

Benthopelagic coupling in Commonwealth Marine Reserves

Report to the Department of the Environment

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1 Introduction

Parks Australia is providing secretariat support to independent panels undertaking the Commonwealth Marine Reserves Review. The Review's Expert Scientific Panel (ESP) has requested a report about the current state of knowledge in relation to the extent to which the pelagic ecosystems are functionally linked to the benthic/demersal realm across the range of environments that are protected in the CMRs.

This brief assessment focuses on several key questions:

- What is the current state of knowledge about the relationship between pelagic and benthic/demersal environments in Australian waters (excluding inner shelf environments)?
- At the spatial scale of relevance to CMR zones, what habitats/communities are characterised by benthic-pelagic coupling?
- What pelagic species/communities are involved in linking benthos and the water column and how are they generally distributed within the CMRs estate e.g. shelf edge - upper slope environments?

We also include:

- A brief summary of existing observational and modelling information on benthic-pelagic links on outer shelf, upper slope, seamounts, submarine canyons and other key large scale features from across Australia represented in Commonwealth Marine Reserves. This assessment is supported by graphic/diagrammatic illustrations of relevant processes/relationships.
- An overview of key gaps and uncertainties in relation to the point above.

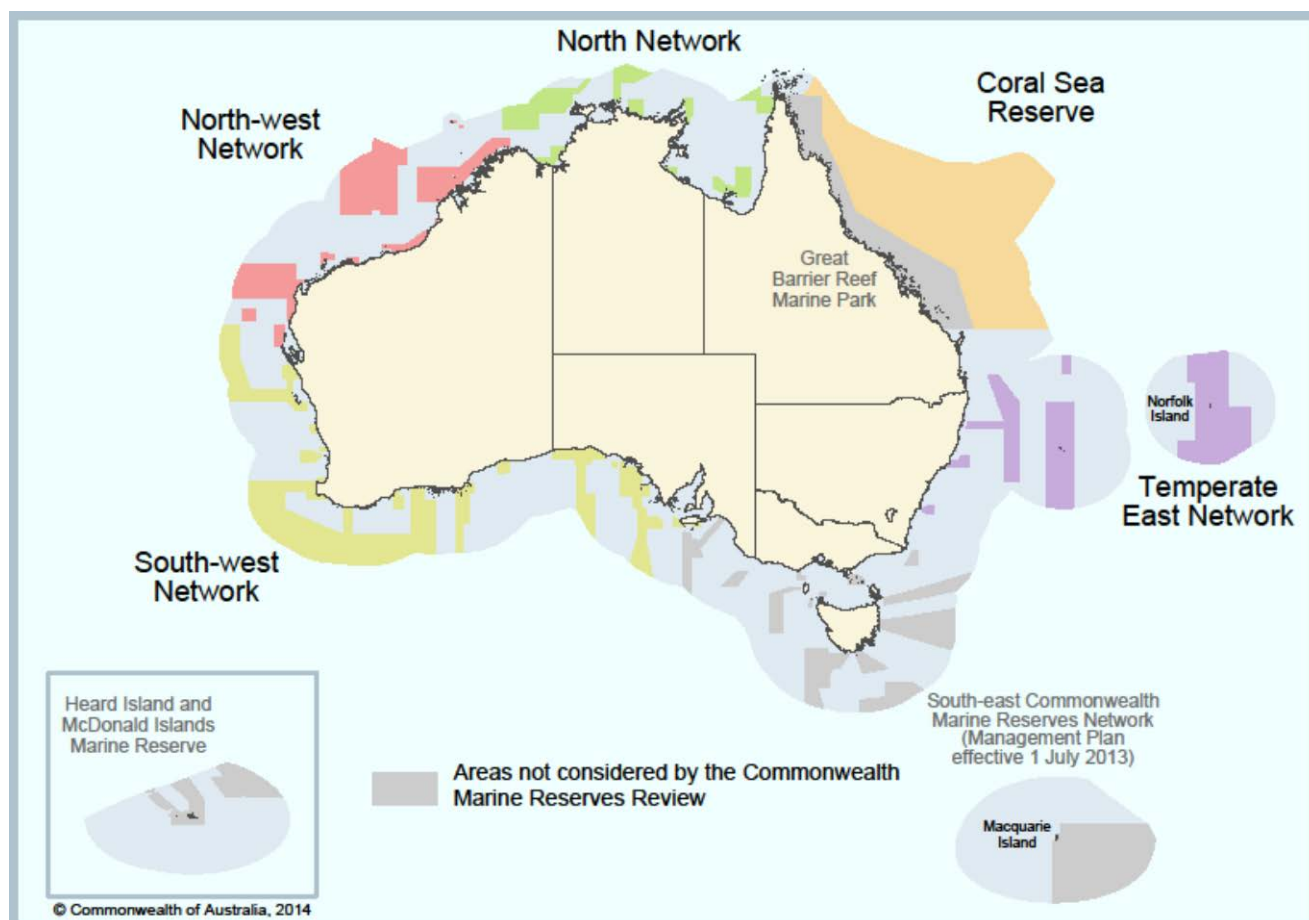
This assessment is necessarily limited due to time restrictions and may not have captured all recent and current research that could address these issues nor is it a comprehensive review of all global literature. We have however sought to provide a broad assessment to the best of our knowledge.

We thank Derek Fulton for modifying figures, Trevor Hutton and Franzis Althaus for providing valuable assistance and information at short notice.

2 Current state of knowledge

In 2007, 14 marine reserves were proclaimed in the South-east Commonwealth marine reserves network under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act). Six years later in 2013, a further 14 marine reserves in the South-west, 13 in the North-west, eight in the North and eight in the Temperate East networks and the Coral Sea Marine Reserve were proclaimed. There are now 59 Commonwealth marine reserves, 58 of which are managed by the Director of National Parks (Figure 1).

Figure 1 Australia's network of marine reserves under review



Source: <http://www.marinereservesreview.gov.au/resources> : accessed 20 May 2015

Extensive research and syntheses of existing data were conducted for each of the marine reserve regions as part of the planning process and this body of information is available on the Department of the Environment website. The large volume of Australia's EEZ has led to an array of opportunistic sampling locations, incrementally building up a view of the many different parts of the marine systems around Australia. The depth, remoteness and extent of the outer shelf and slope system mean that it does not get the same attention as the epipelagic (surface ocean) or near shore waters. Consequently, the observational information relating to processes in deeper waters and how they link to the surface ocean has not grown much in the last 10-15 years. Biodiversity sampling has occurred in new areas (e.g. off the Gascoyne coast of Western Australia) but sampling for process understanding is rarer. Consequently, in this report, we draw on the research reports and assessments used in the marine reserve planning process and supplement it

with the small amount of other literature available for Australian waters. Given resource constraints on this summary work we focus on the reports that discuss trophic system descriptions that illustrate benthic-pelagic coupled systems and, where possible, where or how those systems are situated in relation to the key features of the marine reserves and bioregion more generally (Table 1).

Table 1 Key Ecological Features (KEFs) identified by Dambacher *et al.* (2012a) and features included in proposed reserves

NETWORK	KEY FEATURES	FEATURES INCLUDED	SPECIES OF CONCERN
South-east	East Tasmanian Subtropical Convergence Zone, Bass Cascade, upwelling east of Eden, West Tasmania Canyons, Big Horseshoe Canyon, Seamounts south and east of Tasmania, Bonney Coast upwelling, shelf rocky reefs and hard substrate	10 provincial bioregions and 17 seafloor types	Southern right, blue, fin, sei, humpback whales, Australian sea lions, white shark, Harrison's dogfish, killer and sei whales, Australasian gannet, fairy prion, black-faced cormorant, little penguin, crested tern, several species of seal, penguin, albatross, petrel, shear-water and gulls
South-west	Waters surrounding the Houtman Abrolhos Islands, Recherche archipelago, waters within and adjacent to the west coast inshore lagoon and Geographe Bay, Perth, Kangaroo Island Pool and Albany Canyons and adjacent shelf breaks, Eyre Peninsula and Cape Mentelle upwellings, Naturaliste Plateau, Diamantina Fracture Zone, ancient coastline between 90 and 120 m depth, meso-scale eddies, demersal slope and associated fish communities of the Central Western Province, benthic invertebrate communities of the eastern Great Australian Bight, small pelagic fish of the south-west marine region, western rock lobster	Nine provincial bioregions, nine meso-scale bioregions, 69 depth ranges within provincial bioregions and 16 seafloor types	Southern right, blue, humpback, sperm and killer whales, Australia sea lion, white shark, Indian yellow-nosed albatross, soft-plumaged petrel and migratory seabirds
North-west	Carbonate bank and terrace system of the Sahul Shelf, pinnacles of the Bonaparte Basin, Ashmore Reef and Cartier Island and surrounding waters, Seringapatam Reef and waters of Scott Reef complex, Mermaid Reef and waters around Rowley Shoals, waters adjacent to Ningaloo Reef, demersal fishes on the continental slope, ancient Coastline at 125 m depth contour, canyons Linking the Argo Abyssal Plain and Scott Plateau, and the Cuvier Abyssal Plain and the Cape Range Peninsula, Exmouth Plateau, Wallaby Saddle	Eight provincial bioregions, nine meso-scale bioregions, 81 depth ranges within provincial bioregions, and 15 seafloor types	Olive ridley, green, flatback, loggerhead and hawksbill marine turtles, whale shark, sea snakes, sawfish, migratory seabirds, Australian snubfin dolphin and humpback whales
North	Basin, coastal zone and submerged coral reefs of Gulf of Carpentaria, carbonate banks and terraces of Van Diemen Rise, terraces and pinnacles of the Bonaparte basin, plateau and saddle north-west of the Wellesley islands, shelf break and slope of the Arafura Shelf, tributary canyons of the Arafura Depression	Four provincial bioregions, 14 meso-scale bioregions, 22 depth ranges within provincial bioregions, and 15 seafloor types	Flatback, hawksbill, green and olive ridley turtles, dugongs, migratory seabirds
Temperate East	Shelf rocky reefs, Lord Howe, Tasmantid and Norfolk Ridge seamount chains, upwelling off Fraser Island, Elizabeth and Middleton Reefs, canyons on the eastern continental slope,	Six benthic/demersal and 1 pelagic KEFs, seven provincial bioregions, three meso-scale bioregions, 73 depth ranges within provincial bioregions,	Grey nurse sharks, white shark, Bleekers devil fish, the little tern and other seabirds

NETWORK	KEY FEATURES	FEATURES INCLUDED	SPECIES OF CONCERN
	and the Tasman Front and eddies.	and 15 seafloor types	
Coral Sea Reserve*	Reefs, cays and herbivorous fishes of the Queensland and Marion Plateaux, Tasmantid seamount chain	Three KEFs, all six provincial sub-regions, all 94 depth ranges, all 16 seafloor types.	

*was not identified as a separate region in Dambacher *et al.* (2012a).

2.1 South-east Marine Region: a case study of benthic-pelagic trophic connections

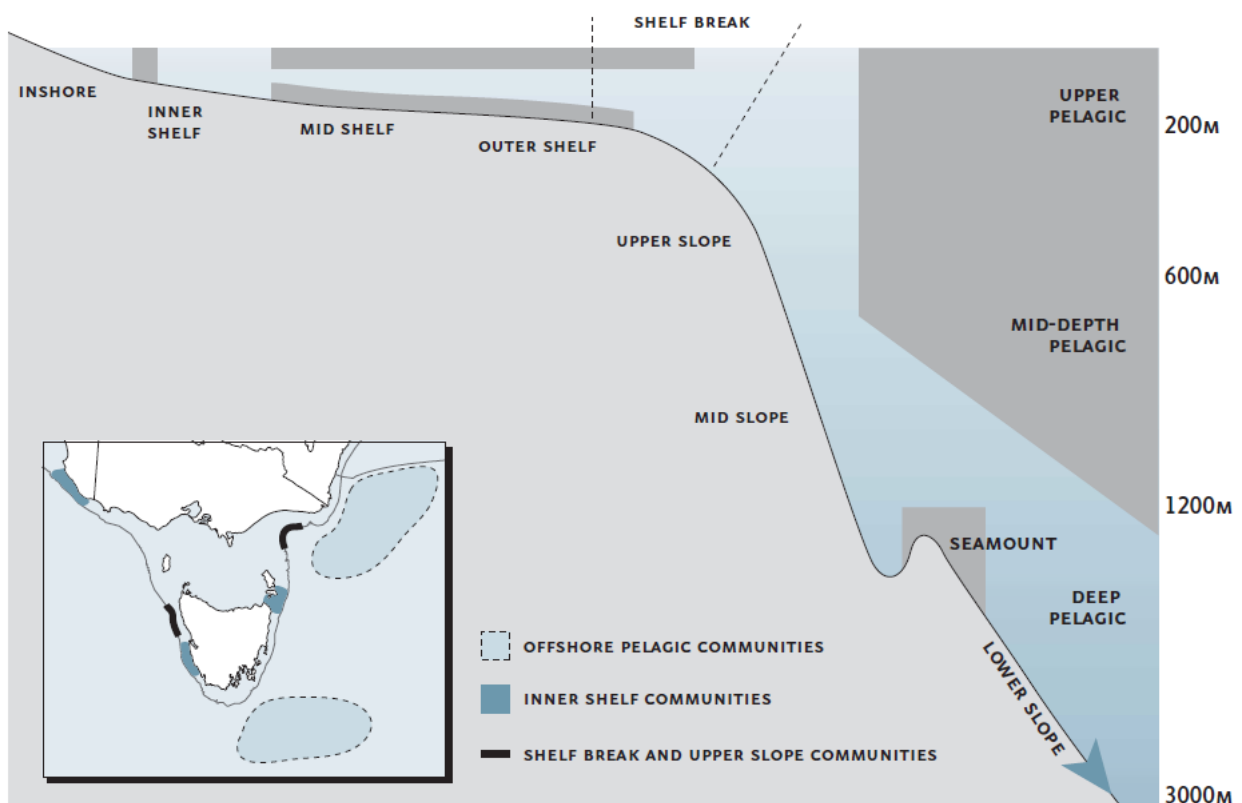
The South-east Marine Region was the first region for which a marine plan was developed. The Assessment report for this region (National Oceans Office 2002) focussed on providing ecosystem-based input into the planning process and thus is the first synthesis of all biological, oceanographic and geological information that was available at the time for this region. While this region is not part of the Marine Reserve Review the assessments of ecosystem structure and function and the synthesis of data into conceptual models illustrating the dynamical ecosystem processes are relevant to this investigation in the absence of region-specific knowledge. This is because the south-east region is perhaps the best-known region in Australia and is thought to be indicative of general patterns that are likely to hold more broadly along the shelf-slope edge of Australia. Where information on a specific region is available it is provided in the following sections and they support the view that the general form displayed in the south-east region is representative. However, it is important to note that much of this information is more than 1-2 decades old and that climate related processes may have shifted (or even added or removed) connections. Until dedicated process studies occur around Australia – either to fill gaps where no such studies have occurred or to update past studies for new ocean conditions – the summary presented here will have a high degree of associated uncertainty. Nevertheless it is the best possible given existing information.

The conceptual models available in National Oceans Office (2002) for the south-east marine ecosystems cover the benthic inshore and inner shelf (0-60m); benthic mid and outer-shelf (60-200m); benthic slope (200-3500m) and pelagic over the shelf, shelf-break and slope (Figure 2). For any readers interested in specific details, further background and key references on these conceptual models are available in National Oceans Office (2002). The report did not describe or illustrate all ecosystem types nor was the coupling of the benthic and pelagic sub-systems explicitly illustrated therefore we will address these.

The characterisation of shelf ecosystems in southern Australia was drawn largely from a study on the southeastern Australian shelf from Wilson's Promontory to Bermagui by CSIRO in the early 1990s (Bax and Williams 2000). This study was complex and multidisciplinary aiming to understand the sources of primary production in the southeast corner of the continental shelf and how this production supported the commercially important fish in the region (Bulman *et al.* 2001). Isotopic analyses of 87 species of fish, marine mammals, penguins, invertebrates, algae, suspended particulate organic matter (POM), and sediments confirmed the main source of primary production in south-east Australia as oceanic phytoplankton, although there was some evidence of a seagrass contribution to the benthos (Davenport and Bax 2002). In terms of diet, over 70 species of demersal fish were examined to determine the contribution made by pelagic *cf* benthic prey. About half of the fish species ate pelagic prey; moreover, nearly two-thirds of the

commercial species—18 of 28 species—ate pelagic prey. While pelagic prey were not always dominant for all the species, and at all locations and times sampled, the presence of pelagic prey in the diets of demersal fish indicates that a link exists. Modelling (e.g. using Atlantis; Fulton *et al.* (2014), Johnson (2011), Smith *et al.* (2011)) indicates that the strength of the link may vary through time and space depending on the state of other ecosystem components (e.g. the depletion of mesopelagic fish increases the dependence of demersal fish on other prey sources, including pelagic prey species; Johnson 2011, Smith *et al.* 2011).

Figure 2 General ecosystem subdivisions for the South-east Marine region



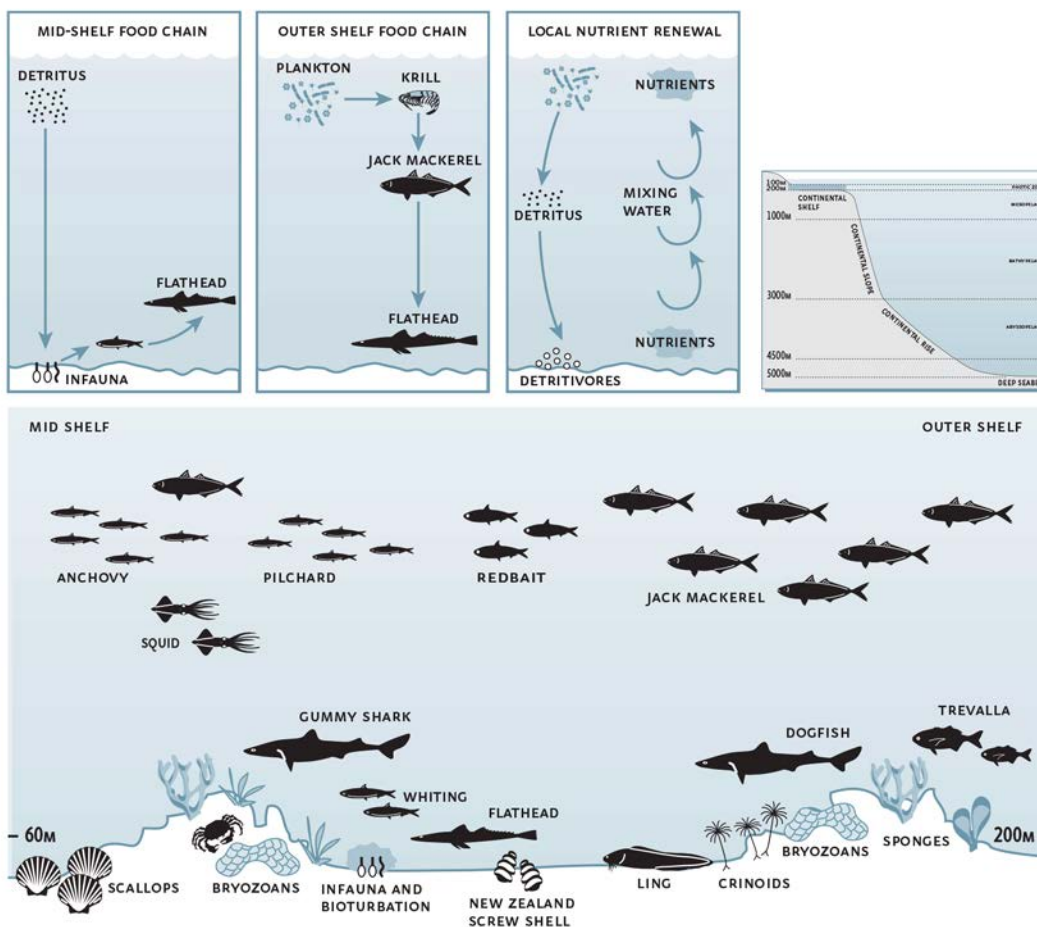
Source: National Oceans Office (2002) reproduced with permission from Department of the Environment.

On the shelf the links between pelagic prey and benthic/demersal predators begins with small to medium-sized pelagic fishes e.g. Australian sardine *Sardinops sagax*, anchovy *Engraulis australis*, jack mackerel *Trachurus declivis*, redbait *Emmelichthys nitidus*. These species commonly eat a wide variety of small and large phytoplankton and zooplankton and represent the most obvious and direct pelagic trophic pathway (Figure 3) which has been well-studied elsewhere in southern Australia (Goldsworthy *et al.* 2013, Ward *et al.* 2006). These “small pelagics” in turn are eaten by a wide variety of species (and trophic levels) from squid and fish through to seabirds and marine mammals thus splitting the trophic pathway across several domains - pelagic, benthopelagic, benthic and terrestrial. Small pelagics also support large fisheries e.g. South Australian Sardine Fishery and to a lesser —and more variable— extent, the Small Pelagic Fishery. Apart from the small pelagic fishes, pelagic prey taken on the shelf also includes **mesopelagic fish** e.g. the myctophids Hector’s lanternfish *Lampanyctodes hectoris* and Dana lanternfish *Maurolicus muelleri*), cephalopods (squid) and gelatinous nekton such as pyrosomes and salps

(Bulman *et al.* 2001) which are usually associated with more offshore pelagic ecosystems (Figure 4).

In addition to these fish based links, the information and qualitative models developed by Hosack *et al.* (2012) indicates that in locations like the Bonney upwelling, euphausiids and other planktonic prey (e.g. copepods) are prey of benthic invertebrates, which in turn are the prey of sedentary benthic predators and mobile benthopelagic predatory fish. This indicates that the links between pelagic and benthic/demersal systems can be physically moderated by vertical migration and sinking (plankton, small detrital rain and larger items such as whale carcasses) rather than simply connecting in trophic level steps across depths.

Figure 3 A conceptual model of pelagic shelf ecosystem in the South-east Marine Region

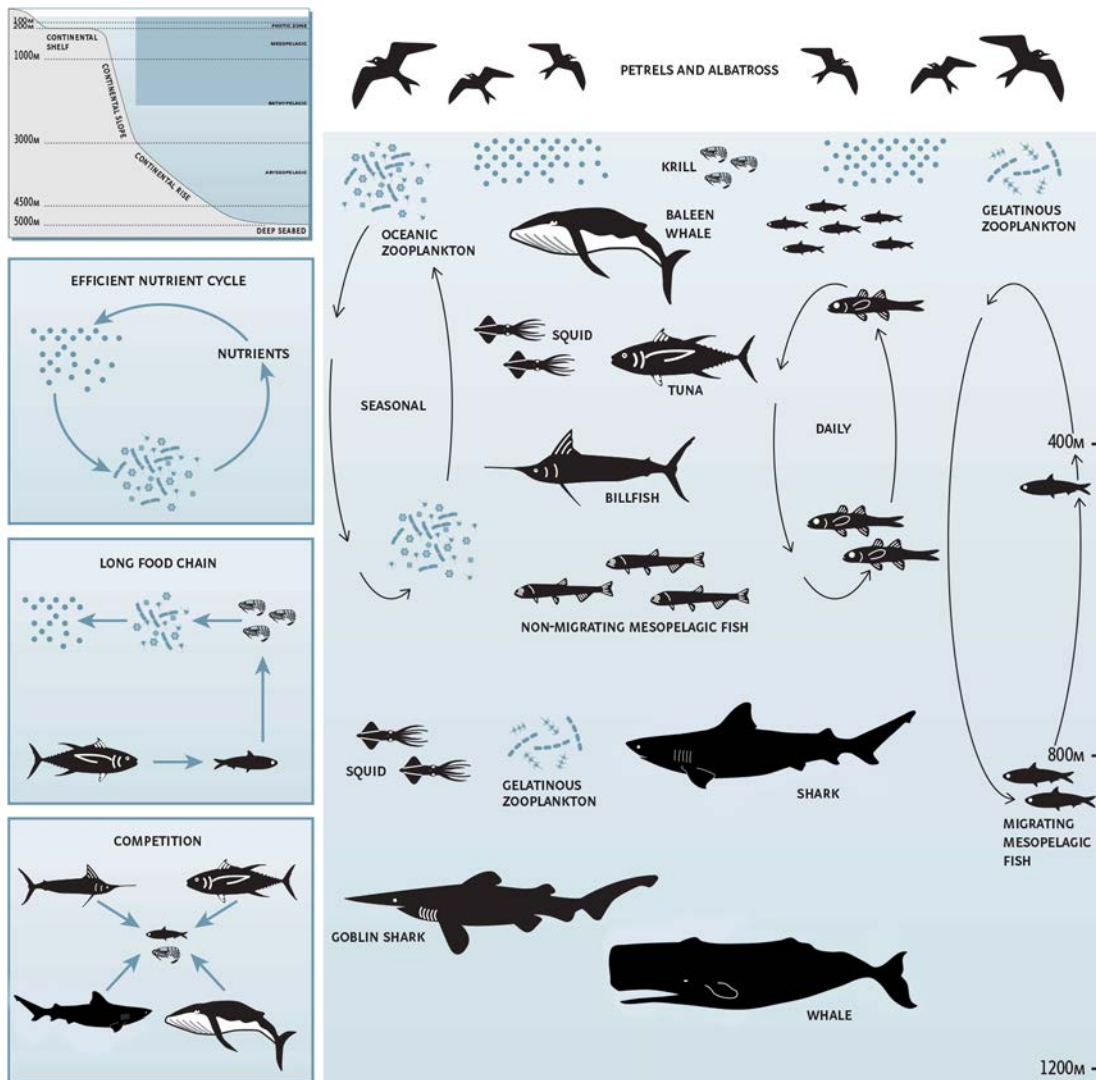


Source: National Oceans Office (2002) reproduced with permission from Department of the Environment.

Behaviour of the dominant predatory demersal fish in shelf systems can be characterised by the highly piscivorous benthic species, such as flathead *Platycephalus richardsoni*, which consistently ate *L. hectoris* in the 1990s study and jack mackerel to a smaller extent. A recent study by CSIRO, which has re-examined diets of a few of the species from this area using both visual and DNA techniques, found these connections have persisted but that flathead also took sardine and red bait in small quantities (Berry *et al.* (in prep), C. Bulman CSIRO pers. comm. 25 May 2015). John dory *Zeus faber* also eat a both demersal and pelagic planktivores such as sardines and red bait. Similarly, *Platycephalus* spp. from the Western Australian shelf also eat clupeids (Platell and Potter

1998b, Salini *et al.* 1990) confirming a similar benthopelagic connection in the western Australian shelf ecosystem.

Figure 4 Conceptual model of offshore pelagic ecosystem in the South-east Marine region.



Source: National Oceans Office (2002) reproduced with permission from Department of the Environment.

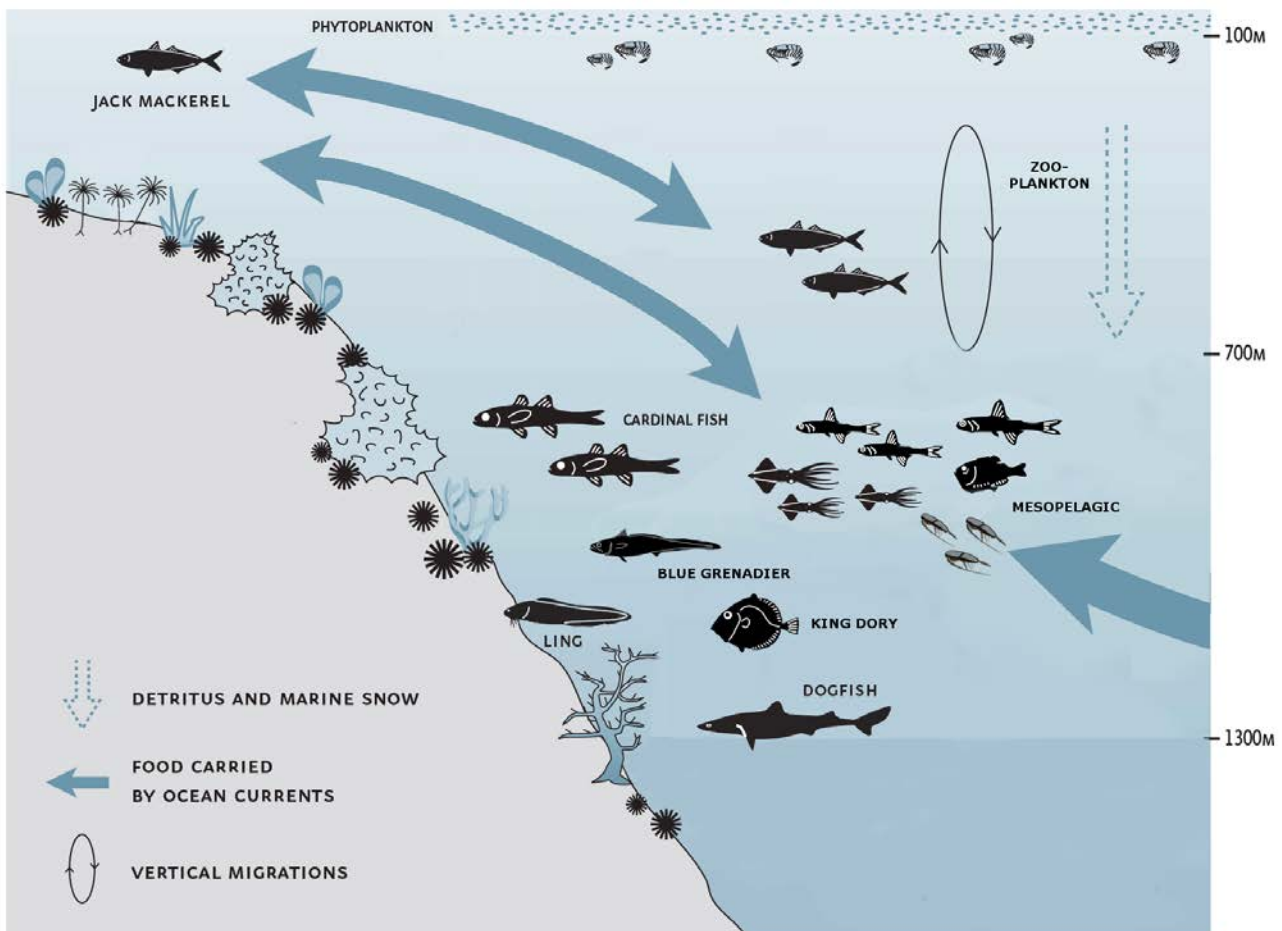
Gelatinous pelagic prey such as pyrosomes, salps, and cnidarians, and fish larvae also provide a pathway to larger benthic or benthopelagic fish. Ocean perch *Helicolenus percoides* consistently eat pyrosomes and other zooplankton (up to 30% of spring diet in 1990s; Bulman *et al.* (2001), Bulman *et al.* (2000)). Blue warehou *Seriola lalandi* feed on salps and zooplankton (Bulman *et al.* 2001) and the recent DNA studies (CSIRO unpublished) suggest that fish larvae may be another important contribution to their diet.

While these observations represent a coupling of pelagic and benthic resources on the shelf, the eastern Australian study also reveals coupling of mesopelagic and benthic resources. Particularly evident was the preference for small piscivorous slope fishes of demersal species on the outer shelf. Pink ling *Genypterus blacodes* (also found on the upper slope) and jackass morwong *Nemadactylus macropterus* consumed other small pelagic piscivores such as three-spined cardinal fish *Apogonops anomalus*, jack mackerel and toothed whiptail *Lepidorhynchus denticulatus*, all of which eat lanternfish. All species especially the lanternfish were found to be abundant over the

upper slope of eastern Tasmania (Blaber and Bulman 1987, Bulman *et al.* 2001, May and Blaber 1989). **This represents a longer, two-step link between the shelf demersal species and mesopelagic resources from the upper slope pelagic system.**

Cephalopoda are a constant and sometimes significant cornerstone of diets of fishes from the shelf to the deep slope (Condie *et al.* 2014). Arrow squid *Nototodarus gouldi* on the shelf eat other squid, pelagic fishes and larvae (such as sardines and barracouta; (O’Sullivan and Cullen 1983, Smith 1983). In turn, squids are eaten by most predators, for many species this is a small or variable component of broader diets, but species like john dory on the shelf and the oreos on the mid-slope eat up to ~20% squid. **Squid are an equivalent step to that of a small pelagic piscivorous fish.** Despite the seemingly insignificant role of squid in most fish diets, the impact on the ecosystem from loss of squid was predicted by qualitative models(Condie *et al.* 2014) and Atlantis and EwE models for the south-east to be large (Johnson *et al.* 2010, Smith *et al.* 2011). Moreover while the role of squid in the deeper slope here is unknown, studies in the Balearic basin of the Mediterranean over 450-2200m found three depth-associated assemblages and two trophic pathways (Fanelli *et al.* 2012). One pathway **links cephalopods to benthic resources** which were influenced by river discharge effects and transport of organic matter to the benthos and the other pathway link cephalopods to the **pelagic foodweb through active vertical migration** and influenced by phytoplankton and zooplankton. Such connections are plausible for Australian slope waters too.

Figure 5 Conceptual model of shelf break- upper slope-mesopelagic ecosystem (modified form original)



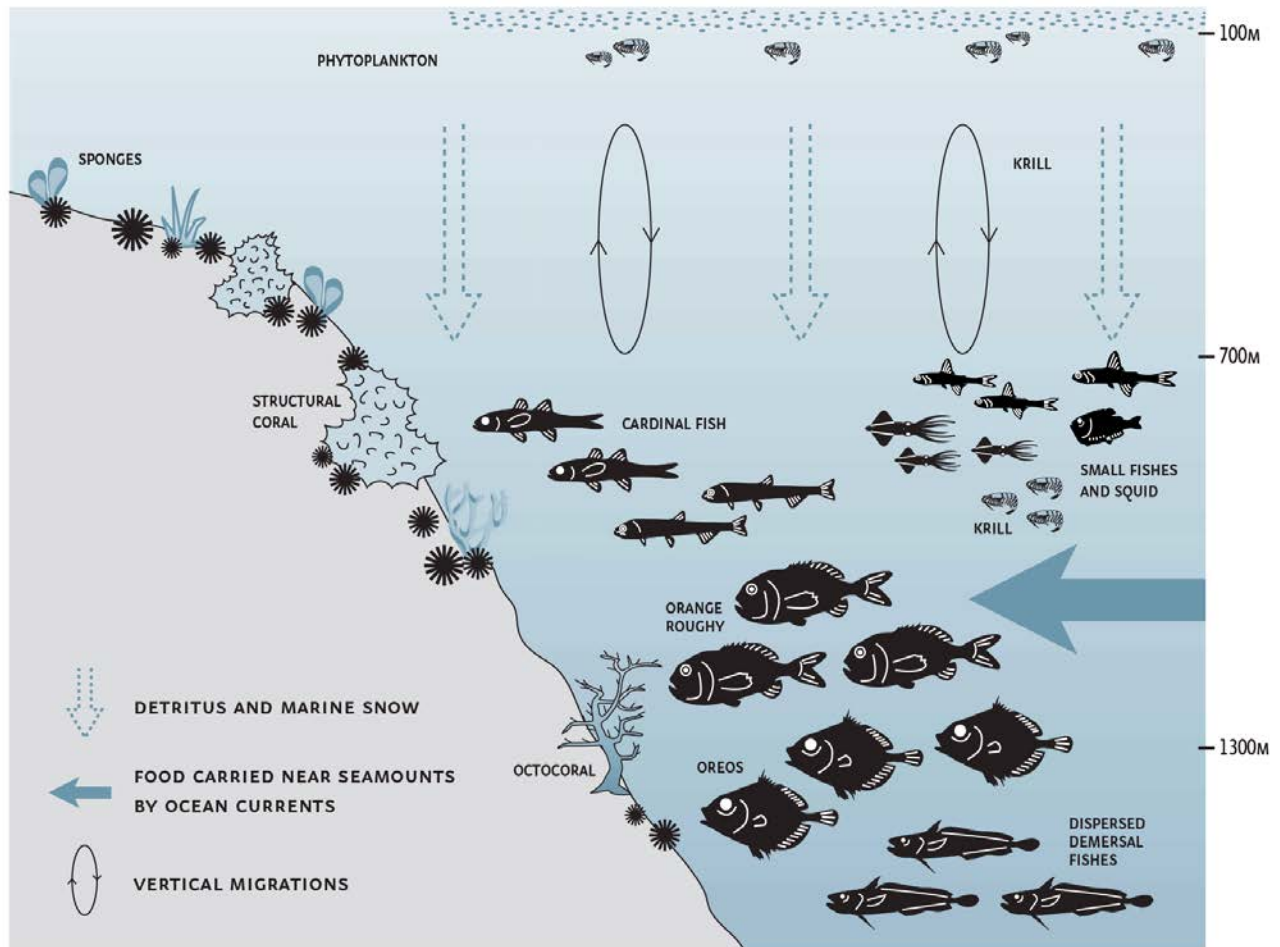
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In the study of **upper slope** fishes (Blaber and Bulman 1987), **the mesopelagic fishes, crustacean and squid were found to provide the coupling to benthopelagic fishes** such as blue grenadier *Macrurus novaezelandiae*, brier shark *Deania calceus*, king dory *Cyttus traversi*, spikey oreo *Neocyttus rhomboidalis* and to many macrourids (Figure 5). Gelatinous nekton is also eaten by spikey oreos and ocean perch. Euphausiids (which can move from deeper water to the surface either daily or over the course of their lifetime) were also heavily consumed (50-60% by energy contribution) by toothed whiptail and the deepsea cardinal fishes *Epigonus* spp and *Apogonops anomalus*.

Connections through oceanic micronekton which includes meso- and bathy-pelagic fish, crustacean and squid are likely to be significant. May and Blaber (1989) estimated myctophids biomass at 65-518 g m⁻² off the slope of eastern Tasmania, probably resulting from the more dispersed oceanic biomass being concentrated by the abrupt shallowing of the continental slope. The importance of the link could be higher still as these species may be a much more abundant resource than previously thought. Acoustic observations in the Tasman Sea have estimated that the biomass of this resource could be 5-58 times greater than net-sampling would normally suggest (Kloser *et al.* 2009). The acoustic sampling and models (e.g. Atlantis) suggest that millions of tonnes of micronekton likely inhabit waters around south-east Australia.

Further down the slope and deeper seamount ecosystems (Figure 6), connectivity between demersal species in this mid slope region with shallower ecosystems is more distant. At this depth, the warty oreo *Allocyttus verrucosus* and the squalids *Centroscymnus crepidater* and *Deania calcea* eat either migrating or non-migrating myctophids, while orange roughy *Hoplostethus atlanticus* eat generally non-migrating bathylagid fishes and carid prawns (Bulman *et al.* 2002c, Bulman and Koslow 1992). Macrourids eat mostly pelagic crustacea particularly gammarids, calanoid copepods and carid prawns. The alepocephalids (slickheads), the spikey oreo and the smooth oreo *Pseudocyttus maculatus* eat primarily gelatinous nekton. While all these nektonic prey are abundant in the bathypelagic zone (Williams and Koslow 1997), the standing primary productivity of the overlying euphotic zone (that could be delivered by the vertical migrating species and by sedimentation processes) was insufficient to support dense populations of demersal predators that occur on the seamounts off southern Tasmania without augmentation by advection of allochthonous production (Bulman 2002, Bulman *et al.* 2002a, Koslow 1997, Parslow *et al.* 1996). Bulman *et al.* (2002a) tested this hypothesis and connectivity with the surface by developing a trophic model for the seamounts, and found that the model-estimated immigration rates of bathypelagic micronekton required to support the seamount fish populations were easily achieved by the average current speed at those depths (in the Sub-Antarctic Mode Water (300-700m) and Antarctic Intermediate Water (800-1200m)). **This implies that the primary production supporting these deepwater communities via the advected production originates some distance away, i.e. it is allochthonous, and probably over a much larger surface area than the seamount area.**

Figure 6 A conceptual model of the seamounts on the mid-slope off southern Tasmania



Source: National Oceans Office (2002) reproduced with permission from Department of the Environment.

While no Australian data yet exists to verify this hypothesis, the model based view of a coupled benthopelagic community on the seamount and mid-slope is consistent with studies of abundance and isotopic composition of demersal fishes between 500-1500m on the northwest Atlantic slope by Trueman *et al.* (2014). This study found that the abundance of benthopelagic feeding fish increased below 1000m with a peak at 1500m, and that their diet became increasingly benthopelagic (from less than 50% at depths less than 1000 m to greater than 75% at depths greater than 1000 m). They suggested that high biomass of benthopelagic feeding fish occurring at ~1000-1500m was tightly coupled to pelagic production at 500m through diurnally vertically migrating fish, calanoid copepods and other zooplankton which concentrate at depth overlapping that of the fish during daylight hours (Figure 7).

Figure 7 Conceptual model of energy transfer on the northwest Atlantic slope by Trueman *et al.* (2014).

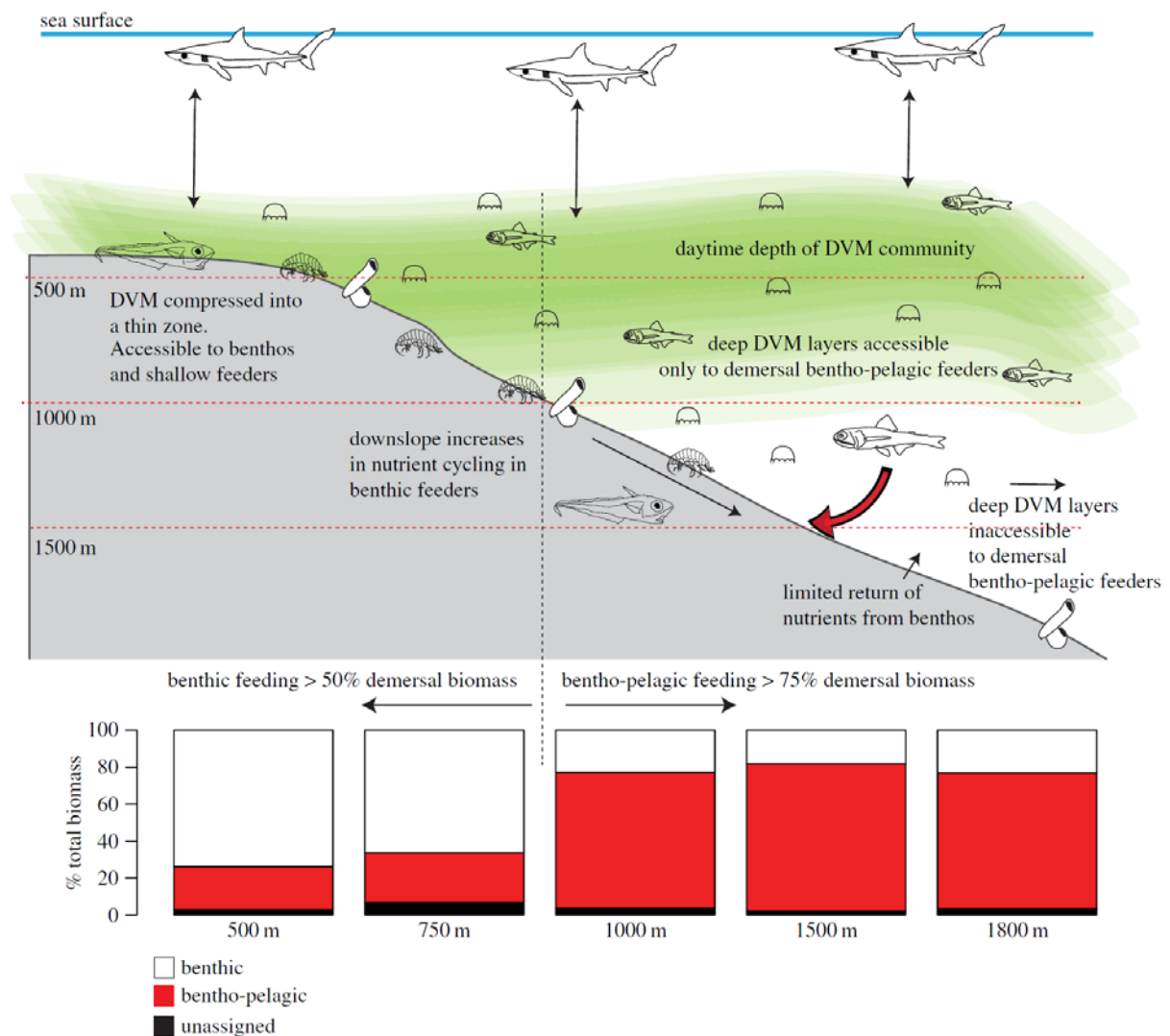


Figure 6. Schematic diagram of important nutrient flow pathways operating on the continental slope and overlying water column as inferred from stable isotope and biomass data. Shaded area represents the daytime depth of organisms within the DVM community. Lower barplot shows the relative biomass of the trawled community assigned to either a benthic or benthic-pelagic diet based on stomach content data.

Source: Reproduced from Trueman *et al.* (2014) under the Creative Commons BY licence (<http://creativecommons.org/licenses/by/4.0/>).

Within Australia, studies on the deeper slope and seamounts have been mostly descriptive, taxonomic studies of the benthos, which have been incorporated into the marine planning advice already. However recent studies (Thresher *et al.* 2011, Thresher *et al.* 2014) using a remotely operated underwater vehicle on Tasmanian seamounts and Tasman fracture have discovered dense communities of megabenthos below 2000m not seen before outside hydrothermal vent communities. The geographical extent of these communities is unknown although it is suspected to be widespread. The mechanism by which this extraordinarily high biomass is maintained is also unknown; the sinking of large detritus like whale carcasses (Higgs *et al.* 2014)) will have some role but are only part of the delivery mechanism. Thresher *et al.* (2011) suggest that high rates of carbon exported from the surface to the deep in around the Southern hemisphere at this latitude might be the supporting energy source. This discovery aligns with the modern view of the functioning of deep-ocean ecosystems presented by Gage (2003) who suggested that major and highly variable losses from the upper pelagic ecosystems to deep ocean environments “leads to

benthic-pelagic coupling that may be dynamic and highly variable, just as it is on the continental shelf” (p314: Gage (2003).

Overlaid on these general trophic structures are the influences of seasonality and interannual variability, of ontogeny due to size-related dietary preferences or life history **migratory patterns** (e.g. species that have shallow dwelling or pelagic feeding prey moving into deeper waters and shifting to more mesopelagic prey species with age), **and changing distribution patterns of predator and prey due to climate change**. All these factors, to a greater or lesser degree depending on depth, will impact our interpretation of the trophic structure and benthopelagic coupling.

Significant gaps in our knowledge include trophic connections in the canyons and on the deep abyssal plains and will need to be inferred from what we understand of the seamount/midslope environments and from studies elsewhere e.g. Clark *et al.* (2010), Pitcher *et al.* (2007), Rowden *et al.* (2010). As we have seen from past and present studies in analogous systems elsewhere in the world, for example in the northwest Atlantic (Haedrich and Merrett 1990, Mauchline and Gordon 1984, Trueman *et al.* 2014), off the Californian coast (Drazen *et al.* 2009, Drazen *et al.* 2008) and New Zealand (Clark 1985, Clark *et al.* 1989, Rosecchi *et al.* 1988), the communities at greater depths tend to be similar in functionality if not composition. This is not the case at shallower depths where the faunal compositions and the ecosystem environmental drivers can be vastly different throughout the Australian marine regions.

2.1.1 South-west

The South-west Marine Region spans approximately 1.3 million square kilometres of temperate and subtropical waters and abuts the coastal waters of South Australia and Western Australia from the eastern end of Kangaroo Island in South Australia to Shark Bay in Western Australia (DSEWPaC 2012). Encompassed by this marine region are physical features from a narrow continental shelf on the west coast to the broad shelf of the Great Australian Bight, steep muddy continental slopes and several deep canyons, abyssal plains, fracture zones of rugged terrain at great depths, deep plateaux, sub-tropical and temperate islands and reefs and complex and energetic oceanographic conditions. The region is also host to hotspots of biodiversity particularly around the Houtman-Abrolhos Islands, the overlap between tropical and temperate fauna along the west coast, the Recherche Archipelago and the soft sediment ecosystems in the Great Australian Bight.

In 2006, a workshop was conducted to summarise knowledge of the key ecological characteristics of the south-west marine ecosystem (McClatchie *et al.* 2006). They found that diets of benthic invertebrates were poorly known for the shelf and slope and little was known of the pelagic links to benthic food webs.

The key ecological features of the South-west region (Table 1) range from topography (such as canyons, plateaux, and coastlines to upwellings) to biological communities such as slope fish and benthic communities. Canyon processes were especially considered by McClatchie *et al.* (2006) as they were likely to be hotspots of productivity based on a review of international studies and their summary follows:

“Abrupt topography and the biophysical mechanisms of prey aggregation are becoming more recognised as creating key hotspots of productivity in the oceans (Genin 2004); these hotspots are vitally important to sustaining fish production. Overseas studies in the Mediterranean, Georges Bank, and off the Oregon and Canadian west coasts have shown that canyons generate complex flows, the net result of which can be higher regional productivity. As such, they form important hotspots of biological production. Dense krill concentrations accumulate in the heads of the canyons off Georges Bank (Greene 1988), providing a "prey subsidy" that helps to sustain high fish production on the banks. While smaller zooplankton and phytoplankton are advected by the deep and temporally variable flows generated around canyons, swimming and vertically migrating micronekton such as krill and mesopelagic fish can maintain position by behavioural interaction with the flow field (Macquart-Moulin & Patrini 1996; Mackas et al. 1997; Allen et al. 2001). These aggregations of micronekton are preyed upon by commercial species such as *Sebastes* on the North American west coast (Pereyra et al., 1969), and provide a rich food source for cetaceans (Bosley et al. 2004). Astoria canyon off Oregon is an important fishery area with extensive groundfish dependent upon the rich prey field of the canyon (Pereyra et al. 1969). Work on the South Australian canyons, scheduled for 2007, will be the first effort to expand these findings into the Southwest Marine Region and to investigate the importance of the canyons as key habitats underpinning the fisheries within the Region.” (McClatchie et al. 2006).

A recent literature review of the Great Australian Bight area compiled by Rogers *et al.* (2013) concluded that there was limited data and understanding of the pelagic ecosystem and trophodynamics, and most of which was focussed on the eastern GAB (Goldsworthy *et al.* 2011, Goldsworthy *et al.* 2013). Specific knowledge gaps identified included the composition and abundance of plankton communities, primary and secondary productivity, microbial loop dynamics, and trophic linkages of zooplankton and nekton to apex predators. The benthic shelf ecosystem is better known particularly over the past two decades and for the demersal fish fauna.

Since the compilation and analyses for this region, there have been many studies of taxonomy (~30) and diversity of the benthos arising from research being conducted which have added considerably to the knowledge of deep benthic fauna of the western bathyal margin of Western Australia (McCallum *et al.* 2013, McEnnulty *et al.* 2011, Poore *et al.* 2014, Przeslawski *et al.* 2013, Williams *et al.* 2010a, Williams *et al.* 2010c, Woolley *et al.* 2013) and shallower fauna of Western Australia (Fromont *et al.* 2012), and the benthic fauna of eastern GAB canyons ((Currie and Sorokin 2011, Currie *et al.* 2007, Currie *et al.* 2008); and also to predicting biodiversity (Althaus *et al.* 2012, Dunstan *et al.* 2012), to geomorphology (Huang *et al.* 2014a, Huang *et al.* 2014c, Williams and Althaus 2015) and of bio-physical processes and modelling (England *et al.* 2013, Gallop *et al.* 2012, Loneragan *et al.* 2013, Lourey *et al.* 2013). In particular, the benthic faunal studies on the Western Australian coast found that species richness of polychaetes and some crustaceans were strongly correlated with net primary productivity determined by local oceanography (McCallum *et al.* 2014), while decapod diversity was largely predicted by latitude (McCallum *et al.* 2013). Woolley *et al.* (2013) also found that distribution of benthic invertebrates was correlated with environmental gradients.

The ongoing Great Australian Bight (GAB) Research Program is collating information about the marine resources of the GAB and will provide important new information on the distribution,

diversity and ecology of the deepwater biota and fauna of the central and eastern GAB. However, explicit trophic information for the deepwater fauna is not expected and therefore will remain a gap in our knowledge.

The trophic relationships of the demersal fish of the shelf ecosystems both on the western and southern coasts are well-studied particularly over the past two decades and for the demersal fish fauna ; see for example French *et al.* (2013), Goldsworthy *et al.* (2011), Hyndes *et al.* (1998), Hyndes *et al.* (1999), Morton *et al.* (2008), Platell and Potter (1998a), Platell *et al.* (2006), Platell and Potter (1998b), Platell and Potter (1999), Platell and Potter (2001), Platell *et al.* (1998a), Platell *et al.* (1998b), Platell *et al.* (1997), Schafer *et al.* (2002), Sommerville *et al.* (2011), White *et al.* (2004), Wildsmith *et al.* (2005). However, the trophic relationships of the outer-shelf and deeper slope ecosystems are poorly studied apart from some deepwater surveys of orange roughy in the late 1980s from which some dietary information for the eastern region of the GAB was obtained (Bulman and Koslow 1992, Koslow *et al.* 1994).

The qualitative models described in Hayes *et al.* (2012) identify at least some connections between pelagic production and benthic/demersal components for the waters off the Houtman Abrolhos Islands and in the Perth Canyon. For the Houtman-Abrolhos Islands *Sargassum* supported a trophic web through small invertebrates to both small pelagic and benthic fish on to large pelagic, piscivorous fish and seabirds (such as the crested turns). In contrast, large invertebrates connected benthic production of kelp to the large pelagic fish. The structure in the Perth Canyon resembled the deeper water conceptual models described above for the south-east with micronekton or filter feeding invertebrates mediating the connection from surface plankton to deeper water predatory fish and detrital fall (e.g. carcasses) supplying energy to sedentary benthic invertebrates.

In conclusion, we are not aware of any further information that improves our knowledge of benthopelagic coupling in this marine region particularly for the canyon areas, and deeper slope and plateaux.

2.1.2 North-west

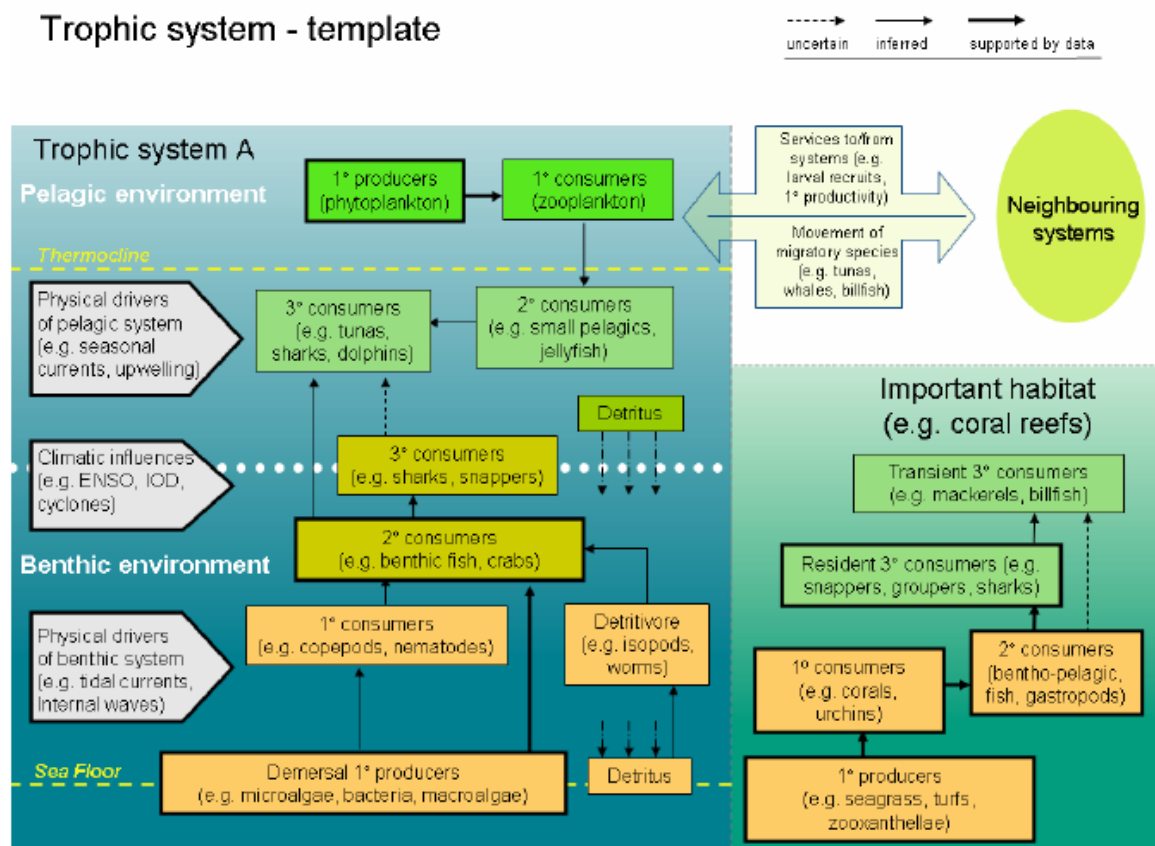
The North-west Marine Region covers 1.07 million square kilometres of water under Commonwealth jurisdiction from Kalbarri in the south to the WA/NT border in the north. It extends from the state waters (3 nautical miles from the coastal baseline) out to the extent of Australia's EEZ up to about 700 kilometres offshore at its widest extent. It is distinguishable from other regions by a number of features: a wide continental shelf, very high tides, very high cyclone frequency, unique western boundary currents and warm oligotrophic waters (Brewer *et al.* 2007b). The Ningaloo Reef, Exmouth Plateau slope and offshore reefs and a unique benthic fauna are also key features of this region.

Brewer *et al.* (2007b) compiled a comprehensive report broadly describing the trophic ecosystems of the region. They compartmentalised the region into 11 subregions based on the IMCRA and pelagic bioregionalisation (Last 2005, Lyne *et al.* 2005) and detailed drivers of the system, features, key species interactions and information gaps. For each sub-region, a schema of the presumed trophodynamics was drawn (Fig 8).

In general more is known about the shelf trophic ecosystems in this region, with practically nothing about the slope and canyons, abyssal plains or plateaux. The physical processes are quite

well described and play a large part in regulating productivity from the Indonesian Through Flow in the north to the Leeuwin and Ningaloo Currents in the south. The low nutrient but high energetic surface waters have led to recycling organisms such as picoplankton and microbial and filter feeders playing a key role in sustaining production in surface waters, but at depth, subsurface upwellings are thought to have a key role in supplying productivity (Brewer *et al.* 2007b). The link between the pelagic and benthic communities is stronger in the inshore part of the shelf which is more affected by tides and currents, monsoonal winds and sporadic cyclones, which serve to mix the water column and associated nutrients. The pelagic and benthic communities on slope and deeper regions are presumed to be less connected. There is some mixing of the deeper, more nutrient rich waters into the oligotrophic surface layer due to strong currents, winds and cyclones, and upwellings as well as breaking internal waves which may support a high biomass of small pelagic fishes. There are also species that migrate between the two habitats, including plankton (e.g. calanoid copepods), micronekton (e.g. lanternfish and shrimps), some tunas and cetaceans. The diversity of reef, atolls, islands and shoal habitats is a key ecological feature in this marine region (Table 1, see Figure 9 as an example of a deep plateau). However the trophic structures for these habitats are only assumed. Direct observation of the large pelagic fish in the region (e.g. tuna) indicates that, as found elsewhere, they do feed opportunistically on the migrating mesopelagics (Fulton unpublished data collected in collaboration with recreational fishers on the Gascoyne coast).

Figure 8 Template used by Brewer *et al.* (2007b) to conceptualise the North-west Marine Region.



Source: Brewer *et al.* (2007b) reproduced with permission from the author.

In comparison to the rest of the region, the North West Shelf (NWS) subregion is relatively well-studied having been the focus of CSIRO investigations in the late 1980s before and after the

closure of foreign fishing and intermittently since. The NWS Joint Environmental Management Study aimed to develop and demonstrate practical and science-based methods that supported integrated regional planning and management of marine ecosystems to achieve ecologically sustainable development. As part of that study, two ecosystem models were developed for the NWS: an Ecopath with Ecosim (EwE) trophic model (Figure 10) and an In Vitro agent-based integrated model. These models were based on trophic data from the region, but also data for the same or similar species from adjacent or similar areas (Bulman 2006). The major connections are captured in Figure 10, which shows that squid and small benthopelagic fish have a linking role across the pelagic and benthic realms. Note however that again these data were collected two decades ago and so connections may have changed.

Figure 9 Conceptual diagram of a plateau by Brewer *et al.* (2007b).

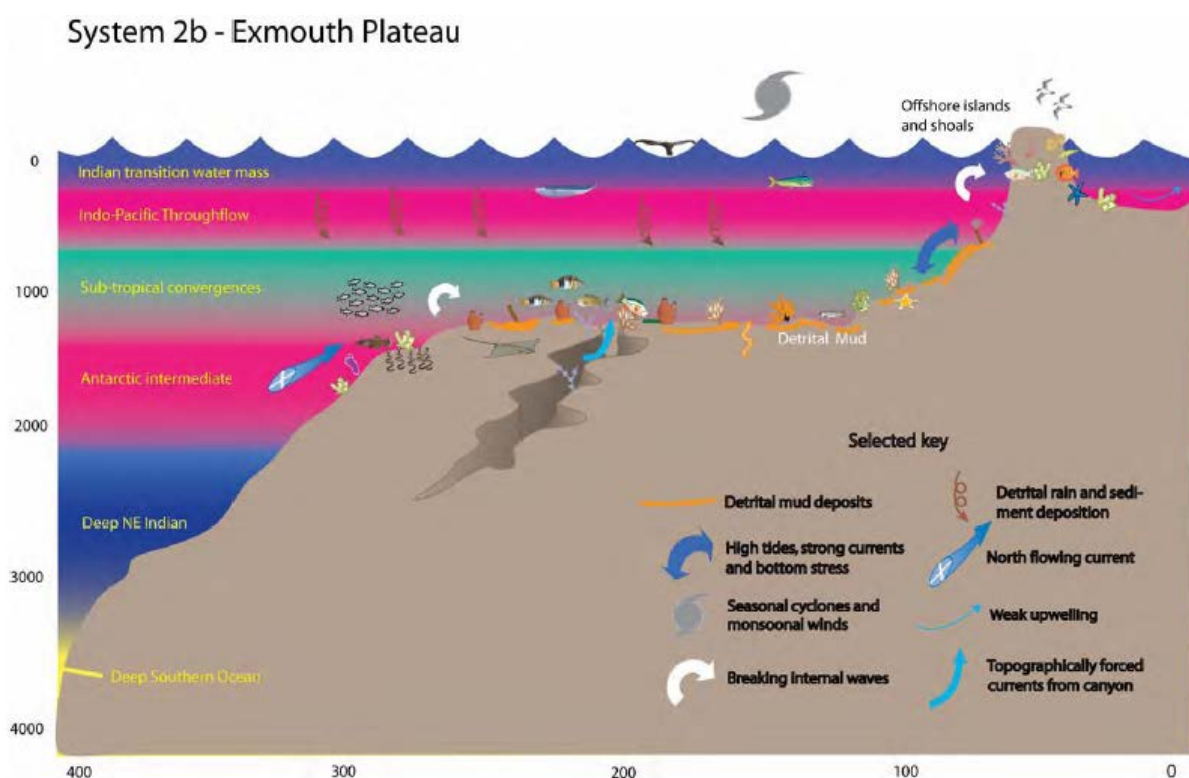
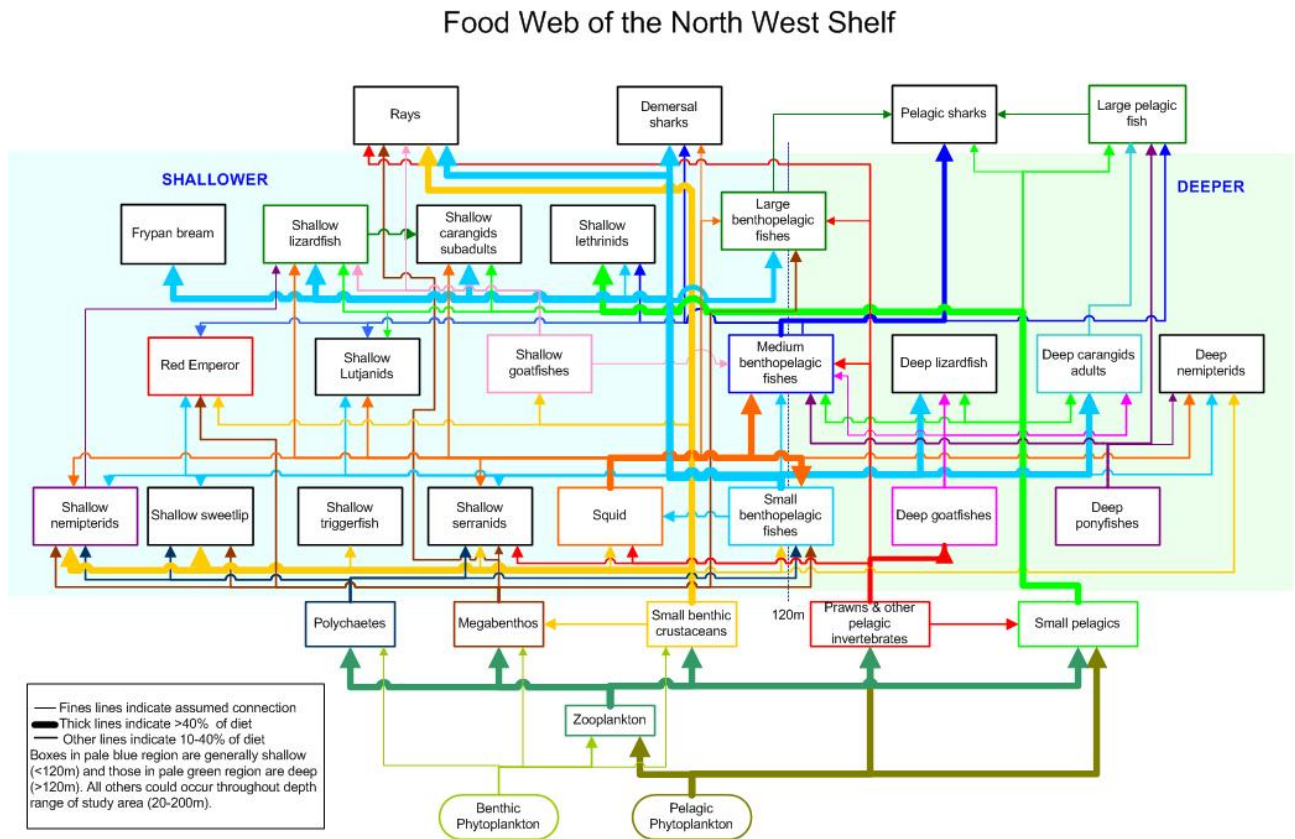


Figure 6-33 Habitat diagram of the Exmouth Plateau sub-region showing selected important drivers and features. 70-100 m deep chlorophyll maxima not shown.

Source: Brewer *et al.* (2007b) Reproduced with permission of the author

Figure 10 Foodweb diagram for the NWS trophic model of Bulman (2006).



In conclusion, we are not aware of any further research in this region that would improve our knowledge of benthopelagic coupling in the northwest marine region. All of the qualitative models discussed by Hosack *et al.* (2012) for the region concentrate on reefs, where links are via filter feeders consuming plankton or mobile fish carrying invertebrate or benthic primary production out to pelagic predators and seabirds. The canyon areas, and deeper slope and plateaux and plains are poorly known; however several voyages have added considerably to the knowledge of deep benthic fauna (McCallum *et al.* 2013, McEnulty *et al.* 2011, Poore *et al.* 2014, Przeslawski *et al.* 2013, Schonberg and Fromont 2012, Williams *et al.* 2010a, Williams *et al.* 2010c, Woolley *et al.* 2013) and shallower fauna (Bruce 2012, Bruce 2014, Duncan and Wilson 2012, Falter *et al.* 2012, Johansson *et al.* 2013, Penny and Willan 2014, Przeslawski *et al.* 2013), predicting biodiversity (Althaus *et al.* 2012, Fromont *et al.* 2012, Huang *et al.* 2014a) of geomorphology (Huang *et al.* 2014c, Kloser *et al.* 2015) and of bio-physical processes (Falter *et al.* 2012, Loneragan *et al.* 2013, Lourey *et al.* 2013, O'Shea *et al.* 2012, Rayson *et al.* 2012, Rousseaux *et al.* 2012).

2.1.3 North

The North Marine region is largely a shallow, soft sediment tropical marine environment covering 625,689 square kilometres. 97% of the area is shallower than 200 m and much of it less than 70 m and therefore has the shallowest ocean and most extensive shelf of any marine region. There are three main sub-regions: Gulf of Carpentaria, Arafura Sea and Joseph Bonaparte Gulf. These regions were further subdivided based largely on geomorphology (North Marine Planning Section 2007).

There are two large and relatively deep mud basins (Bonaparte Basin and Gulf of Carpentaria basin), an extensive system of carbonate banks (Oceanic Shoals CMR) and a series of shallow canyons extending off shelf. Submerged reefs are an important feature of the region many of which support living corals. The seafloor is dominated by soft sediments. The tropical monsoon climate and shallowness of the region creates a unique environment, which can result in widespread turbidity and mobilisation of sediments. Large rivers from Papua New Guinea and Indonesia also deliver sediments, freshwater and nutrients into the ocean. There is the Arnhem current in this region (Condie 2011) and strong tides inshore around islands and reefs, and offshore in canyons, channels and valleys.

The inshore and estuarine demersal fish fauna are well studied particularly in relation to the commercial prawn fisheries (Rochester *et al.* 2007). The feeding ecology of inshore and estuarine fishes of the Gulf of Carpentaria has been studied, particularly in relation to consumption of commercially important prawns. Many species are generalists or opportunistic, such as the larger trevallies and snappers that eat a range of teleosts, crustaceans, and molluscs. In contrast, there are several species that are specialists such as detritivorous mullets and milkfish, and a weasel shark that eats octopus almost exclusively. The diets of pelagic fishes have not been studied.

The most recent research conducted in the North Marine Region was in the western part of the Oceanic Shoals CMR in 2012 by the NERP Marine Biodiversity Hub (Nichol 2013). These surveys added greatly to the knowledge of the biodiversity of this region, in particular, of sponge communities but also of other benthic and pelagic communities. These surveys have also added to our knowledge of the seabed features and the associations of pelagic vertebrates, benthic invertebrates with hard ground and infaunal species associated with soft sediments.

Both qualitative and quantitative models for Albatross Bay were developed to investigate the banana prawn catch decline. The Gulf of Carpentaria EwE model (Bustamante *et al.* 2011) focused on the benthic-pelagic ecosystem of the tiger-endeavour prawn fishing grounds of the Northern Prawn Fishery (NPF), the most valuable prawn species of this fishery. This ecosystem model was based on all ecological and trophic data available. Hosack *et al.* (2012) present qualitative models for the Gulf of Carpentaria, and Caley *et al.* (2015) present one for the Oceanic Shoals (Figure 11). The observations and models indicate the kinds of reef driven connections identified above for the north-west, but also other associated links (e.g. via mobile grazers like dugongs and turtles that feed on benthic production but move into the domain of pelagic sharks and toothed whales). Turtles are also a species that link the pelagic and benthic/demersal systems through the course of their life history, although at quite large scales.

Ceccarelli *et al.* (2013) sub-divided the Coral Sea into 3 regions (Figure 12) each with specific features: “The northern Coral Sea is predominantly an open-water habitat (>4000 m), with the Hiri Gyre having a strong influence on pelagic ecology. The central Coral Sea hosts the highest density of coral reefs and islands, creating a network of stepping stones characterised by three prominent rises with abundant seamounts, separated by deep basins and trenches (>3500 m) and influenced by the proximity of the oceanographic boundary of the Tasman Front between the Australian coast and [GBR Great Barrier Reef] in the west and the islands of New Caledonia and Vanuatu in the east. The southern Coral Sea is characterised by three prominent rises with abundant seamounts, separated by deep basins and trenches (>3500 m) and influenced by the proximity of the oceanographic boundary of the Tasman Front.”

Ceccarelli *et al.* (2013) in their comprehensive review of 70 years of research on Coral Sea geology, oceanography, ecology and fisheries found that there was “virtually no knowledge of benthic ecological processes, including benthopelagic coupling.” There was also little known of the fate of productivity; zooplankton and micronekton communities; and basic biology, population dynamics and trophodynamics of unfished species and other non-fish fauna. However, key knowledge that was identified included the role of myctophids and squid in aggregations of top predators such as tuna and billfishes, the importance of the jelly food web in the northern Coral Sea, and good knowledge of shallow reef communities. The Coral Sea micronekton is distinct from that of the Tasman Sea consistent with identified biogeographical boundaries; and also differs between seamounts, the open ocean and reefs and islands.

Given that no further information on benthopelagic coupling is available for either region, the inferences made by Brewer *et al.* (2007a) remain unchanged i.e. similar to those described in the South-east case study section. The assumed similarity of the deeper water processes along the east coast of Australia is also assumed by Dambacher *et al.* (2012b). Their qualitative models of the Lord Howe Seamount Chain and Norfolk Ridge identify the same kinds of links discussed for the south-east. Phytoplankton and detrital rain are consumed by benthic invertebrates e.g. sessile filter feeders or bivalves, which are consumed by mid-trophic level consumers like rays and demersal fish which are in turn consumed by the top predators (often benthic but also potentially vertically migrating species). An extra benthopelagic pathway links coralline algae and pelagic micro-crustaceans to demersal fish in the Norfolk Ridge model. Similarly the qualitative model of the upwelling off Fraser Island has similar linking roles for planktonic production and micronekton as for the south-east upwellings although the particular role of gelatinous species is stressed more strongly in the model of the Fraser Island upwelling. For the shallower reef systems captured in the Elizabeth and Middleton Reefs and other reefs and cays of the Queensland Plateau the links mirror those identified above for other reef systems.

Figure 12 Key features of the three regions of the Coral Sea (from Ceccarelli *et al.* (2013)).

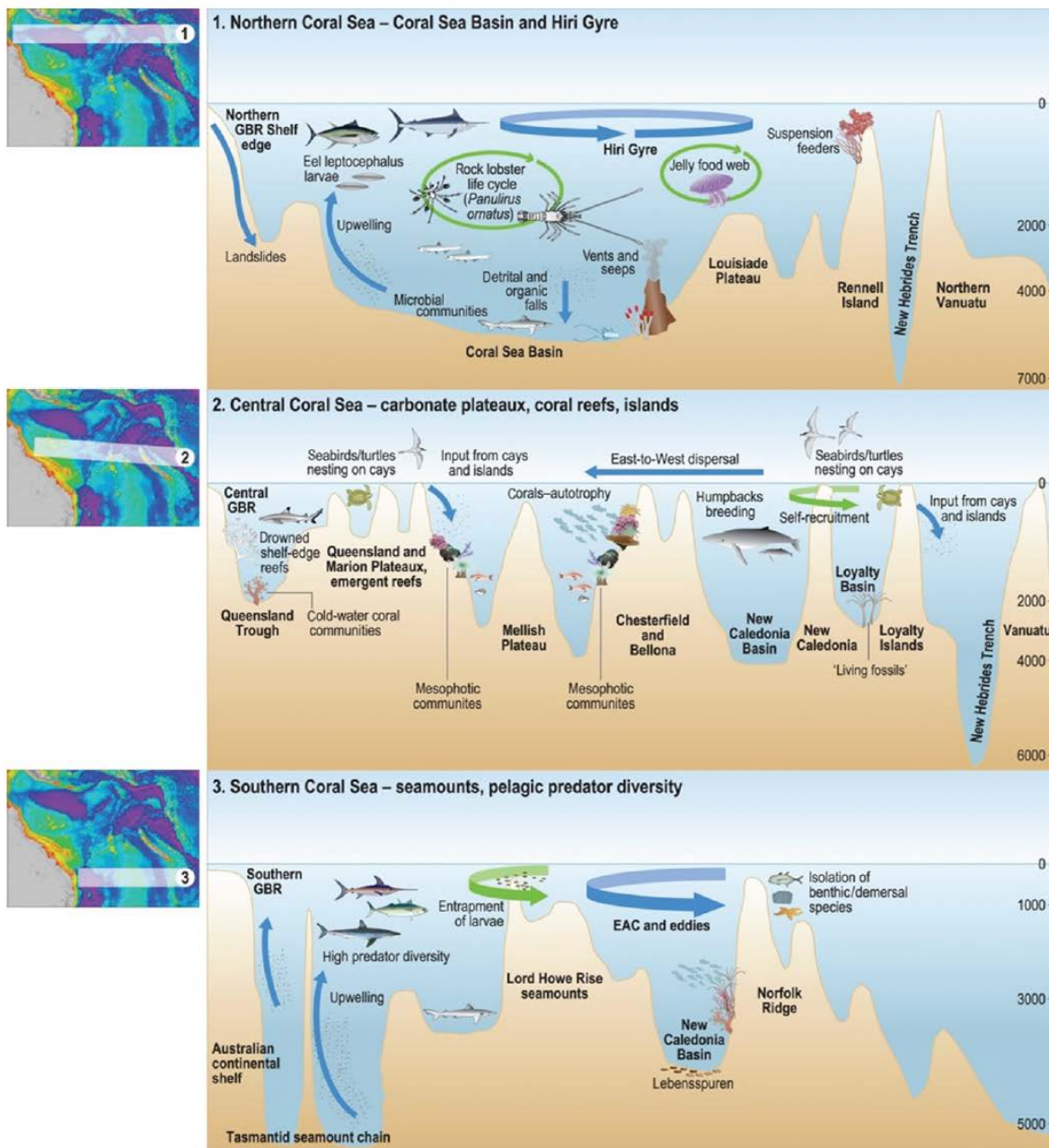


Figure 4.14 Schematic diagram of key features and defining characteristics of the northern, central and southern Coral Sea. Cross-section profiles were adapted from bathymetry data provided by Robin Beaman

Source: This figure was originally published in *Advances in Marine Biology*, Vol. 66. Ceccarelli *et al.* (2013). Chapter Four - The Coral Sea: Physical Environment, Ecosystem Status and Biodiversity Assets. pp. 213-290. Copyright 2013 Elsevier Ltd.

2.2 Model-based Information

Pelagic ecosystems in Australian waters have been reviewed for a white paper on biodiversity (Constable *et al.* 2014). The review compiled a comprehensive list of relevant models of various types (Table 2) i.e. from conceptual and simple through medium complexity to complex and

coupled. Models were broadly described by scale from small-scale at species level to large scale or global, their maturity or readiness for application - usually in a fishery context. Some of these models also couple the benthic and benthopelagic systems and are therefore the most useful of the models with which to holistically explore marine ecosystems as a whole. However all models are designed with specific purposes in mind and can't address all questions. There are even attempts to couple different types of models in order to take advantage of characteristics and capabilities peculiar to that model type. We have adapted the table to include comments on what information these models provide on benthic-pelagic coupling (largely summarised in the sections above).

Table 2 Summary review of the status of pelagic ecosystem models in 7 regions of Australia

AREA	TYPES OF MODELS DEVELOPED
Antarctic and Subantarctic	Conceptual models on ecosystem structure (Melbourne-Thomas <i>et al.</i> , 2013), a partial model of biogeochemistry and production for Kerguelen region as well as whole of Southern Ocean; simple predator-krill models are available but driven by knowledge from Antarctic Peninsula and Atlantic sector; a NetLogo and Atlantis models almost ready for trials (rudimentary heading for mature; Bedford pers. comm. UTAS, Fulton pers. comm. CSIRO).
South-East Australia	Conceptual models exist (e.g. (Hosack & Dambacher, 2012), mature Ecopath with Ecosim (EwE) models exist for small sections of this region (Bulman <i>et al.</i> , 2006), mature Atlantis model (Atlantis-SPF; Fulton) also exists (other Atlantis models exist for the region too but more demersally focused; (Fulton EA, 2014)).
Great Australia Bight and SA Gulfs	Conceptual models exist (Hayes <i>et al.</i> , 2012), mature BGC model exists for Spencer Gulf (Doubell et al), mature EwE model exists (Goldsworthy <i>et al.</i> , 2013), an Atlantis model is being currently calibrated (rudimentary heading for mature; (Fulton & Gorton, 2014)
South-West Australia	Conceptual models exist (Hayes <i>et al.</i> , 2012), a couple of small scale rudimentary EwE models (mainly for demersal species; (Lozano-Montes <i>et al.</i> , 2011) exists and Atlantis model is under calibration (pers. comm. Lozano-Montes CSIRO)
North-West Australia	Conceptual models exist (Hosack <i>et al.</i> , 2012), rudimentary-mature models exist for Gascoyne and Pilbara both InVitro (Fulton <i>et al.</i> , 2011; Gray, 2006) and EwE (Bulman, 2006; Fulton <i>et al.</i> , 2011), but in terms of pelagic components more rudimentary and simplified than for demersal stocks and habitats.
Northern Australia including Gulf of Carpentaria	Conceptual models exist (Hosack <i>et al.</i> , 2012), Gulf of Carpentaria has a mature EwE model (Dichmont <i>et al.</i> , 2013; Okey, 2006), again more demersally focused, plus MICE models (focused on commercial crustaceans, (Plagányi <i>et al.</i> , 2014; Plagányi <i>et al.</i> , 2011) and numerous multispecies models. Biggest gap in dynamic models is across NT.
North-East Australia (including GBR)	Conceptual models exist (Dambacher <i>et al.</i> , 2012); mature Atlantis model exists for the Coral Sea (pers. comm. Hutton CSIRO) and offshore waters down the east coast, MICE and EwE models exists for ETBF region (Griffiths et al 2010, pers. com. Hillary CSIRO). Mature EwE models also complete for GBR ((Gehrke, 2007; Gribble, 2009), Atlantis models under development (pers. comm. Fulton CSIRO). eReefs – coupled physical and biogeochemical model of the Great Barrier Reef
Whole of Australia (Earth System, biogeochemistry)	Partial models exist (e.g. biogeochemical plankton models, (Matear, 2013)) with project proposals in place for an Australia wide for a size-based model to be developed.

Source: National Marine Science Plan White Paper Submissions for Biodiversity Conservation and Ecosystem Health- Pelagic Ecosystems.

<http://frdc.com.au/environment/NMSC->

[WHITE/Documents/Submissions/Biodiversity%2c%20conserv%2c%20eco%20health%20subtheme%20paper%20-%20Pelagic%20Ecosystems.pdf](http://frdc.com.au/environment/NMSC-WHITE/Documents/Submissions/Biodiversity%2c%20conserv%2c%20eco%20health%20subtheme%20paper%20-%20Pelagic%20Ecosystems.pdf)

accessed 20 May 2015.

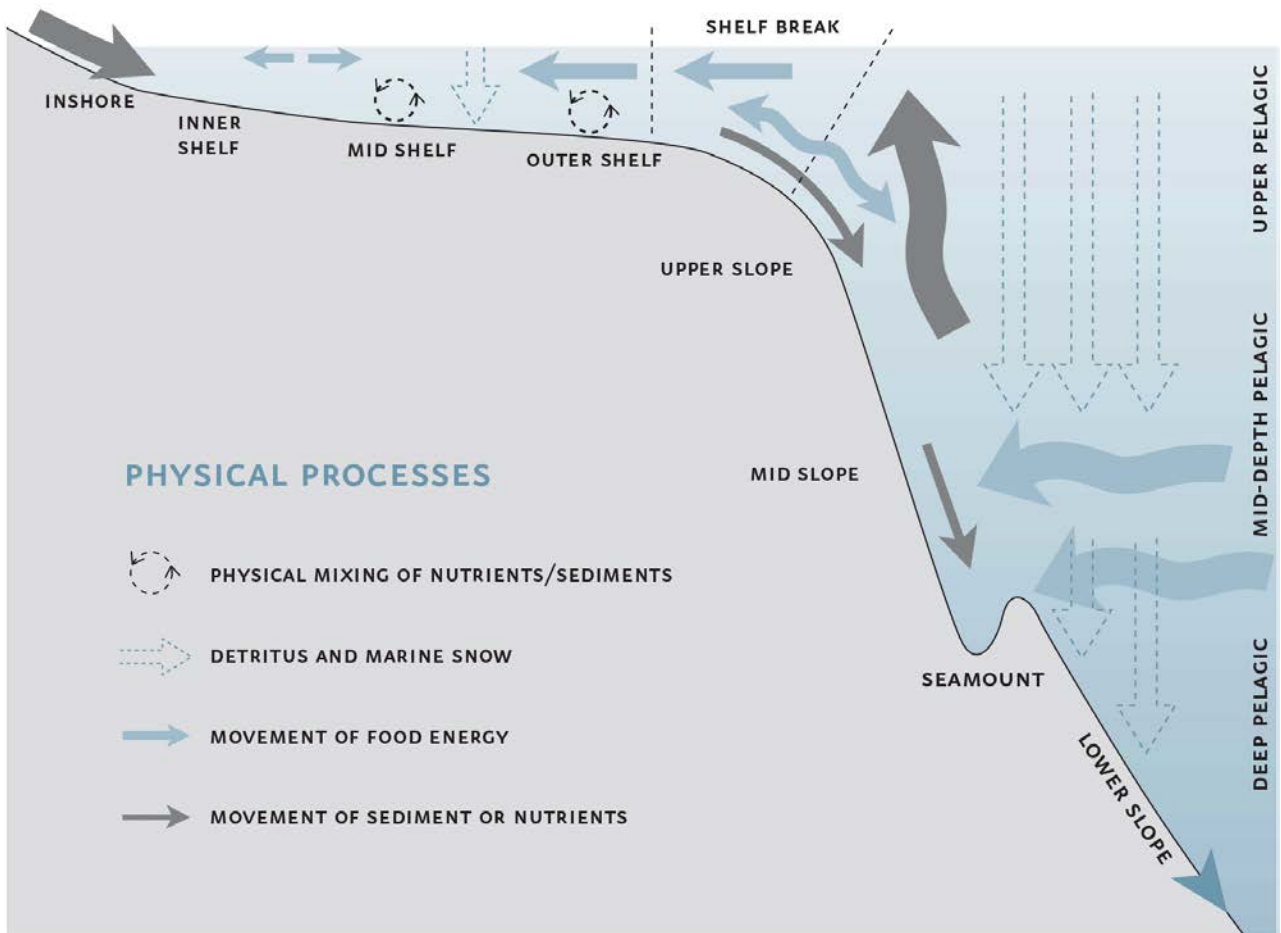
3 Conclusions

This brief report summarises the current state of knowledge on marine benthic-pelagic coupling around Australia. It is clear there are many geographic gaps and that much of the data is aging and so may be uncertain given broader environmental shifts due to ocean warming and acidification, and shoaling of oxygen contours.

Our best available knowledge suggests that in shallow systems (like reefs) pelagic and benthic pelagic production flows in both directions, mediated through invertebrates and fish and their predators. In upper slope waters the linkages are more one way (at least at shorter time scales) where pelagic production filters to depth through physical settling as well as via trophic links mediated by horizontal and some vertical movement of epipelagic species such as jack mackerel, and by micronekton like mesopelagic fish, squid and gelatinous species. At deeper depths on seamounts and the rugged terrain of steep slopes, the return of pelagic production from overlying waters via settling diminishes even further and the dense populations of demersal fishes found in these can only be supported by advected allochthonous production originating from probably quite some distance away. On longer time scales physical and chemical linkages also operate, where deep water nutrients are brought to the surface by current systems and upwellings – though we have put less attention on such linkages here. Comparing what is known around Australia with similar depths elsewhere suggests that these general patterns seem to hold fairly broadly.

Our best understanding of marine trophodynamics comes from the southern areas of Australia and in particular in the South-east Marine Region (Figure 13). Gaps in our knowledge for the South-east Marine Region are of trophic connections in the canyons and on the deep slope and abyssal plains and will need to be inferred from what we understand about the seamount/midslope environments and from similar environments elsewhere. As we have seen from past and present studies either, for example in the northwest Atlantic (Haedrich and Merrett 1990, Mauchline and Gordon 1984, Trueman *et al.* 2014), off the Californian coast (Drazen *et al.* 2009, Drazen *et al.* 2008) and New Zealand (Clark 1985, Clark *et al.* 1989, Rosecchi *et al.* 1988), the communities at greater depths tend to be similar in functionality if not composition. This is not the case at shallower depths where the faunal compositions and the ecosystem environmental drivers are vastly different throughout the Australian marine regions. However, our conceptual model of the outer-shelf–upper slope energy pathways is slightly improved.

Figure 13 Conceptual models of the physical and biological processes in the South-east Marine Region. Additional links are movement of food energy between mesopelagic-upper slope-shelf regions (wiggly blue line).



Source: National Oceans Office (2002). Reproduced with permission of Department of the Environment.

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