Pelagic ecology of the Ningaloo region, Western Australia: influence of the Leeuwin Current

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Abstract

The Ningaloo region of Western Australia (WA), best known for its fringing coral reef system, is also an oceanographically unique area that recent studies have revealed as one of the most productive in Australia. Despite the suppression of major upwelling along the WA coast by the poleward-flowing Leeuwin Current (LC), localised seasonal upwelling at Ningaloo is effected by the wind-driven, northward-flowing Ningaloo Current that periodically flows inshore of the LC and enhances nutrient concentrations within the euphotic zone. Under the upwelling-favourable conditions generated during El Niño years, levels of primary production can episodically reach 3000–8000 mg C m^{-2} d^{-1} (as compared to 200 mg C m^{-2} d^{-1} within the bulk of the LC). The diverse copepod fauna of the region is dominated by small, upwelling-ready species that should benefit from these sporadic phytoplankton blooms. However, copepod production rates are generally low (~ 13 mg C m^{-2} d^{-1}) and do not mirror the trends observed with phytoplankton. This disparity is potentially a result of the highly pulsed nature of the upwelling, a strongly advective physical environment and the dominance of microbial processes. It is notable that grazing on picoplankton biomass is extremely high (100%), while the lower (60%) grazing rates on the total phytoplankton community indicate that a substantial portion may be available for export to the benthos. Whale sharks are more abundant at Ningaloo Reef in years in which the Leeuwin Current is strong, but links between the strength of the LC and the seasonal aggregation of other megafauna are weaker. There is also likely significant connectivity between the pelagic production dynamics off Ningaloo and the benthic fauna of the region, although this is currently an under-researched area.

Keywords: Leeuwin Current, Ningaloo Current, Western Australia, primary production, zooplankton, secondary production, megafauna

Introduction

The Ningaloo region of Western Australia (WA), bordering the Cape Range peninsula from about 21°40'S to 23°35'S (Figure 1), is a unique marine environment that supports the most extensive (260 km) western fringing coral reef in the world. The Ningaloo Marine Park was established in 1987 and incorporates most of Ningaloo Reef, in addition to the seabed and overlying waters on the continental slope and shelf to an average distance of 18.5 km offshore. While the region's relatively isolated location has served to limit negative anthropogenic influences as compared to other continental marine parks (Moore 2000), it has also placed some logistical constraints on research efforts. However, over the past two decades or so, oceanographic research programs have increasingly been conducted in the waters off Ningaloo. Here, we review the current state of knowledge on the influence of the Leeuwin Current on the pelagic ecology of the Ningaloo region, including nutrient fluxes, pelagic primary productivity, zooplankton dynamics, and the characteristic marine megafauna of the region.

Physical oceanographic setting

The large-scale oceanographic dynamics off Ningaloo can be characterised by two main scenarios, depending on season. Whilst the poleward-flowing Leeuwin Current is present year-round (Figure 2), the flow rate and volume transport is largest between April and September (Godfrey & Ridgway 1985). The presence of an extensive coral reef at Ningaloo is closely linked with the LC, as this warm, downwelling current serves to increase ambient temperatures as compared to similar latitudes off the west coasts of South America and Africa, particularly during winter (Pearce 1991; Morton 2003). Physical connectivity between the Leeuwin Current and reef waters is particularly facilitated towards the

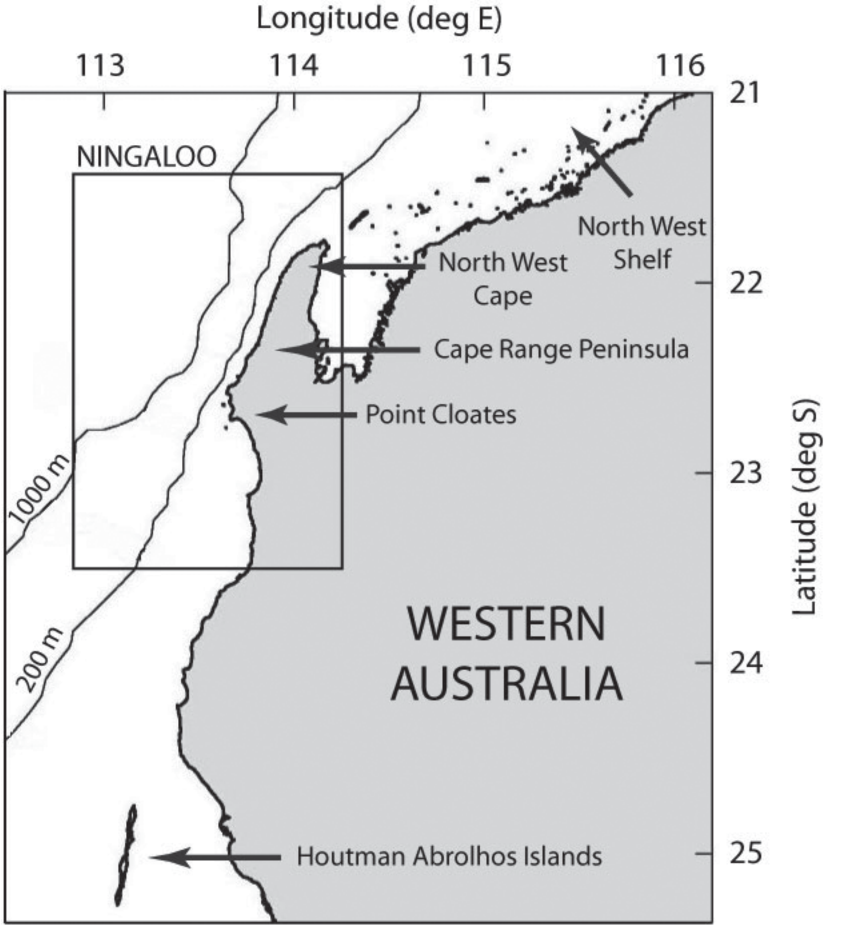

Figure 1. Location of the Ningaloo region of Western Australia.

northern extent of the Ningaloo region, where the continental shelf is the narrowest in Australia (6–10 km).

During summer, strong southerly winds generate a northward current, the Ningaloo Current (NC), on the continental shelf between the LC and the reef front (Figure 2b). The NC generally predominates on the shelf from September to April, forming a wide (30 km) flow on the broad shelf off Point Cloates (Figure 1) that rapidly tapers to 2 km or less as it flows northward along the narrow shelf (Taylor & Pearce 1999). Recent field and modelling data has indicated that a significant proportion of the NC volume is sourced from LC surface waters, via a persistent re-circulation feature at Point Cloates (Figure 2; Woo *et al*. 2006a,b). A contribution to the Ningaloo Current's volume is also sourced from upwelling of deeper (~ 100 m) and colder water from the base of the LC, below the upper mixed layer depth (Hanson *et al*. 2005; Woo *et al*. 2006). However this relatively small-scale upwelling can be fairly cryptic in nature, as the strength of the Ekman transport is not always sufficient to advect the colder water through to the surface where it could be detected by satellite imagery (Hanson *et al*. 2005; Woo *et al*. 2006a; Furnas 2007).

On an interannual basis, the strength and volume of the LC are closely linked to the El Niño/Southern Oscillation (ENSO) cycle. The interannual ENSO signals are transmitted from the Pacific across the Indonesian Throughflow, and travel along the WA coastline as coastally trapped waves (Meyers 1996; Wijffels & Meyers 2003). High coastal sea levels correspond to stronger LC flow during La Niña years, and contrast with low sea levels and weaker flow during El Niño years (Pearce & Phillips 1988; Feng *et al*. 2003, 2004). The latter scenario allows for increased seasonal upwelling activity off northwestern Australia (Wilson *et al*. 2003a; Condie & Dunn 2006; Furnas 2007).

Pelagic ecology off Ningaloo

The Leeuwin Current, Ningaloo Current and primary production

The oligotrophic Leeuwin Current is typified by very low dissolved nutrient levels (generally < 0.2 μM nitrate, < 0.2 μM phosphate) within the upper mixed layer, with a nutricline present between 100 and 200 m depth (Pearce *et al*. 1992; Hanson *et al*. 2005). Accordingly, primary productivity rates within the LC and adjacent oceanic waters can be quite low, measured at a mean of 200 mg C m^{-2} d^{-1} north of the 28°S during the summer (Hanson *et al*. 2005). Though recent field work has shown that the presence of the downwelling LC does not completely suppress Ekman-type upwelling off northwestern Australia (Woo *et al*. 2006a,b), the oligotrophic nature of the LC does place limits on the nutrient levels that are transported into the euphotic zone by the adjacent NC upwelling. During a study in the summer of 2000,

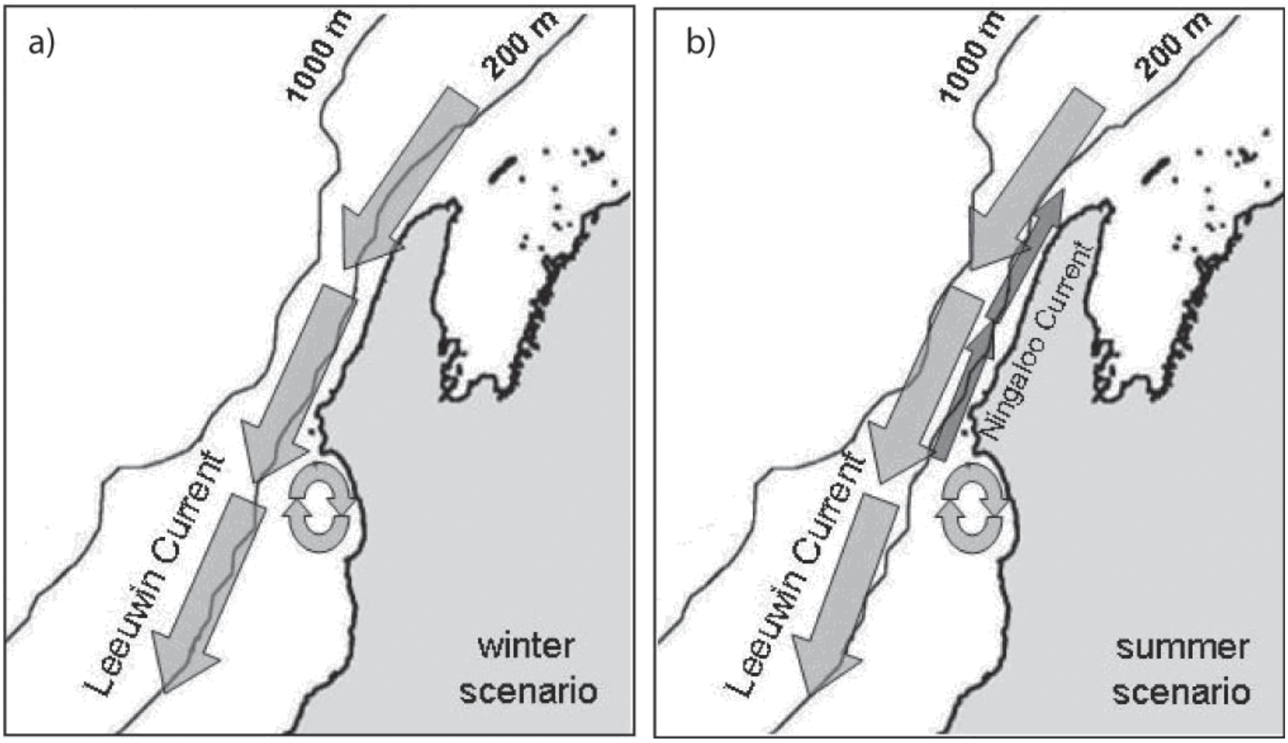

Figure 2. Generalised seasonal circulation patterns off the Ningaloo region, indicating a) the dominance of the Leeuwin Current along the shelf break during the winter months and b) the presence of the northward-flowing Ningaloo Current during the summer months. The re-circulation pattern south of Point Cloates is a persistent feature.

maximum nitrate concentrations were ~ 2–6 mM in upwelled water within the euphotic zone (~100 m) off North West Cape (Hanson *et al*. 2005), substantially lower than in the major upwelling regions associated with equatorward eastern boundary currents (*e.g.*, up to 20–30 mM NO_3^- in the eastern Pacific; Dickson & Wheeler 1995; Kudela *et al*. 1997).

The relatively modest level of nutrient enrichment (~ 2–6 mM nitrate) resulting from upwelling generates primary production rates off Ningaloo that are significantly higher than in the LC proper. Total water column productivity off the Cape Range peninsula ranged between 850 and 1300 mg C m^{-2} d^{-1} (Hanson *et al*. 2005), and have been measured as high as 3000–8000 mg C m^{-2} d^{-1} off North West Cape (Furnas 2007), though these high rates were not sustained. These high rates of primary productivity undoubtedly play an important role in the food web dynamics of the region. For example, it is unlikely to be a coincidence that the highly productive Ningaloo Current is located next to a major coral reef system and adjacent to the rich prawn fishery in Exmouth Gulf, the second largest in WA (770–1500 tonnes yr^{-1}; Kangas *et al*. 2006).

The original view of phytoplankton communities within the LC, primarily obtained via ocean colour satellite imagery (Pearce *et al*. 2000), was one of extremely low biomass (0.1 mg chl *a* m^{-3}). However, recent *in situ* measurements found significant vertical biomass gradients, with phytoplankton forming a deep chlorophyll maximum (DCM) associated with the nitracline at the base of the LC's mixed layer (Hanson *et al*. 2005, 2007a). These DCMs (which are also maxima of phytoplankton carbon) can have chlorophyll concentrations of 0.9 mg m^{-3} or higher, and in the LC are associated with a maximum of 30 to 70% of total water column production. However off the Ningaloo region, the upwelling dynamics and shoaled nutricline can result in a DCM layer that is relatively shallow (~ 30–40 m depth; Hanson *et al*. 2007). The large phytoplankton populations in these layers are able to take advantage of higher light levels at these depths, resulting in an extremely productive DCM that can account for 80–95% of total water column production and yet remains largely beyond the range of surface-based satellite biomass measurements.

During the summer of 2000, phytoplankton community composition within the Leeuwin Current and offshore waters showed only 40–55 % similarity to Ningaloo Current waters (based on HPLC pigment analysis), displaying high proportions of picoplankton such as cyanobacteria in surface waters and prochlorophytes at the DCM (Hanson *et al*. 2007b). In contrast, diatoms and haptophytes were found to be more prevalent in the Ningaloo Current. The size-fractionated work by Furnas (2007) showed that large phytoplankton > 10 mm (particularly centric diatoms) were common off NW Cape during upwelling conditions. These species are classically associated with nutrient-rich conditions with significant 'new' inputs of nitrate, leading to the relatively short and productive 'herbivorous' food chain from large phytoplankton to copepods to fish (Cushing 1989). Yet interestingly, Hanson *et al*. (2007b) found that ammonium-driven 'regenerated' production (which is typically based on recycling of nitrogenous nutrients within the food web) can dominate throughout the study region, accounting for over 80% of total nitrogen uptake even in the upwelling-influenced Ningaloo Current. Nitrogen recycling via the multi-layered microbial food web (which leads from bacteria and picoplankton to protozoa, ciliates and microzooplankton; Azam *et al*. 1983; Cushing 1989) has been shown to complement the shorter nitrate-based herbivorous food chain within upwelling zones (Codispoti 1983; Probyn *et al*. 1990; Bode *et al*. 2004), and in the Ningaloo region seems to play a large part in sustaining productivity levels that may have initially been generated by advective nitrate fluxes.

The biological impact of upwelling in the Ningaloo region is a function of: (a) conditions within the Leeuwin Current (*e.g.*, depth of mixed layer and nutricline), (b) the strength and duration of upwelling-favourable winds (*i.e.*, the intensity of upwelling), and (c) geographical location, primarily with respect to the width of the continental shelf and resultant proximity of upwelling flows to deep nutrient pools (Hanson *et al*. 2005). Furnas (2007) compared the effect of different physical forcing scenarios occurring El Niño and La Niña years on phytoplankton and bacterial dynamics. During El Niño years, the Leeuwin Current is weaker, with a thinner mixed layer and a higher associated frequency of coastal upwelling events (Condie & Dunn 2006; Furnas 2007). During upwelling events in the El Niño summer of 1997/98, there were episodes of very high primary production – up to 8000 mg C m^{-2} d^{-1} (as measured by the incorporation of ^{14}C-bicarbonate). These production events were strongly pulsed – measurements at the same slope station a few days apart differed by over a factor of four (Furnas 2007) and did not generally persist. However, during the La Niña of 1998/99 a stronger Leeuwin Current suppressed the tendency of the system to upwell, and resulted in generally lower rates of primary production, and fewer instances of production exceeding 2000 mg C m^{-2} d^{-1}.

Measurements of oxygen flux in the water column indicate that the waters immediately adjacent to Ningaloo Reef are strongly autotrophic, with P:R ratios between 2 and 6 (Table 1). Respiration rates frequently exceed 1000 mg C m^{-2} d^{-1}, possibly reflecting bacterial degradation of detrital material within the water column, and net primary productivity rates using the oxygen flux method frequently exceed 2000 mg C m^{-2} d^{-1}. Bacterial production rates on the slope off North West Cape, measured from the incorporation of ^{3}H-thymidine, were correlated with primary productivity rates (~18% of primary production), and were on average 6-fold higher in El Niño conditions than in La Niña conditions (median 620 mg m^{-2} d^{-1}, cf 110 mg m^{-2} d^{-1}; Furnas 2007).

The intensity of coastal upwelling (most prevalent during El Niño years) is also closely linked to the ambient wind field (Barber & Smith 1981), further highlighting the episodic nature of any associated nutrient fluxes. The large phytoplankton biomass and high productivity measured off Ningaloo may provide a seasonally predictable, but patchily distributed, input of food resources to the micro- and mesozooplankton populations within the region (discussed below), which in turn are regularly exploited by the large filter feeders (*e.g.*, manta rays and whale sharks) that are seasonal visitors to this region (Taylor 1994). The extent of such bottom-up control of trophic structure off Ningaloo is certainly one area requiring further research.

Zooplankton dynamics

There is no data available on the zooplankton communities of the Leeuwin Current per se, though studies are in progress (Strzelecki *pers. com.*). Further south (31°), off Perth, the microzooplankton (Paterson *et al*. 2007) and mesozooplankton (Strzelecki *et al*. 2007) communities of warm core rings largely originating from the LC have been described. Microzooplankton abundance in the vicinity of North West Cape was 620 cells L^{-1} (Moritz *et al*. 2006), but 1500–2600 cells L^{-1} in the warm core eddy off Perth (Paterson *et al*. 2007). Tranter (1977a) and co-workers described copepod, euphausiid, amphipod and euthecostome communities in the eastern Indian Ocean along the 110° E meridian between 9° and 32° S, and taken together with the study of Strzelecki *et al*. (2007) the data straddle the area of influence of the LC but do not include it. Moreover, differences in sampling methodology (plankton net mesh size and sampling strategy) make direct comparisons between mesozooplankton studies difficult.

Copepods are the dominant organisms in the mesozooplankton of the Ningaloo area (McKinnon & Duggan 2001), and >120 species were recorded from stations occupied around North West Cape. Small calanoid copepods belonging to the families Paracalanidae and Clausocalanidae dominate, together with small cyclopoid copepods belonging to the Oithonidae, Corycaeidae and Oncaeidae (McKinnon *et al*. 2008). The dominant genera of small calanoid copepods (*e.g*., *Calocalanus*, *Paracalanus*, *Clausocalanus*) are common

Table 1

Community respiration (CR) and net primary production (NPP) at Ningaloo Reef in April of 2003 and 2004. The P:R ratio represents the ratio of gross primary production (CR+NPP):CR. See McKinnon *et al*. (2007) for methods.

Date	Latitude	Longitude	Depth (m)	CR (mg C m^{-2} d^{-1})	NPP (mg C m^{-2} d^{-1})	P:R
11-Apr-02	21 35.95	113 59.68	250	550.29	561.28	2.02
16-Apr-02	22 41.03	113 32.93	100	1735.71	2680.39	2.54
19-Apr-02	22 43.35	113 36.35	52	1250.91	2260.16	2.81
24-Apr-03	22 43.88	113 38.30	28	597.02	1647.35	3.76
26-Apr-03	22 44.27	113 36.78	56	1045.14	2503.35	3.40
28-Apr-03	22 45.14	113 32.96	70	1171.29	5517.64	5.71
29-Apr-03	22 43.10	113 36.27	50	579.96	2142.32	4.69

generalist suspension feeders that are pre-adapted to upwelling, in that they are able to achieve life cycle closure under these advective conditions (Peterson 1998). The most notable absence from the Ningaloo fauna is *Calanoides carinatus*, a copepod that is characteristic of upwelling regimes, despite its occurrence in the broader region (Tranter 1977b). It therefore appears that upwelling is too infrequent and episodic to sustain a zooplankton fauna specific to upwelling regimes.

Generally, the action of the Leeuwin Current entrains a southward flow of water off the shallow NW shelf. McKinnon *et al*. (2003) documented the effect of Cyclone Tiffany on the plankton communities of the NW shelf. This cyclone moved in a SW direction, pushing the water and plankton ahead of it down to the vicinity of NW Cape, causing an elevation in water temperature, and a shift in plankton communities toward those typical of the inshore tropical environments to the north. The movement of the Leeuwin Current probably has the same effect, by entraining shallow water tropical coastal communities southward – as indicated by the contribution of small, typically inshore calanoid copepods such as *Bestiolina similis* and *Parvocalanus crassirostris* to the copepod communities in the vicinity of Ningaloo.

Macrozooplankton, as sampled by light traps, were more abundant in El Niño conditions than in La Niña conditions, primarily because of the greater contribution of amphipods (Wilson *et al*. 2003a). Subsequent macrozooplankton research in the vicinity has focused on krill (Euphausiacea), as these were believed to be important resources targeted by megafauna (see below). The most abundant euphausiid in the area is *Pseudeuphausia latifrons* (98% of euphausiid catches), though 3 other species do occur (Wilson *et al*. 2003b). *P. latifrons* was more abundant in La Niña conditions, possibly because of a preference for warmer water (Wilson *et al*. 2003b).

Unfortunately, despite the obvious abundance of gelatinous zooplankton in the area, there is no published information.

Bongo net collections made in the vicinity of NW Cape contained the larvae of 76 families of fishes (Sampey *et al*. 2004). In the two summers of that study, there was a similar community composition in each year, though some families (*e.g*., Pomacentridae, Carangidae) showed differences in abundance. Most larvae preyed upon copepods, and individual families of fishes exhibited strong selection for particular taxa (Sampey *et al*. 2007). Late stage larvae sampled with light traps were threefold higher in La Niña conditions, and differed markedly in community composition between El Niño and La Niña years (Meekan *et al*. 2006a), and richest catches occurred at stations characterised by high mixing.

Secondary production and food chains

Dilution experiments conducted near NW Cape indicate that ~100% of picoplankton (*Synechococcus* and *Prochlorococcus*; counted by flow cytometry) production is grazed each day, but only ~60% of the total phytoplankton community (as indicated by chlorophyll a concentration) is grazed by micrograzers (McKinnon *et al*. unpublished); these estimates are consistent with those of Paterson *et al*. (2007, 2008), further south. This implies that the balance of primary production is consumed within the water column by meso- and macrozooplankton or settles out to become available to benthic consumers. One of the unresolved challenges in the ecology of the NW is to account for the carbon source which drives benthic food chains in the area. Exmouth Gulf, in particular, has a very productive prawn fishery; in the absence of significant terrigenous inputs the only source of primary production that could drive this fishery is pelagic.

In spite of the differences observed by Furnas (2007) in primary production rates near NW Cape between El Niño (weak LC) and La Niña years, copepod production rates measured on the same cruises did not differ substantially (McKinnon & Duggan 2001, 2003), and were generally low (~13 mg C m^{-2} d^{-1}). We suspect the cause of the anomaly between high rates of primary production and low rates of secondary production is the highly pulsed nature of upwelling, a strongly advective physical environment and a domination of food web structure by microbial processes. The dominance of microbial processes hinted at from the results of the dilution experiments can be confirmed by a comparison of primary and secondary production rates (Table 2). Copepods are highly inefficient grazers of particles <2μm in size; therefore restricting the primary production numbers to the range of cell sizes available to copepod grazers and comparing that to their production rates, we find that the food web linking primary production to mesozooplankton is only ~1% efficient. Similar calculations on upwelling systems, such as the Benguela, result in trophic efficiencies of the order of 10%.

Low rates of secondary (copepod) production off the coast of NW Australia are reflected further up the food chain by fisheries statistics. Catches of finfish species off the Western Australian coast are low by world standards (Lenanton *et al*. 1991), and the large biomass of pelagic planktivores characteristic of other eastern boundary current ecosystems does not occur. Meekan *et al*. (2003) compared the growth rates of the coral reef fish *Pomacentrus coelestis* in El Niño (upwelling favourable, high plankton production) and La Niña years (lower incidence of upwelling, lower plankton production, higher water temperatures). Fish grew faster in the La Niña year, suggesting that in this case, temperature rather than food supply was more important in determining growth rate.

Table 2

Pelagic food chain efficiency. Primary production is taken from the data of Furnas (2007), and copepod production from McKinnon & Duggan (2003), meaned over 10 field trips in two summers (Oct–Feb).

		Shelf	Shelf Break
>2μm primary production	mg C m^{-3} d^{-1}	38	13
Copepod production	mg C m^{-3} d^{-1}	0.4	0.1
Transfer efficiency	%	1.2	1.1

The Leeuwin Current and the movement of megafauna

The seasonal aggregation of whalesharks at Ningaloo Reef between March and June of each year is one of the best known features of the area, and is the basis of a lucrative ecotourism industry. The cause of this predictable occurrence is still open to speculation, but the most likely explanation is a trophic one. Taylor (1994) proposed that whale sharks fed on aggregations of zooplankton and small fish associated with the coral spawning that occurs at this time of year. However, such short-lived events do not explain the occurrence of whale sharks in the area for a period of months. Whale sharks are known to feed on aggregations of chaetognaths (Rowat *et al* 2008), plankton (Taylor 1996), tropical krill (Wilson & Newbound 2001; Jarman & Wilson 2004), fish spawn (Heyman *et al*. 2001) and baitfishes (Wilson *et al*. 2006). At present there is nothing known about the annual patterns in abundance or behaviour of plankton and their predators in waters adjacent to Ningaloo, in part because of the logistic difficulty of sampling in offshore waters year-round. However, the occurrence of episodically high plankton production and the seasonal aggregation of large planktivores in the same geographic area is a co-incidence too large to ignore.

The Leeuwin Current is strongest between April and September (Godfrey & Ridgeway 1985). There is currently no data to indicate where whale sharks arriving at Ningaloo have come from, but it is known that many sharks return to the area each year (Meekan *et al*. 2006b; Bradshaw *et al*. 2007). Whale shark abundance at Ningaloo is negatively correlated to the SOI, indicating that there are more sharks in years in which there is a strong LC (Sleeman *et al*. in press). In this case, it may be that the sharks "ride" the Leeuwin Current to arrive at Ningaloo (as suggested by Wilson *et al*. 2001). Tagging studies of whale sharks indicate that the animals move in a northerly direction, toward Indonesia, when they leave Ningaloo Reef, in which case they would be swimming against the LC and possibly using it as a directional cue (Wilson *et al*. 2006) . Archival tagging studies (Wilson *et al*. 2006) indicate whale sharks are easily capable of diving to considerable depth, and could avoid the influence of the current by diving beneath it. Despite this, the depth records shown by Wilson *et al*. (2006) are predominantly shallow.

Other megafauna occur in waters adjacent to Ningaloo Reef, including humpback and pygmy blue whales, dolphins, sharks, turtles, manta rays and dugongs. However, biophysical variables, including those such as SST that may be correlated with the influence of the Leeuwin Current, accounted for only a small proportion of the variance in abundance of megafauna (Sleeman *et al*. 2007).

Links to the benthos

To date, investigations into the coupling between pelagic and benthic dynamics at Ningaloo have been limited. The physical effect of the Leeuwin Current on dispersal of benthic (and also pelagic) organisms is two-fold. Firstly, the net movement of propagules is southward with the dominant current flow, and is responsible for the occurrence of tropical animals in SW Australia (Hutchins 1991 and papers therein). Secondly, the formation of the NC forms a closed cell in which local propagules may well be retained, and coral spawning within the Ningaloo region may be timed to coincide with the presence of the NC (Taylor & Pearce 1999). Simpson (1991) examined the mass spawning of scleractinian corals along the WA coast, which generally coincides with periods of maximum seawater temperatures (March/April at Ningaloo) and the annual intensification of the Leeuwin Current, which would provide a physical mechanism for the southward dispersal of coral planulae. As also suggested by Babcock *et al*. (1994), this would potentially result in unidirectional (southward) gene flow between WA coral reefs (*e.g*., from Ningaloo to reefs at the Abrolhos Islands; Figure 1). However, recent genetic studies by Whitaker (2004, 2006) on three species of broadcast spawning corals at Ningaloo found restricted genetic mixing even at distances of 7–24 km, suggesting that large-scale dispersal from the Ningaloo region may be relatively infrequent.

There is likely to be significant connectivity between the pelagic production dynamics off Ningaloo and the benthic fauna of the region, although there is little published work on this theme. In 2004, a series of deep water (to 200 m depth) biodiversity surveys off Ningaloo revealed significant populations of benthic filter feeding organisms, particularly sponges and gorgonian corals (Rees *et al*. 2004). It is interesting to speculate on the potential links between the nutrition of these filter feeders, the productive deep chlorophyll maximum layers within the Leeuwin and Ningaloo Currents, and seasonal influxes of live and detrital particulate material associated with summer upwelling blooms. In shallower waters, there is significant exchange between shelf waters and those of the reef lagoon, with wave action transporting shelf water over the reef front and lagoon waters escaping to the shelf through the reef gaps (Taylor & Pearce 1999). Studies currently underway aim to quantify the fraction of reef productivity driven by oceanic nutrient sources at Ningaloo, using biomarker techniques and coral laboratory studies (A. Wyatt, *pers. comm*.).

Conclusions

The Leeuwin Current is the primary physical forcing factor determining the pelagic ecology of the Ningaloo region off Western Australia, with the key dynamics highlighted in this paper illustrated schematically in Figure 3. Series of episodic, cryptic upwelling events have been observed during the summer months off Ningaloo, especially during El Niño years when the Leeuwin Current is weaker and the wind-driven Ningaloo Current is stronger. Under these conditions, Ekman transport results in moderate influxes of nutrients within the euphotic zone that can generate localised events of high phytoplankton productivity. Based on grazing rates and levels of mesozooplankton production, it is apparent that microbial-scale processes may be key to the pelagic trophodynamics of the region (Figure 3). There are many unresolved challenges in understanding the ecology of the waters off Ningaloo, including determining annual patterns in both primary and secondary production, and quantifying the links between pelagic and benthic dynamics.

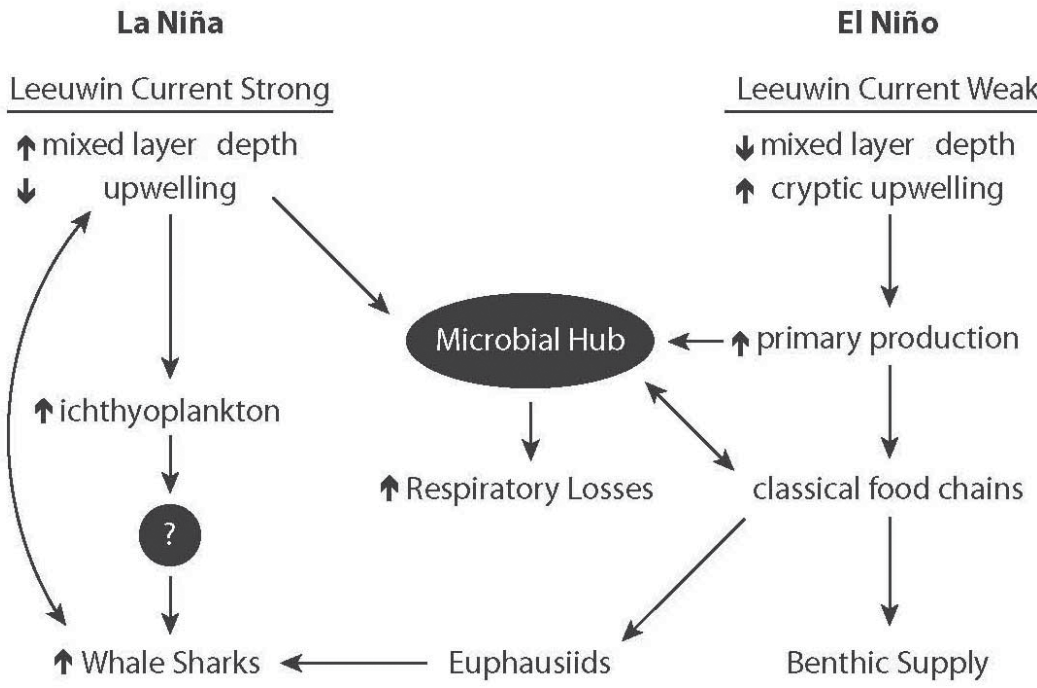

Figure 3. Schematic indicating the key linkages within the pelagic ecology of the Ningaloo region, and the impact of the contrasting physical forcing scenarios under La Niña and El Niño conditions.

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