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Habitat-specific food webs and trophic interactions supporting coastal-dependent fishery species: an Australian case study

Kátya G. Abrantes · Adam Barnett · Ronald Baker · Marcus Sheaves

Abstract Coastal ecosystems such as estuaries, tidal wetlands and shallow coastal waters are often highly productive and provide important habitats to many recreationally and commercially important fish and invertebrates that use these areas as nursery, feeding and/or reproduction grounds. The diversity of coastlines found worldwide results in differences in types of provisioning and function, and in community structure and trophic organisation. Since almost all coastal fishery species require particular components of the seascapes during specific stages of their life-cycles, it is important to understand the way fish use different habitats throughout ontogeny. Access to rich feeding environments is a key contributor to habitat value, and so knowledge on food webs and feeding relationships, and how these vary over space and time, is central to understanding the importance of the different coastal environments. However, the functional roles of the different habitats in supporting fishery species are still not well understood for most regions. In this study, we review and discuss the available literature to identify key knowledge gaps in the understanding of habitat- and context-specific food webs and trophic interactions supporting fisheries species relying on coastal ecosystems. We use Australia and Australian fisheries species as a case-study, as Australia's extensive coastline encompasses many of the coastal ecosystems and habitats found globally. Given the ever increasing transformation of coastal landscapes by either direct human action or by sea level rise and changing climate, these knowledge gaps need to be urgently addressed for appropriate management and mitigation of various impacts.

Keywords Connectivity · Critical habitats · Fish · Fisheries · Primary producers

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Introduction

Food webs represent fundamental interactions that underpin ecosystem function, community structure, and population dynamics (Link et al. 2006; Pasquaud et al. 2007). Understanding the food webs that support fishery species throughout all stages of their lives is critical for effective management (Sheaves et al. 2015). The loss or disruption of key productivity sources, densities and/or composition of predators or prey, or food web connectivity can lead to population collapses or prevent recovery from population

declines (Swain and Sinclair 2000; Link 2002) and have cascading effects on ecosystems (Pinnegar et al. 2000; Altieri et al. 2012). As a result, even when fisheries themselves and the key habitats supporting them are well managed, fish stocks may decline if important trophic links are altered (Bostrom et al. 2011; Fogarty 2014).

Coastal ecosystems such as estuaries, tidal wetlands and shallow coastal waters are among the most valuable natural systems on earth (Costanza et al. 1997) and support a diversity of commercial, artisanal and recreational fisheries around the globe by providing crucial spawning (e.g. Gray and Miskiewicz 2000), feeding (e.g. Begg and Hopper 1997) and nursery grounds (e.g. Beck et al. 2001; Sheaves et al. 2015) to a large proportion of fishery species. However, they are also among the most threatened systems (Elliott and Kennish 2011). Their location at the interface of land and sea makes them highly prized for a diversity of human activities, leading to unprecedented and rapidly increasing threats from growing populations (Bassett et al. 2013; Waycott et al. 2009).

While coastal species and the ecosystems they occupy are studied at a range of spatial and temporal scales, management actions tend to focus on discrete and static spatial units that can be most easily defined and mapped, from broad bioregions (e.g. Fernandes et al. 2005) or whole estuaries (e.g. Vasconcelos et al. 2011), to individual systems or habitat units such as mangrove forests, seagrass beds, or individual reefs (e.g. Barbier et al. 2011; Vasconcelos et al. 2014). However, many coastal fishery species progressively move through a series of habitats or seascape units during their lives, showing strong ontogenetic shifts in both habitat use and diet (Nagelkerken et al. 2013). While some life stages may occupy discrete habitats that provide all the resources needed (Tupper 2007), others may move across the seascape linking habitats and transferring production through regular foraging migrations (Sheaves and Molony 2000; Krumme 2009; Davis et al. 2014). As a consequence, the management of static spatial units may be effective in sustaining some species or life stages if all the resources required are contained within the protected unit, but will be ineffective where supporting food webs transcend the identified units of habitat (Sheaves 2009; Edwards et al. 2010).

The aim of this paper is to review our understanding of food webs that support fishery species in coastal systems. We firstly focus on some of the most commonly managed habitat units: mangroves, salt-marshes, seagrass beds and reefs (Beck et al. 2001). We then investigate how food webs connect among and across these habitat units and through time rather than being static relationships specific to particular units of habitat. We end by identifying the most important knowledge gaps and proposing the most productive avenues for future research to support and advance the management of fishery species and their supporting habitats. We use Australia and Australian fisheries species as a case-study, as Australia's extensive coastline, with its contrasting geology, geomorphology, oceanography and climate, encompasses most of the coastal ecosystems and habitats found globally. While this review takes an Australian focus, it draws on examples from around the globe and makes points pertinent to the management of coastal fishes elsewhere. We conclude that understanding the key prey resources and food web linkages that support all life-stages of fishery species is a high priority for their sustainable management, especially for species that participate in food webs that transcend the individual habitat units that are the common focus of management.

Habitat-specific food webs

The spatial arrangement of habitats coupled with consumer foraging behavior within and amongst these habitats, inherently influences food web ecology (McCann et al. 2005; Rezende et al. 2009). For example, the two broad (but not mutually exclusive) views of food web ecology, compartmentalization of food webs and connectivity/trophic flows between food webs in different habitats, are interconnected with spatial ecology. Here, compartmentalization refers to food webs being organized in compartments, where the species from each compartment interact more frequently among themselves than with species from other compartments (Rezende et al. 2009; Stouffer and Bascompte 2011). Although theory suggests that compartmentalization of food webs may be primarily driven by a number of mechanisms such as body size or phylogeny (Rezende et al. 2009), habitat boundaries may also play a key role (Pimm and Lawton 1980; Girvan and Newman 2002; Rezende et al. 2009). Hence, while trophic connectivity across

habitat boundaries is a widely recognised phenomenon (e.g. Nagelkerken 2009), strong habitat-specific food webs are likely in many coastal systems.

Unlike the rich body of theoretical literature on aquatic food webs (e.g. Belgrano et al. 2014 and chapters therein), few empirical studies have detailed habitat-specific aquatic food webs that span from primary producers to top consumers. Food webs have mostly been studied in relatively closed systems that are easier to work in such as lakes (e.g. Gu et al. 1996; Vander Zanden et al. 1999) or in less diverse systems such as rivers (e.g. Fisher et al. 2001; Jepsen and Winemiller 2002) (see review by Vander Zanden and Fetzer 2007). Even large open ocean areas (Davenport and Bax 2002; Sherwood and Rose 2005), deep sea (Fry 1988) and Polar Regions (e.g. Gillies et al. 2012) have had a number of relatively detailed food web studies published. Yet, surprisingly given the easy access and significance in supporting fisheries production, there are still few relatively comprehensive food web studies in coastal habitats. Indeed, with few exceptions (e.g. Abrantes and Sheaves 2009a; Nyunja et al. 2009; Mazumder et al. 2011; Vinagre et al. 2011; Vaslet et al. 2012; Zagars et al. 2013; Abrantes et al. 2014a), most coastal food web studies do not consider a comprehensive assemblage of primary producers and of consumers of the different trophic levels and trophic ecologies. In other cases, data from a range of habitats is combined and used to describe a general food web (e.g. Abrantes et al. 2014a). This lack of information is more striking given the wide diversity of coastal environments found around the world.

Compared to most offshore and oceanic waters, coastal environments are highly productive (Alongi 1996) and receive rich and diverse inputs of nutrients, supporting high biomasses of juveniles that use these areas for critical growth and development (Sogard 1992; Deegan et al. 2000). Many of these juveniles then become prey components in trophic relays (Kneib 1997; Le Quesne 2000; Nemerson and Able 2004) that move nutrients to offshore waters (Deegan 1993). Coastal ecosystems are also important feeding areas for predators that make regular inshore migrations to access prey-rich coastal areas (Begg and Hopper 1997; Barnett and Semmens 2012). So, while detailed food web studies in coastal habitats are sparse, important processes that structure food webs in these areas are becoming better understood.

In terms of fisheries research, perhaps the most extensively studied coastal ecosystems in the world are the *Spartina alterniflora* saltmarshes along the northern Gulf of Mexico and Atlantic coasts of the USA. The long history of research in these systems has provided much of our understanding of the function and value of coastal habitats in general, and their roles as nurseries supporting fisheries production (e.g. Teal 1962; Boesch and Turner 1984; Kneib 1997; Minello et al. 2003). While detailed individual food web studies of these saltmarshes are more numerous than elsewhere in the world, they are still relatively few, yet as a combined body of work, our understanding of the food webs supporting fishery species in these salt-marshes is amongst the best for any coastal system (e.g. Weinstein and Kreeger 2000 and chapters therein).

Spartina alterniflora represents a conspicuous high biomass primary producer that was long considered to fuel aquatic food webs through detrital pathways (Teal 1962; Odum 1968), ultimately supporting massive fisheries production in adjacent coastal waters (Turner 1977). While these marshes do appear critical in supporting some of the highest yielding fisheries in the USA (Deegan et al. 2000), the outwelling of detritus from the marsh is a dynamic process that may be significant at particular locations or conditions (Odum 2000), but less important in other areas (Nixon 1980). Stable isotope studies have revealed the importance of less conspicuous but more palatable producers in the marsh seascape, including microphytobenthos and phytoplankton (Sullivan and Moncreiff 1990; Currin et al. 1995; Galván et al. 2008). However, *S. alterniflora* also makes important contributions to the support of a wide variety of aquatic consumers (e.g. Currin et al. 2003; Winemiller et al. 2007).

The variety of production sources on the marsh surface and the adjacent shallow waters, which together make up the marsh complex (Minello et al. 2008), support high densities of juveniles of many fishery species including blue crabs (*Callinectes sapidus*) (Fantle et al. 1999; Dittel et al. 2000), penaeid shrimps (*Farfantepenaeus aztecus* and *Litopenaeus setiferus*) (McTigue and Zimmerman 1991; Riera et al. 2000; Fry 2008), and gulf menhaden (*Brevoortia patronus*) (Deegan 1993). In addition to their direct value to fisheries, these species in turn form important prey for other fishery species such as red drum (*Sciaenops ocellatus*) (e.g. Scharf and

Schlicht 2000) and flounder (*Paralichtys lethostigma*) (e.g. Minello et al. 1989).

Broader concepts about the functioning of coastal food webs have emerged from saltmarsh research in the USA. The passive outwelling of detrital material from coastal wetlands (Odum 2000) together with the active translocation of nutrients through the movement of animals (Deegan et al. 2000; Kneib 2000) result in production flows within and among systems (Bouillon and Connolly 2009), that directly and indirectly support coastal and offshore fisheries production (Hyndes et al. 2014). In particular, trophic relays involving the transfer of production from producers in one habitat to fishery species in another via mobile intermediate consumers (Kneib 1997) may represent the most significant vector for the support of coastal fisheries by wetlands (Deegan 1993). Trophic relays can link across food webs in different habitats and ecosystems, and the recognition of their significance greatly expands our understanding of the value of coastal systems in supporting fisheries (Sheaves et al. 2015).

Australia: coastal habitats in focus

The diversity of coastal ecosystems and seascape mosaics found around Australia results from differences in climate, geomorphology, and the range, distribution, and availability of habitats and of primary producers within habitats. This in turn leads to differences in community structure and trophic organisation. For example, the estuaries of tropical eastern Australia comprise a range of interconnected intertidal habitats, including seagrass beds, mangrove forests, saltmarsh and salt pans, intertidal flats, as well as littoral floodplain forests, coastal lagoons and swamps that are seasonally connected by flooding to estuaries. This mosaic of coastal habitats provides a diversity of feeding opportunities for species with diverse feeding strategies, from species such as flathead (*Platycephalus* spp.) that spend the bulk of their lives feeding in one habitat type (Baker and Sheaves 2005, 2006) to others such as barramundi (*Lates calcarifer*) which range widely, connecting food webs across the coastal seascape (Russell and Garrett 1983, 1988; Sheaves et al. 2007; Sheaves and Johnston 2008). In the high wave energy south west coast of Western Australia, coastal habitats are characterised by extensive subtidal seagrass meadows and limestone reefs dominated by macroalgae. Exposed sandy beaches with abundant wrack deposits are separated from the terrestrial environment and coastal wetlands by sand dunes which, coupled with the restricted seasonal rainfall, limits connectivity between the marine environment, other coastal wetlands and the terrestrial environment. In the end of this spectrum, in the high limestone cliffs that dominate the high energy coastline bordering the arid Nullarbor Plain on the Great Australian Bight (southern Australia), there are almost no estuaries or coastal wetlands for thousands of kilometers. These contrasting environments generate very different contexts for the development of food webs supporting fishery species. In the following section we review what is known about the food webs supporting fishery species in coastal waters around Australia. We focus on the key habitat units that are widely studied and generally considered in management such as mangroves, saltmarshes, seagrass beds and reefs.

Mangroves

Situated in the high intertidal, mangrove forests are widely considered critical in supporting fisheries production in Australia (Manson et al. 2005a; Meynecke et al. 2007) and elsewhere in the world (Manson et al. 2005b; Nagelkerken et al. 2008). Mangroves occur in low wave energy environments; in Australia mostly around the northern and eastern coasts (Fig. 1a). They are ubiquitous in the tropics and extend down the east coast to Corner Inlet in southern Victoria, where the most southerly and highest latitude mangroves in the world occur (Duke 2006). Mangroves are absent from Western Australia's temperate coasts except for a relict stand at Bunbury in the far southeast. Juvenile nekton of many species primarily occupy mangroves and associated subtidal channels, reflecting the global importance of mangrove ecosystems as key nursery grounds for fish (Blaber and Blaber 1980; Nagelkerken et al. 2008) and invertebrates such as banana prawns (*Penaeus merguiensis*) (Vance et al. 1990; Sheaves et al. 2012) and mud crabs (*Scylla serrata*) (Hill 1976; Demopoulos et al. 2008).

Despite their recognised importance, most studies on mangrove habitats are limited to comparisons of animal communities between these habitats and adjacent seagrass beds or unvegetated habitats (e.g.

Fig. 1 The distribution of the different coastal habitats along the Australian coastline. *Squares* represent 50 km grids cells. *Source*: OzCoasts (2009)
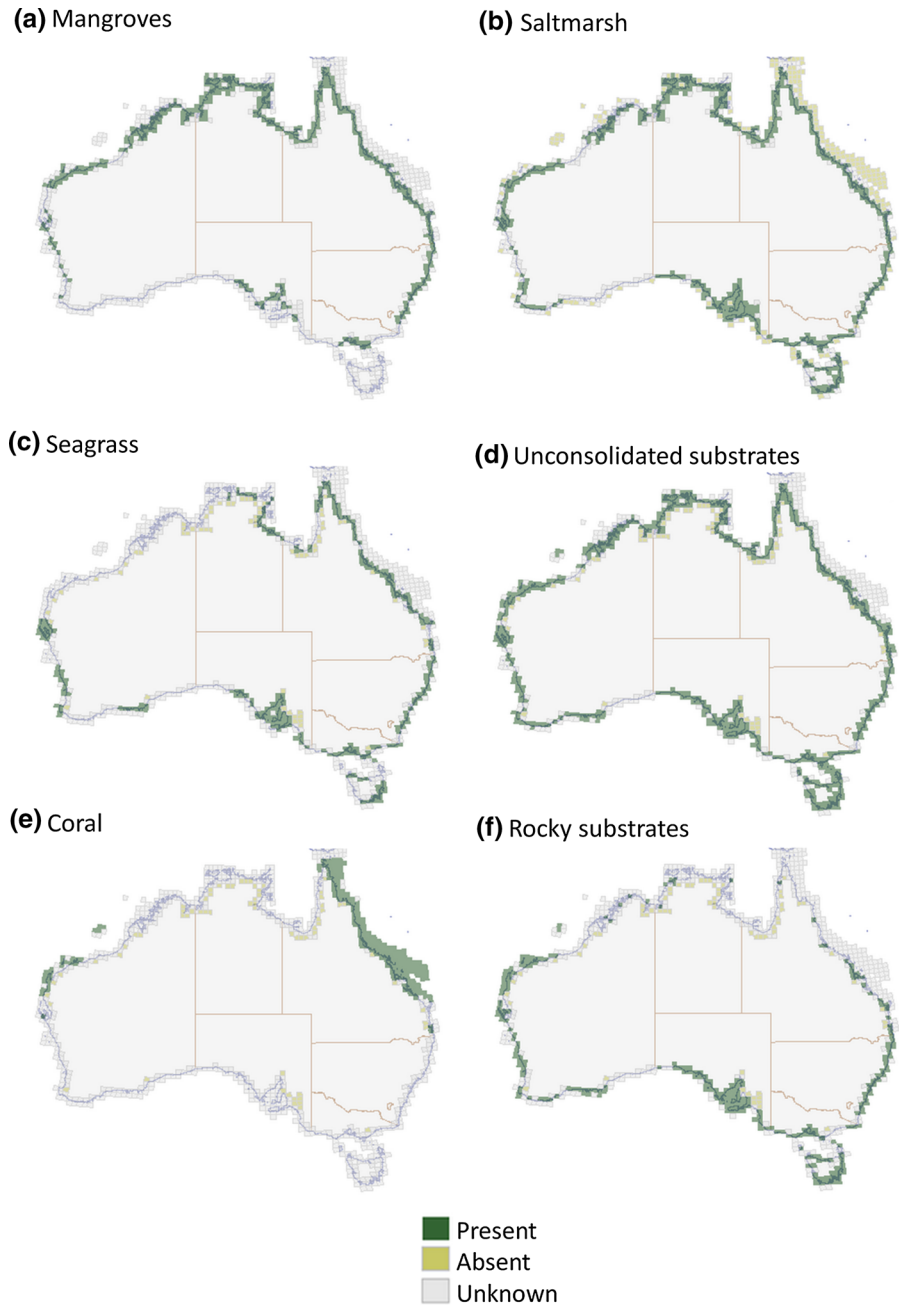
Robertson and Duke 1987; Laegdsgaard and Johnson 1995), and there is still much debate on the energetic links between mangrove production and aquatic consumers (Fry and Ewel 2003; Layman 2007; Bouillon et al. 2008; Igulu et al. 2013). The mangrove forests of northern Australia are highly productive (Bunt et al. 1979; Clough 1998) and contribute to a large proportion of the available organic carbon in estuarine waters [e.g. mangroves contribute up to 56 % of the total organic carbon in the Hinchinbrook Channel in North Queensland (Alongi et al. 1998)]. Although mangrove material is of poor nutritional quality (Alongi et al. 1998), it enters estuarine food webs through direct grazing by herbivorous

invertebrates such as sesarmid crabs and mangrove snails (Robertson and Daniel 1989; Micheli 1993; Bui and Lee 2014) and through detrital pathways (Abrantes and Sheaves 2008, 2009b; Oakes et al. 2010). However, despite the large expanses of mangrove forests and high availability of mangrove-derived carbon, its importance as a direct source of nutrition for fishery species is limited, with food webs in mangrove areas mostly based on a combination of more easily assimilated aquatic producers such as phytoplankton, seagrass and microphytobenthos (Loneragan et al. 1997; Abrantes and Sheaves 2008, 2009b; Oakes et al. 2010). A notable exception are groupers (*Epinephelus* spp.), snappers (*Lutjanus* spp.) and bream (*Acanthopagrus* spp.) which in northern Queensland feed extensively on mangrove-feeding sesarmid crabs, as part of a very short food chain from mangroves to large predatory fish (Sheaves and Molony 2000; Sheaves et al. 2014). In temperate eastern Australia (Victoria, South Australia, New South Wales), mangroves are confined to sheltered shores such as estuaries, embayments and inlets, while in Western Australia these are mostly distributed through the northern and western shores, and are abundant only in the northern regions of the Kimberley and Pilbara. Studies in these areas also indicate that mangroves are of little importance to consumer nutrition, and that aquatic producers are the most important contributors (Boon et al. 1997; Hadwen et al. 2007; Heithaus et al. 2011).

Indeed, the view of mangroves as key primary producers that fuel coastal food webs and support fisheries throughout their global range (Odum and Heald 1975) has shifted with evidence from stable isotope studies that indicate a general minor role of mangrove production in aquatic food webs (Layman 2007; Igulu et al. 2013 and references therein). However, the importance of mangrove production depends on the relative availability of mangrove material and other sources, with higher contributions of mangrove carbon in relatively isolated systems such as small mangrove-lined creeks and mangrove ponds (Lugendo et al. 2007; Giarrizzo et al. 2011; Vaslet et al. 2012; Zagars et al. 2013; Abrantes et al. 2014b). Note also that some studies may have underestimated the contributions of mangrove carbon to fishery species due to incorrect assumptions about trophic fractionation through intermediate consumers (Bui and Lee 2014). Nevertheless, even where mangrove production plays only a minor role in supporting fishery species, mangrove forests provide rich foraging habitats with prey supported by a variety of sources (Igulu et al. 2013), and fishery landings are higher in areas adjacent to mangrove forests (Manson et al. 2005a, b; Meynecke et al. 2007). While the detailed mechanisms are yet to be resolved, recent work in Australia and elsewhere indicates that where together with coral reefs and seagrass beds, mangroves are an integral component of tropical coastal seascapes that support abundant and diverse communities, including fishery species (Nagelkerken et al. 2008; Olds et al. 2012).

Saltmarshes

Saltmarshes around Australia (Fig. 1b) are used by a range of fish and invertebrates, including juveniles of commercially important species. In tropical regions, saltmarshes generally occur landward of mangrove forests, while in southern temperate regions vast expanses of saltmarsh occur in place of mangroves directly adjacent to subtidal waterways. Although saltmarshes are more extensive in the northern half of the continent (Bucher and Saenger 1991), most saltmarsh research has been conducted in temperate regions, especially southeast Queensland (e.g. Morton et al. 1987; Thomas and Connolly 2001; Hollingsworth and Connolly 2006), with some studies also from South Australia (Connolly et al. 1997; Bloomfield and Gillanders 2005), Victoria (Crinall and Hindell 2004) and New South Wales (Mazumder et al. 2006; Saintilan et al. 2007). Work in the tropics has concentrated on permanent (Sheaves et al. 2007; Sheaves and Johnston 2008; Davis et al. 2012) and temporary (Russell and Garrett 1983) saltmarsh pools. Juveniles of a number of species use both types of pools which, together with freshwater wetlands, are considered important juvenile habitats for species such as the iconic barramundi (*L. calcarifer*) (e.g. Russell and Garrett 1983; Sheaves et al. 2007).

As noted earlier, much of our understanding of the importance of saltmarshes in supporting aquatic food webs and fishery species is based on more extensive research in southeastern USA. In that region, various producers within the marsh complex directly support juveniles of a variety of fishery species including penaeid prawns, portunid crabs, and various fish (Deegan et al. 2000). Together with passive

outwelling (Odum 1968) and the active transfer of production via trophic relays (Kneib 2000) and life-cycle migrations (Deegan 1993), these saltmarshes support some of the largest and most valuable fisheries in the USA (Deegan et al. 2000).

Unlike those in the USA (Minello et al. 2012), most saltmarsh habitats in northern Australia occur high in the intertidal and are only submerged during the highest spring tides and for relatively short periods of time (Connolly 2009; Davis et al. 2012). Since the trophic importance of saltmarsh plants for fish and invertebrates is partly regulated by the duration of marsh flooding (Baker et al. 2013), the use of these habitats, including their trophic and nursery function, is likely to be very different to that of saltmarshes in the Northern Hemisphere (Connolly 2009), and to vary among regions around Australia due to differences in marsh flooding patterns. Nevertheless, a number of Australian studies reported the consumption of saltmarsh invertebrates by fish. For example, stable isotope studies have confirmed the incorporation of saltmarsh material by invertebrates such as crabs, penaeid prawns and gastropods in tropical (Abrantes and Sheaves 2008, 2009b) and subtropical (Guest and Connolly 2004, 2006; Guest et al. 2006) estuaries, meaning that despite the low frequency of inundation, saltmarsh carbon can be important for fishery species. Also, juveniles of fish such as yellowfin bream (*Acathopagrus australis*) feed substantially on terrestrial invertebrates such as flies, spiders, grasshoppers, dragonflies and even skink lizards in saltmarsh habitats (Morton et al. 1987), further increasing the importance of saltmarsh productivity for aquatic food webs.

Overall, the few studies that provide quantitative information on the incorporation of either saltmarsh or mangrove material by Australian fishery species indicate that these producers have limited importance for consumers in tropical (Abrantes and Sheaves 2008, 2009b), subtropical (Melville and Connolly 2003; Connolly et al. 2006), and temperate regions (Boon et al. 1997; Svensson et al. 2007), and that food webs supporting adjacent fisheries rely mostly on aquatic sources such as plankton, microphytobenthos and seagrass. However, because the importance of saltmarsh/mangroves to fish and invertebrates depends on the assemblage and relative availability of different habitats/sources (Polis et al. 1997; Svensson et al. 2007), the different producers are likely to have

different patterns of importance, depending on the environmental conditions of each area. For example, riparian vegetation is likely to have greater importance for consumers in intermittently open estuaries due to increased water residency time compared to open estuaries (Hadwen et al. 2007), while the importance of aquatic and terrestrial production is likely to alternate in areas with extreme hydrological seasonality (Abrantes and Sheaves 2010). Finally, while mangrove and marsh production itself may be of limited importance for fishery species, these wetland plants are foundation species that support a diversity of other production sources and rich prey that may be critical for fishery species (Igulu et al. 2013).

Seagrass meadows

Major seagrass areas occur around Australia, especially along the low wave energy northern coastlines (Fig. 1c). In the high energy southern coast, seagrass distribution is patchy and generally restricted to estuaries, protected bays and coastal lagoons. As with mangroves and saltmarshes, seagrass habitats have long been recognised as important nursery grounds (Heck et al. 2003). Australia's seagrass habitats support high diversities and abundances of invertebrates and fish, including many fishery species (e.g. Blaber and Blaber 1980; Edgar and Shaw 1995a; Haywood et al. 1995; Jenkins et al. 1997; Travers and Potter 2002).

In northern Australia, important fisheries species such as tiger (*Penaeus esculentus* and *P. semisulcatus*) and endeavour (*Metapenaeus endeavouri*) prawns use on seagrass beds as nurseries (Haywood et al. 1995). However, juvenile penaeids rely on different production sources depending on their position in the seascape; for example, in the Embley River, Cape York Peninsula, animals in seagrass habitats depend mostly on seagrass and their epiphytes, while those in macroalgae beds in mangrove creeks depend mostly on macroalgae and seston (Loneragan et al. 1997). Since penaeid prawns are a major prey for many fishery species including barramundi, bream and snappers (Robertson 1988; Salini et al. 1990), the nutrient flow from seagrass to these fish via penaeids must be significant. However, because penaeid prawns undergo important ontogenetic variations in diet (Abrantes and Sheaves 2009b), and can rely on different sources depending on habitat (Loneragan

et al. 1997; Abrantes and Sheaves 2009b), the sources of nutrition for penaeid juveniles and their predators is likely to be quite variable among regions.

Seagrass meadows are also important nurseries for other commercially important crustaceans such as blue swimmer crabs (Portunus pelagicus) and rock lobsters (Panulirus cygnus) in south western Australia. Juveniles of these species forage on invertebrates and plant material in seagrass meadows, but stable isotope studies have shown that macroalgae, rather than seagrass, is their main source of nutrition (Joll and Phillips 1984; Jernakoff 1987; de Lestang et al. 2000; MacArthur et al. 2011). However, different sized juveniles forage in different habitats, and as for penaeid prawns there can be variations in diet between sites and seasons (Joll and Phillips 1984). So, while the importance of seagrass production for these species will vary depending on the seascape context, seagrass could be an important production source during particular life-history stages.

Besides garfish (Hyporamphus spp.) (Edgar and Shaw 1995b; Carseldine and Tibbetts 2005; Tibbetts and Carseldine 2005), no other Australian commercial finfish species is known to feed substantially on seagrass. The primarily herbivorous luderick (Girella tricuspidata) also occur in seagrass habitats (Kingsford 2002) but feed mostly on macroalgae, with seagrass making only a small contribution to their diet (Clements and Choat 1997; Raubenheimer et al. 2005). Nevertheless, seagrass is directly or indirectly (through the detrital pathway) consumed by a range of macroinvertebrates, which are then prey for carnivorous fish such as flathead (Platycephalus spp.) whiting (Sillago spp. and Sillaginodes punctatus), and therefore contributes to important fishery food webs (Howard 1984; Robertson 1984; Hindell 2006). Indeed, stable isotope and fatty acid studies indicate that seagrass carbon is ultimately important for a range of fishery species including flathead in Victoria (Klumpp and Nichols 1983; Nichols et al. 1986), whiting in South Australia (Connolly et al. 2005), tarwhine (Rhabdosargus sarba) and whiting in Western Australia (Belicka et al. 2012), and queenfish (Scomberoides spp.) and trevallies (e.g. Caranx spp., Carangoides spp.) in Queensland (Abrantes and Sheaves 2009a).

Seagrass meadows also support high biomass of invertebrates that feed on seagrass epiphytes, in what appears to be a global phenomenon (Valentine and Duffy 2006). Some detailed work in Victoria showed

that these invertebrates form important prey for a diversity of fish species (Edgar and Shaw 1995b) and that these seagrass areas support much higher fish densities than adjacent unvegetated habitats (Edgar and Shaw 1995a), therefore indirectly supporting fish production (Edgar and Shaw 1995c). While these studies noted relatively low abundances of fisheries species in the studied habitats, seagrass support of fisheries is still likely to be significant as the abundant fish and invertebrates are likely important prey for fisheries species. Furthermore, detritus from seagrass meadows can be an important source of production supporting fishery species in adjacent habitats (e.g. Connolly et al. 2005; Heck et al. 2008; see section on Exchange of material between habitats, below).

Although similarly detailed understanding is lacking in many other regions around Australia, the trophic contribution of seagrass to fisheries is likely to vary between regions depending on the availability of alternate producers in the seascape, the extent and productivity of seagrass meadows, and the nature of consumer assemblages. For example, in Torres Strait (Queensland) and Shark Bay (Western Australia), where some of the largest seagrass areas in Australia occur, shallow and relatively clear waters mean that food webs rely mostly on benthic producers such as benthic microalgae and seagrass (Fry et al. 1983; Belicka et al. 2012; Speed et al. 2012). In systems like the relatively turbid Hinchinbrook Channel, however, seagrass productivity is limited by turbidity, so its relative importance is reduced and consumers rely on a combination of sources including seagrass, plankton, microphytobenthos, and mangroves (Abrantes and Sheaves 2009a).

Recent reviews have highlighted that despite considerable research effort around the world, gaps in our knowledge of seagrass food webs limit our understanding of their support of fishery species (e.g. Butler and Jernakoff 1999), and of the overall structure and function of seagrass ecosystems (Valentine and Duffy 2006). As for mangroves and saltmarshes, although seagrass production may be significant for only a limited range of fishery species, seagrass ecosystems appear to form critical components of coastal seascapes that support a diversity of fishery species.

Coastal rocky and coral reefs

Coastal reefs, including rocky reefs and fringing coral reefs, provide important habitat for many fisheries

species. Fringing coral reefs occur in tropical shallow waters, where they can extend as reef flats to the shore, and also around continental islands. These structures occur mainly along Western Australia, particularly in the Kimberly region and Ningaloo coast, in the Northern Territory and also in Queensland, especially along the eastern Cape York Peninsula (Short 2006) (Fig. 1e). Ningaloo Reef, in Western Australia, is Australia's largest fringing reef, reaching up to 1400 m in width, and stretching for 260 km along the coast (Short 2006). A range of primary producers is available in these areas, including micro- and macro-algae, and seagrass, supporting important fisheries such as rock lobsters (*P. cygnus* and *P. ornatus*), groupers and trout (Serranidae, particularly the coral trout *Plectropomus leopardus*), emperors (Lethrinidae), snappers (Lutjanidae) and sweetlips (Haemulidae). Despite the plethora of coral reef ecology studies in Australia and overseas, there have been no detailed and quantified food web studies on fringing reefs. As in other coastal systems, there are likely several trophic pathways in coral reef systems, based on different producers (planktonic and benthic microalgae, macroalgae and seagrass). For example, many species feed directly on reef macroalgae, including sea urchins and rabbitfish (*Siganus* spp.), sea chubs (*Kyphosus* spp.) and unicornfishes (*Naso* spp.) (Clements and Choat 1997; Hoey 2010; Michael et al. 2013), and these support some fisheries and are also important food for predatory fish such as emperors, groupers and sharks (Westera et al. 2003; Johansson et al. 2013), transporting this macroalgal carbon up the food chain. On the other hand, small planktivores (e.g. clupeids) are also abundant in the waters around reefs, and primarily from the base of the diet of pelagic carnivores such as scombrids, sphyraenids and carangids, in another important pathway. In a recent study in Ningaloo Reef, Wyatt et al. (2012) found that detritivorous and corallivorous fish species rely on benthic reef productivity throughout the reef width, while carnivores, herbivores and planktivores rely increasingly on oceanic productivity with distance from the shore. While a number of stomach content studies on coral reef fishery species are available (e.g. Connell 1998; St John 1999), the multiplicity of primary producers in close proximity makes it difficult to quantify the contributions of different sources for consumers, even if based on techniques such as stable isotope and fatty acid analysis (e.g. Wyatt et al. 2012). As a consequence, the relative balance of the various reef-based and pelagic production sources in supporting coral reef fishery species remains largely unknown.

Rocky reefs occur in <20 % of Australia's coastline (Fairweather and Quinn 1995; Fig. 1f), and are particularly abundant in temperate southern Australia, providing habitat for recreationally important invertebrate species such as abalone (*Haliotis* spp.), octopus (*Octopus* spp.) and rock lobster, and for fish such as luderick (*Girella* spp.), bream, tailor (*Pomatomus saltator*), morwong (*Cheilodactylus* spp.) and wrasses (*Notolabrus* spp.). The main sources of nutrition for rocky reef consumers will likely depend on factors such as hydrology, geomorphology and seascape characteristics. For example, in intertidal and subtidal rock flats, surfaces are often covered in algae, including turf and coralline algae, that are food for grazing invertebrates (e.g. gastropods, crabs) and fish (e.g. luderick, sea chubs, leatherjackets) (e.g. Jones and Andrew 1990; Guest et al. 2008). Sessile filter-feeders (e.g. sponges, ascidians, bryozoans, bivalves) are also common in these habitats, and feed mostly on plankton (Young 1990), providing a pathway to incorporate plankton-based production into local reef food webs. Similarly, other areas such as the western coast of south Western Australia, which is characterized by a series of limestone ridges that run parallel to the coastline, are dominated by macroalgae interspersed with unvegetated sand and seagrass meadows, also allowing different trophic pathways to co-occur. However, in regions such as in the Nullarbor Cliffs in the Great Australian Bight, Port Campbell (Victoria), around Sydney (New South Wales) and in southern Tasmania, vertical cliffs and high wave energy waters limit the areas suitable for attachment of sessile organisms, thus limiting the range of available producers and the number of possible trophic pathways. There, plankton is likely to have a greater importance than in shallow, low energy coastlines. However, in those regions, subtidal rocky reefs often support dense kelp forests (Steneck et al. 2002) that support important species such as rock lobsters, abalone, and snapper (Sparidae). While little is known about food webs on Australian rocky reefs, more detailed studies have been done elsewhere (e.g. Jennings et al. 1997; Fredriksen 2003).

Other habitats

Although mangroves, saltmarshes, seagrass meadows and reefs generally attract more attention and are most often considered in management (Beck et al. 2001; Harborne 2009), other habitats such as sand and mudflats and coastal pelagic habitats such as deeper areas of bays and off coastal headlands, for example, can also be important for a range of fishery species.

Sand- and mudflat habitats occupy a large proportion of Australia's coastal zone (Short 2006) (Fig. 1d) and include intertidal habitats like beaches, sand and mud banks in estuaries and coastal lagoons, as well as subtidal areas of consolidated and mobile sands and muds. In general, these habitats are characterised by limited macroscopic vegetation or other complex structure. The physical properties (e.g. wave energy, slope, grain size,) and seascape settings (assemblage of habitats available) play a major role in determining food web structure and the significance of local versus imported production in these environments (Degré et al. 2006; Bergamino et al. 2011). Large intertidal and/or subtidal sand and mudflats often occur adjacent to estuarine and lagoonal habitats such as mangroves, saltmarshes, seagrass meadows and reefs. Fish and invertebrates can move between habitats and this connectivity between habitats is important to maintain the ecological value of these systems (Sheaves 2009; Nagelkerken 2009). In some of these areas, high microphytobenthos productivity (MacIntyre et al. 1996) can support local food webs (e.g. Middelburg et al. 2000; Al-Zaidan et al. 2006; Galván et al. 2008; Shahraki et al. 2014) and even subsidize food webs in neighboring habitats through dispersal of suspended benthic microalgae produced on the flats (e.g. Yoshino et al. 2012). In other regions, however, fishery species in mudflats rely mostly on carbon imported from adjacent habitats such as seagrass beds (Melville and Connolly 2005; Connolly et al. 2005). The presence of a range of habitats dominated by different primary producers in close proximity and the movement of carbon through the seascape through water and animal movement means that food webs in these flats are likely to rely on a range of sources. The relative importance of each source will depend on the productivity of the different primary producers in the different habitats that constitute the coastal mosaic, as well as on the level of connectivity among habitats.

In beaches not associated to estuaries or lagoons, however, intertidal and subtidal flats are generally only neighbored by the terrestrial environment and open water habitats. Sandy beaches are often highly dynamic and provide little structural complexity (McLachlan and Hesp 1984; Robertson and Lenanton 1984), and so are unsuitable for many species. However, they can provide alternative habitats for some species generally associated with estuaries such as whiting and bream (Lenanton 1982; Robertson and Lenanton 1984; Lenanton and Potter 1987; Ayvazian and Hyndes 1995). Although high energy beaches have low in situ primary production (McLachlan and Brown 2006), in some areas high concentrations of diatoms accumulate in the surf zones (Campbell 1996) and can fuel local food webs, but to date no research has been done on the importance of these producers for fishery species occupying beaches in Australia or elsewhere. However, in most cases, food webs depend mostly on allochthonous inputs from offshore, from land and/or from other coastal habitats (McLachlan and Brown 2006). For example, detached macrophytes are often transported from distant areas and accumulate in surf zones, forming beach wrack, which is particularly abundant along the wave-dominated coasts of temperate Australia (e.g. Duong and Fairweather 2011). Much work on the importance of this wrack for aquatic consumers has been done in Australia (e.g. Lenanton et al. 1982; Crawley et al. 2006, 2009) and overseas (see review by Colombini and Chelazzi 2003). Macrophyte subsidies increase productivity in these otherwise nutrient poor and unproductive environments (Kirkman and Kendrick 1997), providing important food and habitat for macroinvertebrates (Ince et al. 2007) and fish (Lenanton et al. 1982; Robertson and Lenanton 1984; Crawley et al. 2006). Bacteria that break down beach wrack are responsible for most secondary production in these areas (McLachlan 1985). Benthic macrofauna, dominated by large populations of amphipods, with isopods and insects also present, is consistently more abundant on high-wrack beaches (McLachlan 1985; Ince et al. 2007). These invertebrates are in turn important prey for fish, including fishery species such as whiting, bream and Australian salmon (Lenanton et al. 1982; Robertson and Lenanton 1984; Crawley et al. 2006), forming short and simple food webs from macrophyte detritus through colonising microbes, to detritivorous invertebrates and fish. Because algae are generally more easily

assimilated than seagrass (Klumpp et al. 1989), the algal component of wrack is often preferred by detritivores (Crawley et al. 2009; Doropoulos et al. 2009). However, there are no quantitative estimates of the relative importance of the different wrack components and other sources such as marine plankton to fishery species that use these habitats. This importance is likely to vary both spatially and seasonally depending on factors such as wrack availability and species composition and abundance, as well as the assemblage of primary consumer invertebrates.

In coastal pelagic habitats such as deeper areas of large bays and off coastal headlands, mobile piscivores such as queenfish (*Scomberoides* spp.), mackerels (*Scomberomorus* spp.), trevallies (e.g. *Caranx* spp., *Carangoides* spp.), kingfish (*Seriola* spp.), Australian salmon (*Arripis* spp.) and sharks, especially Charcharinids, are some of the most important fisheries species. Some of these species, such as mackerels and Australian salmon, feed mostly on small pelagic prey such as clupeids and engraulids (Begg and Hopper 1997; Hughes et al. 2013), as part of strong plankton-based food webs. Others, such as queenfish, trevallies and sharks (Salini et al. 1994; Yick et al. 2012), feed on a range of pelagic and benthic fish and invertebrates. These deeper areas can also support high densities of important invertebrates such as penaeid prawns (Somers et al. 1987), cephalopods (Dunning et al. 1994) and scallops (Tracey and Lyle 2011). Depending on environmental factors such as depth, turbidity, substrate type and seascape characteristics, pelagic and benthic producers will have different contributions to food webs supporting these species in different regions.

Multiple trophic pathways, temporal variations in source contributions and cross-linking

Food webs in the different habitats often rely on various sources of nutrition, including local primary production (autochthonous sources) and material imported from adjacent habitats (allochthonous sources). The relative importance of these contrasting sources depends on the availability and assemblage of sources, and this partially depends on factors such as productivity and spatial distribution of habitats (Polis et al. 1997). Cross-linking between food webs is widespread, as material is transported from one habitat

to another and as consumers move among habitats (Nagelkerken 2009). Thus, multiple trophic pathways, with different strengths or importance, are generally present within a food web, and the relative strength of these pathways varies both spatially and temporarily at different scales.

Multiple trophic pathways and temporal variations in source contributions

Coastal food webs are generally composed by multiple food chains, based on different primary producers (e.g. Abrantes and Sheaves 2009a; Belicka et al. 2012). The different food chains generally have different contributions to the overall food web, and the relative importance of each pathway varies between species, depending on the relative contribution of different sources to their nutrition. There can also be spatial and temporal variations in importance of the different pathways, depending on ecological (e.g. changes in community assemblage) and environmental (e.g. temperature, salinity, water flow, turbidity) conditions. However, assessments of the contributions of different pathways to the nutrition of particular species are rare, and there is still no information on how important each trophic pathway is for fisheries species and productivity, or for preserving the resilience of the overall biotic community. While spatial differences in importance of the different pathways have been explored in a number of studies (e.g. Loneragan et al. 1997; Guest and Connolly 2006), few studies focused on temporal aspects, and those that have only considered short periods of time, often only two seasons (e.g. Connolly et al. 2009; Schlacher and Connolly 2009; Abrantes and Sheaves 2010). These temporal variations can however be of great importance because they can lead to variations in biomass of different species, including fishery species. Also, several species use coastal habitats only during certain times of the year, leading to strong seasonal differences in food web structure. Seasonal connectivity by animal movement can be an important driver of temporal variability in importance of different trophic pathways. In the coastal bays of southeast Tasmania, for example, almost the entire chondrichthyan assemblage, including the most important predators (some of which important fishery species), leaves over winter (Barnett and Semmens 2012), linking spatially separated food webs and significantly changing the

food web structure of their summer coastal habitats. This seasonal movement also means that these species rely on different primary producers in different seasons.

Despite the importance of understanding the temporal dynamics in food web structure, few studies considered this aspect in detail. While some stable isotope-based studies that incorporated a temporal aspect in their analysis found no evidence of differences in food web organisation between seasons (Nyunja et al. 2009; Shahraki et al. 2014), others found evidence of seasonal differences in food web structure (Degré et al. 2006; Bergamino et al. 2011; Vinagre et al. 2011; Abrantes et al. 2014a). Also, different anthropogenic impacts (e.g. deforestation of rivers' catchments, overfishing) have been found to affect the seasonality of main sources and trophic pathways fuelling fishery species (Abrantes et al. 2013, 2014a) and, consequently, food web structure (Abrantes et al. 2014a), with implications for fisheries management. For example, overfishing can have negative impacts over the overall food web organisation, affecting both targeted and non-targeted species, and its effects can be evident only years after the onset of impact (Jackson et al. 2001; Scheffer et al. 2005). The alteration of the natural temporal patterns of nutrient source and availability can also negatively affect recruitment of coastal organisms, affecting the whole food web, including fishery species (Barth et al. 2007). Understanding the responses of the different species' life-stages to the various impacts is essential for appropriate management as it helps us predict the effects of different human activities on fishery stocks.

Temporal variations in importance of the different trophic pathways occur not only because of natural seasonal patterns related to temperature and rainfall regimes (e.g. Vinagre et al. 2011; Abrantes et al. 2013), but also due to more sporadic events such as cyclones, due to human activities such as localised dredging, or localised inputs of nutrients and organic matter from agriculture or aquaculture, or due to temporal changes in community composition that result from animal migrations. Since different fishery species rely on different trophic pathways (e.g. piscivores such as queenfish and mackerel rely mostly on pelagic pathways, while benthivores such as flathead and whiting rely mostly on benthic pathways), different species will be affected differently by temporal changes in source availability (Abrantes

and Sheaves 2010). For example, the input of organic matter from the terrestrial environment during wet seasons leads to increased detritus availability, fuelling detritus-based food webs, as in floodplain pool habitats in North Queensland (Abrantes and Sheaves 2010). At the same time, an increase in nutrient availability stimulates aquatic primary (Waycott et al. 2005; Schlacher et al. 2008) and secondary (Connolly et al. 2009; Schlacher et al. 2009) production, fuelling algae-based food webs in estuaries and adjacent coastal areas. Increases in nutrient input from agriculture may also strengthen plankton-based food chains, supporting greater biomasses of zooplanktivorous, benthivorous and piscivorous fish (Gehrke 2007), while the resulting shading from increased phytoplankton biomass can lead to decreases in seagrass abundance (Carruthers et al. 2002) and consequent decrease of importance of this trophic pathway. In contrast, a reduction of nutrient inputs may lead to weaker pelagic and benthic trophic chains, leading to reductions in biomass of piscivores, benthivores, detritivores and herbivores (Gehrke 2007). This effect will vary between regions and systems, depending on the environmental settings of each area (e.g. Abrantes and Sheaves 2010).

All these fluctuations have implications for the spatio-temporal dynamics of biotic assemblages and, consequently, food web structure. For example, there are often large spatial and temporal variations in seagrass occurrence and abundance (Kerr and Strother 1990; McKenzie 1994; Lanyon and Marsh 1995). Temporal variations can be seasonal (Kerr and Strother 1990; McKenzie 1994), or result from episodic events like large floods and cyclones (Preen et al. 1995; Carruthers et al. 2002; Campbell and McKenzie 2004; Waycott et al. 2005), making seagrass contribution difficult to track and likely to vary by orders of magnitude over time. Variable seagrass availability can exert bottom-up control on consumer assemblages in seagrass areas and adjacent habitats, and even over the whole estuary (Hughes et al. 2009). For instance, in times of high seagrass abundance, there would be more nutrition available for both seagrass/epiphyte- and detritus-based food webs, fuelling detritus and benthic food webs. However, this would not affect planktivores in plankton-based food webs. Although this is an over simplistic view of the interactions among the different food web components, as many other factors affect this dynamic, this

shows how changes in the patterns of contribution from the different trophic pathways can lead to shifts in assemblage composition. The temporal variability in importance of different sources and consequent shifts in assemblage composition is however rarely included in food web studies. Estimates of biomass of the different trophic guilds are also almost non-existent for most regions, but are fundamental for a better understanding of the importance of different producers for fisheries production (Polis 1999).

Exchange of material between habitats

Different habitats are often interconnected by a number of physical, chemical and biological processes (Polis et al. 1997). For example, organic dissolved or particulate matter from vegetation and detritus moves between habitats via water movement (tides, currents, waves), and animal movement and trophic relays (i.e. chains of predator–prey interactions) also link food webs in different habitats (Bouillon and Connolly 2009; Grober-Dunsmore et al. 2009). Therefore, food webs within a habitat are often connected with those in other habitats.

Imported material

Imported material can support food webs in both productive habitats such as inshore reefs and seagrass and algal beds, as well as in unproductive habitats such as sandy beaches (Polis et al. 1997; Heck et al. 2008). Several studies from around Australia have identified important exchanges of material between distant aquatic habitats, e.g. subsidies of detached macrophytes fuelling food webs in otherwise unproductive beaches (e.g. Lenanton et al. 1982; Robertson and Lenanton 1984), in adjacent seagrass beds and in less productive inshore reefs inshore reefs (Wernberg et al. 2006; Vanderklift and Wernberg 2008; Hyndes et al. 2012), and seagrass subsidies supporting food webs in adjacent mudflats (Connolly et al. 2005, 2006). In Tasmania, seagrass detritus transported offshore during storms support larval stages of blue grenadier (*Macruronus novaezelandiae*) recruiting into coastal habitats (Thresher et al. 1992), forming an important energetic link between inshore and offshore habitats for a fishery species. Mass spawning of corals can also fuel pelagic and benthic food webs in adjacent habitats, as gametes and larvae are

consumed by planktivorous organisms (Westneat and Resing 1988; Pratchett et al. 2001), and the deposition of gametes on the sediments (Wolanski et al. 1989) serves as food for benthic consumers, representing an important nutrient subsidy to these habitats (Wild et al. 2008).

Coastal food webs can also receive important subsidies from the adjacent terrestrial environment (Connolly et al. 2009; Schlacher and Connolly 2009; Abrantes et al. 2013). For example, in North Queensland, terrestrial material transported from the Herbert River catchment is estimated to contribute 27 % of the total organic carbon input for the Hinchinbrook Channel, a contribution much higher than that of aquatic sources such as plankton and microphytobenthos, which together have estimated a contribution of only ∼17 % (Alongi et al. 1998; Alongi 2009). Freshwater flows allow the delivery of nutrients, organic matter and sediments from river catchments to the coastal zone, stimulating phytoplankton growth and fuelling phytoplankton-based food webs (McComb and Humphries 1992; Connolly et al. 2009; Schlacher et al. 2009), leading to increases in fishery production (Loneragan and Bunn 1999; Meynecke et al. 2006; Connolly et al. 2009; Gillson et al. 2009). Nevertheless, although several studies have linked freshwater flows to fisheries production of several species (see reviews by Gillanders and Kingsford 2002; Robins et al. 2005; Meynecke et al. 2006; Gillson 2011), the mechanisms responsible for these relationships are not yet clarified for the great majority of species. Because freshwater flows are highly seasonal, there is also strong seasonality in importance of different sources to coastal food webs. Other scales of temporal variability also affect this energetic connectivity, including interannual variations related to large floods and cyclonic events, or to the El Niño/ La Niña-Southern Oscillation (ENSO). Identifying and understanding the different links is important for fisheries management as the disruption of connectivity either by changing the strengths of the linking agents (e.g. changes in currents due to ENSO events), by breaking the links (e.g. by construction of barrages that limit runoff of terrestrial nutrients from catchment to coastal habitats) or by altering productivity of the donor habitat can compromise the trophic support of fishery species in receiving habitats, negatively affecting fisheries by reducing recruitment and/or survival.

Animal movement

Animal movement can link spatially separated food webs at a range of spatial and temporal scales, from small dial migrations between adjacent habitats to broader scale migrations, e.g. by moving between foraging and spawning/mating grounds, by seasonally moving into coastal areas to exploit temporarily abundant prey or even by leaving these areas to avoid seasonal fluctuations in environmental conditions (Polis et al. 1997; Grober-Dunsmore et al. 2009; Hyndes et al. 2014). Furthermore, many fishery species shift habitats during ontogeny, even if remaining within the same system (Grober-Dunsmore et al. 2009; Hyndes et al. 2014; Nagelkerken et al. 2013).

At smaller spatial scales, many fishery species often move relatively small distances (up to 10 s of meters) between adjacent habitats. For example, during high tides, many species move into previously unavailable mangrove and saltmarsh habitats to feed (e.g. Sheaves and Molony 2000; Meynecke et al. 2008b; Krumme 2009), while others migrate daily between sheltering habitats such as mangroves and reefs to feed on sand/mud, seagrass or algal habitats at night (Linke et al. 2001; Verweij and Nagelkerken 2007; Nagelkerken et al. 2008; Hyndes et al. 2014). These migrations may be important to fuel food webs in sheltering habitats (Layman et al. 2011; Hyndes et al. 2014). Although opportunistic feeding is also likely to occur in sheltering habitats most nutrients are likely transferred in the foraging to sheltering habitat direction (Nagelkerken and van der Velde 2004; Verweij et al. 2006).

At larger spatial scales, the migration of some species to reproductive sites can be an important vector of connectivity across marine habitats, as nutrients are transported in the gametes and adult fish biomass moving to and from reproductive areas (Nemeth 2009). Many fishery species aggregate to spawn (Sadovy de Mitcheson et al. 2008), including female mud crabs (*Scylla serrata*), which in Australia migrate up to 95 km from estuarine habitats to offshore spawning sites (Hill 1994) and king prawns (*Penaeus plebejus*), which can migrate over 1000 km from their estuarine nursery grounds into offshore waters (Ruello 1975; Montgomery 1990). Other species like anchovies (*Engraulis australis*) and pilchards (*Sardinops sagax*) move into estuaries and bays to spawn (e.g. Hoedt and Dimmlich 1995; Hoedt

et al. 1995), representing an import of carbon from offshore. In the spawning areas, adults contribute to local food webs by becoming prey for larger predators, and by supplying food to smaller species via their gametes and larvae (Nemeth 2009). These gametes and larvae enter local food webs via consumption by resident planktivores and can also contribute to neighbouring or distant food webs through dispersal via currents. Adults also contribute to local food webs by feeding while at the spawning sites. The interactions between migrants and local food webs vary depending on their trophic ecology, ecological requirements, and the length of time they spend in the spawning area (Nemeth 2009).

Spawning aggregations are vulnerable to fishing pressure, and a high proportion of these aggregations is in decline (Sadovy de Mitcheson et al. 2008). Moreover, and because overfishing at spawning sites can affect food webs in all involved habitats, understanding the importance of these energetic connectivities is critical for the management not only of the spawning species, but also of other fishery species that are part of food webs in the different habitats involved. Protecting spawning aggregations can therefore benefit not only the population of the spawning species, but can also maintain food web stability in multiple habitats by ensuring the preservation of important connectivity.

Like spawning, larvae and juvenile recruitment into coastal habitats represents an input of offshore carbon into coastal food webs and is therefore also a vector of connectivity between habitats (Deegan 1993; Beck et al. 2001). For example, the recruitment of penaeid prawns (e.g. *Penaeus* spp. and *Metapenaeus* spp.), portunid crabs (e.g. *Portunus* spp. and *Scylla serrata*), and fish such as clupeoids (e.g. *S. sagax* and *E. australis*), eels (*Anguilla* spp.), tarwhine (*R. sarba*) and snappers (*Lutjanus* spp.) (Dall et al. 1990; Robertson and Duke 1990; Smith and Suthers 2000) from offshore or coastal reefs into estuaries may constitute important seasonal subsidies of marine carbon to estuarine food webs (Baker and Sheaves 2009). Since flooding regime and magnitude affect recruitment, survival and growth of several species (Robins et al. 2005), this input is likely to vary in importance between years. In the opposite direction, ontogenetic inshore-offshore movements of species such as snappers (*Lutjanus* spp.), groupers (*Epinephelus* spp.) (Sheaves 1995) and some sharks

such as the blackip reef shark *Carcharhinus me-lanopterus* (Chin et al. 2013), represents a transfer of nutrients accumulated in their biomass during their juvenile phase to offshore habitats (Hyndes et al. 2014). Additionally, some species seasonally move into coastal areas to feed or breed (e.g. Begg and Hopper 1997; Barnett et al. 2011) and, when leaving, export coastal nutrients in their biomass to offshore food webs, increasing connectivity between inshore and offshore regions.

There can also be important connectivities between coastal food webs and their adjacent terrestrial habitats. The transport of terrestrial invertebrates (e.g. ants, spiders, grasshoppers) into coastal habitats with the wind and flood waters can subsidize the diets of carnivorous aquatic species (Nakano et al. 1999; Balcombe et al. 2005), while seasonal floods allow the connectivity between habitats such as main channels and floodplain wetlands, providing an opportunity for animals to move into different habitats and access different sources (e.g. Sheaves and Johnston 2008; Abrantes and Sheaves 2010). Vertebrates such as birds and fruit bats are also important connectivity agents in coastal areas. These are highly mobile and often use habitats such as mangroves, saltmarshes and dunes to nest, roost, feed, or as refuge (Palmer and Woinarski 1999; Kutt 2007; Spencer et al. 2009). Since most of these species use other habitats for feeding (e.g. intertidal flats, rainforests, marine-pelagic waters), their movements allow the transport of nutrients between spatially separated food webs (Nagelkerken et al. 2008; Huijbers et al. 2013). For example, piscivorous birds like herons, egrets and sea eagles can link food webs across distanced systems (e.g. between estuarine and freshwater reaches, coastal and marine-pelagic environments, or between distanced estuaries). For bats and birds that roost/nest in mangrove forests but forage in different habitats, for example, their feces can constitute an important nutrient subsidy to mangrove habitats, enhancing the productivity of these areas (Onuf et al. 1977). The importance and strength of these energetic links will vary seasonally, depending on migratory/reproductive cycles of the different species. These different types of subsidies and connectivities are potentially very important for the different receiving habitats and the fisheries they support (Meynecke et al. 2007, 2008a; Sheaves 2009).

Critical knowledge gaps on the trophic support of coastal habitats to fishery species

It is evident that the definition of what constitutes a habitat varies among studies, as habitats are often defined at very different spatial scales depending on the context of each study. For example, *marine habitats* could be anything from the vast open ocean to the roots of mangrove trees. The issue of differences in scale considered was most apparent in estuaries, where some studies were made at the scale of the overall system, with data from all its different habitats considered together, while others focused on defined habitats separately, e.g. on the mangrove or seagrass habitat. For appropriate management of fishery species, we suggest that studies should be made at this habitat scale, e.g. at the mangrove/saltmarsh/seagrass level, rather than at whole estuary level whenever possible. This scale considers discrete and easily identifiable habitats that can function as ecological units, in a hierarchical framework (Guarinello et al. 2010). By collecting data at this scale, a more complete understanding of habitat use and food web processes can be obtained, and information can be later scaled up to the system level if more appropriate for management. Extrapolation in the opposite direction is not possible, i.e. it is not possible to estimate food web contributions to species from each individual habitat based on information from the overall system. A greater understanding of habitat use and food webs at the appropriate scales means that offsets such as habitat protection can be better directed. Although habitats can be further broken down into smaller units, e.g. forest edge of the mangrove habitat, these are likely too small to lend themselves useful to most management applications.

While there are examples of where we have a good understanding of food webs supporting fishery species (e.g. the USA saltmarshes, as described in the "Introduction" section), for many species our understanding remains deficient across a range of issues. Throughout this review on the situation for Australian fishery species, many knowledge gaps related to the trophic function and use of coastal habitats were identified, which need to be filled for a complete understanding of food webs from specific habitats. The most critical gaps are presented below. The first three refer to the most basic gaps, which need to be filled before more complex issues (gap 4 onwards) can

be addressed. Because of the patchy nature of our understanding, it is not possible to generalise about the priority of each gap, since different management concerns will face varying critical knowledge gaps depending on the species, location, and context. However, the gaps we identify are those that we consider represent the greatest hindrance to the effective sustainable management of coastal fishery species around Australia. In many cases these gaps are also relevant for fisheries management elsewhere in the world. Where appropriate, we propose the best way forward to addressing these gaps. Given the immensity of work involved to fulfill these gaps for all species and habitats, it is unrealistic to claim that such knowledge can be achieved for all species and habitats, given the resource limitations. However, efforts can be focused in specific studies depending on the fishery and on the management question in hand.

Basic dietary information is lacking for many species

Basic dietary information is missing for many species, and available studies rarely cover a size range that accounts for ontogenetic variations in diet or provide information on the habitat-specific diets of small (<5 cm) juveniles. Dietary data is generally obtained using stomach content analysis and gives information on the most important food items and on the food chains the different consumers are part of. This is important for management because of the need to protect critical resources to preserve fisheries species. For example, if shrimps found in seagrass beds are a major component of the diet of a fishery species, then seagrass beds, along with its shrimps, should be considered a high value habitat to be preserved. Dietary data is needed not only for the relevant fishery species, but also for other species that are part of their food web. Indeed, dietary composition of competitors and predators is also important as competition and predation affect mortality and population sizes of targeted species (Walters et al. 2008), with obvious implications for management.

Largely unknown range of habitats used by different life-cycle stages

Basic information on habitat-related distribution of fishery species is lacking for most coastlines, but this

information is fundamental for understanding the importance of the different components of the seascapes. Despite that the availability, quality and spatial distribution of habitats used at the different life stages are the primary determinants of a system's contribution to fisheries (Sheaves et al. 2015), even for the most well studied regions, basic information on habitat use, either for food, shelter, or reproduction, is still lacking for most species, resulting in an incomplete understanding of habitat needs and major gaps in knowledge about key food resources used by those life stages. For example, even for the well-studied Gulf of Mexico salt marshes, there is still uncertainty on the relative importance of threatened habitats supporting some of the most important fishery species (Minello et al. 2008; Fry 2008). This information is fundamental to determine which habitats need to be prioritised in conservation and management. Basic surveys using sampling techniques such as netting and trapping can be used to address this gap.

Geographic patchiness of available data

While a good understanding of fishery food webs is available for some areas, habitat and food web research is incomplete and irregularly distributed around Australia and around the world, meaning that the available data are geographically patchy, both within and among regions. Since the nature of food web organisation and the patterns of temporal change vary greatly throughout the world depending on environmental conditions, generalisations, extrapolations and spatial and temporal comparisons need to be done carefully.

Importance of different producers to fishery species

Since much of the value of habitats is derived from their ability to provide food, precise understanding of both the main habitats (e.g. seagrass meadows) and specific primary producers within each habitat (e.g. seagrass epiphytes) supporting the different life-stages of the different species is paramount. For example, when a species relies mostly on material transported from an adjacent habitat for nutrition, it is important to also preserve that donor habitat even if that particular species does not occur in it. Most of the available trophic data are based on gut content analysis but

although this method gives important information on the ingested material, it does not identify the sources of nutrition at the base of the food web. Methods such as stable isotope and lipid analyses can provide quantitative estimations on the contribution of different producers to nutrition of fishery species and should be used in combination with stomach content data for a more precise identification of the ultimate sources of nutrition and specific habitats used for feeding. These methods need however to become more accessible and widely used. Because of the frequent similarities in stable isotope and/or fatty acid composition between primary producers it is often impossible to separate the importance of all sources. More advanced techniques such as stable isotope labeling and compound-specific stable isotope analyses have the potential to provide more precise estimates, but these are technically difficult and expensive, and so rarely used.

Deficient understanding of the required physical connectivities between habitats

Most coastal fishery species require the access to a range of habitats for appropriate nutrition and/or refuge (e.g. access to intertidal mangroves and to subtidal mud banks), and the required assemblage of habitats can vary between life-cycle stages. This means that those species can be part of different food webs and link spatially separated food webs. It is thus important to have a good understanding of the required physical connectivity between habitats, at appropriate spatial and temporal scales, but this aspect is often not considered. Studies based on tracking using biologgers (e.g. acoustic tracking) or on biogeochemical tracers (e.g. stable isotope analysis) can be useful to determine the movements of animals throughout the seascape and, therefore, to identify the required physical connectivity between habitats. This information is crucial for fisheries management as it will allow identifying the habitats and physical connectivities that need to be preserved to maintain recruitment and survival of the different live stages of fishery species.

Deficient understanding of the energetic connectivities between habitats and their importance for fishery food webs

Throughout the world, degradation of coastal habitats and their connectivities is ever increasing, e.g. with the construction of barriers that prevent salt intrusion or increase the area of usable land, roads that cut off wetlands from their estuaries, or dams that prevent movement of carbon and animals between freshwater and estuarine reaches. Despite the recognised importance of energetic connectivity and subsidies for several systems, few studies attempted to identify and quantify these linkages in food webs supporting fishery species. It is also important to determine the regulating mechanisms controlling these connectivities, the spatial and temporal variability in this importance and the effect of this variability on the overall food web structure. Energetic connectivities can be studied using biogeochemical tracers such as stable isotope and lipid analysis. These techniques are however only useful if the differences in stable isotope/lipid composition between primary producers in the different habitats involved are large enough to allow for the differentiation on energy sources. Although addressing this gap likely requires expensive long-term studies, this information is paramount to determine the habitats involved in nutrition provision and has therefore management implications. For example, if inputs or organic matter from terrestrial catchments are important for a fishery species, then modification or loss of connectivity has implications well beyond the ecosystems occupied by the fishery species, and may have negative impacts on the sustainability of the fishery.

Temporal variability in source availability and importance generally not taken into account

In natural systems, there can be strong temporal variability in source availability and productivity and, consequently, in importance of different sources to fishery food webs. This variability can operate at different scales and affect different species and life-cycle stages differently. Temporal variability in importance of different sources is however rarely included in food web studies as funding cycles generally do not allow research over many years. To address this gap, surveys on the availability, relative abundance and productivity of the different producers, conducted at different times of the year, can be used to determine the temporal variability in source availability, while stable isotope and lipid analysis can be used to estimate the temporal variability in relative importance of these producers to the different

consumers. Although undoubtedly challenging, this is an important gap to fill as it will allow the identification of most important habitats throughout the year. Indeed, information obtained during one season does not necessarily reflect the processes in the other seasons of the year particularly for regions with strong seasonality in environmental conditions (e.g. wet vs. dry season in the tropics).

Biomass estimates

One of the most basic and yet challenging tasks facing the construction of detailed food webs is a clear understanding of the distribution of biomass among different components of the food web. In many ways, fisheries management is focused on biomass, the yield of fish biomass available for harvest. The food webs supporting fishery species represent the flow of biomass through the system. Estimating the biomass of even a single species is challenging enough, yet detailed food webs require data on the biomass of each major link in the system to properly evaluate the significance of different sources, pathways, or trophic interactions in regulating energy flow and population sustainability. Without biomass estimates, it is not possible to quantify the carbon moving through the different trophic pathways even with the use of biogeochemical tracers.

Conclusion

Although coastal habitats are important to many fish and invertebrates, the diversity of coastlines means that there are substantial differences in the way this importance is manifested, including in types and degrees of provisioning and function throughout the different species' ontogeny. Understanding the food resources and trophic linkages that support all life-stages of fishery species in the different habitats is critical for their sustainable management, especially for species that participate in food webs that span several habitat units commonly considered in management. This means that information on the trophic importance of the contributions of the different habitats, as well as on trophic relationships between the key consumers and on how these vary over space and time, is essential. This level of detail is however still not well understood for most coastal seascapes. As

a consequence, models of estuary functioning, evaluations of status and vulnerability, and understanding of ecosystem value are usually extrapolated from other studies, often from systems separated by large distances and with unknown physical or biological similarities to the estuary in question. This can lead to the mismanagement of fishery species and/or used habitats. This review identifies eight critical gaps in our understanding of habitat-specific food webs supporting coastal fishery species, and proposes future research directions to address these gaps. Given the ever-increasing transformation of coastal landscapes, either by direct human action or by sea level rise and changing climatic patterns (Worm et al. 2006; Poloczanska et al. 2007; Koehn et al. 2011), the effective management and mitigation of the diverse impacts requires a greater recognition and understanding of the complexity of the ecosystems (Harris and Heathwaite 2012) that support valuable fisheries and basic food security for people around the globe.

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