# Chapter 18
# The Roles of Seagrasses in Structuring Associated Fish Assemblages and Fisheries

**Glenn A. Hyndes, Patrice Francour, Paolo Guidetti, Kenneth L. Heck Jr. and Gregory Jenkins**

**Abstract** Seagrasses are known to provide important habitats for a diversity of fish and fisheries species. Continued research has allowed us to re-evaluate the generalisations, and identify the gaps in our knowledge regarding these habitats, particularly in an Australian context. Seagrasses generally form part of a mosaic with other habitats within a seascape that contributes to its overall biodiversity of fish. Patterns of abundance and diversity of fish between seagrass and other habitats, such as unvegetated flats and reef habitats, is inconsistent and depends on the region, fish and seagrass species, and sampling method. Edge effects, adjacent habitats, and fragmentation can strongly influence fish assemblages. Seagrass structural complexity can enhance survival and growth of juvenile fishes, but recent studies show that survival rates of individual prey do not vary greatly across seagrass densities when densities of both prey and predators increase with seagrass density. The concept of the nursery habitat has been built on data from studies in estuaries or highly seasonal seagrass habitats, whereas recent studies in marine systems or cool temperate seagrass meadows suggest that this role does not always hold. Direct grazing on seagrasses by fishes occurs mainly in tropical regions,

---

G. A. Hyndes (✉)
Centre for Marine Ecosystems Research, School of Science, Edith Cowan University,
270 Joondalup Drive, Joondalup, WA 6027, Australia
e-mail: g.hyndes@ecu.edu.au

P. Francour · P. Guidetti
University of Nice-Sophia Antipolis, CNRS ECOMERS Laboratory, Parc Valrose,
06108 Nice Cedex 2, France
e-mail: francour@unice.fr

P. Guidetti
e-mail: Paolo.guidetti@unice.fr

K. L. Heck Jr.
Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 36528, USA
e-mail: kheck@disl.org

G. Jenkins
School of BioSciences, The University of Melbourne, Parkville, VIC 3010, Australia
e-mail: gjenkins@unimelb.edu.au

A. W. D. Larkum et al. (eds.), *Seagrasses of Australia*,
https://doi.org/10.1007/978-3-319-71354-0_18

although there is a paucity of data on this process along with several other processes, from tropical Australia. Grazing on seagrasses by fishes appears to be limited in temperate regions, with consumption of seagrass restricted mainly to omnivorous species. However, tropicalisation, that is, the immigration of tropical grazers to higher latitudes due to global ocean warming, is predicted to increase grazing rates on temperate seagrasses. Reductions in seagrass biomass caused by increased grazing will disrupt connectivity processes between seagrass meadows and surrounding habitats, and are likely to have significant ramifications for the biodiversity and ecosystem services those other coastal habitats provide. Although other habitats rely on inputs of seagrass detritus, and the immigration of fish and fisheries species from their juvenile seagrass habitats, quantitative data on this link are limited. Evidence that fisheries declines, either directly or indirectly, have resulted from seagrass loss is equivocal to date, and therefore, the quantification of this role is still needed. Managing seagrass for fisheries is complex, and many fisheries agencies embrace ecosystem-based management, but do not have direct responsibility for seagrass habitat. Significant progress has been made in our knowledge of fish and fisheries in seagrasses, but our review highlights significant knowledge gaps where further research is recommended.

## 18.1 Introduction

Seagrass meadows provide important habitats for a wide range of fish species. The often higher densities and diversity of fish in seagrass meadows compared to other coastal habitats, particularly sand and mud flats, reflects elevated structural complexity, primary and secondary production, and availability of vegetal detritus (Nagelkerken 2009 and references therein; Nanjo et al. 2014). These characteristics, in turn, are likely to provide increased protection from predation and food availability for both adult and juvenile fish compared to less complex habitats (Horinouchi 2007). For these reasons, seagrass meadows are perceived as important "nursery habitats" for fisheries production, and have received considerable attention, leading to several reviews over the last few decades (see Bell and Pollard 1989; Connolly et al. 1999a, b; Gillanders 2006; Heck and Orth 1980; Heck and Valentine 2006; Ogden 1980; Jackson et al. 2001; Whitfield and Pattrick 2015; Ogden 1977).

Many of the early generalisations of seagrass ecology emerged from studies carried out in the 1970s and 1980s, which led to an increasing effort in seagrass research in the 1990s and 2000s. In a search on ISI Web of Science using the keywords "fish*" and "seagrass*", a total of 2,114 papers referred to fish and seagrass between 1992 and 2015. A confirmation process for those papers revealed that a total of 601 papers (not including review papers) specifically examined at least one aspect of fish ecology in seagrass meadows. The number of papers increased from 59 in 1992–95 to 166 in 2004–07, before declining to 84 in 2012–2015 (Fig. 18.1). The majority of papers originated from Australia and North

America in the 1990s, but subsequently, studies from the Caribbean and Europe in the 2000s contributed to the literature (Fig. 18.1). There was also an increase in the number of papers coming from Africa and Asia during the 2000s. Perhaps reflecting the focus of research in narrow geographic ranges, a large number of studies has examined fish assemblages in meadows dominated by *Zostera* and *Thalassia* (200 and 137, respectively) (Fig. 18.1b). Fish in *Posidonia* and *Halodule* meadows received less attention (74 and 66 papers, respectively) (Fig. 18.1b). However, *Posidonia* received far greater attention in the 2000s, mainly associated with increased work in the Mediterranean Sea. Fish assemblages in other seagrasses, including *Amphibolis*, *Cymodocea*, *Enhalus*, *Halophila*, *Syringodium* and *Thalassodendron,* have received little attention.

In this chapter, we examine the importance of seagrass meadows to fish and fisheries, either directly as a habitat and food source, or indirectly through the

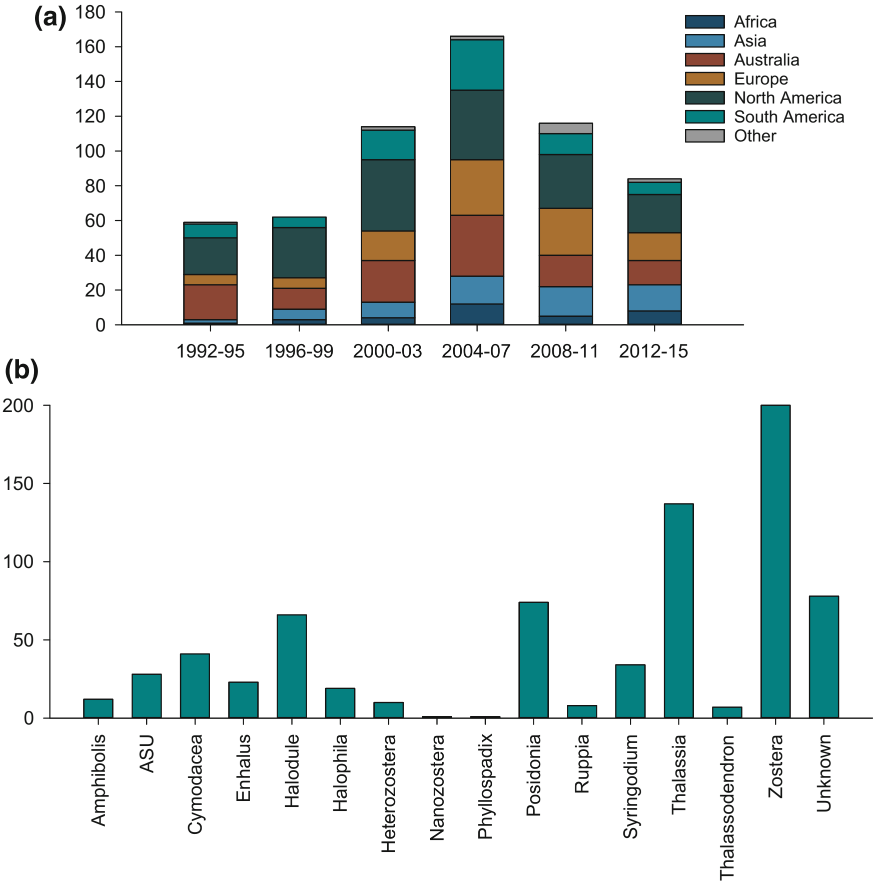

**Fig. 18.1** The number of primary publications examining fish in seagrass meadows in **a** different years and regions, and **b** different seagrass genera

provision of seagrass-associated organic matter to other habitats. We generally focus on finfish, but broaden the scope to include invertebrates when discussing fisheries. A recent increase in the number of published studies examining fish in seagrasses in a range of seagrass genera and regions around the world (Fig. 18.1), allows us to examine whether early generalizations regarding the use of seagrass meadows by fish hold for a broad suite of seagrass genera and geographic regions, and discuss these in the context of Australian seagrasses where possible. We firstly consider the spatial and seascape patterns in diversity of fishes by examining fish assemblages in seagrass meadows compared to other habitats, including comparisons across different seagrass habitats and depths, and exploring the current knowledge of structure, patch size and edge effects. We then focus on assessing the generalisations regarding the nursery function of seagrass meadows to fish and feeding ecology within those systems. We next examine the mechanisms of connectivity between seagrass meadows and coastal and offshore fisheries, focusing particularly on Australian fisheries. Finally, we discuss management issues related to seagrass and the sustainability of fisheries, followed by the main research gaps the literature that we consider need attention.

### *18.1.1 Characteristics of Seagrass Habitats*

The physical characteristics of seagrasses differ markedly among genera. In a classification proposed by Walker et al. (1999), *Zostera* and *Halodule* have low biomass, are characterized by rapid turnover, and are ephemeral (Fig. 18.2). In comparison, *Thalassia, Enhalus* and *Posidonia* have relatively high biomass, slow turnover of biomass, and are persistent (Fig. 18.2, Hemminga and Duarte 2000). The different growth forms respond differently to disturbance, and are likely to interact differently with higher trophic levels (Walker et al. 1999). Furthermore, different genera have different distribution ranges, with *Zostera* exhibiting the greatest latitudinal range from the tropics to cold temperate regions (Moore and Short 2006), while *Thalassia* is restricted mainly to the tropics (Van Tussenbroek et al. 2007) and *Posidonia* to temperate regions of Australia and the Mediterranean Sea (Green and Short 2003). Also, the different forms of seagrasses occur in different coastal environments, and therefore form different associations with neighbouring coastal habitats. For example, *Thalassia* is often associated with mangroves and coral reefs (van Tussenbroek et al. 2007), while *Zostera* is often found in estuaries and *Posidonia* in marine waters (Guidetti et al. 2002; Gobert et al. 2006).

The differences in form and environment affect the interactions of seagrasses with the associated epiphytes and invertebrate fauna, and the combination of all these attributes will affect the associated fish assemblages. Seagrass species with relatively slow turnover such as *Posidonia* spp., and those with extensive and persistent stems such as *Amphibolis* spp., have high levels of epiphytic algae and sessile epifauna (Borowitzka et al. 1990; Jernakoff and Nielsen 1998). These attributes would increase food availability and habitat structure beyond the seagrass

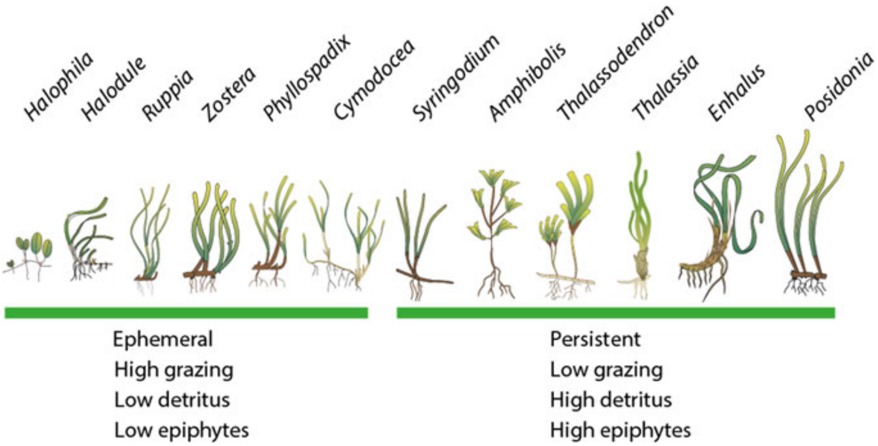

**Fig. 18.2** Conceptual model displaying the life history and functional characteristics of seagrass genera that are relevant for their roles as fish habitats (adapted from Walker et al. 1999)

itself, and influence the densities and diversity of fish assemblages in seagrass meadows. In addition, Heck and Orth (1980) suggested that there is a latitudinal shift in habitat complexity and heterogeneity, with temperate seagrass meadows being the most homogeneous and tropical meadows being the most heterogeneous through the occurrence of associated organisms such as sponges, bryozoans, corals, rhodophytes, and calcareous algae such as *Halimeda* spp. The addition of these other habitats could lead to increased diversity of fishes in seagrass meadows (Nagelkerken et al. 2015).

## 18.2 Spatial and Seascape Patterns in Diversity

In early studies, the value of seagrass as a fish habitat was often based on comparisons between seagrass meadows and adjacent unvegetated sediments. The greater diversity and densities of fish, particularly juveniles, in seagrass meadows led to the general acceptance that seagrasses provide critical nursery habitats for fish, and this was often attributed to their greater structural complexity that enhances growth and survival of juvenile fish. More recently, fish assemblages of seagrass meadows have been examined in a broader spatial and seascape context, comparing them to other structured habitats or among meadows comprising different seagrass species or different spatial configurations representing fragmentation. Also, a greater focus has been placed on the influence of connectivity between seagrass meadows and other habitats at the seascape scale through the movement of fish and organic matter between habitats. Below, we discuss the role of spatial and seascape factors in influencing the value of seagrass meadows as fish habitats.

### *18.2.1 Seagrass Versus Unvegetated Sediments*

Species richness and densities of fish are most often higher in seagrass meadows than unvegetated sediment throughout the world, including Australia (Ferrell and Bell 1991; Franco et al. 2006; Connolly 1994b), but there are exceptions (Heck and Thoman 1984). While those general conclusions have often been based on meadows comprising smaller species, such as *Zostera* spp, they have also been observed for meadows of larger seagrasses, such as *Posidonia* or *Amphibolis.* In expansive studies across southern Australia, Edgar and Shaw (1993, 1995) showed that fish production was usually, but not always, greater in shallow seagrass meadows comprising either *Posidonia* or *Zostera* than adjacent unvegetated sediment. At some locations, fish production and abundances were far higher over sand than in *Posidonia* meadows (Edgar and Shaw 1993, 1995), while other studies have shown similar abundances between *Posidonia* or *Zostera* meadows and adjacent sandy areas (Hyndes et al. 2003; Gray et al. 2011). Furthermore, abundances of fish are not always greater in seagrass compared to sandy areas in *Thalassia* meadows of the Caribbean Sea/Central America region (Adams and Ebersole 2004; Arrivillaga and Baltz 1999; Sheridan et al. 1997) and *Enhalus* meadows in Japan (Nakamura and Sano 2004). These inconsistent patterns likely relate to the landscape structure or density of the seagrasses (Hyndes et al. 2003), or other factors such as sampling bias and diel differences in fish assemblages.

Many studies have compared fish assemblages across habitats during the day, but fish assemblages can shift between day and night (Harmelin-Vivien 1982; Gray et al. 1998; Johnson et al. 2008). Such diel shifts can reflect the movement of certain species in and out of seagrass during the diel cycle. For example, a comparison of fish in Australian *Posidonia* meadows and adjacent bare sediment by Hyndes (unpublished data) showed far higher densities of fish in the former habitat during the day, but no differences at night. However, these results reflected the pronounced diel differences in densities of schooling species within the family Atherinidae, whose members appear to move into shallow sandy areas adjacent to seagrass at night (Humphries and Potter 1992). This has also been observed for labrid and sparid species in *P. oceanica* meadows in the Mediterranean Sea (Guidetti 2000). However, such conclusions need to consider the ability of some species to avoid capture during the day, as highlighted by Gray et al. (1998) for the schooling *Liza argentea*. From the above, any assessment of seagrass meadows as fish habitat against unvegetated sediments needs to consider location of the habitat, species of seagrass, and potential sampling biases (e.g. time of day and type of sampling gear).

### *18.2.2 Differences Among Seagrass Species*

Coastal environments can contain a mosaic of seagrass meadows comprising a number of species, and it is overly simplistic to assume that all seagrass meadows provide the same functions. While there has been considerable attention paid to the role of meadow structure, few studies have compared fish assemblages across different seagrass habitats that vary markedly in their species composition and physical structure (Fig. 18.2). For example, species diversity and densities of fishes differ substantially between meadows of *Enhalus acroides* and *Thalassia testudinum* in Zanzibar (Gullström et al. 2008) and *Halodule wrightii*, *Thalassia hemprichii* and *Syringodium filiforme* in the Gulf of Mexico (Ray et al. 2014). In Australia, several studies have shown that fish assemblages differ between meadows of *P. australis* and *Z. capricorni* in eastern Australia (Middleton et al. 1984; Rotherham and West 2002; Young 1981), although these differences may reflect depth gradients across different seagrass species. Similarly, fish assemblages in *P. oceanica* beds differ from those in beds of the smaller *Zostera* and *Cymodocea* species (Bussotti and Guidetti 1999), which may reflect the seasonal dynamics of the seagrasses. That is, the canopy of *P. oceanica* is present year round (Guidetti et al. 2002), while that of small-sized seagrasses almost disappears in the winter (Guidetti and Bussotti 2000). Also, on the west coast of Australia, fish assemblages in *Posidonia sinuosa* and *Amphibolis griffithii* differ (Fig. 18.3, Travers and Potter 2002; Hyndes et al. 2003). Hyndes et al. (2003) suggested that the greater biomass and size of fish in *Amphibolis* meadows is related to the space among the long, permanent stems below the canopy of *Amphibolis,* along with the high load of epiphytes on those stems, allowing larger fish to occupy and forage in those gaps. The influence of seagrass structure on fish assemblages has been tested using simpler structural characteristics such as leaf density and height (see later section), but more complex measures of structural complexity as well as food availability need to be examined.

Even for seagrass species of the same genus, fish assemblages can differ substantially. This is highlighted through comparisons of Australian *Posidonia* species, in which species richness and densities can be greater in *P. sinuosa* than over sand, while such differences are not apparent for *P. coriacea* (Hyndes et al. 2003). *Posidonia coriacea* belongs to the *Posidonia ostenfeldii* group of species that form patchy clumps of seagrass in more dynamic sandy environments compared to *P. sinuosa* in the *P. australis* group that form continuous meadows in more stable environments (Gobert et al. 2006). The lack of differences between fish assemblages in *P. coriacea* and sand (Fig. 18.3) likely reflects the presence of large sand patches within this habitat. At the finer patch scale, fish assemblages are likely to differ between seagrass and sand, but the degree of such differences will depend on patch size and edge effects (see below). Thus, the landscape structure of seagrass species, even within a genus, could have a profound influence on fish assemblages occupying seagrass habitats.

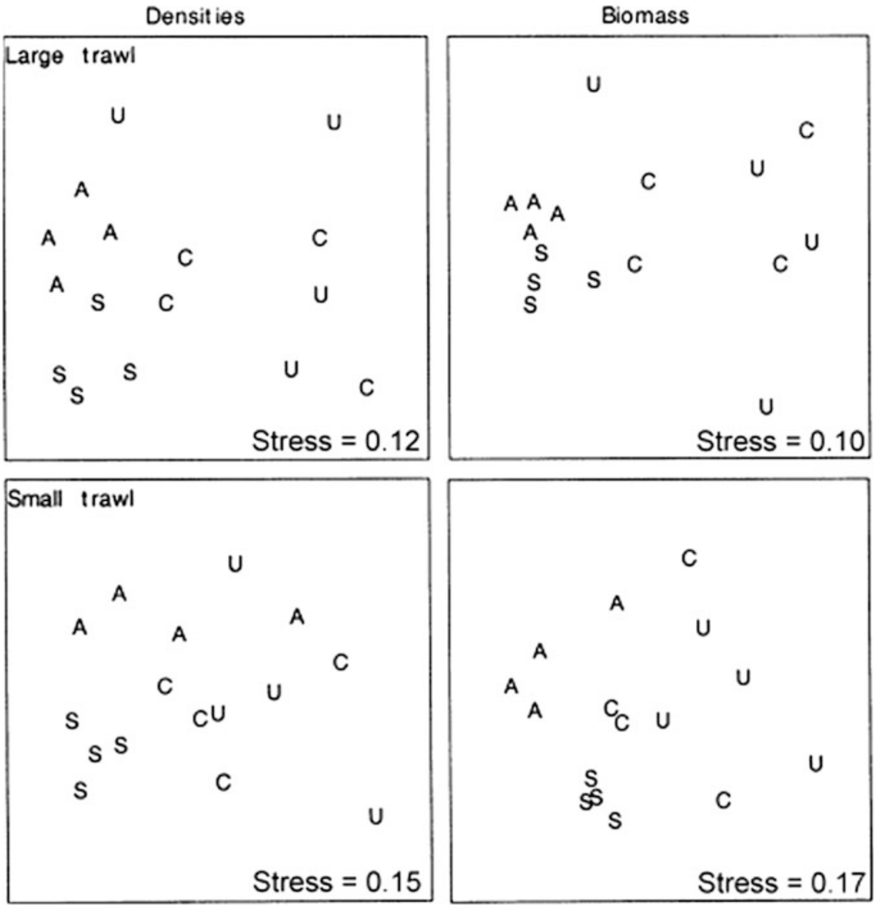

**Fig. 18.3** From Hyndes et al. (2003). nMDS ordination plots of the denisties and biomass of fish assemblages recorded in seagrass meadows comprising different seagrass species and unvegetated areas in south-western Australia using two different trawling methods. A = *Amphibolis griffithii*, C = *Posidonia coriacea*, S = *Posidonia sinuosa*, U = unvegetated areas

The different forms of seagrasses and their meadows, and their associated organisms, such as macroalgae, mangroves, corals and sponges, introduce additional layers of complexity when attempting to generalise about the role of seagrass for fish communities. Clearly, the mosaic of different seagrass species in the coastal region contributes to its overall biodiversity of fish, and the threat of replacement of one seagrass species with another (Pogoreutz et al. 2012) is likely to have significant ramifications for the biodiversity and ecosystem services these coastal ecosystems provide.

### *18.2.3 Seagrass Versus Other Structured Habitats*

Much of the discussion on the value of seagrass as a habitat has focused on seagrass versus unvegetated sediment (see above), while few studies have compared fish assemblages between seagrass and other forms of structured habitats such as reefs. Jenkins and Wheatley (1998) showed that fish assemblages were more similar between structured habitats (*Zostera* and algal reef) than unvegetated sediment, while densities and species richness did not differ between the two structured habitats. In comparison, Sogard and Able (1991) showed a hierarchy in densities of fish in habitats, firstly those in *Zostera*, then the filamentous green alga *Ulva*, and then unvegetated mud. Guidetti (2000) showed that species richness was greater in *P. oceanica* than on nearby rocky reefs with macroalgal cover, while densities of fish were similar in the two habitats. While the species composition differed between the two habitats, they were more similar to each other than when compared to unvegetated sediment (Guidetti 2000). Species that make part of artisanal fishing catches, like the sparids *Diplodus annularis* and *S. cantharus* and the labrid *S. ocellatus* occurred predominantly in *P. oceanica*, while the economically and ecologically relevant sparid *D. sargus* and a range of labrids occurred mainly over rocky reef. However, *D. annularis* also settles into macroalgae of the northern Adriatic where seagrasses are not present (Guidetti and Bussotti 1997). In another study, densities of larger *S. ocellatus* were higher over rocky reef than *P. oceanica*, but medium-sized fish were more abundant in the seagrass (Mouillot et al. 1999). In comparison to those studies, Francour (1994) showed that, in Corsica, the density and biomass of fish were lower in *P. oceanica* than in rocky areas, particularly inside a marine reserve. However, outside the no-take area, densities were similar in the two habitats. Thus, there appears to be no consistent pattern among regions, but results may be strongly dependent on local fishing pressure (Minello et al. 2003; Sheridan and Hays 2003). In addition, the methods used to assess fish density or biomass could have influenced these trends. For example, large species mainly inhabit reefs at adult stages, while juveniles occupy seagrass meadows (Francour 1994; Dorenbosch et al. 2005; Campbell et al. 2011). If the sampling technique does not effectively record these large-sized species, the calculated density or biomass will be underestimated.

### *18.2.4 Influence of Depth*

Amongst seagrasses that form beds of dense and tall plants, the species with the widest depth distribution is *P. oceanica* (from the surface to 40 m; den Hartog 1970). Several species of *Halophila* occur from the surface to depths of 30 m or more (Den Hartog 1970), but the diminutive *Halophila* species modify the environment much less than *P. oceanica*, which forms a thick mat of dead and living rhizomes and roots. There have been limited comparisons between fish faunas in shallow versus deeper meadows, but a greater biomass of herbivorous fish has been observed in shallow (1–5 m) versus deep (15–20 m) *P. oceanica* meadows of the Mediterranean (Francour 1997), and juvenile sparids (*D. annularis* and *S. cantharus*), and the labrid (*Symphodus* spp.), were observed mainly in shallower waters (Francour 1997; Bussotti and Guidetti 1999; Francour and Le Direach 1994, 1998). Similarly, Travers and Potter (2002) showed greater species richness and densities of fish in shallower meadows of both *Posidonia australis* and *Amphibolis antarctica* across depths in Shark Bay on the west coast of Australia. Based on this, differences in the fish assemblages in *Posidonia australis* and *Zostera capricorni* in Australia (Middleton et al. 1984) and *P. oceanica* and a complex of *Cymodocea nodosa* and *Zostera noltii* in the Mediterranean (Guidetti 2000) could be confounded by the smaller seagrass species being located in shallower water. Middleton et al. (1984) showed that smaller species and smaller individuals of some species occupied *Z. capricorni* while larger individuals occupied *P. australis*. This could result from larvae of some species settling preferentially into *Zostera* and subsequently migrating to *Posidonia* meadows (Middleton et al. 1984) or preferentially settling into shallow habitats, regardless of structure, where predation levels may be lower (Ruiz et al. 1993) and growth rates higher (Sogard 1992).

### *18.2.5 Structural Complexity*

There is considerable longstanding evidence of a significant positive relationship between seagrass density and the abundance of small resident and transient fishes, and this type of relationship has been reported from individual seagrass meadows across the globe (see Gillanders 2006 for a review). However, this significant relationship between seagrass density and fish abundance does not always exist at larger spatial scales (that is, among, as opposed to within, seagrass meadows), and sparse meadows may sometimes harbor higher fish densities than dense meadows, a point made and discussed in some detail by Bell and Westoby (1986) in south-eastern Australia 30 years ago. The usual explanations for the large number of juvenile fishes in seagrass meadows is that they survive and grow at higher rates in structurally complex habitats like seagrass meadows, and data generally, but not always, support these explanations (Fig. 18.4, Heck et al. 2003). Bell and Westoby (1986) and Bell et al. (1987) tried to understand the reasons for such differences and proposed that stochastic settlement from the plankton could explain the inconsistencies at larger scales, with young-of-the-year fish choosing to settle in the first, but not necessarily the most dense, meadows they encountered when recruiting from offshore waters, and later redistributing themselves into preferred parts of the meadows in which they settled.

Recent studies, using different experimental procedures, help understand the variance existing between local and regional seagrass density and juvenile finfish and shellfish abundance of the type discussed by Bell and Westoby (1986). Earlier tank experiments increased only prey, not predator densities, with increasing

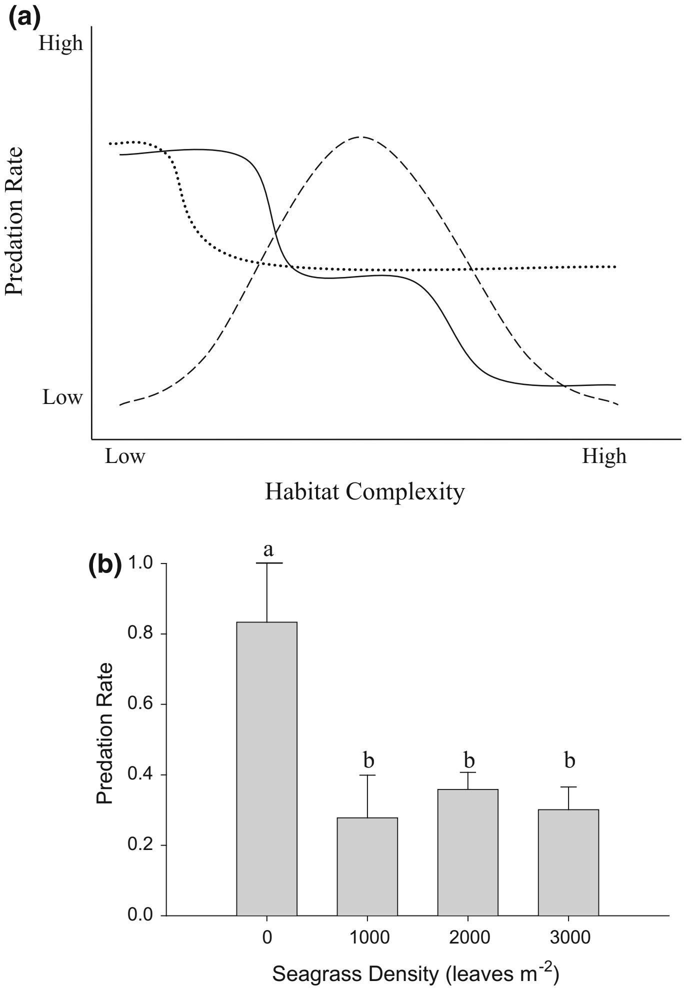

**Fig. 18.4** **a** Models describing the relationship between habitat complexity and predator success: (dotted line) Canion and Heck (2009), (solid line) Nelson (1979) and (dashed line) Crowder and Cooper (1982). **b** Predation rate (mean ± S.E.) of *Lagodon rhomboides* on *Palaemonetes pugio* in field experiments in Perdido Bay, FL by Canion and Heck (2009). Letters indicate significant differences (One-way ANOVA, $p < 0.005$)

seagrass density to examine the relationship between seagrass density and predation rate. However, recent studies of predator-prey relationships in mesocosms (e.g. Canion and Heck 2009, Mattila et al. 2008; Scheinin et al. 2012) showed that when densities of both prey and predators were increased with seagrass density (as they typically do in nature), the survival rate of individual prey was no different among a wide range of seagrass densities (Fig. 18.4). Survival in any density of seagrass was, however, clearly higher than on unvegetated substrates, thereby demonstrating the survival benefits of recruiting into seagrass habitats regardless of shoot density. Thus, it is likely that the first meadow encountered by a post-larval fish is a good choice for settlement.

### *18.2.6 Edge Effects and Fragmentation*

Seagrass meadows are often spatially heterogeneous (patchy) habitats from fine spatial scales to seascape scales, resulting from variation in a range of environmental and biological factors that affect their distribution (Bostrom et al. 2006). These heterogeneous characteristics are often expressed as seagrass patch sizes, edge characteristics and fragmentation patterns. Understanding the effect of fragmentation of seagrass meadows on fish assemblages is crucial due to the ongoing worldwide loss of seagrass (Waycott et al. 2009) and the associated fragmentation of seagrass meadows. The resulting smaller, fragmented patches of seagrass increase edge to area ratios, which can either negatively or positively affect fish depending on their preference for the interior or edge of the meadow. Fragmentation is a process, but many studies that have examined its effect on fish assemblages have used a static state as a representation of the process of fragmentation (Bostrom et al. 2006; Macreadie et al. 2009). Studies in south-eastern Australia that simulated fragmentation using artificial seagrass units (ASUs) showed that loss of seagrass area during fragmentation may not lead to reduced fish abundances if fish are more abundant at the edge of seagrass meadows (due to increased perimeter/area ratio), as occurred in this case with pipefish (Macreadie et al. 2009). Moreover, these studies showed that treatments that were actively fragmented had higher species richness than those already fragmented at the start of the study, illustrating the difference in the effects of fragmentation compared to static patchiness (Fig. 18.5) (Macreadie et al. 2009). In the Mediterranean Sea, Vega Fernandez et al. (2005) reported interesting results based on a *P. oceanica* meadow that was partially destroyed by excavation, resulting in areas of seagrass habitat of equal shoot density but different degree of fragmentation. The fish assemblages associated with differently fragmented beds showed fairly variable patterns: (i) for some species, the abundance was positively related to the degree of fragmentation, (ii) some species were more abundant in fragmented beds, without any difference related to with the degree of fragmentation, (iii) some species were more abundant in large seagrass patches or in the continuous meadow.

Earlier studies did not show strong evidence for seagrass edge effects on fish distributions (Connolly and Hindell 2006). Most studies showed no edge effect, and for those that did show an effect, fish abundances either increased (positive effect) or decreased (negative affect) near the edge. Many studies inferred edge effects from studies of different patch sizes (smaller patches have a larger perimeter/area ratios (Bell et al. 2001), but assumptions that changes in faunal abundance in differing patch sizes are due to edge effects is not well founded (Connolly and Hindell 2006). However, recent studies have made more direct measurements of the

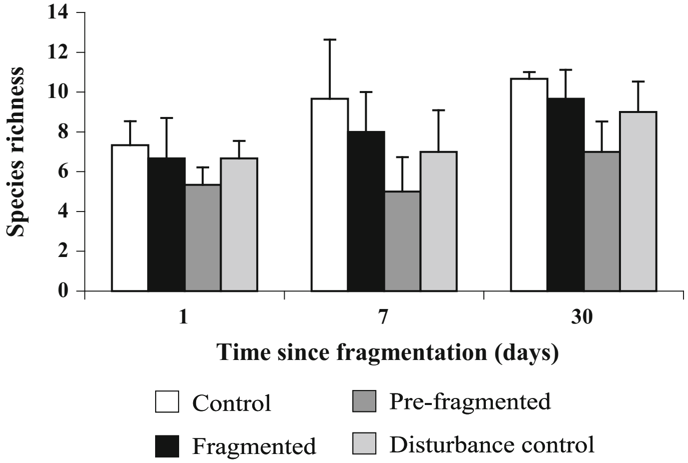

**Fig. 18.5** Modified from Macreadie et al. (2009). Mean species richness (±standard error) in artificial seagrass units. Treatments for the fragmentation experiment were constructed from artificial seagrass units (1 $m^2$) and included: Control, a continuous 9-$m^2$ patch; Fragmented, a 9-$m^2$ patch fragmented to 4 single 1-$m^2$ patches (resulting in a 56% loss of seagrass habitat); Pre-fragmented (PF), 4 single 1-$m^2$ patches; and Disturbance control, fragmented and then immediately restored to a continuous 9-$m^2$ patch

distribution of fish in seagrass meadows, or have used an experimental approach with artificial seagrass units (ASUs). Direct measurements of fish distribution in *Zostera* beds in south-eastern Australia showed strong edge effects for some species: pipefish (Syngnathidae), weedfish (Clinidae) and gobies (Gobiidae) showed positive effects, while garfish (Hemirhamphidae) and weed whiting (Labridae) showed negative effects (Smith et al. 2008, 2012). These effects were, however, not uniform in space or time. For example, pipefish were influenced by edge effects on the seaward but not landward edge of the beds, while weedfish only showed an effect at night (Smith et al. 2008). Edge effects for both these taxa varied with patch size, indicating that patch size cannot be used as a simple proxy for edge effects, and that both patch size and edge effects must be considered (Smith et al. 2010). Furthermore, edge effects may vary over the life cycle of fish. For example, King George whiting (Sillaginidae) showed a negative edge effect for small recruits (Smith et al. 2011) but a positive edge effect for older juveniles (Smith et al. 2012).

Heterogeneous characteristics of seagrass meadows, such as patch size and edge effects, can influence fish assemblages by altering: (1) water flow, physical disturbance and sediment structure; (2) predation pressure; (3) movement and behaviour of fish; and (4) reproductive strategies of fish (Bostrom et al. 2006; Macreadie et al. 2009). In support of some of these mechanisms, recent studies in south-eastern Australia showed that fish displaying edge effects were influenced by variation in the physical structure of seagrasses (Smith et al. 2008), the distribution of food resources (Macreadie et al. 2010), and the influence of predators (Smith et al. 2011).

Experiments using ASUs showed that the positive edge effect for pipefish in *Zostera* was related to food resources (Macreadie et al. 2010), in particular the supply of copepod prey in the water column for these ambush predators (Macreadie et al. 2010; Warry et al. 2009). In contrast, negative edge effects for King George whiting recruits are likely the result of predation effects, with tethering studies showing that predation by piscivorous fish was much higher near the edge of the bed than its interior (Smith et al. 2011). In summary, recent mensurative and manipulative experiments in temperate Australia show that many fish species exhibit strong, but variable, responses to seagrass edges and fragmentation.

## 18.3 Role of Seagrass as a Habitat

The functional roles of seagrasses as habitat varies among species, which use seagrass beds as permanent and seasonal residents, transients and occasional migrants (Kikuchi 1974). Much research has focused on seasonal residents, particularly those recruiting into meadows as larvae or juveniles before migrating to other habitats, which has led to seagrasses being considered critical "nursery" habitats for many economically important species.

### *18.3.1 Nursery Role*

For decades, seagrass meadows have been considered to provide critical nursery habitats, principally due to many earlier studies demonstrating high abundances of juveniles in seagrass meadows compared to unvegetated substrates (see Beck et al. 2001), and the large number of economically important species using seagrass meadows as juveniles. The underlying premise of the nursery role is that juveniles in a putative nursery habitat should disproportionately contribute to the adults in other habitats, through some combination of greater densities, growth rates and survival of juveniles in the nursery habitat, followed by their successful movement to adult habitats (Fig. 18.6, Beck et al. 2001). In support of the nursery role of seagrass meadows, a meta-analysis by Heck et al. (2003) showed that density, survival and growth of fish were generally greater in seagrass meadows, although this generality did not hold as well between seagrass and unvegetated areas in the Southern Hemisphere, or between seagrass and other structured habitats, such as saltmarshes (Heck et al. 2003). Heck et al. (2003) showed that growth rates of fish are generally greater than in surrounding unvegetated areas, but not necessarily other structured habitats. This suggests that structure and presumably increased food availability associated with habitat structure, play major roles in supporting increased growth rates. Similarly, structurally complex habitats increase survival by reducing the foraging success of predators (Heck et al. 2003). Nevertheless, there is still limited evidence that seagrass meadows disproportionately support juveniles

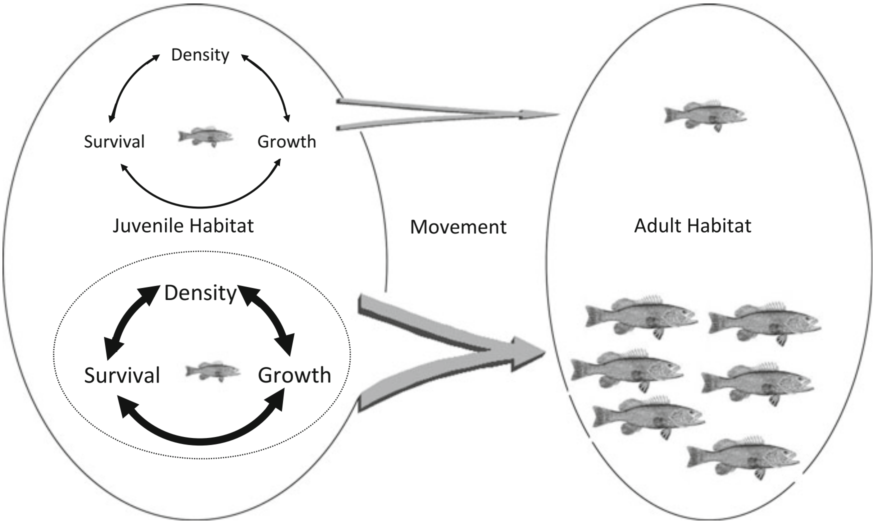

**Fig. 18.6** Conceptual diagram of the nursery role concept (adapted from Beck et al. 2001). Size of symbols represents the relative magnitude

that contribute to the adult stages of fish populations, due to the difficulty of assessing the movement patterns of juveniles from seagrass meadows into adult habitats. A recent, update meta-analysis by McDevitt et al. (2016) confirmed most of the generalisations reported by Heck et al. (2003), thereby strengthening the support for the seagrass nursery hypothesis.

Dahlgren et al. (2006) have further developed the discourse around the nursery role hypothesis by proposing the new term “Effective Juvenile Habitat” or “EJH”, in which an EJH should contribute more juveniles on average to adult habitats than the average of all juvenile habitats. However, this can only be evaluated by determining the proportion of fish in adult habitats that originate from all possible juvenile habitats. Recent advances in microtagging, otolith microchemistry and stable isotopes are allowing this to be tested (e.g. Gillanders and Kingsford 1996), but progress has been slow due to the complexity and cost of such studies.

Extensive meadows of many seagrass species are restricted to the protected waters of estuaries (see Green and Short 2003), which can be extensively used as juvenile habitats (Sogard 1992), regardless of whether seagrass is present. The concept of the nursery habitat was built around the focus of many studies on estuaries (Beck et al. 2001), leading to a bias towards estuarine systems (e.g. Chesapeake Bay, Jones 2014). Indeed, the meta-analysis by Heck et al. (2003) indicated that warm temperate and tropical seagrasses in the Northern Hemisphere appeared to play a more important nursery role than those in cool temperate and boreal waters (Heck et al. 1989; Heck and Coen 1995). In Australia, seagrass meadows are extensive in sheltered estuarine and marine waters as well as more exposed and open marine waters (Abrantes et al. 2015). In this context, in expansive studies across southern Australia, Edgar and Shaw (1993) and Edgar and Shaw (1995) demonstrated the highly variable use of seagrass as a juvenile habitat for fish. Edgar and Shaw (1995) considered the lower abundances of juvenile fish in seagrass meadows along southern, as compared to eastern Australia, to be related to the focus of studies on estuarine versus marine environments in the respective regions. This was supported by studies of more exposed waters along the west coast of Australia, where seagrasses played a minimal role as a juvenile habitat (Travers and Potter 2002; Hyndes et al. 2003).

Although not mutually exclusive, the dynamics of seagrass as a habitat provides another explanation of the observed variation in the role of seagrasses as juvenile habitats. Many species of seagrass are highly seasonal in above-ground biomass, e.g. *Halodule*, *Zostera* and *Thalassia* (Hemminga and Duarte 2000). The highly ephemeral nature of these seagrasses means that habitat availability is not consistent throughout the year, and therefore, it is perhaps not surprising that fish do not use these habitats throughout their life cycles. For example, the seasonal variability in leaf density of *Cymodocea nodosa* and *Zostera noltii* compared to *P. oceanica* in the Mediterranean Sea appears to result in different fish assemblages in those habitats (Guidetti 2000). However, persistent (or perennial) species such as those of *Posidonia* provide above-ground biomass throughout the year, allowing fish species to occupy these productive habitats throughout their lifecycles, and therefore resulting in a smaller proportion of fish utilizing seagrasses as juvenile habitats alone (see section below). In southern Australia, the seagrasses *Posidonia australis*, *P. sinuosa* and *Amphibolis antarctica* and *A. griffithii* form extensive meadows, and studies in these meadows have formed the majority of those concerning seagrass-associated fish in the region (Travers and Potter 2002; Hyndes et al. 2003; Edgar and Shaw 1993, 1995). The perennial nature of these seagrasses would allow resident species to occupy structured habitats throughout their life cycles, and these species characterize those meadows in southern Australia (see below). Conversely, the ephemeral nature of other seagrass species would prevent species that require structure to remain in those habitats when the above-ground biomass is absent in the winter months. Supporting this hypothesis, meadows of *Zostera capricorni* in estuaries on Australia's east coast provide a juvenile habitat for a range of species (Smith and Sinerchiab 2004). The seasonality of seagrass meadows would alter the availability of this habitat through the year, which would have presumably had a profound effect on the evolution of life history strategies of fish in coastal waters.

The economically important *Sillaginodes punctatus* provides a useful cautionary example of generalizations regarding the role of seagrasses as a nursery habitat. Young-of-the-year of this species recruit into *Zostera* meadows in south-eastern Australia (Robertson 1977; Connolly 1994a, c; Jenkins et al. 1997; 1998), but can also recruit to reef algae (Jenkins and Wheatley 1998) and sandy areas in some locations (Jenkins and Hamer 2001). In comparison, the species appears to recruit only into sheltered sandy areas rather than *Posidonia australis* meadows in south-western Australia (Hyndes et al. 1997; 1998). The presence of seagrass, therefore, does not appear to be the primary requirement for successful recruitment of this species. Indeed, the higher recruitment of *S. punctatus* into more sheltered unvegetated habitats where food availability is higher (Jenkins and Hamer 2001), suggests that food availability drives habitat choice of the recruiting juveniles of this species. In support of this conclusion, experiments by Connolly (1994b, c) showed that juvenile abundances were not affected by the removal of *Zostera,* and the species' choice for *Zostera* as a habitat was over-ridden by food availability. However, higher predation on juvenile *S. punctatus* in unvegetated areas (Hindell et al. 2002), suggests that there is a trade-off between high food availability and predation in the sheltered unvegetated habitats. In addition, proximity of seagrass meadows to the currents and wind conditions that transport larvae into coastal habitats appears to play a major role in the recruitment of this species (Jenkins et al. 2000) and others (Ford et al. 2010) into juvenile habitats in the region.

### *18.3.2 Seagrass for Residents*

The ability of fish species to complete their life cycles in seagrasses would require the persistence of the habitat in suitable conditions for reproduction to occur. Firstly, as stated above, many studies on seagrass-associated fish have been carried out in estuaries, which are used for extensive periods by the juveniles of many species before returning to the marine environment to spawn (Potter et al. 2015). While not mutually exclusive, the presence of above-ground biomass of particularly persistent species of seagrasses, such as *Posidonia* spp. in coastal marine waters of southern Australia and the Mediterranean Sea, is likely to provide habitat for juveniles and adults of many seagrass-associated species throughout the year (Bell and Harmelin-Vivien 1982; Edgar and Shaw 1993; Harmelin-Viven 1984; Hyndes et al. 2003). Resident species, therefore, appear to be common in meadows in coastal marine waters, but the proportion of life-long residents may also be related to depth, since *P. oceanica* meadows in shallow (3 m depth) waters of the Mediterranean Sea contain more juveniles (Francour 1997; Guidetti and Bussotti 1997; 1998) than those in relatively deep (12–18 m) waters (Bell and Harmelin-Vivien 1982; Harmelin-Viven 1984).

Fish assemblages in persistent, marine seagrass meadows are likely to be influenced by the reproductive and early life history strategies of resident species. For example, several resident fish families common to *Posidonia* meadows, e.g. Syngnathidae, Apogonidae and Monacanthidae (Kendrick and Hyndes 2003; Steffe et al. 1989) and Labridae (Bell and Harmelin-Vivien 1982; Francour 1997) are characterized by parental care such as mouth brooding, giving birth to live young, or depositing demersal eggs in nests (Patzer 2008). The larvae from species with these reproductive strategies may therefore recruit directly and earlier into the natal or nearby seagrass meadows of their parents, and bypass the high potential for mortality in the pelagic phase and other recruitment processes and potential bottlenecks that influence the settlement of pelagic larvae into seagrass meadows.

## 18.4 Feeding Ecology of Fish Assemblages

A range of feeding guilds occurs in the fish assemblages in seagrass meadows worldwide: (1) predators of fish and other larger nekton; (2) meso-carnivores feeding mainly on small crustaceans, such as copepods and amphipods, shrimps or molluscs; (3) omnivores that feed on mobile or sessile epifauna, as well as epiphytic algae and/or seagrass; (4) herbivores that feed on epiphytic algae and/or seagrass; and (5) detritivores that consume detritus within the meadow. Fish assemblages in southern Australian seagrass meadows are dominated by meso-carnivores feeding mainly on small crustaceans or molluscs (Edgar and Shaw 1993, 1995; Connolly et al. 2004), which in turn, often feed on epiphytes and detritus (Cook et al. 2011; Ebrahim et al. 2014). These meso-grazers play critical roles in controlling epiphytic algae on seagrass leaves in Australia (Cook et al. 2011; Ebrahim et al. 2014) and elsewhere (Myers and Heck 2013; Whalen et al. 2013), and contribute to secondary production (Lepoint et al. 2000; Smit et al. 2005, 2006; Vizzini and Mazzola 2003; Vizzini et al. 2002).

Evidence for direct grazing on seagrasses comes mainly from tropical systems (Valentine and Duffy 2006). However, it must be recognized that the trophic structure we see in seagrasses today may not reflect those of the past due to the direct and indirect effects of historical over-harvesting of large predators and grazers (Jackson et al. 2001). Apart from supporting dugongs, manatees and green turtles, tropical seagrass meadows can support a diversity of herbivorous fish, with species typically belonging to the families Labridae (Sparisoma clade), Acanthuridea and Siganidae (see Valentine and Duffy 2006 and references therein). Species within these families often move from coral reefs to adjacent seagrass meadows, where they can create "haloes" of unvegetated areas due to high levels of grazing (Randall 1965; Ogden 1977). Indeed, *Sparisoma radians* has been shown to consume nearly all daily seagrass production in some locations in the Gulf of Mexico (Kirsch et al. 2002). However, species richness and abundance of herbivores decrease with increasing latitude and decreasing water temperature (Floeter et al. 2005, González-Bergonzoni et al. 2012). While the processes leading to this pattern are not well understood (Clements et al. 2009), grazing on temperate seagrasses by fish is considered to be limited.

*Sarpa salpa* (Sparidae) in the Mediterranean Sea is an exception to the above generalisation. Early studies suggested a mixed diet for this species, comprising seagrass, epiphytes and reef algae (Havelange et al. 1997; Lepoint et al. 2000), with an ontogenetic shift towards seagrass (Verlaque 1990). Early studies also suggested that *S. salpa* consumed 4–15% of daily production of *P. oceanica* (Havelange et al. 1997; Velimirov 1984), but more recently, Tomas et al. (2005) found that consumption rates can exceed local production rates of temperate seagrass meadows. In some locations, seagrass biomass was reduced by as much as 50%, while epiphytic load was reduced by about 30% (Tomas et al. 2005). As a consequence, Valls et al. (2012) regarded this species as a keystone modifier (sensu Mills et al. 1993) in *P. oceanica* meadows.

Direct grazing by fishes on temperate Australian seagrasses appears to be very limited. Some consumption of seagrass has been observed in species of Labridae (from the Odacine clade), Hemirhamphidae, Monacanthidae, Tetraodontidae and Terapontidae, but these species are omnivorous, feeding predominantly on epiphytes and macro-invertebrates, and not seagrasses (Bell et al. 1978; Bell and Harmelin-Vivien 1983; Burchmore et al. 1984; Burkholder et al. 2012; Conacher et al. 1979; Macarthur and Hyndes 2007; Kwak et al. 2015). Despite evidence of some grazing on seagrasses, there is limited evidence that fish significantly influence seagrass production. Through exclusion experiments and observations, Burkholder et al. (2012) inferred that the terapontid *Pelates octolineatus* was responsible for grazing large portions of the *Halodule* and *Halophila* seagrasses in Shark Bay, Western Australia, but this species is omnivorous, feeding largely on epiphytic algae (Edgar and Shaw 1993) and therefore is likely to play a greater role in controlling epiphytes on seagrass leaves. As is true for many omnivorous species, the proportion seagrass in the diets of *Monacanthus chinensis* (Bell et al. 1978) and *Haletta semifasciata* (Macarthur and Hyndes 2007) increases with fish size. It may therefore be relevant that several omnivorous species attain relatively large sizes in perennial *Posidonia* or *Amphibolis* seagrass meadows (Hyndes et al. 2003) that form extensive meadows in southern Australia. These species are therefore likely to play a considerable role in the removal of particularly epiphytic algae in those meadows. There is limited information on grazing on seagrasses by fishes in tropical Australia, and this is clearly a research gap. Kwak et al. (2015) showed that the juveniles of a range of fish species in seagrass meadows of northern Queensland consumed very little seagrass. However, the parrotfish *Leptoscarus vaigiensis* is common in tropical Australia (Lim et al. 2016), and has been shown to consume up to 10 times the rate of local seagrass growth another Indo-Pacific region (Unsworth et al. 2007a, b). The species, therefore, has the capacity to remove considerable biomass of seagrass in the tropics. Also, with global ocean warming and the movement of tropical species to higher latitudes (Fig. 18.7), grazing on seagrasses in more temperate regions is predicted to increase (Hyndes et al. 2016).

Grazing on seagrass can vary among seagrass species. For example, *Thalassia testudium* appears to have a greater resistance to grazing than *Halodule wrightii* in Florida, USA (Armitage and Fourqurean 2006), and elevated nitrogen content can influence grazing (Goecker et al. 2005). In Western Australia, consumption rates were greater on the low-nutrient, slow-growing *Posidonia* and *Amphibolis* species compared to high nutrient, faster growing *Halodule* and *Halophila* species (Burkholder et al. 2012). Despite the low nutrient content of *Posidonia* species, approximately 80% of the organic soluble content of *P. oceanica* is assimilated during gut passage in *S. sarpa* (Velimirov 1984). This suggests that the species gains nutrients from seagrass even though seagrass fragments in its hindgut appear to be undigested. Similarly, *Monacanthus chinensis* and *Hyporhamphus melanochir* assimilate nutrients from *Posidonia* leaves (Conacher et al. 1979; Nichols et al. 1986), providing evidence that *Posidonia* supports the energetic requirements of some (albeit a small number of) fish species in both the Mediterranean Sea and Australia.

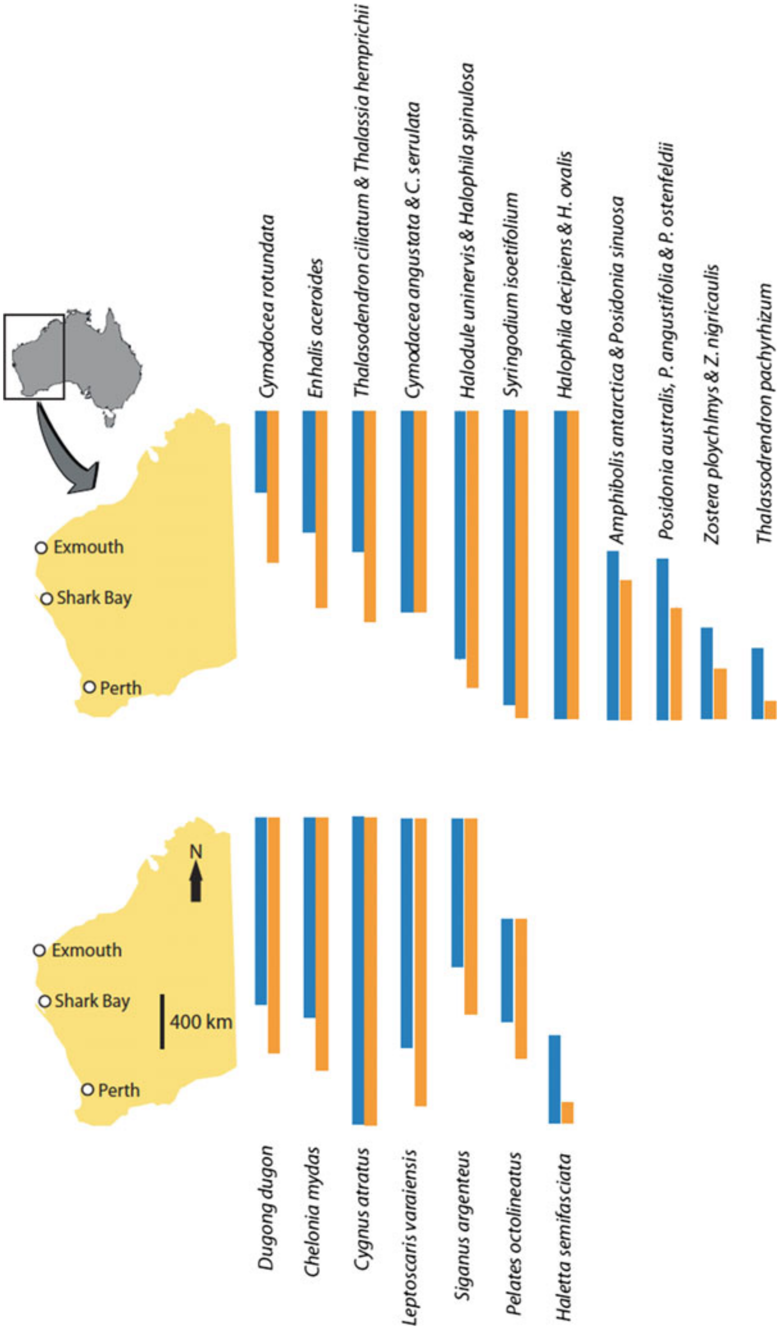

**Fig. 18.7** The current (blue) and predicted end-of-century (orange) distributions of seagrasses (top) and herbivores (bottom) along the west coast of Western Australia. See the supplemental material for methods to determine distributions and their shifts. From Hyndes et al. (2016)

## 18.5 Connectivity Across Seascapes

A major source of seascape connectivity is the process of larval dispersal from spawning in adult habitat, settlement into different juvenile habitats, and subsequent movement back to the adult habitat (Ford et al. 2010; Fowler and Short 1996; Haywood and Kenyon 2009; Verweij et al. 2008). Indeed, seascape connectivity via propagule (eggs and larvae) dispersal (at a biogeographic scale of hundreds of kms) is considered to critically affect the dynamics of fish communities associated with *P. oceanica* beds in the Adriatic Sea, in both space and time (Melià et al. 2016). The larvae of fish settling in seagrass habitats are often derived from adults in different, sometimes distant, habitats (Jenkins et al. 2000; Ford et al. 2010; Hyndes et al. 1998). This pattern of connectivity occurs in both tropical and temperate systems, with the adults of tropical species utilising coral reefs or deeper sedimentary habitats as adults (Huijbers et al. 2013, 2015; Mcmahon et al. 2012; Nagelkerken 2009; Verweij et al. 2008), and temperate species occupying coastal and offshore rocky reefs and sedimentary habitats (Ford et al. 2010, Gillanders and Kingsford 1996; Hyndes et al. 1998; Gillanders 2002; Jenkins and Wheatley 1998), and the juveniles occupying seagrass habitats in estuaries and embayments.

Use of a mosaic of juvenile habitats, termed the 'seascape nursery' (Nagelkerken et al. 2015), may follow a sequential pattern (Jenkins and Wheatley 1998; Pardieck et al. 1999). For example, Grol et al. (2014) showed that larvae of a coral-reef fish species initially settled into rubble habitat before moving into seagrass and then mangrove habitat with increasing size. With further growth, juvenile fish may gradually move into deeper waters before making the migration offshore (Hyndes et al. 1998). These movements from juvenile to adult habitats can occur over kilometres to 100s of kilometres (Gillanders et al. 2003; Huijbers et al. 2013; Mcmahon et al. 2012). If the adult habitat is a relatively short distance from the juvenile habitat then there may be a movement back and forth between the habitats before residence is taken up in the adult habitat (Huijbers et al. 2015). The timing of the ontogenetic migration from the seagrass nursery habitat to adult habitat may be a trade-off between higher survival in the juvenile habitat versus higher growth rates in the adult habitat (Nagelkerken 2009), or coincide with reproductive maturity and the onset of spawning (Hyndes et al. 1997, 1998).

The movement and migration of fish across a range of habitats, including seagrass meadows, significantly contributes to seascape connectivity (Olds et al. 2012; Grober-Dunsmore et al. 2008, 2009). This movement and migration may be part of the daily ambit of the individual or may have a regular diel or tidal periodicity (Krumme 2009), or may occur in the process of adults forming spawning aggregations (Nemeth 2009). Many studies have focused on fish assemblages associated with coral reefs and their proximity to seagrass habitats (Berkström et al. 2013; Olds et al. 2012; Grober-Dunsmore et al. 2009), with a general consensus that proximity of seagrass meadows to coral reefs has a significant positive effect on the assemblage structure of reef fish (Berkström et al. 2013; Olds et al. 2012). Focusing more on seagrass-associated fish, Unsworth et al. (2008) found that assemblages in seagrass were influenced by proximity to mangroves and reef, with a marked increase in fish abundance and species richness in seagrass meadows near mangroves. These links can be associated with strong diurnal and tidal migrations of fish (Krumme 2009). For example, grunts (Haemulidae) rest on patch reefs during the day but forage in surrounding seagrass meadows at night (Krumme 2009; Nagelkerken et al. 2008), while parrotfish (Scarine in Labridae) forage in seagrass during the day but hide on the reef at night (Krumme 2009). Similarly, tidal migrations of fish can connect subtidal seagrass meadows with intertidal mangrove habitats (Jelbart et al. 2007), subtidal habitats with intertidal seagrass meadows (Robertson 1980), and coral reefs with seagrass meadows (Unsworth et al. 2007a, b).

The sequential movement of fish from juvenile to adult habitats likely provides an important process for transferring nutrients across seascapes, with the series of predator-prey interactions along that path, i.e. trophic relay (sensu Kneib 1997), contributing to a net flow of nutrients to other habitats in coastal or offshore waters (Hyndes et al. 2014). This is highlighted by the estimated export of 7400 t of silver perch *Bairdiella chrysoura* from *Zostera* meadows to other coastal habitats in Chesapeake Bay, USA (Sobocinski and Latour 2015). Similarly, the ontogenetic shift of the pinfish *Lagodon rhomboides* from seagrass meadows to offshore Gulf of Mexico (GOM) is estimated to contribute approximately 25% of the overall potential production in the northeastern GOM (Nelson et al. 2013). Thus, the maintenance of the connectivity of fish assemblages between seagrass and other habitats has significant implications for conservation planning, including habitat restoration, the location of marine protected areas, and the management of fisheries. Planning must include consideration of the mosaic of inter-connected habitats in an area rather than just the characteristics of individual habitats (Berkström et al. 2013; Cheminée et al. 2014; Olds et al. 2012, 2014, 2016). In Australia, few studies have directly examined this process for fish (but see Jelbart et al. 2007), although our understanding of this process has been compiled from a range of studies for some economically important finfish species, e.g. the King George whiting *S. punctatus* (Hyndes et al. 1998, Jenkins et al. 2000), and invertebrate species, e.g. the Western Rock lobster *P. cygnus* (Chittleborough and Phillips 1975; Chittleborough 1970; Macarthur et al. 2008).

## 18.6 Seagrass Links to Fisheries

### *18.6.1 Direct Links*

There is strong evidence around the world that numerous fish and invertebrate species that support important fisheries use resources available in seagrass habitats at some stage in their life cycles (Connolly et al. 1999a, b; Jackson et al. 2001; Verweij et al. 2008; Haywood and Kenyon 2009; Mizerek et al. 2011; Jones 2014;

Lilley and Unsworth 2014; Seitz et al. 2014; Jackson et al. 2015), although the relative usage seems to vary regionally, which may in part simply reflect the amount of research in a region (Jackson et al. 2001). The usage of seagrass habitat by fisheries species is particularly well documented for Australia (Mcneill et al. 1992; Haywood et al. 1995; Jenkins et al. 1997; Connolly et al. 1999a, b; Curley et al. 2013), where species have been shown to use seagrass meadows as juvenile habitats, foraging habitats, or spawning habitats. For example, seagrass meadows in Australia are used as juvenile habitat by the King George Whiting *Sillaginodes punctatus* (Jenkins et al. 1996; Robertson 1977; Connolly 1994a) and prawns (Coles et al. 1987, 1993; Loneragan et al. 1998), a foraging habitat for the juveniles and sub-adults of the Western rock lobster *P. cygnus* (Macarthur et al. 2008, 2011), a foraging habitat for the adults of the rock flathead *Platycephalus laevigatus* (Klumpp and Nichols 1983b; Jenkins et al. 1997), and a spawning habitat for the Southern Calamari *Sepioteuthis australis* (Pecl et al. 2006). Some species, such as the grass whiting *Haletta semifasciata* and the six-spine leatherjacket *Meuschenia freycineti* are associated with seagrass throughout their entire life cycles (Jenkins et al. 1997). The southern sea garfish, *Hyporhamphus melanochir*, has an unusual link to seagrass in that the species feeds on seagrass tissue (either directly or as fragments in the water column) during the day and diurnally migrating invertebrates over seagrass beds at night (Robertson and Klumpp 1983; Klumpp and Nichols 1983a). Seagrass meadows are considered to enhance the value of fisheries linked to that habitat in south-eastern Australia by ~$A32,000 $\text{ha}^{-1}$ $\text{year}^{-1}$ (Blandon and Zu Ermgassen 2014). In the gulf waters of South Australia alone, seagrass has been estimated to contribute $A114 M per year to the economy (Blandon and Zu Ermgassen 2014; Mcarthur and Boland 2006). Similarly, the seagrass meadows of Cairns Harbour were estimated in the 1990s to contribute 178 t and $A1.2 M per year to the prawn fishery in tropical Australia (Watson et al. 1993). Based on the link between seagrass and other important fisheries around Australia, its contribution to the economy of Australia will be substantially higher. For example, in Western Australia, the fishery for the western rock lobster, whose juveniles and sub-adults in the southern part of the population forage in seagrass meadows, was valued at ~$A234 M in 2013. However, the quantification of the role of seagrasses in supporting fisheries is less clear in other regions. For example, many papers state that seagrasses, including *Posidonia oceanica*, have important nursery roles for many fishes, including commercial species in the Mediterranean. However, the quantification of this role is still in its infancy (Guidetti et al. 2009) and there has been no assessment of the related economic benefits for fisheries in that region.

### 18.6.2 *Indirect Links Through Trophic Relays and Outflow of Organic Matter*

Seagrass meadows can export, on average, 0.22 kg C $m^{-2}$ $year^{-1}$, mostly in the form of leaves (Heck et al. 2008; Hyndes et al. 2014). This exported detrital material can accumulate in a range of coastal and offshore habitats. For example, accumulations of seagrass and seagrass epiphyte detritus in unvegetated mudflats adjacent to seagrass meadows of subtropical Australia support the food chain to fish, including the economically important whiting, *Sillago schomburgkii* (Connolly et al. 2005). Similarly, the transfer of seagrass detritus to nearby coral reefs in the region appears to contribute to the food resources of the labrid *Pseudolabrus guentheri* (Davis et al. 2014). The export of seagrass to more distant habitats can also support fisheries species. In south-western Australia, seagrass leaves (and kelp thalli) provide an important juvenile habitat in the surf zones for a range of economically important fish species (Lenanton 1982; Crawley et al. 2006). Furthermore, prawns in offshore waters in northern Australia (Loneragan et al. 1997), and larvae of the blue grenadier *Macruonus novaezelandiae* in offshore waters of south-eastern Australia (Thresher et al. 1992), are likely to be supported by transported seagrass detritus. Thus, the export of seagrass detritus to near and distant habitats can, at least partly, support fisheries in other coastal habitats, but direct evidence of this link is still limited.

### 18.6.3 *Evidence of Links Through Seagrass Loss and Fisheries Production*

A strong dependence on seagrass by fisheries should be reflected in declining catches when seagrass is lost, however, the evidence to date is largely equivocal with seagrass loss resulting in fishery declines in some regions but not others (Connolly et al. 1999a, b; Gillanders 2005). One clear example of impacts to fisheries from seagrass loss was the marine wasting disease that caused catastrophic loss of eelgrass, *Zostera marina*, in the Atlantic basin in the early 1930s and subsequent collapse of the fishery for bay scallop, *Argopecten irradians*, on the east coast of the United States (Fonseca and Uhrin 2009). In Australia, a 70% decline in eelgrass, *Zostera*, over 10 years from the early 1970s in Western Port, Victoria, resulted in catch declines of about 40% for species known to be associated with seagrass, but not for other fishery species (Macdonald 1992; Jenkins et al. 1993). King George whiting provides a good example of this link. Prior to the 1970s, catches were variable but showed an increasing trend in three bays in Victoria (Fig. 18.8). However, after the seagrass loss in Western Port, catches declined, whereas they continued to increase in the two other nearby bays (Port Phillip and Corner Inlet).

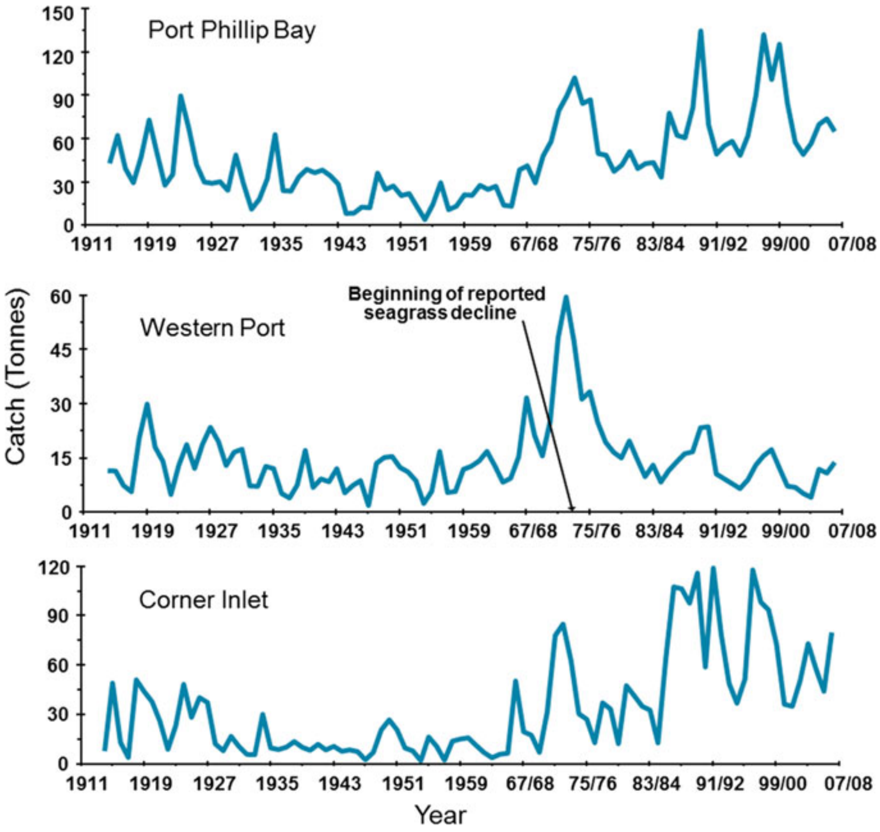

**Fig. 18.8** Historical annual catches of King George whiting from Port Phillip Bay, Western Port and Corner Inlet. Arrow indicates beginning of reported seagrass decline

In many cases, seagrass loss has not resulted in declines in fisheries linked to seagrass habitats, but this is likely to depend on the targeted species and the degree of its dependence on seagrass. For example, there was no catastrophic collapse of European fisheries associated with the eelgrass wasting disease in the early 1930s (Gillanders 2005). The equivocal link between seagrass loss and declines in fishery catches is most likely explained by facultative use of seagrass by many species, which can also use other structured habitats (Jenkins and Wheatley 1998; Heck et al. 2003). Therefore, the loss of seagrass may be ameliorated to some extent if alternative structured habitats that provide similar resources are present (Gillanders 2005; Jenkins et al. 2015). However, the level of facultative use of alternative habitats is often unknown or not quantified, making it difficult to determine the effect of seagrass loss and adaptively manage fisheries when seagrass is being lost. But if several structured habitats simultaneously decline, as is occurring in the

Mediterranean Sea for shallow *Posidonia oceanica* meadows due to coastal building (Duarte 2002) and *Cystoseira* forest due to overgrazing (Gianni et al. 2013), declines of small-scale fisheries are likely.

### *18.6.4 Management of Seagrass-Associated Fisheries*

Ecosystem-based management of fisheries is a goal now embraced by many countries including Australia (Fletcher et al. 2010; Hobday et al. 2011), and as such, includes consideration of both fishing and external impacts on seagrass (Hobday et al. 2011). Most fisheries management agencies, however, do not have direct responsibility for seagrass habitat, but rather take on an advocacy role to influence the policies of coastal and catchment managers that directly influence impacts on seagrass. Fisheries management agencies can, however, have a direct policy role in the case of fishery methods and practices that have a destructive impact on seagrass meadows (Short and Wyllie-Eciieverria 1996; Airoldi and Beck 2007) and also in the development of aquaculture areas and their associated impacts on seagrass (Delgado et al. 1997). Where seagrass is lost, fisheries managers may advocate for seagrass restoration to support and improve fisheries (Tanner et al. 2014). In the Mediterranean, the “Habitat Directive” developed by the EU provides the framework to member states to protect *Posidonia oceanica*, which is a habitat forming species of ‘priority importance’ for protection. Management occurs via the creation of Natura 2000 sites or other types of marine protected areas (MPAs) at national or trans-boundary levels. Also, the adoption of the Marine Strategy Framework Directive and Common Fishery Policy by EU countries drives an effort to adopt an ensemble of protection/management measures aimed at protecting the marine biodiversity and ecosystem functioning, while simultaneously supporting fisheries.

## 18.7 Gaps and Future Directions

Since the 1990s, studies on fish assemblages in seagrass meadows have expanded in terms of both the geographic range and the seagrass species forming the habitat. This has allowed us to broaden our understanding of the role of seagrass habitats to fish assemblages, but there are still a number of gaps that need addressing: (i) how seagrass loss will impact fish assemblages linked to seagrass, particularly as juveniles and their contribution to fisheries production; (ii) how habitat fragmentation versus habitat loss affects fish assemblages; (iii) how fish species interact with seagrass meadows in tropical Australia; and (iv) how temperate seagrass habitats respond to warming sea temperatures with global warming.

The 29% global areal loss of seagrass meadows since the late 1800s, and more rapid losses in the last two decades (Waycott et al. 2009), causes major concerns regarding the various ecosystem services they provide, including its importance as a habitat for fish assemblages and particularly fisheries species. Interpretation of the potential effects of seagrass loss requires a thorough understanding of the role of not only seagrass habitat in the life history of the fish, but also the potential role of alternate habitats. For many seagrass associated fish species, assumptions about the importance of seagrass habitat have been based only on sampling in seagrass habitat rather than a broader suite of potential habitats. While seagrass meadows have been estimated to enhance the value of fisheries in south-eastern Australia by ~$A32,000 $\text{ha}^{-1}$ $\text{year}^{-1}$ (Blandon and Zu Ermgassen 2014), there is limited empirical data linking seagrass-associated fish to fisheries production usually in more offshore waters, and limited data on the relative importance of different juvenile habitats in their contribution to the adult population (Beck et al. 2001; Dahlgren et al. 2006). More studies using approaches, such as otolith microchemistry and stable isotopes (e.g. (Gillanders and Kingsford 1996), are therefore needed to quantify the contribution of juveniles from seagrass meadows to adult spawning habitats for particularly fishery species. This may be more difficult to assess when fisheries in offshore regions are influenced through trophic relays of fauna originating from seagrass meadows, thereby diluting the contribution of seagrass to the offshore production. However, this export from seagrass meadows can be an important means of carbon transfer from tropical systems (Hyndes et al. 2014), and deserves attention.

While understanding fragmentation of seagrass and its effect on associated fishes is important, novel approaches are needed to separate the effects of fragmentation from seagrass loss. Seagrass loss and fragmentation tend to occur together, and therefore, the two processes tend to be confounded (Fahrig 2003). Furthermore, fragmentation is a process rather than a state, and most studies actually consider habitat configuration rather than fragmentation (Boström et al. 2006, 2011). Moreover, fragmentation effects can be further confounded by differences in within-patch structural characteristics of seagrass. Some of these issues can be addressed experimentally using ASUs (Macreadie et al. 2009), however, the scale of the experiments is inevitably small compared with seascape scales. Novel research approaches are therefore required to determine the relative importance of habitat fragmentation and habitat loss to seagrass associated fishes at seascape scales.

With less than 10% of the published studies on fishes in Australian seagrass meadows being undertaken in the tropics, there is a clear need to gain more expansive data on the role of seagrasses for fish assemblages in this climatic region. For example, our understanding of grazing by fishes on seagrasses comes mainly from tropical systems (Valentine and Duffy 2006), but predominantly from Caribbean/Gulf of Mexico region and more recently, Indonesia and Africa. Few papers (Kwak et al. 2015) have examined trophic interactions between fish and seagrasses in tropical Australia. Since species richness and abundance of herbivores is higher in lower latitudes (Floeter et al. 2005; González-Bergonzoni et al. 2012), we would expect relatively high grazing on tropical seagrasses in the region. However, this pattern needs to be confirmed, and its importance is becoming even more pronounced with global warming and the poleward shifts in the distribution of tropical species in the region.

Globally, warming waters have also increased the presence of tropical species in the harvest of finfish from temperate waters (Cheung et al. 2013), and lush kelp forests have dramatically shifted to barrens in some regions such as Australia, Mediterranean and Japan due to the poleward shift in herbivores (Verges et al. 2014). Less is known about this process known as “tropicalisation” and its impacts on temperate seagrasses. Tropical herbivores have, however, moved into seagrass meadows in temperate Gulf of Mexico, where it has been predicted that with continued immigration of those herbivores, seagrass meadows could be grazed to the “height of closely mowed lawn” (Heck et al. 2015). Hyndes et al. (2016) predicted that the influx of tropical herbivores into the temperate seagrass meadows of south-western Australia will have major consequences on the ecosystem services they provide, including a shift in food web structure from one that is detrital based to one that is mostly based on direct consumption. This would lead to reductions in the abundances of seagrass-associated fauna through reduced habitat structure and food availability (Hyndes et al. 2016). With future projections of sea temperature rises, this is clearly an issue that needs research attention in Australia and elsewhere.

**Acknowledgements** We thank Paul Lavery and Mathew Vanderklift for their comments on earlier versions of this chapter, and Rob Cole for his comments on a later version. We also thank Lorraine Wyse for her help with compiling the literature, production of Fig. 18.1 and formatting of references.

## References

Abrantes KG, Barnett A, Baker R, Sheaves M (2015) Habitat-specific food webs and trophic interactions supporting coastal-dependent fishery species: an Australian case study. Rev Fish Biol Fisheries 25:337–363

Adams AJ, Ebersole JP (2004) Processes influencing recruitment inferred from distributions of coral reef fishes. Bull Mar Sci 75:153–174

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology

Armitage AR, Fourqurean JW (2006) The short-term influence of herbivory near patch reefs varies between seagrass species. J Exp Mar Biol Ecol 339:65–74

Arrivillaga A, Baltz DM (1999) Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala’s Atlantic coast. Bull Mar Sci 65:301–319

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Bell JD, Burchmore JJ, Pollard DA (1978) Feeding ecology of three sypatric species of leatherjackets (Pisces: Monacanthidae) from a *Posidonia* seagrass habitat in New South Wales. Aust J Mar Freshw Res 29:631–643

Bell JD, Harmelin-Vivien ML (1982) Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 1. Community structure. Tethys 10:337–347

Bell JD, Harmelin-Vivien ML (1983) Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 2. Feeding habits. Tethys 11:1–14

Bell JD, Westoby M (1986) Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. J Exp Mar Biol Ecol 104:249–274

Bell JD, Westoby M, SA S (1987) Fish larvae settling in seagrass: do they disciminate between beds of different leaf density? J Exp Mar Biol Ecol 111:133–144

Bell SJM, Pollard DA (1989) Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum AWD, Mccomb AJ, Sheperd SA (eds) Biology of seagrasses: a treatise on the biology of seagrasses with specieal reference to the australian region. Elsevier, Amsterdam

Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biol Cons 100:115–123

Berkström C, Lindborg R, Thyresson M, Gullström M (2013) Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. Biol Cons 166:43–53

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Blandon A, Zu Ermgassen PSE (2014) Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. Estuar Coast Shelf Sci 141:1–8

Borowitzka MA, Lethbridge RC, Charlton L (1990) Species richness, spatial distribution and colonisation pattern of algal and invertebrate epiphytes on the seagrass *Amphibolis griffithii*. Mar Ecol Prog Ser 64:281–291

Bostrom C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: A review. Estuar Coast Shelf Sci 68:383–403

Burchmore JJ, Pollard DA, Bell JD (1984) Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. Aquat Bot 18:71–87

Burkholder DA, Heithaus MR, Fourqurean JW (2012) Feeding preferences of herbivores in a relatively pristine subtropical seagrass ecosystem. Mar Freshw Res 63:1051

Bussotti S, Guidetti P (1999) Fish communities associated with different seagrass systems in the Mediterranean Sea. Naturalista Sicil 23:245–259 (Suppl.)

Campbell SJ, Kartawijaya T, Sabarini EK (2011) Connectivity in reef fish assemblages between seagrass and coral reef habitats. Aquat Biol 13:65–77

Canion CR, Heck KL (2009) Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. Mar Ecol Prog Ser 393:37–46

Cheminée A, Feunteun E, Clerici S, Cousin B, Francour P (2014) Management of infralittoral habitats: towards a seascape scale approach. In: Musard O, Le Dû-Blayo L, Francour P, Beurier JP, Feunteun E, Talassinos L (eds) Underwater seascapes—from geographical to ecological perspectives. Springer Science & Business Media, pp 161–183

Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. Nature, 497:365

Chittleborough RG, Phillips BF (1975) Fluctuations of year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). Aust J Mar Freshw Res 26:317–328

Chittleborough RG (1970) Studies on recruitment in the western rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust J Mar Freshw Res 21:131–148

Clements KD, Raubenheimer D, Choat JH (2009) Nutritional ecology of marine herbivorous fishes: ten years on. Funct Ecol 23:79–92

Coles RG, Lee Long WJ, Squire BA, Squire LC, Bibby JM (1987) Distribution of seagrasses and associated juvenile commercial penaeid prawns in north-eastern Queensland waters. Aust J Mar Freshw Res 38:103–119

Coles RG, Lee Long WJ, Watson RA, Derbyshire KJ (1993) Distribution of seagrasses, and their fish and penaeid prawn communities, in Cairns Harbour, a tropical estuary, northern Queensland, Australia. Aust J Mar Freshw Res 44:193–210

Conacher MJ, Lanzing WJR, Larkum AWD (1979) Ecology of Botany Bay II. Aspects of the feeding ecology of the fanbellied leatherjacket *Monocanthus chinensis* in *Posidonia australis* seagrass beds. Aust J Mar Freshw Res 30:387–400

Connolly R, Jenkins G, Loneragan N (1999a) Seagrass dynamics and fisheries sustainability. In: Butler A, Jernakoff P (eds) Seagrass in Australia: strategic review and development of an R & D plan. CSIRO, Melbourne

Connolly RM (1994a) A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. Aust J Mar Freshw Res 45:1033–1044

Connolly RM (1994b) Removal of seagrass canopy—effects on small fish and their prey. J Exp Mar Biol Ecol 184:99–110

Connolly RM (1994c) The role of seagrass as preferred habitat for juvenile *Sillaginodes-punctata* (cuv and val) (Sillaginidae, Pisces)—habitat selection of feeding. J Exp Mar Biol Ecol 180: 39–47

Connolly RM, Guest MA, Melville AJ, Oakes JM (2004) Sulfur stable isotopes separate producers in marine food-web analysis. Oecologia 138:161–167

Connolly RM, Hindell JS (2006) Review of nekton patterns and ecological processes in seagrass landscapes. Estuar Coast Shelf Sci 68:433–444

Connolly RM, Hindell JS, Gorman D (2005) Seagrass and epiphytic algae support nutrition of a fisheries species, *Sillago schomburgkii*, in adjacent intertidal habitats. Mar Ecol Prog Ser 286:69–79

Connolly R, Jenkins G, Loneragan N (1999b) Seagrass dynamics and fisheries sustainability. Seagrass in Australia. CSIRO Publishing, Collingwood, pp 23–64

Cook K, Vanderklift MA, Poore AGB (2011) Strong effects of herbivorous amphipods on epiphyte biomass in a temperate seagrass meadow. Mar Ecol Prog Ser 442:263–269

Crawley KR, Hyndes GA, Ayvazian SG (2006) Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches. Mari Ecol Prog Ser 307:233–246

Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–1813

Curley BG, Jordan AR, Figueira WF, Valenzuela VC (2013) A review of the biology and ecology of key fishes targeted by coastal fisheries in south-east Australia: identifying critical knowledge gaps required to improve spatial management. Rev Fish Biol Fish 23:435–458

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats: concepts and applications. Mar Ecol Prog Ser 312:291–295

Davis JP, Pitt KA, Fry B, Olds AD, Connolly RM (2014) Seascape-scale trophic links for fish on inshore coral reefs. Coral Reefs 33:897–907

Delgado O, Grau A, Pou S, Riera F, Massuti C, Zabala M, Ballesteros E (1997) Seagrass regression caused by fish cultures in Fornells Bay (Menorca, Western Mediterranean). Oceanol Acta 20:557–563

Den Hartog C (1970) Seagrasses of the World. North-Holland Publishing Company, Amsterdam

Dorenbosch M, Grol MGG, Christianen MJA, Nagelkerken I, van der Velde G (2005) Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. Mar Ecol Prog Ser 302:63–76

Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29:192–206

Ebrahim A, Olds AD, Maxwell PS, Pitt KA, Burfeind D, Connolly RM (2014) Herbivory in a subtropical seagrass ecosystem: separating the functional role of different grazers. Mar Ecol Prog Ser 511:83–91

Edgar GJ, Shaw C (1993) Inter-relationships between sediments, seagrasses, benthic invertebrates and fishes in shallow marine habitats off south-western Australia. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) Proceedings of the fifth international marine biological workshop: the marine flora and fauna of Rottnest Island, Western Australia. Western Australian Museum, Perth

Edgar GJ, Shaw C (1995) 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. J Exp Mar Biol Ecol 194:83–106

Ferrell DJ, Bell JD (1991) Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Mar Ecol Prog Ser 72:15–24

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fletcher WJ, Shaw J, Metcalf SJ, Gaughan DJ (2010) An ecosystem based fisheries management framework: the efficient, regional-level planning tool for management agencies. Marine Policy 34:1226–1238

Floeter SR, Behrens MD, Ferreira CEL, Paddack MJ, Horn MH (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. Mar Biol 147:1435–1447

Fonseca MS, Uhrin AV (2009) The status of eelgrass, *Zostera marina*, as bay scallop habitat: consequences for the fishery in the western Atlantic. Marine Fish Rev 71:20–33

Ford JR, Williams RJ, Fowler AM, Cox DR, Suthers IM (2010) Identifying critical estuarine seagrass habitat for settlement of coastally spawned fish. Mar Ecol Prog Ser 408:181–193

Fowler AJ, Short DA (1996) Temporal variation in the early life-history characteristics of the King George whiting (*Sillaginodes punctata*) from analysis of otolith microstructure. Mar Freshw Res 47:809–818

Franco A, Franzoi P, Malavasi S, Riccato F, Torricelli P (2006) Fish assemblages in different shallow water habitats of the Venice Lagoon. Hydrobiologia 555:159–174

Francour P (1994) Pluriannual analysis of the reserve effect on Ichthyofauna in the Scandola Natural Reserve (Corsica, Northwestern Mediterranean). Oceanol Acta 17:309–317

Francour P (1997) Fish assemblages of *Posidonia oceanica* beds at Port Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. Mar Ecol 18:157–173

Francour P, Le Direach L (1994) Recrutement de l'ichtyofaune dans l'herbier superficiel à Posidonia oceanica de la réserve naturelle de Scandola (Corse, Méditerranée nord-occidentale): données préliminaires. Travaux scientifiques du Parc Naturel Régional et des Réserves Naturelles de Corse 46:71–91

Francour P, Le Direach L (1998) Recrutement de *Diplodus annularis* (Sparidae) dans la réserve naturelle de Scandola (Corse). Travaux scientifiques du Parc Naturel Régional et des Réserves Naturelles de Corse 57:42–75

Gianni F, Bartolini F, Airoldi L, Ballesteros E, Francour P, Meinesz A, Thibaut T, Mangialajo L (2013) Conservation and restoration of marine forests in the Mediterranean Sea and the potential role of Marine Protected Areas. Adv Oceanogr Limnol 4:83–101

Gillanders BM (2002) Connectivity between juvenile and adult fish populations: do adults remain near their recruitment estuaries? Mar Ecol Prog Ser 240:215–223

Gillanders BM (2005) Seagrasses, fish, and fisheries. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology, and their conservation. Springer, Berlin

Gillanders BM (2006) Seagrasses, fish and fisheries. In: Larkum A, Orth R, Duarte C (eds) Seagrasses: biology, ecology and conservation. Springer, Berlin

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser 247:281–295

Gillanders BM, Kingsford MJ (1996) Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. Mar Ecol Prog Ser 141:13–20

Gobert S, Cambridge M, Velimirov B, Pergent G, Bouquegneau M, Dauby P, Pergent-Martini C, Walker D (2006) Biology of posidonia. In: Larkum A, Orth R, Duarte C (eds) Seagrasses: biology, ecology and conservation. Springer, Dordrecht

Goecker M, Heck K, Valentine J (2005) Effects of nitrogen concentrations in turtlegrass *Thalassia testudinum* on consumption by the bucktooth parrotfish *Sparisoma radians*. Mar Ecol Prog Ser 286:239–248

González-Bergonzoni I, Meerhoff M, Davidson TA, Mello FT, Baattrup-Pedersen A, Jeppesen E (2012) Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. Ecosystems 15:492–503

Gray CA, Chick RC, Mcelligott DJ (1998) Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. Estuar Coast Shelf Sci 46:849–859

Gray CA, Rotherham D, Johnson DD (2011) Consistency of temporal and habitat-related differences among assemblages of fish in coastal lagoons. Estuar Coast Shelf Sci 95:401–414

Green EP, Short FT (2003) World atlas of seagrasses. University of California Press, Berkeley

Grober-Dunsmore R, Frazer TK, Beets JP, Lindberg WJ, Zwick P, Funicelli NA (2008) Influence of landscape structure on reef fish assemblages. Landscape Ecol 23:37–53

Grober-Dunsmore R, Pittman SJ, Caldow C, Kendall MS, Frazer TK (2009) A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Netherlands

Grol MGG, Rypel AL, Nagelkerken I (2014) Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. Mar Ecol Prog Ser 502:229–244

Guidetti P (2000) Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuar Coast Shelf Sci 50:515–529

Guidetti P, Bussotti S (1997) Recruitment of Diplodus annularus and *Spodyliosoma cantharus* (Sparidae) in shallow seagrass beds along the Italian coasts (Mediterranean Sea). Marine Life 7:47–52

Guidetti P, Bussotti S (1998) Juveniles of littoral fish species in shallow seagrass beds: preliminary quail-quantitative data. Biol Marina Mediterr 5:1–10

Guidetti P, Bussotti S (2000) Fish fauna of a mixed meadow composed by the seagrasses *Cymodocea nodosa* and *Zostera noltii* in the Western Mediterranean. Oceanol Acta 23: 759–770

Guidetti P, Beck MW, Bussotti S, Ciccolella A, D'Ambrosio P, Lembo G, Spedicato MT, Boero F (2009) Nuersery habitats for Mediterranean coastal fishes: the need for a quantitative approach. Biol Mar Mediterr 16:197–200

Guidetti P, Lorenti M, Buia MC, Mazzella L (2002) Temporal dynamics and biomass partitioning in three Adriatic seagrass species: *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina*. PSZN Marine Ecol 23:51–67

Gullström M, Bodin M, Nilsson PG, Öhman MC (2008) Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. Mar Ecol Prog Ser 363:241–255

Harmelin-Vivien ML (1982) Ichtyofaune des herbiers de posidonies du Parc National de Port-Cros: I. composition et variations spatio-temporelles. Trav Sci Parc Nation Port-Cros 8:69–92

Harmelin-Viven ML (1984) Ichtyofaune des herbiers de *Posidonies* du Parc Naturel Regional De Corse. In: Jeudy De Grissac A, Olivier J (eds) International workshop *Posidonia oceanica* Beds, 1984 Boudouresque. GIS Posidonie, pp 291–301

Havelange S, Lepoint G, Dauby P, Bouquegneau JM (1997) Feeding of the sparid fish *Sarpa salpa* in a seagrass ecosystem: diet and carbon flux. Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 18:289–297

Haywood MDE, Kenyon RA (2009) Habitat shifts by decapods-an example of connectivity across tropical coastal ecosystems. Ecological Connectivity among Tropical Coastal Ecosystems

Haywood MDE, Vance DJ, Loneragan NR (1995) Seagrass and algal beds as nursery habitats for tiger prawns (*Penaeus semisulcatus* and *P. esculentus*) in a tropical Australian estuary. Mar Biol 122:213–223

Heck KL, Able KW, Fahay MP, Roman CT (1989) Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. Estuaries 12:59–65

Heck KL, Carruthers TJB, Duarte CM, Hughes AR, Kendrick G, Orth RJ, Williams SW (2008) Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems 11:1198–1210

Heck KL, Coen LD (1995) Predation and the abundance of juvenile blue crabs: a comparison of selected east and gulf coast (USA) studies. Bull Mar Sci 57:877–883

Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows [Review]. Mar Ecol Prog Ser 253:123–136

Heck KL, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy VS (ed) Estuarine Perspective. Academic Press, New York

Heck KL, Thoman TA (1984) The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7:70–92

Heck KL, Valentine JF (2006) Plant-herbivore interactions in seagrass meadows. J Exp Mar Biol Ecol 330:420–436

Heck KL, Fodrie FJ, Madsen S, Baillie CJ, Byron DA (2015) Seagrass consumption by native and a tropically associated fish species: potential impacts of the tropicalization of the northern Gulf of Mexico. Mar Ecol Prog Ser 520:165–173

Hemminga M, Duarte C (2000) Seagrass ecology. Cambridge University Press

Hindell JS, Jenkins GP, Keough MJ (2002) Variability in the numbers of post-settlement King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier) in relation to predation, habitat complexity and artificial cage structure. J Exp Mar Biol Ecol 268:13–31

Hobday AJ, Smith ADM, Stobutzki IC, Bulman C, Daley R, Dambacher JM, Deng RA, Dowdney J, Fuller M, Furlani D, Griffiths SP, Johnson D, Kenyon R, Knuckey IA, Ling SD, Pitcher R, Sainsbury KJ, Sporcic M, Smith T, Turnbull C, Walker TI, Wayte SE, Webb H, Williams A, Wise BS, Zhou S (2011) Ecological risk assessment for the effects of fishing. Fish Res 108:372–384

Horinouchi M (2007) Distribution patterns of benthic juvenile gobies in and around seagrass habitats: Effectiveness of seagrass shelter against predators. Estuar Coast Shelf Sci 72:657–664

Huijbers CM, Nagelkerken I, Debrot AO, Jongejans E (2013) Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. Ecology 94:1859–1870

Huijbers CM, Nagelkerken I, Layman CA (2015) Fish movement from nursery bays to coral reefs: a matter of size? Hydrobiologia 750:89–101

Humphries P, Potter IC (1992) The fish community in the shallows of a temperate australian estuary: Relationships with the aquatic macrophyte *Ruppia megacarpaand* environmental variables. Est Cstl Shelf Sci 34:325–346

Hyndes GA, Heck KL, Vergés A, Kendrick G, Orth RJ, Pearce A, Mcmahon KW, Lavery PS, Whiting S, Wilson S, Wernberg T, Vanderklift MA, Harvey ES (2016) Accelerating tropicalization and the transformation of temperate seagrass meadows. Bioscience 66:938–948

Hyndes GA, Kendrick AJ, Macarthur LD, Stewart E (2003) Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. Mar Biol 142:1195–1206

Hyndes GA, Nagelkerken I, Mcleod RJ, Connolly RM, Lavery PS, Vanderklift MA (2014) Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol Rev Camb Philos Soc 89:232–254

Hyndes GA, Platell ME, Potter IC, Lenanton RCJ (1998) Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia. Fish Bull 96:258–270

Hyndes GA, Potter IC, Platell M (1997) Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Mar Biol 128:585–598

Jackson EL, Rees SE, Wilding C, Attrill MJ (2015) Use of a seagrass residency index to apportion commercial fishery landing values and recreation fisheries expenditure to seagrass habitat service. Conserv Biol 29:899–909

Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB (2001) The importance of seagrass beds as a habitat for fishery species. Oceanogr Mar Biol Annu Rev 39:269–303

Jelbart JE, Ross PM, Connolly RM (2007) Fish assemblages in seagrass beds are influenced by the proximity of mangrove forests. Mar Biol 150:993–1002

Jenkins GP, Black KP, Hamer PA (2000) Determination of spawning areas and larval advection pathways for King George whiting in southeastern Australia using otolith microstructure and hydrodynamic modelling. I. Victoria. Mar Ecol Prog Ser 199:231–242

Jenkins GP, Edgar GJ, May HMA, Shaw C (1993) Ecological basis for parallel declines in seagrass habitat and catches of commercial fish in Western Port Bay, Victoria. In: Hancock DA (ed) Sustainable fisheries through sustaining fish habitat. Australian Society for Fish Biology Workshop, Victor Harbour, SA, 12–13 August, Bureau of Resource Sciences Proceedings. AGPS, Canberra

Jenkins GP, Hamer PA (2001) Spatial variation in the use of seagrass and unvegetated habitats by post-settlement King George whiting (Percoidei: Sillaginidae) in relation to meiofaunal distribution and macrophyte structure. Mar Ecol Prog Ser 224:219–229

Jenkins GP, Kenner T, Brown A, Coleman R (2015) Fish assemblages in locations with alternative structured habitats in an eelgrass, *Zostera*, dominated bay: Biodiversity value and potential for refuge. Estuar Coast Shelf Sci 161:25–37

Jenkins GP, Keough MJ, Hamer PA (1998) The contributions of habitat structure and larval supply to broad-scale recruitment variability in a temperate zone, seagrass-associated fish. J Exp Mar Biol Ecol 226:259–278

Jenkins GP, May HMA, Wheatley MJ, Holloway MG (1997) Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. Estuar Coast Shelf Sci 44:569–588

Jenkins GP, Wheatley MJ (1998) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef algal, and unvegetated habitats, with emphasis on their importance to recruitment. J Exp Mar Biol Ecol 221:147–172

Jenkins GP, Wheatley MJ, Poore AGB (1996) Spatial variation in recruitment, growth and feeding of post-settlement King George whiting, *Sillaginodes punctata*, associated with seagrass beds of Port Phillip Bay, Australia. Can J Fish Aquat Sci 53:96–105

Jernakoff P, Nielsen J (1998) Plant-animal associations in two species of seagrasses in Western Australia. Aquat Bot 60:359–376

Johnson MP, Hanley ME, Frost NJ, Mosley MWJ, Hawkins SJ (2008) The persistent spatial patchiness of limpet grazing. J Exp Mar Biol Ecol 365:136–141

Jones CM (2014) Can we predict the future: Juvenile finfish and their seagrass nurseries in the Chesapeake Bay. ICES J Mar Sci 71:681–688

Kendrick AJ, Hyndes GA (2003) Patterns in the abundance and size-distribution of syngnathid fishes among habitats in a seagrass-dominated marine environment. Estuar Coast Shelf Sci 57:631–640

Kikuchi T (1974) Japanese contributions on consumer ecology in eelgrass (*Zostera marina* L.) beds, with special reference to trophic relationships and resources in inshore fisheries. Aquaculture 4:145–160

Kirsch KD, Valentine JF, Heck KL (2002) Parrotfish grazing on turtlegrass *Thalassia testudinum*: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. Mar Ecol Prog Ser 227:71–85

Klumpp DW, Nichols PD (1983a) Nutrition of the southern sea garfish *Hyporhamphus melanochir*: gut passage rate and daily consumption of two food types and assimilation of seagrass components. Mar Ecol Prog Ser 12:207–216

Klumpp DW, Nichols PD (1983b) A study of food chains in seagrass communities II. Food of the rock flathead, *Platycephalus laevigatus* Cuvier, a major predator in a *Posidonia australis* seagrass bed. Aust J Mar Freshw Res 34:745–754

Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. Oceanogr Mar Biol Annu Rev 35:163–220

Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. Ecological Connectivity among Tropical Coastal Ecosystems

Kwak SN, Klumpp DW, Park JM (2015) Feeding relationships among juveniles of abundant fish species inhabiting tropical seagrass beds in Cockle Bay, North Queensland, Australia. NZ J Mar Freshwat Res 49:205–223

Lenanton RCJ (1982) Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. Aust J Mar Freshw Res 33:881–900

Lepoint G, Nyssen F, Gobert S, Dauby P, Bouquegneau JM (2000) Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets. Mar Biol 136:513–518

Lim IE, Wilson SK, Holmes TH, Noble MM, Fulton CJ (2016) Specialization within a shifting habitat mosaic underpins the seasonal abundance of a tropical fish. Ecosphere *7*

Lilley RJ, Unsworth RKF (2014) Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. Global Ecol Conserv 2:367–377

Loneragan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar Biol 130:289–300

Loneragan NR, Kenyon RA, Staples DJ, Poiner IR, Conacher CA (1998) The influence of seagrass type on the distribution and abundance of postlarval and juvenile tiger prawns (Penaeus esculentus and P. semisulcatus) in the western Gulf of Carpentaria, Australia. J Exp Mar Biol Ecol 228:175–195

Macarthur LD, Hyndes GA (2007) Varying foraging strategies of Labridae in seagrass habitats: herbivory in temperate seagrass meadows? J Exp Mar Biol Ecol 340:247–258

Macarthur LD, Hyndes GA, Babcock RC, Vanderklift MA (2008) Nocturnally active western rock lobsters *Panulirus cygnus* forage close to shallow coastal reefs. Aquat Biol 4:201–210

Macarthur L, Phillips D, Hyndes G, Hansen C, Vanderklift M (2011) Habitat surrounding patch reefs influences the diet, nutrition and trophic linkages of western rock lobsters, Panulirus cygnus. Mar Ecol Prog Ser 436:191–205

Macdonald CM (1992) Fluctuations in seagrass habitats and commercial fish catches in Westernport Bay and the Gippsland Lakes, Victoria. In: Hancock DA (ed) Recruitment processes. Australian Society for Fish Biology Workshop, Hobart, 21 August 1991, Bureau of Rural Resources Proceedings No. 16. AGPS, Canberra

Macreadie PI, Hindell JS, Jenkins GP, Connolly RM, Keough MJ (2009) Fish responses to experimental fragmentation of seagrass habitat. Conserv Biol 23:644–652

Macreadie PI, Hindell JS, Keough MJ, Jenkins GP, Connolly RM (2010) Resource distribution influences positive edge effects in a seagrass fish. Ecology 91:2013–2021

Mattila J, Heck KL, Millstein E, Miller E, Gustafsson C, Williams S, Byron D (2008) Increased habitat structure does not always provide increased refuge from predation. Mar Ecol Prog Ser 361:15–20

Mcarthur LC, Boland JW (2006) The economic contribution of seagrass to secondary production in South Australia. Ecol Model 196:163–172

McDevitt-Irwin JM, Iacarella JC, Baum JK (2016) Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. Mar Ecol Prog Ser 557:133–143

Mcmahon KW, Berumen ML, Thorrold SR (2012) Linking habitat mosaics and connectivity in a coral reef seascape. Proc Natl Acad Sci USA 109:15372–15376

Mcneill SE, Worthington DG, Ferrell DJ, Bell JD (1992) Consistently outstanding recruitment of five species of fish to a seagrass bed in Botany Bay, NSW. Aust J Ecol 17:359–365

Middleton MJ, Bell JD, Burchmore JJ, Pollard DA, Pease BC (1984) Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. Aquatic Botany, 18

Melia P, Schiavina M, RTossetto M, Gatto M, Fraschetti S, Casagrandi R (2016) Looking for hotspots of marine metacommunity connectivity: a methodological framework. Scientific Reports 6:23705 https://doi.org/10.1038/srep23705

Mills LS, Soule ME, Doak DF (1993) The keystone-species concept in ecology and conservation. Bioscience 43:219–224

Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar Ecol Prog Ser 246:39–59

Mizerek T, Regan HM, Hovel KA (2011) Seagrass habitat loss and fragmentation influence management strategies for a blue crab *Callinectes sapidus* fishery. Mar Ecol Prog Ser 427: 247–257

Moore KA, Short FT (2006) Biology of *Zostera*. In: Larkum A, Orth R, Duarte C (eds) Seagrasses, ecology and conservation. Springer, Netherlands

Mouillot D, Culioli J-M, Lepretre A, Tomasini J-A (1999) Dispersion statistics and sample size estimates for three fish species (*Symphodus ocellatus*, *Serranus scriba* and *Diplodus annularis*) in the Lavezzi Islands Marine Reserve (South Corsica, Mediterranean Sea). Mar Ecol 20:19–34

Myers JA, Heck KL (2013) Amphipod control of epiphyte load and its concomitant effects on shoalgrass *Halodule wrightii* biomass. Mar Ecol Prog Ser 483:133–142

Nagelkerken I (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. Ecological Connectivity among Tropical Coastal Ecosystems

Nagelkerken I, Bothwell J, Nemeth RS, Pitt JM, Van Der Velde G (2008) Interlinkage between Caribbean coral reefs and seagrass beds through feeding migrations by grunts (*Haemulidae*) depends on habitat accessibility. Mar Ecol Prog Ser 368:155–164

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish 16:362–371

Nakamura Y, Sano M (2004) Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: importance of the seagrass bed as juvenile habitat. Fish Sci 70:788–803

Nanjo K, Kohno H, Nakamura Y, Horinouchi M, Sano M (2014) Differences in fish assemblage structure between vegetated and unvegetated microhabitats in relation to food abundance patterns in a mangrove creek. Fish Sci 80:21–41

Nelson JA, Stallings CD, Landing WM, Chanton J (2013) Biomass transfer subsidizes nitrogen to offshore food webs. Ecosystems 16:1130–1138

Nemeth RS (2009) Dynamics of reef fish and decapod crustacean spawning aggregations: underlying mechanisms, habitat linkages, and trophic interactions. Ecological Connectivity among Tropical Coastal Ecosystems

Nichols PD, Klumpp DW, Johns RB (1986) Lipid components and utilization in consumers of a seagrass community: an indication of carbon source. Comp Biochem Physiol Part B 83: 103–113

Ogden JC (1977) Carbonate-sediment production by Parrot Fish and Sea Urchins on Caribbean Reefs In: Frost S, Weiss M, Saunders J (eds) Reefs and related carbonates—ecology and sedimentology AAPG studies in geology. American Association of Petroleum Geologists

Ogden JC (1980) Faunal relationships in Caribbean seagrass beds. In: Phillips RC, Mcroy CP (eds) Handbook of seagrass biology: an ecosystem perspective. Garland Publishing Inc, New York

Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. Mar Ecol Prog Ser 462:191–203

Olds AD, Connolly RM, Pitt KA, Maxwell PS, Aswani S, Albert S (2014) Incorporating surrogate species and seascape connectivity to improve marine conservation outcomes. Conserv Biol 28:982–991

Olds AD, Connolly RM, Pitt KA, Pittman SJ, Maxwell PS, Huijbers CM, Moore BR, Albert S, Rissik D, Babcock RC, Schlacher TA (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. Glob Ecol Biogeogr 25:3–15

Pardieck RA, Orth RJ, Diaz RJ, Lipcius RN (1999) Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab. Mar Ecol Prog Ser 186:227–238

Patzer RA (2008) Fish reproduction. CRC Press, Boca Raton

Pecl GT, Tracey SR, Semmens JM, Jackson GD (2006) Use of acoustic telemetry for spatial management of southern calamary *Sepioteuthis australis*, a highly mobile inshore squid species. Mar Ecol Prog Ser 328:1–15

Pogoreutz C, Kneer D, Litaay M, Asmus H, Ahnelt H (2012) The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadows. Estuar Coast Shelf Sci 107:58–68

Potter IC, Tweedley JR, Elliott M, Whitfield AK (2015) The ways in which fish use estuaries: a refinement and expansion of the guild approach. Fish Fish 16:230–239

Randall JE (1965) Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. Ecology 46:255–260

Ray BR, Johnson MW, Cammarata K, Smee DL (2014) Changes in seagrass species composition in northwestern Gulf of Mexico estuaries: effects on associated seagrass fauna. PLoS One 9: e107751

Robertson AI (1977) Ecology of juvenile King George whiting *Sillaginodes punctatus* (Cuvier and Valenciennes) (Pisces: Perciformes) in Western Port, Victoria. Aust J Mar Freshw Res 28: 35–43

Robertson AI (1980) The structure and organization of an eelgrass fish fauna. Oecologia 47:76–82

Robertson AI, Klumpp DW (1983) Feeding habits of the southern Australian garfish *Hyporhamphus melanochir*: a diurnal herbivore and nocturnal carnivore. Mar Biol 10:197–201

Rotherham D, West RJ (2002) Do different seagrass species support distinct fish communities in south-eastern Australia? Fish Manage Ecol 9:235–248

Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar Ecol Prog Ser 99:1–16

Scheinin M, Scyphers SB, Kauppi L, Heck KL, Mattila J (2012) The relationship between vegetation density and its protective value depends on the densities and traits of prey and predators. Oikos 121:1093–1102

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal habitats for commercially and ecologically important species. ICES J Mar Sci 71:648–665

Sheridan P, Mcmahan G, Conley G, Williams A, Thayer G (1997) Nekton use of macrophyte patches following mortality of turtlegrass, *Thalassia testudinum*, in shallow waters of Florida Bay (Florida, USA). Bull Mar Sci 61:801–820

Sheridan PF, Hays CG (2003) Aare mangroves nursery habitat for transient fishes and decapods? Wetlands 23:449–458

Short FT, Wyllie-Eciieverria S (1996) Natural and human-induced disturbance of seagrasses. Environ Conserv 23:17–27

Smit AJ, Brearley A, Hyndes GA, Lavery PS, Walker DI (2005) Carbon and nitrogen stable isotope analysis of an *Amphibolis griffithii* seagrass bed. Estuar Coast Shelf Sci 65:545–556

Smit AJ, Brearley A, Hyndes GA, Lavery PS, Walker DI (2006) $\delta^{15}$N and $\delta^{13}$C analysis of a *Posidonia sinuosa* seagrass bed. Aquat Bot 84:277–282

Smith KA, Sinerchiab M (2004) Timing of recruitment events, residence periods and post-settlement growth of juvenile fish in a seagrass nursery area, south-eastern Australia. Environ Biol Fishes 71:73–84

Smith TM, Hindell JS, Jenkins GP, Connolly RM (2008) Edge effects on fish associated with seagrass and sand patches. Mar Ecol Prog Ser 359:203–213

Smith TM, Hindell JS, Jenkins GP, Connolly RM (2010) Seagrass patch size affects fish responses to edges. J Anim Ecol 79:275–281

Smith TM, Hindell JS, Jenkins GP, Connolly RM, Keough MJ (2011) Edge effects in patchy seagrass landscapes: The role of predation in determining fish distribution. J Exp Mar Biol Ecol 399:8–16

Smith TM, Jenkins GP, Hutchinson N (2012) Seagrass edge effects on fish assemblages in deep and shallow habitats. Estuar Coast Shelf Sci 115:291–299

Sobocinski KL, Latour RJ (2015) Trophic transfer in seagrass systems: estimating seasonal production of an abundant seagrass fish, *Bairdiella chrysoura*, in lower Chesapeake Bay. Mar Ecol Prog Ser 523:157–174

Sogard SM (1992) Variability in growth of juvenile fishes in different estuarine habitats. Mar Ecol Prog Ser 85:35–53

Sogard SM, Able KW (1991) A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuar Coast Shelf Sci 33:501–519

Steffe AS, Westoby M, Bell JD (1989) Habitat selection and diet in two species of pipefish from seagrass: sex differences. Mar Ecol Prog Ser 55:23–30

Tanner JE, Irving AD, Fernandes M, Fotheringham D, Mcardle A, Murray-Jones S (2014) Seagrass rehabilitation off metropolitan Adelaide: a case study of loss, action, failure and success. Ecol Manag Restor 15:168–179

Thresher RE, Nichols PD, Gunn JS, Bruce BD, Furlani DM (1992) Seagrass detritus as the basis of a coastal planktonic food chain. Limnol Oceanogr 37:1754–1758

Tomas F, Turon X, Romero J (2005) Effects of herbivores on a *Posidonia oceanica* seagrass meadow: importance of epiphytes. Mar Ecol Prog Ser 287:115–125

Travers MJ, Potter IC (2002) Factors influencing the characteristics of fish assemblages in a large subtropical marine embayment. J Fish Biol 61:764–784

Unsworth RKF, Bell JJ, Smith DJ (2007a) Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific. J Mar Biol Assoc United Kingdom 87:1287–1296

Unsworth RKF, De León PS, Garrard SL, Jompa J, Smith DJ, Bell JJ (2008) High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. Mar Ecol Prog Ser 353:213–224

Unsworth RKF, Taylor JD, Powell A, Bell JJ, Smith DJ (2007b) The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. Estuar Coast Shelf Sci 74:53–62

Vega Fernández T, Milazzo M, Badalamenti F, D'Anna G (2005) Comparison of the fish assemblages associated with *Posidonia oceanica* after the partial loss and consequent fragmentation of the meadow. Estuar Coast Shelf Sci 65:645–653

Valentine JF, Duffy JE (2006) The central role of grazing in seagrass ecosystems. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation. Springer, Berlin

Valls A, Gascuel D, Guenette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214

Van Tussenbroek BI, Vonk JA, Stapel J, Erftemeijer PLA, Middelburg JJ, Zieman JC (2007) The biology of Thalassia: paradigms and recent advances in research. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation, 1 edn, Springer, Netherlands

Velimirov B (1984) Grazing of *Sarpa salpa* L. on *Posidonia oceanica* and utilisation of soluble compounds. In: Boudouresque CF, Jeudy De Grissac A, Olivier J (eds) International workshop on *Posidonia oceanica* beds. GIS Posidonie Publication, France

Verges A, Steinberg PD, Hay ME, Poore AG, Campbell AH, Ballesteros E, Heck KL Jr, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, Van Sebille E, Gupta AS, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Biol Sci 281:20140846

Verlaque M (1990) Relations entre *Sarpa salpa* (Linnaeus, 1758) (Téléostéen, Sparidae), les autres poissons broteurs et le phytobenthos algal méditerranéen. Oceanol Acta 13:373–388

Verweij MC, Nagelkerken I, Hans I, Ruseler SM, Mason PRD (2008) Seagrass nurseries contribute to coral reef fish populations. Limnol Oceanogr 53:1540–1547

Vizzini S, Mazzola A (2003) Seasonal variations in the stable carbon and nitrogen isotope ratios (C-13/C-12 and N-15/N-14) of primary producers and consumers in a western Mediterranean coastal lagoon. Mar Biol 142:1009–1018

Vizzini S, Sara G, Michener RH, Mazzola A (2002) The role and contribution of the seagrass *Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis. Acta Oecologica Int J Ecol 23:277–285

Walker DI, Denninson W, Edgar GJ (1999) Status of Australian seagrass research and knowledge. In: Butler A, Jernakoff P (eds) Seagrass in Australia: strategic review and development of an R & D plan. CSIRO Publishing, Australia

Watson RA, Coles RG, Lee Long WJ (1993) Simulation estimates of annual yield and landed value for commercial penaeid prawns from a tropical seagrass habitat, northern Queensland, Australia. Aust J Mar Freshw Res 44:211–219

Warry F, Hindell J, Macreadie P, Jenkins G, Connolly R (2009) Integrating edge effects into studies of habitat fragmentation: a test using meiofauna in seagrass. Oecologia 159:883–892

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL Jr, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Whalen M, Duffy JE, Grace J (2013) Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. Ecology 94:510–520

Whitfield AK, Pattrick P (2015) Habitat type and nursery function for coastal marine fish species, with emphasis on the Eastern Cape region, South Africa. Estuar Coast Shelf Sci 160:49–59

Young PC (1981) Temporal changes in the vagile epibenthic fauna of two seagrass meadows (*Zostera capricorni* and *Posidonia australis*). Mar Ecol Prog Ser 5:91–102