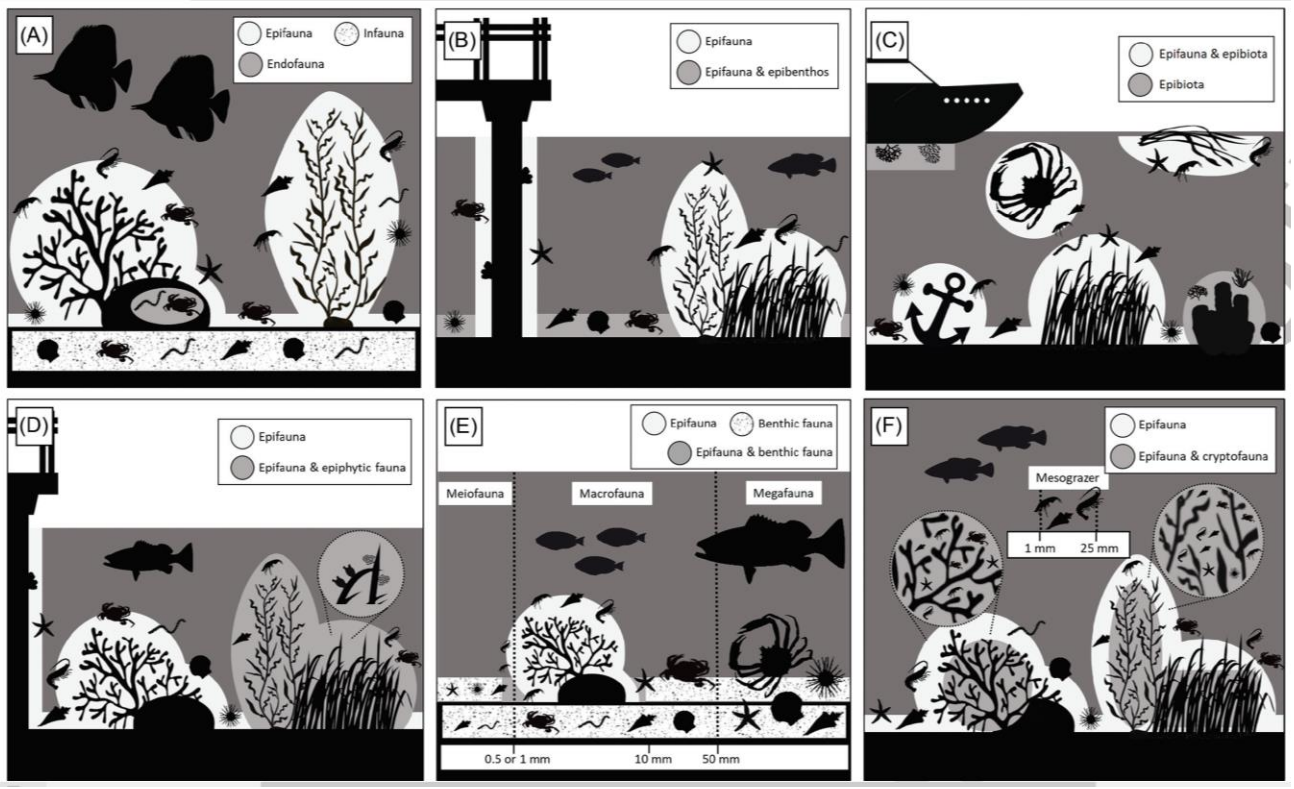

Figure 2.2 Conceptual representation of the relationship between terms used interchangeably within the literature to refer to epifaunal organisms and highlighting of the distinctions between such terms under a strict definitional approach. (A) The distinction between marine epifauna and infauna (including endofauna). (B) The relationship between epifauna and epibenthos. (C) The relationship between epifauna and epibiota. (D) The relationship between epifauna and epiphytic fauna. (E) The relationship between epifauna and macrofauna/macrobenthos. (F) The distinction between epifauna, cryptofauna and mesograzers.

As uncontroversial as this definition of epifauna might seem, challenges nevertheless arise when undertaking a review of the topic, due to the use of alternative terminology to refer either to the same or similar groups of organisms within marine ecosystems. For example, many studies limit their classification of epifauna to mobile taxa only (Edgar 1990a, Martin-Smith 1993, Viejo & Åberg 2003, Arponen & Boström 2012, Bedini et al. 2014, Tano et al. 2016, Wee et al. 2019, Fraser et al. 2020a), whereas others include sessile organisms such as sea anemones, bryozoans and ascidians in their definition of epifauna (Shin 1981; Fowler & Laffoley 1993, Bradshaw et al. 2003, Hepburn et al. 2006, Demers et al. 2016, Kaiser et al. 2018). For reasons of historical legacy (the fact that most of the early studies of epifauna were based in temperate, deep sea habitats), some will think only of sessile, primarily planktivorous, invertebrates when using the term epifauna. Most researchers limit their classification of epifauna to invertebrate communities, but some include vertebrates such as small (<10 cm), benthic-dwelling fishes (Viejo 1999, Hovel et al. 2002). Others use the term in its broadest sense to refer to any organism living on the surface of another, for example Buckle & Harris (1980) used the term ‘epifauna’ to refer to the community of fleas living on a red fox (*Vulpes* vulpes). At the same time, some authors that studied epifauna may have also studied small plants/algae (i.e., not just fauna) and may have used the broader term ‘epibiota’ to include both small animals and plants/algae living on top of substrata (Johnston et al. 2011, Marzinelli et al. 2011, 2012, Clark et al. 2015). A search of the literature relating just to ‘epifauna’ may therefore miss some such studies.

By contrast, depending on the sampling method used or the particular research question asked, some investigators do not use the term at all, even though their study organisms fall under the classification of epifauna (Baden 1990, Irving et al. 2007, Stella et al. 2011, Kramer et al. 2012, Ellis et al. 2013, Kramer et al. 2014, Kramer et al. 2015, Kramer et al. 2017, Nakamoto et al. 2018). Alternative terms fall into one of two categories: (1) terms that might be considered close synonyms in that they represent some form of overlap with the term epifauna (e.g., epibenthic fauna, epibenthos, epibiota) (Table 2.1) and (2) terms that, strictly speaking, have a different meaning to ‘epifauna’, in terms of either the size of organism they refer to, the broader class of organisms included, or the differential habitat niche that they reference (e.g., macrobenthos, cryptofauna) (Table 2.1). This diversity of terms has little parallel with the floral equivalent term ‘epiphyte’, which is widely used for organisms growing on seagrasses or macroalgae.

Table 2.1 Summary of synonyms and alternative terms used within the scientific literature to refer to epifaunal organisms within marine ecosystems, including a commonly accepted definition of the term within the marine context, and examples used in the literature.

Nomenclature	Definition and relationship to the term 'epifauna'	Examples
Epifauna nomenclature		
Epibenthic fauna *Epibentho* *Epibenthic assemblage* *Epibenthic invertebrate* *Epibenthic community* *Epibenthic macrofauna*	Epibenthic fauna are those organisms that live on or just above the bottom substrate in a body of water. Although 'epibenthic' is often used interchangeably with 'epifauna', epibenthos should be considered a smaller subset of epifauna, as it refers only to animals on the bottom substrate (or benthos), as opposed to animals on any type of surface (upright and benthic) within a given habitat (Figure 2.2B).	Howard (1985), Kaiser et al. (1994), Edgar & Shaw (1995), Prena et al. (1999), Cocito et al. (2000), Cohen et al. (2000), Ellis et al. (2000), Jennings et al. (2001a), Zühlke et al. (2001), Callaway et al. (2002a,b), Koch & Wolff (2002), Stachowicz et al. (2002), Colloca et al. (2003), Polte et al. (2005a,b), Hosack et al. (2006), Walker et al. (2007), Nagelkerken et al. (2008), Neumann et al. (2008, 2017), Wilkie et al. (2012), Brandt et al. (2013), Gribben et al. (2013), Michaelis et al. (2019a,b), González-García et al. (2020), Proudfoot et al. (2020)
Epibiont *Epibiota* *Epibiotic invertebrate* *Epibiotic organism* *Epibiotic community*	Strictly speaking, an epibiont refers to an organism living on the surface of another *living* organism, although there can be different interpretations in common usage (see text above). For example, many studies may use the broader term 'epibiota' to include both small animals and plants/seaweeds living on top of substrata (live or inert) The term 'epibiota' therefore could refer to	Daniel & Robertson (1990), Hopkinson et al. (1991), Nalesso et al. (1995), Connell & Anderson (1999), Glasby (1998, 1999a–c, 2000), Bradshaw et al. (2003), Wernberg et al. (2004), Schmidt & Scheibling (2006), Harries et al. (2007), Summerhayes et al. (2009), Johnston et al. (2011), Marzinelli et al. (2011, 2012), Byers et al. (2012), Gribben et al. (2013), Blake et al.

	epifauna when animal groups are included but in this case should exclude phytal communities (Figure 2.2C).	(2014), Clark et al. (2015), Cúrdia et al. (2015), Arnold et al. (2016), Gribben et al. (2017), Kniesz et al. (2018), Powell et al. (2019), Ledbetter & Hovel (2020)
Epiphytic fauna *Epiphytic organism* *Epiphytic macrofauna* *Epiphytic community* *Epiphytal fauna* *Epiphytal arthropod assemblage*	Epiphytes in marine systems – as distinct from terrestrial epiphytes – are species of algae, bacteria, fungi, sponges, bryozoans, ascidians, protozoa, crustaceans, molluscs and any other *sessile* organism that grow on the surfaces of marine macrophytes. The term should therefore be considered a smaller subset of epifauna (i.e., referring just to the subset of non-mobile epifauna that are found on living surfaces, although common usage can sometimes extend to mobile organisms within these classifications living on plant surfaces) (Figure 2.2D).	Cancino et al. (1987), Anderson et al. (1991), Russo (1991), Nakaoka et al. (2001), Schmidt & Scheibling (2006), Hirst (2007), Popadić et al. (2013), Chen et al. (2015), Belattmania et al. (2018a,b), Jacobucci et al. (2019)
Related terms		
Macrobentho *Macrobenthic invertebrate* *Macrobenthic community* *Macrobenthic fauna*	Organisms living on, in or near the benthic substrate that are greater than 1mm in size (in some classification systems >0.5 mm). Macrobenthos are therefore defined by their size *and* habitat. As in the case of 'epibenthos', macrobenthic organisms are essentially a subset of epifauna that excludes animals living on macrophytes or artificial	McDonald (1983), Lana & Guiss (1991), Migné & Davoult (1995), Kühne & Rachor (1996), Wright et al. (1997), Flynn et al. (1998), Gage et al. (2000), Thrush et al. (2001), Smith & Rule (2002), Pagliosa & Lana (2005), Jing et al. (2007), McKinnon et al. (2009), Tang & Kristensen (2010), Sokołowski et al. (2015), Zharikov & Lysenko (2016), Hossain (2019)

	structures, although infauna are also sometimes included (Figure 2.2E).	
Macrofauna *Macroepifauna* *Macro-epibenthic fauna*	Macrofauna are classified as organisms that are 1–50 mm in size. (>0.5 mm in some classifications). The term ‘macrofauna’ makes no presumption of location of the animal and can refer to infaunal organisms, e.g., those living within marine sediments (Figure 2.2E), unless specified as macro-epibenthic.	Webb & Parsons (1991), Jean & Hilly (1994), Ellis et al. (1996), Russo (1997), Bologna & Heck (1999), Hovel et al. (2002), Tanaka & Leite (2003), O’Brien et al. (2006), Garcia et al. (2008), Kon et al. (2011), Leopardas et al. (2014), Ge et al. (2020)
Benthic community *Benthic faunal assemblage* *Benthic macrofauna* *Benthic invertebrate* *Benthic organism*	Community of organisms that live on, in or near the seabed (the benthic zone). These are typically invertebrates and will include mobile and sessile organisms, and can include organisms >50 mm, for example sea anemones, sponges, corals, sea stars, sea urchins. Therefore, likely to include a much larger set of organisms than just ‘epifauna’, unless the study refers to a specific size range within the benthic faunal assemblage that would exclude animals not considered to be epifauna (e.g., large sea stars) (Figure 2.2E).	Howard (1985), Edgar (1990b), Aller & Stupakoff (1996), Aller (1997), Collie et al. (1997), Engel & Kvitek (1998), Jewett et al. (1999), Dumbauld et al. (2001), Jennings et al. (2001b), Sfriso et al. (2001), Edgar & Barrett (2002), Witman et al. (2004, 2008), Osman & Whitlatch (2004), Kon et al. (2010), Pagliosa et al. (2012), Broszeit et al. (2013), Riera et al. (2013), Leopardas et al. (2014), Lambert et al. (2017), Henseler et al. (2019), Yeager et al. (2019), Noble-James et al. (2020)
Mesograzer *Mesoherbivore* *Epifaunal mesograzer*	The term ‘mesograzer’ is chiefly used to describe small benthic herbivorous invertebrates that live and feed on their macrophytal hosts (e.g., macroalgae, seagrasses). They are generally less than 25 mm in length, and can include juveniles of some	Viejo & Arrontes (1992), Schaffelke et al. (1995), Hay (1997), Ruesink (2000), Taylor et al. (2003), Dick et al. (2005), Jaschinski & Sommer (2008), Best & Stachowicz (2012), Berthelsen & Taylor (2014),

	larger species. The term 'mesograzer' therefore refers to just a single trophic component of epifauna (the herbivorous component) and tends to include a larger size range of organisms than might typically be thought of under a strict definition of epifauna (Figure 2.2F).	Martínez-Crego et al. (2015), Campbell et al. (2018)
Phytal fauna	'Phytal' from the term coined by Remane (1933) to denote a third main habitat in the marine environment as distinct from benthic and pelagic. Phytal refers to areas with major vegetation as well as sessile animal growths (e.g., hydroids, corals and bryozoans). Phytal fauna typically refers to motile animals living on macrophytes. Can include organisms belonging to meiofaunal size classes (nematodes, copepods, ostracods and mites), but excludes sessile organisms (e.g., bryozoans, foraminiferans, sponges, sedentary polychaetes, bivalve molluscs and brachiopods). This term has tended to fall out of common usage.	Moore (1981), Edgar (1983), Zander et al. (2015)
Cryptobentho *Cryptofauna* *Cryptic epifauna* *Cryptic invertebrate*	The term 'cryptofauna' strictly refers to animals concealed within a microhabitat or within intra- and inter-skeletal voids formed by framework structures, although the term is also commonly used to refer to cryptobenthic fishes such as gobies and blennies that inhabit branches of	Fishelson & Haran (1986), Todd & Turner (1986), Baden (1990), Enochs (2012), Kramer et al. (2012)

	corals. Cryptofauna would therefore be considered distinct from epifauna by virtue of their different microhabitat usage (Figure 2.2F).	
Fouling community *Fouling organism*	Fouling communities are assemblages of fauna and flora found on artificial substrates, commonly comprised of sessile organisms such as ascidians, bryozoans, sponges and barnacles. They can have negative economic impacts (e.g., block fishing nets and cages, damage boats and buoys, increase hydrodynamic volume and hydrodynamic friction of a vessel which leads to more fuel consumption). This term tends to include a range of organisms in terms of both size (can be megafauna) and taxonomy (can be algae) than 'epifauna'.	Walker et al. (2007), Osman et al. (2010), Johnston et al. (2011), Karlson & Osman (2012), Marzinelli et al. (2012), Fernandez-Gonzalez & Sanchez-Jerez (2017), Carmen & Grunden (2019)

The use of multiple terms for epifaunal communities has been a persistent feature of the field from its inception and continues to challenge researchers when attempting to synthesise the literature (Table 2.1). A summary of the alternative descriptions of epifauna within the field highlights the absence of any strong temporal trends in usage of particular terms, other than potentially a decline in the use of 'epiphytic', as the teaching of Latin in schools decreases and scholars lose their childhood links to Latin nomenclature. In most cases, although the terms are indeed linked to the definition of epifauna, they are not strict synonyms and instead represent either a smaller subset of the epifaunal community (e.g., for terms excluding fauna on vertical living surfaces) or a larger group of organisms that include algae and/or animals that typically would not be considered epifauna (e.g., spider crabs, sponges and sea-stars greater in size than 50 mm) (Table 2.1). In addition, we note that terminology provided here is not exhaustive and excludes terms that appear relatively infrequently (e.g., ‘suprabenthos’ (Cartes et al. 2002), ‘macroscopic epifauna’ (Saarinen et al. 2018), ‘meio-epifaunal community’ (Raes & Vanreusel 2005), ‘macrozoobenthic fauna’ (de Jong et al. 2015), ‘zoobenthic community’ (Davidson 2005)), or that represent organisms that are generally not considered part of the epifaunal community, as in the case of ‘megabenthos’ (Diaz et al. 2004, Kenchington et al. 2007), ‘megabenthic’ (Ramos 1999), or ‘mega-epifauna’ (Du Preez et al. 2016), where the epithet ‘mega’ would typically only be applied to organisms greater than 50 mm.

A primary challenge therefore in synthesising the existing literature on marine epifaunal communities and in carrying out a review of the topic is a lack of consensus in the application of the term ‘epifauna’. What size class of organisms is included? Is the term restricted to invertebrate classes or does it include small vertebrates? Is the epifaunal community composed only of sessile organisms, or mobile organisms, or both? In many cases, the use of one particular term over another relates to the methods used to obtain samples for the study and the level of precision afforded by those methods. The most commonly used quantitative sampling methods for epifauna are: underwater visual survey, towed gear sampling, vacuum or suction sampling, core sampling, full-enclosure sampling, and light traps (Table 2.2). For example, sampling by towed gears will usually result in the collection of all benthic fauna, including megafauna, as well as some infaunal samples. A researcher using this sampling method is unlikely to be able to distinguish between cryptofauna and epifauna and it is arguable as to whether the distinction between the two is even important, depending on the research question. However, even in those cases where the study aims do not require a distinction to be made (e.g., in cases where habitat or trophic specificity is unimportant), it is important that nomenclature be used consistently. To this end, we advocate for the careful and precise application of terminology at the community level, based on the lexicon presented in Table 2.1. Where distinctions between particular parts of the community are important, for example where it is critical to exclude animals living on macrophytes or artificial structures, or to distinguish between the epifaunal community as a whole and those animals living just on benthic surfaces within a particular habitat (the epibenthos or macrobenthos), then the different terms must persist. However, where such distinctions are unimportant, use of the broader term ‘epifauna’ could lend cohesion. For example, although not a redundant distinction, viewed from the perspective of community function, how important is it to distinguish between sessile (epiphytal fauna) and motile epifauna? Undoubtedly there will still be the need, on occasion, to differentiate between the two, making it unlikely that terms can drop out of use completely. However, consideration should certainly be given to elimination of redundant terms: those cases where alternative terms have the same definitional meaning (e.g., benthic community/benthic faunal assemblage/benthic macrofauna). This kind of rationalisation would have the benefit of making the literature more accessible to those new to the field and of facilitating future comparative analyses. At the same time, provision of clear hypotheses, descriptions of sampling methods used, and sufficient detail with respect to key traits of the organisms included in sampling will aid in future comparative studies and meta-analyses to be conducted on the literature within this field.

Table 2.2 Summary of techniques most commonly used for collecting quantitative samples of epifauna.

Sampling method	Description	Examples
Underwater visual survey	This underwater observation is usually applied for epifauna, macrobenthic fauna (e.g., sponges, sea stars, scallops) or megafauna which can be detected by eye. *In situ* photos and/or videos of epifauna are taken by SCUBA divers or ROVs (remotely operated vehicle).	Collie et al. (2000a), Kollmann & Stachowitsch (2001), Valente (2006), Hughes (2014), Zharikov & Lysenko (2016), Michaelis et al. (2019a,b), Lopez-Garrido et al. (2020)
Towed gear sampling	This method usually involves collections of macrofauna on the benthic substrata with coarse mesh size (e.g., >10 mm), conducted by towed gears such as dredge sleds, research vessels or fishing vessels.	Jean & Hilly (1994), Kaiser et al. (1994), Prena et al. (1999), Hamazaki et al. (2005), Kenchington et al. (2006), Lange & Griffiths (2014), Piras et al. (2016)
Vacuum/suction sampling	This sampling is conducted by using an underwater vacuum or suction sampler. Epifauna are directly taken from the sediments or structurally simple habitats such as turf algae and EAM (epilithic algal matrix). A fine filter (e.g., 0.05 mm mesh	Taylor et al. (1995), Taylor (1998a,b), Roberts & Poore (2006), Cowles et al. (2009), Kramer et al. (2012), Berthelsen &

	size) is attached to retain particles for further processing.	Taylor (2014), Fraser et al. (2020a)
Core sampling	Cores are used for collecting the fine, soft bottom sediments (e.g., <0.5 mm particle size) with associated epifauna. After extraction from the core, epifauna are usually sorted by sieves that fractionise these core samples by mesh size.	Webb & Parsons (1991), Parker et al. (2001), Thrush et al. (2001), Commito et al. (2008), Norkko et al. (2010), Smeulders et al. (2014), Rosli et al. (2016)
Enclosure sampling	This sampling method is chiefly for harvesting epifauna from marine macrophytes (e.g., macroalgae, seagrass). It involves using bags to fully enclose the whole plant before detaching the plant from the benthic substrata. Bags are then immediately sealed to prevent epifauna from escaping from macrophytal canopies. Harvested plants with associated epifauna are size-fractionated by using a series of nested sieves with different mesh size (proposed by Edgar 1990b).	Baden (1990), Edgar & Aoki (1993), Jernakoff & Nielsen (1998), Gartner et al. (2010), Tuya et al. (2014), Tano et al. (2016), Chen et al. (2020)
Light trap	This is an emerging technique in the sampling of benthic fauna including epifauna, although it has been more typically used for sampling of plankton, fish larvae and pelagic fauna. It involves using light sources to attract organisms with minimal damage of habitats and specimens	Holmes & O’Connor (1988), Cohen & Oakley (2017), Costello et al. (2017), McLeod & Costello (2017)

Methods for systematic mapping of the term epifauna within primary literature

In order to map the use of the term ‘epifauna’ and the contexts in which the term has been applied and defined, we conducted a search of the peer-reviewed scientific literature using

ISI Web of Science. All research articles (in English only) published between 1953 and July 2020 including the terms ‘epifauna’ or ‘epifaunal’ in their research titles, abstracts, keywords and/or keyword plus, were included to establish a broad initial search. This initial search yielded a total of 2632 potential papers. We then refined the results using the Web of Science ‘categories’ function in order to exclude studies from terrestrial and freshwater habitats, or those with a non-biological focus. Specifically, we excluded studies listed under the following categories: geology, limnology, engineering, paleontology, biotechnology and microbiology. This process resulted in a total of 1780 studies. We also excluded studies conducted in polar (Arctic and Antarctic) marine ecosystems to focus on tropical, subtropical and temperate zones that share more similar habitat conditions, environmental factors and economic/fishery value. For inclusion in the final database, we then applied the following criteria to each paper: (1) studies that used the term epifauna on three or fewer occasions in the main text, or where the term epifauna was used only in the Discussion were excluded as not having sufficient focus on the biological or ecological role of epifauna; (2) studies where the term epifauna was used less than 10 times were screened to confirm that the aims of the study did indeed relate to the ecology of this group; (3) papers where the title and/or abstract revealed that the study did not lie within the relevant scope of this review (i.e., epifaunal communities) for example where the study focused on a single species within the epifaunal community. In order to confirm no omission of significant studies in the field and to ensure we had encompassed the synonyms and related terms detailed in Table 2.1, we conducted a second scan with cross-checks using the search strings ‘macrobenth*’, ‘macrofaun*’ and ‘cryoptofaun*’ in combination with ‘epi*’ (with the exception of ‘mesograzer’, unless the authors also used the term epifauna in their abstract or keywords). From this cross-check and refinement process we identified 993 studies of the biology and ecology of marine epifaunal communities (Appendix 2.1). All searches and study assessments were done by a single observer (Y-Y.C). At the end of the screening process, this observer re-assessed the first 20% of studies in order to check for consistency in the application of the refinement criteria (1–3 above) over the assessment period. Of these re-assessed studies, only one was differently categorised in the repeat exercise.

For each study within our final database, we recorded the following details: (1) date of publication; (2) the geographic region in which the study was performed, with regions categorised by latitude (tropical: 0°± 23.5°; subtropical: 23.5°–35°; temperate: 35°–66.5° excluding studies within the Antarctic Polar Front; Arctic and Antarctic studies are therefore not included in this review); (3) nomenclature used to describe epifauna, with synonyms (if presented); (4) the size range of animals classed as epifauna within the study; and (5) the habitat(s) in which the study was conducted (Appendix 2.2).

Development of the field and trends in the literature on marine epifauna

The field of marine epifaunal biology and ecology research grew at a steady pace in the 1970s and 1980s, predominantly via the work of researchers such as Moore and Seed (e.g., Seed & Boaden 1977, Moore 1981, and review by Seed & O'Connor 1981b). Moore's initial work focused on epifaunal organisms occupying kelp holdfasts, where a major contribution highlighted habitat niche partitioning among epifaunal communities: showing that the organisms found on kelp holdfasts were predominantly of different trophic status to those on leaves and fronds (Moore 1972, 1977, 1981, McKenzie & Moore 1981). Later, Buchanan & Moore (1986) were among the first to investigate the effects of temperature on macrofaunal communities as part of a long-term monitoring program, showing that species diversity declined following cold winters for macrofaunal communities along the UK Northumberland coast. In the 1980s, the focus on epifaunal communities associated with macroalgal kelp continued with the work of Seed, whose contributions included documenting the epifauna found on kelp fronds from coastal intertidal habitats in the UK including Northern Ireland (Seed 1976, Seed & Harris, 1980, Seed et al. 1981) and Wales (Wood & Seed 1980, Seed & O'Connor 1981a, Oswald & Seed 1986). Much of this early work on epifauna was directed towards understanding community structure, the role of classical ecological processes (i.e., competition, predation) in shaping communities and recovery from disturbance events (e.g., Dauvin & Gentil 1990). Epifaunal communities were found to possess a large component of species with rapid recolonisation rates (Edgar 1992, Martin-Smith 1994), including 'demersal zooplankton' species that swim at night (Alldredge & King 1977, 1980, Hammer 1981).

A major broadening of studies of marine epifauna occurred in the 1980s and 1990s, with extended focus on temperate macroalgal habitats (Edgar 1983, Edgar & Moore 1986), seagrass (Heck & Whetstone 1977, Orth & Van Montfrans 1984, Orth et al. 1984, Edgar 1990a, Edgar & Robertson 1992, Heck et al. 1995) and standardised artificial marine habitats (Edgar 1991a,b) (Figure 2.3). This expansion was also marked by a fundamental shift in the focus of research on epifaunal communities, from descriptive studies interested in patterns to manipulative studies involving processes, particularly caging studies for assessing effects of predation (Heck & Orth 1980, Heck & Thoman 1981, Howard 1982, Van Montfrans et al. 1982, Robertson & Lucas 1983, Robertson & Lenanton 1984, Leber 1985), investigations of the critical functional role played by epifaunal grazers in reducing epiphyte loads on seagrasses and macroalgae (Howard 1982, Duffy 1990, Duffy & Hay 2000, Duffy & Harvilicz 2001, Duffy et al. 2001) and interactions involving algal chemical defences, epifauna and predatory fishes (Duffy & Hay 1990, 1991, 1994, Duffy & Paul 1992).

While most investigations to 2000 continued to contrast roles of predation, resource limitation and abiotic drivers, new empirical methods based on metabolic theory also allowed the productivity of marine epifaunal communities to be estimated (Robertson 1979, Banse & Mosher 1980, Edgar 1990b). This provided an altered perspective on epifauna, from use as a model system for understanding classic ecological principles to recognition of their value as a critical component of marine ecosystem processes (nutrient cycling and productivity flows) (Edgar 1992, 1993, 1994, Edgar et al. 1994). Epifaunal communities of varying composition had varying abilities to support biomass of higher-order consumers, meaning that the ability of different habitats to support different levels of fish production could be linked back to the epifaunal communities they harboured (Edgar & Shaw 1995). One unexpected finding was that secondary production of shallow-water epifauna is extremely consistent and predictable worldwide (Edgar 1993, Edgar & Aoki 1993).

Despite these publications highlighting the importance of marine epifaunal communities in food webs and energy flows, and important subsequent contributions (Taylor 1998a,b, Taylor & Rees 1998, Glasby 1999a,b, 2000, 2001, Metcalfe & Glasby 2008), the increase in published studies within the field of epifauna lagged behind the overall growth in scientific literature in the new century. By 2010, the field fell well behind general growth in scientific publications; less than 200 papers were published on the topic of epifauna in the second half of the decade, compared to an expected number of 346 (Figure 2.3A). In the last five years, based on our search criteria (studies using the terms ‘epifauna’ or ‘epifaunal’ in their research titles, abstracts, keywords and/or keyword plus), only 215 studies have been published on the topic of marine epifauna, compared to an expectation of 748 (Figure 2.3A). The understudied nature of the field is clearly evident when research on marine epifauna is contrasted with publication rates in related fields such as the study of infauna, plankton and coral reefs, where a total of 603 (infauna), 3634 (plankton) and 8394 (corals) studies have been published in the last five years (Figure 2.3B).

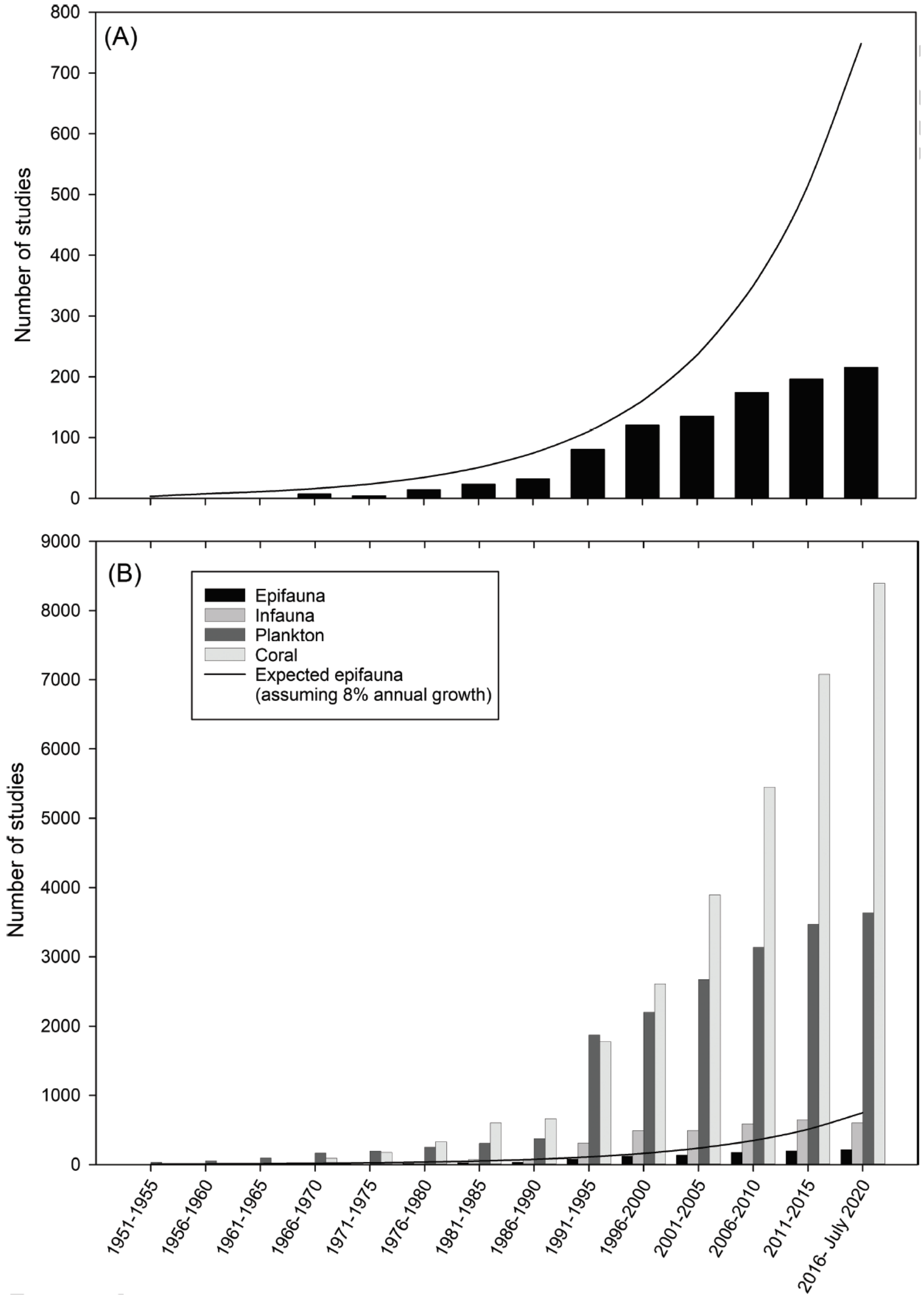

Figure 2.3 (A) Number of research articles on marine epifauna published within each half decade spanning the period (1950–2020) (grey bars), and expected growth across all scientific publications (black line) estimated by Bornmann & Mutz (2015) to be 8% p.a. (B) Growth in the published research on epifauna relative to related fields of ‘infauna’, ‘plankton’ and ‘corals’. Results for epifauna research articles are based on a literature search conducted in the ISI Web of Science database in July 2020 using the terms ‘epifauna’ and ‘epifaunal’.

A notable finding when conducting this review was that many authors provided no taxonomic definition of what constituted the epifauna category of animal (e.g., whether vertebrates were included), or biological or ecological traits of the animals (mobile only or inclusive of sessile organisms), or size range. In the extreme, this resulted in some cases where animals larger than 100 mm were classified as epifauna (e.g., Viejo 1999, Meyer et al. 2016). Of the 993 studies within our database, only 78 provided a definition of the size range of animals classified as epifauna within that study. Nearly 50% (485) provided no detail of the size of animals classified as epifauna within the study or recorded as part of the epifaunal community (Figure 2.4).

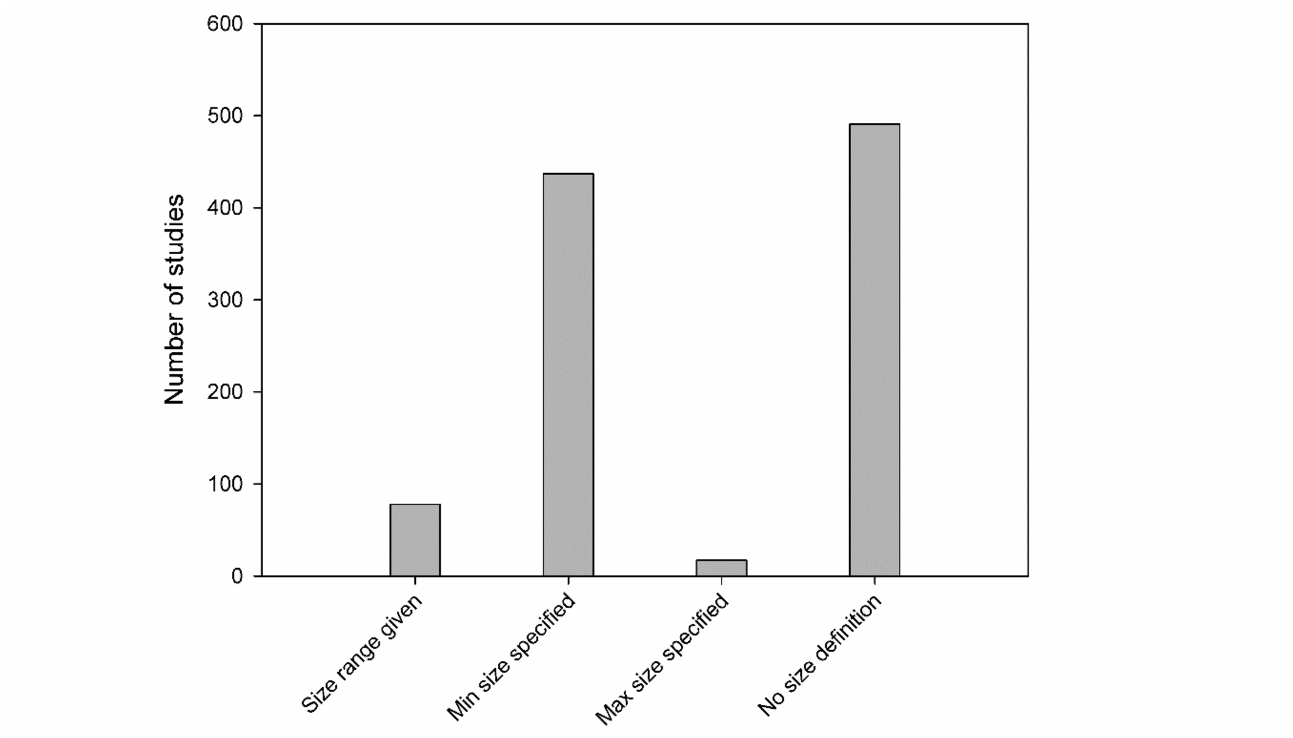

Figure 2.4 Number of studies within the published literature on marine epifauna that define epifaunal organisms according to their size within the publication text. Studies were assigned to one of the following four categories: (1) size range of animals defined; (2) only minimum size specified; (3) only maximum size specified; and (4) no size definition of epifauna given. Results are based on a literature search conducted in the ISI Web of Science database in July 2020 using the terms ‘epifauna’ and ‘epifaunal’.

Towards a unified framework for the study of epifauna within marine ecosystems

Based on the lexicon presented in Table 2.1, better precision is clearly needed when defining what is meant by an epifaunal community within a particular context, and when epifauna might be considered distinct from some of the terms that have previously been used synonymously. To resolve these issues, we suggest that researchers provide within their written methods section, at a minimum: (1) habitat sampled (e.g., seagrass bed, macroalgal meadow); (2) habitat niche, i.e., the precise nature or location of surfaces sampled (e.g., seagrass leaf blades, macroalgal thalli and leaves); (3) method of sampling; (4) organism size range; and (5) organism mobility. Non-essential, but potentially useful extra definitional elements could cover relevant biological and ecological traits of the target community such as taxonomic classes included; whether specific trophic levels are included or excluded; whether both living and artificial surfaces are included.

A majority of studies consider epifauna to refer only to invertebrates. However, excluding two animal classes (Osteichthyes and Chondrichthyes) has little phylogenetic or ecological validity. For example, small vertebrates such as gobiesocid clingfishes living attached to the surfaces of macrophytes exist within epifaunal communities and have overlap in functional roles with small shrimps and crabs. We therefore suggest that arbitrary taxonomic exclusions are not applied to ‘epifauna’. Nevertheless, inclusion of larger cryptobenthic fishes such as gobies and blennies would be inconsistent with most views of epifauna, and a defined size range is needed. Recognition that epifaunal organisms are constrained within a defined size range would allow a distinct separation from the totality of marine macrobenthos and also be helpful in establishing the identity of the functional group of epifauna as a distinct entity. A summary of the size range of organisms considered ‘epifauna’ for those studies within the scientific literature where a size range, a maximum size, or a minimum size are defined in the publication text indicates that most authors consider epifauna to be organisms between 0.5 and 10 mm in size (Figure 2.5).

Overall, within the ‘macrofauna’, we therefore define epifaunal communities through general consensus as those animals, 0.5–10 mm in size (most usually, but not always invertebrates) found living on the surface of sediment, turf algae, marine macrophytal canopies, marine macrophytal rafts, other biogenic habitats and artificial structures. They usually, but not always, range freely over surfaces; sessile organisms such as bryozoans, ascidians and barnacles also fall within the definition when attached to surfaces and in the 0.5–10 mm size range (Figure 2.6). In terms of habitat niche, we consider that all surfaces (living and artificial) within marine habitats should be considered as hosting epifaunal communities. Artificial surfaces are explicitly included because their associated communities contribute in a similar way as natural surfaces to nutrient cycling, energy transfer and other ecosystem processes. Epifauna must live at the interface between microhabitat surfaces and water, excluding cryptofaunal organisms living within the intra- and inter-skeletal voids formed by framework structures (Figure 2.6).

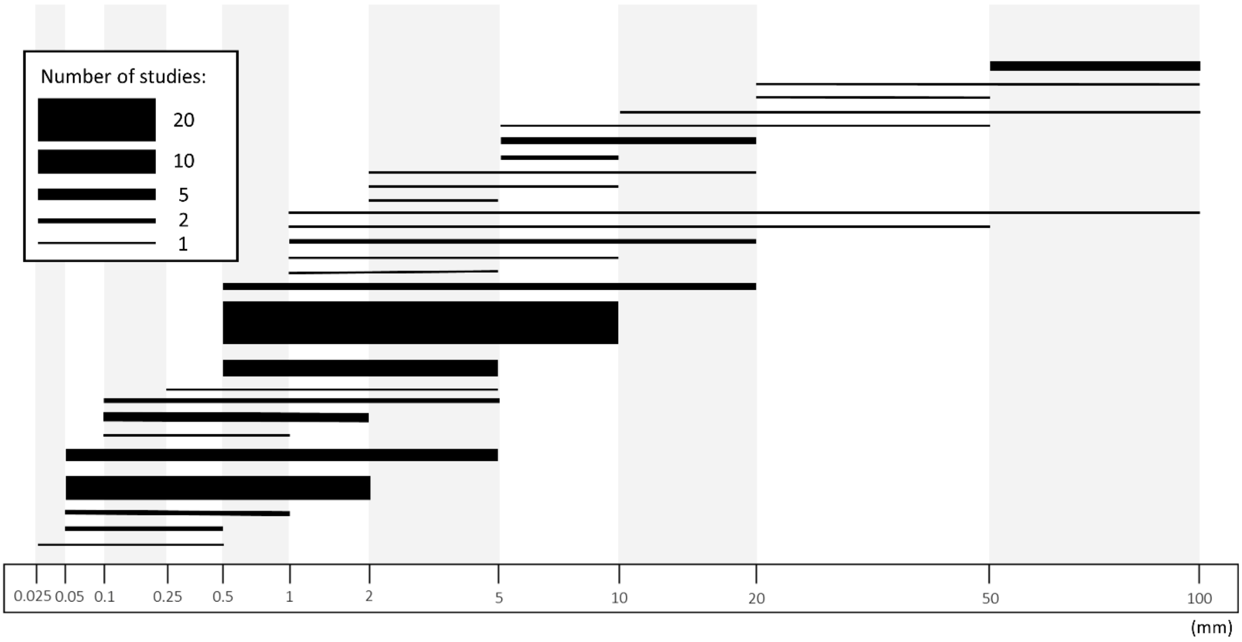

Figure 2.5 Summary of the size range of organisms considered as ‘epifauna’ within the published scientific literature based on a search conducted in the ISI Web of Science database in July 2020 using the terms ‘epifauna’ and ‘epifaunal’. Data are presented only for those studies where a size range is defined in the publication text. Thickness of the bar for each size range represents the number of studies using that particular definition. Note that size (mm) on the *x*-axis is presented on an ordinal scale.

Epifaunal communities may be composed of individuals belonging to multiple trophic levels, including herbivores, carnivores, detritivores and filter-feeders. Likewise, epifaunal communities which fall in the 0.5–10 mm size range can comprise assemblages with no distinction between different ontogenetic developmental stages such as adults, juveniles or larvae, since they are functionally serving the same role within that community. For example, juveniles of the bivalve scallop *Chlamys* (Pectinidae) may be found in seagrass meadows, where they attach to the leaves until they pass on to larger free-swimming stages. These juveniles would be classified as epifauna under our proposed consensus definition, given that they are functionally part of the surface-dwelling community.

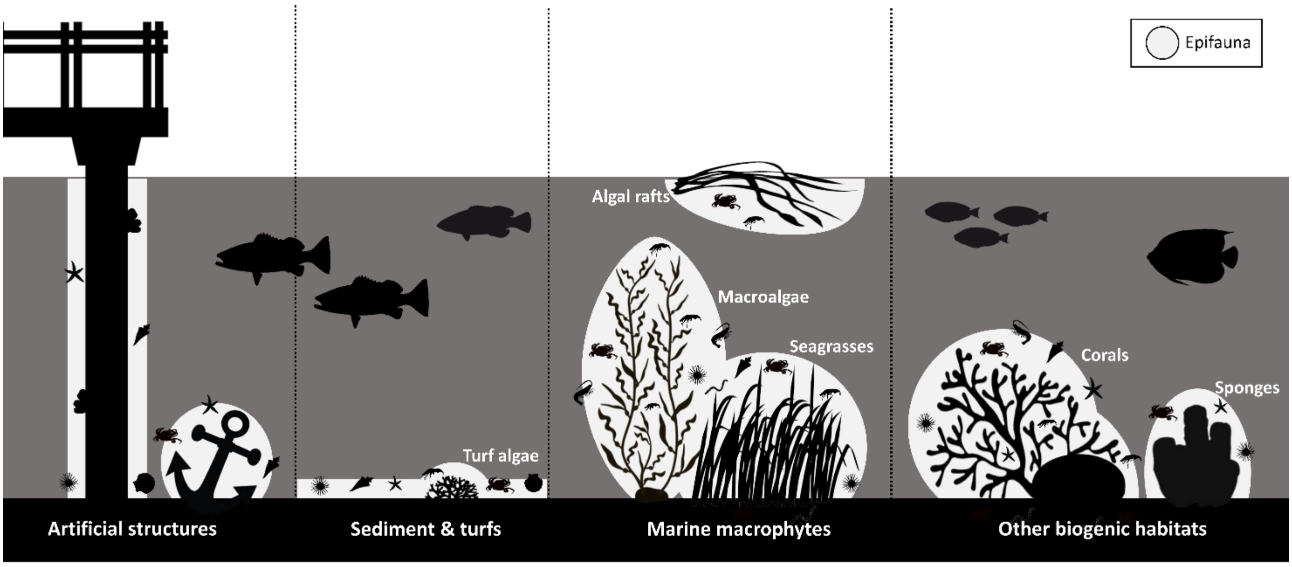

Figure 2.6 Schematic representation of the consensus view of marine epifaunal communities. The diagram shows the predominant living and non-living substrata on which epifauna are typically found within marine ecosystems.

Based on the lexicon presented in Table 2.1, the epifaunal community of a particular marine habitat is thus defined as

$$\text{epifauna} = \sum\nolimits_{k=0.5\,\text{mm}}^{10\,\text{mm}} \left(\text{epibenthic fauna} + \text{epiphytic fauna}\right) - \left(\text{cryptofauna} + \text{infauna}\right)$$

where a particular marine habitat contains no surfaces other than the benthos (i.e., no macrophytes or vertical structures) then the definition of epifauna above essentially collapses to that of ‘epibenthos’ or ‘macrobenthos’, with the important distinction that epifauna fall within the size range of 0.5–10 mm, and are thus a smaller subset than the epibenthic/macrobenthic community, which could be taken to include organisms > 10 mm, for example sea anemones, sponges, corals, sea stars, and sea urchins.

The role of epifauna in marine ecosystem processes

Having established the scope of this review, we next address the question: why care about epifaunal communities? The answer primarily relates to the key roles of epifauna in marine ecosystem processes. Epifauna, by virtue of their ubiquity and abundance, are important contributors to two marine ecosystem processes: (1) they function as mediators between nutrients in the water column and microbes in the benthos, contributing to the biogeochemical cycling of carbon and nitrogen, and (2) they function in the transfer of energy along the marine food web via their role as secondary producers, connecting primary producers to higher-order consumers such as carnivorous invertebrates and invertivorous fishes (Edgar 1994, Taylor 1998a, Cowles et al. 2009, Newcombe & Taylor 2010, Wenger et al. 2018).

Epifauna as mediators within marine ecosystems

Depending on habitat, epifauna can contribute greatly to cycling of carbon, nitrogen and other nutrients between the water column and microbes in the benthos. Epifauna interact with microbes through multiple processes, including ecosystem engineering, grazing and symbiosis. Stief (2013) reviews how these interactions contribute to nitrogen retention, nitrogen removal, and ammonium and nitrous oxide emissions. The effects of ecosystem engineering occur predominantly through the influence of infauna on nitrogen cycling in marine sediments, rather than epifauna (see review by Herbert 1999). However, sessile epifauna can play a role in terms of providing an enlarged surface area for microbial colonisation, thereby increasing nitrogen recycling (Hepburn et al. 2012, Stief 2013). The ingestion of free-living and particle-attached bacteria by epifauna can, however, result in a decline in metabolic activity of grazing-sensitive bacteria and reduced nitrification activity. Nevertheless, epifaunal grazing on the microbes themselves is thought to have only small or neutral effects on nitrogen cycling overall (Stief 2013). Epifaunal processing of macrophytic detritus, on the other hand, contributes to the microbial-macrofaunal shredder loop (part of the microbial loop, *sensu* Azam et al. 1983, Fenchel 2008). Epifaunal grazers, such as amphipods in the genera *Gammarus* and *Allorchestes*, ‘shred’ leaves and other particulate organic matter, breaking down macrophyte debris into finer fractions (Robertson & Lucas 1983, Robertson & Lenanton 1984). This process facilitates the remineralisation of nitrogen by microbes, making it available faster. For systems where phytoplankton and macrophytes are the dominant primary producers, this rapid regeneration of nitrogen can enhance primary production and ultimately increase the overall productivity of the ecosystem in terms of the biomass that can be supported (Taylor & Rees 1998, Hepburn et al. 2012, Stief 2013).

Epifauna as secondary producers: Quantifying the contribution to energy transfer within marine ecosystems

Epifauna also have a role as secondary producers in their own right. Secondary production by epifauna facilitates the flow of energy through the ecosystem from primary producers to higher-order consumers. Epifaunal secondary production is therefore one of the most important ecological parameters needed to understand population dynamics, trophic flow and environmental variability. Classical methods for estimating the secondary production of epifauna have been applied to individual species or to populations based on their change in body mass over time. Population production is then primarily a function of three major factors: (1) the metabolic rate–body size relationship of individuals, (2) the distribution of body sizes and (3) ambient temperature. However, even if these factors could be directly ascertained, getting an estimate of total production in this way is generally impractical because measurement of sizes of all individuals and determination of a body size–production relationship for each species is logistically challenging. Estimates of epifaunal secondary production at the community level are therefore relatively rare because of methodological and sampling difficulties.

Several empirical methods have been proposed to circumvent these challenges (reviewed in Dolbeth et al. 2012). These empirical models are chiefly based on multiple regression equations for production or the P/B ratio (P: secondary production, B: biomass) and include population characteristics (e.g., population biomass, metabolic rate, life span) as predictors and environmental parameters (e.g., water temperature, depth) as coefficients (Robertson 1979, Schwinghamer et al. 1986, Edgar 1990b, Brey 1990, 1999, 2001, Tumbiolo & Downing 1994, Cusson & Bourget 2005).

Biomass determinations are necessary for secondary production assessments, and ash-free dry weight (AFDW) provides arguably the best predictor for invertebrate biomass given that it minimises issues dealing with heavy calcareous shells and gelatinous tissues. However, measuring AFDW requires the incineration of dried samples at high temperature (commonly 520°C), which can require long periods of time, significant research effort and the destruction of the sample. Several empirical models utilise conversion factors to convert wet weight (WW) or dry weight (DW) to AFDW (Ricciardi & Bourget 1998, Brey et al. 2010). Brey et al. (2010) build a global data bank of conversion factors in aquatic organisms. It covers ratios between body mass (i.e., WW, DW, AFDW), body composition (i.e., protein, carbohydrate, lipid), macro-elements (i.e., C, P, N) and energy content, making it much easier to estimate biomass and production of marine fauna.

Edgar's sieve method (1990b), Brey's general model (1990, 2001) and global data bank (2010) are some of the most commonly adopted models for quantifying secondary production and energy content. Edgar's sieve method entails pouring samples through a series of nested sieves with decreasing mesh size (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.7 and 0.5 mm) and counting the number of individuals belonging to major morphological groups on each sieve (crustaceans, molluscs, polychaetes, platyhelminthes and caprellid amphipods). The latter are separated due to a propensity for their thin appendages to become entangled over coarser sieves, leading to potential overestimation of biomass. Total mean biomass (AFDW) of different functional groups retained by different-sized sieves can then be predicted based on known mean AFDW values of each sieve size. Associated allometric equations make it possible to estimate the productivity of epifauna at the assemblage level by predicting epifaunal secondary productivity as a function of body mass and water temperature. Error involved in predicting the productivity of individual species using this method can be high, but tends to cancel out in assemblage-level estimates (Edgar 1990b). This method has been widely adopted by subsequent investigators assessing benthic faunal secondary production in both temperate and tropical regions due to its tractability.

The nature and significance of epifaunal communities within marine habitats

In reviewing the published literature on epifauna, we found a strong Northern Hemisphere bias, with 73% of studies concentrating on marine habitats within the Northern Hemisphere (Figure 2.7). Of these Northern Hemisphere studies, 534 out of 778 (69%) focused on temperate marine habitats. Across both hemispheres, only 189 (17%) of published studies of marine epifauna considered tropical habitats (Figure 2.7). The neglect of tropical studies is not surprising: epifauna tend to be less abundant and conspicuous within tropical marine ecosystems, making them a much less ‘visible’ component of the system. However, given that these tropical ecosystems account for almost half of the world’s fish catches and that epifauna are a critical link in the food chain supporting such fisheries, the relative paucity of studies of epifauna within tropical marine habitats is a noteworthy gap in the existing literature. We advocate for a research emphasis on epifaunal communities within tropical habitats.

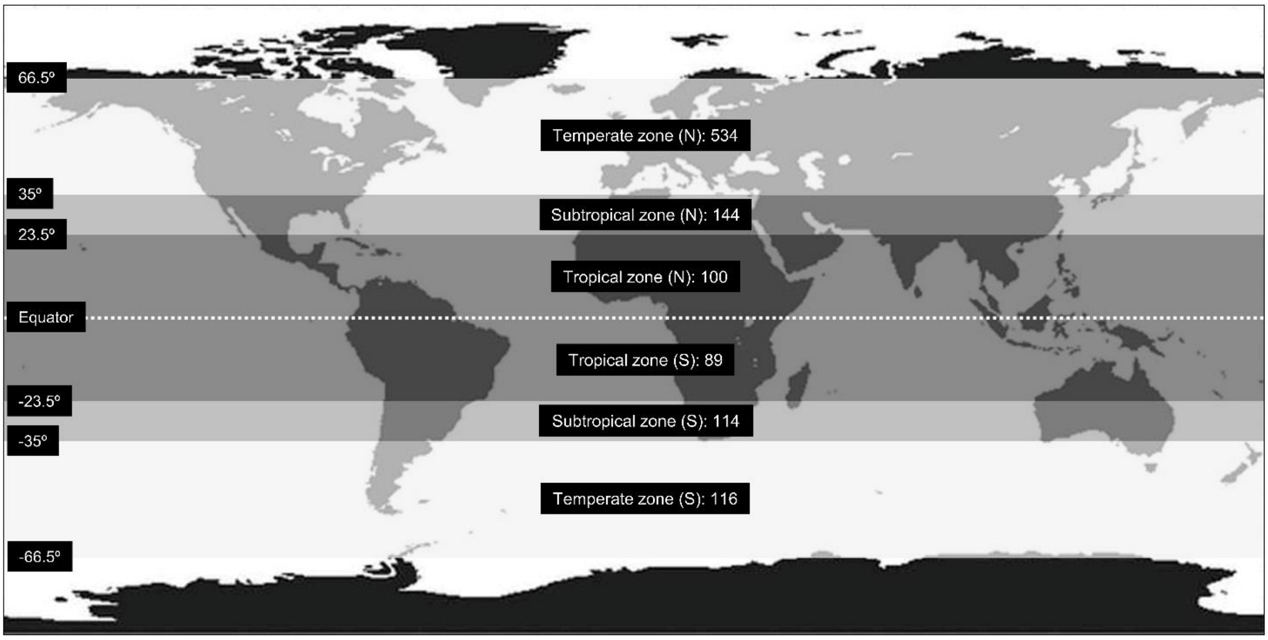

Figure 2.7 Number of studies within the published literature on marine epifaunal communities conducted within each latitudinal zone (tropical: 0°± 23.5°; subtropical: 23.5°–35°; temperate: 35°–66.5°) excluding polar (Arctic and Antarctic) zones. Numbers are based on a search conducted in ISI Web of Science database, up to and including July 2020, using the terms ‘epifauna’ and ‘epifaunal’. Note that the numbers here sum to 1097 (greater than the 993 studies listed in Appendix 2.2) as some studies extend across more than one latitudinal zone.

At the local scale, the nature of a community whose etymology relates to habitat surfaces necessarily links the community to that particular habitat. Thus, epifaunal communities in seagrass habitats, for example, are bound by definition to the nature and structure of seagrass canopies. Variation of epifaunal communities will be underpinned by variation in habitat type and quality across different locations. Recent evidence demonstrating that habitat is the most important correlate of variation in epifaunal assemblage has come from the work of Fraser et al. (2020a), who showed that reef-associated epifaunal assemblages varied significantly across 21 benthic microhabitat types sampled from temperate to tropical latitudes (28.6° latitudinal span), with much less variation according to latitude. Similarly, assemblage size distributions were much more affected by microhabitat type than latitude (Fraser et al. 2020b). In this section, we focus attention on the current status of knowledge of epifaunal communities in temperate and tropical latitudes across the two best studied habitats: seagrass meadows and macroalgal beds.

Seagrass meadows

Seagrasses are marine flowering plants that create key shallow-water habitats across all parts of the globe except Antarctica. Their dense canopies and associated deposition of organic matter in sediments provide food and shelter for a large community of organisms, including commercially important invertebrates and fishes. By forming extensive meadows connected with a mosaic of adjacent habitats, seagrasses are among the most productive marine ecosystems that supply ecosystem goods (e.g., maintenance of fisheries, supporting food security) and services (e.g., erosion control, coastal protection) to humanity.

Latitudinal differences in seagrass habitat structure exist, with temperate seagrass meadows typically monospecific (plus some macroalgae), while tropical meadows display greater habitat heterogeneity, with seagrass interspersed with corals, sponges and calcareous green algae (Virnstein et al. 1984, Duffy 2006). Seagrass habitats harbour abundant epifaunal invertebrates (Edgar 1990c, Nakamura & Sano 2005, Moore & Hovel 2010), such as gammarid amphipods and gastropods, which provide trophic pathways connecting seagrass primary production to larger invertebrates and carnivorous fishes. Epifaunal community composition and production is therefore an important metric for managers with responsibility for these habitats (Duffy 2006, Wong 2018).

Epifauna in seagrass beds have been more extensively studied than in coral, mangrove and algal turf habitats (Figure 2.8). In particular, the diversity and community structure of mobile and sessile epifauna within Neptune grass (*Posidonia* spp., dominant in the Mediterranean Sea), eelgrass (*Zostera* spp., globally widespread) and turtlegrass (*Thalassia* spp., chiefly distributed in Indo-Pacific and West Atlantic) meadows are relatively well documented (Virnstein et al. 1984, Knowles & Bell 1998, Sánchez-Jerez et al. 1999, Wong & Dowd 2015, Demers et al. 2016, McDonald et al. 2016, Tano et al. 2016, Boyé et al. 2017). Numerous published studies focus on plant–animal interactions and energy flows within seagrass meadows (Jernakoff & Nielsen 1998, Lepoint et al. 1999, Lewis & Anderson 2012, Hammerschlag-Peyer et al. 2013).

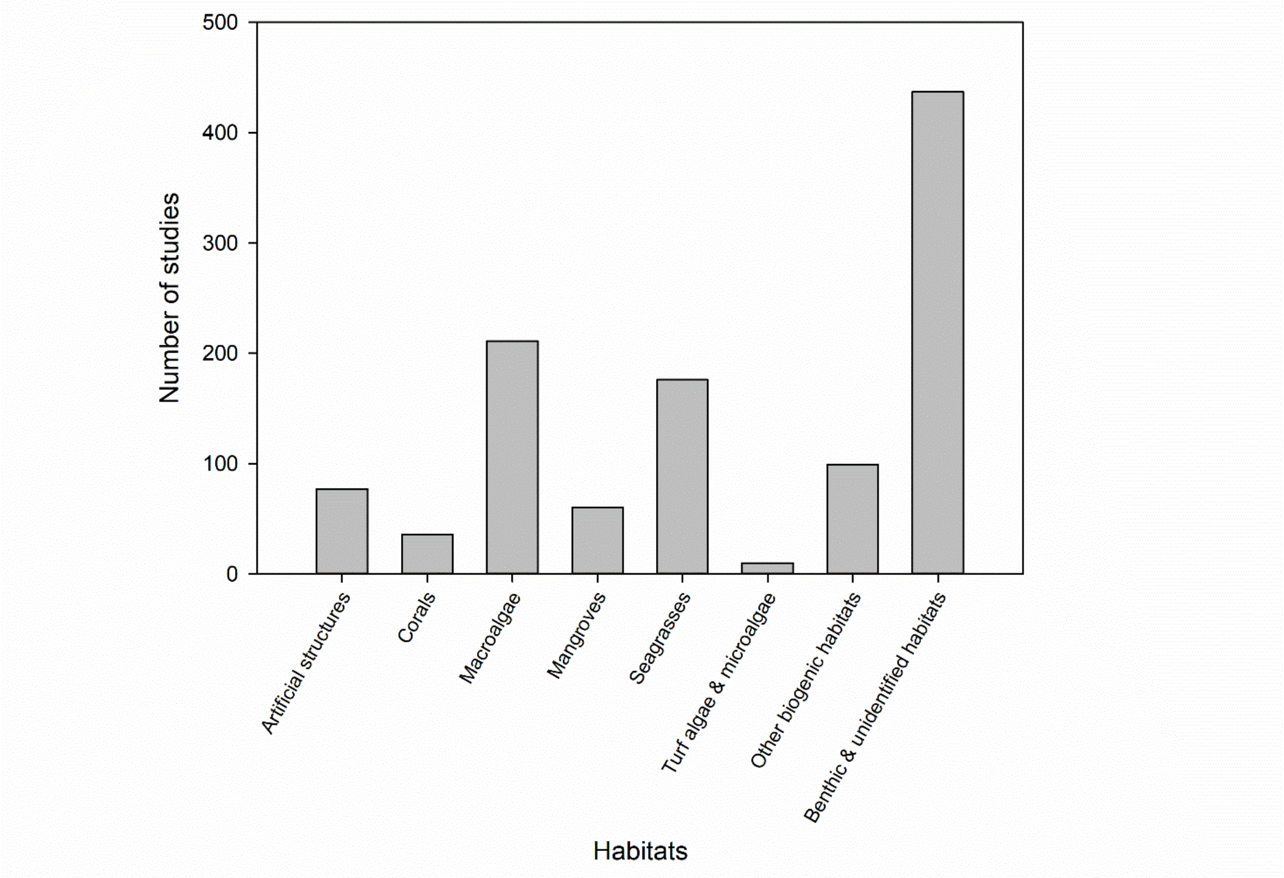

Figure 2.8 Number of studies conducted on epifaunal communities within particular marine habitats. Values are based on a search conducted in ISI Web of Science database in July 2020 using the terms ‘epifauna’ and ‘epifaunal’.

Overall, seagrass systems are much less studied in the tropics (although see Ansari et al. 1991, Klumpp et al. 1992, Prieto et al. 2003, Unsworth et al. 2007, Leopardas & Nakaoka 2014, Tano et al. 2016, Cavalcante et al. 2019) than temperate latitudes (Hootsmans & Vermaat 1985, Edgar & Shaw 1995, Heck et al. 1995, Nakamura & Sano 2005, Polte et al. 2005a,b, Spivak et al. 2009, Gullström et al. 2012, Wong & Dowd 2015, Lefcheck & Duffy 2015, Lefcheck et al. 2016, Boyé et al. 2017, Wong 2018) or subtropical zones (Edgar 1990c, Connolly 1995, Lemmens et al. 1996, Jernakoff & Nielsen 1998, Alfaro 2006, Micheli et al.

2008, Lewis & Anderson 2012, Hammerschlag-Peyer et al. 2013, McDonald et al. 2016, Douglass et al. 2018, Ledbetter & Hovel 2020). Limited tropical evidence does, however, suggest that latitudinal influences are likely less significant than differences between epifaunal communities at the level of microhabitat structure (Fraser et al. 2020a).

The abundance, biomass and secondary production of epifaunal invertebrates is high in seagrass meadows and among canopy-forming macroalgae relative to marine habitats, including corals, mangroves and bare sediments, across tropical, subtropical and temperate zones (Edgar 1990c, Ansari et al. 1991, Heck et al. 1995, Connolly 1997, Nakamura & Sano 2005, Polte et al. 2005a,b, Alfaro 2006, Bologna 2006, Wong 2018). Tropical seagrass ecosystems tend to include a large component of sessile invertebrates such as sponges and ascidians (Duffy 2006). In general, epifaunal abundance, biomass and diversity are positively associated with seagrass canopy size in terms of above-ground biomass, rhizome density, percent cover (Connolly 1995, Gil et al. 2006, Meysick et al. 2019, Yeager et al. 2019), macrophytal complexity (Edgar & Robertson 1992, Nakamura & Sano 2005) and meadow patch size (Källén et al. 2012, Yeager et al. 2019). Ecological patterning appears regulated at various scales by multiple structural elements such as degree of patchiness or proximity to patch edges (Bologna & Heck 2002, Hovel et al. 2002, Healey & Hovel 2004, Tanner 2005, 2006, Moore & Hovel 2010).

Seagrass meadows around the world show strong seasonal patterns of growth and change in canopy structure. Seagrasses often exhibit summer growth as vertical and horizontal elongation of plants, followed by winter decay of above-ground blades (Marbà et al. 1996, Cebrián et al. 1997, Fourqurean et al. 2001, Metz et al. 2020). This results in strong seasonal variations in primary production that make seagrasses ephemeral hosts for epifauna attaching on their leaves. Such seasonal dynamics of seagrass canopies and primary production can significantly affect the distribution and abundance of epifauna, manifest as temporal fluctuations in epifaunal communities (Edgar 1990a, Gambi et al. 1992, Nakaoka et al. 2001, Kouchi et al. 2006).

Extensive losses of seagrass habitat have been reported from many coastal regions worldwide over the past decade, resulting in an overall annual decline of 7% globally (Waycott et al. 2009, Boström et al. 2011, Unsworth et al. 2018). These losses are predominantly due to anthropogenic activities (e.g., mooring, anchor damage, plant harvesting) and to climate-associated disturbances (Thomson et al. 2015, Hyndes et al. 2016). Such degradation and loss of seagrass habitats arising from multiple perturbations presumably affect epifaunal communities (i.e., abundance and diversity) over large scales, and the functions they provide (e.g., levels of secondary production) (Meysick et al. 2019, Tuya et al. 2019). In addition, loss and fragmentation of seagrass meadows result in significant declines in epifaunal diversity and abundance (Reed & Hovel 2006, Gustafsson & Salo 2012, Cadier & Frouws 2019, Githaiga et al. 2019), with potential implications for higher-order predators reliant on epifaunal production, and perturbations to food web structures. Nevertheless, some studies have shown the opposite response, with increases in epifaunal abundance following seagrass fragmentation (Tanner 2005, Arponen & Boström 2012), although this occurred in situations where the distance between fragments was low. Critical tipping points may thus exist, beyond which epifaunal communities will respond negatively to habitat disturbance. In addition, the net rate of decline in coverage of some seagrass species has slowed and even experienced a reversal in certain areas (for example, rates of coverage of *Posidonia* and *Zoster*a meadows in Europe). This has often been due to management interventions including improvement of water quality, reduction of industrial sewage discharge, and introduction of regulations governing anchoring and trawling. These reversals of seagrass habitat decline offer hope that associated ecosystem services, including the contribution to habitat quality by the epifaunal communities in terms of secondary production and food resources for invertivorous fishes within these meadows, can also recover (Vaudrey et al. 2010, Dolch et al. 2013, de los Santos et al. 2019).

Macroalgal meadows

Along with seagrasses, macroalgae rank among the most important contributors to global carbon and oxygen cycles in shallow marine environments (Hatcher 1990, Titlyanov & Titlyanova 2012, Unsworth et al. 2018). While seagrasses occupy soft sediment areas surrounding reefs, adjacent areas of hard pavement can be dominated by a great diversity of macroalgae, ranging from short algal turfs that form an epilithic algal matrix (EAM), to foliose understory macroalgae without canopies (e.g., *Dictyota* spp., *Padina* spp.), to fleshy canopy-forming laminarian (*Laminaria* spp.) and fucoid species (e.g., *Sargassum* spp., *Cystoseira* spp.) that attain heights over 1 m. In tropical marine ecosystems, macroalgal meadows have been estimated to cover 16–46% of shallow inshore habitats (Fulton et al. 2019).

Although macroalgae can be highly productive components of these ecosystems, they generally attract less attention than coral-dominated areas in coastal conservation and management (Fulton et al. 2019). Nevertheless, in clear tropical waters, macroalgae can produce up to 0.5 $kg \cdot C \cdot m^{-2} \cdot yr^{-1}$, suggesting that the net primary production of dense macroalgal communities within tropical marine ecosystems is as vital as the energy produced by corals (Hatcher 1990, Schaffelke & Klumpp 1997, Eidens et al. 2014). Notably, corals have tight symbiotic cycling of photosynthetic materials between the coral host and zooxanthellae, meaning that relatively low amounts of their net production become available to consumers (Hatcher 1990). The reverse is true for macroalgae, where the net production of primary biomass can be readily consumed by a range of invertebrate and vertebrate herbivores, aiding transfer of energy and nutrients to carnivores (Titlyanov & Titlyanova 2012, Fulton et al. 2019). In tropical macroalgal meadows, abundant and diverse epifauna are a key food resource, making macroalgal meadows important feeding sites for a large variety of reef fishes (Wilson et al. 2014, Tano et al. 2016, van Lier et al. 2018).

Macroalgae belonging to the genus *Sargassum* (family Sargassaceae) are dominant canopy-forming species globally. The large and dense meadows of *Sargassum* trap nutrients from sea water and contribute to high primary productivity within these habitats. They generally harbour abundant and diverse invertebrate assemblages through expanded surface area and complex canopy structure (Taylor & Cole 1994). *Sargassum* canopies host a broad biodiversity of epifaunal invertebrates that are targeted by carnivorous fishes (Edgar 1990b, Edgar & Aoki 1993, Tano et al. 2016). For example, gammarid amphipods, harpacticoid copepods, tanaidaceans, gastropods, bivalves, ophiuroids and polychaetes are common epifauna in the canopy-forming *Sargassum* meadows of Ningaloo Reef, Western Australia, where an individual *Sargassum* can host more than 6000 invertebrates, providing sufficient food for a large guild of higher-order predators (Wenger et al. 2018, Chen et al. 2020).

The biomass and canopy structure of *Sargassum* meadows fluctuate seasonally with sea temperature, influencing the biodiversity, abundance and trophodynamics of associated animals such as epifaunal invertebrates and reef fishes. While a basic knowledge of seasonal fluctuations in *Sargassum* biomass exists (Santelices 1977, Glenn et al. 1990, Trono & Lluisma 1990, Vuki & Price 1994, Schaffelke & Klumpp 1997, Leite & Turra 2003, Hwang et al. 2004, Tsai et al. 2004, Wong & Phang 2004, Ateweberhan et al. 2005, Ang 2006, Ateweberhan et al. 2006, 2008, 2009, Mattio et al. 2008, Lefevre & Bellwood 2010, Fulton et al. 2014, Wilson et al. 2014, Lim et al. 2016), we still have little understanding of how such fluctuations may influence the biodiversity of associated invertebrates, as well as trophic flows within tropical reef ecosystems. In temperate macroalgal meadows, seasonal fluctuations in epifaunal abundance and composition have been recorded (Edgar 1983, Taylor 1998b), with faunal densities reaching a peak in late summer and dropping to low levels in winter. In some cases, this pattern corresponds with seasonal variations in canopy size and shape structure (Edgar & Klumpp 2003, Ba-Akdah et al. 2016, Tano et al. 2016).

In highly productive tropical *Sargassum* meadows, epifaunal fluctuations can show typical annual cycles (Leite & Turra 2003, Ba-Akdah et al. 2016), with seasonality related to the growth and decay of the canopy, which in turn presumably responds to a variety of physical (e.g., light, sea temperature, wave action) and biological (e.g., food resource, competition, predation) drivers. Shifts in habitat availability and complexity can alter habitat area, food supply and/or niche availability for epifaunal different species, as well as influence the strength of biological interactions (e.g., predation, competition; Ledet et al. 2018, Wenger et al. 2018, Chen et al. 2020).

Moving from tropical to temperate macroalgal habitats, research has focused on the community structure and spatio-temporal variation of epifaunal communities associated with the habitat-forming fucoids *Cystoseira* (Fraschetti et al. 2002, Bedini et al. 2014, Casamajor et al. 2019) and *Laminaria* (Seed & Harris 1980, Schmidt & Scheibling 2006, Cacabelos et al. 2010, Tuya et al. 2011, Walls et al. 2016). *Laminaria*-associated epifauna have been particularly well studied in terms of their community structure, secondary production, contribution to energy flows, spatio-temporal variation, biological interactions and response to disturbances. Strong seasonality in these temperate marine environments will have the potential to trigger large trophic cascades associated with the temporal fluctuations in algal biomass. Understanding the responses of epifaunal communities to seasonal habitat changes within these important temperate marine ecosystems represents a key research priority.

The contribution of epifauna to seagrass and macroalgal 'nurseries'

Notably, the roles described above of epifauna as contributing to the quality and quantity of food resources provided by seagrass and macroalgal meadows make them a contributor to the critical role meadows play in providing nursery habitats for juvenile reef fish species, including species that are key fisheries targets (Nagelkerken et al. 2000, Evans et al. 2014, Fulton et al. 2020). Nursery habitats can only be defined as such if their contribution to the adult population biomass is greater than the average production of all juvenile habitats (see Dahlgren et al. 2006, Nagelkerken 2009). Given this definition, high food abundance is likely to be one of the key contributing factors to making a particular area 'nursery' habitat. This means that macroaglae-associated and seagrass-associated epifauna are fundamental to the development of fish nurseries and to the quality of that nursery habitat in terms of its nutritional load. Studies have shown, via use of stable isotopes and gut content analysis, that epifauna, in particular small crustaceans, are an important contributor to the diet of juvenile fishes within these habitats (de la Morinière et al. 2003) and that food availability is a key factor in attracting juvenile fishes to particular nursery sites (Verweij et al. 2006). In this sense, epifaunal communities associated with seagrass and macroalgal habitats are likely to be integral to the development of fish nurseries and, hence, to the life cycle of many commercially important reef fish species.

Effects of environmental disturbance on epifaunal communities

Although some studies have looked at the effects of natural disturbance events on epifaunal communities (such as typhoons, tsunamis and storm events (Posey et al. 1996, Roberts et al. 2007, Lomovasky et al. 2011, Salmo et al. 2019), coastal habitat alteration (such as marina operations (Turner et al. 1997), construction of pier pilings (on the artificial substrata *per se*, Glasby 1999a,b, or on macroalgae growing on pilings, Marzinelli et al. 2009, 2011) and coastal structures (Sedano et al. 2020) in the context of invasive species, or pollution (e.g., Johnston et al. 2011), investigations of effects of anthropogenic disturbance on epifauna have historically focused on impacts of fishing, including trawling and dredging (e.g., Hutchings 1990, Collie et al. 1997, Freese et al. 1999, Collie et al. 2000a,b, Rumohr & Kujawski 2000, Veale et al. 2000, Jennings et al. 2001a,b, Thrush et al. 2001, Gage et al. 2005, de Juan et al. 2007, 2011, de Juan & Demestre 2012, Strain et al. 2012). Together, these studies demonstrate high sensitivity of epifaunal communities to fishing, which can affect population size structure (Hinz et al. 2009), alter community composition (Hinz et al. 2009) and reduce the maximum size of organisms within the community (e.g., 17% reduction in mean size, Lambert et al. 2011), overall epifaunal biomass (Hinz et al. 2009, Lambert et al. 2011) and species richness. The focus on benthic habitat degradation via fishing methods continues to the present (e.g., Mangano et al. 2013, Lambert et al. 2017, Lundquist et al. 2018), although research on impacts of other environmental factors is expanding, such as shifts driven by eutrophication (Cebrian et al. 2014) and coastal acidification (Hossain 2019, Hossain et al. 2019), along with interactions between environmental factors and trawling effort (e.g., Couce et al. 2020).

Somewhat surprisingly, far fewer studies have investigated potential effects of climate change (e.g., pulse heatwaves, ocean warming, ocean acidification) on marine epifaunal communities. Only a handful of studies to date have considered likely changes in epifaunal community structure wrought by climate-related factors (e.g., Osman et al. 2010, Powell et al. 2019). Two studies have demonstrated the potential for experimental mesocosms to enhance our understanding of the effects of global change on epifauna. In a five-week study, Eklöf et al. (2015) tested the effect of temperature (ambient versus + 3.2°C), ocean acidification and simulated consumer loss (the omnivorous crustacean, *Gammarus locusta*), on the diversity and composition of macrofaunal communities in eelgrass (*Zostera marina*) beds. While acidification had little impact on macrofaunal communities over this relatively short study period, rapid warming and loss of consumer diversity led to an increase in macrofauna richness and abundance, but shifted the balance of organisms with particular life-history traits: warmer conditions favoured poorly defended epifaunal crustaceans such as tube-building amphipods and organisms that brooded their offspring.

The suggestion that epifaunal communities will be more affected by rapid warming than by rapid ocean acidification echoes the findings of Nagelkerken et al. (2020). In their mesocosm study, replicated benthic communities including primary producers (cyanobacteria and algae) and primary and secondary consumers typical of epibenthic communities (e.g., molluscs, copepods, polychaetes, fish) were established within 1800 L tanks and exposed to different temperature and acidification conditions. Alterations to food web structure, biomass and productivity under each scenario were documented. Food web structure was relatively unaffected by temperature and acidification, whereas biomass and productivity significantly changed. Secondary consumer biomass and productivity actually increased under combined warming and acidification, but primary consumption decreased. Over the longer term, this imbalance is obviously unsustainable and suggests that this particular climate scenario could ultimately see the system tip into a new stable state dominated by primary producers, with an associated reduction in the higher-order consumers, such as fish species that are the target of food fisheries (see Figure 1 in Chown 2020).

Managing the effects of environmental disturbance: The inextricable link to habitat

While the idea of ‘managing’ organisms <10 mm in size may seem a somewhat sisyphean task, it is nevertheless a critical one. As described above, the inextricable link to habitat means that the task of ‘managing’ epifaunal communities essentially reduces to managing marine habitats. Research findings clearly indicate that changes in habitat structural elements flow on to taxonomic changes in the epifaunal community (Taylor & Cole 1994). This is evident for macroalgal canopies (Chemello & Milazzo 2002, Marzinelli et al. 2009, 2011, 2012, 2016) and coral reefs (Stella et al. 2010, Kramer et al. 2014). The abundance, biomass and size structure of epifaunal communities can all vary with different structural aspects of the particular habitat (Edgar et al. 1994, Taylor 1998a,b, Kramer et al. 2014, 2017), meaning that any disturbance that causes a habitat change will also affect epifaunal community structure and function.

Potential drivers of structural changes to individual marine habitats and their associated epifaunal communities include marine heatwave events that induce loss of macroalgal canopy structure (Smale & Wernberg 2013, Wernberg et al. 2013, 2016), heat-induced coral bleaching events (Hughes et al. 2017), high-intensity cyclones (Salmo et al. 2019) or coastal development (Partyka & Peterson 2008, Blake et al. 2014, Callaway et al. 2020a) (Figure 2.9). Changes in habitat structural characteristics could result in, for example, eutrophication-driven loss of parts of the seagrass canopy that leads to fragmentation of the remaining habitat (e.g., Waycott et al. 2009). Evidence for the effects of seagrass fragmentation on epifauna is currently somewhat equivocal, with some studies showing higher species richness in a number of small patches compared to a large patch of the same area (e.g., McNeill & Fairweather 1993, Eggleston et al. 1999, Reed & Hovel 2006), but with variable responses through time among individual taxa (Healey & Hovel 2004). Studies looking at edge effects on densities of epifauna in seagrass habitats have also yielded inconsistent results, with some showing positive effects (Bowden et al. 2001, Warry et al. 2009, Arponen & Boström 2012), some negative (Hovel & Lipcius 2002, Uhrin & Holmquist 2003) and some no effect (Connolly & Hindell 2006). In reality, as Warry et al. (2009) point out, patchy landscapes will benefit certain taxa (e.g., harpacticoid copepods), but the net effect will ultimately be dependent on how patchiness came about, as well as patch size and distances between patches (Arponen & Boström 2012).

In other cases, disturbance events could set the ecosystem onto a new trajectory, with the habitat undergoing a phase shift and tipping into a new stable state (Holling 1973). For example, a thermal anomaly leading to a severe coral bleaching event that results in coral death and the overgrowth of dead skeleton by algal turf. Fraser et al. (2020a) found that live branching coral and turfing algae are host to significantly different epifaunal communities, meaning that as the ecosystem shifts from coral to turf following a bleaching event, invertebrate communities are likely to transform in predictable ways. We still, however, need to understand the implications of habitat change on ecosystem nutrient cycling and production levels. For each of the cases highlighted in Figure 2.9, knowledge gaps include whether the changes will lead to reduced or enhanced epifaunal abundance and biomass (and lower or higher secondary production levels, respectively), or sustained community abundance but altered biodiversity or size structure, and hence altered biomass and production.

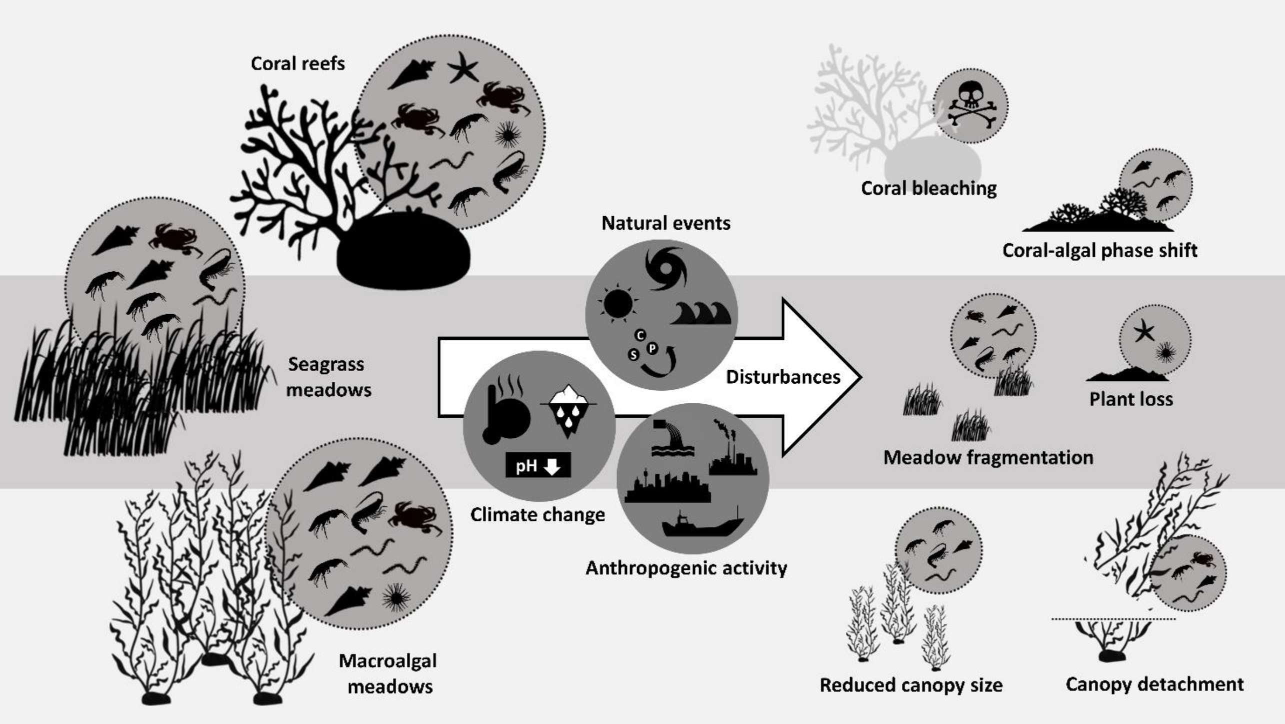

Figure 2.9 Potential impacts of disturbance events on the structure of three main marine habitats: coral reefs, seagrass meadows and macroalgal meadows, and the associated consequences for epifaunal communities associated with those microhabitats. Healthy habitats and their associated epifaunal communities are pictured on the left of the figure. Examples of disturbance events that could impact these habitats are given within centre grey circles, while the white arrow points in the direction of potential changes to habitat structure following such events. On the right-hand side of the figure, the altered habitat is shown, along with the potential impact on the epifaunal community.

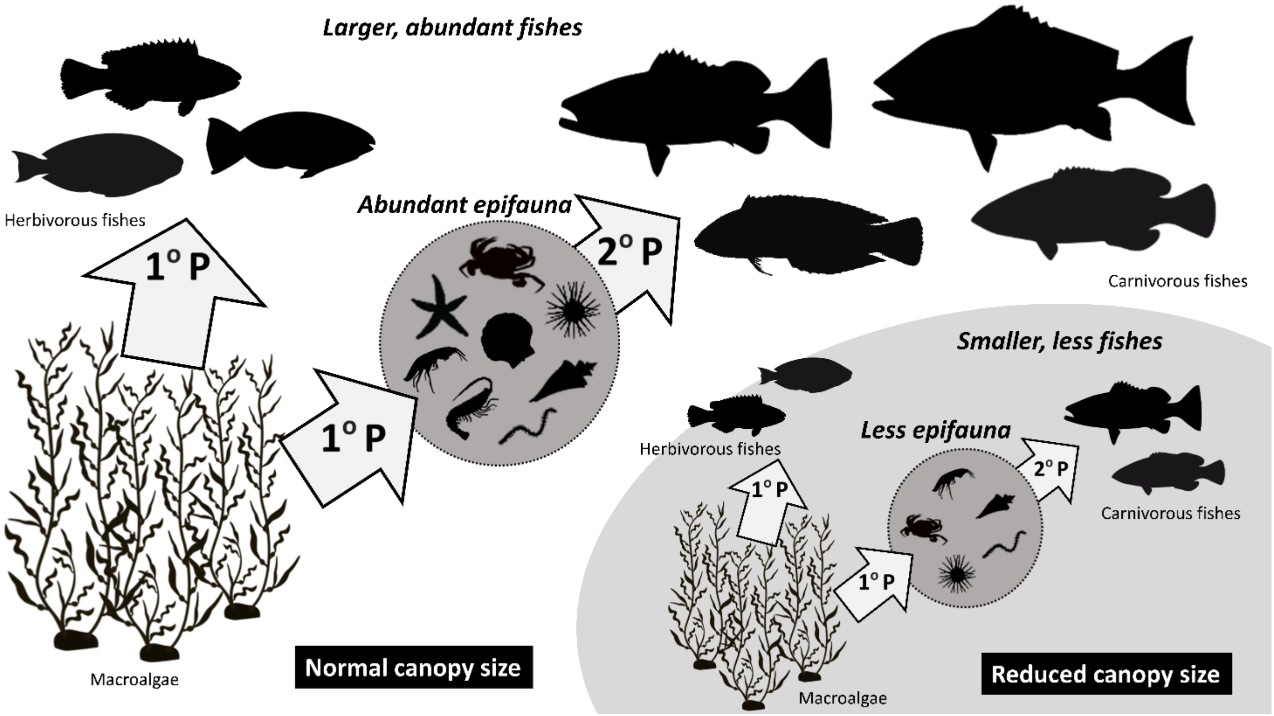

Figure 2.10 Conceptual diagram highlighting the potential consequences of climate-driven alterations to tropical *Sargassum* canopy structure over and above those currently experienced on a seasonal basis, and the flow-on food chain effects for epifaunal communities and higher-order consumers (invertivorous and carnivorous fishes). (1°P: primary production, 2°P: secondary production)

The fact that minor changes in habitat structure might fundamentally alter a community of organisms almost too small for the eye to see is a powerful reminder of the need to consider all the potential consequences of environmental change, before they yield unforeseen consequences, including impacts on fisheries production and human food security. Thus, a better understanding of epifaunal assemblages in anthropogenically altered habitats should be seen as a research priority in the current era of rapid change in marine ecosystems. For example, we know that *Sargassum* meadows display temporal fluctuations in canopy structure (e.g., biomass, cover, canopy height) corresponding to variations in sea temperature (Glenn et al. 1990, Ateweberhan et al. 2006, Fulton et al. 2014) (Figure 2.10), but currently have little understanding of how changes to *Sargassum* growth and survival driven by warming ocean temperatures (e.g., Graba-Landry et al. 2020) may influence epifaunal production. While current evidence indicates *Sargassum* supports elevated abundance and diversity of epifaunal invertebrates and fishes (Wilson et al. 2014, Tano et al. 2016, Wenger et al. 2018), we lack good information on mechanisms underlying tropical reef ecosystems, including the size structure and diversity of fish populations that can be supported by different levels of epifaunal secondary production (Figure 2.10). Similarly, better understanding is needed as to how subtle changes to structural elements within marine habitats will impact the abundance, population size structure and productivity of epifaunal communities within those habitats, and ultimately their ability to maintain current levels of ecosystem production and food web stability.

Conclusions and future research directions

This review has explored the history of the study of epifauna and considered the different nomenclature used within the research field to describe similar communities with similar ecosystem functions. We highlight the challenge that this can pose when trying to present a unified perspective on the contribution of these organisms to marine ecosystems. Much of the confusion surrounding nomenclature can be avoided by defining organisms according to the role they play in marine ecosystems, i.e., by considering a functional rather than a taxonomic or habitat-based classification.

This review has also highlighted that, despite their ubiquity, epifauna are a relatively poorly studied group of animals. Three main reasons likely contribute to this: (1) their small body size and cryptic habits; (2) challenges associated with quantitatively sampling and processing communities within structurally diverse habitats; and (3) the difficulty of providing high taxonomic resolution when describing the constituent organisms within diverse epifaunal samples. However, new sampling techniques have immense potential to break down some of these barriers, providing an opportunity for a renaissance in the field in coming years. A quantum advance in epifaunal research is likely through eDNA sampling and analysis of metagenomic structure (Kelly et al. 2017, Stæhr et al. 2017, Garlapati et al. 2019), advances that can surmount all three sampling and taxonomic challenges listed above. An important research front that is currently very active is the estimation of abundance, which remains to be accurately assessed using eDNA methodologies (Kelly et al. 2016, Garlapati et al. 2019, Leduc et al. 2019).

Epifaunal communities potentially provide a critical indicator of marine ecosystem health, including as an early warning sign of issues higher up the food chain. Reduced cost barriers associated with sampling and processing also open up the possibility of repeated sampling of individual locations over the longer term, and the ability to build long-term datasets that can offer insights into community responses to changing environmental conditions. Long-term databases will also likely be key to improving our understanding of the impact of epifaunal production and nutrient cycling on marine ecosystems, and for modelling projections of the biomass of higher-order consumers that can be supported under various climate scenarios.

Additional opportunities for breaking down barriers associated with sampling and taxonomic identification are provided through citizen science. Technological developments that offer more tractable sampling protocols could see the routine inclusion of epifaunal community metrics in marine ecosystem management plans, as well as the chance to build large teams of citizen scientists engaged in sampling eDNA, and monitoring epifaunal communities across broad scales (Duffy et al. 2019). This approach builds on the success of other citizen science programs, such as iNaturalist, eBird and Reef Life Survey (Edgar et al. 2021).

Experimental approaches also offer exciting opportunities to explore how ecological interactions may alter under future climate scenarios (Edgar et al. 2016), as highlighted by the recent study by Nagelkerken et al. (2020). Mesocosm studies, which replicate marine benthic communities and then quantify how food web structure, biomass and productivity are altered under various environmental scenarios, have the potential to yield further insights into the resilience of marine ecosystems under global change. Coordinated experimental networks, where controlled manipulative experiments are replicated in different regions worldwide, similarly include huge capacity for expanding generality of knowledge. Thus, both mesocosm and experimental network approaches are likely to offer important insights into changes to marine trophic structures, including impacts on fish populations and global food security. Epifaunal communities, by virtue of their critical role in marine food web structures, need to feature more significantly in marine research agendas. This is more than a ‘research push’, but a call for investment in studies that can fill the gaps in our understanding of the quantitative contribution that epifauna make to global biodiversity and services provided by marine ecosystems, as well as the potential impacts of global change on abundance, community composition and biomass of epifauna themselves.

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Appendix 2.1

Published studies on marine epifaunal communities based on a literature search conducted in the ISI Web of Science database up to and including 21 July 2020 using the terms 'epifauna' and 'epifaunal'.

Year	Authors	Title	Journal
1953	Allen	Observations on the epifauna of the deep-water muds of the Clyde Sea Area, with special reference to *Chlamys septemradiata* (Müller)	Journal of Animal Ecology
1964	Pequegnat	Epifauna of California siltstone reef	Ecology
1967	Calder & Brehmer	Seasonal occurrence of epifauna on test panels in Hampton Roads, Virginia	International Journal of Oceanology and Limnology
1967	Driscoll	Attached epifauna-substrate relations	Limnology and Oceanography
1967	Richards & Riley	Benthic epifauna of Long Island Sound	Bulletin of the Bingham Oceanographic Collection
1968	Fager	A sand-bottom epifaunal community of invertebrates in shallow water	Limnology and Oceanography
1968	Matthews	Folliculinids (protozoa) of Ago Bay, Japan, and their relation to epifauna of pearl oyster (*Pinctada martensii*)	Pacific Science
1968	Pequegnat	Distribution of epifaunal biomass on a sublittoral rock-reef	Pacific Science
1968	Snell	The Lithothamnion community in Nord-Möre, Norway with notes on the epifauna of *Desmarestia viridis* (Müller)	Sarsia
1971	Bourget & Lacroix	Two simple durable epifaunal collectors	Journal of the Fisheries Research Board of Canada

1972	Sassaman & Mangum	Adaptations to environmental oxygen levels in infaunal and epifaunal sea anemones	Biological Bulletin
1973	Bourget & Lacroix	Seasonal aspects of settlement of benthic epifauna on infralittoral stratum of Saint Lawrence Estuary	Journal of the Fisheries Research Board of Canada
1973	Jackson et al.	Epifaunal invertebrates of ornate diamondback terrapin, *Malaclemys terrapin macrospilota*	American Midland Naturalist
1977	Koechlin	Settlement of epifauna of *Spirographis spallanzani*, *Sycon ciliatum* and *Ciona intestinalis* in harbor of Lezardrieux	Cahiers De Biologie Marine
1978	Anger	Development of a subtidal epifaunal community at the island of Helgoland	Helgoländer wissenschaftliche Meeresuntersuchungen
1978	Davis & Vanblaricom	Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow-water	Limnology and Oceanography
1978	Karlson	Predation and space utilization patterns in a marine epifaunal community	Journal of Experimental Marine Biology and Ecology
1979	Conover	Effect of gastropod shell characteristics and hermit crabs on shell epifauna	Journal of Experimental Marine Biology and Ecology
1979	Peterson	The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey	Oecologia
1980	Beckley & McLachlan	Studies on the littoral seaweed epifauna of St. Croix Island 2. Composition and summer standing stock	South African Journal of Zoology
1980	Fradette & Bourget	Ecology of benthic epifauna of the estuary and Gulf of St. Lawrence: factors influencing their distribution and abundance on buoys	Canadian Journal of Fisheries and Aquatic Sciences
1980	Jokiel	Solar ultraviolet radiation and coral reef epifauna	Science
1980	Russ	Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community	Journal of Experimental Marine Biology and Ecology
1980	Seed & Harris	The epifauna of the fronds of *Laminaria digitata* Lamour in Strangford Lough, Northern Ireland	Proceedings of the Royal Irish Academy Section B: Biological

			Geological and Chemical Science
1980	Stoner	Perception and choice of substratum by epifaunal amphipods associated with seagrasses	Marine Ecology Progress Series
1980	Vandolah & Bird	A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods	Estuarine and Coastal Marine Science
1980	Wood & Seed	The effects of shore level on the epifaunal communities associated with *Fucus serratus* (L) in the Menai Strait, North Wales	Cahiers De Biologie Marine
1981	Kay & Keough	Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia	Oecologia
1981	Seed & O'connor	Epifaunal associates of *Fucus serratus* at Dale, southwest Wales	Holarctic Ecology
1981	Seed et al.	The composition and seasonal changes amongst the epifauna associated with *Fucus serratus* L. in Strangford Lough, Northern Ireland	Cahiers De Biologie Marine
1981	Shin	The development of sessile epifaunal communities in Kylesalia, Kilkieran Bay (west coast of Ireland)	Journal of Experimental Marine Biology and Ecology
1982	Bak et al.	Complexity of coral interactions: influence of time, location of interaction and epifauna	Marine Biology
1982	Beckley	Studies on the littoral seaweed epifauna of St. Croix Island 3. *Gelidium pristoides* (Rhodophyta) and its epifauna	South African Journal of Zoology
1982	Lewis & Hollingworth	Leaf epifauna of the seagrass *Thalassia testudinum*	Marine Biology
1982	Russ	Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks	Oecologia
1983	Fletcher & Day	The distribution of epifauna on *Ecklonia radiata* (C. Agardh) J. Agardh and the effect of disturbance	Journal of Experimental Marine Biology and Ecology
1983	Karlson & Shenk	Epifaunal abundance, association, and overgrowth patterns on large hermit crab shells	Journal of Experimental Marine Biology and Ecology

1983	McDonald	A sampler for quantitatively assessing the macrobenthic epifaunal community of a hard substrate	Estuarine, Coastal and Shelf Science
1983	Shepherd	The epifauna of megaripples: specie's adaptations and population responses to disturbance	Australian Journal of Ecology
1983	Sheridan & Livingston	Abundance and seasonality of infauna and epifauna inhabiting a *Halodule wrightii* meadow in Apalachicola Bay, Florida	Estuaries
1983	Ward & Young	The depauperation of epifauna on *Pinna bicolor* near a lead smelter, Spencer Gulf, South Australia	Environmental Pollution Series A: Ecological and Biological
1984	Keough	Dynamics of the epifauna of the bivalve *Pinna bicolor*: interactions among recruitment, predation, and competition	Ecology
1984	Lópezjamar et al.	Contribution of infauna and mussel-raft epifauna to demersal fish diets	Marine Ecology Progress Series
1984	Patterson	Distribution patterns of some epifauna in the Irish Sea and their ecological interactions	Marine Biology
1984	Schmidt & Warner	Effects of caging on the development of a sessile epifaunal community	Marine Ecology Progress Series
1984	Virnstein et al.	Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained?	Estuaries
1985	Dewitt & Levinton	Disturbance, emigration, and refugia: how the mud snail, *Ilyanassa obsoleta* (Say), affects the habitat distribution of an epifaunal amphipod, *Microdeutopus gryllotalpa* (Costa)	Journal of Experimental Marine Biology and Ecology
1985	Hootsmans & Vermaat	The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions	Aquatic Botany
1985	Howard	Measurements of short-term turnover of epifauna within seagrass beds using an *in situ* staining method	Marine Ecology Progress Series
1985	Woodhead & Jacobson	Epifaunal settlement, the processes of community development and succession over two years on an artificial reef in the New York bight	Bulletin of Marine Science

1986	Fishelson & Haran	Epifauna of algae on a rocky platform near Mikhmoret (Mediterranean Sea, Israel): composition and dynamics	Israel Journal of Zoology
1986	Oswald & Seed	Organization and seasonal progression within the epifaunal communities of coastal macroalgae	Cahiers De Biologie Marine
1986	Persson & Olafsson	Distribution and abundance of mobile epifauna and macrozoobenthos in south Swedish shallow marine areas	Ophelia
1986	Todd & Turner	Ecology of intertidal and sublittoral cryptic epifaunal assemblages. I. Experimental rationale and the analysis of larval settlement	Journal of Experimental Marine Biology and Ecology
1987	Cancino et al.	Effects of epifauna on algal growth and quality of the agar produced by *Gracilaria verrucosa* (Hudson) Papenfuss	Hydrobiologia
1987	Demurguia & Seed	Some observations on the occurrence and vertical-distribution of mites (Arachnida: Acari) and other epifaunal associates of intertidal barnacles on two contrasted rocky shores in North Wales	Cahiers De Biologie Marine
1987	Howard	Diel variation in the abundance of epifauna associated with seagrasses of the Indian River, Florida, USA	Marine Biology
1987	Johnson & Scheibling	Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus Vesiculosus* in Nova Scotia, Canada	Marine Ecology Progress Series
1987	Lewis	Crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, USA	Marine Biology
1987	Rosman et al.	Epifaunal aggregations of Vesicomyidae on the continental slope off Louisiana	Oceanographic Research Papers
1987	Virnstein & Howard	Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. 1. Comparisons among three species of seagrasses from adjacent beds	Bulletin of Marine Science
1987	Virnstein & Howard	Motile epifauna of marine macrophytes in the Indian River Lagoon, Florida. 2. Comparisons between drift algae and three species of seagrasses	Bulletin of Marine Science
1988	Feder & Pearson	The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. V. Biology of the dominant soft-bottom epifauna and their interaction with the infauna	Journal of Experimental Marine Biology and Ecology

1988	Hall & Bell	Response of small motile epifauna to complexity of epiphytic algae on seagrass blades	Journal of Marine Research
1988	Okamura	The influence of neighbors on the feeding of an epifaunal bryozoan	Journal of Experimental Marine Biology and Ecology
1988	Todd & Turner	Ecology of intertidal and sublittoral cryptic epifaunal assemblages. II. Nonlethal overgrowth of encrusting bryozoans by colonial ascidians	Journal of Experimental Marine Biology and Ecology
1989	Basford et al.	The epifauna of the Northern North Sea (56°–61°N)	Journal of the Marine Biological Association of the United Kingdom
1989	Costello & Myers	Breeding periodicity and sex ratios in epifaunal marine amphipoda in Lough Hyne, Ireland	Estuarine, Coastal and Shelf Science
1989	Harrison	Are deep-sea asellote isopods infaunal or epifaunal	Crustaceana
1989	Mullineaux	Vertical distributions of the epifauna on manganese nodules: implications for settlement and feeding	Limnology and Oceanography
1990	Baden	The cryptofauna of *Zostera marina* (L.): abundance, biomass and population dynamics	Netherlands Journal of Sea Research
1990	Basford et al.	The infauna and epifauna of the northern North Sea	Netherlands Journal of Sea Research
1990	Daniel & Robertson	Epibenthos of mangrove waterways and open embayments: community structure and the relationship between exported mangrove detritus and epifaunal standing stocks	Estuarine, Coastal and Shelf Science
1990	Davoult	Biofacies and trophic structure of the "pebbles-with-sessile-epifauna" community in the Dover Strait	Oceanologica Acta
1990	Edgar	Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass	Journal of Experimental Marine Biology and Ecology
1990	Edgar	Predator-prey interactions in seagrass beds. III. Impacts of the western rock lobster *Panulirus cygnus* George on epifaunal gastropod populations	Journal of Experimental Marine Biology and Ecology

1990	Edgar	The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production	Marine Biology and Ecology
1990	Hendrickx	The stomatopod and decapod crustaceans collected during the GUAYTEC II Cruise in the Central Gulf Of California, mexico, with the description of a new species of *Plesionika* Bate (Caridea, Pandalidae)	Revista De Biologia Tropical
1990	Hutchings	Review of the effects of trawling on macrobenthic epifaunal communities	Australian Journal of Marine and Freshwater Research
1990	Kunitzer	The infauna and epifauna of the central North Sea	Meeresforschung-Reports on Marine Research
1990	Lambshead & Gooday	The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic: the assemblage response	Deep Sea Research Part I: Oceanographic Research Papers
1991	Anderson et al.	*Gelidium pristoides* in South Africa	Hydrobiologia
1991	Ansari et al.	Seagrass habitat complexity and macroinvertebrate abundance in Lakshadweep coral reef lagoons, Arabian Sea	Coral Reefs
1991	Edgar	Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese *Sargassum* bed	Hydrobiologia
1991	Edgar	Distribution patterns of mobile epifauna associated with rope fibre habitats within the Bathurst Harbour estuary, south-western Tasmania	Estuarine, Coastal and Shelf Science
1991	Hopkinson et al.	Community metabolism and nutrient cycling at Gray's Reef, a hard bottom habitat in the Georgia Bight	Marine Ecology Progress Series
1991	Karande	Use of epifaunal communities in pollution monitoring	Journal of Environmental Biology
1991	Lana & Guiss	Influence of *Spartina alterniflora* on structure and temporal variability of macrobenthic associations in a tidal flat of Paranagua Bay (southeastern Brazil)	Marine Ecology Progress Series

1991	Marshall et al.	New southern geographical records of intertidal sea urchins (Echinodermata: Echinoidea), with notes on abundance	South African Journal of Zoology
1991	Rainer & Unsworth	Ecology and production of *Nebalia* sp. (Crustacea: Leptostraca) in a shallow-water seagrass community	Australian Journal of Marine and Freshwater Research
1991	Russo	Do predatory fishes affect the structure of an epiphytal amphipod assemblage on a protected algal reef in Hawaii?	Hydrobiologia
1991	Schneider & Mann	Rapid recovery of fauna following simulated ice rafting in a Nova Scotian seagrass bed	Marine Ecology Progress Series
1991	Schneider & Mann	Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies	Journal of Experimental Marine Biology and Ecology
1991	Schneider & Mann	Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation	Journal of Experimental Marine Biology and Ecology
1991	Stephens & Bertness	Mussel facilitation of barnacle survival in a sheltered bay habitat	Journal of Experimental Marine Biology and Ecology
1991	Takeuchi & Hirano	Growth and reproduction of *Caprella danilevskii* (Crustacea: Amphipoda) reared in the laboratory	Marine Biology
1991	Turner & Todd	The effects of *Gibbula cineraria* (L.), *Nucella lapillus* (L.) and *Asterias rubens* L. on developing epifaunal assemblages	Journal of Experimental Marine Biology and Ecology
1991	Ward & Thorpe	Distribution of encrusting bryozoans and other epifauna on the subtidal bivalve *Chlamys opercularis*	Marine Biology
1991	Webb & Parsons	Impact of predation-disturbance by large epifauna on sediment-dwelling harpacticoid copepods: field experiments in a subtidal seagrass bed	Marine Biology
1991	Zvyagintsev	Seasonal changes in the epifauna on valvas of the oyster *Crassostrea gigas* in Amur Bay, the Sea of Japan	Biologiya Morya-Marine Biology
1992	Ardisson & Bourget	Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna	Marine Ecology Progress Series

1992	Aronson	Biology of a scale-independent predator-prey interaction	Marine Ecology Progress Series
1992	Bingham	Life histories in an epifaunal community: coupling of adult and larval processes	Ecology
1992	Dalby & Young	Role of early post-settlement mortality in setting the upper depth limit of ascidians in Florida epifaunal communities	Marine Ecology Progress Series
1992	Dewarumez et al.	Is the 'muddy heterogeneous sediment assemblage' an ecotone between the pebbles community and the *Abra alba* community in the southern bight of the North Sea?	Netherlands Journal of Sea Research
1992	Edgar	Patterns of colonization of mobile epifauna in a Western Australian seagrass bed	Journal of Experimental Marine Biology and Ecology
1992	Edgar & Robertson	The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian *Amphibolis* bed	Journal of Experimental Marine Biology and Ecology
1992	Eleftheriou & Robertson	The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community	Netherlands Journal of Sea Research
1992	Hily & Floch	Structure of subtidal algal assemblages on soft-bottom sediments: fauna/flora interactions and role of disturbances in the Bay of Brest, France	Marine Ecology Progress Series
1992	Isaksson & Pihl	Structural changes in benthic macrovegetation and associated epibenthic faunal communities	Netherlands Journal of Sea Research
1992	Klumpp et al.	The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community	Aquatic Botany
1992	Lana & Guiss	Macrofauna-plant-biomass interactions in a euhaline salt marsh in Paranagua Bay (SE Brazil)	Marine Ecology Progress Series
1992	Namikawa et al.	Role of the tentaculozooids of the polymorphic hydroid *Stylactaria conchicola* (Yamada) in interactions with some epifaunal space competitors	Journal of Experimental Marine Biology and Ecology
1992	Pearson & Rosenberg	Energy flow through the SE Kattegat: a comparative examination of the eutrophication of a coastal marine ecosystem	Netherlands Journal of Sea Research

1992	Takeuchi & Hirano	Duration and size of embryos in epifaunal amphipods *Caprella danilevskii* Czerniavski and *C. okadai* Arimoto (Crustacea: Amphipoda: Caprellidea)	Journal of Experimental Marine Biology and Ecology
1992	Takeuchi & Hirano	Growth and reproduction of the epifaunal amphipod *Caprella okadai* Arimoto (Crustacea: Amphipoda: Caprellidea)	Journal of Experimental Marine Biology and Ecology
1993	Duineveld et al.	The trawlfauna of the Mauritanian shelf (Northwest Africa): density, species composition, and biomass	Hydrobiologia
1993	Edgar	Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index	Oecologia
1993	Edgar & Aoki	Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*	Oecologia
1993	Fowler & Laffoley	Stability in Mediterranean-Atlantic sessile epifaunal communities at the northern limits of their range	Journal of Experimental Marine Biology and Ecology
1993	Gonzalez et al.	Epifauna of *Spondylus princeps unicolor* (Mollusca: Bivalvia) in Puerto Escondido, Gulf of California, Mexico	Revista De Biologia Tropical
1993	Martin-Smith	Abundance of mobile epifauna: the role of habitat complexity and predation by fishes	Journal of Experimental Marine Biology and Ecology
1993	Mellors & Marsh	Relationship between seagrass standing crop and the spatial distribution and abundance of the natantian fauna at Green Island, Northern Queensland	Australian Journal of Marine and Freshwater Research
1993	Trowbridge	Local and regional abundance patterns of the ascoglossan (= sacoglossan) opisthobranch *Alderia modesta* (Loven, 1844) in the northeastern Pacific	Veliger
1993	Turner & Todd	The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews Bay, N.E. Scotland	Journal of Experimental Marine Biology and Ecology
1993	Wang & Widdows	Calorimetric studies on the energy metabolism of an infaunal bivalve, *Abra tenuis*, under normoxia, hypoxia and anoxia	Marine Biology
1994	Cattrijsse et al.	Nekton communities of an intertidal creek of a European estuarine brackish marsh	Marine Ecology Progress Series

1994	Connolly	Removal of seagrass canopy: effects on small fish and their prey	Journal of Experimental Marine Biology and Ecology
1994	Cruzabrego et al.	Community ecology of marine gastropods (Molusca: Gastropoda) in Contoy Island, Mexico	Revista De Biologia Tropical
1994	Edgar	Observations on the size-structure of macrofaunal assemblages	Journal of Experimental Marine Biology and Ecology
1994	Edgar et al.	Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria	Journal of Experimental Marine Biology and Ecology
1994	Everett	Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages	Journal of Experimental Marine Biology and Ecology
1994	Gee & Warwick	Body-size distribution in a marine metazoan community and the fractal dimensions of macroalgae	Journal of Experimental Marine Biology and Ecology
1994	Gee & Warwick	Metazoan community structure in relation to the fractal dimensions of marine macroalgae	Marine Ecology Progress Series
1994	Hardin et al.	Spatial variation in hard-bottom epifauna in the Santa Maria basin, California: the importance of physical factors	Marine Environmental Research
1994	Hostens & Hamerlynck	The mobile epifauna of the soft bottoms in the subtidal Oosterschelde estuary: structure, function and impact of the storm-surge barrier	Hydrobiologia
1994	Jean & Hilly	Quantitative sampling of soft-bottom macroepifauna for assessing the benthic system in the Bay of Brest (France)	Oceanologica Acta
1994	Kaiser et al.	Improving quantitative surveys of epibenthic communities using a modified 2m-beam trawl	Marine Ecology Progress Series
1994	Levin et al.	Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on fieberling Guyot	Journal of Marine Research
1994	Mangum	Multiple sites of gas exchange	American Zoologist
1994	Martin-Smith	Short-term dynamics of tropical macroalgal epifauna: patterns and processes in recolonization of *Sargassum fissifolium*	Marine Ecology Progress Series

1994	Matsumasa	Effect of secondary substrate on associated small crustaceans in a brackish lagoon	Journal of Experimental Marine Biology and Ecology
1994	Monteforte & Garcia-Gasca	Spat collection studies on pearl oysters *Pinctada mazatlanica* and *Pteria sterna* (Bivalvia, Pteriidae) in Bahia de La Paz, South Baja California, Mexico	Hydrobiologia
1994	Rathburn & Corliss	The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea	Paleoceanography
1994	Taylor & Cole	Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand	Marine Ecology Progress Series
1994	Todd & Keough	Larval settlement in hard substratum epifaunal assemblages: a manipulative field study of the effects of substratum filming and the presence of incumbents	Journal of Experimental Marine Biology and Ecology
1995	Bingham & Young	Stochastic events and dynamics of a mangrove root epifaunal community	Marine Ecology
1995	Connolly	Effects of removal of seagrass canopy on assemblages of small, motile invertebrates	Marine Ecology Progress Series
1995	Edgar & Shaw	The production and trophic ecology of shallow-water fish assemblages in southern Australia II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria	Journal of Experimental Marine Biology and Ecology
1995	Klitgaard	The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic	Sarsia
1995	McDermott & Fives	The diet of an assemblage of small demersal fish in the western Irish Sea	Biology and Environment: Proceedings of the Royal Irish Academy
1995	Migné & Davoult	Multi-scale heterogeneity in a macrobenthic epifauna community	Hydrobiologia
1995	Nalesso et al.	Tube epifauna of the Polychaete *Phyllochaetopterus socialis* Claparède	Estuarine, Coastal and Shelf Science
1995	Nelson	Amphipod crustaceans of the Indian River Lagoon: current status and threats to biodiversity	Bulletin of Marine Science
1995	Osman & Whitlatch	Predation on early ontogenic life stages and its effect on recruitment into a marine epifaunal community	Marine Ecology Progress Series

1995	Takeuchi & Hirano	Clinging behavior of the epifaunal caprellids (Amphipoda) inhabiting the *Sargassum* zone on the Pacific coast of Japan, with its evolutionary implications	Journal of Crustacean Biology
1995	Taylor et al.	A portable battery-powered suction device for the quantitative sampling of small benthic invertebrates	Journal of Experimental Marine Biology and Ecology
1995	Ulrich et al.	Tube-building in two epifaunal amphipod species, *Corophium insidiosum* and *Jassa falcata*	Helgolander Meeresuntersuchungen
1995	Vilela	Ecology of Quaternary benthic foraminiferal assemblages on the Amazon shelf, northern Brazil	Geo-Marine Letters
1995	Virnstein	Anomalous diversity of some seagrass-associated fauna in the Indian-River Lagoon, Florida	Bulletin of Marine Science
1996	Aller & Stupakoff	The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes	Continental Shelf Research
1996	Barry et al.	Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980	Estuaries
1996	Barthel et al.	A wandering population of the hexactineliid sponge *Pheronema carpenteri* on the continental slope off Morocco, northwest Africa	Marine Ecology
1996	Benedetti-Cecchi et al.	Estimating the abundance of benthic invertebrates: a comparison of procedures and variability between observers	Marine Ecology Progress Series
1996	Boaden	Habitat provision for meiofauna by *Fucus serratus* epifauna with particular data on the flatworm *Monocelis lineata*	Marine Ecology
1996	Castricfey	Richness and biodiversity in megatidal seas: rocky sublittoral communities of the Trebeurden-Ploumanach region (Northern Brittany, France)	Cahiers De Biologie Marine
1996	Chauvaud et al.	Experimental collection of great scallop postlarvae and other benthic species in the Bay of Brest: settlement patterns in relation to spatio-temporal variability of environmental factors	Aquaculture International
1996	Connolly & Butler	The effects of altering seagrass canopy height on small, motile invertebrates of shallow Mediterranean embayments	Marine Ecology
1996	Davenport et al.	Mixed fractals and anisotropy in subantarctic marine macroalgae from south Georgia: implications for epifaunal biomass and abundance	Marine Ecology Progress Series

1996	Drake & Arias	The effect of epibenthic predators and macroalgal cover on the benthic macroinvertebrate community of a shallow lagoon in the Bay of Cádiz (SW Spain)	Hydrobiologia
1996	Ellis et al.	Effects of gas producing platforms on continental shelf macroepifauna in the northwestern Gulf of Mexico: abundance and size structure	Canadian Journal of Fisheries and Aquatic Sciences
1996	Gee & Warwick	A study of global biodiversity patterns in the marine motile fauna of hard substrata	Journal of the Marine Biological Association of the United Kingdom
1996	Gooday	Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes	Deep Sea Research Part I: Oceanographic Research Papers
1996	Jacobi & Langevin	Habitat geometry of benthic substrata: effects on arrival and settlement of mobile epifauna	Marine Biology and Ecology
1996	Kuhne & Rachor	The macrofauna of a stony sand area in the German Bight (North Sea)	Helgolander Meeresunters
1996	Lemmens et al.	Filtering capacity of seagrass meadows and other habitats of Cockburn Sound, Western Australia	Marine Ecology Progress Series
1996	Levin et al.	Succession of macrobenthos in a created salt marsh	Marine Ecology Progress Series
1996	Li et al.	Foraminiferal biofacies on the mid-latitude Lincoln Shelf, South Australia: oceanographic and sedimentological implications	Marine Geology
1996	Posey et al.	Influence of storm disturbance on an offshore benthic community	Bulletin of Marine Science
1996	Rathburn et al.	Comparisons of the ecology and stable isotopic compositions of living (stained) benthic foraminifera from the Sulu and South China Seas	Deep Sea Research Part I: Oceanographic Research Papers
1996	Schlacher & Wooldridge	Origin and trophic importance of detritus - evidence from stable isotopes in the benthos of a small, temperate estuary	Oecologia
1996	Schrijvers et al.	Resource competition between macrobenthic epifauna and infauna in a Kenyan *Avicennia marina* mangrove forest	Marine Ecology Progress Series
1996	Thomas	Origin and community structure of the Harrington Sound Notch, Bermuda	Bulletin of Marine Science
1996	Williamson & Creese	Small invertebrates inhabiting the crustose alga *Pseudolithoderma* sp. (Ralfsiaceae) in northern New Zealand	New Zealand Journal of Marine and Freshwater Research

1997	Aller	Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region	Deep Sea Research Part I: Oceanographic Research Papers
1997	Boström & Bonsdorff	Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea	Journal of Sea Research
1997	Buhs & Reise	Epibenthic fauna dredged from tidal channels in the Wadden Sea of Schleswig-Holstein: spatial patterns and a long-term decline	Helgolander Meeresuntersuchungen
1997	Collie et al.	Effects of bottom fishing on the benthic megafauna of Georges Bank	Marine Ecology Progress Series
1997	Connolly	Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary	Hydrobiologia
1997	LeClair & LaBarbera	An *in vivo* comparative study of intersegmental flexibility in the ophiuroid arm	Biological Bulletin
1997	Livingston	Trophic response of estuarine fishes to long-term changes of river runoff	Bulletin of Marine Science
1997	Livingston et al.	Freshwater input to a gulf estuary: long-term control of trophic organization	Ecological Applications
1997	Manley & Shaw	Geotaxis and phototaxis in *Elphidium crispum* (Protozoa: Foraminiferida)	Journal of the Marine Biological Association of the United Kingdom
1997	McClanahan & Sala	A Mediterranean rocky-bottom ecosystem fisheries model	Ecological Modelling
1997	McCorkle et al.	Vertical distributions and stable isotopic compositions of live (stained) benthic foraminifera from the North Carolina and California continental margins	Deep Sea Research Part I: Oceanographic Research Papers
1997	McKnight & Probert	Epibenthic communities on the Chatham Rise, New Zealand	New Zealand Journal of Marine and Freshwater Research
1997	Russo	Epifauna living on sublittoral seaweeds around Cyprus	Hydrobiologia
1997	Sala	The role of fishes in the organization of a Mediterranean sublittoral community II: epifaunal communities	Journal of Experimental Marine Biology and Ecology

1997	Takeuchi & Hino	Community structure of caprellid amphipods (Crustacea) on seagrasses in Otsuchi Bay, northeastern Japan, with reference to the association of *Caprella japonica* (Schurin) and *Phyllospadix iwatensis* Makino	Fisheries Science
1997	Turner et al.	Changes in epifaunal assemblages in response to marina operations and boating activities	Marine Environmental Research
1997	Warner	Occurrence of epifaunshers on the periwinkle, *Littorina littorea* (L.), and interactions with the the polychaete *Polydora ciliata* (Johnston)	Hydrobiologia
1997	Wright et al.	Biological mediation of bottom boundary layer processes and sediment suspension in the lower Chesapeake Bay	Marine Geology
1998	Bacon et al.	Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles: I. Feeding activity and selection	Journal of Experimental Marine Biology and Ecology
1998	Chapman	Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution	Marine Ecology Progress Series
1998	Engel & Kvitek	Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary	Conservation Biology
1998	Flynn et al.	Macrobenthic associations of the lower and upper marshes of a tidal flat colonized by *Spartina alterniflora* in Cananeia Lagoon estuarine region	Bulletin of Marine Science
1998	Glasby	Estimating spatial variability in developing assemblages of epibiota on subtidal hard substrata	Marine and Freshwater Research
1998	Hata & Nakata	Evaluation of eelgrass bed nitrogen cycle using an ecosystem model	Environmental Modelling & Software
1998	Hatcher	Epibenthic colonisation patterns on slabs of stabilised coal-waste in Poole Bay, UK	Hydrobiologia
1998	Jernakoff & Nielsen	Plant–animal associations in two species of seagrasses in Western Australia	Aquatic Botany
1998	Knowles & Bell	The influence of habitat structure in faunal-habitat associations in a Tampa Bay seagrass system, Florida	Bulletin of Marine Science

1998	MacDonald et al.	Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles: II. Absorption efficiency and scope for growth	Journal of Experimental Marine Biology and Ecology
1998	Magorrian & Service	Analysis of underwater visual data to identify the impact of physical disturbance on horse mussel (*Modiolus modiolus*) beds	Marine Pollution Bulletin
1998	Mazouni et al.	Influence of oyster culture on water column characteristics in a coastal lagoon (Thau, France)	Hydrobiologia
1998	Osman & Whitlatch	Local control of recruitment in an epifaunal community and the consequences to colonization processes	Hydrobiologia
1998	Sardá et al.	The impact of epifaunal predation on the structure of macroinfaunal invertebrate communities of tidal saltmarsh creeks	Estuarine, Coastal and Shelf Science
1998	Sasekumar & Chong	Faunal diversity in Malaysian mangroves	Global Ecology and Biogeography
1998	Schrijvers et al.	The infaunal macrobenthos under East African *Ceriops tagal* mangroves impacted by epibenthos	Journal of Experimental Marine Biology and Ecology
1998	Tanaka & Leite	The effect of sieve mesh size on the abundance and composition of macrophyte-associated macrofaunal assemblages	Hydrobiologia
1998	Taylor	Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates	Marine Ecology Progress Series
1998	Taylor	Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand	Hydrobiologia
1998	Taylor	Short-term dynamics of a seaweed epifaunal assemblage	Journal of Experimental Marine Biology and Ecology
1998	Taylor & Rees	Excretory products of mobile epifauna as a nitrogen source for seaweeds	Limnology and Oceanography
1998	Thrush et al.	Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery	Ecological Applications

1998	Walsh & Mitchell	Factors associated with variations in abundance of epifaunal caridean shrimps between and within estuarine seagrass meadows	Marine and Freshwater Research
1998	Whitlatch & Osman	A new device for studying benthic invertebrate recruitment	Limnology and Oceanography
1998	Widdows et al.	Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface	Estuaries
1998	Wieczorek & Todd	Inhibition and facilitation of settlement of epifaunal marine invertebrate larvae by microbial biofilm cues	Biofouling
1998	Wildish & Fader	Pelagic–benthic coupling in the Bay of Fundy	Hydrobiologia
1998	Witman & Grange	Links between rain, salinity, and predation in a rocky subtidal community	Ecology
1998	Wolff et al.	A trophic flow model of the Golfo de Nicoya, Costa Rica	Revista De Biologia Tropical
1999	Bologna & Heck	Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics	Journal of Experimental Marine Biology and Ecology
1999	Brown & Taylor	Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal	Journal of Experimental Marine Biology and Ecology
1999	Connell	Effects of surface orientation on the cover of epibiota	Biofouling
1999	Connell & Anderson	Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size	Journal of Experimental Marine Biology and Ecology
1999	Cranfield et al.	Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand	Aquatic Conservation: Marine and Freshwater Ecosystems
1999	Davenport et al.	Epifaunal composition and fractal dimensions of marine plants in relation to emersion	Journal of the Marine Biological Association of the United Kingdom
1999	Edgar	Experimental analysis of structural versus trophic importance of seagrass beds. I. Effects on macrofaunal and meiofaunal invertebrates	Vie et Milieu - Life and Environment

1999	Edgar	Experimental analysis of structural versus trophic importance of seagrass beds. II. Effects on fishes, decapods and cephalopods	Vie et Milieu - Life and Environment,
1999	Freese et al.	Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska	Marine Ecology Progress Series
1999	Glasby	Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia	Estuarine, Coastal and Shelf Science
1999	Glasby	Effects of shading on subtidal epibiotic assemblages	Journal of Experimental Marine Biology and Ecology
1999	Glasby	Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages	Marine Ecology Progress Series
1999	Hily & Bouteille	Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) (Brittany, France)	Comptes Rendus de l'Académie des Sciences
1999	Jewett et al.	'Exxon Valdez' oil spill: impacts and recovery in the soft-bottom benthic community in and adjacent to eelgrass beds	Marine Ecology Progress Series
1999	Kenyon et al.	Abundance of fish and crustacean postlarvae on portable artificial seagrass units: daily sampling provides quantitative estimates of the settlement of new recruits	Journal of Experimental Marine Biology and Ecology
1999	Lavery et al.	Ecological effects of macroalgal harvesting on beaches in the Peel-Harvey Estuary, Western Australia	Estuarine, Coastal and Shelf Science
1999	Lepoint et al.	Fauna vs flora contribution to the leaf epiphytes biomass in a *Posidonia oceanica* seagrass bed (Revellata Bay, Corsica)	Hydrobiologia
1999	Morri et al.	Biodiversity of marine sessile epifauna at an Aegean island subject to hydrothermal activity: Milos, eastern Mediterranean Sea	Marine Biology
1999	Prena et al.	Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna	Marine Ecology Progress Series
1999	Ramos	The megazoobenthos of the Scotia Arc islands	Scientia Marina

1999	Rees et al.	A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas	ICES Journal of Marine Science
1999	Rees et al.	Surveys of the epibenthos of the Crouch Estuary (UK) in relation to TBT contamination	Journal of the Marine Biological Association of the United Kingdom
1999	Rose et al.	Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay	Marine Ecology Progress Series
1999	Saiz-Salinas & Urkiaga-Alberdi	Use of faunal indicators for assessing the impact of a port enlargement near Bilbao (Spain)	Environmental Monitoring and Assessment
1999	Sánchez-Jerez et al.	Comparison of the epifauna spatial distribution in *Posidonia oceanica*, *Cymodocea nodosa* and unvegetated bottoms: importance of meadow edges	Acta Oecologica
1999	Sánchez-Jerez et al.	Daily vertical migrations in the epifauna associated with *Posidonia oceanica* meadows	Journal of the Marine Biological Association of the United Kingdom
1999	Smallwood et al.	Megafauna can control the quality of organic matter in marine sediments	Naturwissenschaften
1999	Smith & Witman	Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment	Ecology
1999	Tarasov et al.	Effect of shallow-water hydrothermal venting on the biota of Matupi Harbour (Rabaul Caldera, New Britain Island, Papua New Guinea)	Continental Shelf Research
1999	Viejo	Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain	Aquatic Botany
2000	Cocito et al.	First survey of sessile communities on subtidal rocks in an area with hydrothermal vents: Milos Island, Aegean Sea	Hydrobiologia
2000	Cohen et al.	Epibenthic community structure in Port Phillip Bay, Victoria, Australia	Marine and Freshwater Research
2000	Collie et al.	A quantitative analysis of fishing impacts on shelf-sea benthos	Journal of Animal Ecology
2000	Collie et al.	Photographic evaluation of the impacts of bottom fishing on benthic epifauna	ICES Journal of Marine Science
2000	Dando et al.	Hydrothermal studies in the Aegean Sea	Physics and Chemistry of the Earth, Part B:

			Hydrology, Oceans and Atmosphere
2000	Edgar & & Barrett	Effects of catchment activities on macrofaunal assemblages in Tasmanian estuaries	Estuarine Coastal and Shelf Science
2000	Ellis et al.	Demersal assemblages in the Irish Sea, St George's Channel and Bristol Channel	Estuarine, Coastal and Shelf Science
2000	Gage et al.	Patterns in deep-sea macrobenthos at the continental margin: standing crop, diversity and faunal change on the continental slope off Scotland	Hydrobiologia
2000	Glasby	Surface composition and orientation interact to affect subtidal epibiota	Journal of Experimental Marine Biology and Ecology
2000	Jablonski et al.	Analysing the latitudinal diversity gradient in marine bivalves	Evolutionary Biology of the Bivalvia*
2000	Kaiser et al.	Fishing-gear restrictions and conservation of benthic habitat complexity	Conservation Biology
2000	Roy et al.	Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves	Proceedings of the Royal Society B: Biological Sciences
2000	Rumohr & Kujawski	The impact of trawl fishery on the epifauna of the southern North Sea	ICES Journal of Marine Science
2000	Sagasti et al.	Epifaunal communities thrive in an estuary with hypoxic episodes	Estuaries
2000	Sánchez-Moyano et al.	The molluscan epifauna of the alga *Halopteris Scoparia* in southern Spain as a bioindicator of coastal environmental conditions	Journal of Molluscan Studies
2000	Smith	The effects of a small sewage outfall on an algal epifaunal community at Macquarie Island (sub-Antarctic): a drop in the southern ocean?	Marine Pollution Bulletin
2000	Sutherland et al.	Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes	Marine Biology
2000	Tuck et al.	The impact of water jet dredging for razor clams, *Ensis* spp., in a shallow sandy subtidal environment	Journal of Sea Research
2000	Veale et al.	Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats	Marine Biology

2001	Beaulieu	Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks	Deep Sea Research Part I: Oceanographic Research Papers
2001	Beaulieu	Life on glass houses: sponge stalk communities in the deep sea	Marine Biology
2001	Bradshaw et al.	The effect of scallop dredging on Irish Sea benthos: experiments using a closed area	Hydrobiologia
2001	Brooks & Bell	Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/sand ecotones	Journal of Experimental Marine Biology and Ecology
2001	Cranfield et al.	Promising signs of regeneration of blue cod and oyster habitat changed by dredging in Foveaux Strait, southern New Zealand	New Zealand Journal of Marine and Freshwater Research
2001	Dean & Jewett	Habitat-specific recovery of shallow subtidal communities following the Exxon Valdez oil spill	Ecological Applications
2001	Duffy et al.	Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test	Ecology
2001	Dumbauld et al.	Response of an estuarine benthic community to application of the pesticide carbaryl and cultivation of pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington	Marine Pollution Bulletin
2001	Glasby	Development of sessile marine assemblages on fixed versus moving substrata	Marine Ecology Progress Series
2001	Gooday et al.	The foraminiferan macrofauna from three North Carolina (USA) slope sites with contrasting carbon flux: a comparison with the metazoan macrofauna	Deep Sea Research Part I: Oceanographic Research Papers
2001	Henry	Hydroids associated with deep-sea corals in the boreal north-west Atlantic	Journal of the Marine Biological Association of the United Kingdom
2001	Jennings et al.	Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities	Marine Ecology Progress Series
2001	Jennings et al.	Trawling disturbance can modify benthic production processes	Journal of Animal Ecology
2001	Kollmann & Stachowitsch	Long-term changes in the benthos of the northern Adriatic Sea: a phototransect approach	Marine Ecology
2001	Lee et al.	The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds	Journal of Experimental Marine Biology and Ecology

2001	Mancinelli & Rossi	Influence of allochthonous plant detritus on *Gammarus insensibilis* Stock (Amphipoda) occurrence in the soft-bottom epifauna of the northern Adriatic Sea	Mediterranean Ecosystems: Structures and Processes
2001	Maughan	The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community	Journal of Experimental Marine Biology and Ecology
2001	Nakaoka et al.	Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan	Marine Ecology
2001	Oh et al.	Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea	Marine Ecology Progress Series
2001	Parker et al.	Plant species diversity and composition: experimental effects on marine epifaunal assemblages	Marine Ecology Progress Series
2001	Prieto et al.	Mollusc diversity in an *Arca zebra* (Mollusca : Bivalvia) community, Chacopata, Sucre, Venezuela	Revista De Biologia Tropical
2001	Robinson et al.	The impact of scallop drags on sea urchin populations and benthos in the Bay of Fundy, Canada	Hydrobiologia
2001	Sagasti et al.	Effects of periodic hypoxia on mortality, feeding and predation in an estuarine epifaunal community	Journal of Experimental Marine Biology and Ecology
2001	Sánchez-Moyano et al.	Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal variation of invertebrate macrofauna	Aquatic Botany
2001	Sfriso et al.	Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds	Marine Environmental Research
2001	Smith	Historical regulation of local species richness across a geographic region	Ecology
2001	Sudo & Azeta	The microhabitat and size of gammarid species selectively predated by young red sea bream *Pagrus major*	Fisheries Science
2001	Thrush et al.	Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment systems	Marine Ecology Progress Series
2001	Vytopil & Willis	Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef:	Coral Reefs

		implications of coral morphology and habitat complexity	
2001	Wright	*In situ* modification of modern submarine hyaloclastic/pyroclastic deposits by oceanic currents: an example from the Southern Kermadec arc (SW Pacific)	Marine Geology
2001	Zühlke et al.	Epibenthic diversity in the North Sea	Senckenbergiana maritima
2002	Bologna & Heck	Impact of habitat edges on density and secondary production of seagrass-associated fauna	Estuaries
2002	Brooks et al.	Environmental effects associated with marine netpen waste with emphasis on salmon farming in the Pacific northwest	Responsible Marine Aquaculture*
2002	Brown et al.	Small-scale mapping of sea-bed assemblages in the eastern English Channel using sidescan sonar and remote sampling techniques	Estuarine, Coastal and Shelf Science
2002	Burton et al.	Assessment of out-of-kind mitigation success of an artificial reef deployed in Delaware Bay, USA	ICES Journal of Marine Science
2002	Callaway et al.	Diversity and community structure of epibenthic invertebrates and fish in the North Sea	ICES Journal of Marine Science
2002	Callaway et al.	Mesh-size matters in epibenthic surveys	Journal of the Marine Biological Association of the United Kingdom
2002	Cartes et al.	Comparing production-biomass ratios of benthos and suprabenthos in macrofaunal marine crustaceans	Canadian Journal of Fisheries and Aquatic Sciences
2002	Dolmer	Mussel dredging: impact on epifauna in Limfjorden, Denmark	Journal of Shellfish Research
2002	Dulvy et al.	Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient	Journal of Experimental Marine Biology and Ecology
2002	Edgar & Barrett	Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables	Journal of Experimental Marine Biology and Ecology
2002	Fraschetti et al.	Spatio-temporal variation of hydroids and polychaetes associated with *Cystoseira amentacea* (Fucales: Phaeophyceae)	Marine Biology

2002	Germano & Read	Natural recovery at a submarine wood waste site	Remediation and Beneficial Reuse of Contaminated Sediments*
2002	Holloway & Keough	An introduced polychaete affects recruitment and larval abundance of sessile invertebrates	Ecological Applications
2002	Holloway & Keough	Effects of an introduced polychaete, *Sabella spallanzanii*, on the development of epifaunal assemblages	Marine Ecology Progress Series
2002	Hovel et al.	Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds	Marine Ecology Progress Series
2002	Jayaprada	Composition and distribution of epigrowth fauna in Visakhapatnam harbor, east coast of India	Indian Journal of Marine Sciences
2002	Koch & Wolff	Energy budget and ecological role of mangrove epibenthos in the Caete estuary, North Brazil	Marine Ecology Progress Series
2002	Labarta et al.	Enzymatic digestive activity in epifaunal (*Mytilus chilensis*) and infaunal (*Mulinia edulis*) bivalves in response to changes in food regimes in a natural environment	Marine Biology
2002	Mancinelli et al.	Role of microorganisms and macrofauna in benthic phosphorus dynamics in the po river-Adriatic Sea frontal system: an experimental approach	Chemistry and Ecology
2002	Matsumoto & Kohda	The effect of feeding habitats on dietary shifts during the growth in a benthophagous suction-feeding fish	Zoological Science
2002	Nakaoka et al.	Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed	Ecological Research
2002	Saier	Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna	Helgoland Marine Research
2002	Sánchez-Moyano et al.	Effect of environmental factors on the spatial variation of the epifaunal polychaetes of the alga *Halopteris scoparia* in Algeciras Bay (Strait of Gibraltar)	Hydrobiologia
2002	Smith & Rule	Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool?	Journal of Experimental Marine Biology and Ecology

2002	Stachowicz et al.	Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process	Ecology
2002	Steimle et al.	Benthic macrofauna productivity enhancement by an artificial reef in Delaware Bay, USA	ICES Journal of Marine Science
2002	Thiel	The zoogeography of algae-associated peracarids along the Pacific coast of Chile	Journal of Biogeography
2002	Velasco & Navarro	Feeding physiology of infaunal (*Mulinia edulis*) and epifaunal (*Mytilus chilensis*) bivalves under a wide range of concentrations and qualities of seston	Marine Ecology Progress Series
2002	Yu et al.	Seasonal zonation patterns of benthic amphipods in a sandy shore surf zone of Korea	Journal of Crustacean Biology
2003	Ashton et al.	A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia	Journal of Tropical Ecology
2003	Beaver et al.	Secondary productivity within biotic fouling community elements on two artificial reef structures in the northwestern Gulf of Mexico	Fisheries, Reefs, and Offshore Development*
2003	Bolduc & Afton	Effects of structural marsh management and salinity on invertebrate prey of waterbirds in marsh ponds during winter on the Gulf Coast Chenier Plain	Wetlands
2003	Bone et al.	Ecological aspects of syllids (Annelida : Polychaeta : Syllidae) on *Thalassia testudinum* beds in Venezuela	Hydrobiologia
2003	Bradshaw et al.	To what extent does upright sessile epifauna affect benthic biodiversity and community composition?	Marine Biology
2003	Burrows et al.	Topography as a determinant of search paths of fishes and mobile macrocrustacea on the sediment surface	Journal of Experimental Marine Biology and Ecology
2003	Colloca et al.	Pattern of distribution and diversity of demersal assemblages in the central Mediterranean Sea	Estuarine, Coastal and Shelf Science
2003	Deidun et al.	Low faunal diversity on Maltese sandy beaches: fact or artefact?	Estuarine, Coastal and Shelf Science
2003	Diaz & Arana	Epifaunal polychaetes on *Pinctada imbricata* Röding, 1798 (Bivalvia : Pteriidae) from the Gulf of Cariaco, Venezuela	Interciencia

2003	Edgar & Klumpp	Consistencies over regional scales in assemblages of mobile epifauna associated with natural and artificial plants of different shape	Aquatic Botany
2003	Haggitt & Babcock	The role of grazing by the lysianassid amphipod *Orchomenella aahu* in dieback of the kelp *Ecklonia radiata* in north-eastern New Zealand	Marine Biology
2003	Hirst	Encounter 2002 Expedition to the Isles of St Francis, South Australia: peracarid crustacean epifauna of subtidal macroalgal canopies	Transactions of the Royal Society of South Australia
2003	Kumagai & Aoki	Seasonal changes in the epifaunal community on the shallow-water gorgonian *Melithaea flabellifera*	Journal of the Marine Biological Association of the United Kingdom
2003	Leite & Turra	Temporal variation in *Sargassum* biomass, *Hypnea* epiphytism and associated fauna	Brazilian Archives of Biology and Technology
2003	Nash	Interactions of Atlantic salmon in the Pacific Northwest: VI. A synopsis of the risk and uncertainty	Fisheries Research
2003	Pardo & Dauer	Particle size selection in individuals from epifaunal versus infaunal populations of the nereidid polychaete *Neanthes succinea* (Polychaeta: Nereididae)	Hydrobiologia
2003	Prieto et al.	Diversity and abundance of molluscs in *Thalassia testudinum* prairies of the Bay of Mochima, Mochima National Park, Venezuela	Revista De Biologia Tropical
2003	Ribeiro et al.	Macrofauna associated to *Mycale microsigmatosa* (Porifera, Demospongiae) in Rio de Janeiro State, SE Brazil	Estuarine, Coastal and Shelf Science
2003	Sagasti et al.	Estuarine epifauna recruit despite periodic hypoxia stress	Marine Biology
2003	Schreider et al.	Effects of height on the shore and complexity of habitat on abundances of amphipods on rocky shores in New South Wales, Australia	Journal of Experimental Marine Biology and Ecology
2003	Sepúlveda et al.	The peracarid epifauna associated with the ascidian *Pyura chilensis* (Molina, 1782) (Ascidiacea : Pyuridae)	Journal of Natural History
2003	Tanaka & Leite	Spatial scaling in the distribution of macrofauna associated with *Sargassum stenophyllum* (Mertens) Martius: analyses of faunal groups, gammarid life habits, and assemblage structure	Journal of Experimental Marine Biology and Ecology

2003	Tanner	Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities	Oikos
2003	Tanner	The influence of prawn trawling on sessile benthic assemblages in Gulf St. Vincent, South Australia	Canadian Journal of Fisheries and Aquatic Sciences
2003	Thorbjorn & Petersen	The epifauna on the carbonate reefs in the Arctic Ikka Fjord, SW Greenland	Ophelia
2003	Velasco & Navarro	Energetic balance of infaunal (*Mulinia edulis* King, 1831) and epifaunal (*Mytilus chilensis* Hupé, 1854) bivalves in response to wide variations in concentration and quality of seston	Journal of Experimental Marine Biology and Ecology
2003	Viejo & Åberg	Temporal and spatial variation in the density of mobile epifauna and grazing damage on the seaweed *Ascophyllum nodosum*	Marine Biology
2003	Witman & Smith	Rapid community change at a tropical upwelling site in the Galápagos Marine Reserve	Biodiversity & Conservation
2004	Bouillon et al.	Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter	Marine Ecology Progress Series
2004	Diaz et al.	Potential impacts of sand mining offshore of Maryland and Delaware: part 2 - biological considerations	Journal of Coastal Research
2004	Escapa et al.	The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia	Journal of Shellfish Research
2004	Gaymer et al.	Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community	Journal of Experimental Marine Biology and Ecology
2004	Hargrave et al.	Benthic epifauna assemblages, biomass and respiration in The Gully region on the Scotian Shelf, NW Atlantic Ocean	Marine Ecology Progress Series
2004	Healey & Hovel	Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA	Journal of Experimental Marine Biology and Ecology
2004	Henry & Kenchington	Ecological and genetic evidence for impaired sexual reproduction and induced clonality in the hydroid *Sertularia cupressina* (Cnidaria: Hydrozoa) on commercial scallop grounds in Atlantic Canada	Marine Biology

2004	Hinz et al.	Seasonal and annual variability in an epifaunal community in the German Bight	Marine Biology
2004	Kaiser et al.	Demersal fish and epifauna associated with sandbank habitats	Estuarine, Coastal and Shelf Science
2004	Larsen & Gilfillan	Preliminary survey of the subtidal macrobenthic invertebrates of Cobscook Bay, Maine	Northeastern Naturalist
2004	Mathot et al.	Evidence for sexual partitioning of foraging mode in Western Sandpipers (*Calidris mauri*) during migration	Canadian Journal of Zoology
2004	Osman & Whitlatch	The control of the development of a marine benthic community by predation on recruits	Journal of Experimental Marine Biology and Ecology
2004	Tanaka & Leite	Distance effects on short-term recolonization of *Sargassum stenophyllum* by mobile epifauna, with an analysis of gammarid life habits	Journal of the Marine Biological Association of the United Kingdom
2004	Welsh & Castadelli	Bacterial nitrification activity directly associated with isolated benthic marine animals	Marine Biology
2004	Wernberg et al.	Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark)	Helgoland Marine Research
2004	Wikström & Kautsky	Invasion of a habitat-forming seaweed: effects on associated biota	Biological Invasions
2004	Witman et al.	The relationship between regional and local species diversity in marine benthic communities: a global perspective	Proceedings of the National Academy of Sciences of the United States of America
2005	Andersen et al.	Feeding ecology and growth of age 0 year *Platichthys flesus* (L.) in a vegetated and a bare sand habitat in a nutrient rich fjord	Journal of Fish Biology
2005	Bishop	Compensatory effects of boat wake and dredge spoil disposal on assemblages of macroinvertebrates	Estuaries
2005	Brown	Epifaunal colonization of the Loch Linnhe artificial reef: influence of substratum on epifaunal assemblage structure	Biofouling
2005	Castañeda-Fernández-de-Lara et al.	Feeding ecology of juvenile spiny lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico	New Zealand Journal of Marine and Freshwater Research

2005	Clark & Johnston	Manipulating larval supply in the field: a controlled study of marine invasibility	Marine Ecology Progress Series
2005	Davidson et al.	Structural gradients in an intertidal hard-bottom community: examining vertical, horizontal, and taxonomic clines in zoobenthic biodiversity	Marine Biology
2005	Gage et al.	Potential impacts of deep-sea trawling on the benthic ecosystem along the Northern European continental margin: a review	Benthic Habitats and the Effects of Fishing*
2005	Govenar et al.	Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats	Marine Ecology Progress Series
2005	Hamazaki et al.	Analyses of Bering Sea bottom-trawl surveys in Norton Sound: absence of regime shift effect on epifauna and demersal fish	ICES Journal of Marine Science
2005	Hepburn & Hurd	Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna	Marine Ecology Progress Series
2005	Jewett et al.	Epifaunal disturbance by periodic low levels of dissolved oxygen: native vs. invasive species response	Marine Ecology Progress Series
2005	Klumpp & Kwak	Composition and abundance of benthic macrofauna of a tropical sea-grass bed in North Queensland, Australia	Pacific Science
2005	Luckenbach et al.	Oyster reef habitat restoration: relationships between oyster abundance and community development based on two studies in Virginia and South Carolina	Journal of Coastal Research
2005	McConnaughey et al.	Effects of chronic bottom trawling on the size structure of soft-bottom benthic invertebrates	Benthic Habitats and the Effects of Fishing*
2005	Nakamura & Sano	Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan	Fisheries Science
2005	Nakaoka	Plant–animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics	Population Ecology
2005	Pagliosa & Lana	Impact of plant cover removal on macrobenthic community structure of a subtropical salt marsh	Bulletin of Marine Science
2005	Polte et al.	Effects of current exposure on habitat preference of mobile 0-group epibenthos for intertidal seagrass beds (*Zostera noltii*) in the northern Wadden Sea	Estuarine, Coastal and Shelf Science

2005	Polte et al.	The contribution of seagrass beds (*Zostera noltii*) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea	Marine Biology
2005	Prieto et al.	Diversity and abundance of mollusks in the sublittoral epifaunal community of Punta Patilla, Venezuela	Revista De Biologia Tropical
2005	Raes & Vanreusel	The metazoan meiofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic)	Cold-Water Corals and Ecosystems*
2005	Rule & Smith	Spatial variation in the recruitment of benthic assemblages to artificial substrata	Marine Ecology Progress Series
2005	Sgro et al.	Functional responses and scope for growth of two non-indigenous bivalve species in the Sacca di Goro (northern Adriatic Sea, Italy)	Italian Journal of Zoology
2005	Stone et al.	Effects of bottom trawling on soft-sediment epibenthic communities in the Gulf of Alaska	Benthic Habitats and the Effects of Fishing*
2005	Tanner	Edge effects on fauna in fragmented seagrass meadows	Austral Ecology
2005	Thomasson & Tunberg	Composition and vertical distribution of the motile epifauna on a vertical rock wall in Gullmarsfjorden, western Sweden, using an alternative sampling approach	Marine Biology Research
2005	Velasco & Navarro	Feeding physiology of two bivalves under laboratory and field conditions in response to variable food concentrations	Marine Ecology Progress Series
2005	Winston & Migotto	A new encrusting interstitial marine fauna from Brazil	Invertebrate Biology
2006	Alfaro	Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand	Estuarine, Coastal and Shelf Science
2006	Beaumont et al.	Evaluation of techniques used in the assessment of subtidal epibiotic assemblage structure	Biofouling
2006	Burone & Pires-Vanin	Foraminiferal assemblages in Ubatuba Bay, south-eastern Brazilian coast	Scientia Marina
2006	Cruz-Rivera & Paul	Feeding by coral reef mesograzers: algae or cyanobacteria?	Coral Reefs
2006	Eklöf et al.	Effects of tropical open-water seaweed farming on seagrass ecosystem structure and function	Marine Ecology Progress Series

2006	Gil et al.	Nutrient impacts on epifaunal density and species composition in a subtropical seagrass bed	Hydrobiologia
2006	Guerra-García et al.	Assessing a quick monitoring method using rocky intertidal communities as a bioindicator: a multivariate approach in Algeciras Bay	Environmental Monitoring and Assessment
2006	Henry et al.	Impacts of otter trawling on colonial epifaunal assemblages on a cobble bottom ecosystem on Western Bank (northwest Atlantic)	Marine Ecology Progress Series
2006	Hepburn et al.	Colony structure and seasonal differences in light and nitrogen modify the impact of sessile epifauna on the giant kelp *Macrocystis pyrifera* (L.) C Agardh	Hydrobiologia
2006	Hinchey et al.	Responses of estuarine benthic invertebrates to sediment burial: the importance of mobility and adaptation	Hydrobiologia
2006	Hooper & Davenport	Epifaunal composition and fractal dimensions of intertidal marine macroalgae in relation to emersion	Journal of the Marine Biological Association of the United Kingdom
2006	Hosack et al.	Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats	Estuaries and Coasts
2006	Kenchington et al.	Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean	Journal of Sea Research
2006	Kogan et al.	ATOC/Pioneer Seamount cable after 8 years on the seafloor: observations, environmental impact	Continental Shelf Research
2006	Kouchi et al.	Effects of temporal dynamics and vertical structure of the seagrass *Zostera caulescens* on distribution and recruitment of the epifaunal encrusting bryozoa *Microporella trigonellata*	Marine Ecology
2006	Lindsay et al.	Recruitment in epifaunal communities: an experimental test of the effects of species composition and age	Marine Ecology Progress Series
2006	Mendez	Deep-water polychaetes (Annelida) from the southeastern Gulf of California, Mexico	Revista De Biologia Tropical
2006	O'Brien et al.	Effects of *Sabella spallanzanii* physical structure on soft sediment macrofaunal assemblages	Marine and Freshwater Research

2006	Pereira et al.	Biogeographic patterns of intertidal macroinvertebrates and their association with macroalgae distribution along the Portuguese coast	Hydrobiologia
2006	Rae & Vanreusel	Microhabitat type determines the composition of nematode communities associated with sediment-clogged cold-water coral framework in the Porcupine Seabight (NE Atlantic)	Deep Sea Research Part I: Oceanographic Research Papers
2006	Reed & Hovel	Seagrass habitat disturbance: how loss and fragmentation of eelgrass *Zostera marina* influences epifaunal abundance and diversity	Marine Ecology Progress Series
2006	Reiss et al.	Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments	ICES Journal of Marine Science
2006	Roberts & Poore	Habitat configuration affects colonisation of epifauna in a marine algal bed	Biological Conservation
2006	Roberts et al.	Ecological consequences of copper contamination in macroalgae: effects on epifauna and associated herbivores	Environmental Toxicology and Chemistry
2006	Rodney & Paynter	Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland	Journal of Experimental Marine Biology and Ecology
2006	Royer et al.	Presence of spionid worms and other epibionts in Pacific oysters (*Crassostrea gigas*) cultured in Normandy, France	Aquaculture
2006	Schmidt & Scheibling	A comparison of epifauna and epiphytes on native kelps (*Laminaria species*) and an invasive alga (*Codium fragile* ssp *tomentosoides*) in Nova Scotia, Canada	Botanica Marina
2006	Sibaja-Cordero & Vargas-Zamora	The vertical zonation of epifauna and algae species in rocky substrates of the Gulf of Nicoya, Costa Rica	Revista De Biologia Tropical
2006	Sirota & Hovel	Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the epifaunal community of San Diego Bay, California, USA	Marine Ecology Progress Series

2006	Skilleter et al.	Effects of physical disturbance on infaunal and epifaunal assemblages in subtropical, intertidal seagrass beds	Marine Ecology Progress Series
2006	Smith et al.	Effects of dredging activity on epifaunal communities – Surveys following cessation of dredging	Estuarine, Coastal and Shelf Science
2006	Sun et al.	The effect of primary productivity and seasonality on the distribution of deep-sea benthic foraminifera in the North Atlantic	Deep Sea Research Part I: Oceanographic Research Papers
2006	Tanner	Landscape ecology of interactions between seagrass and mobile epifauna: the matrix matters	Estuarine, Coastal and Shelf Science
2006	Valente	Response of benthic infauna and epifauna to ocean disposal of red clay dredged material in the New York Bight: a study using sediment-profile imaging, surface imaging and traditional methods	Journal of Marine Systems
2006	Vizzini & Mazzola	Sources and transfer of organic matter in food webs of a Mediterranean coastal environment: evidence for spatial variability	Estuarine, Coastal and Shelf Science
2006	Ward et al.	Epifaunal assemblages of the eastern Great Australian Bight: effectiveness of a benthic protection zone in representing regional biodiversity	Continental Shelf Research
2006	Yahel et al.	Phytoplankton grazing by epi- and infauna inhabiting exposed rocks in coral reefs	Coral Reefs
2006	Zintzen et al.	Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf	Hydrobiologia
2007	Aníbal et al.	Mudflat surface morphology as a structuring agent of algae and associated macroepifauna communities: a case study in the Ria Formosa	Journal of Sea Research
2007	Antoniadou & Chintiroglou	Zoobenthos associated with the invasive red alga *Womersleyella setacea* (Rhodomelacea) in the northern Aegean Sea	Journal of the Marine Biological Association of the United Kingdom
2007	Aravind et al.	Life history and population dynamics of an estuarine amphipod, *Eriopisa chilkensis* Chilton (Gammaridae)	Estuarine, Coastal and Shelf Science
2007	Bates & DeWreede	Do changes in seaweed biodiversity influence associated invertebrate epifauna?	Journal of Experimental Marine Biology and Ecology

2007	de Juan et al.	Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea)	Marine Ecology Progress Series
2007	Duineveld et al.	Effects of an area closed to fisheries on the composition of the benthic fauna in the southern North Sea	ICES Journal of Marine Science
2007	Fujiwara et al.	Three-year investigations into sperm whale-fall ecosystems in Japan	Marine Ecology
2007	Ganesh & Raman	Macrobenthic community structure of the northeast Indian shelf, Bay of Bengal	Marine Ecology Progress Series
2007	Govenar & Fisher	Experimental evidence of habitat provision by aggregations of *Riftia pachyptila* at hydrothermal vents on the East Pacific Rise	Marine Ecology
2007	Harries et al.	The establishment of the invasive alga *Sargassum muticum* on the west coast of Scotland: a preliminary assessment of community effects	Journal of the Marine Biological Association of the United Kingdom
2007	Hirst	Vertical stratification of mobile epiphytal arthropod assemblages between the canopy and understorey of subtidal macroalgae	Marine Biology
2007	Huntley et al.	Towards establishing a modern baseline for paleopathology: trace-producing parasites in a bivalve host	Journal of Shellfish Research
2007	Ince et al.	Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat	Estuarine, Coastal and Shelf Science
2007	Irving et al.	Priority effects on faunal assemblages within artificial seagrass	Journal of Experimental Marine Biology and Ecology
2007	Itoh et al.	Fate of organic matter in faecal pellets egested by epifaunal mesograzers in a *Sargassum* forest and implications for biogeochemical cycling	Marine Ecology Progress Series
2007	Jing et al.	Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China	Ecological Research
2007	Jorgensen et al.	Top-down and bottom-up stabilizing mechanisms in eelgrass meadows differentially affected by coastal upwelling	Marine Ecology Progress Series
2007	Juan et al.	Effects of commercial trawling activities in the diet of the flat fish *Citharus linguatula* (Osteichthyes:	Journal of Experimental Marine Biology and Ecology

		Pleuronectiformes) and the starfish *Astropecten irregularis* (Echinodermata: Asteroidea)	
2007	Kenchington et al.	Multi-decadal changes in the megabenthos of the Bay of Fundy: the effects of fishing	Journal of Sea Research
2007	Leite et al.	Diel density variation of amphipods associated with *Sargassum* beds from two shores of Ubatuba, Southeastern, Brazil	Iheringia Serie Zoologia
2007	McDermott	Ectosymbionts of the non-indigenous Asian shore crab, *Hemigrapsus sanguineus* (Decapoda: Varunidae), in the Western North Atlantic, and a search for its parasites	Journal of Natural History
2007	Murray et al.	Changes in the biodiversity of mussel assemblages induced by two methods of cultivation	Journal of Shellfish Research
2007	O'Neill et al.	Lack of epifaunal response to the application of salt for managing the noxious green alga *Caulerpa taxifolia* in a coastal lake	Hydrobiologia
2007	Owada et al.	Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia : Mytilidae): a third functional clade	Marine Biology
2007	Powers et al.	Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes	Marine Ecology Progress Series
2007	Roberts et al.	MBACI sampling of an episodic disturbance: stormwater effects on algal epifauna	Marine Environmental Research
2007	Robertson & Weis	Interactions between the grass shrimp *Palaemonetes pugio* and the salt marsh grasses *Phragmites australis* and *Spartina alterniflora*	Biological Invasions
2007	Rule & Smith	Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs	Journal of Experimental Marine Biology and Ecology
2007	Sánchez-Moyano et al.	Effects of temporal variation of the seaweed *Caulerpa prolifera* cover on the associated crustacean community	Marine Ecology
2007	Szarek et al.	Living deep-sea benthic foraminifera from the warm and oxygen-depleted environment of the Sulu Sea	Deep Sea Research Part II: Topical Studies in Oceanography

2007	Unsworth et al.	Faunal relationships with seagrass habitat structure: a case study using shrimp from the Indo-Pacific	Marine and Freshwater Research
2007	Voultsiadou et al.	The habitat engineering tunicate *Microcosmus sabatieri* Roule, 1885 and its associated peracarid epifauna	Estuarine, Coastal and Shelf Science
2007	Walker et al.	Spatial heterogeneity of epibenthos on artificial reefs: fouling communities in the early stages of colonization on an East Australian shipwreck	Marine Ecology
2008	Asch & Collie	Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure	Fishery Bulletin
2008	Commito et al.	Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales	Journal of Experimental Marine Biology and Ecology
2008	Erbland & Ozbay	Comparison of the macrofaunal communities inhabiting a *Crassostrea vircinica* oyster reef and oyster aquaculture gear in Indian River Bay, Delaware	Journal of Shellfish Research
2008	Felley et al.	Small-scale distribution of deep-sea demersal nekton and other megafauna in the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge	Deep Sea Research Part II: Topical Studies in Oceanography
2008	Fukunaga	Invertebrate community associated with the macroalga *Halimeda kanaloana* meadow in Maui, Hawaii	International Review of Hydrobiology
2008	Garcia et al.	Macrofauna associated with branching fire coral *Millepora alcicornis* (Cnidaria : Hydrozoa)	Thalassas
2008	Guillén et al.	Alteration of bottom roughness by benthic organisms in a sandy coastal environment	Continental Shelf Research
2008	Guyonnet et al.	Modified otter trawl legs to reduce damage and mortality of benthic organisms in North East Atlantic fisheries (Bay of Biscay)	Journal of Marine Systems
2008	Hirst	Surrogate measures for assessing cryptic faunal biodiversity on macroalgal-dominated subtidal reefs	Biological Conservation
2008	Jennings et al.	Body-size dependent temporal variations in nitrogen stable isotope ratios in food webs	Marine Ecology Progress Series
2008	Kochmann et al.	Shift from native mussels to alien oysters: differential effects of ecosystem engineers	Journal of Experimental Marine Biology and Ecology

2008	Lam et al.	Shell-bearing Mollusca (Bivalvia and Gastropoda) from submarine caves in Hong Kong	Journal of Natural History
2008	Metcalfe & Glasby	Diversity of polychaeta (Annelida) and other worm taxa in mangrove habitats of Darwin Harbour, northern Australia	Journal of Sea Research
2008	Micheli et al.	Alteration of seagrass species composition and function over two decades	Ecological Monographs
2008	Morton & Bamber	The joint Swire Institute of Marine Science, Hong Kong, and Natural History Museum, London, Hong Kong Submarine Caves Expedition, 2002: discussion, conclusions and recommendations for conservation	Journal of Natural History
2008	Moura et al.	Is surface orientation a determinant for colonisation patterns of vagile and sessile macrobenthos on artificial reefs?	Biofouling
2008	Muir & Bamber	New polychaete (Annelida) records and a new species from Hong Kong: the families Polynoidae, Sigalionidae, Chrysopetalidae, Pilargiidae, Nereididae, Opheliidae, Ampharetidae and Terebellidae	Journal of Natural History
2008	Mutlu & Ergev	Spatio-temporal distribution of soft-bottom epibenthic fauna on the Cilician shelf (Turkey), Mediterranean Sea	Revista De Biologia Tropical
2008	Nagelkerken et al.	The habitat function of mangroves for terrestrial and marine fauna: a review	Aquatic Botany
2008	Nakaoka et al.	Animals on marine flowers: does the presence of flowering shoots affect mobile epifaunal assemblage in an eelgrass meadow?	Marine Biology
2008	Neumann et al.	Effects of cold winters and climate on the temporal variability of an epibenthic community in the German Bight	Climate Research
2008	Neumann et al.	Spatial variability of epifaunal communities in the North Sea in relation to sampling effort	Helgoland Marine Research
2008	Paetzold et al.	Responses of *Mitrella lunata* and *Caprella* spp., potential tunicate micropredators, in Prince Edward Island estuaries to acetic acid anti-fouling treatments	Aquaculture
2008	Partyka & Peterson	Habitat quality and salt-marsh species assemblages along an anthropogenic estuarine landscape	Journal of Coastal Research

2008	Prescott & Cudney-Bueno	Mobile 'reefs' in the northeastern Gulf of California: aggregations of black murex snails *Hexaplex nigritus* as habitat for invertebrates	Marine Ecology Progress Series
2008	Printrakoon et al.	Distribution of molluscs in mangroves at six sites in the upper Gulf of Thailand	Raffles Bulletin of Zoology
2008	Raes et al.	Walking with worms: coral-associated epifaunal nematodes	Journal of Biogeography
2008	Rees et al.	Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. III. Crevice, sediment infauna and epifauna from targeted cores	Journal of the Marine Biological Association of the United Kingdom
2008	Riedel et al.	Oxygen depletion under glass: behavioural responses of benthic macrofauna to induced anoxia in the Northern Adriatic	Journal of Experimental Marine Biology and Ecology
2008	Roberts et al.	Biomonitors and the assessment of ecological impacts: distribution of herbivorous epifauna in contaminated macroalgal beds	Environmental Pollution
2008	Roberts et al.	Contamination of marine biogenic habitats and effects upon associated epifauna	Marine Pollution Bulletin
2008	Roberts et al.	Field and laboratory simulations of storm water pulses: behavioural avoidance by marine epifauna	Environmental Pollution
2008	Rueda & Salas	Molluscs associated with a subtidal *Zostera marina* L. bed in southern Spain: linking seasonal changes of fauna and environmental variables	Estuarine, Coastal and Shelf Science
2008	Sanderson et al.	Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. II. Epifauna recorded by divers and cameras	Journal of the Marine Biological Association of the United Kingdom
2008	Thistle et al.	Large, motile epifauna interact strongly with harpacticoid copepods and polychaetes at a bathyal site	Deep Sea Research Part I: Oceanographic Research Papers
2008	Tomašových	Substrate exploitation and resistance to biotic disturbance in the brachiopod *Terebratalia transversa* and the bivalve *Pododesmus macrochisma*	Marine Ecology Progress Series
2008	Vázquez-Bader et al.	Seasonal changes in the density and species composition of the epifaunal echinoderms recorded from the southwestern Gulf of Mexico	Revista De Biologia Tropical
2008	Vázquez-Luis et al.	Changes in amphipod (Crustacea) assemblages associated with shallow-water algal habitats	Marine Environmental Research

		invaded by *Caulerpa racemosa* var. *cylindracea* in the western Mediterranean Sea	
2008	Vermeij et al.	The trans-Atlantic history of diversity and body size in ecological guilds	Ecology
2008	Witman et al.	The relation between productivity and species diversity in temperate-arctic marine ecosystems	Ecology
2009	Armitage & Fourqurean	Stable isotopes reveal complex changes in trophic relationships following nutrient addition in a coastal marine ecosystem	Estuaries and Coasts
2009	Bates	Host taxonomic relatedness and functional-group affiliation as predictors of seaweed-invertebrate epifaunal associations	Marine Ecology Progress Series
2009	Blanchard et al.	How does abundance scale with body size in coupled size-structured food webs?	Journal of Animal Ecology
2009	Brusati & Grosholz	Does invasion of hybrid cordgrass change estuarine food webs?	Biological Invasions
2009	Bruschetti et al.	An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon	Journal of Experimental Marine Biology and Ecology
2009	Cannicci et al.	Effects of urban wastewater on crab and mollusc assemblages in equatorial and subtropical mangroves of East Africa	Estuarine, Coastal and Shelf Science
2009	Carbines & Cole	Using a remote drift underwater video (DUV) to examine dredge impacts on demersal fishes and benthic habitat complexity in Foveaux Strait, Southern New Zealand	Fisheries Research
2009	Cartes et al.	The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: environmental gradients influencing assemblages composition and biomass trends	Journal of Sea Research
2009	Collie et al.	Recolonization of gravel habitats on Georges Bank (northwest Atlantic)	Deep Sea Research Part II: Topical Studies in Oceanography
2009	Dafforn et al.	Shallow moving structures promote marine invader dominance	Biofouling

2009	de Juan et al.	Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: a Mediterranean case study	Marine Policy
2009	Gheerardyn et al.	Harpacticoida (Crustacea: Copepoda) associated with cold-water coral substrates in the Porcupine Seabight (NE Atlantic): species composition, diversity and reflections on the origin of the fauna	Scientia Marina
2009	Grizzle et al.	Effects of a large fishing closure on benthic communities in the western Gulf of Maine: recovery from the effects of gillnets and otter trawls	Fishery Bulletin
2009	Gustafsson et al.	Effects of plant species richness and composition on epifaunal colonization in brackish water angiosperm communities	Journal of Experimental Marine Biology and Ecology
2009	Gutow et al.	Rapid changes in the epifaunal community after detachment of buoyant benthic macroalgae	Journal of the Marine Biological Association of the United Kingdom
2009	Hinz et al.	Trawl disturbance on benthic communities: chronic effects and experimental predictions	Ecological Applications
2009	Jacobucci et al.	Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore	Aquatic Ecology
2009	Jeffreys et al.	Influence of oxygen on heterotrophic reworking of sedimentary lipids at the Pakistan margin	Deep Sea Research Part II: Topical Studies in Oceanography
2009	Johnson et al.	Large-scale manipulations reveal that top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna	Marine Ecology Progress Series
2009	Margreth et al.	Benthic foraminifera as bioindicator for cold-water coral reef ecosystems along the Irish margin	Deep Sea Research Part I: Oceanographic Research Papers
2009	Marzinelli et al.	Do modified habitats have direct or indirect effects on epifauna?	Ecology
2009	McKinnon et al.	Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats	Marine Ecology Progress Series
2009	Montagna et al.	Long-term biological effects of coastal hypoxia in Corpus Christi Bay, Texas, USA	Journal of Experimental Marine Biology and Ecology

2009	Morsan	Impact on biodiversity of scallop dredging in San Matías Gulf, northern Patagonia (Argentina)	Hydrobiologia
2009	Neumann et al.	Temporal variability in southern North Sea epifauna communities after the cold winter of 1995/1996	ICES Journal of Marine Science
2009	Neumann et al.	Variability of epifauna and temperature in the northern North Sea	Marine Biology
2009	Poore et al.	Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed	Journal of Ecology
2009	Rabaoui et al.	Associated fauna of the fan shell *Pinna nobilis* (Mollusca: Bivalvia) in the northern and eastern Tunisian coasts	Scientia Marina
2009	Rueda et al.	A highly diverse molluscan assemblage associated with eelgrass beds (*Zostera marina* L.) in the Alboran Sea: micro-habitat preference, feeding guilds and biogeographical distribution	Scientia Marina
2009	Rueda et al.	Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea)	Journal of the Marine Biological Association of the United Kingdom
2009	Spivak et al.	Epifaunal community composition and nutrient addition alter sediment organic matter composition in a natural eelgrass *Zostera marina* bed: a field experiment	Marine Ecology Progress Series
2009	Summerhayes et al.	Effects of oyster death and shell disarticulation on associated communities of epibiota	Journal of Experimental Marine Biology and Ecology
2009	Yu et al.	Seasonal variation in diel and tidal effects among benthic amphipods with different lifestyles in a sandy surf zone of Korea	Crustaceana
2010	Ayres-Peres & Mantelatto	Epibiont occurrence on gastropod shells used by the hermit crab *Loxopagurus loxochelis* (Anomura: Diogenidae) on the northern coast of Sao Paulo, Brazil	Zoologia
2010	Barnes et al.	Oyster reef community interactions: the effect of resident fauna on oyster (*Crassostrea* spp.) larval recruitment	Journal of Experimental Marine Biology and Ecology
2010	Borg et al.	Spatial variation in the composition of motile macroinvertebrate assemblages associated with two bed types of the seagrass *Posidonia oceanica*	Marine Ecology Progress Series

2010	Cacabelos et al.	Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae	Estuarine, Coastal and Shelf Science
2010	Gartner et al.	Light reductions drive macroinvertebrate changes in *Amphibolis griffithii* seagrass habitat	Marine Ecology Progress Series
2010	Gedan & Bertness	How will warming affect the salt marsh foundation species *Spartina patens* and its ecological role?	Oecologia
2010	Gestoso et al.	Variability of epifaunal assemblages associated with native and invasive macroalgae	Marine and Freshwater Research
2010	Khan et al.	Biodiversity of epibenthic community in the inshore waters of southeast coast of India	Biologia
2010	Kon et al.	Effects of the physical structure of mangrove vegetation on a benthic faunal community	Journal of Experimental Marine Biology and Ecology
2010	Marenghi et al.	A comparison of the habitat value of sub-tidal and floating oyster (*Crassostrea virginica*) aquaculture gear with a created reef in Delaware's Inland Bays, USA	Aquaculture International
2010	Martinetto et al.	High abundance and diversity of consumers associated with eutrophic areas in a semi-desert macrotidal coastal ecosystem in Patagonia, Argentina	Estuarine, Coastal and Shelf Science
2010	Moore & Hovel	Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities	Oikos
2010	Newcombe & Taylor	Trophic cascade in a seaweed-epifauna-fish food chain	Marine Ecology Progress Series
2010	Nikula et al.	Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans	Marine Ecology Progress Series
2010	Norkko et al.	Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft-sediment communities	Marine Ecology Progress Series
2010	Osman et al.	Thresholds and multiple community states in marine fouling communities: integrating natural history with management strategies	Marine Ecology Progress Series
2010	Poirier et al.	Influence of hydro-sedimentary factors on mollusc death assemblages in a temperate mixed tide-and-	Continental Shelf Research

		wave dominated coastal environment: implications for the fossil record	
2010	Reiss et al.	Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea	ICES Journal of Marine Science
2010	Sellheim et al.	Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities	Marine Ecology Progress Series
2010	Smyth & Roberts	The European oyster (*Ostrea edulis*) and its epibiotic succession	Hydrobiologia
2010	Stella et al.	Variation in the structure of epifaunal invertebrate assemblages among coral hosts	Coral Reefs
2010	Tang et al.	Associations between macrobenthos and invasive cordgrass, *Spartina anglica*, in the Danish Wadden Sea	Helgoland Marine Research
2010	Tanner & Fernandes	Environmental effects of yellowtail kingfish aquaculture in South Australia	Aquaculture Environment Interactions
2010	Valanko et al.	Strategies of post-larval dispersal in non-tidal soft-sediment communities	Journal of Experimental Marine Biology and Ecology
2010	Vanreusel et al.	The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity	Marine Ecology
2010	Voultsiadou et al.	Sponge epibionts on ecosystem-engineering ascidians: the case of *Microcosmus sabatieri*	Estuarine, Coastal and Shelf Science
2010	Zintzen & Massin	Artificial hard substrata from the Belgian part of the North Sea and their influence on the distributional range of species	Belgian Journal of Zoology
2011	Anderson et al.	Deep-sea bio-physical variables as surrogates for biological assemblages, an example from the Lord Howe Rise	Deep Sea Research Part II: Topical Studies in Oceanography
2011	Atkinson et al.	Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages	Marine Ecology Progress Series
2011	Burone et al.	Benthic foraminiferal distribution on the southeastern Brazilian shelf and upper slope	Marine Biology
2011	Carr et al.	Spatial patterns of epifaunal communities in San Francisco Bay eelgrass (*Zostera marina*) beds	Marine Ecology
2011	Currin et al.	The role of cyanobacteria in Southern California salt marsh food webs	Marine Ecology

2011	de Juan et al.	Exploring the degree of trawling disturbance by the analysis of benthic communities ranging from a heavily exploited fishing ground to an undisturbed area in the NW Mediterranean	Scientia Marina
2011	Douglass et al.	Food web structure in a Chesapeake Bay eelgrass bed as determined through gut contents and ^{13}C and ^{15}N isotope analysis	Estuaries and Coasts
2011	Drouin et al.	Higher abundance and diversity in faunal assemblages with the invasion of *Codium fragile* ssp. *fragile* in eelgrass meadows	Marine Ecology Progress Series
2011	Ellis et al.	The benthos and fish of offshore sandbank habitats in the southern North Sea	Journal of the Marine Biological Association of the United Kingdom
2011	Fleddum et al.	Impact of hypoxia on the structure and function of benthic epifauna in Tolo Harbour, Hong Kong	Marine Pollution Bulletin
2011	Fraser et al.	Oceanic rafting by a coastal community	Proceedings of the Royal Society B: Biological Sciences
2011	Freeman & Creese	Predation as a driver of gastropod distribution in north-eastern New Zealand kelp forests	Marine and Freshwater Research
2011	Freestone & Osman	Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity	Ecology
2011	Harris	Benthic environments of the Lord Howe Rise submarine plateau: introduction to the special volume	Deep Sea Research Part II: Topical Studies in Oceanography
2011	Harwell et al.	Landscape aspects of oyster reefs: effects of fragmentation on habitat utilization	Journal of Experimental Marine Biology and Ecology
2011	Hellyer et al.	Manipulating artificial habitats to benefit seahorses in Sydney Harbour, Australia	Aquatic Conservation: Marine and Freshwater Ecosystems
2011	Hinz et al. 2011	Effects of scallop dredging on temperate reef fauna	Marine Ecology Progress Series
2011	Johnson	High-marsh invertebrates are susceptible to eutrophication	Marine Ecology Progress Series
2011	Kon et al.	Influence of a microhabitat on the structuring of the benthic macrofaunal community in a mangrove forest	Hydrobiologia

2011	Lambert et al.	Quantification and prediction of the impact of fishing on epifaunal communities	Marine Ecology Progress Series
2011	Liuzzi & Gappa	Algae as hosts for epifaunal bryozoans: role of functional groups and taxonomic relatedness	Journal of Sea Research
2011	Lomovasky et al.	Macro benthic community assemblage before and after the 2007 tsunami and earthquake at Paracas Bay, Peru	Journal of Sea Research
2011	Luo et al.	Community characteristics of macrobenthos in waters around the Nature Reserve of the Chinese sturgeon *Acipenser sinensis* and the adjacent waters in Yangtze River Estuary	Journal of Applied Ichthyology
2011	Metaxas	Spatial patterns of larval abundance at hydrothermal vents on seamounts: evidence for recruitment limitation	Marine Ecology Progress Series
2011	Moura et al.	Estimation of secondary production of the faro/ancao artificial reefs	Brazilian Journal of Oceanography
2011	Navarro et al.	Filtering capacity and endoscopic analysis of sympatric infaunal and epifaunal bivalves of southern Chile	Journal of the Marine Biological Association of the United Kingdom
2011	Neumann & Kröncke	The effect of temperature variability on ecological functioning of epifauna in the German Bight	Marine Ecology
2011	Nikula et al.	Evolutionary consequences of microhabitat: population-genetic structuring in kelp- vs. rock-associated chitons	Molecular Ecology
2011	Paavo et al.	Macrofaunal community patterns of adjacent coastal sediments with wave-reflecting or wave-dissipating characteristics	Journal of Coastal Research
2011	Pacciardi et al.	Effects of *Caulerpa racemosa* invasion on soft-bottom assemblages in the Western Mediterranean Sea	Biological Invasions
2011	Stevens & Dunn	Different food preferences in four sympatric deep-sea Macrourid fishes	Marine Biology
2011	Tanner	Utilisation of the invasive alga *Caulerpa taxifolia* as habitat by faunal assemblages in the Port River–Barker Inlet Estuary, South Australia	Estuaries and Coasts
2011	Tsubaki et al.	Pattern and process of diversification in an ecologically diverse epifaunal bivalve group Pterioidea (Pteriomorphia, Bivalvia)	Molecular Phylogenetics and Evolution

2011	Tuya et al.	Patterns of abundance and assemblage structure of epifauna inhabiting two morphologically different kelp holdfasts	Hydrobiologia
2011	Wong et al.	Evaluating estuarine habitats using secondary production as a proxy for food web support	Marine Ecology Progress Series
2012	Anderson & Lovvorn	Seasonal dynamics of prey size mediate complementary functions of mussel beds and seagrass habitats for an avian predator	Marine Ecology Progress Series
2012	Arponen & Boström	Responses of mobile epifauna to small-scale seagrass patchiness: is fragmentation important?	Hydrobiologia
2012	Bishop et al.	Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves	Ecology
2012	Byers et al.	Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast	Biological Invasions
2012	Cutajar et al.	Impacts of the invasive grass *Spartina anglica* on benthic macrofaunal assemblages in a temperate Australian saltmarsh	Marine Ecology Progress Series
2012	de Juan & Demestre	A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems	Ecological Indicators
2012	Elahi & Sebens	Consumers mediate natural variation between prey richness and resource use in a benthic marine community	Marine Ecology Progress Series
2012	Gestoso et al.	Effects of macroalgal identity on epifaunal assemblages: native species versus the invasive species *Sargassum muticum*	Helgoland Marine Research
2012	Gullström et al.	Spatial patterns and environmental correlates in leaf-associated epifaunal assemblages of temperate seagrass (*Zostera marina*) meadows	Marine Biology
2012	Gustafsson & Salo	The effect of patch isolation on epifaunal colonization in two different seagrass ecosystems	Marine Biology
2012	Hamilton et al.	One species of seagrass cannot act as a surrogate for others in relation to providing habitat for other taxa	Marine Ecology Progress Series
2012	Haupt et al.	Intra-regional translocations of epifaunal and infaunal species associated with cultured Pacific oysters *Crassostrea gigas*	African Journal of Marine Science

2012	Hepburn et al.	Uptake and transport of nitrogen derived from sessile epifauna in the giant kelp *Macrocystis pyrifera*	Aquatic Biology
2012	Janiak & Whitlatch	Epifaunal and algal assemblages associated with the native *Chondrus crispus* (Stackhouse) and the non-native *Grateloupia turuturu* (Yamada) in eastern Long Island Sound	Journal of Experimental Marine Biology and Ecology
2012	Källén et al.	*Seagrass*-epifauna relationships in a temperate South African estuary: interplay between patch-size, within-patch location and algal fouling	Estuarine, Coastal and Shelf Science
2012	Karlson & Osman	Species composition and geographic distribution of invertebrates in fouling communities along the east coast of the USA: a regional perspective	Marine Ecology Progress Series
2012	Lambert et al.	Implications of using alternative methods of vessel monitoring system (VMS) data analysis to describe fishing activities and impacts	ICES Journal of Marine Science
2012	Lewis & Anderson	Top-down control of epifauna by fishes enhances seagrass production	Ecology
2012	Macias	Faunistic analysis of the caridean shrimps inhabiting seagrasses along the NW coast of the Gulf of Mexico and Caribbean Sea	Revista De Biologia Tropical
2012	Martinez et al.	Spatial distribution of epibenthic molluscs on a sandstone reef in the Northeast of Brazil	Brazilian Journal of Biology
2012	Marzinelli et al.	Artificial structures influence fouling on habitat-forming kelps	Biofouling
2012	Mosch et al.	Factors influencing the distribution of epibenthic megafauna across the Peruvian oxygen minimum zone	Deep Sea Research Part I: Oceanographic Research Papers
2012	Nerot et al.	Stable isotope variations in benthic filter feeders across a large depth gradient on the continental shelf	Estuarine, Coastal and Shelf Science
2012	Pagliosa et al.	Influence of piers on functional groups of benthic primary producers and consumers in the channel of a subtropical coastal lagoon	Brazilian Journal of Oceanography
2012	Przeslawski et al.	Deep-sea *Lebensspuren* of the Australian continental margins	Deep Sea Research Part I: Oceanographic Research Papers

2012	Ragnarsson & Burgos	Separating the effects of a habitat modifier, *Modiolus modiolus* and substrate properties on the associated megafauna	Journal of Sea Research
2012	Riedel et al.	Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: a realistic scenario	Marine Ecology Progress Series
2012	Spicer & Widdicombe	Acute extracellular acid–base disturbance in the burrowing sea urchin *Brissopsis lyrifera* during exposure to a simulated CO_2 release	Science of The Total Environment
2012	Strain et al.	The long-term impacts of fisheries on epifaunal assemblage function and structure, in a Special Area of Conservation	Journal of Sea Research
2012	Tait & Hovel	Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat?	Journal of Experimental Marine Biology and Ecology
2012	Tyrrell et al.	Salt marsh fucoid algae: overlooked ecosystem engineers of north temperate salt marshes	Estuaries and Coasts
2012	Wilkie et al.	Are native *Saccostrea glomerata* and invasive *Crassostrea gigas* oysters' habitat equivalents for epibenthic communities in south-eastern Australia?	Journal of Experimental Marine Biology and Ecology
2012	Yorke & Metaxas	Relative importance of kelps and fucoids as substrata of the invasive epiphytic bryozoan *Membranipora membranacea* in Nova Scotia, Canada	Aquatic Biology
2013	Barnes et al.	Biodiversity in saline coastal lagoons: patterns of distribution and human impacts on sponge and ascidian assemblages	Diversity and Distributions
2013	Bell et al.	Lebensspuren of the bathyal Mid-Atlantic Ridge	Deep Sea Research Part II: Topical Studies in Oceanography
2013	Bilkovic et al.	Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages	Ecological Engineering
2013	Bishop et al.	Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves	Ecology
2013	Bowden et al.	Cold seep epifaunal communities on the Hikurangi Margin, New Zealand: composition, succession, and vulnerability to human activities	Plos One

2013	Brandt et al.	Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems	Deep Sea Research Part II: Topical Studies in Oceanography
2013	Broszeit et al.	Seasonal oxygen-driven migration of mobile benthic fauna affected by natural water column stratification	Estuarine, Coastal and Shelf Science
2013	Cartes et al.	Geomorphological, trophic and human influences on the bamboo coral Isidella elongata assemblages in the deep Mediterranean: to what extent does Isidella form habitat for fish and invertebrates?	Deep Sea Research Part I: Oceanographic Research Papers
2013	Coleman et al.	Using a no-take zone to assess the impacts of fishing: sessile epifauna appear insensitive to environmental disturbances from commercial potting	Journal of Experimental Marine Biology and Ecology
2013	Cook et al.	The substantial first impact of bottom fishing on rare biodiversity hotspots: a dilemma for evidence-based conservation	Plos One
2013	Dauvin et al.	Interactions between aggregations and environmental factors explain spatio-temporal patterns of the brittle-star *Ophiothrix fragilis* in the eastern Bay of Seine	Estuarine, Coastal and Shelf Science
2013	de Juan et al.	Benthic habitat characterisation of soft-bottom continental shelves: integration of acoustic surveys, benthic samples and trawling disturbance intensity	Estuarine, Coastal and Shelf Science
2013	Delgado et al.	Spatial characterization of megabenthic epifauna of soft bottoms around mud volcanoes in the Gulf of Cadiz	Journal of Natural History
2013	Dhib et al.	Contrasting key roles of *Ruppia cirrhosa* in a southern Mediterranean lagoon: reservoir for both biodiversity and harmful species and indicator of lagoon health status	Marine Pollution Bulletin
2013	Do et al.	Limited consequences of seagrass decline on benthic macrofauna and associated biotic indicators	Estuaries and Coasts
2013	Ellis et al.	Epibenthic assemblages in the Celtic Sea and associated with the Jones Bank	Progress in Oceanography

2013	Engelen et al.	Faunal differences between the invasive brown macroalga *Sargassum muticum* and competing native macroalgae	Biological Invasions
2013	Fleddum et al.	Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa	Journal of the Marine Biological Association of the United Kingdom
2013	Foveau et al.	Distribution patterns in the benthic diversity of the eastern English Channel	Marine Ecology Progress Series
2013	Gartner et al.	Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms	Journal of Experimental Marine Biology and Ecology
2013	Gribben et al.	Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem	Oikos
2013	Hammerschlag-Peyer et al.	Predator effects on faunal community composition in shallow seagrass beds of The Bahamas	Journal of Experimental Marine Biology and Ecology
2013	Krone et al.	Epifauna dynamics at an offshore foundation – implications of future wind power farming in the North Sea	Marine Environmental Research
2013	Laboy-Nieves & Muniz-Barretto	Epifauna associated with the sea cucumber *Holothuria mexicana* in Puerto Rico	Echinoderms in a Changing World*
2013	Lambert et al.	A comparison of two techniques for the rapid assessment of marine habitat complexity	Methods in Ecology and Evolution
2013	MacDonald & Weis	Fish community features correlate with prop root epibionts in Caribbean mangroves	Journal of Experimental Marine Biology and Ecology
2013	Mangano et al.	Evidence of trawl disturbance on mega-epibenthic communities in the Southern Tyrrhenian Sea	Marine Ecology Progress Series
2013	Neumann et al.	Benthos and demersal fish habitats in the German Exclusive Economic Zone (EEZ) of the North Sea	Helgoland Marine Research
2013	Ortiz et al.	Network properties and keystoneness assessment in different intertidal communities dominated by two ecosystem engineer species (SE Pacific coast): a comparative analysis	Ecological Modelling

2013	Pascal et al.	Response of the benthic food web to short- and long-term nutrient enrichment in saltmarsh mudflats	Marine Ecology Progress Series
2013	Popadić et al.	Impact evaluation of the industrial activities in the Bay of Bakar (Adriatic Sea, Croatia): recent benthic foraminifera and heavy metals	Marine Pollution Bulletin
2013	Prato et al.	Seasonal fluctuations of some biological traits of the invader *Caprella scaura* (Crustacea: Amphipoda: Caprellidae) in the Mar Piccolo of Taranto (Ionian Sea, southern Italy)	Scientia Marina
2013	Reinhardt et al.	Effects of temperature on the recruitment phenology and niche overlap of shallow epifaunal assemblages in southern New England	Marine Ecology Progress Series
2013	Riera et al.	Hard and soft-bottom macrozoobenthos in subtidal communities around an inactive harbour area (Gran Canaria, Canary Islands)	Vie et Milieu - Life and Environment
2013	Roff et al.	Macroalgal associations of motile epifaunal invertebrate communities on coral reefs	Marine Ecology
2013	Ross et al.	Spatially variable effects of a marine pest on ecosystem function	Oecologia
2013	Sciberras et al.	Benthic community response to a scallop dredging closure within a dynamic seabed habitat	Marine Ecology Progress Series
2013	Sell & Kröncke	Correlations between benthic habitats and demersal fish assemblages — a case study on the Dogger Bank (North Sea)	Journal of Sea Research
2013	Smith et al.	Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank	Marine Ecology Progress Series
2013	Staszak & Armitage	Evaluating salt marsh restoration success with an index of ecosystem integrity	Journal of Coastal Research
2013	Tuya et al.	Seagrass responses to nutrient enrichment depend on clonal integration, but not flow-on effects on associated biota	Marine Ecology Progress Series
2013	Urra et al.	Seasonal variation of molluscan assemblages in different strata of photophilous algae in the Alboran Sea (western Mediterranean)	Journal of Sea Research
2013	Vitaliano et al.	Broad-scale, dense amphipod tube aggregations on the sea bed: implications for resource species that utilize benthic habitats	Fisheries Oceanography

2013	Wolf et al.	Synergistic effects of algal overgrowth and corallivory on Caribbean reef-building corals	Ecology
2014	Altieri & Witman	Modular mobile foundation species as reservoirs of biodiversity	Ecosphere
2014	Bedini et al.	Mobile epifaunal assemblages associated with *Cystoseira* beds: comparison between areas invaded and not invaded by *Lophocladia lallemandii*	Scientia Marina
2014	Bhagirathan et al.	Impact of bottom trawling on the epifauna off Veraval coast, India	Indian Journal of Geo-Marine Sciences
2014	Blain & Gagnon	Canopy-forming seaweeds in urchin-dominated systems in eastern Canada: structuring forces or simple prey for keystone grazers?	Plos One
2014	Blake et al.	Patterns of seagrass community response to local shoreline development	Estuaries and Coasts
2014	Boulcott et al.	Impact of scallop dredging on benthic epifauna in a mixed-substrate habitat	ICES Journal of Marine Science
2014	Brahim et al.	Bathymetric variation of epiphytic assemblages on *Posidonia oceanica* (L.) Delile leaves in relation to anthropogenic disturbance in the southeastern Mediterranean	Environmental Science and Pollution Research
2014	Buzá-Jacobucci & Pereira-Leite	The role of epiphytic algae and different species of *Sargassum* in the distribution and feeding of herbivorous amphipods	Latin American Journal of Aquatic Research
2014	Carvalho et al.	Biodiversity patterns of epifaunal assemblages associated with the gorgonians *Eunicella gazella* and *Leptogorgia lusitanica* in response to host, space and time	Journal of Sea Research
2014	Cebrian et al.	Eutrophication-driven shifts in primary producers in shallow coastal systems: implications for system functional change	Estuaries and Coasts
2014	Corrêa et al.	Diversity and composition of macro- and meiofaunal carapace epibionts of the hawksbill sea turtle (*Eretmochelys imbricata* Linnaeus, 1822) in Atlantic waters	Marine Biodiversity
2014	Fariñas-Franco & Roberts	Early faunal successional patterns in artificial reefs used for restoration of impacted biogenic habitats	Hydrobiologia

2014	Fernandez et al.	Temporal variation in richness and composition of recruits in a diverse cnidarian assemblage of subtropical Brazil	Journal of Experimental Marine Biology and Ecology
2014	Fukunaga et al.	Epifaunal community structure and ammonium uptake compared for the invasive algae, *Gracilaria salicornia* and *Acanthophora specifera*, and the native alga, *Padina thivyi*	Journal of Experimental Marine Biology and Ecology
2014	Gatune et al.	Growth and survival of post-larval giant tiger shrimp *Penaeus monodon* feeding on mangrove leaf litter biofilms	Marine Ecology Progress Series
2014	Hosono	Temperature explains reproductive dynamics in caprellids at different latitudes	Marine Ecology Progress Series
2014	Huang et al.	Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient?	Global Ecology and Biogeography
2014	Hughes	Benthic habitat and megafaunal zonation across the Hebridean Slope, western Scotland, analysed from archived seabed photographs	Journal of the Marine Biological Association of the United Kingdom
2014	Jones et al.	Asphalt mounds and associated biota on the Angolan margin	Deep Sea Research Part I: Oceanographic Research Papers
2014	Konsulova & Doncheva	Ecological impact assessment of groins in Varna Bay (Black Sea, Bulgaria) - a prerequisite for application of environmentally friendly shore protection structures	Acta Zoologica Bulgarica
2014	Kornijow	A quantitative sampler for collecting invertebrates associated with deep submerged vegetation	Aquatic Ecology
2014	Lambert et al.	Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing	Journal of Applied Ecology
2014	Lange & Griffiths	Large-scale spatial patterns within soft-bottom epibenthic invertebrate assemblages along the west coast of South Africa, based on the Nansen trawl survey	African Journal of Marine Science
2014	Lefcheck et al.	Epifaunal invertebrates as predators of juvenile bay scallops (*Argopecten irradians*)	Journal of Experimental Marine Biology and Ecology
2014	Leopardas et al.	Benthic macrofaunal assemblages in multispecific seagrass meadows of the southern Philippines:	Journal of Experimental Marine Biology and Ecology

		variation among vegetation dominated by different seagrass species	
2014	Esqueda-González et al.	Species composition, richness, and distribution of marine bivalve molluscs in Bahía de Mazatlán, México	ZooKeys
2014	Muntadas et al.	Trawling disturbance on benthic ecosystems and consequences on commercial species: a northwestern Mediterranean case study	Scientia Marina
2014	Navarro-Barranco et al.	Mobile epifaunal community in marine caves in comparison to open habitats	Aquatic Biology
2014	Nordström et al.	Benthic food-web succession in a developing salt marsh	Marine Ecology Progress Series
2014	Palardy & Witman	Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities	Ecology
2014	Pierri-Daunt & Tanaka	Assessing habitat fragmentation on marine epifaunal macroinvertebrate communities: an experimental approach	Landscape Ecology
2014	Png-Gonzalez et al.	Comparison of epifaunal assemblages between *Cymodocea nodosa* and *Caulerpa prolifera* meadows in Gran Canaria (eastern Atlantic)	Journal of the Marine Biological Association of the United Kingdom
2014	Reynolds et al.	Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance	Limnology and Oceanography
2014	Ronowicz et al.	Temporal and spatial variability of zoobenthos recruitment in a north-east Atlantic marine reserve	Journal of the Marine Biological Association of the United Kingdom
2014	Smeulders et al.	Cold-water coral habitats of Rockall and Porcupine Bank, NE Atlantic Ocean: sedimentary facies and benthic foraminiferal assemblages	Deep Sea Research Part II: Topical Studies in Oceanography
2014	Smith et al.	Fish trophic engineering: ecological effects of the invasive ascidian *Didemnum vexillum* (Georges Bank, northwestern Atlantic)	Journal of Experimental Marine Biology and Ecology
2014	Trave & Sheaves	Bimini Islands: a characterization of the two major nursery areas; status and perspectives	Springerplus

2014	Tuya et al.	Ecological structure and function differs between habitats dominated by seagrasses and green seaweeds	Marine Environmental Research
2014	Vassallo et al.	Inventory of invertebrates from the rocky intertidal shore at Montepio, Veracruz, Mexico	Revista Mexicana De Biodiversidad
2014	Veiga et al.	Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species	Marine Environmental Research
2014	Vidović et al.	Benthic foraminifera assemblages as elemental pollution bioindicator in marine sediments around fish farm (Vrgada Island, Central Adriatic, Croatia)	Marine Pollution Bulletin
2015	Barry et al.	Generalizing visual fast count estimators for underwater video surveys	Ecosphere
2015	Bergman et al.	Effects of a 5-year trawling ban on the local benthic community in a wind farm in the Dutch coastal zone	ICES Journal of Marine Science
2015	Carcedo et al.	Macrobenthic surf zone communities of temperate sandy beaches: spatial and temporal patterns	Marine Ecology
2015	Chen et al.	Invasive cordgrass facilitates epifaunal communities in a Chinese marsh	Biological Invasions
2015	Coolen et al.	Reefs, sand and reef-like sand: a comparison of the benthic biodiversity of habitats in the Dutch Borkum Reef Grounds	Journal of Sea Research
2015	Cúrdia et al.	Diversity and abundance of invertebrate epifaunal assemblages associated with gorgonians are driven by colony attributes	Coral Reefs
2015	de Jong et al.	Relationships between macrozoobenthos and habitat characteristics in an intensively used area of the Dutch coastal zone	Ices Journal of Marine Science
2015	de Jong et al.	Short-term impact of deep sand extraction and ecosystem-based landscaping on macrozoobenthos and sediment characteristics	Marine Pollution Bulletin
2015	De Mesel et al.	Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species	Hydrobiologia
2015	DeAmicis & Foggo	Long-term field study reveals subtle effects of the invasive alga *Sargassum muticum* upon the epibiota of *Zostera marina*	Plos One

2015	Dias et al.	Temporal variability in epifaunal assemblages associated with temperate gorgonian gardens	Marine Environmental Research
2015	Eklöf et al.	Community-level effects of rapid experimental warming and consumer loss outweigh effects of rapid ocean acidification	Oikos
2015	Fernandez et al.	A comparison of temporal turnover of species from benthic cnidarian assemblages in tropical and subtropical harbours	Marine Biology Research
2015	Green & Fong	A small-scale test of the species-energy hypothesis in a southern California estuary	Journal of Experimental Marine Biology and Ecology
2015	Greene	Habitat characterization of a tidal energy site using an ROV: overcoming difficulties in a harsh environment	Continental Shelf Research
2015	Gutow et al.	Castaways can't be choosers - homogenization of rafting assemblages on floating seaweeds	Journal of Sea Research
2015	Hemery et al.	Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters	Biodiversity and Conservation
2015	Howarth et al.	Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve	Marine Environmental Research
2015	Huang et al.	Top–down control by great blue herons *Ardea herodias* regulates seagrass-associated epifauna	Oikos
2015	Knight et al.	A comparison of epifaunal invertebrate communities in native eelgrass *Zostera marina* and non-native *Zostera japonica* at Tsawwassen, BC	Marine Biology Research
2015	Kristensen et al.	Establishment of blue mussel beds to enhance fish habitats	Applied Ecology and Environmental Research
2015	Lanham et al.	Beyond the border: effects of an expanding algal habitat on the fauna of neighbouring habitats	Marine Environmental Research
2015	Lee et al.	Baseline seabed habitat and biotope mapping for a proposed marine reserve	PeerJ

2015	Long et al.	Overgrowth of eelgrass by the invasive colonial tunicate *Didemnum vexillum*: consequences for tunicate and eelgrass growth and epifauna abundance	Journal of Experimental Marine Biology and Ecology
2015	McDonald et al.	Effects of geoduck (*Panopea generosa* Gould, 1850) aquaculture gear on resident and transient macrofauna communities of Puget Sound, Washington	Journal of Shellfish Research
2015	McFarlin et al.	Context-dependent effects of the loss of *Spartina altemiflora* on salt marsh invertebrate communities	Estuarine Coastal and Shelf Science
2015	Munari et al.	Epifauna associated to the introduced *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) and comparison with the native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvales) in an Adriatic lagoon	Italian Journal of Zoology
2015	Navarro-Barranco et al.	Colonization and successional patterns of the mobile epifaunal community along an environmental gradient in a marine cave	Marine Ecology Progress Series
2015	Nogueira et al.	Effects of habitat structure on the epifaunal community in *Mussismilia* corals: does coral morphology influence the richness and abundance of associated crustacean fauna?	Helgoland Marine Research
2015	Ortiz et al.	Control Strategy scenarios for the alien lionfish *Pterois volitans* in Chinchorro Bank (Mexican Caribbean): based on semi-quantitative loop analysis	Plos One
2015	Ortiz et al.	Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): comparative network structure and assessment of human impacts	Ecological Modelling
2015	Palmer & Montagna	Impacts of droughts and low flows on estuarine water quality and benthic fauna	Hydrobiologia
2015	Sepúlveda et al.	Ascidian-associated polychaetes: ecological implications of aggregation size and tube-building chaetopterids on assemblage structure in the Southeastern Pacific Ocean	Marine Biodiversity
2015	Sheehan et al.	The ecosystem service value of living versus dead biogenic reef	Estuarine, Coastal and Shelf Science

2015	Sokołowski et al.	Habitat-related patterns of soft-bottom macrofaunal assemblages in a brackish, low-diversity system (southern Baltic Sea)	Journal of Sea Research
2015	Torres et al.	The role of annual macroalgal morphology in driving its epifaunal assemblages	Journal of Experimental Marine Biology and Ecology
2015	Vader & Tandberg	Amphipods as associates of other crustacea: a survey	Journal of Crustacean Biology
2015	van der Zee et al.	Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem	Journal of Experimental Marine Biology and Ecology
2015	Veeragurunathan et al.	Cultivation of *Gracilaria dura* in the open sea along the southeast coast of India	Journal of Applied Phycology
2015	Whomersley et al.	More bang for your monitoring bucks: detection and reporting of non-indigenous species	Marine Pollution Bulletin
2015	Wong & Dowd	Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada	Estuaries and Coasts
2015	Zupo et al.	Chemoreception of the seagrass *Posidonia oceanica* by benthic invertebrates is altered by seawater acidification	Journal of Chemical Ecology
2016	Arnold et al.	The structure of biogenic habitat and epibiotic assemblages associated with the global invasive kelp *Undaria pinnatifida* in comparison to native macroalgae	Biological Invasions
2016	Ba-Akdah et al.	Habitat preference and seasonal variability of epifaunal assemblages associated with macroalgal beds on the Central Red Sea coast, Saudi Arabia	Journal of the Marine Biological Association of the United Kingdom
2016	Bowden et al.	Deep-sea seabed habitats: do they support distinct mega-epifaunal communities that have different vulnerabilities to anthropogenic disturbance?	Deep Sea Research Part I: Oceanographic Research Papers
2016	Clark et al.	The NIWA seamount sled: an effective epibenthic sledge for sampling epifauna on seamounts and rough seafloor	Deep Sea Research Part I: Oceanographic Research Papers
2016	de Jong et al.	Ecosystem-based design rules for marine sand extraction sites	Ecological Engineering

2016	Demers et al.	Under the radar: sessile epifaunal invertebrates in the seagrass *Posidonia australis*	Journal of the Marine Biological Association of the United Kingdom
2016	Du Preez et al.	The structure and distribution of benthic communities on a shallow seamount (Cobb Seamount, northeast Pacific Ocean)	Plos One
2016	Figueroa et al.	Photosynthetic activity estimated as *in vivo* chlorophyll a fluorescence in calcareous red macroalgae	Ciencias Marinas
2016	Filimon et al.	Community structure of zoobenthos associated with *Cystoseira barbata* facies from the southern romanian black sea coast	Journal of Environmental Protection and Ecology
2016	Fritz	Commentary: threatened by mining, polymetallic nodules are required to preserve abyssal epifauna	Frontiers in Marine Science
2016	Hemery & Henkel	Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters: a reassessment	Biodiversity and Conservation
2016	Jimenez et al.	Harvesting effects on functional structure and composition of tropical invertebrate assemblages	ICES Journal of Marine Science
2016	Kollars et al.	Invasive décor: an association between a native decorator worm and a non-native seaweed can be mutualistic	Marine Ecology Progress Series
2016	Lefcheck et al.	Faunal communities are invariant to fragmentation in experimental seagrass landscapes	Plos One
2016	Leite et al.	Temporal variation of epi- and endofaunal assemblages associated with the red sponge *Tedania ignis* on a rocky shore (Sao Sebastiao Channel), SE Brazil	Iheringia Serie Zoologia
2016	Luckenbach et al.	Effects of clam aquaculture on nektonic and benthic assemblages in two shallow-water estuaries	Journal of Shellfish Research
2016	Marzinelli et al.	Does restoration of a habitat-forming seaweed restore associated faunal diversity?	Restoration Ecology
2016	McDonald et al.	Fish, macroinvertebrate and epifaunal communities in shallow coastal lagoons with varying seagrass cover of the northern Gulf of Mexico	Estuaries and Coasts
2016	McSkimming et al.	Habitat restoration: early signs and extent of faunal recovery relative to seagrass recovery	Estuarine, Coastal and Shelf Science

2016	Meyer et al.	*Hyalinoecia artifex*: field notes on a charismatic and abundant epifaunal polychaete on the US Atlantic continental margin	Invertebrate Biology
2016	Muntadas et al.	Assessing functional redundancy in chronically trawled benthic communities	Ecological Indicators
2016	Murat et al.	Silting up and development of anoxic conditions enhanced by high abundance of the geoengineer species *Ophiothrix fragilis*	Continental Shelf Research
2016	Navarro-Barranco et al.	Amphipod community associated with invertebrate hosts in a Mediterranean marine cave	Marine Biodiversity
2016	Neumann et al.	Functional composition of epifauna in the south-eastern North Sea in relation to habitat characteristics and fishing effort	Estuarine, Coastal and Shelf Science
2016	Piló et al.	How functional traits of estuarine macrobenthic assemblages respond to metal contamination?	Ecological Indicators
2016	Piras et al.	A photographic method to identify benthic assemblages based on demersal trawler discards	Fisheries Research
2016	Rodrigues et al.	Patterns of mollusc distribution in mangroves from the São Marcos Bay, coast of Maranhão State, Brazil	Acta Amazonica
2016	Rodríguez-Zaragoza et al.	Trophic models and short-term dynamic simulations for benthic-pelagic communities at Banco Chinchorro Biosphere Reserve (Mexican Caribbean): a conservation case	Community Ecology
2016	Rosli et al.	Differences in meiofauna communities with sediment depth are greater than habitat effects on the New Zealand continental margin: implications for vulnerability to anthropogenic disturbance	PeerJ
2016	Tano et al.	Tropical seaweed beds are important habitats for mobile invertebrate epifauna	Estuarine Coastal and Shelf Science
2016	Theodor et al.	Stable carbon isotope gradients in benthic foraminifera as proxy for organic carbon fluxes in the Mediterranean Sea	Biogeosciences
2016	Vanreusel et al.	Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna	Scientific Reports
2016	Walls et al.	Potential novel habitat created by holdfasts from cultivated *Laminaria digitata*: assessing the macroinvertebrate assemblages	Aquaculture Environment Interactions

2016	Zharikov & Lysenko	The distribution of macrobenthic epifauna in the far eastern marine reserve based on remote underwater video data	Russian Journal of Marine Biology
2017	Agostini et al.	What determines sclerobiont colonization on marine mollusk shells?	Plos One
2017	Alfaro-Lucas et al.	Bone-eating *Osedax* worms (Annelida: Siboglinidae) regulate biodiversity of deep-sea whale-fall communities	Deep Sea Research Part II: Topical Studies in Oceanography
2017	Balestra et al.	Coccolithophore and benthic foraminifera distribution patterns in the Gulf of Cadiz and Western Iberian Margin during Integrated Ocean Drilling Program (IODP) Expedition 339	Journal of Marine Systems
2017	Boyé et al.	Constancy despite variability: local and regional macrofaunal diversity in intertidal seagrass beds	Journal of Sea Research
2017	Collie et al.	Indirect effects of bottom fishing on the productivity of marine fish	Fish and Fisheries
2017	Cox et al.	Community assessment techniques and the implications for rarefaction and extrapolation with Hill numbers	Ecology and Evolution
2017	Davoult et al.	Multiple effects of a *Gracilaria vermiculophylla* invasion on estuarine mudflat functioning and diversity	Marine Environmental Research
2017	Donadi et al.	A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems	Proceedings of the Royal Society B: Biological Sciences
2017	Eddy et al.	Ecosystem effects of invertebrate fisheries	Fish and Fisheries
2017	Fernandez-Gonzalez & Sanchez-Jerez	Fouling assemblages associated with off-coast aquaculture facilities: an overall assessment of the Mediterranean Sea	Mediterranean Marine Science
2017	Foveau & Dauvin	Surprisingly diversified macrofauna in mobile gravels and pebbles from high-energy hydrodynamic environment of the 'Raz Blanchard' (English Channel)	Regional Studies in Marine Science
2017	Gribben et al.	Positive and negative interactions control a facilitation cascade	Ecosphere

2017	Hamilton et al.	Modeling local effects on propagule movement and the potential expansion of mangroves and associated fauna: testing in a sub-tropical lagoon	Hydrobiologia
2017	Lambert et al.	Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance	Scientific Reports
2017	Lavender et al.	Small-scale habitat complexity of artificial turf influences the development of associated invertebrate assemblages	Journal of Experimental Marine Biology and Ecology
2017	Lefcheck et al.	Restored eelgrass (*Zostera marina* L.) as a refuge for epifaunal biodiversity in mid-western Atlantic coastal bays	Estuaries and Coasts
2017	Mach et al.	Nonnative species in British Columbia eelgrass beds spread via shellfish aquaculture and stay for the mild climate	Estuaries and Coasts
2017	Mariani et al.	Habitat structure and zonation patterns of northwestern Mediterranean shoreline strands	Scientia Marina
2017	Neumann et al.	Full-coverage spatial distribution of epibenthic communities in the south-eastern North Sea in relation to habitat characteristics and fishing effort	Marine Environmental Research
2017	O'Carroll et al.	Identifying relevant scales of variability for monitoring epifaunal reef communities at a tidal energy extraction site	Ecological Indicators
2017	O'Carroll et al.	Tidal Energy: the benthic effects of an operational tidal stream turbine	Marine Environmental Research
2017	Pascal et al.	Influences of geothermal sulfur bacteria on a tropical coastal food web	Marine Ecology Progress Series
2017	Ramalho et al.	Deep-sea mega-epibenthic assemblages from the SW Portuguese Margin (NE Atlantic) subjected to bottom-trawling fisheries	Frontiers in Marine Science
2017	Reynolds et al.	Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer	Ecosphere
2017	Salmo et al.	Colonization and shift of mollusc assemblages as a restoration indicator in planted mangroves in the Philippines	Biodiversity and Conservation
2017	Sokołowski et al.	Recruitment pattern of benthic fauna on artificial substrates in brackish low-diversity system (the Baltic Sea)	Hydrobiologia

2017	Suárez-Jiménez et al.	The invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds with comparable morphologies	Marine Ecology Progress Series
2017	Taylor et al.	Assessing oxygen depletion in the Northeastern Pacific Ocean during the last deglaciation using I/Ca ratios from multiple benthic foraminiferal species	Paleoceanography
2017	Vermeij	Shell features associated with the sand-burying habit in gastropods	Journal of Molluscan Studies
2017	Winkler et al.	Seasonal variation in epifaunal communities associated with giant kelp (*Macrocystis pyrifera*) at an upwelling-dominated site	Austral Ecology
2017	Xu et al.	Functional groupings and food web of an artificial reef used for sea cucumber aquaculture in northern China	Journal of Sea Research
2017	Yeager & Hovel	Structural complexity and fish body size interactively affect habitat optimality	Oecologia
2017	Zaabar et al.	Temporal variation and structure of macro-epifauna associated with macrophytes in the Bizerte lagoon (Tunisia, SW Mediterranean Sea)	Journal of Natural History
2018	Alitto et al.	Shallow-water brittle stars (Echinodermata: Ophiuroidea) from Araçá Bay (Southeastern Brazil), with spatial distribution considerations	Zootaxa
2018	Audino & Marian	Comparative and functional anatomy of the mantle margin in ark clams and their relatives (Bivalvia: Arcoidea) supports association between morphology and life habits	Journal of Zoology
2018	Baker et al.	Potential contribution of surface-dwelling *Sargassum* algae to deep-sea ecosystems in the southern North Atlantic	Deep Sea Research Part II: Topical Studies in Oceanography
2018	Belattmania et al.	Similar epiphytic macrofauna inhabiting the introduced *Sargassum muticum* and native fucoids on the Atlantic coast of Morocco	Cryptogamie Algologie
2018	Belattmania et al.	The introduction of *Sargassum muticum* modifies epifaunal patterns in a Moroccan seagrass meadow	Marine Ecology
2018	Brix et al.	Distributional patterns of isopods (Crustacea) in Icelandic and adjacent waters	Marine Biodiversity

2018	Burnett & Koehl	Knots and tangles weaken kelp fronds while increasing drag forces and epifauna on the kelp	Journal of Experimental Marine Biology and Ecology
2018	Coffin et al.	Impacts of hypoxia on estuarine macroinvertebrate assemblages across a regional nutrient gradient	Facets
2018	Cunha et al.	Epiphytic hydroids (Cnidaria, Hydrozoa) contribute to a higher abundance of caprellid amphipods (Crustacea, Peracarida) on macroalgae	Hydrobiologia
2018	das Chagas et al.	Composition of the biofouling community associated with oyster culture in an Amazon estuary, Para State, North Brazil	Revista De Biologia Marina Y Oceanografia
2018	Desmond et al.	Epifaunal community structure within southern New Zealand kelp forests	Marine Ecology Progress Series
2018	dos Santos et al.	*Eretmochelys imbricata* shells present a dynamic substrate for a facilitative epibiont relationship between macrofauna richness and nematode diversity, structure and function	Journal of Experimental Marine Biology and Ecology
2018	Douglass et al.	Fish and seagrass communities vary across a marine reserve boundary, but seasonal variation in small fish abundance overshadows top-down effects of large consumer exclosures	Journal of Experimental Marine Biology and Ecology
2018	Eggleton et al.	How benthic habitats and bottom trawling affect trait composition in the diet of seven demersal and benthivorous fish species in the North Sea	Journal of Sea Research
2018	Esqueda-González et al.	Spatial analysis of bivalve mollusks diversity in Mazatlan Bay, Mexico	Marine Biodiversity
2018	Fariñas-Franco et al.	Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears	Marine Environmental Research
2018	French & Moore	Canopy functions of *R. maritima* and *Z. marina* in the Chesapeake Bay	Frontiers in Marine Science
2018	Gabara et al.	Rhodolith structural loss decreases abundance, diversity, and stability of benthic communities at Santa Catalina Island	Marine Ecology Progress Series
2018	Gavira-O'Neill et al.	Mobile epifauna of the invasive bryozoan *Tricellaria inopinata*: is there a potential invasional meltdown?	Marine Biodiversity

2018	Glaspie et al.	Effects of estuarine acidification on an oyster-associated community in New South Wales, Australia	Journal of Shellfish Research
2018	Ha & Williams	Eelgrass community dominated by native omnivores in Bodega Bay, California, USA	Bulletin of Marine Science
2018	Hamoutene et al.	Linking the presence of visual indicators of aquaculture deposition to changes in epibenthic richness at finfish sites installed over hard bottom substrates	Environmental Monitoring and Assessment
2018	Hemery et al.	Benthic assemblages of mega epifauna on the Oregon continental margin	Continental Shelf Research
2018	Hermosillo-Núñez et al.	Keystone species complexes in kelp forest ecosystems along the northern Chilean coast (SE Pacific): improving multispecies management strategies	Ecological Indicators
2018	Hermosillo-Núñez et al.	Trophic network properties of coral ecosystems in three marine protected areas along the Mexican Pacific Coast: assessment of systemic structure and health	Ecological Complexity
2018	Howarth et al.	Effects of bottom trawling and primary production on the composition of biological traits in benthic assemblages	Marine Ecology Progress Series
2018	Janiak et al.	Artificial structures versus mangrove prop roots: a general comparison of epifaunal communities within the Indian River Lagoon, Florida, USA	Marine Ecology Progress Series
2018	Kaiser et al.	Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear	Journal of Applied Ecology
2018	Kaminsky et al.	Spatial analysis of benthic functional biodiversity in San Jorge Gulf, Argentina	Oceanography
2018	Kennedy et al.	Eelgrass as valuable nearshore foraging habitat for juvenile pacific salmon in the early marine period	Marine and Coastal Fisheries
2018	Kniesz et al.	Peritrich epibionts on the hadal isopod species *Macrostylis marionae* n. sp. from the Puerto Rico Trench used as indicator for sex-specific behaviour	Deep Sea Research Part II: Topical Studies in Oceanography
2018	Little et al.	Long-term fluctuations in epibiotic bryozoan and hydroid abundances in an Irish sea lough	Estuarine, Coastal and Shelf Science

2018	Lundquist et al.	Assessing benthic responses to fishing disturbance over broad spatial scales that incorporate high environmental variation	Frontiers in Marine Science
2018	McGann & Conrad	Faunal and stable isotopic analyses of benthic foraminifera from the Southeast Seep on Kimki Ridge offshore southern California, USA	Deep Sea Research Part II: Topical Studies in Oceanography
2018	Momota & Nakaoka	Seasonal change in spatial variability of eelgrass epifaunal community in relation to gradients of abiotic and biotic factors	Marine Ecology
2018	Monk et al.	An evaluation of the error and uncertainty in epibenthos cover estimates from AUV images collected with an efficient, spatially-balanced design	Plos One
2018	Montereale-Gavazzi et al.	Seafloor change detection using multibeam echosounder backscatter: case study on the Belgian part of the North Sea	Marine Geophysical Research
2018	Moreno et al.	Coupling biophysical processes that sustain a deep subpopulation of *Loxechinus albus* and its associated epibenthic community over a bathymetric feature	Estuarine, Coastal and Shelf Science
2018	Morris et al.	Can coir increase native biodiversity and reduce colonisation of non-indigenous species in eco-engineered rock pools?	Ecological Engineering
2018	Mosbahi et al.	Molluscs associated with intertidal *Zostera noltei* Hornemann beds in southern Tunisia (central Mediterranean): seasonal dynamics and environmental drivers	Vie et Milieu - Life and Environment
2018	Muntadas et al.	A knowledge platform to inform on the effects of trawling on benthic communities	Estuarine, Coastal and Shelf Science
2018	Nakamoto et al.	Phylogenetically diverse macrophyte community promotes species diversity of mobile epi-benthic invertebrates	Estuarine, Coastal and Shelf Science
2018	Namba & Nakaoka	Spatial patterns and predictor variables vary among different types of primary producers and consumers in eelgrass (*Zostera marina*) beds	Plos One
2018	Navarro-Barranco et al.	Impoverished mobile epifaunal assemblages associated with the invasive macroalga *Asparagopsis taxiformis* in the Mediterranean Sea	Marine Environmental Research

2018	Parameswaran et al.	Diversity and distribution of echinoderms in the South Eastern Arabian Sea shelf under the influence of seasonal hypoxia	Progress in Oceanography
2018	Saarinen et al.	Epifaunal community composition in five macroalgal species - what are the consequences if some algal species are lost?	Estuarine, Coastal and Shelf Science
2018	Scheffel et al.	Tropicalization of the northern Gulf of Mexico: impacts of salt marsh transition to black mangrove dominance on faunal communities	Estuaries and Coasts
2018	Schweitzer et al.	Impacts of a multi-trap line on benthic habitat containing emergent epifauna within the Mid-Atlantic Bight	ICES Journal of Marine Science
2018	Singh et al.	Changes in standing stock and vertical distribution of benthic foraminifera along a depth gradient (58–2750 m) in the southeastern Arabian Sea	Marine Biodiversity
2018	Soler-Hurtado et al.	Structure of gorgonian epifaunal communities in Ecuador (eastern Pacific)	Coral Reefs
2018	Sutherland et al.	Influence of salmonid aquaculture activities on a rock-cliff epifaunal community in Jervis Inlet, British Columbia	Marine Pollution Bulletin
2018	Tanner et al.	Benthic biogeographic patterns in the southern Australian deep sea: do historical museum records accord with recent systematic, but spatially limited, survey data?	Ecology and Evolution
2018	Tilot et al.	The benthic megafaunal assemblages of the CCZ (eastern Pacific) and an approach to their management in the face of threatened anthropogenic impacts	Frontiers in Marine Science
2018	Vaughn & Hoellein	Bivalve impacts in freshwater and marine ecosystems	Annual Review of Ecology, Evolution, and Systematics*
2018	Venturelli et al.	Epifaunal foraminifera in an infaunal world: insights into the influence of heterogeneity on the benthic ecology of oxygen-poor, deep-sea habitats	Frontiers in Marine Science
2018	Viola et al.	Anthropogenic disturbance facilitates a non-native species on offshore oil platforms	Journal of Applied Ecology
2018	Waters et al.	Rafting dispersal in a brooding southern sea star (Asteroidea : Anasterias)	Invertebrate Systematics

2018	Wenger et al.	Microhabitat selectivity shapes the seascape ecology of a carnivorous macroalgae-associated tropical fish	Marine Ecology Progress Series
2018	Whippo et al.	Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes	Ecosphere
2018	Williams et al.	Characterising the invertebrate megafaunal assemblages of a deep-sea (200–3000 m) frontier region for oil and gas exploration: the Great Australian Bight, Australia	Deep Sea Research Part II: Topical Studies in Oceanography
2018	Yusa et al.	Spatial–temporal variations in the composition of two *Zostera* species in a seagrass bed: implications for population management of a commercially exploited grass shrimp	Fisheries Science
2018	Zwerschke et al.	Limited impact of an invasive oyster on intertidal assemblage structure and biodiversity: the importance of environmental context and functional equivalency with native species	Marine Biology
2019	Abdelhady et al.	Water chemistry and substrate type as major determinants of molluscan feeding habit and life–mode in lagoon sediments	Estuarine, Coastal and Shelf Science
2019	Audino et al.	Ark clams and relatives (Bivalvia: Arcida) show convergent morphological evolution associated with lifestyle transitions in the marine benthos	Biological Journal of the Linnean Society
2019	Barrientos-Lujan et al.	Ecological and functional diversity of gastropods associated with hermatypic corals of the Mexican tropical Pacific	Marine Biodiversity
2019	Bentley et al.	Fishers' knowledge improves the accuracy of food web model predictions	ICES Journal of Marine Science
2019	Bertolini	Can secondary species maintain a primary role? Consistent inter-regional effects of understory algae on diversity	Marine Biodiversity
2019	Bonaglia et al.	Sulfide oxidation in deep Baltic Sea sediments upon oxygenation and colonization by macrofauna	Marine Biology
2019	Bremec & Schejter	*Chaetopterus antarcticus* (Polychaeta: Chaetopteridae) in Argentinian shelf scallop beds: from infaunal to epifaunal life habits	Revista De Biologia Tropical

2019	Brooks & Crowe	Combined effects of multiple stressors: new insights into the influence of timing and sequence	Frontiers in Ecology and Evolution
2019	Cadier & Frouws	Experimental harvest in a tropical seagrass meadow leads to shift in associated benthic communities	Community Ecology
2019	Campanyà-Llovet & Snelgrove	Influence of phytodetrital quality on macroinfaunal community structure and epifaunal response	Marine Ecology Progress Series
2019	Carmen & Grunden	A preliminary assessment of crab predation on epifaunal fouling organisms attached to eelgrass at Martha's Vineyard, Massachusetts, USA	Management of Biological Invasions
2019	Casamajor et al.	*Cystoseira baccata* meadows along the French Basque coast (Bay of Biscay) as a reference for the implementation of the Water Framework and Marine Strategy EU directives	Continental Shelf Research
2019	Cavalcante et al.	Spatiotemporal dynamics of the molluscan community associated with seagrass on the western equatorial Atlantic	Journal of the Marine Biological Association of the United Kingdom
2019	Ferreira et al.	Temporal variation in peracarid assemblages inhabiting *Caulerpa racemosa* in two Brazilian rocky shores	Marine Biodiversity
2019	Fields et al.	Video sleds effectively survey epibenthic communities at dredged material disposal sites	Environmental Monitoring and Assessment
2019	Foster et al.	The invasive green alga *Avrainvillea* sp. transforms native epifauna and algal communities on a tropical hard substrate reef	Phycological Research
2019	Fulton et al.	Form and function of tropical macroalgal reefs in the Anthropocene	Functional Ecology
2019	Gan et al.	Effects of macroalgal morphology on marine epifaunal diversity	Journal of the Marine Biological Association of the United Kingdom
2019	Gárate et al.	Potential nitrous oxide production by marine shellfish in response to warming and nutrient enrichment	Marine Pollution Bulletin
2019	Garcia et al.	Population and reproductive biology of two caprellid species (Crustacea: Amphipoda)	Nauplius

		associated to *Sargassum cymosum* (Phaeophyta: Fucales) on the southeast coast of Brazil	
2019	Gates et al.	Ecological role of an offshore industry artificial structure	Frontiers in Marine Science
2019	Githaiga et al.	Seagrass removal leads to rapid changes in fauna and loss of carbon	Frontiers in Ecology and Evolution
2019	Guillas et al.	Settlement of juvenile glass sponges and other invertebrate cryptofauna on the Hecate Strait glass sponge reefs	Invertebrate Biology
2019	Hayduk et al.	Evidence for regional-scale controls on eelgrass (*Zostera marina*) and mesograzer community structure in upwelling-influenced estuaries	Limnology and Oceanography
2019	Henseler et al.	Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach	Estuarine, Coastal and Shelf Science
2019	Hossain	Trophic functioning of macrobenthic fauna in a tropical acidified Bornean estuary (Southeast Asia)	International Journal of Sediment Research
2019	Hossain et al.	Epibenthic community variation along an acidified tropical estuarine system	Regional Studies in Marine Science
2019	Iliff et al.	Effects of chronic pesticide exposure on an epibenthic oyster reef community	Marine Pollution Bulletin
2019	Ito et al.	Vertical distribution of epifauna on *Sargassum horneri*, with special reference to the occurrence of bivalve spat	Plankton & Benthos Research
2019	Jacobucci et al.	Influence of a narrow depth gradient on the spatial structure of *Sargassum* peracarid assemblages in Southeastern Brazil	Marine Biodiversity
2019	Janas et al.	Importance of benthic macrofauna and coastal biotopes for ecosystem functioning – oxygen and nutrient fluxes in the coastal zone	Estuarine, Coastal and Shelf Science
2019	Lomeli et al.	Evaluating off-bottom sweeps of a U.S. West Coast groundfish bottom trawl: effects on catch efficiency and seafloor interactions	Fisheries Research
2019	Lozano-Cortés et al.	Marine invertebrates colonizing a causeway in the Manifa offshore oilfield, Saudi Arabia	Marine Biodiversity

2019	Luff et al.	A simple mooring modification reduces impacts on seagrass meadows	Scientific Reports
2019	Lutz et al.	Differences in architecture between native and non-indigenous macroalgae influence associations with epifauna	Journal of Experimental Marine Biology and Ecology
2019	Meysick et al.	Context-dependent community facilitation in seagrass meadows along a hydrodynamic stress gradient	Journal of Sea Research
2019	Michaelis et al.	Epibenthic assemblages of hard-substrate habitats in the German Bight (south-eastern North Sea) described using drift videos	Continental Shelf Research
2019	Michaelis et al.	Hard-substrate habitats in the German Bight (South-Eastern North Sea) observed using drift videos	Journal of Sea Research
2019	Navarro-Barranco et al.	Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the Strait of Gibraltar	Biological Invasions
2019	Olivier et al.	Exploring the temporal variability of a food web using long-term biomonitoring data	Ecography
2019	Outinen et al.	Monitoring of sessile and mobile epifauna - considerations for non-indigenous species	Marine Pollution Bulletin
2019	Piechaud et al.	Automated identification of benthic epifauna with computer vision	Marine Ecology Progress Series
2019	Powell et al.	The intermingling of benthic macroinvertebrate communities during a period of shifting range: the "East of Nantucket" Atlantic Surfclam Survey and the existence of transient multiple stable states	Marine Ecology
2019	Price et al.	Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage	Coral Reefs
2019	Salmo et al.	Recolonization of mollusc assemblages in mangrove plantations damaged by Typhoon Chan-hom in the Philippines	Estuarine, Coastal and Shelf Science
2019	Seitz et al.	Production and vertical distribution of invertebrates on riprap shorelines in Chesapeake Bay: a novel rocky intertidal habitat	Estuarine, Coastal and Shelf Science

2019	Slavik et al.	The large-scale impact of offshore wind farm structures on pelagic primary productivity in the southern North Sea	Hydrobiologia
2019	Smith et al.	Detrital traits affect substitutability of a range-expanding foundation species across latitude	Oikos
2019	Sutherland et al.	Detecting indicator taxa associated with benthic organic enrichment using different video camera orientations	Journal of Coastal Research
2019	Talbot et al.	Uncovering the environmental drivers of short-term temporal dynamics in an epibenthic community from the Western English Channel	Journal of the Marine Biological Association of the United Kingdom
2019	Trannum et al.	Epifaunal and infaunal responses to submarine mine tailings in a Norwegian fjord	Marine Pollution Bulletin
2019	Tuya et al.	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations	Journal of Ecology
2019	Wee et al.	The role of in situ coral nurseries in supporting mobile invertebrate epifauna	Journal for Nature Conservation
2019	Yeager et al.	Trait sensitivities to seagrass fragmentation across spatial scales shape benthic community structure	Journal of Animal Ecology
2019	Zhang & Silliman	A facilitation cascade enhances local biodiversity in seagrass beds	Diversity
2020	Babcock et al.	Changing biogeochemistry and invertebrate community composition at newly deployed artificial reefs in the northeast Gulf of Mexico	Estuaries and Coasts
2020	Barbosa & Taylor	Spatial and temporal trends in diet for pinfish (*Lagodon rhomboides*) from turtle grass (*Thalassia testudinum*) beds with contrasting environmental regimes in the Lower Laguna Madre, Texas	Estuaries and Coasts
2020	Belattmania et al.	Spatiotemporal variation of the epifaunal assemblages associated to *Sargassum muticumon* the NW Atlantic coast of Morocco	Environmental Science and Pollution Research
2020	Callaway et al.	Natural dynamics overshadow anthropogenic impact on marine fauna at an urbanised coastal embayment	Science of The Total Environment

2020	Chen et al.	*Sargassum* epifaunal communities vary with canopy size, predator biomass and seascape setting within a fringing coral reef ecosystem	Marine Ecology Progress Series
2020	Couce et al.	Capturing threshold responses of marine benthos along gradients of natural and anthropogenic change	Journal of Applied Ecology
2020	Cramer et al.	Millennial-scale change in the structure of a Caribbean reef ecosystem and the role of human and natural disturbance	Ecography
2020	Fraser et al.	Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs	Marine Ecology Progress Series
2020	Gagnon et al.	Facilitating foundation species: the potential for plant-bivalve interactions to improve habitat restoration success	Journal of Applied Ecology
2020	Ge et al.	Succession of macrofaunal communities and environmental properties along a gradient of smooth cordgrass *Spartina alterniflora* invasion stages	Marine Environmental Research
2020	González-García et al.	Composition, structure and distribution of epibenthic communities within a mud volcano field of the northern Gulf of Cádiz in relation to environmental variables and trawling activity	Journal of Sea Research
2020	Gracia et al.	Meio-epifaunal wood colonization in the vicinity of methane seeps	Marine Ecology
2020	Kodama et al.	Effect of algal phenology on seasonal dynamics of gammarid assemblages: differences between canopy and understory strata in a *Sargassum yezoense* bed	Marine Ecology Progress Series
2020	Lanham et al.	Facilitation cascades create a predation refuge for biodiversity in a novel connected habitat	Ecosphere
2020	Ledbetter & Hovel	Effects of a habitat-modifying eelgrass epibiont on predator success and epifaunal survival	Journal of Experimental Marine Biology and Ecology
2020	López-Garrido et al.	ROV's video recordings as a tool to estimate variation in megabenthic epifauna diversity and community composition in the Guaymas Basin	Frontiers in Marine Science

2020	Ma et al.	Zonation of mangrove flora and fauna in a subtropical estuarine wetland based on surface elevation	Ecology and Evolution
2020	Namba et al.	The effect of environmental gradient on biodiversity and similarity of invertebrate communities in eelgrass (*Zostera marina*) beds	Ecological Research
2020	Noble-James et al.	Monitoring shallow methane-derived authigenic carbonate: insights from a UK Marine Protected Area	Aquatic Conservation: Marine and Freshwater Ecosystems
2020	Pisapia et al.	Epifaunal invertebrate assemblages associated with branching Pocilloporids in Moorea, French Polynesia	PeerJ
2020	Proudfoot et al.	Seafloor mapping to support conservation planning in an ecologically unique fjord in Newfoundland and Labrador, Canada	Journal of Coastal Conservation
2020	Rouse et al.	Artificial reef design affects benthic secondary productivity and provision of functional habitat	Ecology and Evolution
2020	Rowden et al.	Determining coral density thresholds for identifying structurally complex vulnerable marine ecosystems in the deep sea	Frontiers in Marine Science
2020	Sedano et al.	Do artificial structures cause shifts in epifaunal communities and trophic guilds across different spatial scales?	Marine Environmental Research
2020	Sedano et al.	From sessile to vagile: understanding the importance of epifauna to assess the environmental impacts of coastal defence structures	Estuarine, Coastal and Shelf Science
2020	Shelamoff et al.	Kelp patch size and density influence secondary productivity and diversity of epifauna	Oikos
2020	Simpson et al.	Seahorse hotels: use of artificial habitats to support populations of the endangered White's seahorse *Hippocampus whitei*	Marine Environmental Research
2020	Stelling-Wood et al.	Habitat variability in an underwater forest: using a trait-based approach to predict associated communities	Functional Ecology
2020	Stevens et al.	Diet of six deep-sea grenadiers (Macrouridae)	Journal of Fish Biology

2020	Wei et al.	Seafloor biodiversity of Canada's three oceans: patterns, hotspots and potential drivers	Diversity and Distributions

*book or book chapter or book series

Appendix 2.2

Year	Authors	Latitude zone	Hemisphere	Size	Habitat type
1953	Allen	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1964	Pequegnat	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1967	Calder & Brehmer	Temperate	North	No size definition of epifauna given	Artificial structures
1967	Driscoll	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1967	Richards & Riley	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1968	Fager	Subtropical	North	Size range of animals defined	Benthic & unidentified habitats
1968	Matthews	Temperate	North	No size definition of epifauna given	Artificial structures
1968	Pequegnat	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1968	Snell	Temperate	North	No size definition of epifauna given	Macroalgae
1971	Bourget & Lacroix	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1972	Sassaman & Mangum	Temperate	North	No size definition of epifauna given	Artificial structures, benthic & unidentified habitats
1973	Bourget & Lacroix	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1973	Jackson et al.	Subtropical	North	Only maximum size specified	Other biogenic habitats

1977	Koechlin	Temperate	North	No size definition of epifauna given	Artificial structures
1978	Anger	Temperate	North	No size definition of epifauna given	Artificial structures
1978	Davis & Vanblaricom	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1978	Karlson	Temperate	North	No size definition of epifauna given	Artificial structures
1979	Conover	Subtropical	North	No size definition of epifauna given	Other biogenic habitats
1979	Peterson	Temperate	North	No size definition of epifauna given	Artificial structures, benthic & unidentified habitats
1980	Beckley & McLachlan	Subtropical	South	No size definition of epifauna given	Macroalgae
1980	Fradette & Bourget	Temperate	North	No size definition of epifauna given	artificial structures
1980	Jokiel	Tropical	North	No size definition of epifauna given	Corals
1980	Russ	Temperate	South	No size definition of epifauna given	Artificial structures
1980	Seed & Harris	Temperate	North	No size definition of epifauna given	Macroalgae
1980	Stoner	Subtropical	North	No size definition of epifauna given	Seagrasses
1980	Vandolah & Bird	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1980	Wood & Seed	Temperate	North	No size definition of epifauna given	Macroalgae
1981	Kay & Keough	Temperate	South	No size definition of epifauna given	Artificial structures
1981	Seed & O'connor	Temperate	North	No size definition of epifauna given	Macroalgae

1981	Seed et al.	Temperate	North	No size definition of epifauna given	Macroalgae
1981	Shin	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1982	Bak et al.	Tropical	North	No size definition of epifauna given	Corals
1982	Beckley	Subtropical	South	No size definition of epifauna given	Macroalgae
1982	Lewis & Hollingworth	Tropical	North	No size definition of epifauna given	Seagrasses
1982	Russ	Temperate	South	No size definition of epifauna given	Artificial structures
1983	Fletcher & Day	Temperate	South	No size definition of epifauna given	Macroalgae
1983	Karlson & Shenk	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1983	McDonald	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1983	Shepherd	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
1983	Sheridan & Livingston	Subtropical	North	No size definition of epifauna given	Seagrasses
1983	Ward & Young	Subtropical	South	No size definition of epifauna given	Other biogenic habitats
1984	Keough	Temperate	South	No size definition of epifauna given	Other biogenic habitats
1984	Lópezjamar et al.	Temperate	North	No size definition of epifauna given	Artificial structures
1984	Patterson	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1984	Schmidt & Warner	Temperate	North	No size definition of epifauna given	Macroalgae, benthic & unidentified habitats

1984	Virnstein et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Seagrasses
1985	Dewitt & Levinton	Temperate	North	Size range of animals defined	Mangroves
1985	Hootsmans & Vermaat	Temperate	North	Only minimum size specified	Seagrasses
1985	Howard	Subtropical	North	No size definition of epifauna given	Seagrasses
1985	Woodhead & Jacobson	Temperate	North	No size definition of epifauna given	Artificial structures
1986	Fishelson & Haran	Subtropical	North	No size definition of epifauna given	Macroalgae
1986	Oswald & Seed	Temperate	North	No size definition of epifauna given	Macroalgae
1986	Persson & Olafsson	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1986	Todd & Turner	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1987	Cancino et al.	Temperate	South	No size definition of epifauna given	Macroalgae
1987	Demurguia & Seed	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1987	Howard	Subtropical	North	Only minimum size specified	Seagrasses
1987	Johnson & Scheibling	Temperate	North	Only minimum size specified	Macroalgae
1987	Lewis	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
1987	Rosman et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1987	Virnstein & Howard	Subtropical	North	Only minimum size specified	Seagrasses
1987	Virnstein & Howard	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
1988	Feder & Pearson	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1988	Hall & Bell	Subtropical	North	No size definition of epifauna given	Mcroalgae, seagrasses

1988	Okamura	Temperate	North	No size definition of epifauna given	Macroalgae
1988	Todd & Turner	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1989	Basford et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1989	Costello & Myers	Temperate	North	Only minimum size specified	Other biogenic habitats
1989	Harrison	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1989	Mullineaux	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Baden	Temperate	North	Size range of animals defined	Seagrasses
1990	Basford et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1990	Daniel & Robertson	Tropical	South	No size definition of epifauna given	Mangroves
1990	Davoult	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Edgar	Subtropical	North, south	Size range of animals defined	Seagrasses
1990	Edgar	Suptropical	South	Size range of animals defined	Seagrasses
1990	Edgar	Subtropical	South	Size range of animals defined	Artificial structures, seagrasses, benthic & unidentified habitats
1990	Hendrickx	Suptropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Hutchings	Tropical	South	No size definition of epifauna given	Corals, benthic & unidentified habitats
1990	Kunitzer	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1990	Lambshead & Gooday	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Anderson et al.	Subtropical	South	Only minimum size specified	Macroalgae

1991	Ansari et al.	Tropical	North	Only minimum size specified	Seagrasses
1991	Edgar	Subtropical	North	Only minimum size specified	Arificial structures, macroalgae
1991	Edgar	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1991	Hopkinson et al.	Suptropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Karande	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Lana & Guiss	Suptropical	South	Only minimum size specified	Mangroves
1991	Marshall et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1991	Rainer & Unsworth	Suptropical	South	No size definition of epifauna given	Seagrasses
1991	Russo	Tropical	North	Only minimum size specified	Corals, macroalgae
1991	Schneider & Mann	Temperate	North	Only minimum size specified	Seagrasses
1991	Schneider & Mann	Temperate	North	Only minimum size specified	Seagrasses
1991	Schneider & Mann	Temperate	North	Only minimum size specified	Seagrasses
1991	Stephens & Bertness	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1991	Takeuchi & Hirano	Temperate	North	Only minimum size specified	Macroalgae
1991	Turner & Todd	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1991	Ward & Thorpe	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1991	Webb & Parsons	Temperate	North	Only maximum size specified	Seagrasses
1991	Zvyagintsev	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1992	Ardisson & Bourget	Temperate	North	No size definition of epifauna given	Artificial structures, mangroves
1992	Aronson	Subtropical , temperate	North	No size definition of epifauna given	Other biogenic habitats

1992	Bingham	Subtropical	North	No size definition of epifauna given	Mangroves
1992	Dalby & Young	Suptropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Dewarumez et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Edgar	Subtropical	South	Size range of animals defined	Seagrasses, benthic & unidentified habitats
1992	Edgar & Robertson	Subtropical	South	Only minimum size specified	Seagrasses
1992	Eleftheriou & Robertson	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Hily & Floch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Isaksson & Pihl	Temperate	North	No size definition of epifauna given	Seagrasses
1992	Klumpp et al.	Tropical	North	Only minimum size specified	Seagrasses
1992	Lana & Guiss	Subtropical	South	Only minimum size specified	Seagrasses
1992	Namikawa et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1992	Pearson & Rosenberg	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1992	Takeuchi & Hirano	Temperate	North	No size definition of epifauna given	Macroalgae
1992	Takeuchi & Hirano	Temperate	North	Only maximum size specified	Macroalgae
1993	Duineveld et al.	Tropical	North	Only maximum size specified	Benthic & unidentified habitats
1993	Edgar	Tropical, subtropical, temperate	North, south	Size range of animals defined	Macroalgae, seagrasses
1993	Edgar & Aoki	Subtropical	North	Size range of animals defined	Macroalgae
1993	Fowler & Laffoley	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

1993	Gonzalez et al.	Subtropical	North	No size definition of epifauna given	Other biogenic habitats
1993	Martin-Smith	Tropical	South	Only minimum size specified	Macroalgae
1993	Mellors & Marsh	Tropical	South	Only minimum size specified	Seagrasses
1993	Trowbridge	Temperate	North	No size definition of epifauna given	Macroalgae
1993	Turner & Todd	Temperate	North	No size definition of epifauna given	Artificial structures
1993	Wang & Widdows	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1994	Cattrijsse et al.	Temperate	North	No size definition of epifauna given	Mangroves
1994	Connolly	Subtropical	South	Size range of animals defined	Seagrasses
1994	Cruzabrego et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Edgar	Tropical, subtropical, temperate	North, south	Size range of animals defined	Macroalgae, seagrasses, benthic & unidentified habitats
1994	Edgar et al.	Temperate	South	No size definition of epifauna given	Seagrasses
1994	Everett	Temperate	North	No size definition of epifauna given	Macroalgae
1994	Gee & Warwick	Temperate	North	Size range of animals defined	Macroalgae
1994	Gee & Warwick	Temperate	North	Only minimum size specified	Macroalgae
1994	Hardin et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Hostens & Hamerlynck	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Jean & Hilly	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
1994	Kaiser et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats

1994	Levin et al.	Suptropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1994	Mangum	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1994	Martin-Smith	Tropical	South	Only minimum size specified	Macroalgae
1994	Matsumasa	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1994	Monteforte & Garcia-Gasca	Suptropical	North	Only minimum size specified	Other biogenic habitats
1994	Rathburn & Corliss	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
1994	Taylor & Cole	Temperate	South	Only minimum size specified	Macroalgae
1994	Todd & Keough	Temperate	South	Only minimum size specified	Artificial structures
1995	Bingham & Young	Subtropical	North	No size definition of epifauna given	Mangroves
1995	Connolly	Subtropical	South	Size range of animals defined	Seagrasses
1995	Edgar & Shaw	Temperate	South	Only minimum size specified	Seagrasses
1995	Klitgaard	Temperate	North	Size range of animals defined	Other biogenic habitats
1995	McDermott & Fives	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1995	Migné & Davoult	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1995	Nalesso et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
1995	Nelson	Subtropical	North	Only minimum size specified	Seagrasses
1995	Osman & Whitlatch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1995	Takeuchi & Hirano	Temperate	North	No size definition of epifauna given	Macroalgae
1995	Taylor et al.	Temperate	South	Only minimum size specified	Turf algae & microalgae, benthic & unidentified habitats

1995	Ulrich et al.	Temperate	North	No size definition of epifauna given	Macroalgae, benthic & unidentified habitats
1995	Vilela	Tropical	North, south	Size range of animals defined	Benthic & unidentified habitats
1995	Virnstein	Subtropical	North	No size definition of epifauna given	Seagrasses
1996	Aller & Stupakoff	Tropical	South	Size range of animals defined	Benthic & unidentified habitats
1996	Barry et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Barthel et al.	Suptropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Benedetti-Cecchi et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Boaden	Temperate	North	Only minimum size specified	Macroalgae
1996	Castricfey	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Chauvaud et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Connolly & Butler	Temperate	North	Size range of animals defined	Seagrasses
1996	Davenport et al.	Temperate	South	Only minimum size specified	Macroalgae
1996	Drake & Arias	Temperate	North	Size range of animals defined	Macroalgae
1996	Ellis et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Gee & Warwick	Tropical, subtropical, temperate	North, south	Only minimum size specified	Benthic & unidentified habitats
1996	Gooday	Tropical, subtropical, temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1996	Jacobi & Langevin	Tropical	South	No size definition of epifauna given	Artificial structures
1996	Kuhne & Rachor	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1996	Lemmens et al.	Suptropical	South	Only minimum size specified	Seagrasses

1996	Levin et al.	Subtropical	North	No size definition of epifauna given	Mangroves
1996	Li et al.	Subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1996	Posey et al.	Subtropical	North	No size definition of epifauna given	Artificial structures
1996	Rathburn et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
1996	Schlacher & Wooldridge	Suptropical	South	Only minimum size specified	Benthic & unidentified habitats
1996	Schrijvers et al.	Tropical	South	Only minimum size specified	Mangroves
1996	Thomas	Suptropical	North	Only minimum size specified	Benthic & unidentified habitats
1996	Williamson & Creese	Temperate	South	Size range of animals defined	Turf algae & microalgae
1997	Aller	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1997	Boström & Bonsdorff	Temperate	North	Only minimum size specified	Seagrasses
1997	Buhs & Reise	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1997	Collie et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1997	Connolly	Subtropical	South	Size range of animals defined	Seagrasses, benthic & unidentified habitats
1997	LeClair & LaBarbera	Tropical	North	No size definition of epifauna given	Corals
1997	Livingston	Suptropical	North	Only minimum size specified	Benthic & unidentified habitats
1997	Livingston et al.	Suptropical	North	Only minimum size specified	Benthic & unidentified habitats
1997	Manley & Shaw	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1997	McClanahan & Sala	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1997	McCorkle et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1997	McKnight & Probert	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
1997	Russo	Temperate	North	Only minimum size specified	Macroalgae

1997	Sala	Temperate	North	No size definition of epifauna given	Macroalgae
1997	Takeuchi & Hino	Temperate	North	Only minimum size specified	Seagrasses
1997	Turner et al.	Temperate	South	No size definition of epifauna given	Artificial structures
1997	Warner	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1997	Wright et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1998	Bacon et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
1998	Chapman	Suptropical	South	Only minimum size specified	Mangroves
1998	Engel & Kvitek	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1998	Flynn et al.	Suptropical	South	Only minimum size specified	Mangroves
1998	Glasby	Suptropical	South	No size definition of epifauna given	Benthic & unidentified habitats
1998	Hata & Nakata	Temperate	North	No size definition of epifauna given	Seagrasses
1998	Hatcher	Temperate	North	Only minimum size specified	Artificial structures
1998	Jernakoff & Nielsen	Subtropical	South	Size range of animals defined	Seagrasses
1998	Knowles & Bell	Subtropical	North	Only minimum size specified	Seagrasses
1998	MacDonald et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
1998	Magorrian & Service	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1998	Mazouni et al.	Temperate	North	No size definition of epifauna given	Artificial structures
1998	Osman & Whitlatch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1998	Sardá et al.	Temperate	North	No size definition of epifauna given	Mangroves

1998	Sasekumar & Chong	Tropical	North	No size definition of epifauna given	Mangroves
1998	Schrijvers et al.	Tropical	South	Size range of animals defined	Mangroves
1998	Tanaka & Leite	Tropical	South	Size range of animals defined	Macroalgae
1998	Taylor	Temperate	South	Size range of animals defined	Macroalgae
1998	Taylor	Temperate	South	Only minimum size specified	Macroalgae, turf algae & microalgae, other biogenic habitats
1998	Taylor	Temperate	South	Only minimum size specified	Macroalgae
1998	Taylor & Rees	Temperate	South	Size range of animals defined	Macroalgae
1998	Thrush et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1998	Walsh & Mitchell	Temperate	South	No size definition of epifauna given	Seagrasses
1998	Whitlatch & Osman	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1998	Widdows et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
1998	Wieczorek & Todd	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
1998	Wildish & Fader	Temperate	North	No size definition of epifauna given	Other biogenic habitats
1998	Witman & Grange	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1998	Wolff et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Bologna & Heck	Subtropical	North	Only minimum size specified	Artificial structures, seagrasses
1999	Brown & Taylor	Temperate	South	Only minimum size specified	Turf algae & microalgae
1999	Connell	Temperate	South	No size definition of epifauna given	Artificial structures

1999	Connell & Anderson	Suptropical	South	No size definition of epifauna given	Macroalgae
1999	Cranfield et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
1999	Davenport et al.	Temperate	South	Only minimum size specified	Macroalgae
1999	Edgar	Temperate	South	No size definition of epifauna given	Artificial structures, seagrasses
1999	Edgar	Temperate	South	No size definition of epifauna given	Artificial structures, seagrasses
1999	Freese et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Glasby	Suptropical	South	No size definition of epifauna given	Seagrasses
1999	Glasby	Suptropical	South	Only minimum size specified	Artificial structures, seagrassess, benthic & unidentified habitats
1999	Glasby	Suptropical	South	No size definition of epifauna given	Artificial structures, seagrassess, benthic & unidentified habitats
1999	Hily & Bouteille	Temperate	North	Only minimum size specified	Seagrasses
1999	Jewett et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Kenyon et al.	Tropical	South	Only minimum size specified	Artificial structures, seagrasses
1999	Lavery et al.	Subtropical	South	Only minimum size specified	Macroalgae
1999	Lepoint et al.	Temperate	North	No size definition of epifauna given	Seagrasses
1999	Morri et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Prena et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Ramos	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1999	Rees et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats

1999	Rees et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
1999	Rose et al.	Suptropical	North	Only minimum size specified	Seagrasses
1999	Saiz-Salinas & Urkiaga-Alberdi	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Sánchez-Jerez et al.	Temperate	North	Only minimum size specified	Seagrasses
1999	Sánchez-Jerez et al.	Temperate	North	No size definition of epifauna given	Seagrasses
1999	Smallwood et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
1999	Smith & Witman	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
1999	Tarasov et al.	Tropical	South	No size definition of epifauna given	Artificial structures
1999	Viejo	Temperate	North	Size range of animals defined	Macroalgae
2000	Cocito et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Cohen et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2000	Collie et al.	Tropical, subtropical, temperate	North: temperate south: tropical, subtropical, temperate	No size definition of epifauna given	Benthic & unidentified habitats
2000	Collie et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
2000	Dando et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Edgar & Barrett	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2000	Ellis et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
2000	Gage et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

2000	Glasby	Suptropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2000	Jablonski et al.	Tropical, subtropical, temperate	North: tropical, subtropical, temperate south: tropical	No size definition of epifauna given	Benthic & unidentified habitats
2000	Kaiser et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2000	Roy et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Benthic & unidentified habitats
2000	Rumohr & Kujawski	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Sagasti et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2000	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2000	Smith	Temperate	South	Only minimum size specified	Turf algae & microalgae
2000	Sutherland et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2000	Tuck et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2000	Veale et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Beaulieu	Subtropical	North	Only minimum size specified	Other biogenic habitats
2001	Beaulieu	Suptropical	North	Only minimum size specified	Other biogenic habitats
2001	Bradshaw et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Brooks & Bell	Suptropical	North	No size definition of epifauna given	Macroalgae, seagrasses
2001	Cranfield et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2001	Dean & Jewett	Temperate	North	No size definition of epifauna given	Macroalgae, seagrasses, benthic & unidentified habitats
2001	Duffy et al.	Temperate	North	Only minimum size specified	Seagrasses

2001	Dumbauld et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2001	Glasby	Suptropical	South	Only minimum size specified	artificial structures, benthic & unidentified habitats
2001	Gooday et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2001	Henry	Temperate	North	No size definition of epifauna given	Corals
2001	Jennings et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2001	Jennings et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2001	Kollmann & Stachowitsch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Lee et al.	Tropical	North	Only minimum size specified	Artificial structures, seagrasses
2001	Mancinelli & Rossi	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Maughan	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Nakaoka et al.	Temperate	North	Only minimum size specified	Seagrasses
2001	Oh et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Parker et al.	Temperate	North	Only minimum size specified	Seagrasses
2001	Prieto et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Robinson et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Sagasti et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2001	Sfriso et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses, benthic & unidentified habitats

2001	Smith	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2001	Sudo & Azeta	Suptropical	North	Only minimum size specified	Seagrasses, benthic & unidentified habitats
2001	Thrush et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2001	Vytopil & Willis	Tropical	South	Only minimum size specified	Corals
2001	Wright	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2001	Zühlke et al.	Temperate	North	Only maximum size specified	Benthic & unidentified habitats
2002	Bologna & Heck	Subtropical	North	Only minimum size specified	Seagrasses
2002	Brooks et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Brown et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2002	Burton et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2002	Callaway et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2002	Callaway et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2002	Cartes et al.	Tropical, subtropical, temperate	North, south	Only minimum size specified	Benthic & unidentified habitats
2002	Dolmer	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Dulvy et al.	Tropical	South	Size range of animals defined	Corals
2002	Edgar & Barrett	Temperate	South	Size range of animals defined	Benthic & unidentified habitats
2002	Fraschetti et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2002	Germano & Read	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Holloway & Keough	Subtropical	South	No size definition of epifauna given	Artificial structures

2002	Holloway & Keough	Subtropical , temperate	South	No size definition of epifauna given	Artificial structures
2002	Hovel et al.	Subtropical	North	No size definition of epifauna given	Seagrasses
2002	Jayaprada	Tropical	North	Only minimum size specified	Artificial structures
2002	Koch & Wolff	Tropical	South	No size definition of epifauna given	Mangroves
2002	Labarta et al.	Temperate	South	Size range of animals defined	Macroalgae
2002	Mancinelli et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Matsumoto & Kohda	Suptropical	North	Only minimum size specified	Macroalgae
2002	Nakaoka et al.	Tropical	North	Only minimum size specified	Seagrasses
2002	Saier	Temperate	North	Only minimum size specified	Other biogenic habitats
2002	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae
2002	Smith & Rule	Subtropical	South	Only minimum size specified	Artificial structures, macroalgae, turf algae & microalgae
2002	Stachowicz et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2002	Steimle et al.	Temperate	North	Only minimum size specified	Artificial structures
2002	Thiel	Tropical, subtropical, temperate	South	Only minimum size specified	Macroalgae
2002	Velasco & Navarro	Temperate	South	Size range of animals defined	Macroalgae
2002	Yu et al.	Suptropical	North	Only minimum size specified	Benthic & unidentified habitats
2003	Ribeiro et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
2003	Ashton et al.	Tropical	North	No size definition of epifauna given	Mangroves
2003	Beaver et al.	Suptropical	North	No size definition of epifauna given	Artificial structures
2003	Bolduc & Afton	Suptropical	North	Only minimum size specified	Benthic & unidentified habitats

2003	Bone et al.	Tropical	North	Only minimum size specified	Seagrasses
2003	Bradshaw et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2003	Burrows et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Colloca et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Deidun et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2003	Diaz & Arana	Tropical	North	No size definition of epifauna given	Other biogenic habitats
2003	Edgar & Klumpp	Tropical	South	Size range of animals defined	Artificial structures, macroalgae, seagrasses
2003	Haggitt & Babcock	Temperate	South	Only minimum size specified	Macroalgae
2003	Hirst	Subtropical	South	Only minimum size specified	Macroalgae
2003	Kumagai & Aoki	Subtropical	North	No size definition of epifauna given	Corals
2003	Leite & Turra	Tropical	South	Only minimum size specified	Macroalgae
2003	Nash	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Pardo & Dauer	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
2003	Prieto et al.	Tropical	North	No size definition of epifauna given	Seagrasses
2003	Sagasti et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2003	Schreider et al.	Subtropical	South	Size range of animals defined	Macroalgae
2003	Sepúlveda et al.	Temperate	South	Only maximum size specified	Other biogenic habitats
2003	Tanaka & Leite	Tropical	South	Only minimum size specified	Macroalgae
2003	Tanner	Subtropical	South	Only minimum size specified	Seagrasses

2003	Tanner	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2003	Thorbjorn & Petersen	Temperate	North	Only minimum size specified	Corals, other biogenic habitats, benthic & unidentified habitats
2003	Velasco & Navarro	Temperate	South	Size range of animals defined	Macroalgae
2003	Viejo & Åberg	Temperate	North	No size definition of epifauna given	Macroalgae
2003	Witman & Smith	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2004	Bouillon et al.	Tropical	North, south	No size definition of epifauna given	Mangroves
2004	Diaz et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Escapa et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2004	Gaymer et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Hargrave et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Healey & Hovel	Subtropical	North	No size definition of epifauna given	Artificial structures, seagrasses
2004	Henry & Kenchington	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2004	Hinz et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2004	Kaiser et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2004	Larsen & Gilfillan	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2004	Mathot et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2004	Osman & Whitlatch	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

2004	Tanaka & Leite	Tropical	South	Only minimum size specified	Macroalgae
2004	Welsh & Castadelli	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2004	Wernberg et al.	Temperate	North	Only minimum size specified	Macroalgae
2004	Wikström & Kautsky	Temperate	North	No size definition of epifauna given	Macroalgae
2004	Witman et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Benthic & unidentified habitats
2005	Andersen et al.	Temperate	North	Only minimum size specified	Macroalgae, benthic & unidentified habitats
2005	Bishop	Temperate	North	Only minimum size specified	Seagrasses
2005	Brown	Temperate	North	No size definition of epifauna given	Artificial structures
2005	Castañeda-Fernández-de-Lara et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2005	Clark & Johnston	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2005	Davidson et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Gage et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Govenar et al.	Temperate	North	Size range of animals defined	Other biogenic habitats
2005	Hamazaki et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Hepburn & Hurd	Temperate	South	No size definition of epifauna given	Macroalgae
2005	Jewett et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2005	Klumpp & Kwak	Tropical	South	Only minimum size specified	Seagrasses
2005	Luckenbach et al.	Temperate	North	Only minimum size specified	Other biogenic habitats

2005	McConnaughey et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Nakamura & Sano	Subtropical	North	Only minimum size specified	Corals, seagrasses, benthic & unidentified habitats
2005	Nakaoka	Tropical, subtropical, temperate	North	No size definition of epifauna given	Seagrasses
2005	Pagliosa & Lana	Subtropical	South	Only minimum size specified	Mangroves
2005	Polte et al.	Temperate	North	Size range of animals defined	Seagrasses
2005	Polte et al.	Temperate	North	Size range of animals defined	Seagrasses
2005	Prieto et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Raes & Vanreusel	Temperate	North	Only minimum size specified	Corals
2005	Rule & Smith	Subtropical	South	Size range of animals defined	Artificial structures
2005	Sgro et al.	Temperate	North	Size range of animals defined	Macroalgae
2005	Stone et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Tanner	Subtropical	South	Only minimum size specified	Seagrasses
2005	Thomasson & Tunberg	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2005	Velasco & Navarro	Temperate	South	Size range of animals defined	Macroalgae
2005	Winston & Migotto	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2006	Alfaro	Temperate	South	Only minimum size specified	Mangroves, seagrasses
2006	Beaumont et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Burone & Pires-Vanin	Tropical	South	Only minimum size specified	Benthic & unidentified habitats
2006	Cruz-Rivera & Paul	Tropical	North	Size range of animals defined	Macroalgae, turf algae & microalgae, other biogenic habitats

2006	Eklöf et al.	Tropical	South	Only minimum size specified	Macroalgae, seagrasses
2006	Gil et al.	Subtropical	North	No size definition of epifauna given	Macroalgae, seagrasses
2006	Guerra-García et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2006	Henry et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Hepburn et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2006	Hinchey et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2006	Hooper & Davenport	Temperate	North	Only minimum size specified	Macroalgae
2006	Hosack et al.	Temperate	North	Only minimum size specified	Seagrasses, other biogenic habitats
2006	Kenchington et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Kogan et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Kouchi et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2006	Lindsay et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2006	Mendez	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2006	O'Brien et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2006	Pereira et al.	Temperate	North	Size range of animals defined	Macroalgae
2006	Rae & Vanreusel	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Reed & Hovel	Temperate	North	No size definition of epifauna given	Seagrasses
2006	Reiss et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Roberts & Poore	Subtropical	South	Only minimum size specified	Macroalgae
2006	Roberts et al.	Subtropical	South	No size definition of epifauna given	Macroalgae

2006	Rodney & Paynter	Temperate	North	Only minimum size specified	Other biogenic habitats
2006	Royer et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2006	Schmidt & Scheibling	Temperate	North	Only minimum size specified	Macroalgae
2006	Sibaja-Cordero & Vargas-Zamora	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2006	Sirota & Hovel	Subtropical	North	Only minimum size specified	Seagrasses
2006	Skilleter et al.	Subtropical	South	Only minimum size specified	Seagrasses
2006	Smith et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Sun et al.	Tropical, subtropical, temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Tanner	Subtropical	South	Only minimum size specified	Artificial structures, seagrasses
2006	Valente	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Vizzini & Mazzola	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2006	Ward et al.	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2006	Yahel et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2006	Zintzen et al.	Temperate	North	Only minimum size specified	Artificial structures
2007	Aníbal et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Antoniadou & Chintiroglou	Temperate	North	Only minimum size specified	Macroalgae
2007	Aravind et al.	Tropical	North	No size definition of epifauna given	Mangroves
2007	Bates & DeWreede	Temperate	North	Only minimum size specified	Macroalgae
2007	de Juan et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2007	Duineveld et al.	Temperate	North	Only minimum size specified	Artificial structures
2007	Fujiwara et al.	Subtropical	North	Size range of animals defined	Other biogenic habitats
2007	Ganesh & Raman	Tropical	North	Only minimum size specified	Benthic & unidentified habitats

2007	Govenar & Fisher	Tropical	North	Size range of animals defined	Benthic & unidentified habitats
2007	Harries et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Hirst	Temperate	South	Only minimum size specified	Macroalgae
2007	Huntley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2007	Ince et al.	Subtropical	South	Only minimum size specified	Macroalgae, seagrasses
2007	Irving et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2007	Itoh et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2007	Jing et al.	Subtropical	North	Only minimum size specified	Mangroves
2007	Jorgensen et al.	Temperate	North	Only minimum size specified	Seagrasses
2007	Juan et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2007	Kenchington et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2007	Leite et al.	Tropical	South	Only minimum size specified	Macroalgae
2007	McDermott	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2007	Murray et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2007	O'Neill et al.	Subtropical	South	Only minimum size specified	Macroalgae
2007	Owada et al.	Subtropical, temperate	North	No size definition of epifauna given	Artificial structures, corals, benthic & unidentified habitats
2007	Powers et al.	Temperate	North	Only minimum size specified	Macroalgae
2007	Roberts et al.	Subtropical	South	Only minimum size specified	Macroalgae
2007	Robertson & Weis	Temperate	North	No size definition of epifauna given	Mangroves
2007	Rule & Smith	Subtropical	South	Only minimum size specified	Artificial structures
2007	Sánchez-Moyano et al.	Temperate	North	Only minimum size specified	Macroalgae

2007	Szarek et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2007	Unsworth et al.	Tropical	North	Only minimum size specified	Seagrasses
2007	Voultsiadou et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2007	Walker et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2008	Asch & Collie	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Commito et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2008	Erbland & Ozbay	Temperate	North	Size range of animals defined	Other biogenic habitats
2008	Felley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Fukunaga	Tropical	North	No size definition of epifauna given	Macroalgae
2008	Garcia et al.	Tropical	South	No size definition of epifauna given	Corals
2008	Guillén et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Guyonnet et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Hirst	Subtropical	South	Only minimum size specified	Macroalgae
2008	Jennings et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Kochmann et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2008	Lam et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2008	Metcalfe & Glasby	Tropical	South	No size definition of epifauna given	Mangroves
2008	Micheli et al.	Subtropical	North	Only minimum size specified	Seagrasses
2008	Morton & Bamber	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Moura et al.	Temperate	North	Only minimum size specified	Artificial structures

2008	Muir & Bamber	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2008	Mutlu & Ergev	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Nagelkerken et al.	Na	Na	No size definition of epifauna given	Mangroves
2008	Nakaoka et al.	Temperate	North	Size range of animals defined	Seagrasses
2008	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2008	Paetzold et al.	Temperate	North	Size range of animals defined	Other biogenic habitats
2008	Partyka & Peterson	Subtropical	North	Only minimum size specified	Mangroves
2008	Prescott & Cudney-Bueno	Subtropical	North	Size range of animals defined	Artificial structures, other biogenic habitats
2008	Printrakoon et al.	Tropical	North	Only minimum size specified	Mangroves
2008	Raes et al.	Tropical, temperate	North: temperate south: tropical	Only minimum size specified	Corals
2008	Rees et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2008	Riedel et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Roberts et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2008	Roberts et al.	Subtropical	South	Only minimum size specified	Macroalgae, seagrasses, other biogenic habitats
2008	Roberts et al.	Na	Na	No size definition of epifauna given	Macroalgae
2008	Rueda & Salas	Temperate	North	Only minimum size specified	Seagrasses
2008	Sanderson et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2008	Thistle et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats

2008	Tomašových	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Vázquez-Bader et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Vázquez-Luis et al.	Temperate	North	Only minimum size specified	Macroalgae
2008	Vermeij et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2008	Witman et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Armitage & Fourqurean	Subtropical	North	Only minimum size specified	Seagrasses
2009	Bates	Temperate	North	Only minimum size specified	Macroalgae
2009	Blanchard et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Brusati & Grosholz	Temperate	North	No size definition of epifauna given	Mangroves
2009	Bruschetti et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2009	Cannicci et al.	Tropical, subtropical	South	No size definition of epifauna given	Mangroves
2009	Carbines & Cole	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2009	Cartes et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Collie et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Dafforn et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2009	de Juan et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Gheerardyn et al.	Temperate	North	Only minimum size specified	Corals
2009	Grizzle et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

2009	Gustafsson et al.	Temperate	North	Only minimum size specified	Mangroves
2009	Gutow et al.	Temperate	North	Only minimum size specified	Macroalgae
2009	Hinz et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Jacobucci et al.	Tropical	South	Only minimum size specified	Macroalgae
2009	Jeffreys et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Johnson et al.	Temperate	North	Only minimum size specified	Mangroves
2009	Margreth et al.	Temperate	North	Size range of animals defined	Corals
2009	Marzinelli et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2009	McKinnon et al.	Temperate	South	Only minimum size specified	Macroalgae
2009	Montagna et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2009	Morsan	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2009	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2009	Poore et al.	Subtropical	South	Only minimum size specified	Macroalgae
2009	Rabaoui et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2009	Rueda et al.	Temperate	North	Only minimum size specified	Seagrasses
2009	Rueda et al.	Temperate	North	Only minimum size specified	Seagrasses
2009	Spivak et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2009	Summerhayes et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2009	Yu et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Ayres-Peres & Mantelatto	Tropical	South	No size definition of epifauna given	Other biogenic habitats

2010	Barnes et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2010	Borg et al.	Temperate	North	Only minimum size specified	Seagrasses
2010	Cacabelos et al.	Temperate	North	Only minimum size specified	Macroalgae
2010	Gartner et al.	Subtropical	South	Size range of animals defined	Seagrasses
2010	Gedan & Bertness	Temperate	North	Only minimum size specified	Mangroves
2010	Gestoso et al.	Temperate	North	Only minimum size specified	Macroalgae
2010	Khan et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2010	Kon et al.	Tropical	North	Size range of animals defined	Mangroves
2010	Marenghi et al.	Temperate	North	Only minimum size specified	Artificial structures
2010	Martinetto et al.	Temperate	South	Only minimum size specified	Macroalgae, mangroves, benthic & unidentified habitats
2010	Moore & Hovel	Subtropical	North	Only minimum size specified	Seagrasses
2010	Newcombe & Taylor	Temperate	South	Only maximum size specified	Macroalgae
2010	Nikula et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2010	Norkko et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Osman et al.	Temperate	North	No size definition of epifauna given	Macroalgae, seagrasses, benthic & unidentified habitats
2010	Poirier et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Reiss et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2010	Sellheim et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2010	Smyth & Roberts	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2010	Stella et al.	Tropical	South	Only minimum size specified	Corals

2010	Tang et al.	Temperate	North	Only minimum size specified	Mangroves, benthic & unidentified habitats
2010	Tanner & Fernandes	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2010	Valanko et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2010	Vanreusel et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Benthic & unidentified habitats
2010	Voultsiadou et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2010	Zintzen & Massin	Temperate	North	Only minimum size specified	Artificial structures
2011	Anderson et al.	Tropical, subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Atkinson et al.	Subtropical	South	Only maximum size specified	Benthic & unidentified habitats
2011	Burone et al.	Tropical, subtropical	South	Only minimum size specified	Benthic & unidentified habitats
2011	Carr et al.	Temperate	North	Only minimum size specified	Seagrasses
2011	Currin et al.	Subtropical	North	No size definition of epifauna given	Mangroves
2011	de Juan et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2011	Douglass et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2011	Drouin et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2011	Ellis et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Fleddum et al.	Tropical	North	Only minimum size specified	Artificial structures
2011	Fraser et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Freeman & Creese	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Freestone & Osman	Tropical, subtropical, temperate	North	No size definition of epifauna given	Mangroves, benthic & unidentified habitats

2011	Harris	Tropical, subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Harwell et al.	Subtropical	North	Only minimum size specified	Other biogenic habitats
2011	Hellyer et al.	Subtropical	South	Only minimum size specified	Artificial structures
2011	Hinz et al. 2011	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Johnson	Temperate	North	No size definition of epifauna given	Mangroves
2011	Kon et al.	Tropical	North	Only minimum size specified	Mangroves
2011	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Liuzzi & Gappa	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Lomovasky et al.	Tropical	South	Only minimum size specified	Benthic & unidentified habitats
2011	Luo et al.	Subtropical	North	Only maximum size specified	Benthic & unidentified habitats
2011	Metaxas	Tropical, subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2011	Moura et al.	Temperate	North	Only minimum size specified	Artificial structures
2011	Navarro et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Neumann & Kröncke	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2011	Nikula et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2011	Paavo et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2011	Pacciardi et al.	Temperate	North	Only minimum size specified	Macroalgae
2011	Stevens & Dunn	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2011	Tanner	Subtropical	South	Only minimum size specified	Macroalgae

2011	Tsubaki et al.	Na	Na	No size definition of epifauna given	Corals, benthic & unidentified habitats
2011	Tuya et al.	Temperate	North	Only minimum size specified	Macroalgae
2011	Wong et al.	Subtropical	North	Only minimum size specified	Mangroves, seagrasses, other biogenic habitats, benthic & unidentified habitats
2012	Anderson & Lovvorn	Temperate	North	Only minimum size specified	Seagrasses
2012	Arponen & Boström	Temperate	North	No size definition of epifauna given	Seagrasses
2012	Bishop et al.	Subtropical	South	Only minimum size specified	Mangroves
2012	Byers et al.	Subtropical	North	Only minimum size specified	Macroalgae
2012	Cutajar et al.	Temperate	South	Only minimum size specified	Mangroves
2012	de Juan & Demestre	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Elahi & Sebens	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Gestoso et al.	Temperate	North	Only minimum size specified	Macroalgae
2012	Gullström et al.	Temperate	North	Size range of animals defined	Seagrasses
2012	Gustafsson & Salo	Subtropical	North	Only minimum size specified	Seagrasses
2012	Hamilton et al.	Temperate	South	Only minimum size specified	Seagrasses
2012	Haupt et al.	Subtropical	South	No size definition of epifauna given	Other biogenic habitats
2012	Hepburn et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2012	Janiak & Whitlatch	Temperate	North	No size definition of epifauna given	Macroalgae
2012	Källén et al.	Subtropical	South	No size definition of epifauna given	Seagrasses

2012	Karlson & Osman	Subtropical, temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Lewis & Anderson	Subtropical	North	Only minimum size specified	Seagrasses
2012	Macias	Tropical, subtropical	North	No size definition of epifauna given	Seagrasses
2012	Martinez et al.	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2012	Marzinelli et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2012	Mosch et al.	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2012	Nerot et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Pagliosa et al.	Subtropical	South	Only minimum size specified	Macroalgae
2012	Przeslawski et al.	Subtropical	South	No size definition of epifauna given	Other biogenic habitats
2012	Ragnarsson & Burgos	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Riedel et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Spicer & Widdicombe	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Strain et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2012	Tait & Hovel	Subtropical	North	No size definition of epifauna given	Seagrasses
2012	Tyrrell et al.	Temperate	North	Only minimum size specified	Macroalgae
2012	Wilkie et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats

2012	Yorke & Metaxas	Temperate	North	No size definition of epifauna given	Macroalgae
2013	Barnes et al.	Subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2013	Bell et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2013	Bilkovic et al.	Temperate	North	Only minimum size specified	Mangroves
2013	Bishop et al.	Subtropical	South	No size definition of epifauna given	Macroalgae, mangroves
2013	Bowden et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2013	Brandt et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Broszeit et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Cartes et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Coleman et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Cook et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2013	Dauvin et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	de Juan et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Delgado et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Dhib et al.	Temperate	North	Only minimum size specified	Mangroves
2013	Do et al.	Temperate	North	Only minimum size specified	Seagrasses
2013	Ellis et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Engelen et al.	Temperate	North	Only minimum size specified	Macroalgae
2013	Fleddum et al.	Subtropical	South	Only minimum size specified	Benthic & unidentified habitats

2013	Foveau et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Gartner et al.	Subtropical	North, south	No size definition of epifauna given	Seagrasses
2013	Gribben et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2013	Hammerschlag-Peyer et al.	Subtropical	North	Only minimum size specified	Seagrasses
2013	Krone et al.	Temperate	North	Only minimum size specified	Artificial structures
2013	Laboy-Nieves & Muniz-Barretto	Tropical	North	No size definition of epifauna given	Other biogenic habitats
2013	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	MacDonald & Weis	Tropical	North	No size definition of epifauna given	Mangroves
2013	Mangano et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Ortiz et al.	Tropical, subtropical	South	No size definition of epifauna given	Macroalgae, other biogenic habitats
2013	Pascal et al.	Temperate	North	No size definition of epifauna given	Mangroves
2013	Popadić et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2013	Prato et al.	Temperate	North	Only minimum size specified	Macroalgae
2013	Reinhardt et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Riera et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2013	Roff et al.	Tropical	North	Only minimum size specified	Macroalgae
2013	Ross et al.	Temperate	South	Only minimum size specified	Other biogenic habitats
2013	Sciberras et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

2013	Sell & Kröncke	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2013	Smith et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Staszak & Armitage	Subtropical	North	No size definition of epifauna given	Mangroves
2013	Tuya et al.	Subtropical	North	Only minimum size specified	Seagrasses
2013	Urra et al.	Temperate	North	Size range of animals defined	Macroalgae, seagrasses, benthic & unidentified habitats
2013	Vitaliano et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2013	Wolf et al.	Tropical	North	No size definition of epifauna given	Corals, macroalgae
2014	Altieri & Witman	Tropical	South	No size definition of epifauna given	Other biogenic habitats
2014	Bedini et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2014	Bhagirathan et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Blain & Gagnon	Temperate	North	No size definition of epifauna given	Macroalgae
2014	Blake et al.	Temperate	North	Size range of animals defined	Seagrasses
2014	Boulcott et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Brahim et al.	Subtropical	North	No size definition of epifauna given	Seagrasses
2014	Buzá-Jacobucci & Pereira-Leite	Tropical	South	Only minimum size specified	Macroalgae
2014	Carvalho et al.	Temperate	North	Only minimum size specified	Corals
2014	Cebrian et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2014	Corrêa et al.	Tropical	South	Only minimum size specified	Other biogenic habitats

2014	Esqueda-González et al.	Tropical	North	Size range of animals defined	Artificial structures, other biogenic habitats
2014	Fariñas-Franco & Roberts	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Fernandez et al.	Subtropical	South	No size definition of epifauna given	Macroalgae
2014	Fukunaga et al.	Tropical	North	Only maximum size specified	Mangroves
2014	Gatune et al.	Tropical	South	Only minimum size specified	Macroalgae
2014	Hosono	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Huang et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Benthic & unidentified habitats
2014	Hughes	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Jones et al.	Tropical	South	No size definition of epifauna given	Artificial structures
2014	Konsulova & Doncheva	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2014	Kornijow	Na	Na	Only minimum size specified	Benthic & unidentified habitats
2014	Lambert et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Lange & Griffiths	Suptropical, temperate	South	No size definition of epifauna given	Seagrasses
2014	Lefcheck et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2014	Leopardas et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2014	Muntadas et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Navarro-Barranco et al.	Suptropical, temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Nordström et al.	Subtropical	North	No size definition of epifauna given	Mangroves

2014	Palardy & Witman	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Pierri-Daunt & Tanaka	Tropical	South	Only minimum size specified	Macroalgae
2014	Png-Gonzalez et al.	Tropical	North	Only minimum size specified	Macroalgae, seagrasses
2014	Reynolds et al.	Temperate	North	Only minimum size specified	Seagrasses
2014	Ronowicz et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Smeulders et al.	Temperate	North	Only minimum size specified	Corals, benthic & unidentified habitats
2014	Smith et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2014	Trave & Sheaves	Subtropical	North	No size definition of epifauna given	Seagrasses
2014	Tuya et al.	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2014	Vassallo et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2014	Veiga et al.	Temperate	North	Only minimum size specified	Macroalgae
2014	Vidović et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2015	Barry et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Bergman et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Carcedo et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2015	Chen et al.	Subtropical	North	Only minimum size specified	Mangroves
2015	Coolen et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	Cúrdia et al.	Temperate	North	Only minimum size specified	Corals
2015	de Jong et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	de Jong et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	De Mesel et al.	Temperate	North	Only minimum size specified	Artificial structures

2015	DeAmicis & Foggo	Temperate	North	No size definition of epifauna given	Macroalgae, seagrasses
2015	Dias et al.	Temperate	North	Only minimum size specified	Corals
2015	Eklöf et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses, benthic & unidentified habitats
2015	Fernandez et al.	Tropical	South	No size definition of epifauna given	Artificial structures
2015	Green & Fong	Subtropical	North	Only minimum size specified	Macroalgae
2015	Greene	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Gutow et al.	Temperate	North	Only minimum size specified	Macroalgae
2015	Hemery et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Howarth et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Huang et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2015	Knight et al.	Temperate	North	Only minimum size specified	Seagrasses
2015	Kristensen et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2015	Lanham et al.	Subtropical	South	Only minimum size specified	Macroalgae
2015	Lee et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2015	Long et al.	Temperate	North	Only minimum size specified	Seagrasses
2015	McDonald et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	McFarlin et al.	Temperate	North	Size range of animals defined	Mangroves
2015	Munari et al.	Temperate	North	Only minimum size specified	Macroalgae
2015	Navarro-Barranco et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats

2015	Nogueira et al.	Tropical	South	Only minimum size specified	Corals
2015	Ortiz et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Ortiz et al.	Tropical	South	No size definition of epifauna given	Corals
2015	Palmer & Montagna	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Sepúlveda et al.	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2015	Sheehan et al.	Temperate	North	No size definition of epifauna given	Corals
2015	Sokołowski et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2015	Torres et al.	Temperate	North	Only minimum size specified	Macroalgae
2015	Vader & Tandberg	Na	Na	No size definition of epifauna given	Other biogenic habitats
2015	van der Zee et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2015	Veeragurunathan et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2015	Whomersley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2015	Wong & Dowd	Temperate	North	Only minimum size specified	Seagrasses
2015	Zupo et al.	Temperate	North	Only minimum size specified	Seagrasses
2016	Arnold et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2016	Ba-Akdah et al.	Tropical	North	Only minimum size specified	Macroalgae
2016	Bowden et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2016	Clark et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats

2016	de Jong et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Demers et al.	Temperate	South	No size definition of epifauna given	Seagrasses
2016	Du Preez et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Figueroa et al.	Subtropical, temperate	North	No size definition of epifauna given	Macroalgae
2016	Filimon et al.	Temperate	North	Only minimum size specified	Macroalgae
2016	Fritz	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2016	Hemery & Henkel	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Jimenez et al.	Tropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2016	Kollars et al.	Subtropical	North	No size definition of epifauna given	Macroalgae
2016	Lefcheck et al.	Temperate	North	Only minimum size specified	Seagrasses
2016	Leite et al.	Tropical	South	No size definition of epifauna given	Other biogenic habitats
2016	Luckenbach et al.	Temperate	North	Only minimum size specified	Artificial structure, macroalgae
2016	Marzinelli et al.	Suptropical	South	Only minimum size specified	Macroalgae
2016	McDonald et al.	Subtropical	North	Only minimum size specified	Seagrasses
2016	McSkimming et al.	Temperate	South	Only minimum size specified	Seagrasses
2016	Meyer et al.	Temperate	North	Size range of animals defined	Benthic & unidentified habitats
2016	Muntadas et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2016	Murat et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Navarro-Barranco et al.	Subtropical	North	Only minimum size specified	Other biogenic habitats

2016	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2016	Piló et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Piras et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Rodrigues et al.	Tropical	South	No size definition of epifauna given	Mangroves
2016	Rodríguez-Zaragoza et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Rosli et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats
2016	Tano et al.	Tropical	South	Only minimum size specified	Macroalgae, seagrasses
2016	Theodor et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2016	Vanreusel et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2016	Walls et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2016	Zharikov & Lysenko	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Agostini et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2017	Alfaro-Lucas et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2017	Balestra et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Boyé et al.	Temperate	North	Only minimum size specified	Seagrasses
2017	Collie et al.	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2017	Cox et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Davoult et al.	Temperate	North	Only minimum size specified	Macroalgae
2017	Donadi et al.	Temperate	North	No size definition of epifauna given	Macroalgae

2017	Eddy et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Benthic & unidentified habitats
2017	Fernandez-Gonzalez & Sanchez-Jerez	Temperate	North	Only minimum size specified	Macroalgae, other biogenic habitats
2017	Foveau & Dauvin	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Gribben et al.	Subtropical	South	Only minimum size specified	Seagrasses
2017	Hamilton et al.	Subtropical	North	No size definition of epifauna given	Mangroves
2017	Lambert et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	Lavender et al.	Subtropical	South	Only minimum size specified	Artificial structures
2017	Lefcheck et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2017	Mach et al.	Temperate	North	Only minimum size specified	Seagrasses
2017	Mariani et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Neumann et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2017	O'Carroll et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats, benthic & unidentified habitats
2017	O'Carroll et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Pascal et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Ramalho et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Reynolds et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Salmo et al.	Tropical	North	Only minimum size specified	Mangroves
2017	Sokołowski et al.	Temperate	North	Size range of animals defined	Artificial structures
2017	Suárez-Jiménez et al.	Temperate	South	No size definition of epifauna given	Macroalgae

2017	Taylor et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2017	Vermeij	Tropical	North, south	No size definition of epifauna given	Benthic & unidentified habitats
2017	Winkler et al.	Subtropical	South	Only minimum size specified	Macroalgae
2017	Xu et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2017	Yeager & Hovel	Subtropical	North	No size definition of epifauna given	Seagrasses
2017	Zaabar et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2018	Alitto et al.	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Audino & Marian	Subtropical	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Baker et al.	Tropical	North	Size range of animals defined	Macroalgae
2018	Belattmania et al.	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2018	Belattmania et al.	Subtropical	North	Only minimum size specified	Macroalgae
2018	Brix et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2018	Burnett & Koehl	Temperate	North	No size definition of epifauna given	Macroalgae
2018	Coffin et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2018	Cunha et al.	Tropical	South	Only minimum size specified	Macroalgae
2018	das Chagas et al.	Tropical	South	Only minimum size specified	Artificial structures
2018	Desmond et al.	Temperate	South	Only minimum size specified	Macroalgae, macroalgae
2018	dos Santos et al.	Tropical	South	Only minimum size specified	Other biogenic habitats
2018	Douglass et al.	Subtropical	North	Size range of animals defined	Seagrasses
2018	Eggleton et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

2018	Esqueda-González et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Fariñas-Franco et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2018	French & Moore	Temperate	North	Only minimum size specified	Seagrasses
2018	Gabara et al.	Subtropical	North	No size definition of epifauna given	Turf algae & microalgae
2018	Gavira-O'Neill et al.	Temperate	North	Only minimum size specified	Other biogenic habitats
2018	Glaspie et al.	Subtropical	South	Only minimum size specified	Other biogenic habitats
2018	Ha & Williams	Temperate	North	Only minimum size specified	Seagrasses
2018	Hamoutene et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2018	Hemery et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2018	Hermosillo-Núñez et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2018	Hermosillo-Núñez et al.	Tropical, subtropical, temperate	South	No size definition of epifauna given	Corals
2018	Howarth et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2018	Janiak et al.	Subtropical	North	Only minimum size specified	Artificial structures, mangroves
2018	Kaiser et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Kaminsky et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Kennedy et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2018	Kniesz et al.	Tropical	North	No size definition of epifauna given	Other biogenic habitats
2018	Little et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Lundquist et al.	Temperate	South	Only minimum size specified	Benthic & unidentified habitats

2018	McGann & Conrad	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2018	Momota & Nakaoka	Temperate	North	Only minimum size specified	Seagrasses
2018	Monk et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Montereale-Gavazzi et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Moreno et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Morris et al.	Subtropical	South	Size range of animals defined	Benthic & unidentified habitats
2018	Mosbahi et al.	Subtropical	North	No size definition of epifauna given	Seagrasses
2018	Muntadas et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Nakamoto et al.	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2018	Namba & Nakaoka	Temperate	North	Size range of animals defined	Seagrasses
2018	Navarro-Barranco et al.	Temperate	North	Only minimum size specified	Macroalgae
2018	Parameswaran et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Saarinen et al.	Temperate	North	Only minimum size specified	Macroalgae
2018	Scheffel et al.	Subtropical	North	Only minimum size specified	Mangroves
2018	Schweitzer et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Singh et al.	Tropical	North	Only minimum size specified	Benthic & unidentified habitats
2018	Soler-Hurtado et al.	Tropical	South	Only minimum size specified	Corals
2018	Sutherland et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2018	Tanner et al.	Subtropical, temperate	South	Only minimum size specified	Benthic & unidentified habitats
2018	Tilot et al.	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats

2018	Vaughn & Hoellein	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2018	Venturelli et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2018	Viola et al.	Subtropical	North	No size definition of epifauna given	Artificial structures
2018	Waters et al.	Temperate	South	No size definition of epifauna given	Macroalgae
2018	Wenger et al.	Tropical	South	Only minimum size specified	Macroalgae
2018	Whippo et al.	Temperate	North	Only minimum size specified	Seagrasses
2018	Williams et al.	Subtropical, temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2018	Yusa et al.	Temperate	North	Only minimum size specified	Seagrasses
2018	Zwerschke et al.	Temperate	North	Only maximum size specified	Other biogenic habitats
2019	Abdelhady et al.	Subtropical	North	Only minimum size specified	Benthic & unidentified habitats
2019	Audino et al.	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2019	Barrientos-Lujan et al.	Tropical	North	No size definition of epifauna given	Corals
2019	Bentley et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Bertolini	Temperate	North	No size definition of epifauna given	Macroalgae
2019	Bonaglia et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2019	Bremec & Schejter	Temperate	South	No size definition of epifauna given	Other biogenic habitats
2019	Brooks & Crowe	Temperate	North	No size definition of epifauna given	Artificial structures, macroalgae
2019	Cadier & Frouws	Tropical	South	Only minimum size specified	Seagrasses
2019	Campanyà-Llovet & Snelgrove	Temperate	North	Only minimum size specified	Macroalgae

2019	Carmen & Grunden	Temperate	North	No size definition of epifauna given	Seagrasses
2019	Casamajor et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2019	Cavalcante et al.	Tropical	South	Only minimum size specified	Seagrasses
2019	Ferreira et al.	Tropical	South	Only minimum size specified	Macroalgae
2019	Fields et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Foster et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2019	Fulton et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Macroalgae
2019	Gan et al.	Tropical	North	No size definition of epifauna given	Macroalgae
2019	Gárate et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Garcia et al.	Tropical	South	Only minimum size specified	Macroalgae
2019	Gates et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2019	Githaiga et al.	Tropical	South	Only minimum size specified	Seagrasses
2019	Guillas et al.	Temperate	North	No size definition of epifauna given	Other biogenic habitats
2019	Hayduk et al.	Temperate	North	Only minimum size specified	Macroalgae, seagrasses
2019	Henseler et al.	Temperate	North	Only minimum size specified	Macroalgae
2019	Hossain	Tropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Hossain et al.	Tropical	North	Size range of animals defined	Benthic & unidentified habitats
2019	Iliff et al.	Subtropical	North	Only minimum size specified	Other biogenic habitats
2019	Ito et al.	Temperate	North	Only minimum size specified	Macroalgae

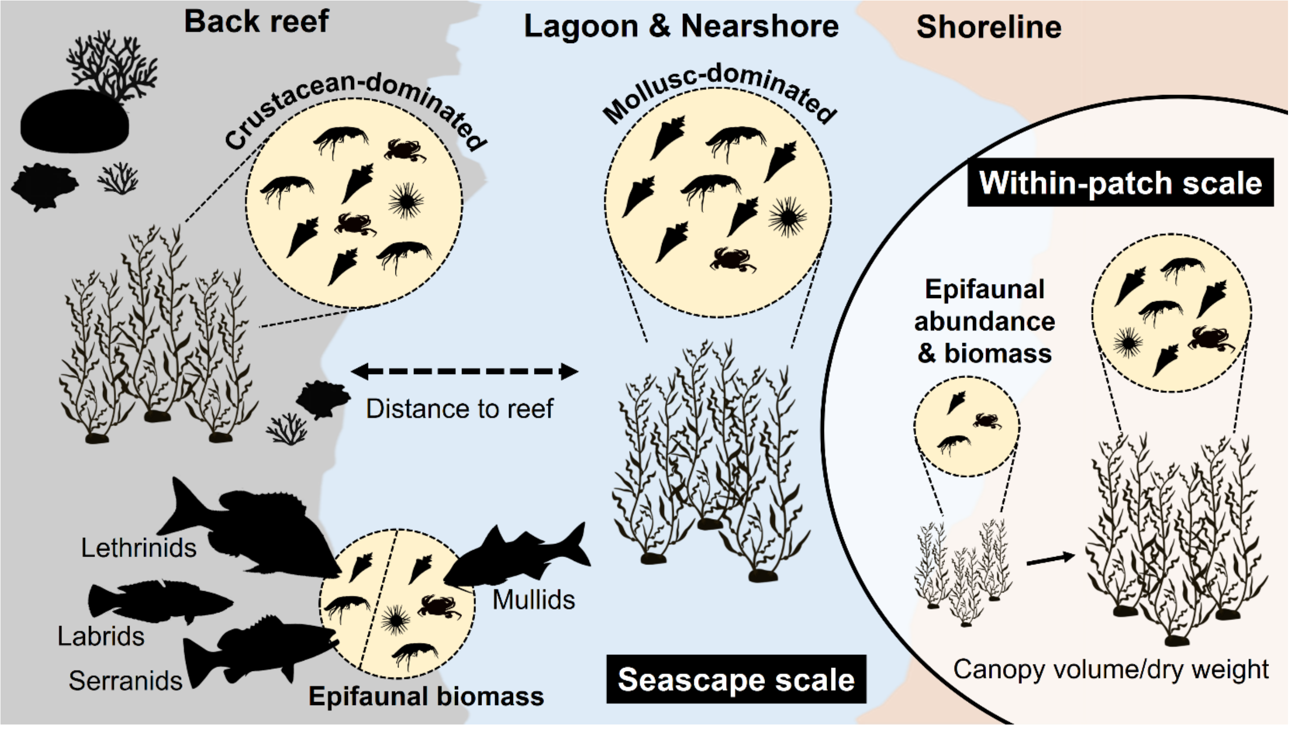
2019	Jacobucci et al.	Tropical	South	Only minimum size specified	Macroalgae
2019	Janas et al.	Temperate	North	Size range of animals defined	Seagrasses
2019	Lomeli et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Lozano-Cortés et al.	Subtropical	North	Only minimum size specified	Artificial structures
2019	Luff et al.	Temperate	North	No size definition of epifauna given	Seagrasses
2019	Lutz et al.	Subtropical	North	Only minimum size specified	Macroalgae
2019	Meysick et al.	Temperate	North	Only minimum size specified	Seagrasses
2019	Michaelis et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Michaelis et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Navarro-Barranco et al.	Temperate	North	Only minimum size specified	Macroalgae
2019	Olivier et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Outinen et al.	Temperate	North	No size definition of epifauna given	Macroalgae, benthic & unidentified habitats
2019	Piechaud et al.	Na	Na	No size definition of epifauna given	Benthic & unidentified habitats
2019	Powell et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Price et al.	Temperate	North	No size definition of epifauna given	Corals
2019	Salmo et al.	Tropical	North	Only minimum size specified	Mangroves
2019	Seitz et al.	Temperate	North	Only minimum size specified	Artificial structures
2019	Slavik et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Smith et al.	Subtropical	North	Only minimum size specified	Mangroves

2019	Sutherland et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2019	Talbot et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2019	Trannum et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2019	Tuya et al.	Subtropical, temperate	North	Only minimum size specified	Seagrasses
2019	Wee et al.	Tropical	North	Only minimum size specified	Corals
2019	Yeager et al.	Subtropical	North	Only minimum size specified	Seagrasses
2019	Zhang & Silliman	Subtropical	North	Only minimum size specified	Macroalgae, seagrasses
2020	Babcock et al.	Subtropical	North	No size definition of epifauna given	Artificial structures, macroalgae
2020	Barbosa & Taylor	Subtropical	North	No size definition of epifauna given	Seagrasses
2020	Belattmania et al.	Subtropical	North	Only minimum size specified	Macroalgae
2020	Callaway et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2020	Chen et al.	Tropical	South	Size range of animals defined	Macroalgae
2020	Couce et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Cramer et al.	Tropical	North	Size range of animals defined	Corals
2020	Fraser et al.	Tropical, subtropical, temperate	South	Only minimum size specified	Corals, macroalgae, turf algae & microalgae, other biogenic habitats
2020	Gagnon et al.	Tropical, subtropical, temperate	North, south	No size definition of epifauna given	Mangroves, seagrasses
2020	Ge et al.	Subtropical	North	Only minimum size specified	Mangroves
2020	González-García et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Gracia et al.	Tropical	North	Only minimum size specified	Other biogenic habitats, benthic & unidentified habitats

2020	Kodama et al.	Temperate	North	No size definition of epifauna given	Macroalgae
2020	Lanham et al.	Temperate	South	Only minimum size specified	Macroalgae
2020	Ledbetter & Hovel	Subtropical	North	Only minimum size specified	Seagrasses
2020	López-Garrido et al.	Subtropical	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Ma et al.	Tropical	North	Only minimum size specified	Mangroves
2020	Namba et al.	Temperate	North	Size range of animals defined	Seagrasses
2020	Noble-James et al.	Temperate	North	Only minimum size specified	Benthic & unidentified habitats
2020	Pisapia et al.	Tropical	South	Only minimum size specified	Corals
2020	Proudfoot et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats
2020	Rouse et al.	Temperate	North	No size definition of epifauna given	Artificial structures
2020	Rowden et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2020	Sedano et al.	Temperate	North	Only minimum size specified	artificial structures
2020	Sedano et al.	Temperate	North	Only minimum size specified	artificial structures
2020	Shelamoff et al.	Temperate	South	Only minimum size specified	Macroalgae
2020	Simpson et al.	Subtropical	South	No size definition of epifauna given	Artificial structures
2020	Stelling-Wood et al.	Subtropical	South	Only minimum size specified	Macroalgae
2020	Stevens et al.	Temperate	South	No size definition of epifauna given	Benthic & unidentified habitats
2020	Wei et al.	Temperate	North	No size definition of epifauna given	Benthic & unidentified habitats

CHAPTER 3

SARGASSUM EPIFAUNAL COMMUNITIES VARY WITH CANOPY SIZE, PREDATOR BIOMASS AND SEASCAPE SETTING WITHIN A FRINGING CORAL REEF ECOSYSTEM



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Abstract

Tropical seascapes are comprised of a range of patch habitat types, yet we have only a partial understanding of how local patch condition and seascape position may influence patterns of marine biodiversity, particularly for invertebrate taxa. We investigated how the epifaunal abundance and biomass of tropical *Sargassum* varied with canopy size (volume, total length and dry weight), local patch conditions (macroalgal composition, canopy structure and invertivorous fish biomass) and seascape setting (nearshore, lagoon and back reef) within the Ningaloo fringing reef ecosystem, Australia. A total of 49431 epifauna, dominated by crustaceans and molluscs, were extracted from the thalli of 81 tropical *Sargassum polycystum*. Epifaunal abundance and biomass were most strongly correlated with host *Sargassum* canopy volume and dry weight, respectively. Epifaunal abundance and biomass also varied significantly among separate *Sargassum* meadow patches, with a significant interaction between canopy size and seascape position. Considerable site-level variations in epifaunal biomass density (mg per g *Sargassum* dry weight) were best predicted by either seascape context or local invertivorous fish biomass. *Sargassum* within meadows furthest from the back reef tended to have the highest epifaunal biomass (dominated by molluscs), while meadows closest to the back reef were dominated by crustacea. *Sargassum* within meadows with a high local abundance of invertivorous labrids and serranids tended to have the lowest epifaunal biomass. Strong *Sargassum* canopy size–epifauna relationships indicate that even small differences in canopy extent have major flow-on effects for the trophic function of tropical marine ecosystems by affecting the epifaunal secondary productivity available to higher-order consumers, such as fishes.

Keywords: Tropical Macroalgae, Epifauna, Invertivorous Fish, Crustacea, Mollusca, Biomass, Patch Habitat

Introduction

Tropical seascapes can be composed of a range of habitat-forming organisms that create patches of coral, seagrass, mangroves, and macroalgae embedded within a matrix of carbonate reef and sand. Emerging evidence indicates that local conditions can interact with the seascape position of these biogenic patch habitats to shape spatial patterns of tropical marine biodiversity and ecosystem function (Berkström et al. 2013, Hensgen et al. 2014, van Lier et al. 2018). For instance, the local abundance of macroaglae-associated fishes has been linked to within-patch habitat complexity and proximity to nearby patches of coral, seagrass and/or macroalgal habitat (Berkström et al. 2013, van Lier et al. 2018). The extent to which these within-patch and seascape effects operate at lower trophic levels (e.g., small-bodied invertebrates), however, remains poorly understood.

Epifauna are invertebrates (typically 0.5–10 mm long) that occupy the living canopy of other organisms, such as macroalgae and corals (Edgar 1990a, Edgar & Aoki 1993, Kramer et al. 2017). Often extremely abundant with rapid rates of turnover (growth and mortality), the productivity of these epifauna can support large populations of higher-order consumers, such as fishes, and underpin major pathways of energy and nutrient transfer in marine ecosystems (Edgar & Aoki 1993, Taylor 1998a, Kramer et al. 2017). In marine ecosystems, epifaunal communities have been documented within abiotic substrata (rubble and sand) as well as within the canopy of corals, seagrasses and macroalgae (Stella et al. 2010, Kramer et al. 2014, Tano et al. 2016). Current evidence suggests that epifaunal abundance and diversity may be highest within macroalgal microhabitats, including both erect canopy-forming taxa as well as turf communities of the epilithic algal matrix (Kramer et al. 2017), which are targeted by a range of invertivorous reef fishes (Kramer et al. 2015, Wenger et al. 2018).

Canopy-forming macroalgae of the genus *Sargassum* are widespread along coastlines of the world, where they can form extensive meadow habitats. *Sargassum* meadows are increasingly being recognised as an integral component of tropical marine ecosystems, where they support primary production and provide habitat for a diversity of juvenile and adult fishes (Fulton et al. 2019). Canopy structure and composition of tropical *Sargassum* meadows and their associated reef fish communities can vary strongly over space and time due to local environmental conditions and seascape context (Ateweberhan et al. 2009, Fulton et al. 2014, van Lier et al. 2018). Moreover, limited evidence suggests tropical *Sargassum* canopies can contain a range of epifaunal invertebrates, which may vary in abundance according to macroalgal canopy size (Leite & Turra 2003, Wenger et al. 2018) and the presence of invertivorous fishes (Edgar & Aoki 1993). However, we lack an understanding of the relative importance of these local factors alongside seascape context for shaping the relative abundance of *Sargassum* epifauna, which are likely to be a key trophic resource for many higher-order consumers found within tropical macroalgal meadows (Berkström et al. 2013).

To better understand the likely drivers of tropical macroalgal epifaunal community structure, we used an extensive network of *Sargassum*-dominated meadows within a fringing coral reef ecosystem to determine (1) to what extent epifaunal abundance (in terms of number of individuals) and biomass are correlated with different measures of host *Sargassum* canopy size (total length, volume and dry weight), (2) whether epifaunal community structure varies with seascape position (nearshore, lagoon and back reef) and (3) if local conditions of within-patch macroalgal composition and invertivorous fish biomass can predict spatial variations in *Sargassum* epifaunal community structure.

Materials and methods

Study location

Ningaloo Reef is a World Heritage site in the eastern Indian Ocean that comprises >290 km of fringing coral reef encompassing a shallow lagoon dominated by >30000 hectares of brown macroalgal meadows dominated by tropical members of the canopy-forming genus *Sargassum* (Kobryn et al. 2013, Fulton et al. 2014). While the taxonomy of *Sargassum* remains to be fully resolved for this tropical region, our collections were focused on the most common morphotype in these meadows which we believe matches the description for *Sargassum polycystum* (Huisman 2019). For this study, which focused on spatial variation in the *Sargassum* epifaunal community, we selected 9 distinct *Sargassum* meadow patches separated by a minimum of 300 m and spread across the 3 distinct seascape positions of nearshore (sites closest to shoreline, which was typically within 50 to 300 m of the shoreline and embedded within ancient reef pavement covered in a layer of sand on an average of 1-3 cm thick), lagoon (>500 m from shoreline and embedded within pavement-sand matrix) and back reef (embedded within pavement-sand surrounded by fringing coral reef), within a 6 km^2 section of the Maud Region of the Ningaloo Marine Park near Coral Bay, Western Australia (Figure 3.1). These seascape positions are relevant to many coastlines where

Sargassum meadows occur alongside coral reefs in the Pacific (e.g., New Caledonia), Indian (e.g., Ningaloo and Tanzania) and Atlantic (e.g., Brazil) Oceans, as well as the Red Sea (Berkström et al. 2013, Tano et al. 2016, Fulton et al. 2019). The macroalgal meadow study sites were an average of 26210 m^2 (± 10605 m^2 SE) in area (van Lier et al. 2018), embedded within a pavement-sand matrix in shallow water (2–6 m deep), and were subject to similar site-level mean sea temperatures (27.3 ± 0.1°C) during the 4 wk field survey and collection period.

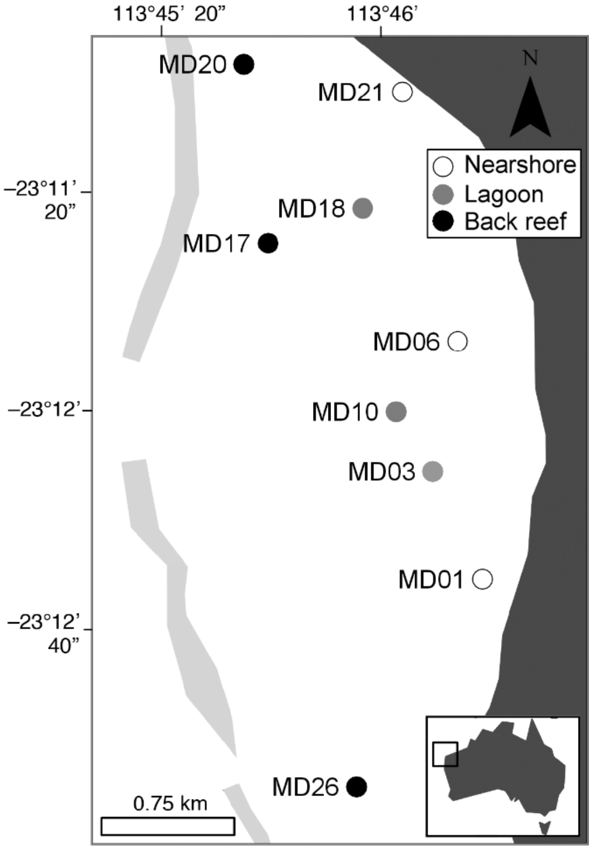

Figure 3.1 Nine *Sargassum*-dominated study sites at 3 seascape positions (nearshore, lagoon, back reef) within the Maud Recreation Zone near Coral Bay, Ningaloo Reef, Western Australia.

Sargassum epifauna sampling

During the late austral summer (February to March) of 2018, we collected 9 entire *S. polycystum* individuals and their epifauna at each of the 9 study sites. Since canopy size can be a key predictor for epifaunal abundance (Edgar 1990c), we haphazardly sub-sampled a cross section of *Sargassum* canopy sizes at each site. To do this, a 15 m line transect across the centre of each study site was used to select the *S. polycystum* individuals closest to the 5 m mark that fell within each of 3 height classes (>60, 30–60 and <30 cm). These height classes corresponded to the top, middle and bottom third of mean canopy sizes recently recorded for this region across sites, years and seasons (Wilson et al. 2014, van Lier et al. 2018). We repeated this procedure at the 10 and 15 m points on the same line transect to collect a total of 9 *S. polycystum* individuals per site (3 per size class). For each selected *S. polycystum* individual, a SCUBA diver gently and fully enclosed the entire *Sargassum* thallus and associated epifauna with a canvas bag, then cut the stipe just above the holdfast before immediately sealing the canvas bag to reduce the risk of epifauna escape. All collected samples were brought back to the research vessel within 30 min and transported in a cooler to the Coral Bay Research Station for processing within 4 h of collection.

Post-collection processing of *S. polycystum* individuals involved immersion in cold freshwater for 10 min before gently shaking and then dislodging all of the chilled epifauna from their *Sargassum* host with a salad spinner. All of the cold freshwater containing the epifauna was then passed through a 125 µm stainless steel sieve so the retained particles could be washed into a labelled zip bag and frozen at –20°C for transport to The Australian National University for further analysis. After all the freshwater was removed from the *S. polycystum* individual, a range of metrics were taken for each host canopy: total extended length from stipe end to tip (to nearest cm), total volume (to nearest millilitre measured via displacement of freshwater in a measuring cylinder) and total wet weight (g). *S. polycystum* individuals were then dried in an oven at 60°C for 48 h to obtain a canopy dry weight (to nearest 0.1 g).

Total abundance of epifauna collected from each *S. polycystum* individual was quantified by defrosting the epifauna and fixing them in a 10% formalin-seawater solution for 1 h, before rinsing in seawater for identification and enumeration under a stereo-microscope with 40× magnification. To allow estimation of epifaunal biomass in terms of ash free dry weight (AFDW), we used the sieve method proposed by Edgar (1990c), which involved passing the now-fixed epifauna samples through a nested series of sieves (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.7 and 0.5 mm stainless steel mesh sizes) that fractionated the epifauna by body size. Epifauna retained on each sieve were then identified to 6 taxonomic groups following Edgar (1990c): crustaceans, molluscs, echinoderms, polychaetes, foraminifera and other animals;

epifaunal abundance was determined by counting all individuals per taxonomic group per sieve size. For epifauna retained on sieve sizes of ≤4.0 mm, we used the empirically derived equations of Edgar (1990c) to estimate the total AFDW of each taxonomic group in the sample. For all epifauna > 5.6 mm, we empirically measured the dry weight and ash weight of each taxonomic group (following 48 h in a 60°C oven or 2 h in a 500°C muffle furnace, respectively) to estimate AFDW by subtracting the ash weight from dry weight.

Macroalgal and invertivorous fish surveys

Macroalgal benthic composition within each site was estimated underwater by SCUBA divers deploying 6 replicate 10 m line transects run in series and separated by a minimum of 5 m. Along each transect, the relative percentage cover of macroalgal genera was estimated by recording the distance occupied under the line (to nearest 5 cm). *Sargassum* canopy structure was also assessed in terms of holdfast density (number within a 0.5 × 0.5 m quadrat) and vertical canopy height (maximum length when manually extended along a ruler to nearest cm) at 2 m intervals (starting at 0 m) to yield 6 replicate measures of each canopy metric per 10 m line transect, following Wilson et al. (2014).

Invertivorous fishes have been identified as common in tropical macroalgal meadows and include species in the 4 diverse families of the Labridae (excluding the Scarinae), Lethrinidae, Mullidae and Serranidae (Wilson et al. 2010, van Lier et al. 2018, Fulton et al. 2019). We estimated the biomass of these fish families within our 9 study sites using the point-census cylinder survey method of Noble et al. (2013). This involved the same observer on SCUBA recording the estimated total length (cm) of all target fishes within 6 replicate 5 m diameter cylinders that were haphazardly spread within each site so as to be separated by at least 5 m from each other. Mean site-level biomass of each fish family was then calculated by converting the total length (cm) of all individuals to an estimated mass (g) using published length-weight relationships for each species (Kulbicki et al. 2005a, Froese & Pauly 2021).

Data analyses

To examine which measures of *Sargassum* canopy size may best predict variation in epifaunal total abundance and biomass, we used least-squares regression to model the relationships between 3 metrics of *Sargassum* canopy size (total length, volume and dry weight) and either total epifaunal abundance or total epifaunal biomass (AFDW) per *S. polycystum* individual. Initial analyses indicated that most relationships were significant and non-linear (see Figure A3.1 in the Appendix), so they were linearised via natural log-log transformations for subsequent analyses.

Epifaunal community structure among sites was then explored in terms of both individual abundance and biomass of the 6 taxonomic groups of epifauna (as dependent variables), with the fixed factor of seascape position (nearshore, lagoon or back reef) and random factor of site (nested in seascape position) in a 2-way multivariate permutational analysis of covariance (PERMANCOVA). *Sargassum* canopy size was included as a covariate (logged volume for epifaunal abundance, logged dry weight for epifaunal biomass). These PERMANCOVAs were performed with Type 1 sum of squares and a maximum of 9999 permutations of resemblance matrices based on the modified Gower (base 2) dissimilarity measure applied to either $\log_{10}(x + 1)$ (abundance) or fourth-root (biomass) transformed data that were used to reduce skew across the dependent variables (Anderson et al. 2006, 2008). Post-hoc explorations of significant terms were explored with threshold-metric multi-dimensional scaling (tmMDS) ordinations of the site-seascape group centroids. Ordination structure in epifaunal individual abundance and biomass was explored with principal components analysis (PCA), optimised with vector overlays to indicate the degree of Pearson's correlation between the epifaunal variables and the ordination structure.

Possible environmental predictors of site-level variation in the relative biomass of the 6 taxonomic groups of *Sargassum* epifauna were explored with best-subsets model selection using distance-based linear models (DistLM) and the Akaike information criterion corrected for finite sample sizes (AICc) to select the most parsimonious model(s), following Burnham & Anderson (2002). We first converted the matrix of dependent data (being epifaunal biomass per taxonomic group) into biomass per *Sargassum* canopy dry weight (mg epifauna g DW^{-1}) to take account of general canopy size effects on epifaunal biomass. This standardised epifaunal biomass was then arranged into a modified Gower (log base 2) resemblance matrix, following a fourth-root transformation to correct for skew. An environmental predictor matrix was assembled, comprising site means for 3 groups of possible predictors: invertivorous fish biomass (per each of the 4 families), *Sargassum* canopy structure (canopy height, holdfast density, percent cover canopy and understory taxa, taxonomic genera richness and Pielou's evenness) and seascape context (meadow patch area, distance to fringing reef, distance to nearest neighbouring meadow and depth).

The most parsimonious environmental model for predicting *Sargassum* epifaunal biomass across the 9 study sites was chosen as the one with the fewest variables within 2 AICc of the top model, which was then visualised by a distance-based redundancy analysis (dbRDA) ordination with the best predictor environmental vectors as an overlay. All analyses were performed in PRIMER (v.7.0.13) with the Permanova+ add-on (Anderson et al. 2008).

Results

A total of 49431 epifauna individuals were extracted from 81 *S. polycystum* individuals, which represented an estimated total biomass of 18619.4 mg (AFDW) of epifauna from 6119.8 g (dry weight) of tropical *Sargassum* canopy biomass. Total abundance and biomass of epifauna per *S. polycystum* individual varied significantly with all 3 measures of *Sargassum* canopy size (Figure 3.2). Pearson's correlation was highest for epifaunal abundance against *Sargassum* canopy volume (Figure 3.2B); correlations were generally lower for epifaunal biomass–canopy relationships, being highest for *Sargassum* canopy dry weight (Figure 3.2F).

Half of the total epifaunal abundance (50.0%) consisted of crustaceans (mainly Amphipoda, Harpacticoida and Isopoda), a third (33.4%) were molluscs (mainly Gastropoda), and the remainder comprised foraminifera (9.1%), echinoderms (2.6%, mostly Ophiuroidea), polychaetes (1.9%) and a mixture of other animals (2.7%, including Nematoda). In biomass terms (estimated as AFDW that excludes skeletal tissues such as shells), however, molluscs were the dominant group (77% of the overall total), followed by crustaceans (20%). Considerable variation was apparent at the sample level, with little apparent structure in either epifaunal abundance or biomass related to seascape position across all of the taxonomic groups (Figures 3.3 & 3.4), perhaps with the exception of crustaceans and molluscs being more abundant in the back reef *S. polycystum* samples (Figure 3.3A,B) that also tended to be at the larger end of the canopy size spectrum across the entire collection (Figure 3.2A–C).

Both epifaunal individual abundance and biomass varied significantly among sites, with a significant interaction between *Sargassum* canopy size and seascape position after taking into account the significant covariance between canopy size and epifauna (Table 3.1, Figure 3.2). Whilst the largest *Sargassum* canopy sizes were sampled in the back reef, there was high variability among sites that created considerable overlap among all 3 seascape positions (Figure 3.5). Focusing on this site-level variation, best-subsets model selection revealed 2 competing models that could provide the best predictors for epifaunal community biomass structure (Table 3.2), which were based on either invertivorous fish biomass (Figure 3.6A,C) or seascape context (Figure 3.6B,D). In general, *Sargassum* at sites characterised by a high biomass of mullid fishes had higher epifaunal biomass for a given canopy size, while a lower epifaunal biomass (particularly molluscs; Figure 3.6C) tended to be found in sites characterised by a high biomass of labrid, serranid and lethrinid fishes (Figure 3.6A,C). Distance to fringing reef was the best single seascape predictor for epifaunal community structure (accounting for >47% of the total variation along dbRDA1), with a trend of increasing epifaunal biomass (particularly molluscs) with increasing distance of the patch from the coral back reef (Figure 3.6B). Depth and distance to the nearest neighbouring *Sargassum* meadow appeared to play a smaller overall role (8% of total variation along dbDRA2) in explaining spatial variations in epifaunal canopy-specific biomass (Figure 3.6B,D).

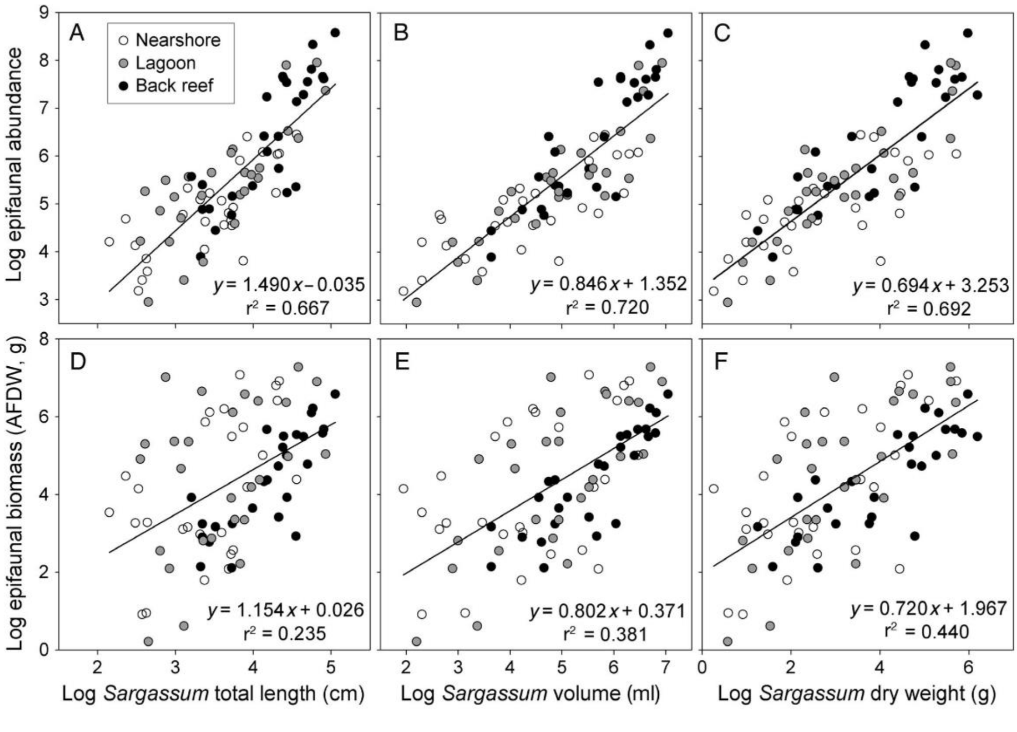

Figure 3.2 Log-log plots of the relationship between different measures of *Sargassum* canopy size (total length, volume, and dry weight) and either (A–C) epifaunal abundance (total individuals per *S. polycystum*) or (D–F) epifaunal biomass (ash free dry weight, AFDW, per *S. polycystum*) collected from 9 study sites at 3 seascape positions (nearshore, lagoon, and back reef) in the Maud region of Ningaloo Reef during summer 2018.

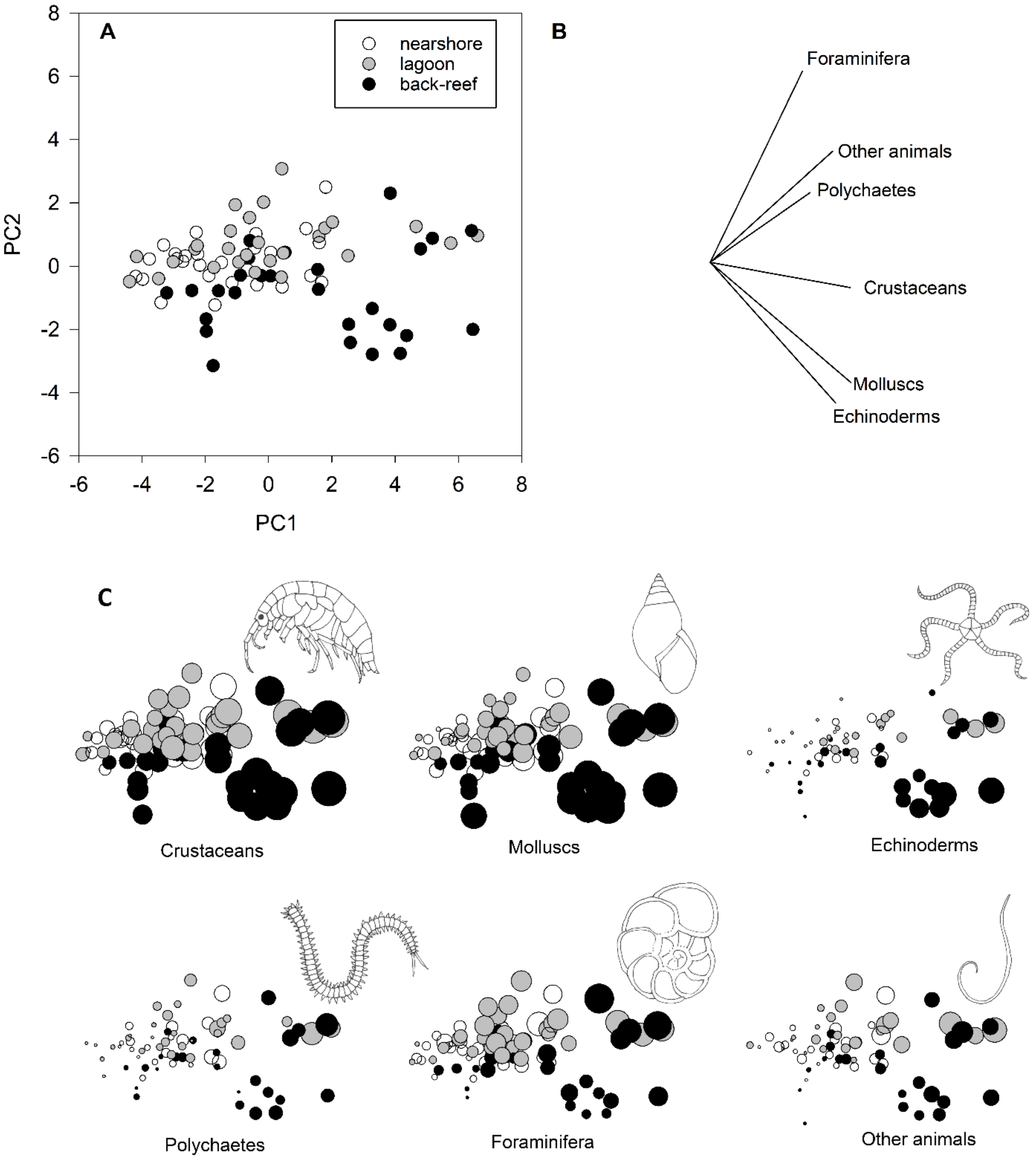

Figure 3.3 Principal component analysis (PCA) of epifaunal abundance on 81 individual *S. polycystum* collected from 9 sites (n = 9 samples per site) at 3 seascape positions (n = 3 sites per position) in Ningaloo during summer 2018. (A) Total epifaunal abundance, (B) vector overlay of epifaunal taxonomic groups strongly correlated with the ordination structure, and (C) ordinations optimised with bubbles scaled to relative abundance of each epifaunal group.

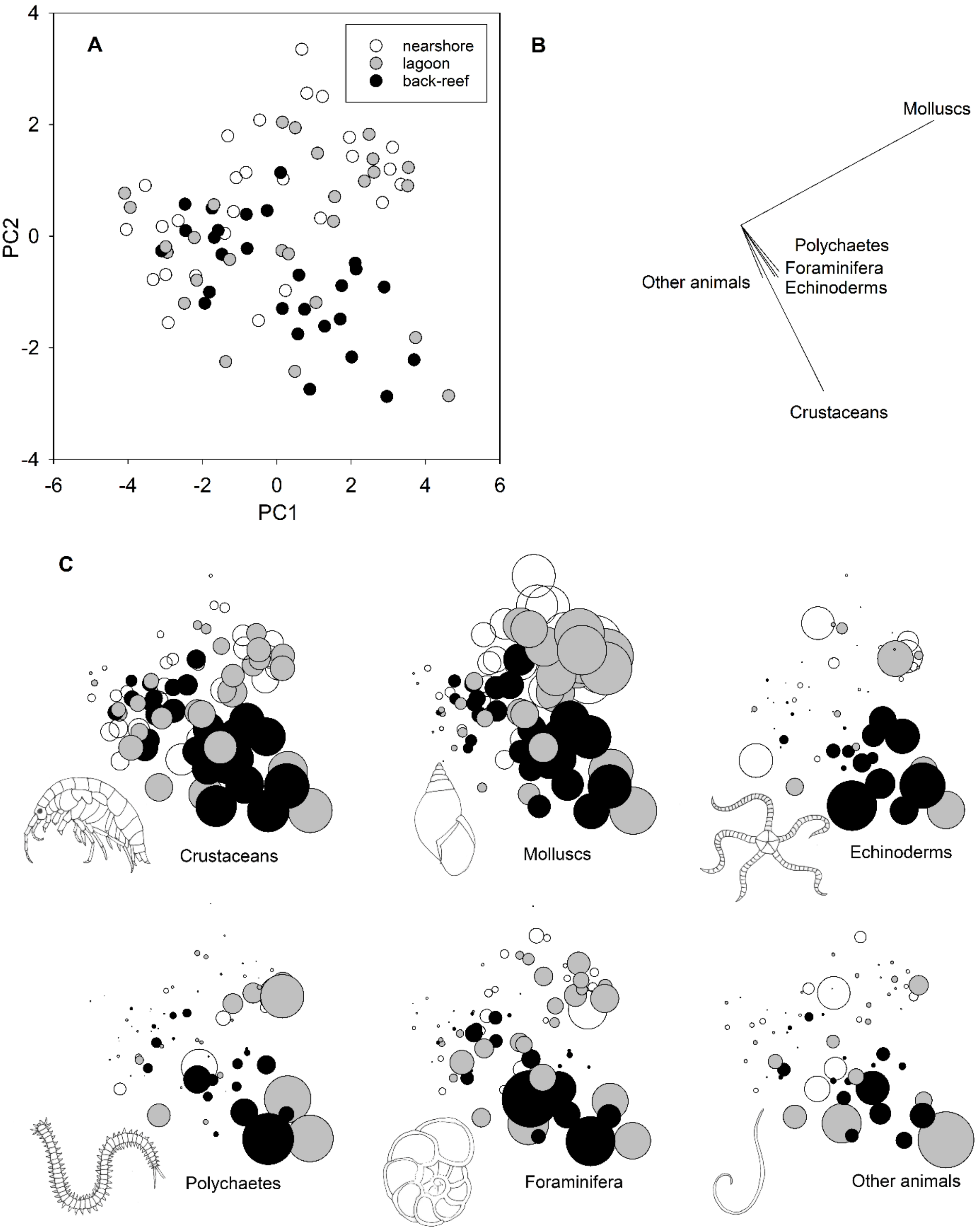

Figure 3.4 PCA of epifaunal biomass on 81 individual *S. polycystum* collected from 9 sites (n = 9 samples per site) at 3 seascape positions (n = 3 sites per position) in Ningaloo during summer 2018. (A) Total epifaunal biomass, (B) vector overlay of epifaunal taxonomic groups strongly correlated with the ordination structure, and (C) ordinations optimised with bubbles scaled to relative biomass of each epifaunal group.

Table 3.1 Summary of PERMANCOVA of *Sargassum* epifaunal (A) individual abundance and (B) biomass across 3 seascape positions (fixed) and 9 study sites (random, nested in seascape) in the Maud region of Ningaloo Reef during summer 2018, with log *Sargassum* canopy size included as a covariate in terms of either (A) volume or (B) dry weight according to the best predictors for the canopy size–epifauna relationships (see Figure 3.2). Significant terms ($P < 0.05$) are highlighted in **bold**.

Source	df	SS	MS	Pseudo-*F*	p-value
(A) Epifaunal individual abundance					
***Sargassum* canopy volume**	1	16.125	16.125	55.990	**<0.01**
Seascape	2	1.139	0.569	1.024	0.454
Site (Seascape)	6	3.445	0.574	3.064	**<0.01**
***Sargassum* canopy volume × Seascape**	2	1.129	0.564	3.012	**<0.05**
Sargassum canopy volume × Site	6	1.812	0.302	1.612	0.079
Residual	63	11.807	0.187		
Total	80	35.456			
(B) Epifaunal biomass					
***Sargassum* canopy dry weight**	1	13.127	13.127	18.134	**<0.01**
Seascape	2	1.865	0.932	0.506	0.827
Site (Seascape)	6	11.365	1.894	4.873	**<0.01**
***Sargassum* canopy dry weight × Seascape**	2	2.817	1.409	3.623	**<0.01**
Sargassum canopy dry weight × Site	6	3.301	0.550	1.415	0.115
Residual	63	24.491	0.389		
Total	80	56.967			

Table 3.2 Summary of best-subsets selection of distance-based linear models for predicting site-level variation in biomass of *Sargassum* epifauna. The most parsimonious models within 2 Akaike information criterion (AICc) units of the top model are indicated in **bold**.

Model	AICc	deltaAICc	r^2
Invertivorous fish biomass	**2.413**	**–**	**0.635**
Seascape context	**3.103**	**0.69**	**0.606**
Canopy structure	88.001	85.59	0.885

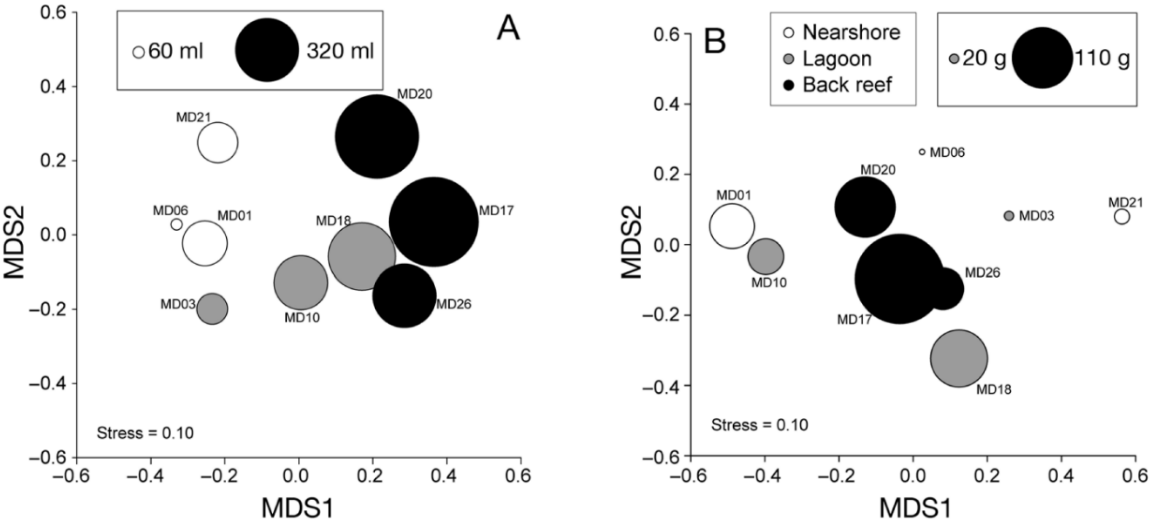

Figure 3.5 Threshold-metric multi-dimensional scaling (tmMDS) ordination of site-level group centroids for *Sargassum* epifaunal (A) abundance and (B) biomass collected at 3 seascape positions (nearshore, lagoon, back reef; n = 3 sites per position) within Ningaloo during summer 2018. Bubble sizes are proportional to site-level mean *Sargassum* canopy (A) volume or (B) dry weight to explore the significant canopy × seascape interaction (see Table 3.1).

Discussion

Our study found 3 key results that significantly increased our understanding of invertebrate biodiversity patterns within tropical seascapes containing macroalgal meadows. First, we found an overarching positive correlation between epifaunal community structure and *Sargassum* canopy size, although the best canopy size metric varied for the measures of epifaunal individual abundance and biomass. Second, we found epifaunal community structure varied significantly among *Sargassum* meadow patches, with a prominent interaction between host canopy size and seascape position. Third, the local biomass of invertivorous fish and the position of macroalgal meadows within the seascape provided some of the best predictors for site-level variations in *Sargassum* epifaunal community structure (Figure 3.7). Given that epifauna are a critical trophic link between the macroalgal production base and higher-order consumers such as fishes, our evidence suggests distinct differences in the trophodynamics of these tropical ecosystems across relatively fine spatial scales (<2 km). Moreover, the strong links between epifaunal biomass and canopy size, and the sensitivity of *Sargassum* canopy growth to sea temperature (Fulton et al. 2014, 2019), suggest climate change is likely to influence flows of primary to secondary production in macroalgal-dominated systems.

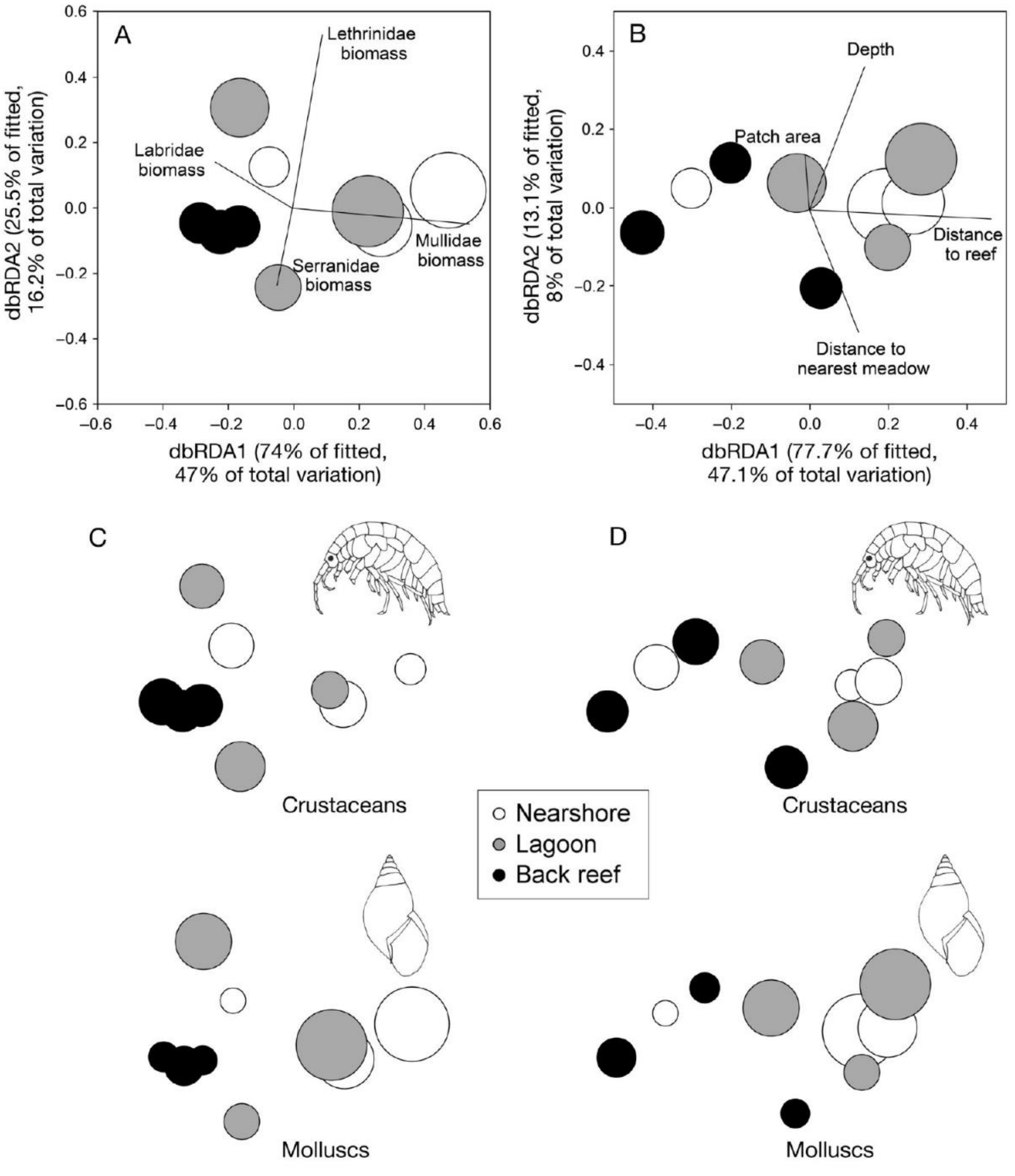

Figure 3.6 Distance-based redundancy analysis (dbRDA) ordination of the most parsimonious best-subsets models for predicting site-level variation in epifaunal biomass across 3 seascape positions (nearshore, lagoon, back reef) in terms of (A) invertivorous fish biomass and (B) seascape context, with optimisations showing bubble sizes scaled to site-level epifaunal biomass for both crustacea and molluscs for each model (C and D, respectively). Vector overlays indicate invertivorous fish family and seascape metric most strongly correlated with each ordination structure.

Strong correlations between epifaunal abundance and *Sargassum* canopy size, such as those found in this study, may arise through habitat amount effects that can govern the size and diversity of ecological communities (Fahrig 2013). However, the differing metrics of canopy size relevant to either individual abundance or biomass of epifauna suggest some nuanced effects related to habitat microstructure. For instance, epifaunal abundance was most strongly correlated with canopy volume (rather than canopy length or biomass), which may point to the importance of overall surface area and microniches for colonisation by mobile animals on fresh *Sargassum* (Carvalho et al. 2018). Indeed, canopy macroalgal meadows have already been found to harbour more epifauna than other macrophyte habitats, such as seagrass meadows (Tano et al. 2016, Belattmania et al. 2018b), the epilithic algal matrix (EAM; Kramer et al. 2012, 2014) or the understory macroalgae (Wenger et al. 2018), due to their complexity and higher volumetric canopy structure. An increased epiphyte load, which increases the structural complexity and surface area of the overall macroalgal canopy, has also been found to support a greater abundance of epifauna (Martin-Smith 1993, Leite & Turra 2003). Our late-summer samples at Ningaloo showed a very low occurrence of *Sargassum* epiphytes (total of 53.65 g epiphytes across 6119.8 g *Sargassum*, dry weight). Epiphyte loads on tropical *Sargassum* can change dramatically with season (Martin-Smith 1993, Lefevre & Bellwood 2010), and such seasonal effects should be a priority for future research in this area. We found epifaunal biomass, however, was most strongly correlated with *Sargassum* canopy dry weight in the Ningaloo samples, which is consistent with prior studies of epifaunal biomass on tropical and temperate *Sargassum* (Mukai 1971, Edgar & Aoki 1993, Edgar & Klumpp 2003, Leite & Turra 2003). Notably, Pearson’s correlations for epifaunal biomass–canopy relationships were generally lower than for epifaunal abundance–canopy relationships, which may arise from biomass estimates of epifauna larger than 5.6 mm that represent a greater amount of biomass (59.14%) relative to their individual abundance (0.86%) of the total epifaunal community. Nonetheless, we found significant positive correlations between the amount of epifauna and *Sargassum* canopy size, which is emerging as a common scenario in tropical *Sargassum* communities (Martin-Smith 1993, Wenger et al. 2018).

Epifaunal communities inhabiting *Sargassum* canopies in Ningaloo were dominated by 2 key taxonomic groups: crustaceans and molluscs. Peracarid crustaceans (amphipods and isopods), harpacticoid crustaceans and gastropod molluscs were the main taxonomic groups contributing to total epifaunal abundance (83.4%) and biomass (94%), followed by ophiuroid echinoderms and polychaetes. Our findings are congruent with previous studies indicating that crustaceans and molluscs are the most abundant mobile epifauna on *Sargassum* in tropical and temperate biomes around the world (Table 3.3). Indeed, studies of epifauna living within turf algae of the EAM (immediately adjacent to corals) or scleractinian corals found crustaceans were most abundant, followed by molluscs, annelids, foraminifera, and nematodes (Stella et al. 2010, Kramer et al. 2012, Kramer et al. 2014). Depending on seascape setting (explored further below), these 2 taxonomic groups may be the most abundant drivers of trophodynamics and nutrient cycling within these macroalgal-dominated ecosystems. Notably, our estimates of total epifaunal density (individual number per g *Sargassum* dry weight) were ~3-fold lower than the average from other studies of tropical and temperate *Sargassum* epifauna (Table 3.3). A previous estimate from a single *Sargassum* meadow at Ningaloo, which was an order of magnitude higher than our estimate (148 individuals per g canopy dry weight; Wenger et al. 2018), provides some insight into the possible source of these differences. Wenger et al. (2018) used 0.12 mm as the finest mesh size while processing their *Sargassum* epifauna, which captured an extremely abundant foraminifera fauna that were subsequently found to not be major prey targets for a *Sargassum*-associated invertivorous fish (Wenger et al. 2018). While there are some wide variations across studies using similar mesh collection sizes, there is a generally higher mean epifaunal density on tropical versus temperate *Sargassum* (Table 3.3). This fits with the notion that production of the ectothermic epifaunal community is higher in warmer sea temperatures (Edgar 1990b).

Consumers can exert strong top-down pressure on prey to shape relative abundance and biomass across space and time. Macroalgal meadows can be important foraging grounds for invertivorous fishes (Edgar & Aoki 1993, Wilson et al. 2014, Tano et al. 2016), which have been found to specifically target mobile epifauna on macroalgae like *Sargassum* (Edgar & Aoki 1993, Wenger et al. 2018), with varying effects. For instance, one study found no significant decrease in epifaunal abundance on *Sargassum* canopies caged to exclude fish foraging activity (Martin-Smith 1993). In contrast, Edgar & Aoki (1993) found that predation by an invertivorous wrasse (Labridae) tended to remove larger epifauna from macroalgae in mesocosm experiments, which freed up resources (through competitive release) for smaller epifauna that subsequently increased in abundance. In other words, it appears predation could drive an increase in the abundance and productivity of *Sargassum* mobile epifauna, which may help explain why higher epifaunal biomass was often found in meadows with greater invertivorous fish biomass at Ningaloo. The biomass of common invertivorous fish species has been positively correlated to *Sargassum* canopy structure

(Wilson et al. 2014, Wenger et al. 2018), with at least one invertivorous fish species found to preferentially target epifaunal crustaceans and molluscs on tropical *Sargassum* (Wenger et al. 2018). Given that invertivorous fishes have previously been shown to vary in abundance with seascape position (van Lier et al. 2018), some of the seascape effects on epifauna condition may arise from these predation effects. Such linkages of invertivorous fishes, epifauna and *Sargassum* in Ningaloo provide a hint of how secondary and higher production may be supported by the underlying *Sargassum* canopy habitat at Ningaloo and across seascapes dominated by *Sargassum* meadows around the world (Fulton et al. 2019). This is clearly a key research front for future work in this arena, requiring empirical study of epifauna–fish interactions and microhabitat foraging preferences to help resolve the relative importance of bottom-up (canopy structure) and top-down influences on macroalgal epifauna.

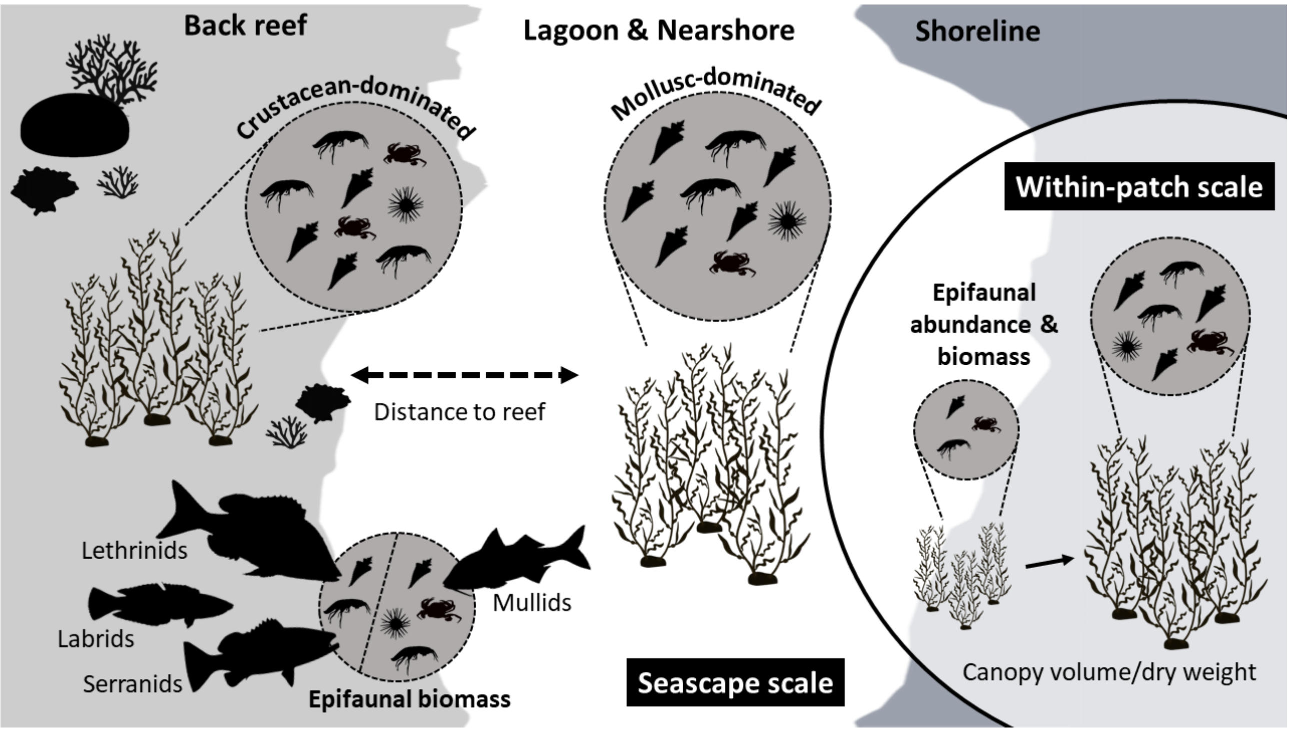

Figure 3.7 Conceptual diagram showing the relationship between macroalgal canopy volume/dry weight and epifaunal abundance/biomass at within-patch scale, and how seascape contexts and the presence of invertivorous fishes affect epifaunal community structure at seascape scales.

Table 3.3 Studies of *Sargassum*-associated epifaunal composition around the world. Epifaunal density is presented as the individual number per gram of *Sargassum* dry weight. The top 3 most abundant taxa (if present) are listed. Most studies used a 0.5 mm mesh size, and studies using 0.1 to 0.3 mm mesh size are marked with an asterisk. *Sargassum* wet weight in some studies was converted to dry weight by following Brey et al. (2010).

Epifaunal density	Most abundant taxa	Focal region	Source
(A) Tropical			
13	Crustaceans > Molluscs > Foraminifera	Ningaloo Reef, Australia (23° 1’ S)	Present study
8	Crustaceans > Molluscs > Polychaetes	Northeast Queensland, Australia (18° 1’–18° 4’ S)	Edgar & Klumpp (2003)
31*	Crustaceans > Polychaetes > Molluscs	The Great Barrier Reef, Australia (19° 1’ S)	Martin-Smith (1993)
12	Crustaceans > Molluscs > Polychaetes	Red Sea, Saudi Arabia (21° 2’ N)	Ba-Akdah et al. (2016)
148*	Foraminifera > Crustaceans > Molluscs	Ningaloo Reef, Australia (23° 1’ S)	Wenger et al. (2018)
66*	Molluscs > Crustaceans > Polychaetes	Flamengo Bay, Brazil (23° 3’ S)	Leite & Turra (2003)
1	Crustaceans > Polychaetes > Molluscs	Lazaro and Tabatinga, Brazil (23° 3’ S)	Tanaka & Leite (1998)
Mean density ± SE: 39.9 ± 19.8			
(B) Temperate			
97	Crustaceans > Platyhelminthes > Molluscs	Tomioka Peninsula, Japan (32° 3’ N)	Edgar & Aoki (1993)
4	Crustaceans > Molluscs > Polychaetes	El Jadida shoreline, Morocco (33° 2’ N)	Belattmania et al. (2018b)
74*	Crustaceans > Polychaetes > Molluscs	Sydney & Illawarra, Australia (34° 2’–34° 4’ S)	Lanham et al. (2015)
3*	Crustaceans > Molluscs > Annelids	Southeast New South Wales, Australia (34° 3’–34° 8’ S)	Marzinelli et al. (2016)
31	Molluscs > Crustaceans	West and south coast, Portugal (37° 1’–37° 4’ N)	Engelen et al. (2013)
14	NA	North coast, Portugal (41° 4’–41° 5’ N)	Veiga et al. (2014)
2	Crustaceans > Molluscs > Polychaetes	Galician coast, Spain (42° 1’–42° 2’ N)	Gestoso et al. (2012)
6	Molluscs > Crustaceans > Nematodes	Galician coast, Spain (42° 2’ N)	Gestoso et al. (2010)
Mean density ± SE: 28.9 ± 13.0			

Our study reveals that local conditions of mean *Sargassum* canopy size can vary considerably over fine spatial scales to provide one of the primary explanations (indicated by the significant interaction term) for variations in epifaunal community structure in a range of seascape contexts. At Ningaloo, *Sargassum* canopy size was not consistent across all meadows, creating a complex mosaic of high/low canopy density, height and cover across meadows spread across the seascape (Wilson et al. 2014, Lim et al. 2016, Wenger et al. 2018). While this was largely irrespective of seascape position, we did find a tendency for higher maximum *Sargassum* canopy size in back reef positions, where the *Sargassum* meadows were embedded among the fringing coral reef. Once these canopy size effects were taken into account, however, seascape position did provide further explanations for spatial variations in *Sargassum* epifaunal community structure. In particular, distance to the back reef provided one of the key predictors for differences in epifaunal community structure at Ningaloo. This was largely because of a shift in the relative dominance of the 2 major epifaunal taxa: crustaceans dominated the *Sargassum* epifauna in macroalgal meadows close to coral reef (i.e., back reef sites), while epifaunal molluscs predominated in nearshore and lagoonal macroalgal meadows. This is significant because these 2 invertebrate groups may have very different levels of growth (secondary production) to support consumption by higher-order consumers like fishes using different strategies for consumption and processing of these 2 prey types (Wainwright 1988, Edgar 1990a,b,c, Kramer et al. 2015). If so, then adjacent macroalgal meadows separated by relatively fine spatial scales (100s of metres to a few kilometres) may have remarkably different trophodynamics.

Strong canopy–epifauna relationships such as those revealed here indicate some broader consequences for the conservation and management of diverse and productive tropical seascapes. Across the range of canopy sizes examined here, which span a typical range of *Sargassum* canopy sizes that have been observed across sites, seasons and years in this region (Wilson et al. 2014, van Lier et al. 2018), we can see that even small reductions in canopy extent can translate to much lower epifaunal abundance with flow-on effects for associated species and overall ecosystem function. A reduction in *Sargassum* canopy from disturbance or seasonal effects is likely to trigger a trophic cascade in reduced productivity at higher trophic levels, with variable consequences across the seascape. The non-linear nature of these effects suggests a particularly severe reduction in epifaunal abundance for canopies below 30 to 60 cm height at Ningaloo. Indeed, similar reductions in canopy size due to seasonal cycles in *Sargassum* phenology have been linked to major declines in the abundance of macroalgal-dependent fishes (Lim et al. 2016, Wenger et al. 2018). Besides a reduction in the overall abundance of epifauna with canopy reductions, there may also be a loss of certain taxa (e.g., shifts in the gammarid crustacean epifauna over seasonal *Sargassum* canopy cycles; Kodama et al. 2020) that are key components in nutrient cycling and trophic flows. A major cause for concern is that one of the key stressors of climate change—sea temperature—is a primary determinant of *Sargassum* canopy growth in tropical reef settings around the world (Fulton et al. 2019). Alongside disturbances like marine heatwaves and cyclones (Fulton et al. 2019) which can dramatically reduce *Sargassum* canopy size in a short time, these climatic effects can drive a bottom-up collapse of trophic flows to higher-order consumers, including fish species that underpin productive tropical fisheries linked to the livelihoods of millions of people across the tropical world (Robinson et al. 2019, Fulton et al. 2019). As such, we suggest that tropical macroalgal canopy conditions should be a key metric in habitat-based fisheries management and spatial approaches to conservation that seek to encompass a representative cross-section of biodiversity across a range of seascape settings. The thermal thresholds that may underpin major shifts in epifaunal abundance and production should be a key priority for future experimental work and targeted multi-season and multi-year field studies.

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Appendix

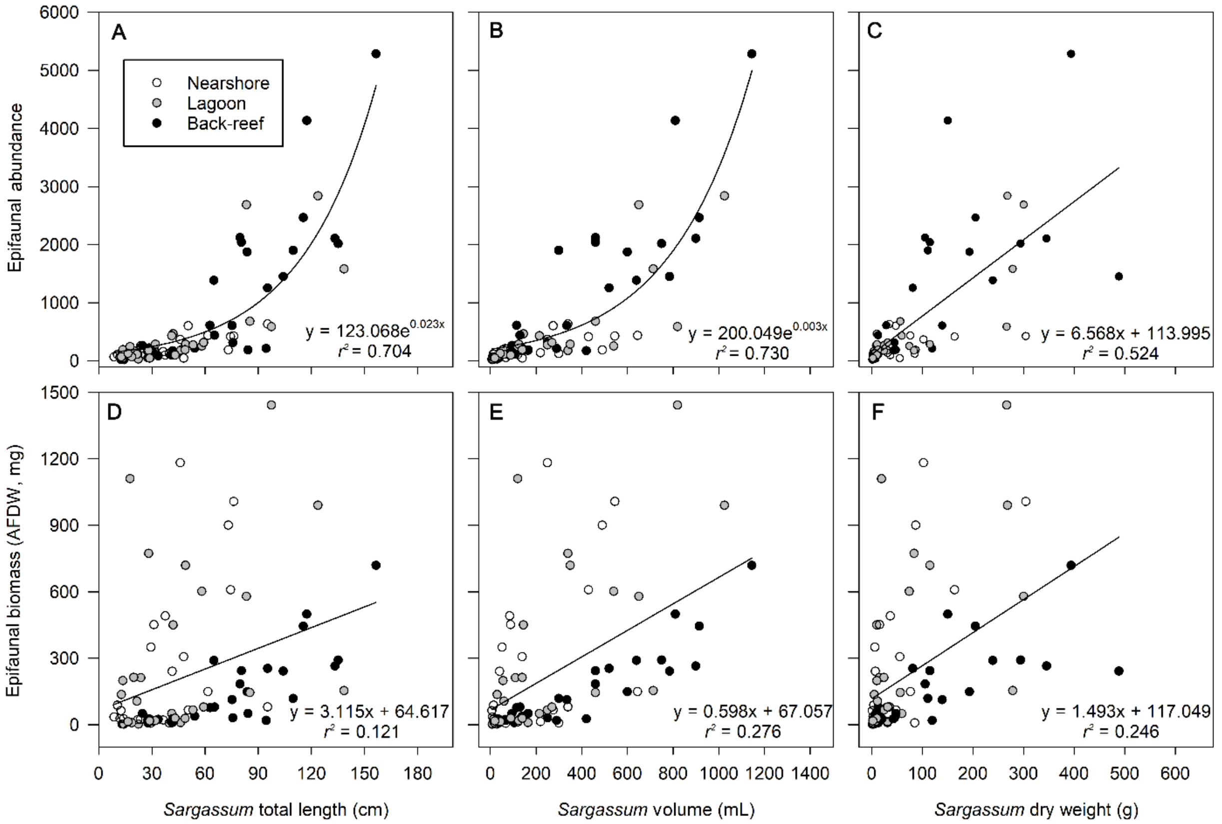
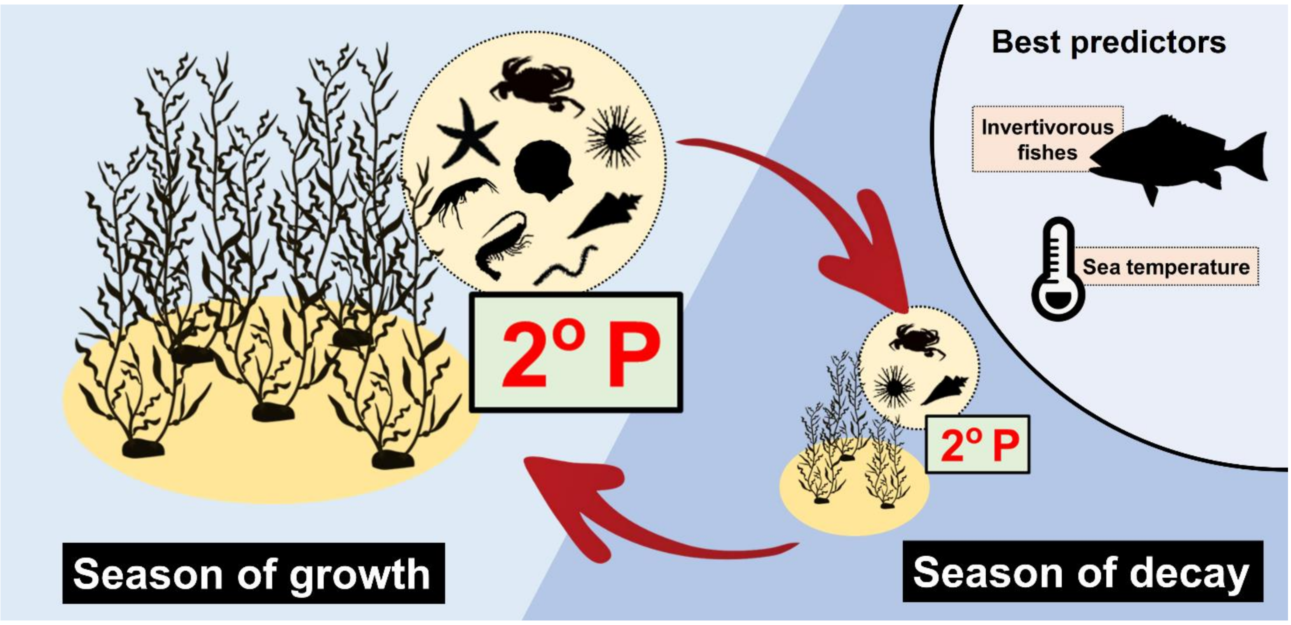


Figure A3.1 Relationship between different measures of *Sargassum* canopy size (total length, volume, and dry weight) and either (A–C) epifaunal abundance (total individuals per *S. polycystum*) or (D–F) epifaunal biomass (ash free dry weight per *S. polycystum*) collected from 9 study sites at 3 seascape positions (nearshore, lagoon, and back reef) in the Maud region of Ningaloo Reef, Australia, during summer 2018.

CHAPTER 4

QUANTIFYING EPIFAUNAL SECONDARY PRODUCTION WITHIN TROPICAL MACROALGAL MEADOWS: SEASONALITY AND SENSITIVITY TO CANOPY STRUCTURE



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Co-authored with Cooper, P., Fulton, C.J. and Fox, R.J.

Abstract

Secondary production connects primary producers with higher-order consumers. The response of secondary production to seasonal variation in primary producers can influence trophic flows that underpin key ecosystem functions and services. Within the canopy-forming macroalgal meadows of Ningaloo Reef, Western Australia, we quantified the secondary production generated by *Sargassum*-associated epifauna across seasons and seascapes. We found a strong positive correlation between overall epifaunal production and *Sargassum* canopy size. Variation in epifaunal production was predominantly driven by seasonal changes in *Sargassum* canopy size. However, these seasonal effects were not uniform across the seascape. Key predictors of spatial and temporal variation in epifaunal production were the presence of invertivorous fish families, as well as daily and monthly fluctuations in sea temperature. Areal estimates of epifaunal productivity were much higher in summer than in winter, due to higher *Sargassum* canopy size and percent cover in summer. Epifaunal production was estimated to be more sensitive to *Sargassum* percentage cover than to canopy height. Modelling a 45% reduction in canopy height and percent cover of *Sargassum* associated with a marine heatwave event revealed a potential 81% drop in the areal rate of secondary production by *Sargassum* epifauna in this tropical fringing reef ecosystem. Disturbances to *Sargassum* canopy structure driven by global change can therefore significantly alter the productivity of these tropical macroalgal meadows and their ability to support higher level consumers within the food web, including important fisheries species. Our results highlight the importance of including epifaunal production estimates in predictive modelling when managing macroalgal-dominated marine ecosystems.

Keywords: Canopy Macroalgae, Climate Change, Ecosystem Functioning, Epifauna, Invertivorous Fishes, *Sargassum* spp., Seasonality, Secondary Production

Introduction

Biological production is essential to the functioning of every aquatic ecosystem. The conversion of sunlight to organic material and subsequent promotion of energy flow through food webs generate the linkage between biodiversity and ecosystem stability which, in turn, underpin all ecosystem processes, services and functions (Falkowski 1980, Mace et al. 2012). Discussion of biological production typically focuses on measuring primary production, determining how these flows are regulated by abiotic and/or biotic factors, with related applications in environmental science (Field et al. 1998, Brown et al. 2010). By contrast, secondary production – or the generation of biomass by heterotrophs – tends to be less well studied in aquatic ecosystems, although is equally important in connecting primary producers with higher-order consumers, integrating individual process and population fitness, and incorporating biotic interactions with abiotic conditions that can influence energy flows (Brey 1989, Benke et al. 2001). Quantification of secondary production is also a useful tool for understanding ecosystem dynamics, the relationships between biodiversity and ecosystem functioning, and the impact of environmental changes on those relationships (Benke & Huryn 2010, Dolbeth et al. 2011, Dolbeth et al. 2012).

Levels of production within an ecosystem are rarely fixed throughout the year. They can be profoundly influenced by temporal fluctuations in physical drivers (e.g., temperature, humidity, light, nutrient). In many cases, these factors can create repeating patterns of seasonality: predictable periods of higher production during certain seasons (usually summer or wet season) with some intervals (usually winter or dry season) experiencing low production (Longhurst 1995, Pennington & Chavez 2000). Seasonality of production affects biodiversity and ecosystem functioning, because both primary producers and higher-order consumers respond to changes in energy fluxes which affect their abundance, biomass and fitness (Longhurst 1995, Dudgeon 2000). Trophic flows can be bi-directionally regulated by top-down and bottom-up effects, meaning that the response of secondary producers to seasonal fluctuations in primary production can result in critical flow-on effects for the ecosystems they support (Benke 2010, Lewis&Anderson 2012). On top of these predictable seasonal changes, the effects of global change can add a layer of uncertainty. Alterations to the timing or phenology of seasonal patterns, as well as moderation or exaggeration of their abiotic extremes (e.g., rising temperatures during winter, increased frequency of extreme weather events during summer) can significantly reshape biological communities, with associated effects on biodiversity and ecosystem functioning (Emmerson et al. 2005, Pennington et al. 2006). Knowledge of baseline seasonal modulations in productivity will be fundamental to our ability to predict the additional effects of global change on production levels within ecosystems.

Within marine ecosystems, one of the largest contributors to secondary production are the epifaunal communities (Edgar 1990a, Edgar 1990b, Taylor 1998a, Cowles et al. 2009). Epifauna are animals found attached to living and/or non-living surfaces, with a wide range of body size but typically 0.5-10 mm long (Chen et al. 2021). Their extreme abundance and rapid turnover rate make them an essential part of the marine food web, connecting benthic primary producers and higher-order consumers such as carnivorous invertebrates and invertivorous fishes (Newcombe & Taylor 2010, Wenger et al. 2018, Chen et al. 2021). Epifauna are typically associated with large macrophytes, such as macroalgae or seagrasses, and previous studies have shown that epifauna can experience seasonal fluctuations in their abundance and biomass (Veiga et al. 2014, Ba-Akdah et al. 2016, Chen et al. 2021), corresponding to seasonality in host morphology (e.g., biomass, volume), habitat conditions (e.g., structural complexity, benthic composition, predation) and environmental parameters (e.g., sea temperature, nutrient concentration) (Edgar 1990a, Taylor & Cole 1994, Taylor 1998a). However, few studies have quantified the associated seasonal changes in secondary production by the epifaunal community, meaning that the response of epifaunal production to seasonal ecosystem dynamics are not well understood (Gan et al. 2019, Fraser et al. 2020a).

One of the most common habitat-forming macrophytes within tropical reef ecosystems are fucoid macroalgae belonging to the genus *Sargassum*. Canopies of *Sargassum* can extend into large meadows, making up a large proportion of the total areal primary production within tropical reef ecosystems (Fulton et al. 2019). *Sargassum* is known to harbour an abundance of epifauna whose community structure varies over space and time in association with *Sargassum* canopy size (e.g., total length, canopy volume, canopy dry weight), canopy structure (e.g., canopy vertical height, holdfast density, canopy percent cover), presence of invertivorous fishes and local environmental conditions (Edgar & Aoki 1993, Leite & Turra 2003, Chen et al. 2020). However, this key habitat-forming macrophyte can exhibit strong temporal shifts in canopy size and structure. In tropical regions, *Sargassum* chiefly shows two patterns of seasonal fluctuations: (1) canopy growth in summer and detachment in winter (Leite & Turra 2003, Lefevre & Bellwood 2010, Fulton et al. 2014); or (2) winter growth followed by summer canopy detachment (Trono & Lluisma 1990, Ang 2006, Ateweberhan et al. 2009). The canopy size and structure of *Sargassum* can, therefore, exhibit strong seasonal fluctuations from shifts in sea temperature (Ateweberhan et al. 2006, Fulton et al.

2014). While these seasonal fluctuations in *Sargassum* canopy structure and the impact on associated epifaunal communities have been documented (Leite & Turra 2003, Ba-Akdah et al. 2016), we currently have little understanding of how such fluctuations influence secondary production by epifauna, and the likely implications for trophic flows within tropical reef ecosystems.

We examined the consequences of seasonal variation in *Sargassum* canopy size for secondary production by associated epifaunal communities with shallow marine habitats of the Ningaloo coast, Western Australia. Using Edgar's empirical equation (1990b), we quantified the seasonal secondary production of epifauna across tropical seascapes to: (1) determine the relationship between epifaunal secondary productivity and macroalgal canopy size; (2) explore the responses of epifaunal secondary productivity to temporal and spatial changes in macroalgal canopies; (3) identify the best predictors for spatial and temporal variations in epifaunal secondary productivity; and (4) estimate the sensitivity of areal estimates of secondary epifaunal productivity to modelled shifts in macroalgal canopy structure.

Materials and methods

Study location

The study was conducted within Ningaloo Marine Park, situated in the northwest coastal region of Western Australia. This area, bordering the Ningaloo Coast, is Australia's largest fringing coral reef (290 km long) and encloses a shallow lagoon dominated by brown macroalgal, chiefly belonging to the canopy-forming genus *Sargassum* which produce dense canopies and anchors themselves into the benthic substrate with holdfasts to form massive meadows. The term 'meadow' is used here in an equivalent sense to the term 'bed', and the two can be considered synonmous. The extensive *Sargassum* meadows cover an area of over 300 km^2 and exhibit dramatic seasonal fluctuations in canopy biomass (Kobryn et al. 2013, Fulton et al. 2014, van Lier et al. 2018; Figure 4.1a, b). Due to the difficulty of providing taxonomically-accurate identification of individual species of *Sargassum* in the field, we focused on the most common morphotype of *Sargassum* present in these meadows (but most likely to be the species *S. polycystum*), thereby ensuring consistency of sampling between meadow patches. Within a 6 km^2 section of the Maud Recreation Zone (south of Coral Bay), we selected nine distinct *Sargassum* meadow patches separated by at least 300 m, distributed across three distinct seascape positions (nearshore, lagoon, back reef, three meadows per seascape position, van Lier et al. 2018; Figure 4.1c). Both nearshore and lagoon patches were embedded within a pavement-sand matrix that was an ancient reef pavement covered with 1-3 cm thick sand. Back reef patches were embedded within the same pavement-sand matrix but surrounded by fringing coral reefs.

Sampling and post-collection processing

To determine the temporal and spatial differences in epifaunal secondary production among habitats, we collected nine whole *Sargassum* individuals with their associated epifauna from each of the nine meadows in austral summer (Feb-Mar 2018) and in again in austral winter (Aug-Sept 2018). Sample sizes were selected based on the desire to maximise within-meadow sampling, subject to the constraint of sample-processing time. One site (B1) was not able to be accessed for the winter sampling, resulting in 71 *Sargassum* samples collected in winter and 81 samples collected in summer (n = 152). As *Sargassum* canopy size (e.g., total length, volume, biomass) is a key predictor for epifaunal abundance and biomass (Edgar 1990b, Wenger et al. 2018, Chen et al. 2020), we sampled a cross-section of *Sargassum* canopy sizes within each meadow patch. Collections were conducted by divers on SCUBA using a line-transect method (following Chen et al. 2020). Briefly, starting from the centre of each meadow patch, we haphazardly ran a 15 m transect tape out to the patch edge. At 5, 10 and 15 m we collected three *Sargassum* individuals of varying thallus length. For each individual, the entire thallus and associated epifauna were fully enclosed within a canvas bag, the stipe cut just above the holdfast, and the bag sealed immediately to prevent loss of any epifauna. All samples were brought back to the research vessel and put on ice, with post-collection processing conducted at the Coral Bay Research Station within 4 hours of collection. Each *Sargassum* individual was immersed in cold freshwater for ten minutes to numb the associated epifauna, then gently shaken and placed into a salad spinner to dislodge the epifauna. These epifauna were washed into a labelled zip bag and frozen at -20°C for transportation to The Australian National University for fixation (10% formalin seawater solution) and further analysis. We also quantified the canopy size of each *Sargassum* host in terms of four measured variables: total length (cm, from stipe end to tip); total volume (mL, measured via displacement of freshwater in a measuring cylinder); total wet weight (g WW); and dry weight (g DW, oven-dried at 60°C for 48 hours).

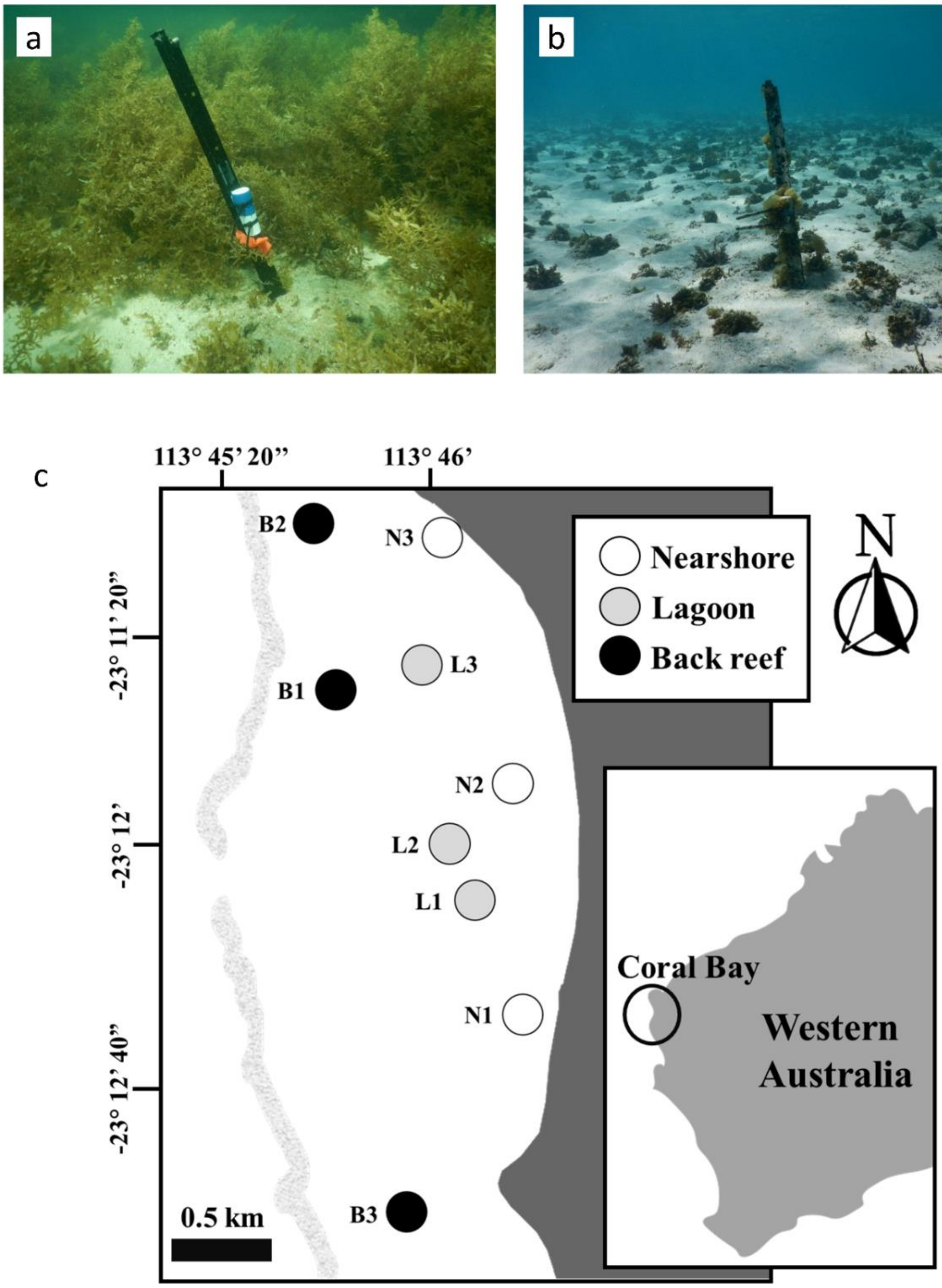

Figure 4.1 (a) Dense, tall canopies of *Sargassum* in Austral summer; (b) sparse coverage and short stipes of *Sargassum* remaining in winter. Images were taken at the same lagoonal meadow patch in (a) March 2018 and (b) August 2018 (Photo credits: David Ellis), showing the huge shifts of *Sargassum* canopy size and percent cover within Ningaloo Marine Park, Western Australia; and (c) Study site and sampling location of the nine *Sargassum* meadow patches sampled in summer and winter 2018 at three seascape positions (nearshore, lagoon, back reef) within Maud Recreation Zone near Coral Bay, Ningaloo Reef, Western Australia.

Estimates of epifaunal biomass and productivity

Estimates of epifaunal productivity (µg day^{-1}) were obtained from the standing epifaunal biomass (ash free dry weight, AFDW, in µg) collected from each *Sargassum* individual. Biomass estimates were obtained following the sieve method of Edgar 1990b (see Chen et al. 2020 for details). Briefly, formalin-fixed epifaunal samples were poured through a series of stainless steel sieves (5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.7 and 0.5 mm mesh sizes) to fractionate the invertebrates by body size. Epifauna retained on each sieve were identified under a stereo microscope with 40x magnification and recorded under one of four taxonomic groups adapted from Edgar (1990b): crustaceans, molluscs, polychaetes and 'other animals'. We excluded from our definition of epifauna any invertebrates > 5.6 mm. Using the number of individuals in each taxonomic group retained per sieve size, we then calculated the total biomass (AFDW) of each group using Edgar's empirically-derived equations (1990b). For each *Sargassum* individual sampled, these biomass estimates were then converted into estimates of daily overall secondary production associated with each taxonomic group using the empirical equation of Edgar (1990b):

$$P = 0.01\, B^{0.78}\, T^{0.68} \qquad (1)$$

where P is overall secondary productivity (µg day^{-1}), B is epifaunal AFDW (µg), and T is mean water temperature T (°C) for a given meadow patch. Finally, we standardised these daily overall rates of epifaunal secondary production based on the canopy dry weight (g) of each *Sargassum* individual from which they were obtained, to adjust for differences in *Sargassum* canopy size (µg day^{-1}g DW^{-1}).

Sampling of associated biotic and abiotic habitat variables

At each meadow patch, in each season, we carried out underwater censuses on SCUBA to estimate the abundance of invertivorous fishes. Using a point-census cylinder survey method (see Noble et al. 2013), we recorded the presence of individuals belonging to the families Labridae (excluding Scarinae), Lethrinidae and Mullidae, known to be the dominant invertivores within tropical macroalgal meadows (Edgar & Aoki 1993, Wilson et al. 2010, Wenger et al. 2018). At each meadow patch we conducted six replicate surveys, with a single diver recording the presence and total length (cm) of individuals within a 5 m diameter cylinder. Abundances were converted to biomass estimates using published length-weight relationships for each species (Kulbicki et al. 2005a, Froese & Pauly 2021) and summed to give areal biomass estimates of each fish family within the meadow patch.

The benthic composition of each meadow patch in summer and winter was recorded via underwater visual censuses conducted by SCUBA. Six replicate 10 m transect tapes were deployed by divers, with percent cover (%) of all macroalgal genera along the transect recorded (total amount of the 10 m covered by each species, to the nearest 5 cm). The habitat context of each meadow in both summer and winter was also quantified from these data, in terms of taxonomic macroalgal genera richness, Pielou's evenness, maximum vertical canopy height of *Sargassum* (to nearest cm) and *Sargassum* holdfast density (holdfast number within a 0.5 × 0.5 m quadrat). Maximum vertical canopy height and holdfast density of *Sargassum* were measured at 2 m intervals (starting at 0 m) to yield six replicates within a line transect, following Wilson et al. (2014).

To record patch-level sea surface temperature, we deployed submersible temperature loggers (Onset HOBO Pro v2) at a height 30 cm above the pavement-sand matrix (cable-tied to a metal stake embedded in the centre of each meadow patch, one logger per meadow). Ambient water temperature was logged at 1-hour intervals over the entire study period (see Figure S4.1 in Supplemental Information). Variables relating to the average water depth at each meadow patch and the distance from each patch to the nearest fringing reef habitat were taken from van Lier et al. (2018) and Chen et al. (2020).

Data analyses

To determine the relationship between overall epifaunal productivity (µg day^{-1}) and its host canopy size (in terms of canopy dry weight, g DW) of each sampled *Sargassum* individual, we used least squares regression. Both variables were log-transformed to meet the assumptions of linearity and normality of distribution. We then conducted a Principal Components Analysis (PCA) to explore the sample-level variation in overall epifaunal productivity across seasons and seascapes, with vector overlays to indicate degree of Pearson's correlation between the overall epifaunal productivity and the ordination structure. Data were $\log_{10}(x+1)$-transformed to reduce skew. To test for the effects of seasonality and seascape position on overall epifaunal productivity, we ran a three-way multivariate permutational analysis of covariance (PERMANCOVA), with productivity of the four taxonomic groups of epifauna as dependent variables. We treated season (summer, winter) and seascape position (nearshore, lagoon, back reef) as fixed factors and meadow patch as a random factor (nested in seascape). We controlled for the observed positive relationship between epifaunal productivity and *Sargassum* canopy size by including *Sargassum* dry weight (log transformed) as a covariate in the model, as previous studies have found that *Sargassum* canopy dry weight is most strongly correlated with epifaunal biomass (Edgar & Aoki 1993, Leite & Turra 2003, Chen et al. 2020). The PERMANCOVA was performed with Type I (sequential) sum of squares and a maximum of 9999 permutations of resemblance matrices based on the modified Gower (base 2) dissimilarity (Anderson et al. 2006, 2008). Post-hoc explorations of significant terms were explored with threshold-metric Multi-Dimensional Scaling (tmMDS) ordinations of the patch-seascape-season group centroids.

To examine possible predictors of patch level variations in epifaunal productivity across seasons, we used distance-based linear models (DistLM) and the Akaike Information Criterion corrected for finite sample sizes (AICc) as best-subsets model selection (following Burnham & Anderson 2002). These analyses were based on mass-standardised estimates of epifaunal productivity (epifaunal productivity per dry weight of sampled *Sargassum* individual, µg $day^{-1}g$ DW^{-1}) to account for the effect of *Sargassum* canopy size on epifaunal productivity (see above) and fourth-root transformed to correct for skew. Data were arranged into a modified Gower (log base 2) resemblance matrix. Our potential driver matrix was based on four groups of possible predictors: (1) invertivorous fish biomass (Labridae, Lethrinidae, Mullidae), (2) habitat context (*Sargassum* canopy height, percent cover of *Sargassum*, percent cover of understory macroalgal taxa, taxonomic genera richness of macroalgae, Pielou's evenness of macroalgae), (3) seascape context (distance to nearest neighbouring meadow, distance to fringing reef, water depth), and (4) sea temperature (average daily minimum temperature, monthly temperature range, average daily temperature fluctuation), because seasonal differences in hourly sea temperature varied significantly between meadow patches (ANOVA, significant season*meadow patch interaction, $F = 10.823$, $P < 0.0001$). The best models for predicting patch-level epifaunal productivity were considered to be those within two AICc units of the overall top model, following Burnham & Anderson (2002). Variations in epifaunal productivity according to the best models were visualised using distance-based redundancy analysis (dbRDA) ordinations (all model subset groups are presented in Supplemental information for completeness, see Figure S4.2). All of the above multivariate analyses were performed in PRIMER (version 7.0.13) with the Permanova+ add-on (Anderson et al. 2008).

To examine the effect of changes in *Sargassum* canopy structure on epifaunal production, we converted our standardised measures of secondary productivity (µg day^{-1} g DW^{-1}) into estimates of areal productivity (mg m^{-2} day^{-1}). First we calculated the mean areal *Sargassum* canopy biomass within each meadow patch using an empirical relationship derived by Fulton and Wilson (unpublished data), combined with estimates of *Sargassum* structure within each patch obtained from our benthic surveys:

$$Y = 216.65\, e^{\,0.435\,(C + H \times D)}, \qquad (2)$$

where Y is the areal canopy wet weight (kg 0.25 m^{-2}), C is the mean *Sargassum* canopy cover under the 10 m line transect (m), H is the mean maximum vertical canopy height of *Sargassum* (m) and D is the mean *Sargassum* holdfast density (0.25 m^{-2}). Conversion factors of Brey et al. (2010) were used to convert the areal canopy biomass from wet weight to dry weight. These estimates of mean areal *Sargassum* canopy biomass within each meadow patch were then multiplied by our mass-standardised measures of epifaunal secondary productivity to yield an overall estimate of areal epifaunal secondary productivity (mg m^{-2} day^{-1}) for each meadow patch in both summer and winter. Compound error terms for the uncertainty around these estimates were calculated using Goodman's estimator for the variance of two independent random variables (following Travis 1982).

We then conducted sensitivity analyses to model predicted rates of epifaunal production associated with three types of environmental scenario: (1) shifts in *Sargassum* canopy vertical height (specifically 30, 60, 90, 120 cm representing the small, medium, large and extreme sizes of *Sargassum* canopy at this location), combined with static 50% canopy cover and 5 holdfasts per 0.25 m^{-2}; (2) shifts in *Sargassum* percent cover (25, 50, 75, 100% representing low, medium, high and full cover of *Sargassum*, respectively) combined with a static assumption of 60 cm vertical canopy height and 5 holdfasts per 0.25 m^{-2}); and (3) a combination of shifting *Sargassum* canopy height and percent cover with static 5 holdfasts per 0.25 m^{-2}.

Results

Overall epifaunal productivity and its relationship with Sargassum canopy size

Water temperatures across the study region as a whole averaged 26.6 ± 0.01°C during the summer, and 21.4 ± 0.01°C during the winter collection periods (Figure S4.1). Strong differences were evident in the secondary production of *Sargassum*-associated epifaunal communities across summer and winter, with secondary production reaching higher magnitudes during summer, but only at sites where extensive canopies were present. In both summer and winter, overall epifaunal productivity was positively correlated with *Sargassum* canopy size in terms of dry weight (Figure 4.2). However, the overall relationship between overall epifaunal productivity and *Sargassum* dry weight varied between seasons and across parts of the seascape (significant interactions recorded between *Sargassum* dry weight and season, and *Sargassum* dry weight and seascape, after controlling for *Sargassum* dry weight as a covariate) (Table 4.1). This was due to high values of *Sargassum* dry weight and productivity being driven by the back reef in summer, versus nearshore and lagoon meadow patches in winter (Figure 4.2a, b).

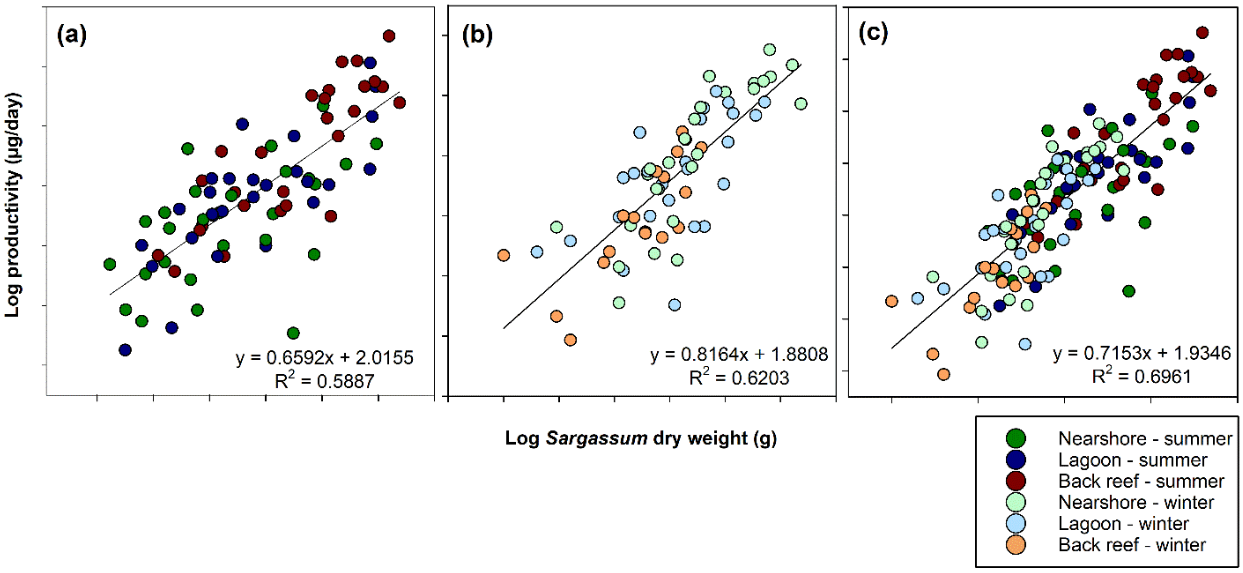

Figure 4.2 Log-log plots of the relationships between overall epifaunal productivity and *Sargassum* canopy size (in terms of dry weight) during (a) summer, (b) winter, and (c) both seasons in 2018, from nine meadow patches (*n* = 9 samples per patch) at three seascape positions in the Maud Recreational Region near Coral Bay, Ningaloo Reef, Western Australia.

Seasonal and spatial variation in epifaunal productivity

Variation in overall epifaunal productivity between samples did not show clear separation by season or by seascape, with samples from summer and winter overlapping along the main axis of variation (70.9% of variation explained) (Figure 4.3a). The positioning of samples along this main axis was positively related to the biomass of all epifaunal taxa, in particular molluscs and crustaceans, which projected the furthest distance along PC1 (Figure 4.3b). Across the two seasons, nearly 90% of the measured productivity was derived from crustaceans (53%) and molluscs (36%), with the remainder derived from polychaetes (2%) and other animals (9%; mostly ophiuroids, nematodes and foraminifera). Summer productivity showed a similar contribution of taxonomic composition, dominated by crustaceans (51%) and molluscs (39%) (Figure 4.3c-f). While in winter, the contribution of molluscs declined substantially (to 14%) and the contribution of crustaceans (64%) and other animals (19%) increased (Figure 4.3c-f). This seasonal switch in the emphasis between molluscs and other animals could be seen in the separation of samples along PC2 (Figure 4.3a, b).

Table 4.1 Summary of PERMANCOVA of epifaunal productivity across two seasons (fixed), three seascape positions (fixed) and nine meadow patches (random, nested in seascape) in the Maud region near Coral Bay of Ningaloo Reef, 2018, with logged *Sargassum* canopy dry weight included as a covariate. Significant terms ($p < 0.05$) are highlighted in **bold**.

Source	**df**	**SS**	**MS**	**Pseudo-*F***	***p*-value**
***Sargassum* dry weight**	1	13.299	13.299	304.19	**0.0001**
Season	1	0.025	0.025	0.139	0.721
Seascape	2	0.052	0.026	0.342	0.697
Meadow patch (Seascape)	6	0.468	0.078	1.871	0.089
***Sargassum* dry weight × Season**	1	1.106	1.106	22.329	**0.0001**
***Sargassum* dry weight × Seascape**	2	0.326	0.163	3.907	**0.0232**
Season × Seascape	2	0.002	0.001	0.005	0.996
Sargassum dry weight × Meadow patch (Seascape)	6	0.184	0.031	0.736	0.615
Season × Meadow patch (Seascape)	5	1.006	0.201	4.821	**0.0011**
Sargassum dry weight × Season × Seascape	2	0.131	0.066	1.573	0.213
Sargassum dry weight × Season × Meadow patch (Seascape)	4	0.233	0.058	1.398	0.240
Residual	119	4.964	0.042		
Total	151	21.796			

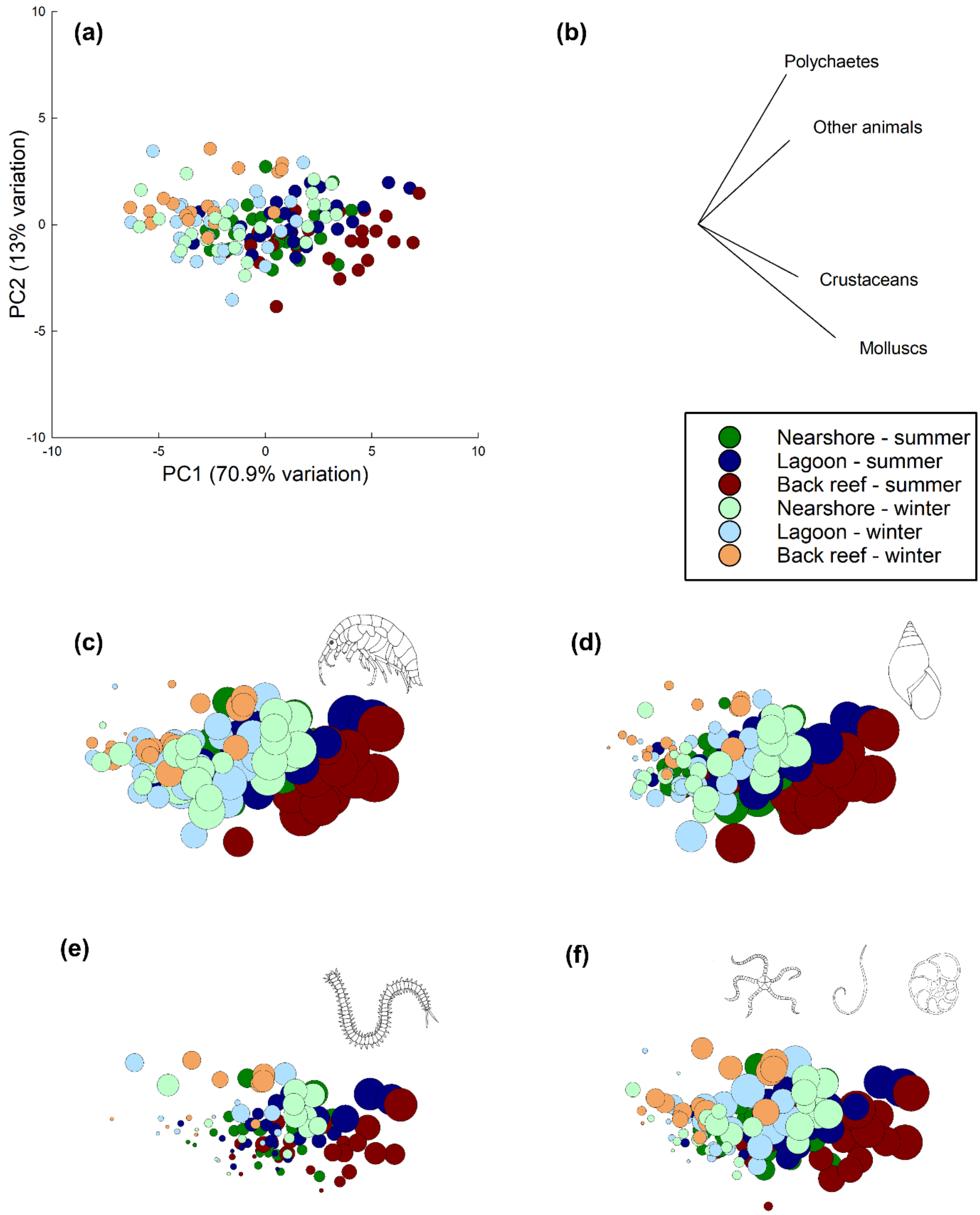

Figure 4.3 Principal Component Analysis (PCA) of overall epifaunal productivity on 152 *Sargassum* individuals collected from nine meadow patches at three seascape positions during summer and winter in the Maud Recreational Region near Coral Bay, Ningaloo Reef. (a) Total overall epifaunal productivity, (b) vector overlays of epifaunal taxonomic groups strongly correlated with the ordination structure, and (c-f) ordinations optimised with bubbles size proportional to relative productivity of each taxonomic group: (c) crustaceans, (d) molluscs, (e) polychaetes and (f) other animals.

The seasonal variation in overall epifaunal productivity was not spatially consistent across the Ningaloo seascapes, with a significant interaction observed between season and meadow patches (nested in seascape positions), controlling for *Sargassum* canopy size (Table 4.1). Whereas back reef and lagoon meadow patches showed strong differences in overall productivity between summer and winter, nearshore meadows showed much weaker seasonal differences in epifaunal productivity (Figure 4.4). In summer particularly, there was high variability of *Sargassum* canopy dry weight among meadow patches within a given seascape zone, particularly for the lagoon and nearshore (Figure 4.4).

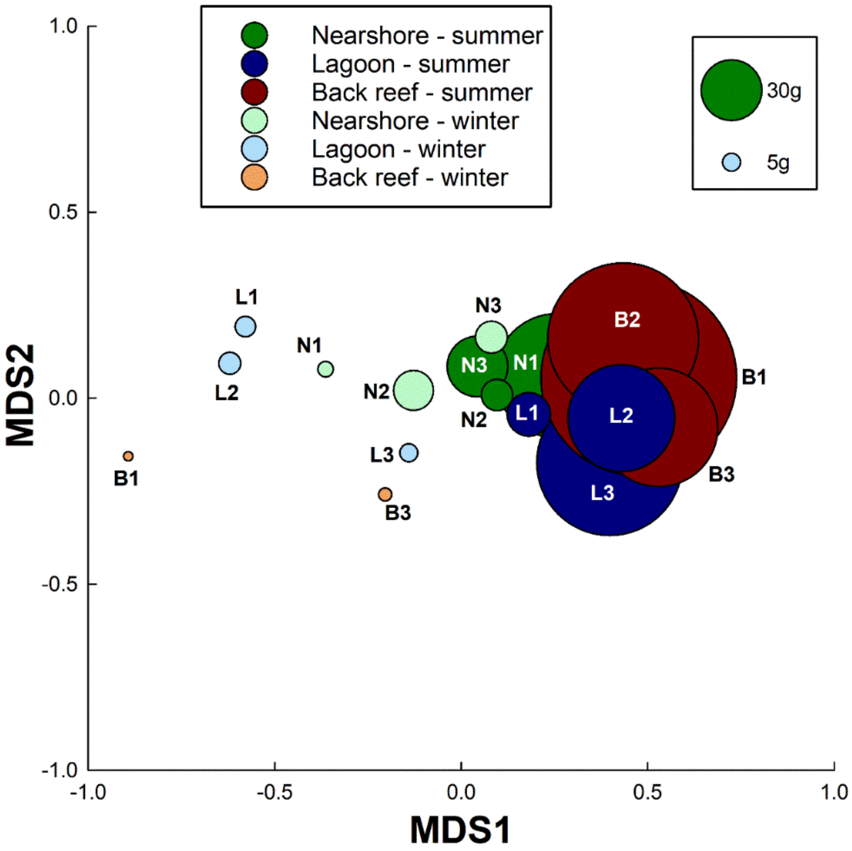

Figure 4.4 Threshold-metric Multi-Dimensional Scaling (tmMDS) ordination of the patch-seascape-season group centroids for overall epifaunal productivity obtained from nine meadow patches at three seascape positions during summer and winter in the Maud Recreational Region near Coral Bay, Ningaloo Reef (stress value: 0.06). Bubble sizes are proportional to patch-level mean *Sargassum* canopy dry weight, to explore the significant interactions among canopy size, seasons, meadow patches and seascape positions (see Table 4.1).

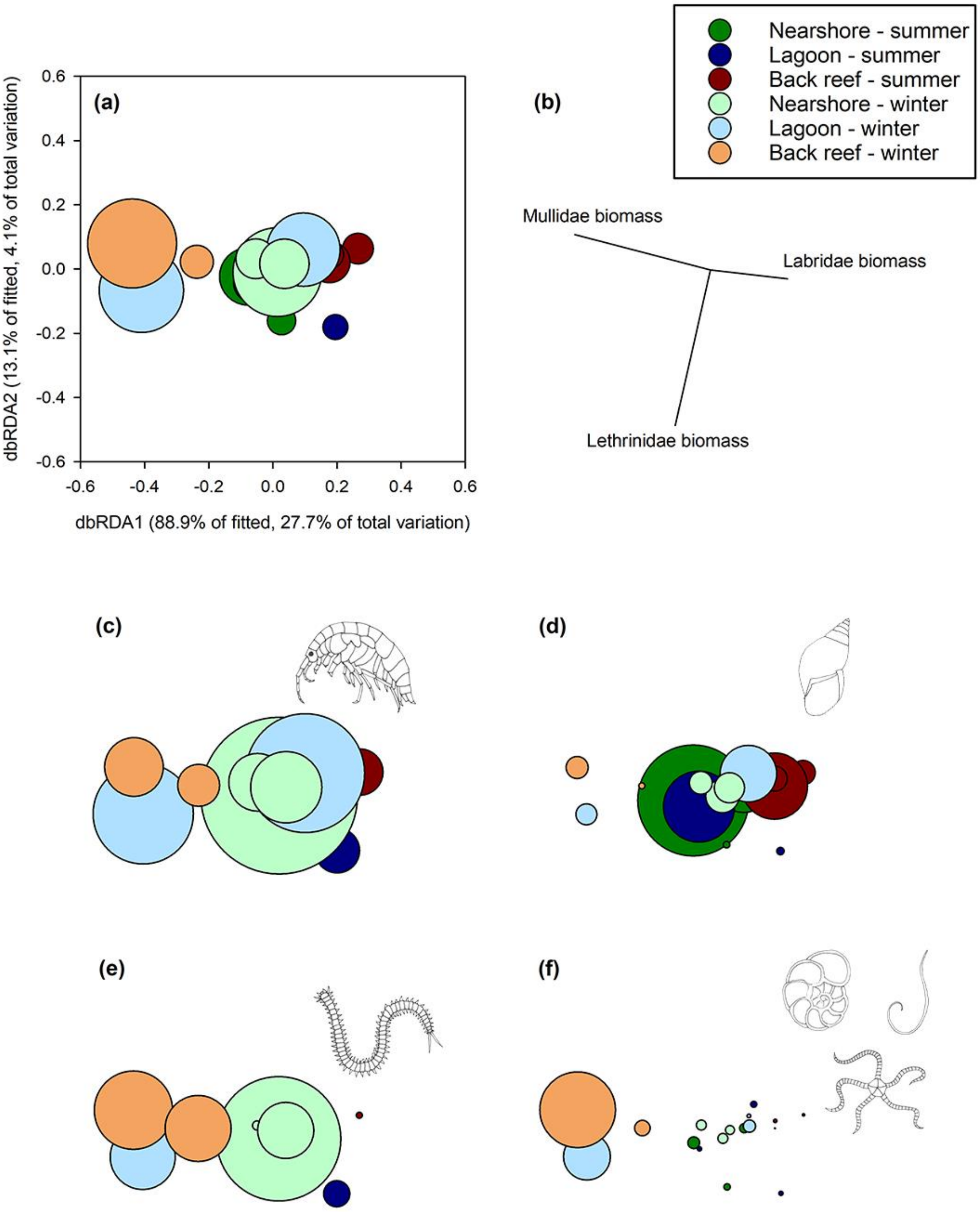

Figure 4.5 Distance-based redundancy analysis (dbRDA) ordination of the most parsimonious best-subsets models in terms of invertivorous fish biomass for predicting the patch-level variations in mass-standardised epifaunal productivity across taxonomic groups from nine meadow patches at three seascape positions during summer and winter in the Maud Recreational Region near Coral Bay, Ningaloo Reef: (a) overall taxonomic groups, (b) vector overlays indicating potential drivers which strongly correlated with each ordination structure, (c) crustaceans, (d) molluscs, (e) polychaetes, and (f) other animals. Bubble sizes are proportional to patch-level productivity that is standardised by *Sargassum* dry weight to take account of the positive correlation between canopy size and epifaunal productivity.

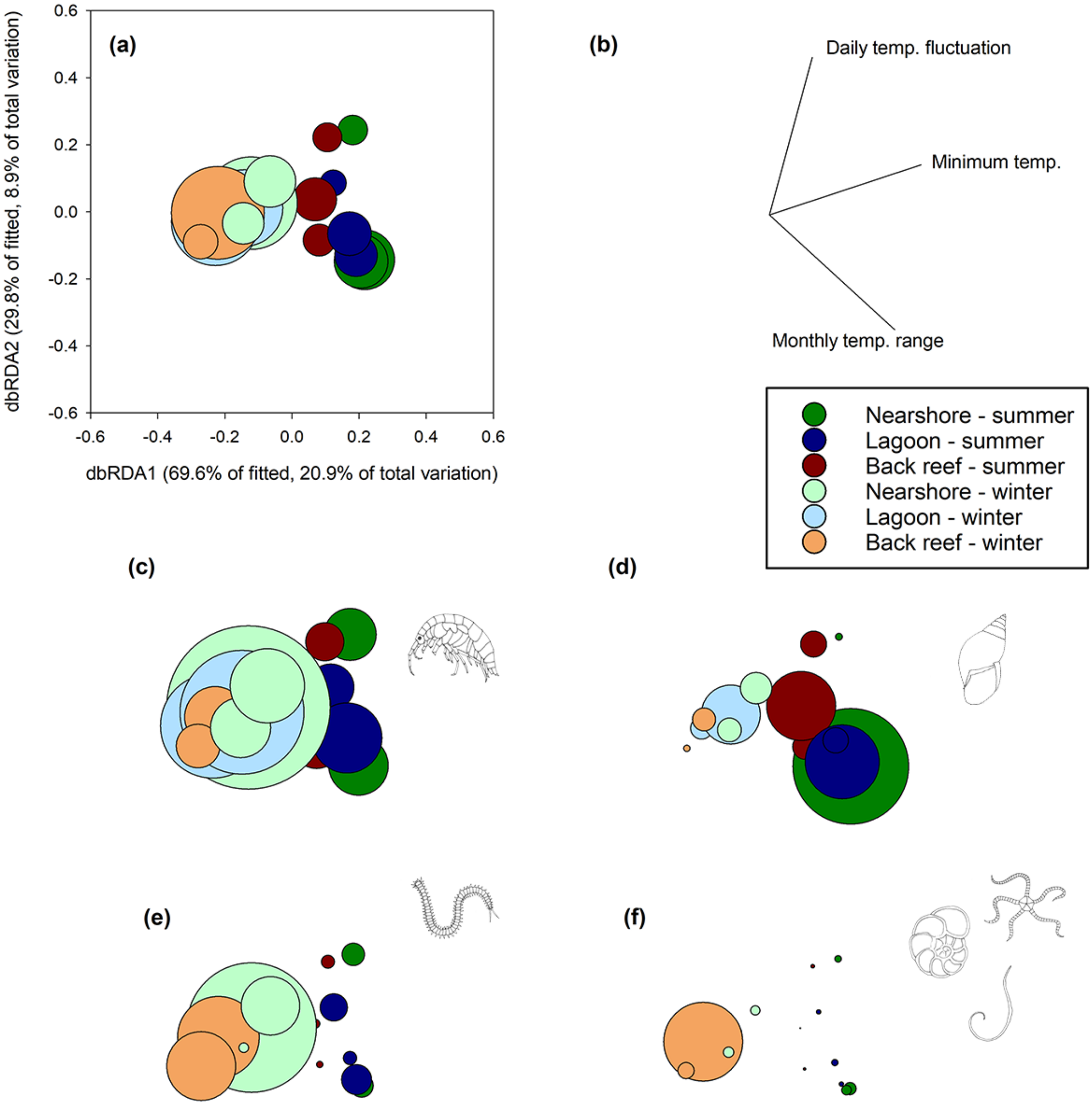

Figure 4.6 Distance-based redundancy analysis (dbRDA) ordination of the most parsimonious best-subsets models in terms of sea temperature for predicting the patch level variations in mass-standardised epifaunal productivity across taxonomic groups from nine meadow patches at three seascape positions during summer and winter in the Maud Recreational Region near Coral Bay, Ningaloo Reef: (a) overall taxonomic groups, (b) vector overlays indicating potential drivers which strongly correlated with each ordination structure, (c) crustaceans, (d) molluscs, (e) polychaetes, and (f) other animals. Bubble sizes are proportional to patch-level productivity that is standardised by *Sargassum* dry weight to take account of the positive correlation between canopy size and epifaunal productivity.

Predictors of observed variation in epifaunal productivity

When values of epifaunal productivity were standardised by *Sargassum* canopy dry weight to account for the positive correlation between canopy size and productivity (converted to µg day^{-1} g DW^{-1}), estimates of mass-standardised winter epifaunal productivity per g of *Sargassum* DW exceeded rates estimated for summer (Figures 4.5, 4.6). The best predictors for spatial and seasonal variation in the mass-standardised epifaunal secondary productivity among *Sargassum* were: (1) biomass of invertivorous fishes, and (2) sea temperature (Table 4.2; Figures 4.5, 4.6). We also found some support for the model based on habitat context as a predictor of variation in epifaunal production (ΔAICc of 2.261 compared to the threshold of 2, Table 4.2). A post-hoc likelihood ratio test showed no significant difference in the fit of habitat context compared to the best model of invertivorous fish biomass (LLR, $\chi 2$ = 0.280, p = 0.870), however it was excluded on the basis of parsimony. In the case of invertivorous fishes, epifaunal production was inversely related to the presence of fishes belonging to the family Labridae and positively related to the presence of Mullidae, although these were predominantly responsible for driving the seasonal separation between back reef and lagoon meadow patches, with little impact on the nearshore productivity levels (Figure 4.5a, b). Most taxonomic groups of epifauna followed this general trend, except molluscs that tended to have an inverse relationship between productivity and presence of invertivorous fishes (Figure 4.5c-f). In terms of sea temperature, the average daily minimum was a key predictor for variations in standardised epifaunal productivity along the main axis, which related to the two sampled seasons (Figure 4.6a, b). Variation within seasons, particularly during summer, seemed to arise from the opposing effects of monthly temperature range and average daily temperature fluctuations, which helped explain differences in epifaunal productivity between meadows along the second axis (Figure 4.6a, b). At the level of individual taxonomic groups, molluscs again showed the inverse trend between monthly temperature range and secondary productivity levels (Figure 4.6c-f).

Areal estimates of epifaunal productivity and sensitivity to changes in Sargassum canopy

Estimates of areal epifaunal secondary productivity (mg m^{-2} day^{-1}) for each meadow across season and seascape showed that summer areal productivity exceeded that in winter, predominantly due to the much larger *Sargassum* canopy size in summer (Figure 4.7). In the back reef meadows, epifaunal production in summer was between 40-300 times higher than in winter, but nearshore and lagoon meadows did not show such large seasonal fluctuations (Figure 4.7). Sensitivity analysis modelling the consequences of change in *Sargassum* canopy height and percent cover for areal epifaunal productivity showed a clear trend of increasing areal epifaunal productivity with increasing canopy size and percent cover (Figure 4.8). However, productivity levels were more sensitive to changes in percentage cover of *Sargassum* than to canopy height (Figure 4.8a, b).

Table 4.2 Summary of best-subsets model selection based on distance-based linear models (DistLM) predicting patch-level variation in mass-standardised epifaunal productivity across two seasons. The most parsimonious models within two AICc of the overall top model are indicated in **bold**.

Model	AICc	ΔAICc	r^2
Invertivorous fish biomass	**-28.898**	**-**	**0.311**
Sea temperature	**-28.621**	**0.277**	**0.300**
Habitat context	-26.637	2.261	0.538
Seascape context	-23.850	5.048	0.073

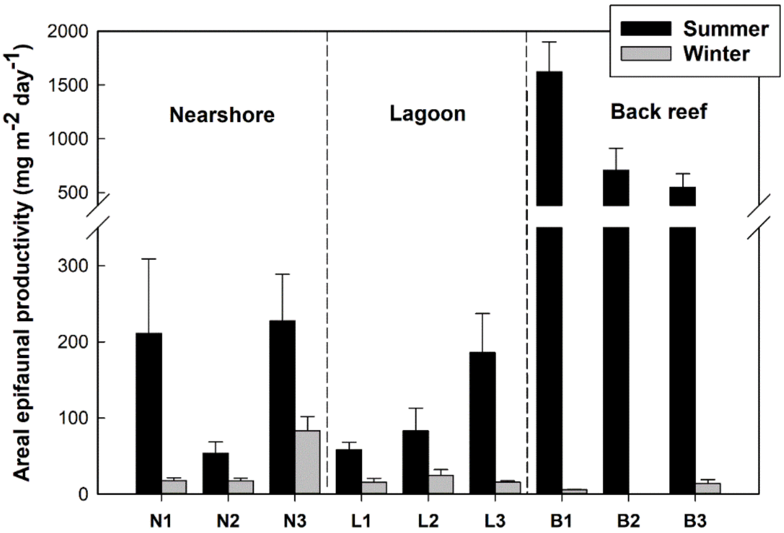

Figure 4.7 Estimates of areal secondary productivity (mg m^{-2} day^{-1}) generated by *Sargassum*-hosted epifauna for nine meadow patches at three seascape positions during summer and winter in the Maud Recreational Region near Coral Bay, Ningaloo Reef (Data are mean ± se).

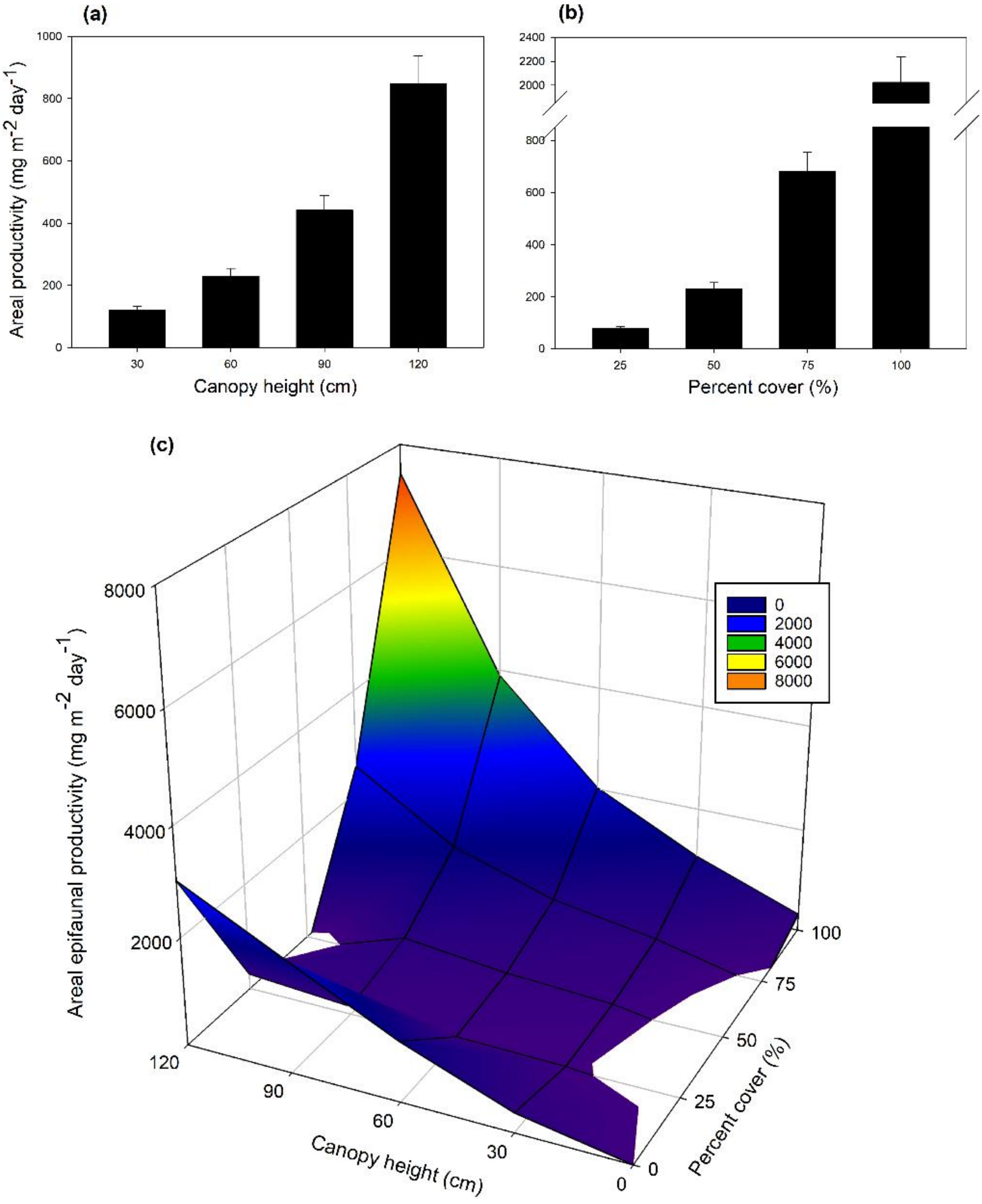

Figure 4.8 Sensitivity analysis modelling the consequences of changes in *Sargassum* canopy structure for areal epifaunal secondary productivity. Areal measures of epifaunal secondary productivity are examined in terms of changes to: (a) *Sargassum* canopy height, (b) percent cover of *Sargassum*, and (c) the combination of *Sargassum* canopy height and percent cover. Data in (a) and (b) are based on the average productivity per g *Sargassum* DW across all meadow patches. Error bars reflect the uncertainty associated with this estimate of mass-standardised daily production (se), multiplied by the volume of *Sargassum* associated with each scenario.

Discussion

Our results show that the canopy size (in terms of dry weight) of the tropical fucoid macroalga *Sargassum* is strongly positively correlated with overall secondary production by associated epifauna*.* Alongside this effect of canopy size, however, our results highlight the potential for more unexpected and subtle interactions between *Sargassum* biomass and mass standardised secondary productivity within particular meadow patches over a seasonal cycle. In particular, nearshore meadow patches showed a much lower amplitude of seasonal fluctuations in epifaunal secondary productivity. When viewed in terms of a standardised measure of secondary productivity per unit weight of *Sargassum*, the most parsimonious predictors of epifaunal secondary productivity within our study system were a mixture of biotic and abiotic factors, namely the presence (Labridae) or absence (Mullidae) of invertivorous fishes, and the site-specific thermal context (daily temperature fluctuations, average daily minimum temperature and monthly temperature range). The characteristics of the *Sargassum* canopy itself, as well as the species composition (richness and evenness) of other understory macroalgae present within the habitats were also found to play a role in explaining variation in epifaunal secondary productivity, although the role of these other habitat variables was less parsimonious as a predictor model. Finally, our estimates of areal epifaunal productivity are among the first to take into account of potential differences across seasons within these critical marine macrophyte habitats. Our sensitivity analysis provides a unique insight into the response of secondary productivity to perturbations in *Sargassum* canopy structure that could result either from press disturbances (sustained, e.g., increasing sea temperature) or pulse disturbances (temporary e.g., marine heatwave).

Sargassum meadows function as critical source of epifaunal secondary production

The strong positive correlation between overall epifaunal secondary productivity and individual *Sargassum* biomass spanning both sampling seasons suggests that larger *Sargassum* canopy size consistently gives rise to greater amounts of secondary production. This could either be because larger thalli provide a greater food resource (level of primary production), increasing the biomass of each individual epifauna, and/or because the larger thallus size generates a greater surface area for epifauna to colonise, increasing the overall abundance of secondary producers. Either way, from a management perspective, *Sargassum* canopy size could be used as a proxy for estimating levels of secondary production by epifauna within these meadow habitats. Previous studies from both tropical and temperate *Sargassum* habitats have reported significant positive correlations between epifaunal biomass and *Sargassum* canopy size (Edgar & Klumpp 2003, Leite & Turra 2003, Kodama et al. 2020). Moreover, larger canopies can provide more complex micro-niches and larger surface areas for epifauna to colonise (Cacabelos et al. 2010, Veiga et al. 2014, Carvalho et al. 2018). Now we show that these observed biomass and canopy size correlations translate to quantity of epifaunal secondary production, based on a snapshot of community composition within tropical macroalgal meadows. This relationship between epifaunal productivity and canopy size can be observed not only in macroalgae, but in other marine macrophytes such as seagrasses whose canopies can offer structurally complex habitats (Wong 2018, Jinks et al. 2019). Interestingly, several studies have found that macroalgal meadow canopies in both tropical and temperate marine coastal systems can potentially harbour more epifauna than other habitats such as seagrass meadows and turf algal matrices (Lewis 1987, Taylor 1998a, Tano et al. 2016), suggesting that higher productivity in canopy macroalgal meadows can be expected. Our results highlight the need to estimate secondary, as well as primary, production associated with macroalgal meadows when considering their role in marine ecosystem functioning and their potential to support higher tropic level consumers, such as fishes that forage within these meadow habitats (Fulton et al. 2019, 2020).

Seasonal swings in epifaunal secondary productivity are not uniform across seascapes

Epifaunal secondary productivity associated with *Sargassum* meadow patches within the Ningaloo Marine Park did fluctuate between seasons, but only insofar as canopy size altered between summer and winter in a given part of the seascape. Within most meadow patches, both overall and areal epifaunal productivity was much lower in winter due to predictable changes in *Sargassum* canopy size associated with the winter reductions in canopy biomass. However, declines in winter productivity were not uniform across all meadows; there was no consistent seasonal effect on epifaunal productivity, rather a canopy effect. Given that seasonal fluctuations in *Sargassum* canopy size and canopy structure are commonly observed in marine habitats across the globe (studies reviewed in Fulton et al. 2019), it is important to consider the associated seasonal fluxes in levels of secondary production when examining the potential for these habitats to support higher-order consumers. Our study also found seasonal fluctuations in the relative contributions of different taxonomic groups within the epifaunal communities to measured secondary production. In summer, production was chiefly generated by crustaceans and molluscs, reflecting their dominance within epifaunal communities associated with *Sargassum*, including within marine macrophyte canopies in cold-water settings (Edgar & Klumpp 2003, Marzinelli et al. 2016, Belattmania et al. 2018a). In winter, production due to molluscs declined substantially, demonstrating that the community composition of epifaunal taxa can also show seasonal patterns. Perhaps unsurprisingly, given the strong link between epifaunal biomass and productivity, this is consistent with studies reporting clear seasonal patterns of epifaunal biomass across a variety of marine habitats in tropical and temperate regions (Leite & Turra 2003, Ba-Akdah et al. 2016, Belattmania et al. 2018a). Nevertheless, the estimation of actual rates of production across seasons in these habitats yields an important additional insight: that we cannot assume a consistent seasonal response across marine seascapes. The differences in seasonal response across individual meadows highlighted by the current study creates the potential for productivity ‘refuges’ in different parts of the seascape during each season that can support the foraging requirements of higher-order consumers. Investigation of the temporal stability across years of these seasonal refugia (and associated seasonal patterns of epifaunal productivity) should be a research priority, particularly given that *Sargassum* canopy extent can be highly variable across years (Fulton et al. 2014, Wilson et al. 2014, van Lier et al. 2018).

Interestingly, the scale of the seasonal effect on epifaunal productivity was not uniform across individual meadow patches within the Ningaloo ecosystem. Season alone was not a significant factor in the observed variation in epifaunal productivity, but rather interacted with meadow patch location. Seasonal differences in epifaunal productivity were most pronounced in the back reef meadows, where areal estimates of epifaunal secondary productivity in winter were at least three orders of magnitude lower than in summer, owing to the fact that the winter detachment in these meadows is significantly greater than in lagoon and nearshore. Parts of the nearshore and lagoon meadow patches showed much lower seasonal swings in areal epifaunal productivity, falling by only 50% in some meadows. At some nearshore meadows (N2, N3), areal levels of secondary productivity in winter were commensurate with levels recorded in summer within other nearshore and lagoon parts of the seascapes, due to a less pronounced seasonal change in canopy height. These patterns highlight the importance of maximising *Sargassum* growth in summer for maintaining high levels of production within back reef patches. Thus, productivity can be strongly site-specific and highly localised, with individual parts of the seascape displaying varying potential to support higher-order consumers over each season. For example, levels of epifaunal secondary productivity observed in back reef meadows in winter would be insufficient to sustain the same population density of consumers as in summer, whereas nearshore habitats show greater potential to support similar populations of higher-order consumers across both seasons. By examining levels of secondary productivity in summer and winter, our results are able to draw out the potential need for season-specific management priorities in terms of protection of critical habitats.

Implications of disturbances for Sargassum epifaunal production

Modelling the effect of changes in *Sargassum* canopy structure (in particular canopy height and percent cover) on secondary productivity by epifauna showed that areal productivity can undergo dramatic shifts in response to changes in canopy structure. We observed high sensitivity of areal productivity in response to reductions in *Sargassum* canopy height and percent cover, due to the underlying empirical relationship between canopy biomass and secondary productivity. Studies have already shown how environmental changes associated with short term (2-8 weeks) thermal anomalies, known as marine heatwaves, impact habitat-forming macroalgae within temperate and sub-tropical marine communities (Bond et al. 2015, Straub et al. 2019). The 2011 temperature anomaly along the west coast of Australia (now known as the Ningaloo Niño, Feng et al. 2013) resulted in range-contraction of the brown alga *Scytothalia dorycarpa* on the west coast of Australia (Smale & Wernberg 2013), along with extensive loss of the keystone kelp species, *Ecklonia radiata* (Wernberg et al. 2013), and reductions in overall macroalgal canopy cover (Wernberg et al. 2016). These pulse events are increasing in frequency and magnitude (Oliver et al. 2019) and are expected to have associated effects on community production (Yang et al. 2018). Temperate and sub-tropical macroalgae experience reductions in survival (e.g., up to 20% reduction in cover, Alestra & Schiel 2015) and reductions in growth when exposed to extreme increases in water temperature (Chu et al. 2012). There is now experimental evidence that tropical macrophytes, such as the *Sargassum* within Ningaloo, may show an even greater sensitivity to heatwave events (Graba-Landry et al. 2020). For instance, propagules of *Sargassum swartzii* showed an 88% decline in survival and a 38% reduction in growth when exposed to water temperatures 3ºC above ambient for a 7-week testing period comparable to a marine heatwave event (Graba-Landry et al. 2020). In the same experiment, adult plants of three species of tropical *Sargassum* showed reductions in growth of ~45% after just 2-weeks exposure to the +3ºC water temperature treatment (Graba-Landry et al. 2020). According to our sensitivity analysis, a reduction in canopy height and percent cover of 45% during the summer period would lead to an 81% drop (from 260 mg m^{-2} day^{-1} to 50 mg m^{-2} day^{-1}) in the areal rate of secondary production by epifauna within the *Sargassum* meadows of Ningaloo. If the heatwave were to occur during a critical reproductive window and impact on propagule survival (percentage cover) to the extent suggested above, then levels of epifaunal secondary productivity could decrease from 780 mg m^{-2} day^{-1} to 90 mg m^{-2} day^{-1}- a decline of 88% for back reef meadow patches. The system-wide implications of these shifts in secondary productivity are likely to be considerable, and should be taken into account when predicting the likely consequences of climate change and anthropogenic activities.

Conclusions

Macroalgal meadows, such as those dominated by *Sargassum*, are an integral part of seascapes. In tropical marine ecosystems, they have been estimated to cover 16-46% of shallow inshore habitats (Fulton et al. 2019). The epifaunal communities associated with these meadows represent a critical, yet understudied, link in the flow of energy from primary producers to higher-order consumers and therefore contribute to the functioning of these ecosystems. *Sargassum* meadows within the Ningaloo marine system have previously been found to be important foraging grounds for species of invertivorous fish (e.g., Wenger et al. 2018). The strong relationship demonstrated here between the abundance of invertivorous fishes and standardised measures of epifaunal productivity confirms the reliance of key fish species within this ecosystem on these epifauna as a source of production. This is important, given that some key species of macroaglae-associated Labridae are targeted for food fisheries in the Indian Ocean (Froese & Pauly 2021, Fulton et al. 2020). Trophic cascades triggered by environmental disturbances to canopy structure described above (including the associated collapse in epifaunal production) could therefore have significant effects on fisheries catches and food security within the Indo-Pacific region. Interestingly, our results also showed that thermal environment was a key predictor of secondary production of macroalgal epifauna. Variables such as daily minimum temperature, average daily temperature fluctuations as well as the overall monthly water temperature range were important in predicting differences in epifaunal productivity between meadows and all of these are likely to be affected by changing climatic conditions associated with global warming. These changes have the potential to drive both positive and negative changes in epifaunal productivity (e.g., increases in daily minimum water temperature during winter could drive higher levels of epifaunal production, but these would be offset by reductions in summer due to heat-induced degradation of canopy structure as discussed above). Similarly, higher amplitudes of daily water temperature fluctuations associated with a changing climate would, according to the current study, lead to reductions in epifaunal production. Overall, it is likely that climate-associated changes to local thermal conditions will significantly alter the nature of trophic flows in macroalgal ecosystems. Given the ubiquity of macroalgal meadows within tropical marine waters, and evidence that anthropogenic activities are generating increasing pressure on such habitats (Harley et al. 2012, Marzinelli et al. 2016, Fulton et al. 2019), future research aimed at examining the effect of changes in epifaunal secondary productivity on populations of higher-order consumers, particularly those that are targeted for food fisheries, should be a priority.

Acknowledgments

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Supplementary Information

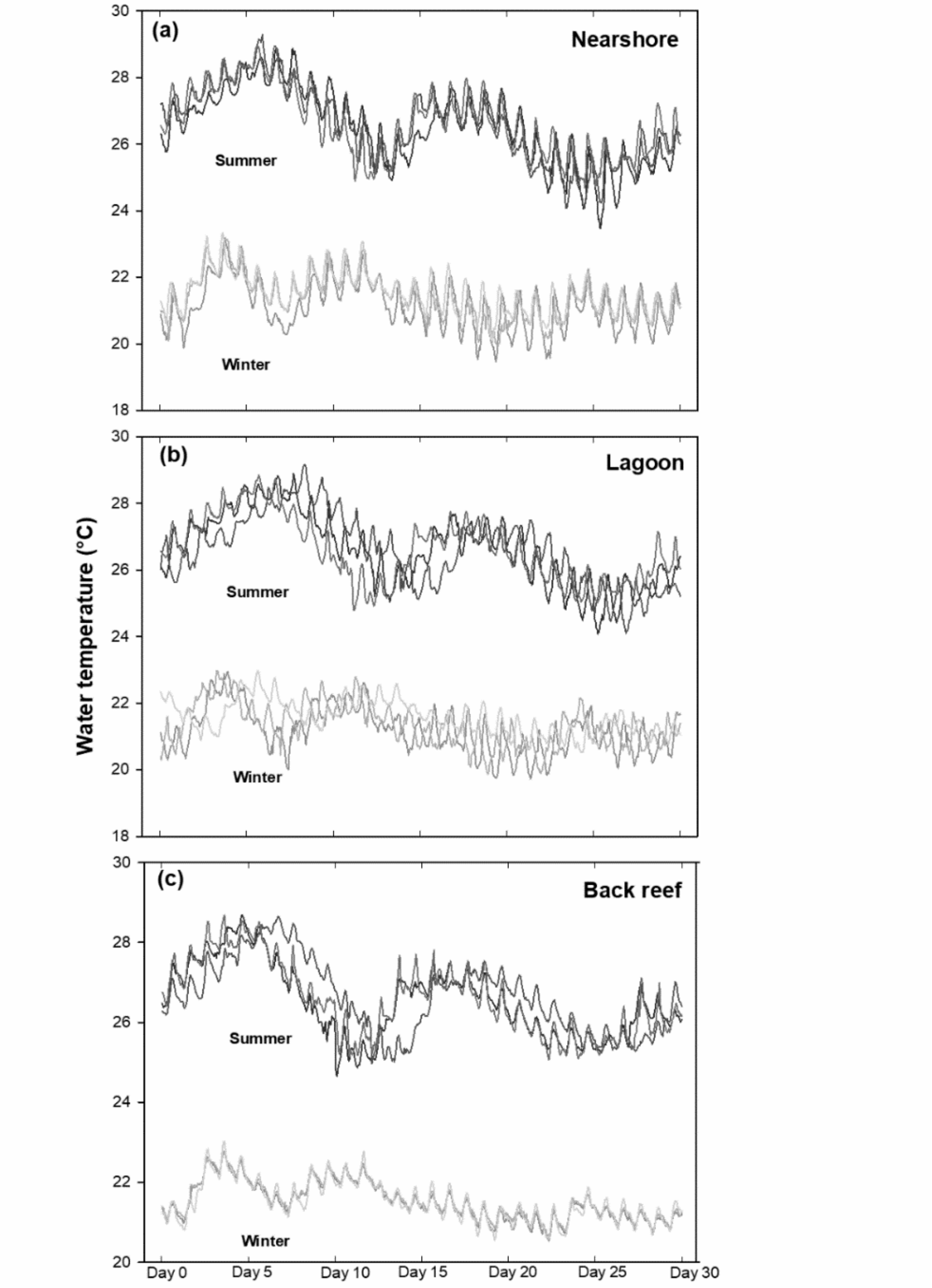


Figure S4.1 Hourly sea temperature over the 30-day study period prior to quantification of epifaunal secondary production within *Sargassum* meadow patches during austral summer and winter 2018, in the Maud Recreational Region near Coral Bay, Ningaloo Reef, Western Australia. Data are presented for each of the three replicate meadows sampled within three seascape positions: (a) nearshore, (b) lagoon, and (c) back reef. These data were used to calculate the mean site-level temperature in both seasons applied in equation (1) to calculate epifauanl production for each site.

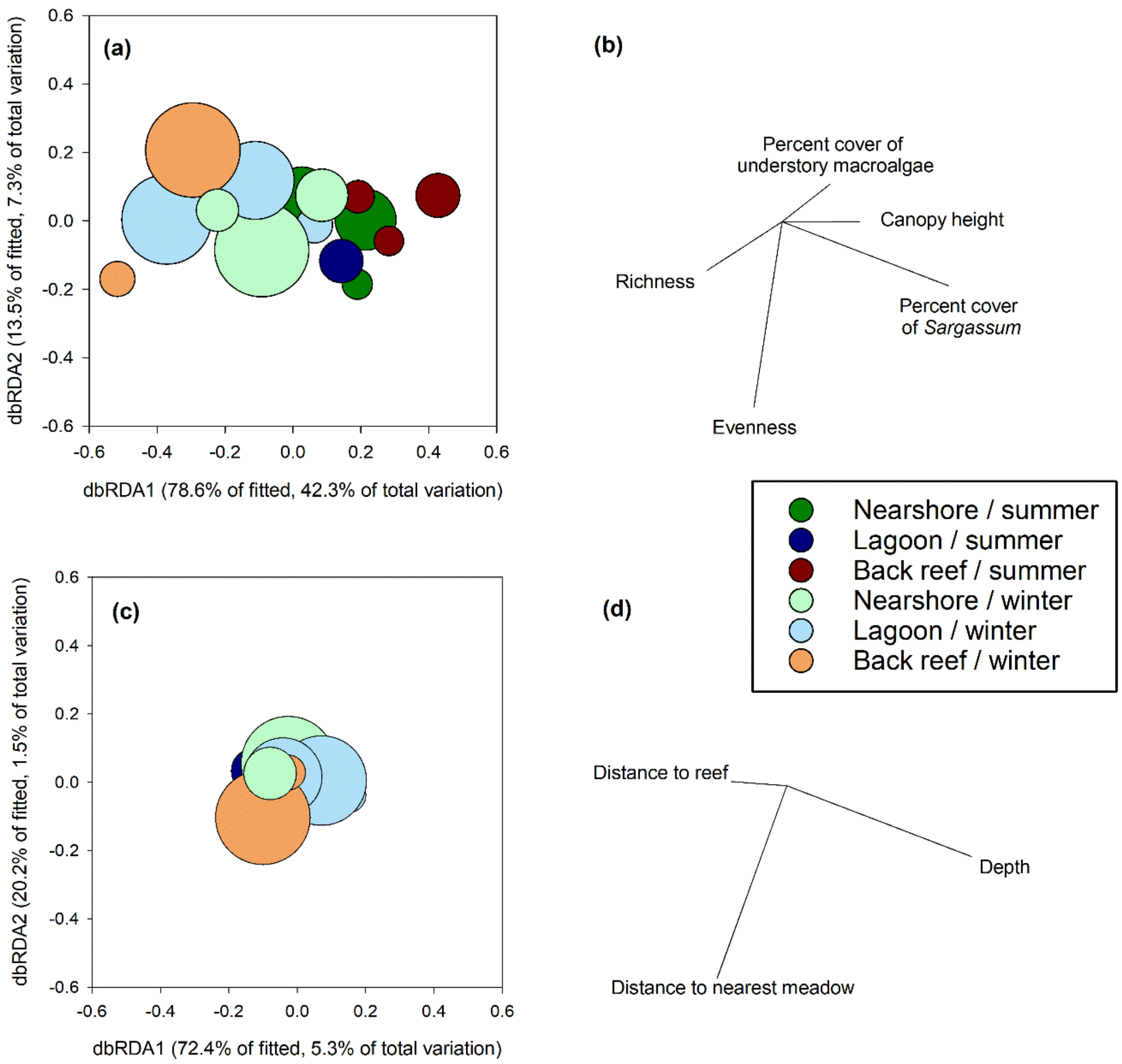
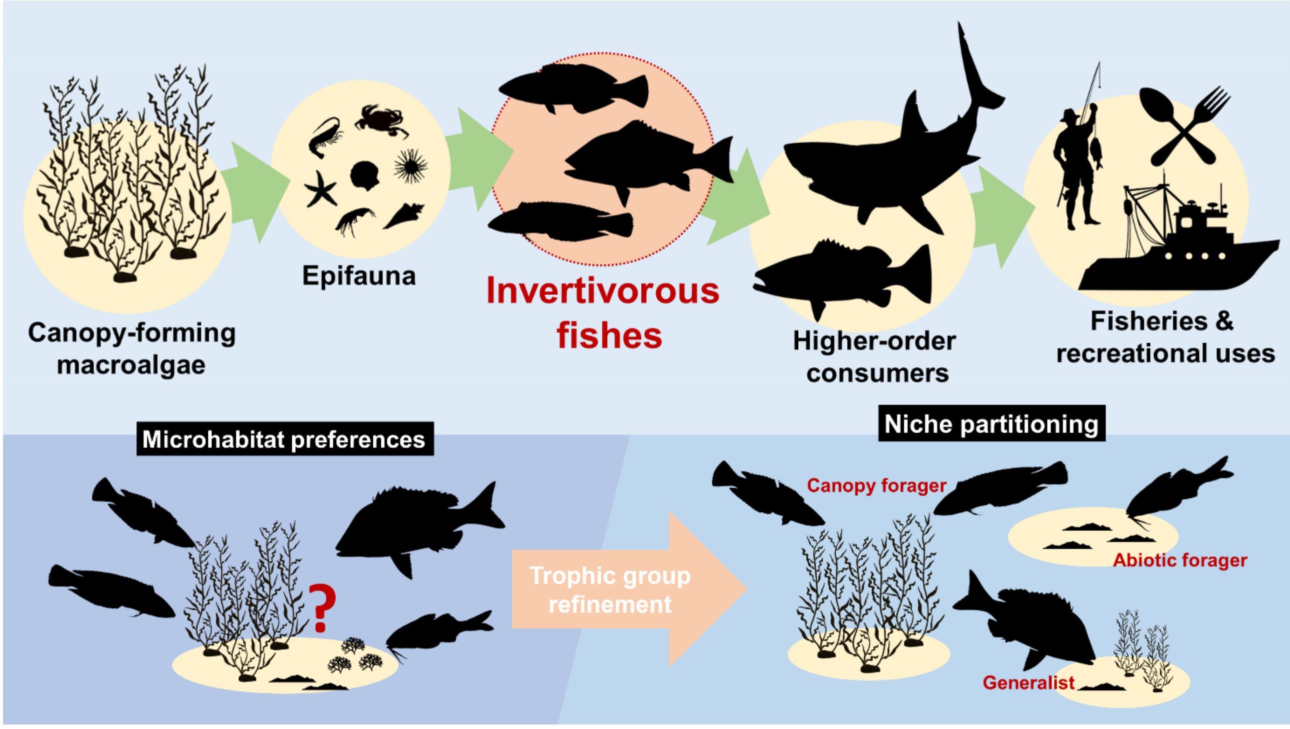


Figure S4.2 Distance-based redundancy analysis (dbRDA) ordination of the subsets used in model selection to predict variation in standardised patch-level epifaunal productivity: (a) habitat context, and (c) seascape context, from nine meadow patches at three seascape positions during summer and winter in the Maud Recreational Region near Coral Bay, Ningaloo Reef. Vector overlays (b) and (d) show variables which strongly correlated with each ordination structure: Bubble sizes are proportional to patch-level epifaunal productivity that is standardised by *Sargsassum* dry weight to take account of the positive correlation between canopy size and epifaunal productivity.

CHAPTER 5

FORAGING MICROHABITAT PREFERENCES OF INVERTIVOROUS FISHES WITHIN TROPICAL MACROALGAL MEADOWS: IDENTIFICATION OF CANOPY SPECIALISTS



This chapter has been submitted to *Coral Reefs*

Co-authored with Jennions, M. and Fox, R.J.

Abstract

Invertivorous fishes are key middle-order consumers that connect energy flows across different trophic levels. However, the potential for distinct functional roles to exist within this trophic guild has not been satisfactorily explored to date, meaning that current assessments of ecosystem resilience are likely to over-estimate the level of functional redundancy within a given invertivorous fish assembly. Our study examined the foraging behaviour and foraging microhabitat preferences of invertivorous fish communities within the productive canopy macroalgal meadows of Ningaloo Marine Park, Western Australia. Our aim was to identify foraging specialisations that could yield distinct functional roles for species belonging to the guild. We found that invertivorous fishes at this location were chiefly represented by species belonging to the Labridae, Lethrinidae and Mullidae. Individual species demonstrated strong preferences for foraging within specific microhabitat types, suggesting that the guild can be grouped into three foraging categories: ‘canopy forager’, ‘generalist’ and ‘abiotic forager’. Our results highlight subtle niche partitioning of foraging microhabitats within the trophic guild of invertivorous fishes associated with tropical macroalgal meadows. Moreover, this partitioning is consistent across seasons, despite significant fluctuations in canopy structure and biomass. The resulting refinement of functional roles has boarder implications as it might provide greater protection to individual species that would otherwise be considered functionally redundant. Our results will help to inform knowledge of the functional impact of particular species, their ecological specialisations, as well as our understanding of trophic flows in marine food webs for appropriate management and conservation.

Keywords: Invertivore, Canopy Forager, Abiotic Forager, Canopy-Forming Macroalgae*,* Ecosystem Resilience, Functional Complementarity

Introduction

In marine ecosystems, invertivorous fishes (i.e., species which primarily feed on invertebrates) can represent one of the dominant feeding guilds (Longo et al. 2019, Parravicini et al. 2020). For example, nearly 70% of fish species on the Great Barrier Reef, Australia have been classified as feeding predominantly on invertebrates (Randall et al. 1997, Kramer et al. 2015, Froese & Pauly 2021), and approximately 30% of fish species recorded from the Fernando de Noronha Archipelago of Brazil are classified as mobile and sessile invertebrate feeders (Krajewski & Floeter 2011). The overall guild of invertivorous fishes comprises a diverse range of families, including Labridae (wrasses, excluding parrotfishes), Lethrinidae (emperors, breams), Mullidae (goatfishes) and Serranidae (sea basses, groupers), many of which are common targets of commercial and recreational fisheries (Sumner et al. 2002, Fulton et al. 2020, Froese & Pauly 2021). The guild therefore makes a significant contribution to ecosystem services globally, firstly in terms of direct food production (van Lier et al. 2018, Fulton et al. 2019, Froese & Pauly 2021). In addition, they have been shown to shape the community structure and production of lower trophic levels in marine food webs, determining the temporal and/or spatial fluctuations in invertebrate abundance within an ecosystem (Choat & Kingett 1982, Edgar & Aoki 1993, Batzer et al. 2000). They also connect energy flows between primary producers and higher-order consumers (Galvan et al. 2008, Newcombe & Taylor 2010, Lewis & Anderson 2012). Invertivorous fishes are the target prey of mesopredatory piscivores (e.g., lizardfishes, groupers) and apex predators (e.g., trevallies, sharks) that are themselves important as both fishery stocks and recreational attractions linked to the livelihoods of millions of people (Ashworth et al. 2014, Bergström et al. 2016, Froese & Pauly 2021). In sum, invertivorous fishes are pivotal middle-order mediators that provide essential connections of energy flows across all trophic levels, both top-down and bottom-up. The trophic links that are facilitated by their predation and foraging preferences underpin fundamental processes of marine ecosystem functioning (Randall et al. 1997, Taylor 1998a, Cowles et al. 2009).

The identification of essential habitats used by fishes is a critical step in the process of ecosystem-based fishery management of commercially and recreationally important species (Beck et al. 2001, Thrush & Dayton 2010, Wilson et al. 2017). Foraging behaviour is a key aspect of habitat use by fishes, and can be documented as preferences relating to particular microhabitat types (Krajewski & Floeter 2011, Fulton et al. 2016, Kramer et al. 2016). For example, strong dependency on preferred microhabitats can lead to dramatic changes in the temporal and spatial dynamics of fish populations or communities following shifts in the availability of those preferred microhabitats. Local extinction of some coral reef fish species can occur when the corals they exclusively prey on are no longer available (Westmacott et al. 2000, Pratchett et al. 2018), and carnivorous fishes can also be vulnerable to the loss of preferred foraging microhabitats (Munday 2004, Wilson et al. 2008a, Wenger et al. 2018). Therefore, information on the role of different microhabitat requirements and the degree of microhabitat preferences can assist in the development of effective management and conservation interventions (Fulton et al. 2016). In addition to which, documenting species' microhabitat specialisations is fundamental to defining their 'ecosystem function' in terms of positioning along the feeding niche resource axis (MacArthur 1958, Hutchinson 1959). The monitoring and management of marine ecosystems is increasingly based around the protection of critical functional groups (Green & Bellwood 2009, Graham et al. 2013, Villéger et al. 2017), where a species' ecosystem function is defined based on its ecological traits (Bellwood et. al. 2019). This approach has led to the recognition that members of particular trophic groupings are not ecological equivalents. For example, on coral reefs, the group of fishes previously defined collectively under the trophic status of 'herbivore' has now been carved up into many different ecosystem functions, based on factors such as mode of feeding ('scrapers' versus 'excavators' (Bellwood & Choat 1990), 'grazers' versus 'browsers' (Choat et al. 2002, Fox & Bellwood 2008, Green & Bellwood 2009, Hoey & Bellwood 2009), and 'croppers' (Green & Bellwood 2009)), or on microhabitat preferences ('crevice-feeders' versus 'open matrix feeders' (Fox & Bellwood 2013, Brandl & Bellwood 2014), 'leaf-biters' versus 'thallus biters' (Streit et al. 2015)). This process of trophic group refinement into functional groupings can help provide a more accurate assessment of ecosystem resilience, by identifying species that perform unique ecosystem functions and yielding a more conservative estimate of the level of functional redundancy associated with the biodiversity present within a particular community structure (Cheal et al. 2010, 2012, Rasher et al. 2013).

Within tropical seascapes such as coral reefs, seagrass and macroalgal meadows, invertivorous fishes have the potential to exploit heterogeneous microhabitats to feed on epifaunal and infaunal invertebrates (Kwak et al. 2015, van Lier et al. 2018, Sambrook et al. 2019). Although strong microhabitat preferences of tropical invertivorous fishes driven by specific dietary targets have previously been documented (Lukoschek & McCormick 2001, Wilson et al. 2008b, Wenger et al. 2018), most studies to date on the microhabitat utilisation of these invertivorous fishes have focused either on well-studied habitats, such as coral reefs, or have looked only at the microhabitat preferences of a single species of invertivore (Layton & Fulton 2014, Brandl et al. 2015, Kramer et al. 2016, Wenger et al. 2018). Current knowledge of how the *overall* collective trophic grouping of invertivorous fish species demonstrate niche partitioning of their foraging microhabitats in non-reef habitats is therefore limited. Theory would predict, however, that within the overall invertivore assemblage, individual species would exploit different portions of the habitat space, exhibiting niche partitioning at a finer scale (Floeter et al. 2007, Berkström et al. 2012, Asher et al. 2017, Brandl et al. 2020). Knowledge of these microhabitat specialisations is therefore an important first step in being able to define the ecosystem function of species within the invertivore trophic guild.

One of the most common and productive non-reef habitats within tropical seascapes are macroalgal meadows, comprised of canopy-forming macroalgae (Tano et al. 2016, Fulton et al. 2020). These macroalgal meadows can extend over significant portions of shallow tropical marine habitats (estimated between 16-46 % of some shallow coastal areas, Fulton et al. 2019), forming complex habitat structures and contributing a large amount of areal primary production. This primary production supports communities of epifaunal invertebrates, which in-turn provide nutrition for invertivorous fishes (Edgar & Aoki 1993, Wenger et al. 2018). Recent studies have highlighted the fact that these macroalgal meadows and their associated epifaunal communities are important foraging grounds for invertivorous fishes, including species that are the targets of commercial fisheries (Chaves et al. 2013, Chen et al. 2020). Macroalgal meadows can, however, exhibit strong temporal shifts in canopy size (in terms of either overall biomass or the length of macroalgal thalli). In tropical regions, these temporal shifts are often characterised by canopy growth in summer and detachment in winter (Leite & Turra 2003, Wong & Phang 2004, Lefevre & Bellwood 2010, Fulton et al. 2014). Seasonal fluctuations in macroalgal canopy size therefore influence the availability of habitat, impacting on abundance and availability of associated epifaunal invertebrate communities (Taylor 1998b, Leite & Turra 2003, Ba-Akdah et al. 2016), and on the invertivorous fishes that prey on epifauna. However, we have little understanding of how individual species of invertivorous fishes might respond to such fluctuations in prey availability. Alongside this, as described above, we lack a basic understanding of the foraging microhabitat preferences of the collective community of macroaglae-associated invertivorous fishes with which to understand niche partitioning within this trophic group and the potential for within-group functional complementarity versus redundancy. The aims of this study were therefore: (1) to document the foraging microhabitat preferences of the dominant invertivorous fish species within macroalgal meadows of the world heritage Ningaloo Marine Park, Western Australia, and determine the potential for functional complementarity based on the microhabitat resource axis within this trophic group; and (2) to examine how these microhabitat preferences (and associated functional roles) respond to seasonal shifts in macroalgal canopy structure (summer to winter).

Methods

Study region

This study was conducted within the Maud Recreation Region of Ningaloo Marine Park near Coral Bay, situated in the northwest of Western Australia (Figure 5.1). As Australia's largest fringing coral reef (~290 km long), shallow waters (3-5 m depth) in this area are dominated by canopy-forming fucoids chiefly belonging to the genus *Sargassum.* These canopies form extensive macroalgal meadow patches covering over 300 km^2, which exhibit strong seasonal fluctuations in macroalgal biomass (Kobryn et al. 2013, Fulton et al. 2014, van Lier et al. 2018, Chen et al. 2020). A total of eight *Sargassum* meadow patches (size: 28893 ± 11627 m^2) were surveyed during late austral summer (February-March) 2018 to confirm the presence of invertivorous fishes and determine habitat composition (Figure 5.1). Only four of these *Sargassum* meadow patches were reinvestigated during the austral winter (August-September) 2018 due to the dramatic seasonal decline of *Sargassum* canopy biomass (Figure 5.1).

Habitat composition of macroalgal meadows

Habitat composition of each *Sargassum* meadow patch in summer and winter was documented via underwater visual censuses conducted by divers on SCUBA, following Lim et al. (2016). At each meadow patch, we haphazardly deployed six replicate 10 m transect tapes, and recorded the distance along each transect (to the nearest 5 cm) occupied by three distinct habitat categories: (1) canopy macroalgae (leathery macrophytes with the canopy height can reach around 10-50 cm, e.g., *Sargassum*, *Sargassopsis*), (2) understory macroalgae (foliose macrophytes without canopies, occupying the floor of meadows, e.g., *Lobophora*, *Dictyota*, *Padina*) and (3) abiotic components (e.g., pavement, sand, dead coral, rubble). Converting these distances to a proportion of the 10 m transect length gave us a percentage composition of the three habitat types within each meadow.

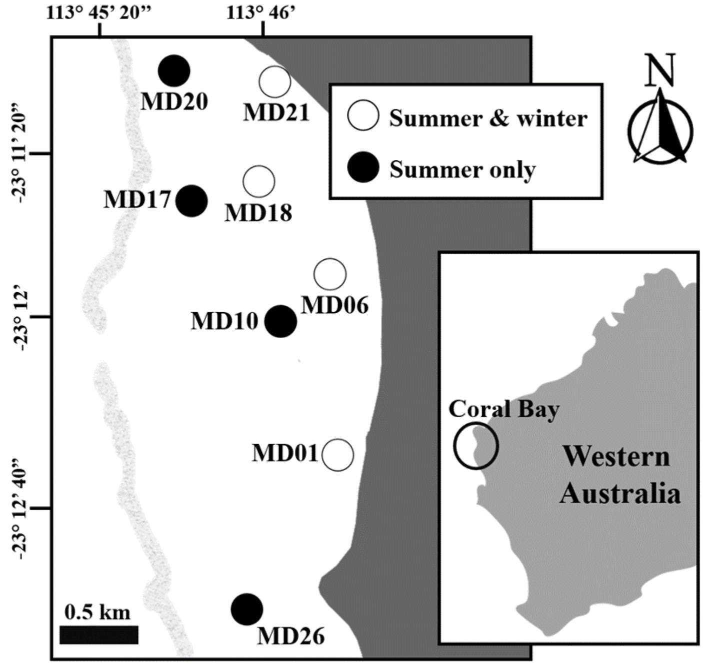


Figure 5.1 Map of study region and surveyed *Sargassum* meadow patches within Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, Western Australia.

Foraging microhabitat preferences of invertivorous fishes

The use of individual foraging microhabitats by species of invertivorous fishes was recorded using underwater visual observations by divers on SCUBA. At each meadow patch during summer and winter, at least three instantaneous focal surveys were conducted (following Wenger et al. 2018) over multiple days to reduce the risk of an abberant day leading to a non-representative measure of behavioural pattern. In brief, a single diver swam a random, non-overlapping path starting from the centre of each meadow patch out to the patch edge. Surveys commenced 5 minutes after the diver had reached the patch centre to allow for fish to acclimate to diver presence. For each invertivorous fish subsequently encountered on the random swim path, the diver noted species identity, total length (TL, to the nearest cm), foraging behaviour (searching/feeding) and microhabitat location (canopy macroalgae to genus/understory macroalgae to genus/abiotic habitat). Within these focal observations of foraging behaviour, 'searching' was strictly defined as the fish having head inclined toward the particular microhabitat but without touching, while 'feeding' was defined by the individual having its mouth in contact with the microhabitat. To avoid problems associated with inferences based on low sample sizes, only invertivorous species represented by more than ten individuals per meadow patch, and for at least three meadow patches during each season, were included in subsequent analyses. Foraging microhabitat preferences of each invertivorous fish species were determined using the electivity index formula of Vanderploeg and Scavia (1979):

$$E_i^* = [W_i - (1/n)] / [W_i + (1/n)], \qquad (1)$$

where E_i^* is the electivity for microhabitat category i, n is the number of microhabitat categories, and Wi is the selective coefficient for microhabitat category i calculated as:

$$W_i = (r_i/p_i) / (\sum_i r_i/p_i), \qquad (2)$$

where r_i is the proportional use of the microhabitat category i, and p_i is the proportional availability of the microhabitat category i. Values of electivity indices (E_i^*) range from -1 to 1, with indication of avoidance (negative value), neutrality ($E_i^* = 0$) and preference (positive value) for a particular microhabitat. Electivity indices were averaged across all patches censused within a given season (n = 8 patches in summer, n = 4 patches in winter) to determine the season-specific foraging-microhabitat associations of individual species of invertivorous fishes in the Maud Recreation Region of Ningaloo Marine Park.

Results

Invertivorous fish communities

A total of 36 invertivorous fish species (34 in summer, 24 in winter) were observed searching and feeding within macroalgal meadows across the two seasons. Of these 36 species, 12 met our criterion of being represented by more than 10 individuals at each meadow patch for at least three meadow patches during each season and were then analysed for their foraging microhabitat preferences (Table 5.1). This resulted in a total of 3207 foraging behaviour records (2538 in summer, 669 in winter). The majority of invertivorous fishes recorded foraging in our surveys belonged to the family Labridae (71% in summer, 75% in winter), followed by Lethrinidae (17% in summer, 10% in winter) and Mullidae (11% in summer, 15% in winter). The dominant species represented within each of the three family were: (1) Labridae: *Anampses geographicus*, *Cheilio inermis*, *Coris caudimacula*, *Halichoeres nebulosus*, *Pseudojuloides elongatus*, *Stethojulis bandanensis*, *Stethojulis interrupta*, *Thalassoma lunare*; (2) Lethrinidae: *Lethrinus atkinsoni*, *Lethrinus nebulosus*; and (3) Mullidae: *Parupeneus barberinoides*, *Parupeneus spilurus* (Table 5.1).

Table 5.1 Invertivorous fish species observed foraging within macroalgal meadows, Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, Western Australia.

Family	Species	Number in summer	Number in winter
Balistidae	*Rhinecanthus aculeatus*	4	
Carangidae	*Gnathanodon speciosus*	2	
Labridae	*Anampses caeruleopunctatus*	1	1
	*Anampses geographicus**	135	56
	Bodianus bilunulatus	1	
	Cheilinus bimaculatus	1	
Labridae	*Cheilinus chlorourus*	2	1
	Cheilinus trilobatus	6	
	*Cheilio inermis**	221	93
	Choerodon rubescens	1	
	Coris auricularis	2	2
	Coris aygula	7	
	*Coris caudimacula**	360	90
	Epibulus insidiator	1	
	*Halichoeres nebulosus**	165	67
	Hemigymnus melapterus	1	
	Hologymnosus annulatus	2	
	Macropharyngodon ornatus	10	2
	*Pseudojuloides elongatus**	160	15
	Pteragogus enneacanthus	30	3
	Pteragogus flagellifera	38	2
	*Stethojulis bandanensis**	127	21
	*Stethojulis interrupta**	182	33
	Stethojulis strigiventer		3
	*Thalassoma lunare**	264	87
	Thalassoma lutescens	67	15
	Xenojulis margaritaceus	30	10
Lethrinidae	*Lethrinus atkinsoni**	216	16
	*Lethrinus nebulosus**	181	20
	Lethrinus variegatus	37	29
Mullidae	*Parupeneus barberinoides**	110	13
	Parupeneus indicus	10	6
	*Parupeneus spilurus**	160	83
	Upeneus australiae		1
	Upeneus tragula	1	
Nemipteridae	*Scolopsis bilineata*	3	

*Valid for calculation of microhabitat preferences

Habitat availability and microhabitat use

Habitat composition in each meadow patch showed that canopy macroalgae was the most dominant microhabitat in summer, followed by abiotic components. The only exception was patch MD06 where the proportion of abiotic components was slightly higher than that of canopy macroalgae (Figure 5.2a). The dominance of canopy macroalgae shifted due to the dramatic seasonal decline in *Sargassum* canopy biomass, resulting in the abiotic component dominating patches in winter (Figure 5.2b). Invertivorous fishes used distinct microhabitats (Figures 5.3, 5.4). During summer, *Anampses geographicus*, *Cheilio inermis*, *Coris caudimacula*, *Pseudojuloides elongatus* and *Thalassoma lunare* were more often observed foraging within canopy macroalgae, with relatively low number of individuals using understory macroalgae or abiotic components. The proportional use of canopy macroalgae was higher than the proportional availability of this microhabitat for these species, suggesting a strong foraging microhabitat preference for canopy macroalgae. The avoidance of abiotic components to forage by these species was also observed, as a low proportion of individuals used the abiotic components even though the proportional availability of this microhabitat was high (Figure 5.3a-e). The opposite pattern of higher proportional use of the abiotic components than expected based on its availability was found for *Halichoeres nebulosus*, *Parupeneus barberinoides*, *Parupeneus spilurus*, *Stethojulis bandanensis* and *Stethojulis interrupta* (Figure 5.3h-l). Interestingly, such patterns (disproportionately using certain microhabitats) were consistent in winter for the four species (*Cheilio inermis*, *Coris caudimacula, Halichoeres nebulosus* and *Parupeneus spilurus*) observed in both summer and winter (Figure 5.4).

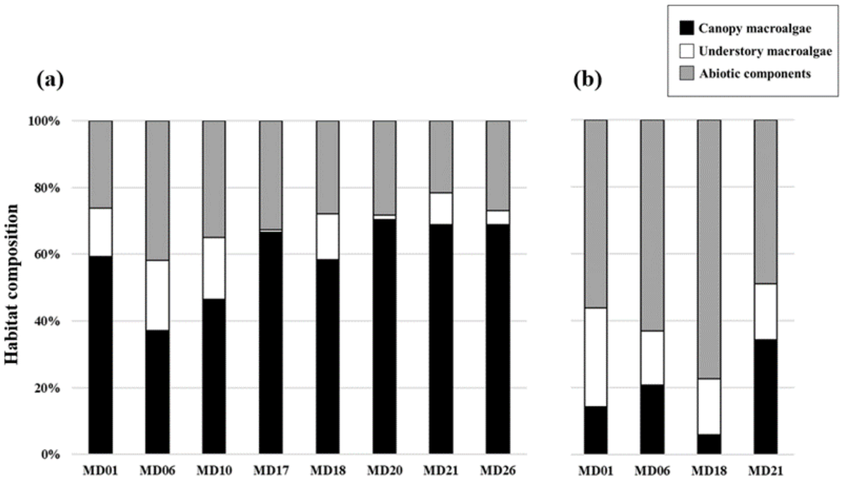


Figure 5.2 Habitat composition of each macroalgal meadow patch during (a) summer and (b) winter in 2018.

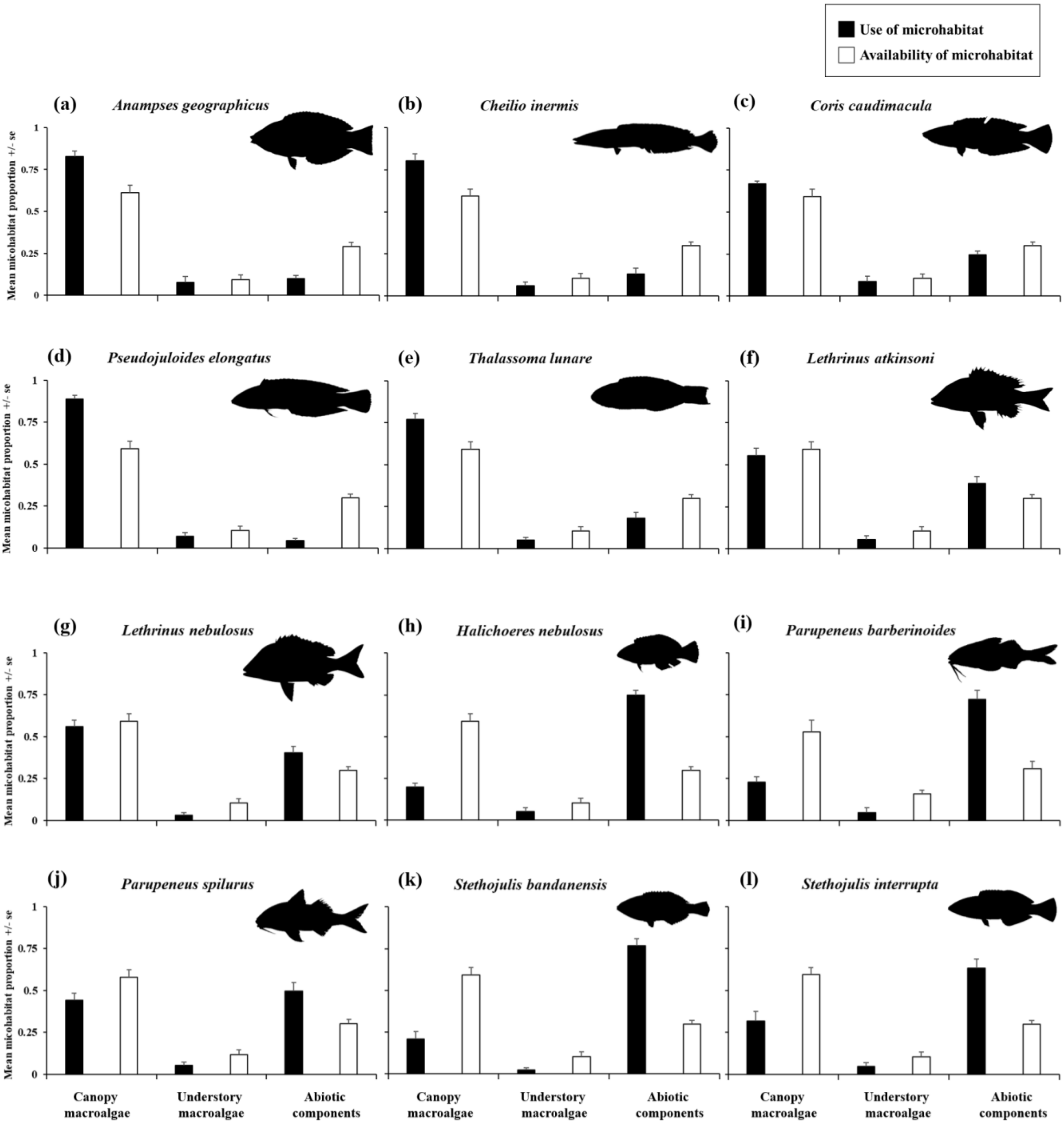


Figure 5.3 Foraging microhabitat use by invertivorous fishes in summer, as indicated by the proportional use and the proportional availability of three microhabitat categories: (a) *Anampses geographicus*, (b) *Cheilio inermis*, (c) *Coris caudimacula*, (d) *Pseudojuloides elongatus*, (e) *Thalassoma lunare*, (f) *Lethrinus atkinsoni*, (g) *Lethrinus nebulosus*, (h) *Halichoeres nebulosus*, (i) *Parupeneus barberinoides*, (j) *Parupeneus spilurus*, (k) *Stethojulis bandanensis* and (l) *Stethojulis interrupta*.

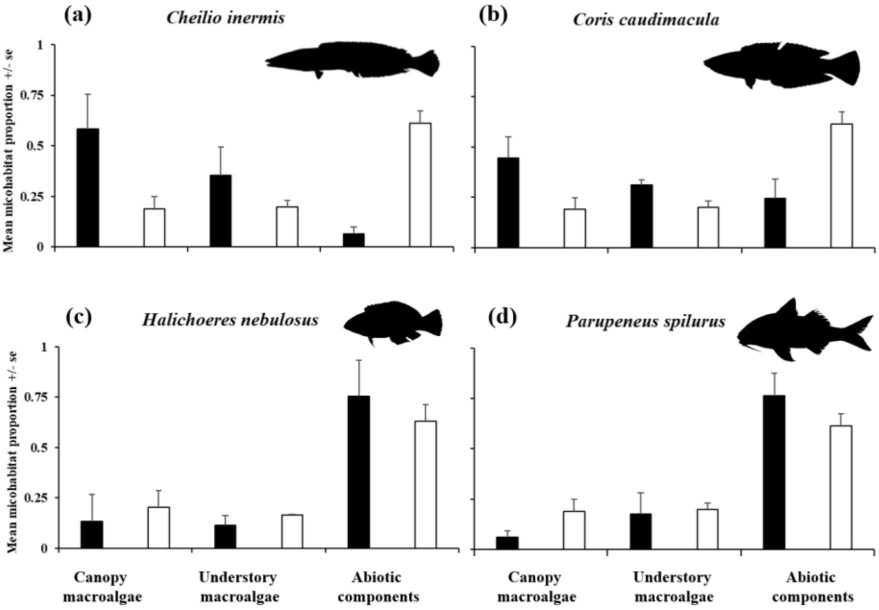


Figure 5.4 Foraging microhabitat use by invertivorous fishes in winter, as indicated by the proportional use and the proportional availability of three microhabitat categories: (a) *Cheilio inermis*, (b) *Coris caudimacula*, (c) *Halichoeres nebulosus* and (d) *Parupeneus spilurus*.

Microhabitat preferences of invertivorous fishes

Electivity indices revealed that invertivorous fishes foraging within macroalgal meadows can be chiefly grouped into three foraging categories: ‘canopy forager’, ‘generalist’ and ‘abiotic forager’. ‘Canopy foragers’ (i.e., those fish that search for prey and feed within macroalgal canopies) were overwhelmingly represented by Labridae, specifically the species *Anampses geographicus*, *Cheilio inermis*, *Coris caudimacula*, *Pseudojuloides elongatus* and *Thalassoma lunare* in summer (Figure 5.5), and *Cheilio inermis* and *Coris caudimacula* in winter (Figure 5.6). All of these species had positive electivity values for canopy macroalgae, as their proportional use of this microhabitat was greater than its proportional availability. Notably, this positive preference for canopy macroalgae was consistent across seasons, even in winter when there was significantly lower availability of macroalgal canopy (Figures 5.5, 5.6). Species belonging to the family Mullidae (*Parupeneus barberinoides* and *Parupeneus spilurus* in summer; *Parupeneus spilurus* in winter) as well as the labrid species (*Halichoeres nebulosus*, *Stethojulis bandanensis* and *Stethojulis interrupta* in summer; *Halichoeres nebulosus* in winter) were found to be ‘abiotic foragers’ (fish that search for prey and feed on pavement, sand, dead coral, rubble). All of these species had positive electivity values for abiotic substrates, as their proportional use of this microhabitat was greater than its proportional availability (Figures 5.5, 5.6). They also exhibited negative electivity values for canopy macroalgae suggesting that they were actively avoiding such habitats (Figures 5.5, 5.6). Finally, species belonging to the family Lethrinidae (*Lethrinus atkinsoni* and *Lethrinus nebulosus*) were found to be 'generalists', showing a positive electivity for foraging within both canopy macroalgae and on abiotic substrates (Figure 5.5). However, none of these generalist species were observed in sufficient number during the winter surveys. Interestingly, all the fish species in this study showed a strong avoidance of foraging within understory macroalgae, despite the high availability of this habitat within the macroalgal patches (Figures 5.5, 5.6).

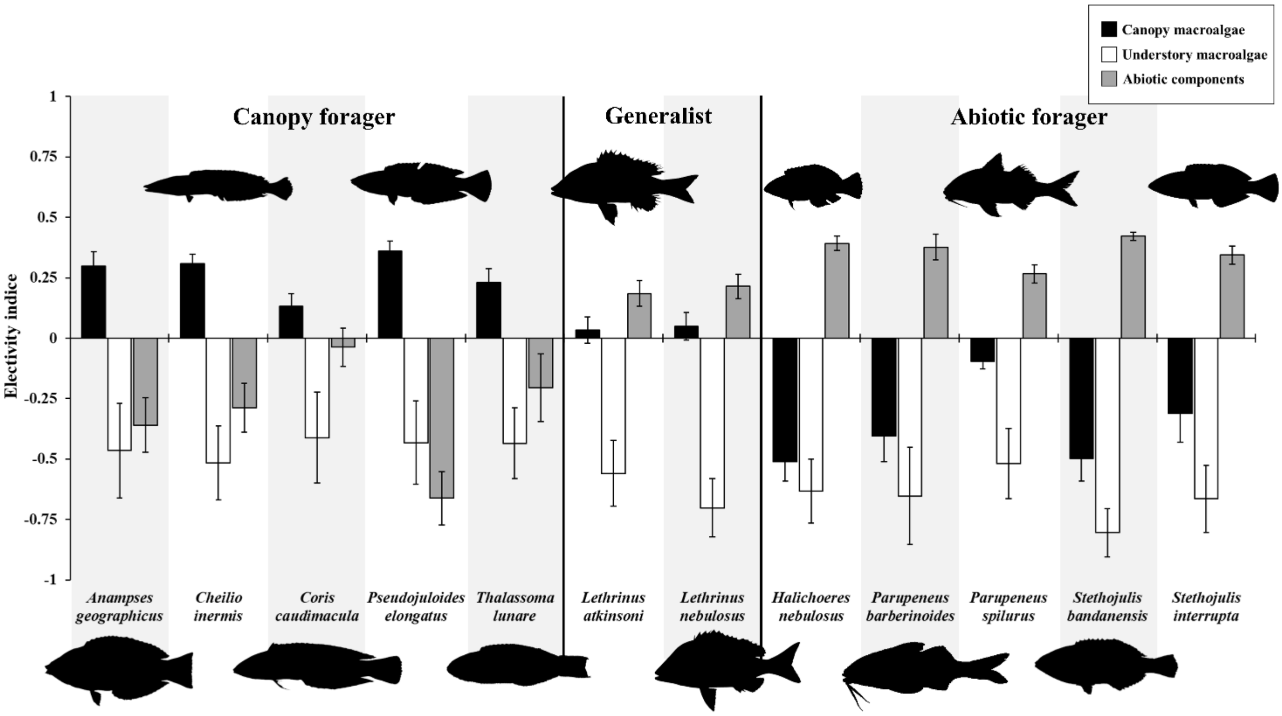


Figure 5.5 Preferences of common invertivorous fishes toward microhabitat categories (canopy macroalgae, understory macroalgae, abiotic components) averaged (± standard error) across 8 meadow patches within Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, during summer season.

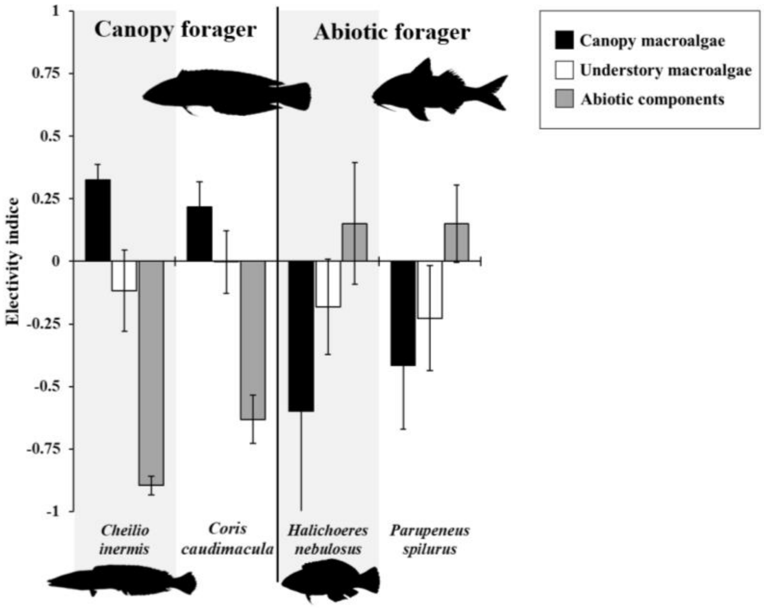


Figure 5.6 Preferences of common invertivorous fishes toward microhabitat categories (canopy macroalgae, understory macroalgae, abiotic components) averaged (± standard error) across 4 meadow patches within Maud Recreation Zone of Ningaloo Marine Park near Coral Bay, during winter season.

Discussion

This study presents the seasonal taxonomic composition and foraging microhabitat utilisation of invertivorous fish communities within tropical macroalgal meadows of Coral Bay, Ningaloo Marine Park, Western Australia. Species belonging to the family Labridae were the most abundant invertivorous taxa within the macroalgal meadows here, making up over 70 % of our foraging observations, followed by the families Mullidae and Lethrinidae. Similar compositions of invertivorous fish communities, particularly in terms of dominance by labrids, have been reported across tropical seascapes, including coral reefs (Chaves et al. 2013; Evans et al. 2014; Sambrook et al. 2019, 2020) and macrophytal habitats such as seagrass (Nakamura et al. 2003; Shibuno et al. 2008; Tano et al. 2016; Sambrook et al. 2019, 2020) and macroalgal meadows (Evans et al. 2014; Tano et al. 2016; Sambrook et al. 2019, 2020). However, our study also found that fishes grouped under the trophic status of 'invertivore' actually have distinct foraging microhabitat preferences, resulting in individual invertivorous species having non-equivalent functional impacts on marine ecosystems. The division of invertivorous fish communities at this location can be divided into three foraging categories: 'canopy forager', 'abiotic forager' and 'generalist' based on their unique microhabitat preferences, highlighting a previously unappreciated aspect of functional complementarity within this particular trophic group.

Species belonging to the family Labridae were the dominant ‘canopy foragers’ with the exception of two species of ‘abiotic forager’, lethrinids dominated the category of ‘generalist’, and mullids were dominant in the category of ‘abiotic forager’. This coordination between taxonomic group and foraging category suggests that the observed division of the microhabitat niche axis is most likely to be based on the sharing of similar morphological traits, social characteristics or the need to acquire particular dietary targets. Canopy macroalgae provide complex microniches and large surface areas, which facilitate the colonisation of abundant epifaunal communities targeted and consumed by invertivorous fishes (Cacabelos et al. 2010; Veiga et al. 2014; Tano et al. 2016; Carvalho et al. 2018; Wenger et al. 2018). This results in a high prey density in a small volume of canopy, meaning that macroalgal canopies are likely to be a rich food resource for canopy foragers. As dominant canopy foragers, labrids characteristically have a pointed snout and prominent canine teeth which project forward at the front of the jaw, making it possible to flip the macroalgal blades to expose the hidden epifauna within the canopies, and with the development of a strong beak and pharyngeal jaw, labrids are able to crush the hard-shelled epifaunal prey such as crustaceans and molluscs while foraging within the canopies (Choat & Bellwood 1998; Froese & Pauly 2021). Previous studies have found that labrids in shallow habitat zones (e.g., inner flat, outer flat) of coral reefs tend to have a much higher fin aspect ratio for their size, suggesting fast swimming ability and high manoeuvrability which they can employ to procure food or to compete against other species (Bellwood & Wainwright 2001; Fulton et al. 2001). These swimming abilities may also be useful for canopy foragers in terms of escape from potential predators while foraging within canopies, particularly given that marine macrophytal habitats (e.g., macroalgae, seagrass) represent ideal places for piscivorous fishes to ambush their prey (Willis & Anderson 2003; Lauren & Brown 2006; Hoey & Bellwood 2011; Kruschel & Schult 2020). The ‘abiotic’ microhabitat preference of mullids documented in the current study undoubtedly reflects their particular morphological and behavioural specialisations. Mullids were consistently observed foraging within sand/rubble based microhabitats, using their sensory barbels to detect epibenthos and infauna, and stirring up sediments using their broad snouts in order to expose their prey (Golani & Galil 1991; McCormick 1995; Lombarte et al. 2000; Uiblein 2007; Esposito et al. 2014). Mullids have been reported foraging in association with many fish species (Lukoschek & McCormick 2001; Froese & Pauly 2021), particularly labrids, and this behaviour was also observed in the current study in the case of the two species of labrids that were also documented as ‘abiotic foragers’. Lethrinids, which in the current study showed no specific foraging microhabitat preference and were therefore classified as ‘generalists’ have previously been shown to use varied marine macrophytal habitats such as seagrass or macroalgal meadows adjacent to coral reefs (Dorenbosch et al. 2005; Kulbicki et al. 2005b; Lugendo et al. 2005; Wilson et al. 2010, 2017; Sambrook et al. 2019). Previous studies have also found that lethrinids consume a diverse range of prey species, showing a great plasticity in diet and trophic range (e.g., from ‘invertivore’ to ‘piscivore’; Kulbicki et al. 2005b; Farmer & Wilson 2011; Froese & Pauly 2021), and they can increase their dietary breadth with increasing body size and mouth size (Kwak et al. 2015), meaning that smaller lethrinids feed on the small sand- or canopy-dwelling prey, while larger individuals tend to hunt more mobile prey (Kulbicki et al. 2005b). In the current study, 55% of foraging observations in lethrinids were juvenile individuals, suggesting that macroalgal canopy habitats provide important nursery habitat for these species and that the epifaunal communities of canopy macroalgae can make a significant contribution to the quality of those nursery habitats, including in terms of their nutritional quality.

Whether foraging microhabitat preferences recorded in the current study were driven by selection of particular dietary targets associated with those individual microhabitat niches is more difficult to assess on the basis of currently-available data. There are surprisingly few published studies that compare epifaunal communities between neighbouring habitats to allow for assessment of whether differences in community composition between habitats may translate either into differences in dietary target or nutritional quality between habitats. We know that epifaunal community structure can vary between habitats across microhabitat and seascapes (Chen et al. 2020; Fraser et al. 2020a). It is therefore likely that particular dietary targets may be more or less abundant within communities at certain locations, driving specialisations in foraging microhabitat preferences of invertivorous fishes. Fraser et al. (2020a) found that peracarid crustaceans can make up more than 75% of epifauna harboured by fucoid macroalgae, while epifauna within abiotic/carbonate microhabitats such coral rubble or dead corals are dominated by decapods, gastropods and polychaetes. Previous studies have highlighted some of the trophic relationships between invertivorous predators and epifaunal prey. For example, gut content analysis of the invertivorous species *Xenojulis margaritaceus*, revealed a dietary preference for AOM (amorphous organic matter) and microcrustaceans (Wenger et al. 2018). There is also correlational evidence for selection of gastropod prey by labrids (Chen et al. 2020). In the current study, we were unable to collect specimens for gut content analysis to verify potential dietary targets that could be driving division of the foraging habitat resource axis. However, this would represent a profitable future direction of research in order to examine and verify the prey selection and dietary targets of invertivorous fish species within macroalgal meadows.

Our study found that, although the taxonomic composition of invertivorous fishes present within the macroalgal meadow habitats of Ningaloo varied across seasons (higher abundance of a greater number of species recorded in summer), the foraging microhabitat preferences of individual species were consistent across seasons. This suggests that the microhabitat niche partitioning observed in the current study are likely to be based on real foraging specialisations, rather than just resulting from microhabitat crowding and resource competition in a given season. For marine macrophytal habitats which undergo systematic and predictable fluctuations that are regulated by regular seasonal changes, associated fish assemblages must periodically migrate or adapt to such changes (Green et al. 2009; Wilson et al. 2014; Lim et al. 2016). In the present study, either the abundance or the foraging behaviour of invertivorous fish species underwent dramatic declines in winter, in accordance with the extent of *Sargassum* canopy loss. Due to the local absence of preferred microhabitats for canopy foragers in winter, they may move to adjacent habitats, since the biomass of *Sargassum* at Ningaloo Reef also demonstrates significant spatial variation, allowing some meadow patches to retain abundant canopies in the same season (Fulton et al. 2014; Wilson et al. 2014; Lim et al. 2016). However, two canopy foraging labrid species '*Cheilio inermis*' and '*Coris caudimacula*' continued to use the decayed meadows in winter, despite the lower resource availability. Also of note is that, along with fewer 'canopy forager' species observed in winter, there were also fewer 'abiotic' foraging species, despite there being no equivalent reduction in foraging microhabitat availability for this category. Only two abiotic foraging species '*Halichoeres nebulosus*' and '*Parupeneus spilurus*' were observed in significant abundances in the vicinity of meadow patches in winter. This contradicts our initial hypothesis that the density of 'generalists' and 'abiotic foragers' would be less influenced by seasonal fluctuations in macroalgal canopy biomass. This suggests that, for such non-canopy foraging species, macroalgal canopies may provide other important functions including nurseries for recruitment or refuge from predators (Tano et al. 2017; Wilson et al. 2017). Once macroalgal canopies start to decay, these satellite functions are lost, meaning that generalist and abiotic foragers are forced to move to adjacent reef habitats to seek out equivalent functionality. Our results therefore highlight the importance of macroalgal canopies as essential microhabitat which provides not only food but other ecological functions.

Surprisingly, all the fish species documented in the current study showed a strong avoidance of foraging on understory macroalgae, despite the high availability of this microhabitat within the macroalgal patches. This accords with the results of previous studies looking at the foraging behaviour of individual fish species within macroalgal meadows (herbivorous *Leptoscarus vaigiensis*: Lim et al. 2016; invertivorous *Xenojulis margaritaceus*: Wenger et al. 2018). Potential factors that may discourage invertivores from foraging in the understory include: (1) nutritional differences and/or, differences in taxonomic structure of epifaunal prey communities associated with the two microhabitats; (2) differential predation threat posed by the two microhabitats. Previous studies have suggested that canopy-forming macroalgae are able to harbour a greater biomass of epifaunal invertebrates and/or to provide better quality of shelters than non-canopy species (e.g., understory macroalgae, turf algae) due to their more complex structure (Taylor & Cole 1994; Cacabelos et al. 2010; Carvalho et al. 2018; O'Brien et al. 2018), meaning that understory macroalgae at Ningaloo Reef may represent the poorer of the two dietary resources.

The refinement of functional roles of invertivorous fishes based on their foraging microhabitat preferences presented here suggests that the functional diversity of fish under the trophic status ‘invertivore’ within tropical canopy macroalgal meadows has previously been underestimated. The discovery of discrete functional roles for invertivorous fishes based on their foraging microhabitat preferences yields a more conservative estimate of the level of functional redundancy within the ecosystem that will be important for management actions going forward. For example, over-exploitation of species that all fall within the ‘canopy forager’ role is likely to have consequences for top-down control of epifaunal invertebrate communities and cascading effects on primary producers. Moreover, as the foraging microhabitat preferences of invertivorous fish species are unravelled further, particular species may be found to play a unique role in facilitating particular trophic links between organisms. For example, previous studies of invertivorous fishes in the canopy macroalgal meadows of Ningaloo have tended to focus on fishery or recreational targets, especially fishes from the family Lethrinidae (Westera 2003; Wilson et al. 2010, 2014, 2017; Farm & Wilson 2011). However, due to the consistency of their abundance and foraging microhabitat preferences across seasons, canopy foragers such as the labrids *Coris caudimacula* and *Cheilio inermis* are also likely to be vital components of macroalgal meadow ecosystems. As these ecosystems come under pressure from climate change, including marine heatwaves and rising sea temperature (Smale & Wernberg 2013; Straub et al. 2019; Graba-Landry et al. 2020), the predicted range-contractions of canopy macroalgal meadows will impact on associated invertivorous fish communities, and especially on canopy specialists such as species belonging to the family Labridae. Future research should aim to examine gut contents, foraging rates and feeding trails to further refine our understanding of the functional roles of the species presented here. This will ensure that the potential implications of loss of macroalgal meadow habitats on the trophic guild of 'invertivores' are better understood to assist in future marine management.

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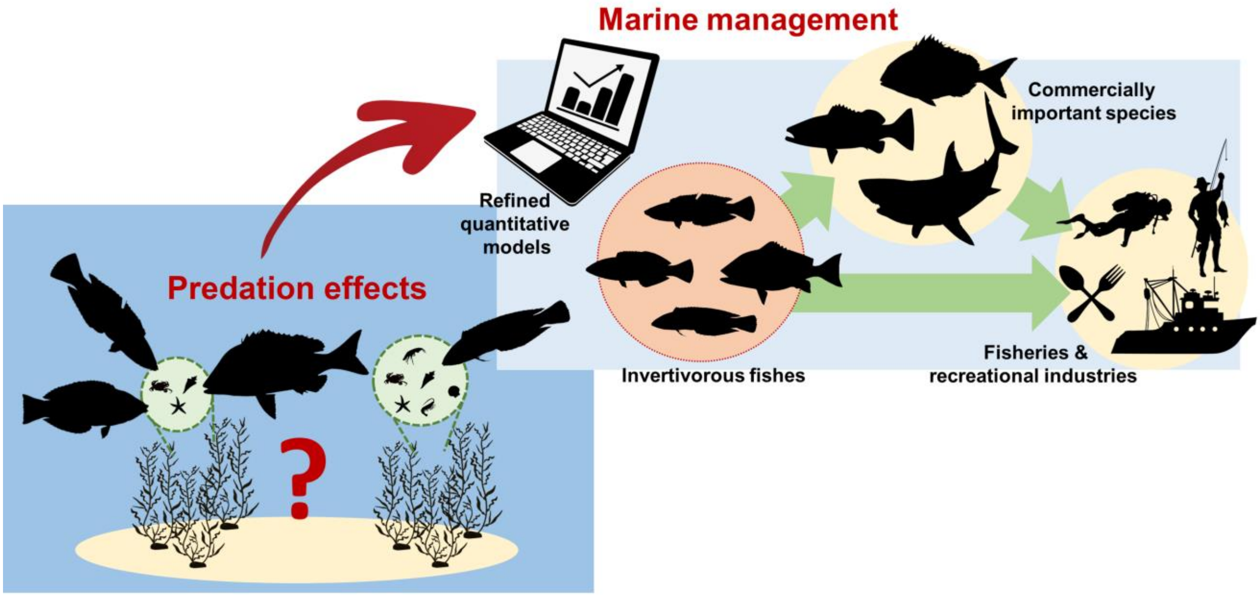
CHAPTER 6

ESTIMATES OF TROPHIC LINKAGES BETWEEN EPIFAUNA AND INVERTIVOROUS FISHES WITHIN A MACROALGAL-DOMINATED REEF HABITAT: AN EXPERIMENTAL APPROACH



This chapter will be submitted to *PeerJ*

Co-authored with Jennions, M. and Fox, R.J.

Abstract

Predation is a biological interaction found in almost all ecosystems that mediates energy flow from prey to predators. Understanding when, who and how predators consume prey therefore brings key insights into studies of trophic dynamics and ecosystem functioning. In tropical seascapes, invertivorous fishes are one of the most abundant trophic guilds, and they have been identified as pivotal predators feeding on epifaunal invertebrates. The trophic link between invertivorous fish and epifauna therefore underpins marine biodiversity and the size of fishery stocks. In this study, we investigated predation in the tropical canopy-forming macroalgal meadows of World Heritage Ningaloo Reef in Western Australia. We quantified the level of predation by invertivorous fishes on macroaglae-associated epifauna by excluding predator from canopy macroalgae in a short-term caging experiment. Our results show that epifaunal biomass varied significantly across caging treatments. We also observed changes in the size distribution of crustacean between treatments where predators were or were not excluded, which offers hints as to preferential selection of certain prey items and/or size by invertivorous fishes. We estimated that the net daily consumption rate of epifaunal biomass by invertivorous fishes in the summertime was 0.218 (mg epifaunal ash free dry weight per g *Sargassum* dry weight), suggesting that predation by invertivorous fishes has the potential to alter epifaunal community structure. We also extended this estimate to predict the total consumption rate of epifauna by fish in the Ningaloo region. We highlight the implications of predation of epifauna by invertivorous fishes for energy transfer to higher trophic levels. The results of this study improve our understanding of tropical macroalgal-based marine food webs, which will help to guide future research, and assist in the design of effective marine management programs.

Keywords: Caging Artefacts, Canopy-Forming Macroalgae, Epifaunal Invertebrate, Invertivorous Fish, Predation, Predator Exclusion, Trophic Flows, Tropical Seascape

Introduction

Predation is a ubiquitous biological interaction found in almost all terrestrial and aquatic ecosystems that affects populations and communities in a variety of ways. Crucially, it determines trophic flow and thereby affects associated ecological processes (Sinclair et al. 2003, Schmitz 2007, Benkendorf & Whiteman 2021). Understanding the effects of predators on prey at both the individual level (e.g., changes in hiding behaviour) and the population level (e.g., changes in density or the sex ratio), can help us to answer key questions in functional ecology. In tropical seascapes, studies on how predators affect the abundance and composition of lower-level communities that include prey species have been an intense focus of research. This is particularly true for studies of mesopredatory fish species on coral reefs (Doherty & Sale 1986, Thillainath et al. 2016, Casey et al. 2017). Predation-prey interaction at lower trophic levels, and in other equally important habitats such as macroalgal meadows are, however, far less well studied.

Invertivorous fishes are usually small to medium sized predators, primarily feeding on invertebrates (Kulbicki et al. 2005, Kramer et al. 2015, Froese & Pauly 2021). In tropical seascapes, they have been documented to consume epifaunal invertebrates that occur in a wide range of habitats, including coral reefs, seagrass and macroalgal meadows (Kramer et al. 2016, Wenger et al. 2018, Froese & Pauly 2021). Invertivorous fishes therefore play an important role in shaping both the community structure and the productivity of lower trophic levels. At the same time, invertivorous fishes are themselves targeted as key food resource by a diverse array of mesopredatory piscivores and other apex predators (Kulbicki et al. 2005b, Ashworth et al. 2014, Froese and Pauly 2021). This makes invertivorous fishes key middle-order mediators that connect energy flows from primary consumers to higher-order consumers: trophic links that involve predation by (and on) invertivorous fishes therefore underpin biodiversity and ecosystem functioning.

Canopy-forming macroalgal meadows are now recognised as one of the most productive seascapes in tropical regions (Tano et al. 2016, Fulton et al. 2019, 2020). Recent studies have highlighted their importance as foraging grounds, shelters and nurseries for many reef fishes, including a diverse array of invertivorous species, because they provide habitat for an abundance of epifauna that live on their structurally complex canopies (Chaves et al. 2013, Tano et al. 2017, Chen et al. 2020). Recent studies have documented the community composition and foraging preference of invertivorous fishes and how their presence is likely to affect epifaunal communities when there are shifts in the habitat created by tropical, canopy-forming macroalgal meadows (van Lier et al. 2018, Wenger et al. 2018, Chen et al. 2020). However, compared to the relatively well studied temperate macrophytal habitats and tropical coral reefs, there have been few investigations of either the effects of invertivorous predation on epifaunal communities, or estimates of the epifaunal biomass consumed by fishes in the '*canopy-forming macroalgae – epifauna – invertivorous fish*' trophic pathway found in tropical seascapes (Edgar & Aoki 1993, Taylor 1998a, Casey et al. 2017).

The trophic links created by invertivorous fish underpin fundamental processes of ecosystem functioning. The supply of ecosystem service that then arise from a healthy ecosystem include the maintenance of fishery stocks that are linked to the livelihoods of millions of people who live along macroalgal-dominated coastlines in the tropics. This makes it essential for us to understand better the trophic cascades triggered by the predatory behaviour of invertivorous fish so that we can more accurately estimate energy flows between different trophic levels. Here, using the canopy-forming macroalgal meadows of Ningaloo Reef as our study system, we ask two key questions. First, how does the exclusion of invertivorous fishes affect the density and size distribution of epifauna harboured by macroalgal canopies? Second, how much epifaunal production is consumed by these invertivorous predators on a regional scale?

Materials & Methods

Study location

This study was conducted within the UNESCO World Heritage Ningaloo Reef, Western Australia (Figure 6.1). Ningaloo Reef is the world's largest fringing reef, stretching 290 km along the western coast of Australia with shallow water covered by extensive macroalgal meadows dominated by canopy-forming fucoids *Sargassum* and *Sargassopsis* (Kobryn et al. 2013, Fulton et al. 2014, van Lier et al. 2018). In the austral summer (January to February) of 2020, we selected two distinct nearshored canopy-forming macroalgal meadow patches (Patch A: -23°11.79, 113°46.24; Patch B: -23°13.46, 113°46.36) within a 6 km^2 section of the Maud Recreation Zone nearby Coral Bay to conduct predator exclusion experiments (Figure 6.1).

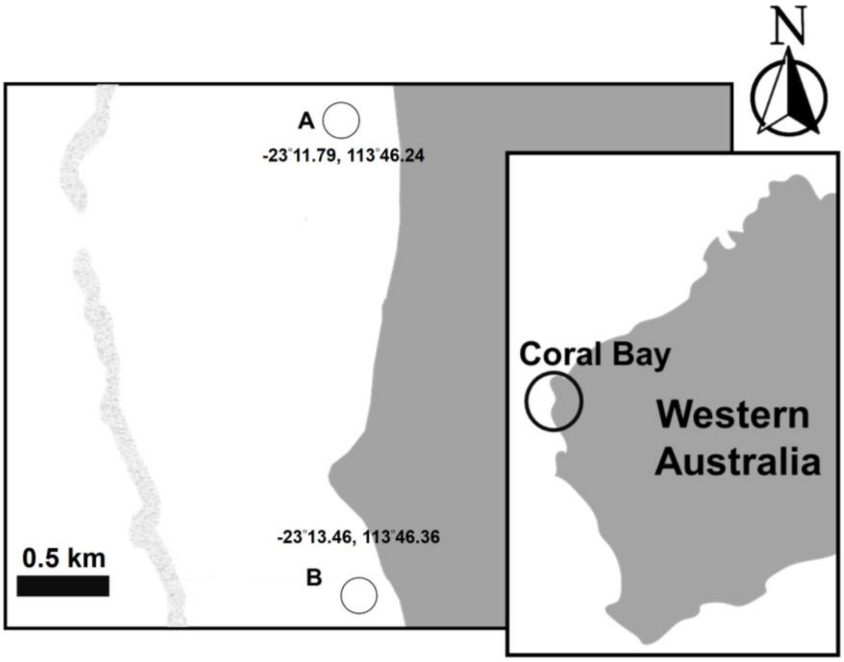


Figure 6.1 Study location of the two canopy-forming macroalgal meadow patches within the Maud Recreation Zone near Coral Bay, Ningaloo Reef, Western Australia.

Benthic habitat composition & invertivorous fish survey

The benthic habitat composition and invertivorous fish density within these macroalgal meadow patches were measured via underwater visual censuses conducted by SCUBA diving. At each meadow patch, we ran 12 replicates of 5 m transects, with each transect separated by at least 5 m. Along each transect, we estimated the percent cover (%) of each benthic habitat category (e.g., sand, pavement, macroalgal genus such as *Sargassum* and *Lobophora*) that we encountered by measuring the total distance of the 5 m occupied by each benthic habitat category. Along the same 5 m transects, we also used a point-census cylinder survey method following Chen et al. (2020) to document the presence of invertivorous fish species that have previously been shown to forage on epifauna within macroalgal canopies at Ningaloo (Chen and Fox, unpublished data). This survey method involves a single diver recording the presence and total length (cm) of individual fish, identified to the species level, within a virtual 5 m diameter cylinder whose base is parallel to the transect. The length and abundance information for each invertivorous species was then converted to biomass using published length-weight relationships (Kulbicki et al. 2005a, Froese & Pauly 2021). These values were then summed to estimate the biomass (g per m^2) of invertivorous fishes within each meadow patch.

Predator exclusion experiments

To quantify the effects of predation by invertivorous fishes on epifauna in canopy-forming macroalgal meadows, we designed a short-term caging experiment with three treatments (full cage, open cage, control) to conduct a field manipulation of predation. Full cages were constructed of galvanised steel (50 cm × 50 cm × 50 cm) with 1 cm mesh netting to enclose macroalgae and exclude any potential invertivorous fishes (Figure 6.2a). Open cages had the same dimensions and mesh size as the full cages, but the mesh netting covered only the roof and the bottom half, so that invertivorous fishes could still gain access to the macroalgae. This cage design was intended to control for any caging artefacts (e.g., lower light intensity, change in temperature, changes in water movement) (Figure 6.2b). For the control treatment we used a 50 cm × 50 cm metal quadrat to mark out an area equivalent in size to that in the full or open cages. In the control treatments, invertivorous fishes could forage freely and there was no possibility for caging artefacts (Figure 6.2c).

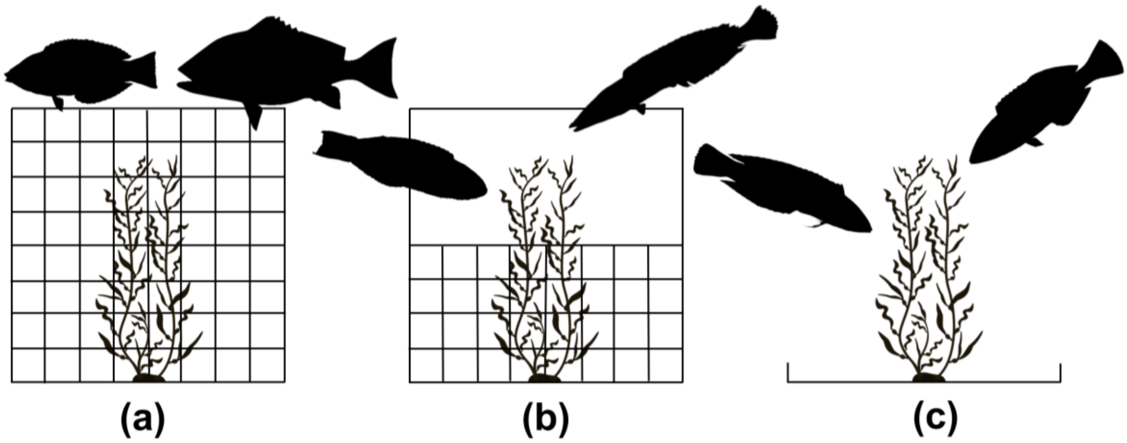


Figure 6.2 Treatments for short-term caging experiment used to test for predation effects and caging artefacts: (a) full cage, (b) open cage and (c) control. The cage size is 50 cm × 50 cm × 50 cm cage size and the mesh size is 1 cm.

At each meadow patch, four replicates of each caging treatment (total *N* = 12 per patch) were deployed, with one replicate located on each of the 12 transects described above. Treatments were randomly assigned to a transect and kept in place for 10 days. The cages were scrubbed, while still in place, on the 6th day to remove any detritus, epiphytes and fouling organisms. This cleaning minimised potential caging artefacts caused by the mesh becoming blocked. We tested directly for potential caging artefacts in each of three treatments at Patch A by installing clod cards to quantify water movement, and submersible loggers (Onset HOBO Pro v2) to record sea temperature and light intensity respectively.

Sampling & post-collection processing of macroalgae with associated epifauna

After ten days the cages were carefully removed by two SCUBA divers. All canopy-forming macroalgae and associated epifauna within each cage (or the equivalent volume for the control) were then collected immediately. For each replicate, the samples of macroalgae were stored separated based on genus. We used canvas bags to fully enclose any macroalgae, and the bag was then sealed as soon as we had detached the thallus to prevent any associated epifauna from escaping. All samples were brought back to the Coral Bay Research Station for post-collection processing within four hours of sampling. We immersed each canopy-forming macroalgal sample in cold freshwater for ten minutes to numb and dislodge its associated epifauna. The dry weight (g DW) of each canopy-forming macroalgal genus for each replicate was then measured after being oven-dried at 60°C for 48 hours. The extracted epifauna were frozen at -20°C and transported to The Australian National University, where they were fixed with 10% formalin for subsequent analysis.

Estimate of epifaunal biomass

We estimated epifaunal biomass following the sieve method of Edgar’s (1990b) (see Chen et al. 2020 for details). In brief, epifauna were fractionated by body size after passing the 10% formalin-fixed samples described above through a series of stainless steel sieves (8.0, 4.0, 2.8, 2.0, 1.4, 1.0, 0.7 and 0.5 mm mesh sizes). The epifauna retained on each sieve were identified individual by individual under a dissecting microscope at 40x magnification. We recorded the abundance of six functional groups (crustaceans, molluscs, echinoderms, polychaetes, forams and ‘other animals’) following the approach of Edgar’s (1990b). We then calculated the total ash free dry weight (mg AFDW) of each functional group per sieve size using Edgar’s empirically-derived equations (1990b). Any organism larger than 8.0 mm or smaller than 0.5 mm was disregarded. We focused on animals between 0.5 and 8.0 mm in body size as these reflect the consensus-based definition of epifauna provided by Chen et al. 2021 (chapter 2).

Data analyses

We first ran three separate one-way ANOVAs with caging treatment as a fixed factor to test for any caging artefacts with either sea temperature (°C), light intensity (Lux) or water movement (mass loss of clod card, g per day) as the dependent variable. There were weak or no detectable effects of the caging treatment on sea temperature (*df* = 2, 9, *F* = 6.063, *p* = 0.021), light intensity (*df* = 2, 9, *F* = 2.569, *p* = 0.131) or water movement (*df* = 2, 9, *F* = 0.255, *p* = 0.780). Even so, we decided to exclude the control treatment from subsequent analyses to distinguish the effect of predator exclusion and presence without any concerns about any subtle artefactual effects of caging. That is, we simply compared full and open cages as in both cases there is a cage present. We treated each replicate as an independent data point, even if they were from the same patch (total N = 16 replicates, 8 full cages, 8 open cages). We did not control for patch identify as a random factor in our models, because it is not possible to estimate the variance associated with patch type based on only two levels. Since *Sargassum* was the dominant canopy-forming genus in each cage, constituting 87.84% ± 4.87% of the DW (mean ± SE), we only included *Sargassum* with its associated epifauna in our subsequent analysis.

We then ran a one-way multivariate analysis of covariance (MANCOVA). The model had logged epifaunal biomass (mg AFDW) of the six functional groups for each of the seven size category as dependent variables, caging treatment (full or open cage) as the fixed factor and log-transformed *Sargassum* biomass (g DW) as the covariate (to take account of the strong positive correlations between macroalgal canopy biomass and epifaunal biomass; Leite & Turra 2003, Wenger et al. 2018, Chen et al. 2020). Both epifaunal biomass and *Sargassum* biomass were log-transformed to meet the assumptions of linearity and normality of distribution. These MANCOVAs were performed with type I sum of squares and a maximum of 9999 permutations of resemblance matrices based on the modified Gower (base 2) dissimilarity. We included the interaction between caging treatment and *Sargassum* biomass to test if the relationship between epifaunal and *Sargassum* biomass differed between full cage and open cage. A significant effect of cage treatment in this MANCOVA is interpreted as changes in the biomass distribution across the 42 size-group categories due to predation. Next, we ran an ANCOVA with logged total epifaunal biomass (mg AFDW) as the dependent variable and caging treatment (full or open cage) as the fixed factor and log-transformed *Sargassum* biomass (g DW) as the covariate with type III sum of squares. We included the interaction between caging treatment and *Sargassum* biomass to test if the relationship between epifaunal and *Sargassum* biomass differed between full cage and open cage. It did, but the effect was small (see results). To gain insight into the main effect of the cage treatment on total epifaunal biomass we then re-ran the model after removing the interaction.

Finally, to estimate the total epifaunal biomass consumed by invertivorous fishes, we divided the total epifaunal biomass by total *Sargassum* biomass for each of the two treatments. The difference between the value for the full and open cage treatment was then divided by the underwater period (10 days) to calculate the net daily rate of epifaunal biomass consumption (mg AFDW epifaunal biomass per g DW *Sargassum*). We chose this approach, rather than using the estimates from the ANCOVA because of the confounding problem of the slight difference in the relationship between epifaunal and *Sargassum* biomass between the two caging treatments, which is likely to reflect a type 1 error given the fairly low number of replicates per treatment.

Results

Ten invertivorous fish species from two families (Labridae: *Anampses geographicus, Cheilio inermis, Coris auricularis, Coris caudimacula, Pseudojuloides elongatus, Pteragogus flagellifera, Thalassoma lunare, Xenojulis margaritaceus*; Lethrinidae: *Lethrinus atkinsoni, Lethrinus nebulosus*) previously identified as foragers targeting canopy-associated epifauna were recorded during our transect surveys. A total of 37518 epifauna individuals were extracted from 2410 g DW of canopy-forming maroalgae that comprised four genera retrieved from the experimental replicates in the two meadow patches (*Sargassum* (92%), *Sargassopsis* (5%), *Sirophysalis* (2%) and *Hormophysa* (1%)).

For the MANCOVA there was a significant positive relationship between *Sargassum* biomass and epifaunal biomass, but the relationship did not differ between full and open cages as there was no significant interaction between *Sargassum* biomass and caging treatment. Controlling for the amount of *Sargassum* there was a significant difference between the full and open cage treatment in the distribution of epifaunal biomass across the six functional groups and seven size categories (p = 0.039; Table 6.1; Figure 6.3).

The functional group responsible for this significant effect is hard to determine. In general, animals of 5.6-8.0 mm were the dominant size class in both caging treatments, and the proportion in each size group in full cages was similar to that in the open cages (Figure 6.4a).

The same trend can also be observed when looking at the biomass of molluscs (Figure 6.4c). However, the size distribution of individuals contributing to crustacean biomass showed a slightly different pattern between full and open cages (Figure 6.4b). A higher proportion of 5.6-8.0 mm individuals contributed to biomass in the full than in the open cage (31% versus 18%). This suggests that invertivorous fishes may preferentially consume larger crustaceans, as they disproportionately removed these individuals from the open cages.

Table 6.1 Summary of one-way MANCOVA of logged epifaunal biomass across two caging treatments (fixed) with logged *Sargassum* biomass included as the covariate, in the Maud region near Coral Bay of Ningaloo Reef, 2020. Significant terms ($p < 0.05$) are highlighted in **bold**.

Source	df	SS	MS	Pseudo-*F*	*p*-value
***Sargassum* dry weight**	1	3.3362	3.3362	13.791	**0.0001**
Caging treatment	1	0.47935	0.47935	1.9814	**0.039**
Sargassum dry weight × caging treatment	1	0.30445	0.30445	1.2585	0.2503
Residual	12	2.903	0.24192		
Total	15	7.023			

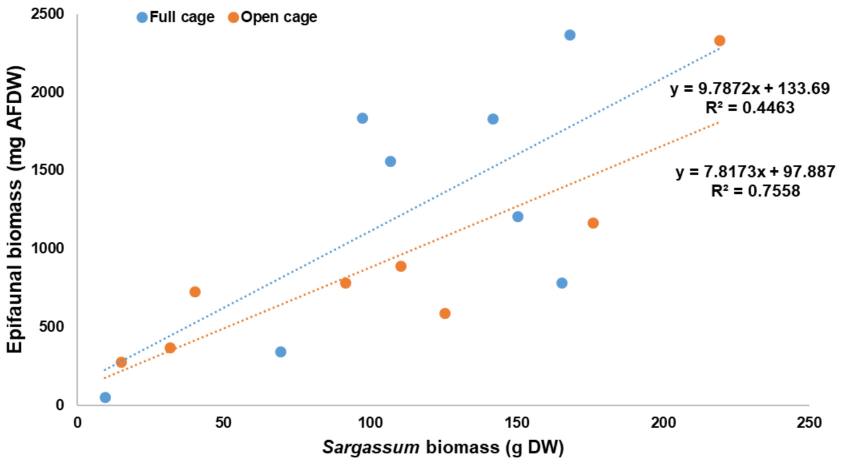


Figure 6.3 Relationships between epifaunal biomass and macroalgal canopy size of the two caging treatments (full cage, open cage) over 10 days in Ningaloo Reef, Western Australia. The model used log-transformed data, but the raw data are shown here to facilitate interpretation.

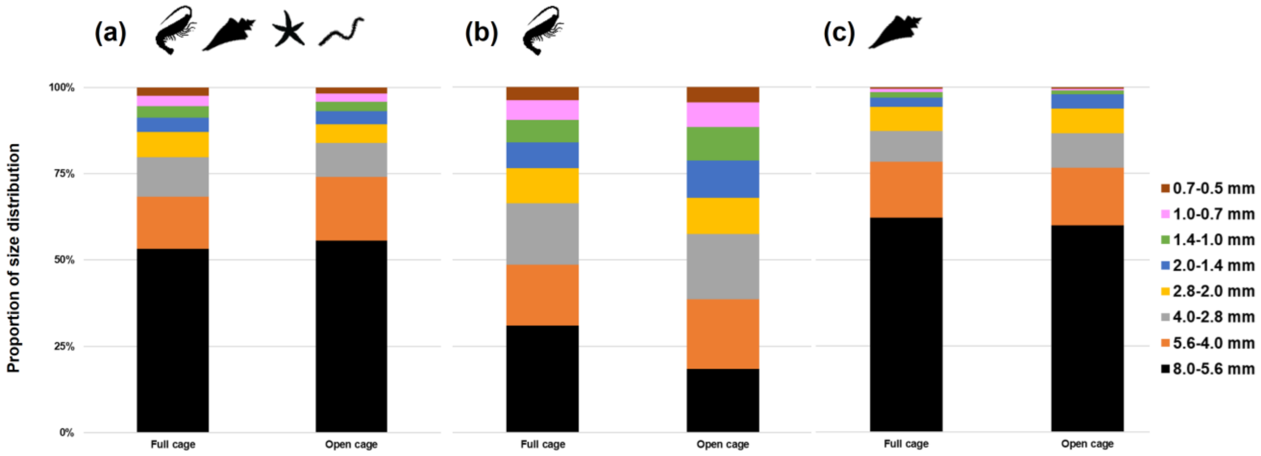


Figure 6.4 Percent contribution to (a) total epifaunal biomass, (b) crustacean biomass, and (c) mollusc biomass of the epifaunal size spectra for the full cage (predator excluded) and open cage (predator not excluded) treatments.

Unfortunately, the effect of the caging treatment on total biomass is slightly difficult to interpret because the relationship between *Sargassum* biomass and total epifaunal biomass differed between full and open cages (p = 0.042). If the interaction is removed from the model, there is no significant difference in the total epifaunal biomass between full cage and open cage (p = 0.849). Indeed, the marginal estimate is slightly higher for the open than full cages, which is biologically difficult to interpret (Table 6.2). Finally, based on pooling data across all replicates we estimated the net daily consumption of epifaunal biomass by invertivorous fishes as 0.218 mg AFDW per 1 g DW of macroalgal canopy.

Discussion

We experimentally manipulated the access of invertivorous fishes to epifaunal prey in tropical canopy-forming macroalgal meadows by deploying a short-term caging experiment. We found that when looking at epifaunal biomass categorised by functional group and size class, the distribution of biomass varied significantly between the caging treatments (MANCOVA). This suggests that predation by invertivorous fishes has the potential to alter epifaunal community composition. More specifically, we noted that there were relatively fewer large individuals contributing towards the biomass of crustacean in the open cages. This suggests that invertivorous fishes may prefer consuming larger crustaceans while selecting prey items. Despite this change in the size distribution, there was no significant decline in total biomass between open and full cages. However, the interpretation of this finding is confounded by the fact that the relationship between *Sargassum* biomass and epifaunal biomass differed between the caging treatments. Finally, pooling across all replicates we quantified the amount of biomass that invertivorous fishes consume from epifauna. This estimate will assist in calculating energy flow through marine food webs, and benefit future work on how marine productivity might response to changes in habitats.

Table 6.2 Summary of ANCOVA of logged epifaunal biomass across two caging treatments (fixed) with logged *Sargassum* biomass included as the covariate, with the interaction between caging treatment and logged *Sargassum* biomass (a) included and (b) excluded, in the Maud region near Coral Bay of Ningaloo Reef, 2020. Significant terms ($p < 0.05$) are highlighted in **bold**.

(a)

Source	df	SS	MS	Pseudo-*F*	*p*-value
Corrected Model	3	2.241	0.747	18.728	0.000
Intercept	1	0.770	0.770	19.303	0.001
***Sargassum* dry weight**	1	2.024	2.024	50.735	**0.000**
Caging treatment	1	0.207	0.207	5.180	**0.042**
***Sargassum* dry weight × caging treatment**	1	0.207	0.207	5.183	**0.042**
Error	12	0.479	0.040		
Total	16	136.307			
Corrected Total	15	2.720			

(b)

Source	df	SS	MS	Pseudo-*F*	*p*-value
Corrected Model	2	2.034	1.017	19.293	0.000
Intercept	1	0.770	0.770	14.599	0.002
***Sargassum* dry weight**	1	2.024	2.024	38.385	**0.000**
Caging treatment	1	0.02	0.02	0.038	0.849
Error	13	0.685	0.053		
Total	16	136.307			
Corrected Total	15	2.720			

The result of our predator exclusion experiment showed that some elements of epifaunal biomass varied significantly with caging treatment, even though we found no significant difference in total epifaunal biomass between full and open cages. This later result may reflect low statistical power due to the modest level of replication, as well as the duration of the experiment being too short to detect any cumulative effect of predation. Even so, by looking at pooled epifaunal biomass there was some evidence that when invertivorous fishes were unable to reach macroalgae, the density of epifauna was higher. Interestingly, the amount of variation in epifaunal biomass explained by *Sargassum* biomass in the full cages (R^2 = 0.4463) was lower than that in the open cages (R^2 = 0.7558), indicating that when predation is excluded, *Sargassum* biomass may be less important in determing the density (abundance or biomass) of epifauna. However, a study with greater replication and a longer duration of experimental treatment with a full analysis that includes the appropriate controls needs to be conducted to examine to what extent *Sargassum* biomass affects the community structure of epifauna under fish predator free conditions. Our study also detected significant caging treatment effects which is in agreement with previous studies that used similar caging manipulation to examine the influences of fish predation on benthic invertebrates in seagrass meadows (Lewis & Anderson 2012, Freestone et al. 2019, Janiak et al. 2020). We therefore suggest that open cages are the best control treatment when investigating the effect of predators on prey communities and should be used in preference to treat open, cageless plots as controls.

We also found that the size distribution of crustacean biomass varied between the two caging treatments. Full cages had a higher proportion of 5.6-8.0 mm sized crustacean than open cages (31% versus 18%). In contrast, all of the remaining six size classes smaller than 5.6 mm made a slightly higher percentage (1-4%) contribution to biomass in the open than full cages. While we were unable to conduct gut content analysis to examine the prey composition of invertivorous fishes, we can still look for other lines of evidence about their diets to infer the trophic links between predators and prey. Crustaceans have been documented as one of the most important food items of invertivorous fishes in a wide variety of tropical seascapes including at Ningaloo Reef (Kulbicki et al. 2005b, Kramer et al. 2015, Wenger et al. 2018, Froese and Pauly 2021). The high abundance of crustaceans, whose biomass is linked to *Sargassum* biomass, in combination with the abundance of invertivorous fishes, strongly suggests that the canopy-forming macroalgal meadows of Ningaloo constitute important foraging grounds for invertivorous fishes (Chen et al. 2020, Chapters 3 and 5). The shift in the size distribution of crustacean between cages where predators were included or excluded in our study therefore suggest that the foraging preference of invertivorous fishes is towards larger crustacean that are visually more apparent. More generally, the secondary production relevant to invertivores is probably also biased towards larger size-classes in other taxonomic groups. Such prey selection of larger epifauna can benefit small individuals and increase net productivity. The removal of larger individuals by predators frees up resources through competitive release that become available for smaller epifauna that then subsequently increase in abundance and biomass (Edgar & Aoki 1993). Although our current experiment was only of a short duration, this competitive release might also partly explain the observed shifts in the size distribution of crustaceans.

The most common concern with the use of cages as a technique to understand the interactions between predators and prey has been the confounding interpretation of caging treatments (Steele 1996, Connell 1997). This is because the cages used may introduce artefacts that cannot be separated from predation effects. To solve this, we employed open cages to evaluate any potential caging artefacts, so that the magnitude of predation effects could be better estimated. Although weak or no significant artefacts were detected in our study, the predator exclusion experiment did have limitations that need to be acknowledged. First, there was a lower than desired level of replication in terms of both the number of replicates per site and the number of sites was unavoidable. This was due to logistic constraints arising from the remote field location. Second, the underwater duration of the treatment was reduced for practical reasons caused by an approaching cyclone. This also halted *in situ* high frame speed filming of invertivorous fish bite rate (to quantify invertivorous fish prey items and dietary composition) and sagittal otolith analysis (to estimate individual somatic growth), which together would have helped to provide more accurate estimates of predation effects and secondary production transferred from epifauna to invertivorous fishes. Even so, the present study is still the first attempt to examine the influence of predation on macroalgal epifauna by invertivorous fishes and thereby estimate the tertiary production arising due to this important trophic pathway. We suggest that future studies should run the predator exclusion experiments for a longer period, and run the empirical studies mentioned above to establish a more detailed database on ‘invertivorous fish – epifauna’ dynamics in tropical macroalgal meadows.

In the present study, we recorded a net daily consumption of 0.218 (mg AFDW per g DW), representing the biomass transferred from canopy-associated epifauna to canopy foraging invertivorous fishes within macroalgal canopies. This value can be used to estimate the areal consumption rate of epifauna in Ningaloo by measuring the area and density of canopy-forming macroalgal meadows. Previous studies mapping the shallow habitats in Ningaloo Reef have identified 762 km^2 of reef environments, which includes 51% of area dominated by macroalgae and turf algae. In these macroalgal and turf algal habitats, canopy-forming species (chiefly focuid *Sargassum*, followed by *Sargassopsis*) can reach up to 80% of benthic cover during summertime, creating massive canopy-forming macroalgal meadows which has a total area of more than 300 km^2 in Ningaloo (Johansson et al. 2010, Kobryn et al. 2013, van Lier et al. 2018). Combined with a mean summer density of canopy-forming macroalgae of 9221.5 (g DW m^{-2}) (see Chen et al. in press (Chapter 4)), the daily epifaunal biomass consumed by invertivorous fishes in Ningaloo's macroalgal meadows is estimated to be around 600 tonnes (AFDW) in summer. Assuming an energy transfer efficiency between trophic levels of 10% (Pauly & Christensen 1995) this means that 60 tonnes AFDW per day can be convert from invertivorous fishes into predators at the next trophic level. These predators include many species that are important fishery and recreational targets (Froese & Pauly 2021).

As tropical macroalgal meadows are sensitive to environmental changes, disturbances such as thermal anomalies can cause extensive loss of macroalgal canopy cover (Fulton et al. 2019, Graba-Landry et al. 2020), triggering associated flow-on effects on higher trophic levels. This could lead to dramatic reductions in fishery production, which is underpinned by epifauna and invertivorous fishes, affecting fishery stocks linked to the livelihoods of millions of people. The quantification of energy flux across multiple trophic levels under different scenario of changing environments is beyond the scope of this study, however, identifying predation-prey interactions and rates of energy flow between epifauna and invertivorous fishes is clearly important to better understand tropical macroalgal-based marine food webs. Our study also sets the stage for work on energy flows and nutrient fluxes in tropical seascapes, as secondary production and predation are core complementary ecological processes in marine habitats, as is also the case in other terrestrial ecosystems (Brandl et al. 2019).

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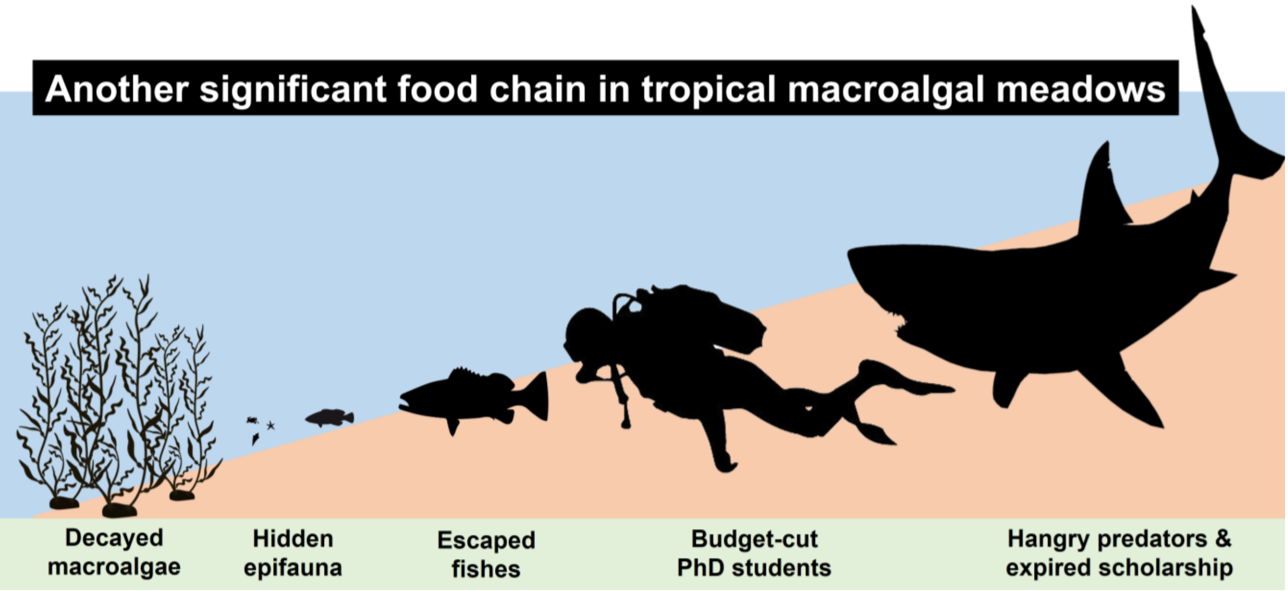
CHAPTER 7

GENERAL DISCUSSION



Marine production dilemma: lack of studies under the challenges of global change

Biological production and trophic interactions are essential to the functioning of every ecosystem on earth. The conversion of solar energy to organic material by photosynthesis, and the subsequent flow of energy through food webs, generates the link between biodiversity and trophic dynamics which, in turn, underpins the sustainability of all ecosystem processes, services and functions (Worm & Duffy 2003, Ives & Carpenter 2007, Mace et al. 2012). Discussions about biological productivity have focused on the measurement of primary production and determining how it is regulated by environmental factors such as limiting nutrients or light levels. This has relevance to applied questions in agriculture and the environmental science, such as sustaining crop yields and supporting greater biodiversity, but researchers have chiefly concentrated on terrestrial rather than aquatic environments (Melillo et al. 1993, Field et al. 1998, Potter et al. 2012). By contrast, secondary and higher-order production, and how they response to primary production, tend to be less well studied phenomena. When secondary and higher-order production are investigated, the emphasis is also mainly on terrestrial habitats, and occasionally freshwater systems. Again, marine ecosystems tend to be less well studied, even though secondary and higher-order production are as important as primary production in energy flow within marine food webs (Polis et al. 1997, Benke et al. 2001, Dolbeth et al. 2012).

Levels of production within any ecosystems are rarely fixed due to temporal and/or spatial fluctuations in key environmental factors, including direct effects of physical, abiotic drivers (e.g., light intensity, temperature, humidity), and indirect effects due to spatial or temporal shifts in biological interactions (e.g., predation, competition). Many ecosystems, including the tropical macroalgal meadows discussed in this thesis, undergo regular and repeatable cycles of fluctuations in the level of production (e.g., daily and/or seasonal shifts in primary production). Temporal changes in production are a natural part of these ecosystems, and species have evolved to be able to persist despite the uneven availability of energy. The net result is that ecosystems have the ability to maintain biodiversity and general stability through the mediated responses of both primary producers and consumers to changes in energy fluxes (Falge et al. 2002, Worm & Duffy 2003, Ives & Carpenter 2007). Despite this, rapid global climate change has added a layer of uncertainty as to the ongoing ability of ecosystems to respond to changes in production that lie outside the historic range. For examples, alterations to temporal patterns of energy availability, shifts in the species that dominate primary production, and more extreme values of upper and lower environmental ranges for many key variables (e.g., temperature, pH, oxygenation levels) can significantly reshape entire biological communities, change the trophic structure of ecosystems, and have associated effects on biodiversity and ecosystem functioning (Emmerson et al. 2005, Ernakovich et al. 2014, Capitani et al. 2021).

Globally, marine ecosystems are currently experiencing dramatic changes which are largely associated with unprecedented disturbances ranging from local, short-term events (e.g., marine heatwave) to large-scaled, long-term threats (e.g., ocean warming, ocean acidification). These abiotic changes can be exacerbated by anthropogenic activities such as pollution, urbanisation and overfishing (Ling et al. 2009, Frölicher et al. 2018, Smale et al. 2019). In tropical seascapes, massive bleaching of coral reefs and the extensive loss of seagrass and macroalgal meadows have recently been reported, and these types of events seem to be occurring at a higher frequency than has historically been the case. These phenomena are predominantly attributed to anthropogenic factors and climate-associated disturbances (Orth et al. 2006, Smale & Wernberg 2013, Hughes et al. 2017). Such habitat loss has critical impacts on associated communities and trophic dynamics, which often begin at basal trophic levels with flow-on effects throughout the entire food web, potentially leading to the collapse of trophic pyramids, and local extinctions. Somewhat surprisingly, in comparison to studies of changes in primary production due to habitat loss, very few studies in marine ecosystems have investigated the potential effects of global change on lower trophic level consumers, such as epifaunal invertebrates and invertivorous fishes, despite their tight conjunction with primary producers. Understanding how these lower trophic level consumers respond to multi-scale variation in primary production in marine food webs in different habitat settings is critical to our ability to predict how ecological processes and ecosystem function will shift under global change. This knowledge is particularly important as we move towards evidence-based marine management and conservation plans that take an ecosystem level approach.

My thesis presents a systematic mapping of, and an ecological investigation into, the potential interactions between different trophic levels within the food chain of '*canopy-forming macroalgae – epifaunal invertebrate – invertivorous fish*' at Ningaloo Reef in Western Australia. My findings are, however, likely to have broader implications for marine biodiversity and ecosystem functioning in tropical macroalgal meadows at many other sites. To start, in Chapter 2 I opened the Pandora's Box of issues that are related to defining marine epifauna, and I offered a consensus-based and functional-based definition of epifauna that should act as an aid to unify different research areas. Next, in Chapter 3, I looked across a range of tropical seascapes in Ningaloo, to document the relationship between the primary producer *Sargassum* and the composition of epifaunal communities to show how epifaunal communities respond to changes in the size of *Sargassum*, the presence of invertivorous fishes and other habitat conditions (e.g., water depth, distance between macroalgal meadows and coral reefs). In Chapter 4, I quantified the secondary productivity generated by epifauna in the macroalgal meadows of Ningaloo. My study is the first to estimate epifaunal production across space and time in the tropics, which I also combined with a sensitivity analysis that models the likely consequences of macroalgal canopy loss on epifaunal productivity. Then, in Chapter 5, I documented the taxonomic composition of invertivorous fish communities in Ningaloo that feed upon canopy-associated epifauna. I further refined the categorization of the trophic guild of 'invertivores' by dividing them into three finer-scale function groups: 'canopy forager', 'abiotic forager' and 'generalist'. Finally, in Chapter 6, I reported on an experimental manipulation of predator exclusion that demonstrated the influence of invertivorous fish predation on epifauna. In so doing, I further calculated the biomass transferred from epifauna to invertivorous fishes which can then be applied to estimates of fishery production on broader spatial scales. My results fill in key knowledge gaps in the ecological processes and ecosystem functioning of tropical canopy-forming macroalgal habitats and provide information on energy flows within coastal food webs that can inform potential action by marine management under likely scenarios for future global change.

The importance of a unified definition of marine epifauna

To date, different nomenclatures have been used by researchers working on marine invertebrates to describe communities that resemble each other in their ecosystem functions. Conversely, the same term (i.e., macrofauna) is sometimes used to refer to organisms which share totally different taxonomic status and ecosystem functions (see studies reviewed in Chen et al. 2021). The plethora of alternative terminologies, and the absence of a unified definition for ‘epifauna’, seems to be a barrier to assimilating existing research knowledge on key communities of small marine organisms. In the past seven decades, the term *epifauna* has been used to refer the organisms living on the surface of microhabitat, where a microhabitat is defined either in a very broad sense or using very strict criteria. Meanwhile, numerous alternative synonyms and related terms have been used to describe other marine communities which closely resemble this definition of marine epifauna (Table 2.1). The lack of a clear definition of the term *epifauna* and the use of multiple nomenclatures have been a persistent feature in marine biology, and it continues to challenge researchers that attempt to synthesis the existing literature. This is detrimental to efforts to develop evidence-based management strategies for the protection of marine habitats: the functional roles of epifauna as key components of marine food webs, and as mediators between lower and higher trophic levels, can easily be overlooked or underestimated. In Chapter 2, I offered a consensus-based definition of marine epifauna, by examining on the functional roles that organisms play in marine ecosystems rather than only considering their taxonomic status or the precise habitat in which they occur. The results are first, a definition that ‘*epifauna are 0.5-10 mm sized animals (usually invertebrates, but not always as similar sized vertebrates sometimes functionally serve the same role within a community), which live on the surface of marine habitat including biogenic habitats, abiotic substrate and artificial structures*’; and second, a suggestion for future researchers (i.e., providing relevant biological and ecological traits of the epifaunal communities focused in their studies) to ensure better application of terminology, which will promote a function-based approach to describing variation among epifaunal communities. This unifying, consistent and detailed rationalisation of the definition of *epifauna* will, if widely adopted, have the benefit of improving the literature by making it easier to locate studies asking similar questions about different communities of small marine organisms, and thereby facilitate future comparative studies and meta-analyses. Given that epifaunal communities are critical indicator of marine ecosystem health, reducing terminological barriers associated with building up long-term datasets on epifauna should improve our knowledge of the consequences of changes in epifaunal production for marine food webs, and offer insights into likely ecosystem shifts in response to global change under various climate scenarios across tropical, subtropical and temperate zones.

Epifauna as tools for predicting how global climate change influences trophic flows

In Chapters 3 and 4, I showed how the community structure and secondary productivity of *Sargassum*-associated epifauna responds to temporal and/or spatial changes in tropical canopy-forming macroalgal meadows. To start, I found strong, positive correlations between *Sargassum* canopy size and epifaunal abundance, biomass and secondary productivity. These relationships highlight the significance of canopy-forming macroalgae as key habitats in Ningaloo for epifauna, and the consequences of canopy loss for epifauna. Previous studies have observed high variation in canopy size and meadow area across sites, seasons, and years in this region (Wilson et al. 2014, Lim et al. 2016, Wenger et al. 2018), which suggests that even small changes in key environmental parameters can have large effects. The persistent environmental changes arising due to global change could therefore have pronounced long-term effects on the total area of algal meadows and/or canopy size. My model predicts that fairly small longer-term reductions in canopy size and/or meadow area could translate into a disproportionate decrease in epifaunal abundance and biomass, hence far less secondary production. This could then have flow-on effects on species that rely on epifauna as prey (e.g., invertivorous fishes) and thereby affect overall ecosystem functions in Ningaloo. Additionally, the strong correlations between canopy features and epifauna are suggestive of broader consequences of the loss of macroalgal habitats for the conservation and management of tropical seascapes which extend beyond Ningaloo to have global implications: marine macrophytal habitats worldwide are undergoing similar pattern of temporal declines in growth and increased disturbance due to global change (Lefevre & Bellwood 2010, Nordlund et al. 2016, Fulton et al. 2019).

Interestingly, my use of model selection suggests that invertivorous fish biomass is the best predictor of site level variation in both epifaunal community structure (Chapter 3) and epifaunal secondary production (Chapter 4). If we make the assumption that there are causal links between fish numbers and epifaunal biomass (i.e., predators affect prey biomass, and *vice versa*), this strongly confirms the reliance of many invertivorous fish species within Ningaloo on epifauna as a key food source, and highlights the relationship between higher-order consumers (invertivorous fishes) and lower trophic levels (epifaunal communities). Some key species of macroaglae-associated Labridae and Lethrinidae are major target of fisheries, and most species of invertivorous fishes are food resources for higher-order and apex predators that also utilize macroalgal meadows, or occur in adjacent seascapes such as coral reefs (Wilson et al. 2014, Fulton et al. 2020, Froese & Pauly 2021). Any environmental disturbances reducing canopy size and meadow area could therefore trigger trophic cascades that might significantly lower fisheries catches and decrease food security. The results of my model selection also indicate that sea temperature is another key predictor of the secondary production generated by macroalgal epifauna (Chapter 4), suggesting that the trophic flows facilitated by epifauna are sensitive to thermal anomalies which lead to the loss of macroalgal habitats. Previous studies on tropical and subtropical macroalgal meadows have already recorded the contraction of canopy cover in response to pulse events of changes in sea temperature (Smale & Wernberg 2013, Fulton et al. 2019, Graba-Landry et al. 2020).

In Chapter 4 I ran sensitivity analyses to model the effects of shifts in *Sargassum* canopy height and percent cover on areal epifaunal productivity. I not only observed high sensitivity of epifaunal productivity to the loss of *Sargassum* canopy, but also, for the first time in this research field, I was able to quantify the overall areal epifaunal productivity given different scenarios of shifts in macroalgal canopies. My findings provide new insights into our ability to predict how trophic flows will change in response to perturbations in habitat conditions that result from climate-associated changes and anthropogenic activities. Given the evidence that climate-associated changes and anthropogenic activities are generating increasing pressure on marine macrophytal habitats (Harley et al. 2012, Marzinelli et al. 2016, Oliver et al. 2018), it is foreseeable that the nature of trophic flows through marine food webs will be significantly altered due to longer, stronger, and more frequent disturbances in the near future. I recommend that interactions between macroalgal canopy conditions and epifaunal communities should be a key priority for future empirical work, especially multi-season/year field studies. The findings will be important for habitat-based marine management to resolve the effects of bottom-up and top-down influences on marine ecosystem functions.

Invertivorous fishes: an essential but often neglected part of marine food webs

One interpretation of the novel findings in the previous chapters is that invertivorous fishes are key consumers of macroaglae-associated epifauna. In the following two chapters (Chapters 5 and 6) I therefore further examined the taxonomic composition, seasonality, and foraging microhabitat utilisation of invertivorous fish assemblages within the macroalgal meadows of Ningaloo. I also conducted an *in situ* experimental manipulation to exclude predators from gaining access to macroalgal epifauna, and used the change in epifaunal biomass to estimate the production transferred to predators to gain insight into the trophic interactions between lower trophic levels (macroaglae-associated epifauna) and higher-order consumers (i.e., invertivorous fishes that were experimentally excluded).

Invertivorous fishes are one of the most abundant tropic guilds within marine ecosystems worldwide, which makes it surprising that they are far less well studied than other guilds for their functional roles and effects on trophic dynamics, especially in tropical macroalgal meadows (Kramer et al. 2015, Fulton et al. 2020, Froese & Pauly 2021). In Chapter 5, I showed that fishes grouped under the trophic status of ‘invertivore’ have a distinct variety of foraging microhabitat preferences. My study is the first to highlight this previously unappreciated aspect of functional complementarity and offers a functional refinement of the classification of tropical macroaglae-associated invertivorous fishes. Since 1990, a series of studies on tropical coral reef fishes have refined the trophic status of ‘herbivore’ into many functional groups (e.g., ‘scrapers’ versus ‘excavators’, ‘grazers’ versus ‘browsers’, ‘crevice-feeders’ versus ‘open matrix feeders’), based on their physical features (e.g., tooth types, fin aspect ratio) and ecological traits such as their foraging mode and microhabitat preferences (Bellwood & Choat 1990, Hoey & Bellwood 2009, Fox & Bellwood 2013). These approaches have led to the recognition that different species in a particular trophic group often have non-equivalent functional effects on marine ecosystems. This refinement of trophic status for herbivorous fishes has been used to improve the monitoring and management of coral reef ecosystems by providing a more accurate assessment of ecosystem functioning and resilience (Green & Bellwood 2009, Graham et al. 2013, Villéger et al. 2017). I expect that the trophic guild refinement of macroaglae-associated invertivorous fishes provided in Chapter 5 will similarly assist in the development of effective management and conservation interventions of tropical macroalgal habitats. It will allow researchers to identify species which perform unique ecosystem functions and yield a more accurate estimate of the level of functional redundancy within a particular community. Ideally, detailed dietary analyses (e.g., gut content, bite rates) by each species is needed to provide robust information about how particular functional group of predatory fish interacts with lower trophic levels and influence ecosystem functioning (Ashworth et al. 2014, Baker et al. 2014). Unfortunately, for my thesis I was unable to collect specimens of invertivorous fishes for gut content analysis to verify potential dietary targets that might drive division of foraging habitat along key resource axes. This happened because the necessary fieldtrips were precluded by the COVID-19 pandemic and travel restrictions. Nevertheless, this would represent a profitable future direction of research that I would like to pursue to verify the prey selection and dietary targets of invertivorous fish species within macroalgal meadows. This additional information would allow us to understand better the potential implications of niche partitioning by invertivorous fishes for ecosystem dynamics in macroalgal meadows.

In Chapter 6, I built on the identification of common invertivorous canopy foragers and generalists (Chapter 5) to examine the influence of fish predation on canopy-dwelling epifauna by conducting caging experiments to exclude invertivorous fishes. The result of this predator exclusion manipulation showed that when invertivorous fishes (and, of course, any other species unable to enter the cages such as large crustaceans) did not have access to macroalga, the density of epifauna ended up being significantly higher. This finding is in agreement with previous studies using similar manipulation to examine the influence of marine fish predation on benthic invertebrates (Connell & Anderson 1999, Lewis & Anderson 2012, Janiak et al. 2020). My results highlight the role that invertivorous fishes play in influencing the structure and function of ecosystems by altering the composition of epifaunal communities. My exclusion experiment did, however, have some limitations that need to be acknowledged. The use of underwater cages has been adopted as a common approach to manipulate predator effects on prey (Steele 1996, Lewis & Anderson 2012, Bolton et al. 2019), but there are concerns about caging artefacts which might distort the effects of predation. This has led to improvements in cage design to minimise caging artefacts, as well as experimental designs and statistical approaches that try to separate cage artefacts from predation effects (see examples in Steele 1996, Connell 1997 and Bolton et al. 2019). Although I did not detect any significant caging artefacts in my study, my predator exclusion experiments had a lower level of replication than I would have liked with respect to both the number of replicates per site and the number of sites. The duration of the predator exclusion period was also shorter than I would have wished. My original plan was to select three distinct macroalgal meadow patches to conduct predator exclusion experiments. Unfortunately, one of the target meadow patches was unsuitable for manipulation when it was visited due to low canopy cover and low fish density, combined with logistic constraints arising from the remote field location. Eventually I had no choice other than to drop that meadow patch from the study. The duration of the treatment was also reduced for practical reasons. An approaching cyclone forced me to retrieve all the cages sooner than intended, which shortening the time they were in place to only ten days. More broadly, this cyclone in early 2020 also halted the sampling of invertivorous fishes for gut content, sagittal otolith analysis and a planned high frame speed filming of fish bite rate. As the COVID-19 pandemic then spread, the subsequent lockdown and strict travel ban into Western Australia made it impossible to return to Ningaloo to complete the intended fieldwork. On the positive side, however, my study in Chapter 6 is still the first attempt to examine the influence of predation on macroalgal epifauna by invertivorous fishes and thereby estimate the tertiary production arising via the important trophic pathway of '*macroalgae – epifauna – invertivorous fish*'. I suggest that future studies should address the current deficiency in field-based predator exclusion experiments run for prolonged periods, and the shortage of empirical studies measuring feeding by invertivorous fishes (e.g., bite rate to estimate the rate of consumption of epifauna). It would also be valuable to link sagittal otolith analysis (to obtain the somatic growth rate of individuals) to monitoring data on the macroalgal state at the time of growth to test whether growth rates are, as predicted, higher when there is more macroalga (hence more epifauna). These studies will allow for more accurate estimates of fish productivity and predation effects.

This thesis as an aid to conservation and management of tropical seascapes

My thesis provides new insights and extensive information about the key trophic pathways in a macroalgal-dominated reef ecosystem. That is, from primary producers (canopy-forming macroalgae) to primary consumers (epifaunal invertebrates), and finally to higher-order consumers (invertivorous fishes). I have highlighted the nature and significance of each of these key components in tropical seascapes, including how each trophic level interacts with others, and how each trophic level is likely to respond to changes in the wider environments, especially those associated with global changes. Most importantly, the results of my thesis have tangible applications to the prediction of energy flows throughout marine food webs, the monitoring of shifts in marine production over space and time, and the modelling of the potential consequences of global climate change for tropical seascapes. For example, by using the sensitivity analysis I ran in Chapter 4, stakeholders can model the consequences of changes in *Sargassum* canopy structure for epifaunal secondary productivity. When combined with the foraging microhabitat preferences of invertivorous fishes in Chapter 5, the authorities should have an improved ability to evaluate to what extent the loss of *Sargassum* meadows and epifaunal productivity under certain circumstances (e.g., normal seasonal shifts, anthropogenic activities, global change) might affect associated fish species that have unique functional roles. This will allow for the identification of species which are more vulnerable to the loss of macroalgal canopies, that can then be included on priority lists for conservation. In brief, the results of my thesis provide information to stakeholders and relevant authorities that should facilitate improved practices to ensure biodiversity conservation and effective marine management to maintain a fishable, but sustainable, future.

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