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S. J. Hawkins, A. L. Allcock, A. E. Bates, A. J. Evans, L. B. Firth,
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Chapter 4

The Oceanography and Marine Ecology of Ningaloo, A World Heritage Area

Mathew A. Vanderklift, Russell C. Babcock, Peter B. Barnes, Anna K. Cresswell, Ming Feng, Michael D. E. Haywood, Thomas H. Holmes, Paul S. Lavery, Richard D. Pillans, Claire B. Smallwood, Damian P. Thomson, Anton D. Tucker, Kelly Waples & Shaun K. Wilson

THE OCEANOGRAPHY AND MARINE ECOLOGY OF NINGALOO, A WORLD HERITAGE AREA

MATHEW A. VANDERKLIFT[1], RUSSELL C. BABCOCK[2], PETER B. BARNES[4], ANNA K. CRESSWELL[1,3,5], MING FENG[1], MICHAEL D. E. HAYWOOD[2], THOMAS H. HOLMES[6], PAUL S. LAVERY[7], RICHARD D. PILLANS[2], CLAIRE B. SMALLWOOD[8], DAMIAN P. THOMSON[1], ANTON D. TUCKER[6], KELLY WAPLES[6] & SHAUN K. WILSON[6]

*[1]CSIRO Oceans & Atmosphere, Indian Ocean Marine
Research Centre, Crawley, WA, 6009, Australia*
[2]CSIRO Oceans & Atmosphere, Queensland Biosciences Precinct, St Lucia, QLD, 4067, Australia
*[3]School of Biological Sciences, The University of Western
Australia, Crawley, WA, 6009, Australia*
[4]Department of Biodiversity, Conservation and Attractions, Exmouth, WA, 6707, Australia
[5]Oceans Institute, The University of Western Australia, Crawley, WA, 6009, Australia
*[6]Marine Science Program, Department of Biodiversity, Conservation
and Attractions, Kensington, WA, 6151, Australia*
*[7]School of Science and Centre for Marine Ecosystems Research,
Edith Cowan University, Joondalup, WA, 6027, Australia*
[8]Department of Primary Industries and Regional Development, Exmouth, WA, 6707, Australia

Abstract   The Ningaloo coast of north-western Australia (eastern Indian Ocean) hosts one of the world's longest and most extensive fringing coral reef systems, along with globally significant abundances of large marine fauna such as whale sharks. These characteristics – which have contributed to its inscription on the World Heritage list – exist because of the unique climatic, geomorphologic and oceanographic conditions. The region is hot and arid, so runoff of water from land is low, facilitating clear water that allows corals to grow close to the shore. The poleward-flowing Leeuwin Current is an important influence, bringing warm water and generally suppressing coastal upwelling. During the austral summer, strong southerly winds generate the equatorward-flowing Ningaloo Current on the inner shelf – this current facilitates sporadic upwelling events that enhance concentrations of nutrients, which in turn enhance pelagic primary productivity that supports the reef's biota. The coast has experienced several marine heatwaves since 2011 that have caused mortality of corals and probably seagrass, albeit relatively less than elsewhere along the coast. Wind-generated surface waves break over the fringing reef crest, causing cooling currents that tend to dampen warming – although this mechanism seems not to have prevented some areas from experiencing damaging heat, and corals in places that do not receive the wave-generated currents have experienced substantial mortality. Herbivores, from fish to green turtles, are abundant, and in the lagoon, extensive stands of large brown algae provide an important habitat for newly recruited fish. There has been a decline in abundance of some fish. Predictions of future pressures include a weaker but more variable Leeuwin Current and increased human use. The ability of Ningaloo's

ecosystems to withstand growing pressures will depend partly on the rate and magnitude of global warming but also on actions that manage local pressures from increasing human use. These actions will rely on continued science to provide the evidence needed to identify the pressures, the changes they create and the ways that we can mitigate them.

Introduction

Ecologists have long noted that the tropics, conventionally defined as the latitudes between the tropics of Cancer and Capricorn (~23.4° N and S of the equator, respectively), host a greater diversity of species than other regions (Barlow et al. 2018). In particular, the diversity of three marine habitat-forming taxa – corals, seagrasses and mangroves – is highest in the tropics. This diversity is especially high in the 'Coral Triangle', which encompasses Indonesia, Malaysia, Papua New Guinea, Philippines, Solomon Islands and Timor-Leste (Hoeksema 2007). This region hosts most of the world's species of reef-building corals, seagrasses and mangroves and a very high proportion of the world's species of fishes and other taxa associated with these habitats. The area covered by these three habitats is declining (Waycott et al. 2009, Polidoro et al. 2010, Hughes et al. 2018), with cascading impacts on the species that inhabit them and the human societies that rely on them.

All three of these habitats are pantropically distributed (and also extend into cooler latitudes). Coral reefs tend to occur mostly between the latitudes of 30°S and N, a distribution which is largely determined by the thermal tolerances of scleractinian (hard) corals and their endosymbiotic dinoflagellates (zooxanthellae: Spalding et al. 2001). These thermal tolerances are now being regularly exceeded, causing corals to bleach (a process in which the zooxanthellae are expelled), which is followed by death if the corals do not regain the zooxanthellae (Hoegh-Guldberg 1999, Hughes et al. 2018). This process, in concert with numerous other injuries arising from poor water quality and direct destruction, has led to a decline in the number and quality of coral reefs worldwide (Spalding & Brown 2015).

Most of the world's coral reefs are already threatened in some way by human activities (Burke et al. 2011, Hughes et al. 2018). One coral reef that has so far mostly escaped the worst degradation is Ningaloo, a predominantly fringing reef that abuts the arid coast of north-western Australia, a thousand or so kilometres south-west of the Coral Triangle. Ningaloo has been relatively unscathed by the global pressures that have caused degradation of many coral reefs (although not every part of Ningaloo has escaped, which we review later in this paper). It is one of only three (of 29) World Heritage–listed coral reefs not expected to experience bleaching at least twice per decade by 2041 (a frequency that is likely to cause total mortality) under Representative Concentration Pathway (RCP) 8.5 climate projections (Heron et al. 2017); however, the same models predict that bleaching will occur at least twice per decade after 2041. This deferral of the fate predicted for so many other coral reefs is due to multiple contributing influences, including unique weather and oceanography and relatively low rates of human use, which we review here. These characteristics make Ningaloo globally important, because a high abundance and diversity of coral (and associated taxa) might persist there after other coral reefs have been severely affected.

Ningaloo is contained within the Ningaloo Coast World Heritage Area (NCWHA), which includes land and sea, and was inscribed in part because of the high diversity of corals and coral-associated species, the globally important annual aggregations of whale sharks and the high abundances of large marine fauna like sea turtles and elasmobranchs (http://whc.unesco.org/en/decisions/4278; accessed 15 March 2019). Much of Ningaloo, including the coral reef and surrounding marine habitats, also falls within marine parks and reserves managed by state (Western Australia) and national (Australia) governments (Figure 1); of this, much is within highly protected 'no-take' (IUCN Category II) reserves (e.g. 34% of the area within the state-managed Ningaloo Marine Park, and 4.8% of the nationally managed Ningaloo Marine Park, is within IUCN Category II reserves).
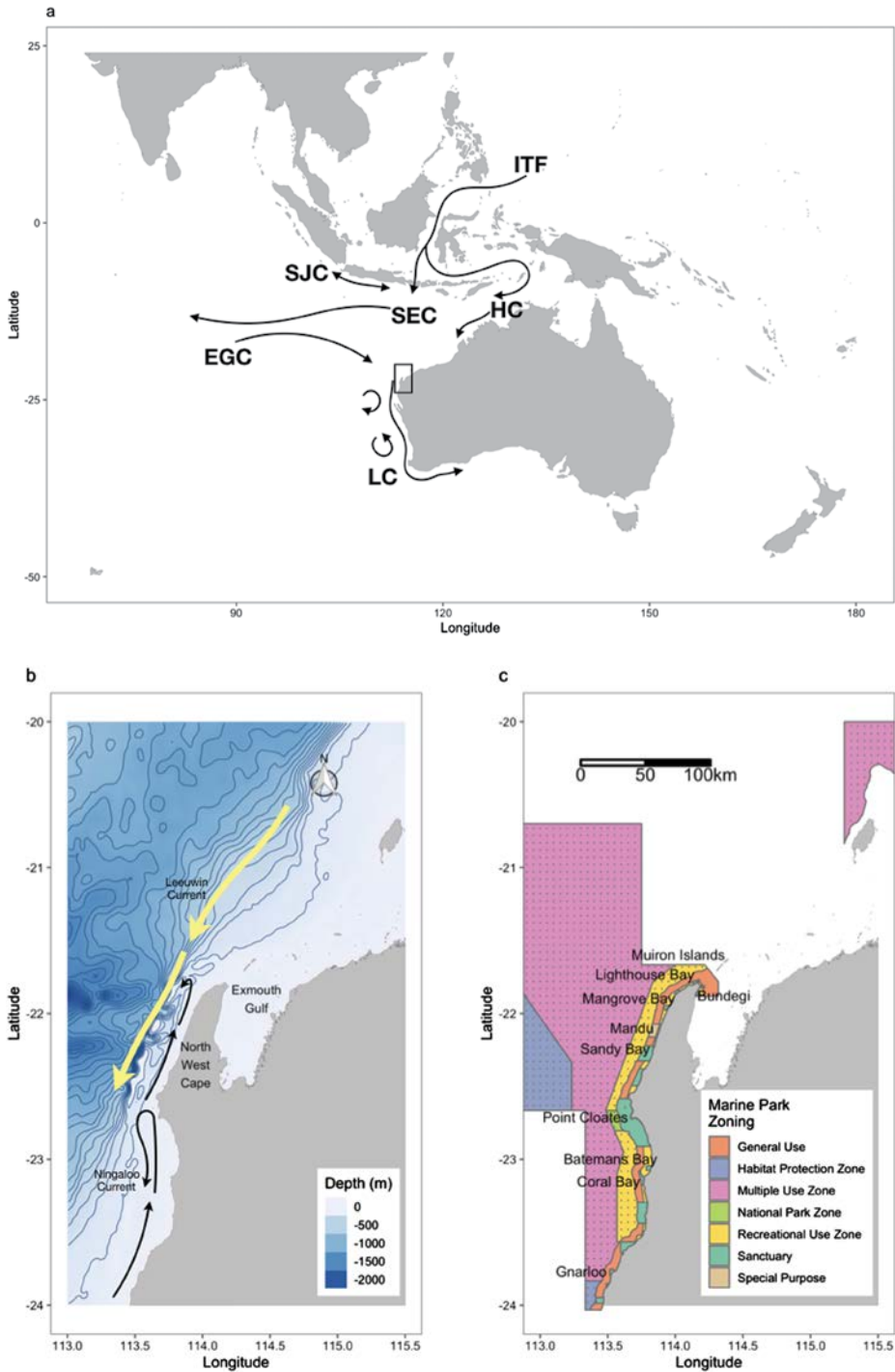
Figure 1 (a) Location of Ningaloo (black rectangle) relative to the major oceanographic currents in the region (EGC, East Gyral Current; ITF, Indonesian Throughflow; HC, Holloway Current; LC, Leeuwin Current; SEC, South Equatorial Current; SJC, South Java Current); (b) bathymetry of Ningaloo, and approximate position of the Leeuwin and Ningaloo Currents and (c) the state and Commonwealth marine park zones (Commonwealth marine park zones are speckled).

In this review, we synthesise more than four decades of research at Ningaloo, placing the knowledge gained in the context of the Indo-Pacific region and coral reefs globally. We critically evaluate our current knowledge about the underpinning climate, geomorphology and oceanography at Ningaloo and the biology and ecology of the habitat-forming taxa (such as corals, seagrass and mangroves) and associated biota, with particular emphasis on the taxa that were fundamental to its inscription on the register of World Heritage Areas. As part of this, we examine the threats Ningaloo faces and the features which have helped its coral reefs survive so far and consider whether we should expect these features to persist into the future. We use the term 'Ningaloo' to refer broadly to the area encompassed by the marine parts of the NCWHA, but because many of the relevant ecological processes span boundaries, we also include information from areas immediately adjacent.

The setting: Climate, oceanography and geomorphology

The coral reefs at Ningaloo encompass ∼300 km of coast (2 degrees of latitude, 21°40 S to 23°34 S), south from North West Cape in north-western Australia (eastern Indian Ocean) (Figure 1). The Muiron Islands, ∼15 km from North West Cape, also have well-developed coral reefs, and we include them in this review. The region is hot and arid, with mean daily maximum air temperatures exceeding 37°C in the austral summer and mean monthly rainfall less than 50 mm all year (Figure 2). Mean monthly potential evaporation exceeds 120 mm all year – on average, potential evaporation is 12 times higher than rainfall. Most rainfall occurs within episodic events associated with tropical low-pressure systems, including cyclones, of which 15 have passed over or adjacent to Ningaloo since 1970 (Figure 3). As a result, there is usually little or no terrestrial runoff, so inshore waters are clear, and corals grow only a few metres from the mean low tide mark in many places.
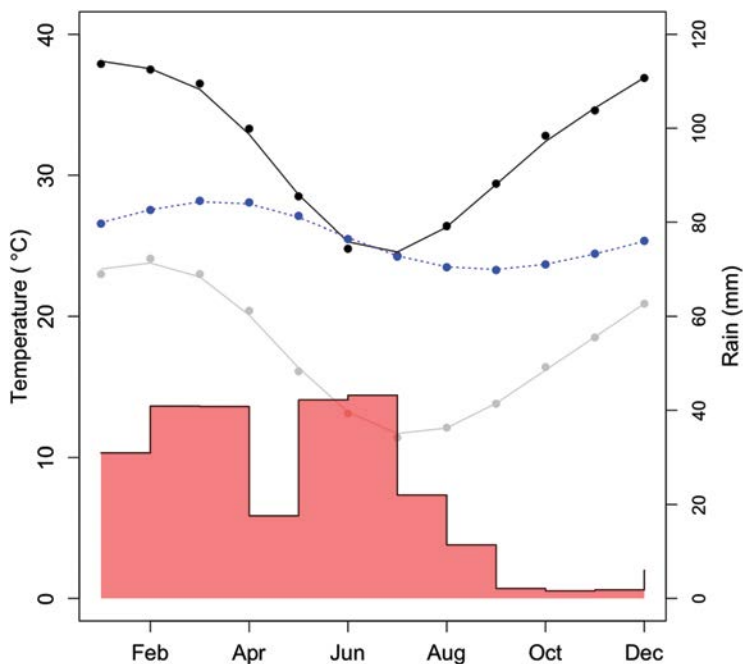

Figure 2 Mean daily maximum (black line) and minimum (grey line) air temperature, mean sea surface temperature (dotted blue line) and mean monthly rainfall (red bars). (Air temperatures and rainfall are from Bureau of Meteorology records from 1970–2018 measured at the Learmonth weather station; sea surface temperatures are from NOAA for 113.5°E, 21.5°S from 1981–2010.)

Cyclones also bring extreme wind conditions, which have the potential to cause significant damage (winds from Cyclone Vance in 1999 were measured at 267 km h^{-1}; http://www.bom.gov.au/cyclone/history/vance.shtml, accessed August 13, 2019). However, the typical wind conditions are also important at Ningaloo – the west side of North West Cape experiences regular strong afternoon sea breezes, exceeding average speeds of 6.6 m s^{-1} (23.7 km h^{-1}) in summer months. These winds bringing cooler water to the reef and facilitate localised upwelling, processes that tend to protect the corals from extreme warming events (Woo et al. 2006).

Situated at the southern edge of the Indo-Pacific warm pool (De Deckker 2016), the ocean currents off Ningaloo are strongly influenced by climate variability in the Indo-Pacific (Zinke et al. 2014). The major oceanographic feature in the region is the poleward-flowing Leeuwin Current (Cresswell & Golding 1980), which is driven by a meridional (i.e. north-south) pressure gradient in the south-eastern Indian Ocean, which in turn is partly caused by the Indonesian Throughflow. This process overrides the normal equatorward flow direction expected for a current on the eastern boundary of an ocean, which would normally bring cooler water. Instead, the Leeuwin Current is a downwelling current, transporting relatively warm, low-salinity (<35.4‰) tropical water southwards (Domingues et al. 2006, Feng et al. 2015).

The Leeuwin Current conveys Pacific Ocean influences into the Indian Ocean through Kelvin and Rossby waves which propagate through the Indonesian archipelago and down the western Australian coast (Feng et al. 2003, Feng et al. 2004, Wijffels & Meyers 2004). These influences include the El Niño-Southern Oscillation (ENSO: the variation in sea surface temperature and wind in the tropical eastern Pacific) and the Interdecadal Pacific Oscillation (long-term increases and decreases in ocean temperature in the Pacific). In 2010–11, a strong La Niña (the phase of ENSO which is associated with cooler water temperatures in the tropical eastern Pacific) caused an unusually strong Leeuwin Current which, combined with a cessation of normal wind patterns, instigated an unprecedented marine heatwave, the 'Ningaloo Niño', off the west coast of Australia
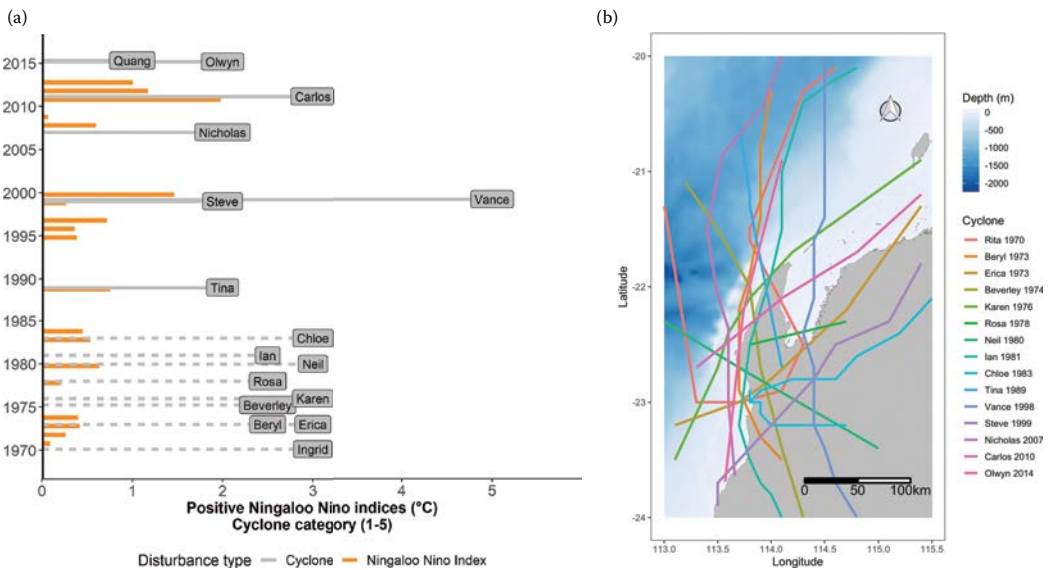
Figure 3 (a) Timeline of two types of ecological disturbance at Ningaloo: cyclones and anomalously high water temperatures. Ningaloo Niños are the strong warming events identified in Feng et al. (2015) from a scaled January–February Ningaloo Niño index. The length of the bar gives an indication of the relative magnitude of the high temperature anomalies (no meaning for the cyclones). (b) Tracks for tropical cyclones that passed over Ningaloo between 1970–2018. (Bureau of Meteorology.)

(Feng et al. 2013; Figure 3). Marine heatwaves in the region can also start from conditions associated with reduced cloud coverage (which causes increased solar radiation) and a weakened Australian monsoon (which causes reduced evaporation) in the Indonesian-Australian basin north of Ningaloo (Benthuysen et al. 2018).

The Leeuwin Current typically contains very low concentrations of dissolved nutrients (e.g. <0.2 μM nitrate), but nutrients can be enhanced during episodes of coastal upwelling. A regular deepening of the mixed layer (within which turbulence mixes the water from the surface to a given depth) in autumn, probably because of a combination of acceleration of the current and heat loss leading to cooler sea surface temperature, also increases nutrient concentrations (Rousseaux et al. 2012). Episodes of coastal upwelling are associated with the Ningaloo Current, a northward-flowing current that runs inshore of the Leeuwin Current, parallel to Ningaloo reef (Taylor & Pearce 1999, Hanson et al. 2005) (Figure 1). The Ningaloo Current brings water with higher nutrient concentrations (up to 2–6 mM nitrate, which is still about an order of magnitude lower than large upwelling systems) onto the continental shelf adjacent to Ningaloo (Hanson et al. 2005). The upwelling is caused by strong southerly winds that occur during late summer and early autumn and by anticlockwise Leeuwin Current eddies in cooler seasons (Rossi et al. 2013, Xu et al. 2015, Zhang et al. 2016). Around northern Ningaloo, the continental shelf is very narrow (in places <10 km wide), so the upwelled water is close to the reef. Upwelling can also be enhanced during El Niño events, when the thermocline (which correlates with the nutricline) is raised closer to the surface (Furnas 2007).

These seasonal or episodic increases in concentrations of dissolved nutrients appear to be important for pelagic primary production. The composition of phytoplankton in the two currents is also different, with the Leeuwin Current dominated by picoplankton, while the Ningaloo Current is dominated by haptophytes and diatoms (Hanson et al. 2007). It seems likely that the nutrients and plankton associated with both upwelling and deepening of the mixed layer are important for reef biota, but the high concentrations of phytoplankton that result from the deepening of the mixed layer in autumn might be more important (Wyatt et al. 2012, Wyatt et al. 2013). Phytoplankton are also food for the zooplankton that probably sustain the seasonal aggregations of whale sharks, but the rates of secondary production are quite low, and trophic pathways remain poorly understood (Hanson & McKinnon 2009, Molony et al. 2011).

An ecologically meaningful feature of water circulation at Ningaloo is wave-induced water flow across the reef and through the lagoon (Figure 4b). Waves breaking on the reef crest cause currents that flow across the reef flat, into the lagoon (Hearn 1999), and then exit the lagoon through reef channels (Figure 4d). Current speeds increase with wave height and are also strongest when tides are 0.2–0.4 m below the mean water level (Taebi et al. 2011). Higher sea levels, such as during La Niña conditions (or in a scenario of sea level rise without concomitant increases in the height of the reef surface), would tend to reduce the wave-driven circulation and increase the amount of time it takes to flush the lagoon (Taebi & Pattiaratchi 2014).

The wave-driven flows across the reef are important for bringing nutrients and food particles. As water flows across the reef, chlorophyll concentrations decline (Wyatt et al. 2010), with many different phytoplankton taxa being removed (Patten et al. 2011), presumably by corals and other suspension feeders. When conditions are favourable for upwelling, the reef appears to be a net nutrient sink, while when upwelling is absent, it is a net source (Wyatt et al. 2012). Since the main oceanographic features (the strength and depth of the Leeuwin Current and the episodes of upwelling) are quite seasonal, it is probable that this is reflected in the ecology of the reef, but our knowledge of these patterns remains scarce.

The wave-driven flows are also an important influence on water temperature over the reef and lagoon. Sea surface temperatures at Ningaloo vary from ∼24–26°C on average (Falter et al. 2014; see also Figure 2) and have warmed over the last century by perhaps more than 1°C (Kuhnert et al. 2000, Zinke et al. 2015), but lagoon water can be cooled as waves bring water over the reef and into the lagoon.
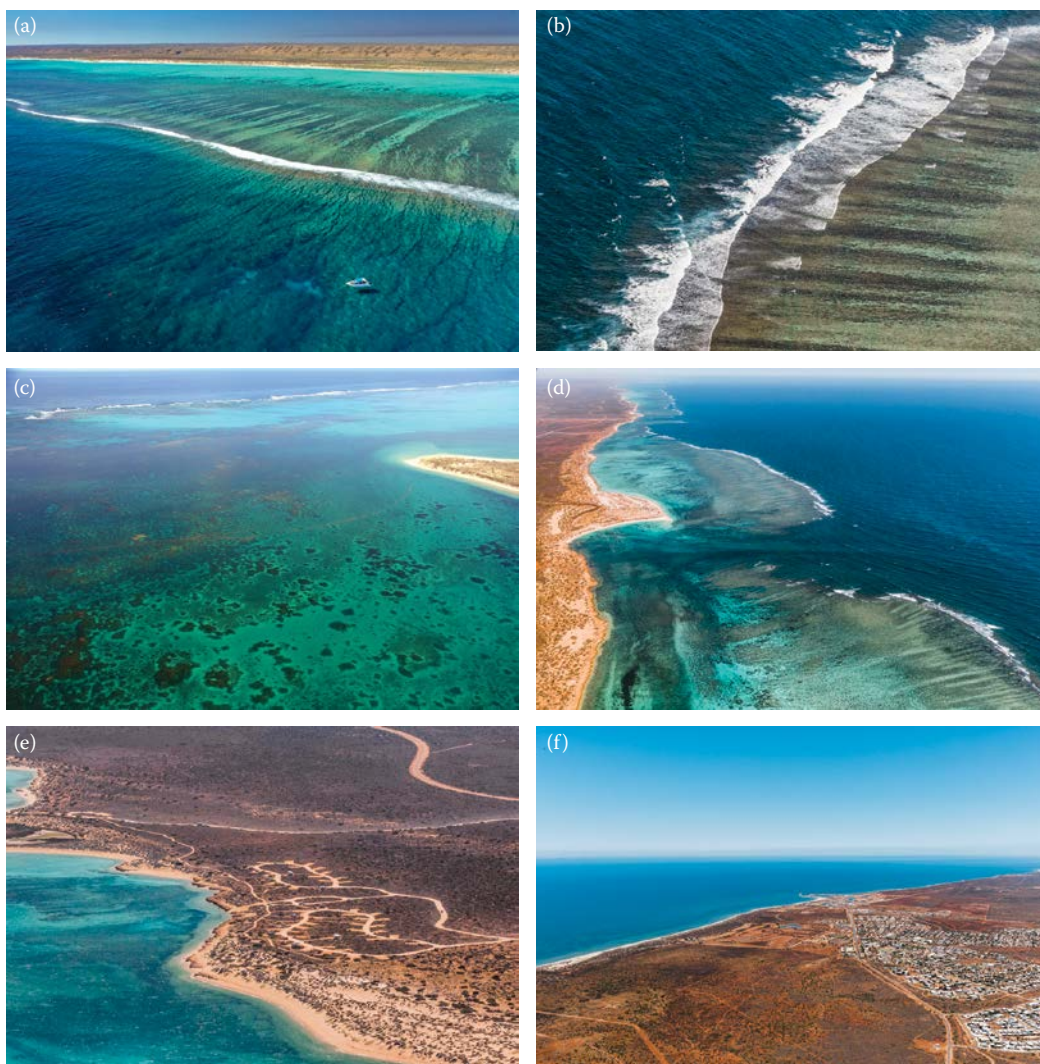
Figure 4 Aerial perspectives of Ningaloo. (a) View from the reef slope towards the lagoon in unusually calm conditions (photo credit: Nick Thake); (b) waves breaking over the reef (photo credit: Violeta Brosig); (c) lagoon with coral bommies (photo credit: DBCA); (d) between sections of the reef at Ningaloo (photo credit: Violeta Brosig); (e) camping area at Osprey Bay (photo credit: Violeta Brosig); (f) town of Exmouth looking towards Exmouth Gulf (photo credit: Violeta Brosig).

Much of Ningaloo is composed of fringing reefs, with a shallow (usually <5 m deep) sand- and low relief limestone-dominated lagoon which is up to 6 km wide, a reef flat (usually <150 m wide) and a reef slope to approximately 30–35 m depth, often characterised by spur-and-groove formations (Cassata & Collins 2008: Figure 4a, Figure 5a). In several sections, the reefs are not contiguous, particularly in the southern parts and on the eastern side of North West Cape, where the reefs are mainly patch reefs (Twiggs & Collins 2010). The geomorphology has a profound influence on the distribution of the major benthic habitat-forming organisms (Figure 5a–g), with hard corals dominating the reef flat and reef slope in depths shallower than 40 m, macroalgae dominating the lagoons and unconsolidated sediments interspersed with patches of suspension-feeding sessile invertebrates occurring in deeper areas (Kobryn et al. 2013, Turner, Babcock et al. 2018).

Corals: The foundation of the reef

Up to 217 species of scleractinian corals have been recorded from Ningaloo (Veron & Marsh 1988, Veron 1995), although this number is likely to be an underestimate (Richards & Rosser 2012). The number of species is similar to that of other parts of north-western Australia (Veron 1995, Richards & Rosser 2012), but numbers drop markedly south of Ningaloo, with the exception of relatively high diversity at the offshore Houtman-Abrolhos Islands, where there are at least 184 species (Veron & Marsh 1988, Veron 1995). Although the number of species is fairly typical for a coral reef at this latitude, the extensive development of the coastal fringing reefs is remarkable (Wilson 2013), and Ningaloo constitutes one of the world's longest and most extensive fringing reef systems. Crustose coralline algae (CCA) are also major sources of reef accretion, while other taxa such as hydrocorals from the genus *Millepora* appear to contribute in wave-exposed or high-current locations, such as in reef passes. Around the Muiron Islands, soft corals (Alcyonaria) are relatively more abundant (Cassata & Collins 2008) and might also make a significant contribution as habitat providers.

Ningaloo's habitats have been mapped using airborne hyperspectral surveys (Kobryn et al. 2013) and multiple discrete habitat types identified (Figure 5). On the seaward side, at the base of the reef slope (∼35 m), the living coral is dominated by encrusting, plate-forming and sub-massive morphs (Turner, Babcock et al. 2018). The percentage cover of living coral at these depths is low (<1%) relative to that reported from similar depths on other coral reefs (Khang et al. 2010). However, many of those studies have been carried out at oceanic locations surrounded by deep water with high water clarity, which allows light – a fundamental requirement of all reef-building corals – to penetrate to greater depths (Turner et al. 2017). At Ningaloo, the reef structure stops at around 35 m, where it transitions to flat, sediment-covered continental shelf. At these depths (∼40 m), low light (1.9% of surface photosynthetically active radiation; Turner, Babcock et al. 2018), which is probably caused by the presence of phytoplankton and resuspended sediment in the water, likely limits the abundance of living coral (Turner, Thomson et al. 2018). The percentage cover of living coral on the reef slope increases to ∼15% at around 25 m; acroporid corals are relatively less abundant here, and poritid corals dominate. Percentage cover of living coral peaks at 3 m, where it approaches 20% and the coral assemblage is dominated by Acroporidae (Turner, Thomson et al. 2018). The shallow reef slope and the reef flat (Figure 5b), which extend up to several hundred metres either side of the reef crest, are characterised by high percentage cover of CCA (∼80%) and living coral (∼20%, mainly digitate Acroporidae). This transitions to a shallow (∼1 m deep) inner reef flat where the percentage cover of living coral can be as high as 90%, with an assemblage dominated by tabular *Acropora*, mainly *A. spicifera* (Figure 5b). Colonies of this species are fragile and can only develop to their full extent on parts of the reef that are sheltered from strong water motion. The reef flat transitions to the back reef (∼2 m deep) where the percentage cover of living coral is 20%–50%, and the assemblage is also dominated by *Acropora*, but is taxonomically and structurally more diverse, containing arborescent and corymbose forms of *Acropora* and greater numbers of massive corals such as Faviidae (Cassata & Collins 2008). The sandy-bottomed lagoon is populated by sparsely distributed colonies of coral growing attached to underlying limestone pavement and by large patch reefs ('bommies') in deeper areas (3–15 m) (Cassata & Collins 2008; Figure 4c). These bommies are frequently associated with (and probably formed around) massive *Porites* colonies, which are often substantially eroded and colonised by multiple taxa of other corals.

The species composition and morphology of corals are also strongly influenced by temperature and hydrodynamic forces, including extreme events such as marine heatwaves and cyclones. Both have influenced coral abundance within the last decade (Gilmour et al. 2019). The abundance of corals has declined substantially in some areas, less in others, and in others has remained relatively unchanged (Depczynski et al. 2013, Holmes et al. 2017; Figure 6). Bundegi, a reef in Exmouth Gulf on the eastern side of North West Cape, suffered from marine heatwave-induced coral bleaching in
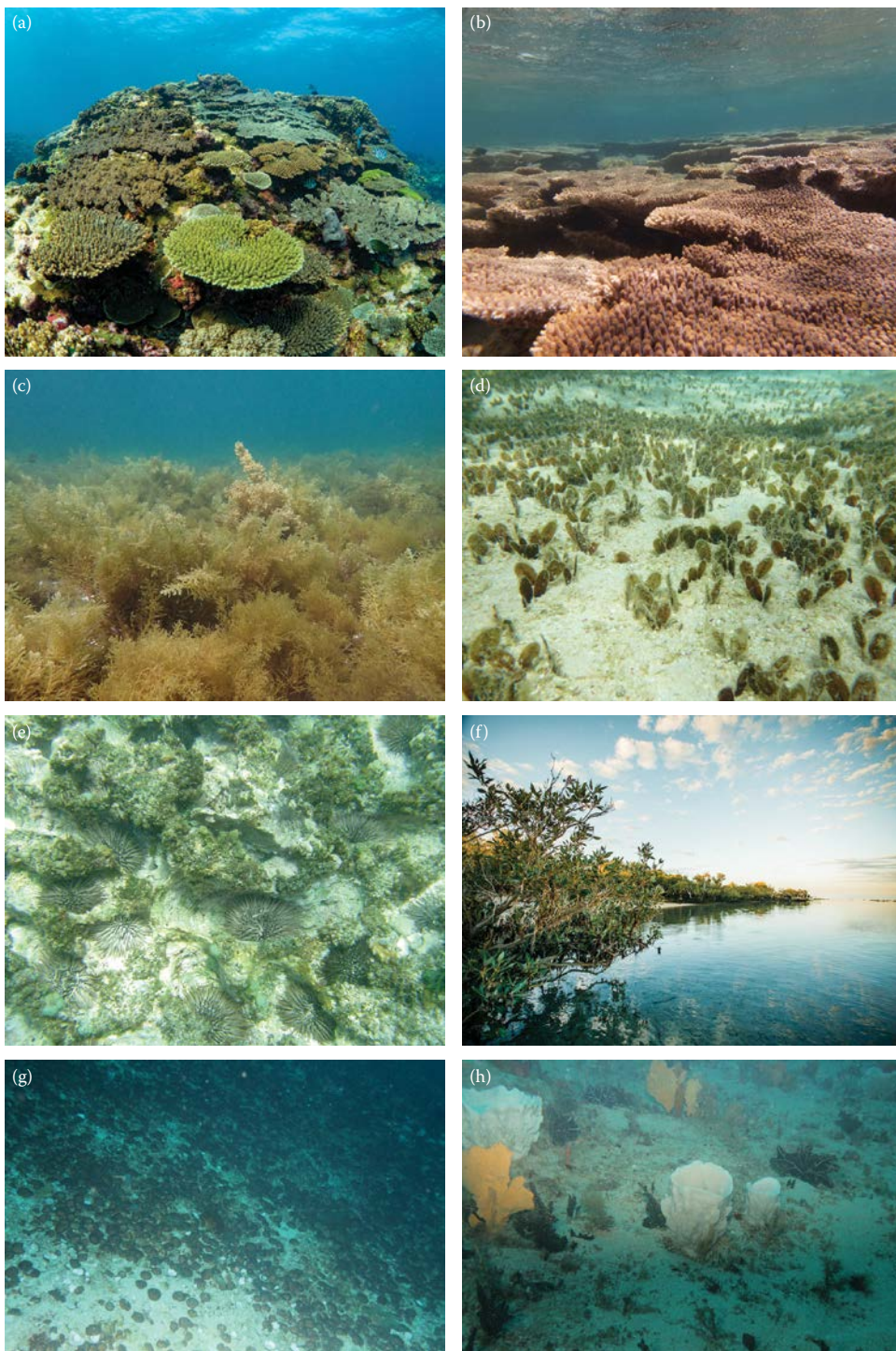
Figure 5 Some of the main habitats present at Ningaloo. (a) Reef slope, (b) reef flat, (c) macroalgae in lagoon, (d) seagrass in lagoon, (e) low-relief limestone with high densities of *Echinometra mathaei*, (f) mangroves (photo credit: Violeta Brosig), (g) dense aggregations of solitary coral *Diaseris* at ∼40 m seaward of the reef slope and (h) assemblage of suspension feeders at ∼42 m seaward of the reef slope.
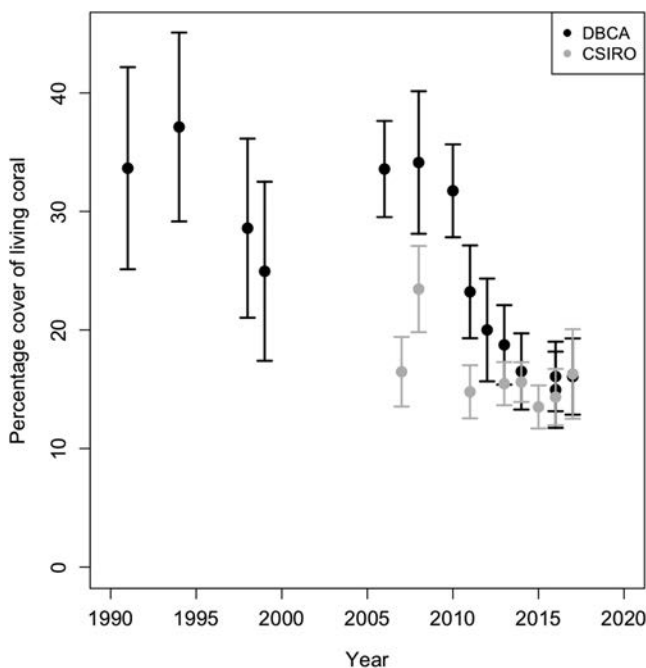
Figure 6 Percentage cover of living coral from 1991–2017, derived from photographs of benthos along transects from long-term ecological research at Ningaloo. DBCA surveys were conducted in back reef and lagoon; CSIRO surveys were conducted in reef flat. (Redrawn from Gilmour, J et al. 2019. *Coral Reefs* **38**, 651–667.)

2011, causing living coral abundance to decrease by up to 95%, while corals at the Muiron Islands decreased by around 50% from a similar event in 2012–2013 (Depczynski et al. 2013, Holmes et al. 2017). In contrast, many reefs on the western side have survived the heatwaves relatively intact, probably because of the cooling effects of the wave-driven currents as they pass over the reef. However, the abundance of corals in some sheltered locations south of Point Cloates has declined steadily since 2011 (Holmes et al. 2017), and localised decreases in coral cover have also occurred north of Point Cloates (e.g. Vanderklift et al. 2019). Cyclones might have caused some mortality, but the declines are coincident with major warming events and seem most likely to be caused by water temperatures exceeding thermal thresholds. Poor water quality has been implicated in degradation of some coral reefs elsewhere, but at Ningaloo, even turbidity associated with high runoff from extreme rainfall events caused no apparent change in percentage cover of living coral (Lozano-Montes et al. 2017).

Over smaller spatial extents (tens of kilometres), localised declines in coral cover have been linked with periodic disturbances. At Coral Bay, multiple episodes have occurred in which accumulations of coral spawn cause anoxia and subsequent mortality of corals (Simpson et al. 1993, van Schoubroeck & Long 2007). Patterns of mortality have typically been patchy even within the bay, and areas with slow currents (high water residence times) were the worst affected. There was recovery from 9% to >40% after 15 years at the worst affected sites (Shedrawi et al. 2017), in contrast to observations at Bundegi, where there has been little recovery following heat stress and cyclones in 2011 (Holmes et al. 2017).

Biological interactions, such as competition, disease and predation, also have the potential to influence the abundance and composition of corals. The incidence of disease at Ningaloo has been estimated to be less than 3% (Onton et al. 2011), which is similar to the background levels of

disease reported in other studies of Indo-Pacific scleractinian corals (Willis et al. 2004, Page et al. 2009, Raymundo et al. 2009), suggesting disease has not been a major cause of mortality. Indeed, the majority of diseased corals from an area with a similar incidence (range: 0%–7.3%) – Barrow Island, approximately 150 km to the north-east of Ningaloo – recovered within weeks and without mortality (Stoddart et al. 2019). Competition between corals is also unlikely to be a major influence, because percentage cover of living coral is less than 50% in most places. The dense stands of tabular *Acropora spicifera* on reef flats are exceptions to this overall pattern, but these areas are almost monospecific, so any competition is likely mostly intraspecific. Macroalgae can attain high biomass on the reef despite the low nutrients and abundant herbivores, so competition between corals and macroalgae might be important. Experimental exclusion of fish in one study led to a proliferation of tall macroalgae, which in turn reduced coral recruitment (Webster et al. 2015). This implies that herbivory by fish is probably an important process that facilitates high coral cover. Other experimental studies of herbivory by fish at Ningaloo support this inference (Doropoulos et al. 2013, Michael et al. 2013).

Outbreaks of the coral-eating gastropod *Drupella cornus* were first noted in the mid-1980s, causing coral mortality as high as 75% in some areas, and leading to extensive loss of coral cover by 1987 (Turner 1994a). *D. cornus* were most commonly recorded on caespitose or corymbose morphs of *Acropora* and reached their highest abundances (up to 19.4 ind. m^{-2}) on the back reef and reef flat (Turner 1994a). The abundance of *D. cornus* appeared to peak around 1989, when they were recorded in high densities throughout the reef (Turner 1994b). The causes of this outbreak remain unknown; variability in abundance can be high, but average densities recorded in the most recent surveys have been mostly <1 ind m^{-2} (Holmes et al. 2017). The overall density at Mandu between 2007 and 2016 was 0.14–0.6 ind m^{-2}, below the estimated outbreak threshold of $\sim$0.95 ind m^{-2} (Bessey et al. 2018). Other known problematic corallivores, such as the crown-of-thorns starfish *Acanthaster solaris*, are rare at Ningaloo.

The accretion and growth of reefs at Ningaloo appear to vary from reef to reef. Although the rate of historical reef growth has been low (Twiggs & Collins 2010), contemporary estimates are in the range of other coral reefs – the mean net carbonate accumulation rate is 2.46 $\pm$ 2.01 kg^{-1} CaCO$_3$ m^{-2} yr^{-1} (Perry et al. 2018). This is higher than many other coral reefs in the central (1.41 $\pm$ 3.02 kg^{-1} CaCO$_3$ m^{-2} yr^{-1}) and western Indian Ocean (1.71 $\pm$ 2.02 kg^{-1} CaCO$_3$ m^{-2} yr^{-1}), where corals have experienced significant mortality (Perry et al. 2018). Fast-growing corals (e.g. *Acropora* and *Pocillopora*) are responsible for the bulk of calcium carbonate production (Perry et al. 2018), but other calcifiers such as CCA are probably more important in wave-exposed areas, where they are abundant (Cassata & Collins 2008). The parrotfish *Chlorurus microrhinos* and the sea urchin *Echinometra mathaei* (Figure 5e) are likely to be the main bioeroders, accounting for up to 95% of the total mass of carbonate excavated from Ningaloo each year (D. Thomson & M. Haywood, unpublished data).

Estimates of net calcium carbonate accumulation (i.e. calcification minus erosion) for Ningaloo are positively correlated with the percentage cover of living coral. The highest rates of carbonate accumulation occur on reefs on the western side of North West Cape (Perry et al. 2018), where the percentage cover of living coral is high (>25%) and the coral assemblage is dominated by *Acropora* and *Pocillopora* (Turner, Babcock et al. 2018). For corals such as these, which have branching and tabulate species, rates of linear extension are a reliable predictor of carbonate production. Linear extension rates for tabulate *A. spicifera* are 12.4 $\pm$ 1.4 cm^{-1} yr^{-1} at north-western Ningaloo and 10.5 $\pm$ 1.2 cm^{-1} yr^{-1} at north-eastern Ningaloo (Stimson 1996), which is high for tabulate *Acropora* (Pratchett et al. 2015). These high growth rates, combined with their high abundance, support the prediction that they are responsible for most of the production of carbonate material. The lowest rates of net carbonate accumulation occur where coral cover is generally low (<10%) and the reef is dominated by CCA and relatively slow-growing corals such as Poritidae and Faviidae. The high net carbonate accumulation rates suggest Ningaloo's reefs have the potential to keep pace with moderate rates of sea level rise over the next 30 years (Perry et al. 2018).

Recovery of reefs after disturbances can occur solely by regeneration from fragments (Hughes 1987), but reproduction and recruitment are vital to the long-term survival of coral reefs (Hughes et al. 1999). This is particularly the case for Acroporidae, which, while often the first corals to be affected by storms or bleaching, are also early colonisers which are important for the recovery of damaged reefs (Doropoulos et al. 2015). The majority of Acroporidae are known to participate in mass spawning (the synchronous release of gamete bundles for external fertilisation), which occurs in autumn at Ningaloo, after full moons between late March and early April (Gilmour et al. 2016). A small proportion of acroporid species are thought to spawn in spring or summer, although the details of these and many other species are not well known, because field observations have been concentrated during the known mass spawning period (Gilmour et al. 2016).

Recruitment of corals at Ningaloo has not been well studied, but a study of coral recruitment onto tiles placed at multiple depths from 3–40 m revealed that the greatest number of settlers was at 25 m, with very little settlement at 40 m (Turner, Thomson et al. 2018). The number of recruits averaged <2.5 dm^{-2} (100 cm^{-2}), which is almost an order of magnitude lower than recruitment measured at coral reefs elsewhere using the same methods (e.g. Hughes et al. 1999, Smith et al. 2005) and is also lower than measurements prior to the 2011 bleaching (Holmes et al. 2017). This low recruitment might mean that corals at Ningaloo would recover slowly from disturbances that cause bleaching and subsequent mortality – this has indeed been the case at Bundegi. This inference is supported by hydrodynamic particle dispersion modelling, which shows that Ningaloo probably receives larvae from the reefs farther north (Feng et al. 2016). Furthermore, the amount of larvae that are transported to Ningaloo varies from year to year, and supply varies among individual reefs, such that recovery times of many reefs are likely to be decades or longer (Boschetti et al. 2019).

Beyond corals: Macroalgae and seagrasses of Ningaloo

Macroalgae, including filamentous turf, cover more than 50% of the seafloor at Ningaloo (Kobryn et al. 2013), particularly within the lagoons (Figure 5c), where large meadows of canopy-forming macroalgae can be found (Cassata & Collins 2008). Fucalean algae from the family Sargassaceae are the main canopy-forming taxa, particularly those from the genera *Sargassum* and *Sargassopsis*, though other brown algae such as *Lobophora* and *Dictyota* are also common (Fulton et al. 2014). In the summer months, the density, height and percentage cover of canopy-forming Sargassaceae increases (Wilson et al. 2014, Lim et al. 2016), and these are highest during La Niña years when water temperatures are warmer (Wilson et al. 2018a,b). Seasonal changes in abundance of macroalgae are closely aligned with water temperature, with biomass typically peaking in February and March when water is warmest (Fulton et al. 2014). There is, however, considerable spatial variation in the composition of macroalgae beds from place to place (Wilson et al. 2014).

In the lagoon, away from coral bommies or reef structure, herbivory is negligible (Verges et al. 2011, Downie et al. 2013) and consumption of macroalgae is mainly by small herbivores that inhabit the macroalgae, such as the parrotfish *Leptoscarus vagiensis* (Lim et al. 2016) and green turtles *Chelonia mydas* (M. Vanderklift, unpublished data). Most uneaten biomass detaches in the early autumn months (Fulton et al. 2014), and the detached thalli form wrack within nearby subtidal and intertidal habitats, or rafts on the sea surface. Both processes probably provide an additional source of nutrients for fauna in adjacent or distant habitats (Fulton et al. 2019), although the relative importance of this process at Ningaloo is unknown.

On the reef, macroalgae range from tall taxa with bushy morphs (like *Sargassum* and *Turbinaria*) to small filamentous taxa; the latter typically grow mixed with sediment and detritus in a combination often called the 'epilithic algal matrix' (Wilson et al. 2003). Compared to many other coral reefs, the interactions between algae, corals and herbivores on the reef has been little studied at Ningaloo. On the reef flat, herbivore exclusion experiments (cages) led to marked increases in the biomass of macroalgae (Webster et al. 2015). Other evidence also suggests that herbivory is likely to be

an important determinant of the composition and distribution of macroalgae. Bare 'halos' around patch reefs indicate intense herbivory by fish inhabiting the reefs (Downie et al. 2013). Browsing acanthurids (surgeonfish) and kyphosids (drummer) are the main consumers of tall macroalgae like *Sargassum* (Michael et al. 2013), and proximity to reefs facilitates access to macroalgae in the lagoon by reef-dwelling fish (van Lier et al. 2018). Acoustic telemetry of the drummer *Kyphosus bigibbus* (Pillans et al. 2017) demonstrated that schools of fish on adjacent patch reefs have distinct core areas of use which did not overlap despite very similar habitats. Home range estimates of *K. bigibbus* (mean 95% KUD = 1.61 km²) are the largest values for a herbivorous coral reef fish recorded to date.

Seagrasses are another important marine plant in sheltered waters at Ningaloo (Figure 5d) and are likely to be a key food and habitat source for some species. For example, the distribution of seagrass is likely to be a primary influence on the distribution of dugong *Dugong dugon* (Holley et al. 2006). Up to 12 species of seagrass occur at Ningaloo. Three species appear to have their northern-most distribution limits at Ningaloo: *Posidonia coriacea* (observed growing in Batemans Bay), *Amphibolis antarctica* (observed near the Muiron Islands) and *P. australis* (drift samples observed at several locations at Ningaloo) (Van Keulen & Langdon 2011, M. Vanderklift unpublished observations; https://naturemap.dpaw.wa.gov.au, accessed 5 March 2019).

On the east side of North West Cape, in Exmouth Gulf, the composition and abundance of seagrass varies from year to year, and the variation appears to be related to a pattern of disturbance (from events like cyclones and marine heatwaves) and recovery (Loneragan et al. 2013, Vanderklift et al. 2016). These fluctuations have implications for other parts of the ecosystem: for example, declines in abundance of dugong (Gales et al. 2004) and brown tiger prawns *Penaeus esculentus* (Loneragan et al. 2013), followed loss of seagrass due to Cyclone Vance.

Variation in abundance and composition of seagrass tends to be less at Bundegi and the Muiron Islands. At Bundegi (in Exmouth Gulf), the abundance of seagrass tends to be highest in late summer and lowest in winter, while at South Muiron Island, abundance of *Halophila ovalis* and *Thalassia hemprichii* remained low during 2.5 years of surveys (Vanderklift et al. 2016).

Other than abundance, the ecology of seagrasses at Ningaloo remains poorly known. The small-leaved *H. ovalis* has been observed flowering at Bundegi in summer, but the importance of seeds and asexual reproduction in maintaining populations is unclear. However, patterns of moderate to high genetic diversity in *H. ovalis* suggest that both sexual reproduction and vegetative growth are present (McMahon et al. 2017). Genetic diversity in *Halodule uninervis* is more variable – *H. uninervis* from Exmouth Gulf are genetically distinct from those in the central and eastern Pilbara – and patterns imply that some populations probably rely on vegetative growth (McMahon et al. 2017). *T. hemprichii* at the Muiron Islands are genetically diverse and exhibit moderate to high connectivity with populations in the Pilbara, a pattern which might be due to dispersal of propagules (McMahon et al. 2017).

Patterns of growth and consumption relative to other places are also poorly known. At Coral Bay, mean photosynthetic rates of 12 ± 0.68 mg O_2 g DW hr^{-1}, with a temperature optimum at about 27°C, were recorded for *H. ovalis* (Said 2017), comparable to the rates recorded for this species and *Halophila spinulosa* in other tropical reef systems (Mohammad et al. 2006), but about four times higher than for the same species from temperate sites. Rates of production of *A. antarctica* at Ningaloo are high compared to a cool temperate region, but rates of consumption are also higher, and ~30% of leaf production is consumed by herbivores – especially fish (Verges et al. 2018).

Mangroves are not abundant on the coast west of North West Cape, but there are some significant stands of mangroves in the southern reaches of Exmouth Gulf. Three species of mangroves are present: *Avicennia marina* (the grey mangrove), *Rhizophora stylosa* (the red mangrove) and *Bruguiera exaristata* (the rib-fruited mangrove, which is rare). *A. marina* is the most abundant species. A small mangrove forest at Mangrove Bay appears to be vulnerable to sea level changes associated with ENSO, and two dieback events have coincided with extremely low sea levels and

associated increases in soil salinity, which also seemed to result in reduced reproductive success (Lovelock et al. 2017).

The mangroves are used by a range of marine species, but perhaps one of the more unique features is a trophic subsidy whereby kangaroos which feed on adjacent grasslands transfer nutrients into mangroves when they shelter in the shade the trees provide during the day (Reef et al. 2014).

Mobile inhabitants of the reef: Fish and invertebrates

Ningaloo hosts at least 500 species of fishes from 234 genera and 86 families (Allen 1980, May et al. 1983, Hutchins 1994, CALM 2005), though the true number may be much higher. Underestimates may have resulted from studies at Ningaloo relying primarily on visual surveys of a restricted group of families, and so many cryptic and nocturnal species may not have been recorded (Hutchins 1994, Hutchins 2001, Babcock et al. 2008, Watson et al. 2010). Nonetheless, endemism is low, and most species are widely distributed across the tropical Indo-Pacific or temperate Australia (Hutchins 2001). There are also latitudinal gradients with the number of species declining from north to south, with distinctive assemblages at the geographic extremes: Bundegi, the Muiron Islands, Lighthouse Bay (all in the north) and Gnaraloo (in the south), which all differed from the central west coast of North West Cape (Babcock et al. 2008).

As well as latitudinal and regional patterns, the composition of fish assemblages varies across the reef from the reef slope towards the lagoon (Babcock et al. 2008), a pattern which is consistent with fringing reefs elsewhere in the world (Chabanet et al. 1997, Núñez-Lara et al. 2005). This is at least partly due to differences in structural complexity (Wilson et al. 2012), but depth (Fitzpatrick et al. 2012) and wave energy (Fulton et al. 2005) are also likely to be important influences. More species have been recorded from the reef slope than the other reef zones (Babcock et al. 2008).

Compared to the species from shallow habitats, there is very little information about the species that inhabit deep water at Ningaloo. Many of these species are slow growing and long lived and tend to aggregate around isolated patches of favourable structure. In deep water, the majority of unique species have been recorded from areas with assemblages of suspension feeders. The composition of fish assemblages was best predicted by a combination of benthos (filter feeders, macroalgae, sand or rubble zones) and depth (Babcock et al. 2008).

Relatively more research has been done further north on the North West Shelf, because of the commercially important trap and trawl fisheries (e.g. Moran & Stephenson 2000, Newman 2002), but there are some important differences in bathymetry and oceanography (e.g. the continental shelf is much wider north of Ningaloo: Wilson 2013), as well as a long history of trawling in parts of the North West Shelf that has probably changed the biota (Sainsbury 1991); these differences limit the extent to which knowledge can be transferred. Two large submarine canyons (Cape Range Canyon and the Cloates Canyon) extend offshore from the Ningaloo coast – these features remain largely unexplored.

In a survey of fish encompassing depths from 1–110 m, Fitzpatrick et al. (2012) found that the number of species and abundance declined with increasing depth, but average length and trophic level increased. For some species, larger (and presumably older) individuals were found in deeper habitats, a pattern which implies that there might be ontogenetic changes in habitat use.

In an extensive study of demersal fish assemblages south of 21°S, Williams et al. (2001) used nets to survey continental slope habitats in 200–1500 m. They identified a northern shelf break assemblage in 200–310 m depths off Ningaloo, characterised by five species (some not yet identified) that were almost exclusively found in this area (*Squalus* sp. D, *Chlorophthalmus* sp. B, *Lepidotrigla* sp. A, *Lepidotrigla* sp. B and *Citharoides macrolepidotus*). The remainder of species found in this area comprised a variety of tropical fishes whose range extends south from NW Australia (Williams et al. 2001).

Overall, estimates of fish biomass based on underwater visual census (788 kg ha^{-1}, Wilson et al. 2018a) are similar to those from other well-enforced no-take marine reserves in the Indian Ocean (McClanahan et al. 2009) but are less than the 1,000 kg ha^{-1} expected in the total absence of fishing (MacNeil et al. 2015). There tend to be more individual fish and species of fishes inside sanctuary zones, but differences in the number of species are not maintained after controlling for the number of individuals (Vanderklift et al. 2013).

The first documented surveys of fish assemblages at Ningaloo Reef were conducted by Ayling & Ayling (1987) in Sandy Bay in 1987. These surveys included counts of some species targeted by recreational fishers and revealed high densities of two species of lethrinids (emperors): *Lethrinus nebulosus* and *L. atkinsoni* (Ayling & Ayling 1987). Surveys have continued and become more frequent and widespread in the region, with most data collected since 2005 (Cresswell et al. 2019). Babcock et al. (2008) compared results from surveys in 2006–07 with those of previous surveys (Ayling & Ayling 1987, Westera et al. 2003) and found lower abundance of lethrinids, suggesting that their abundance has declined over time. Ten years of surveys by Vanderklift et al. (2019) support this, finding parallel declines inside and outside the Mandu Sanctuary Zone. The abundance of Labridae (wrasses) and Chaetodontidae (butterflyfish) have also declined, while other families, including parrotfish and surgeonfish, do not appear to have changed. Various plausible explanations for the observed declines exist, including fishing, localised declines in the abundance of coral and long-term climate variability (Holmes et al. 2017, Wilson et al. 2017). However, attributing causes is complicated when some trends may be part of long-term cycles – necessitating a deeper understanding of processes influencing mortality and recruitment.

There is some evidence that declines are not limited to fish. A commercial fishery (hand collection by snorkel diving) for rock lobster *Panulirus* spp. (mainly *P. cygnus*) existed at Ningaloo in the 1950s and 1960s and supported at least one full-time professional fisher (Halkyard 2005). Anecdotal reports describe a single diver harvesting 20–30 kg of lobsters within 30 minutes. The commercial fishery ceased to operate in the 1970s, by which time catches were declining (Halkyard 2005), and abundances remain low (Depczynski et al. 2009). The reason behind a lack of recovery in abundance of lobster decades after the closure of the commercial fishery is not clear, although changes in ocean currents might have contributed to ongoing low abundance by influencing recruitment (Ningaloo is the northern distribution limit of *P. cygnus*).

The majority of fish recruitment at Ningaloo likely occurs on the back reef and in the macroalgae that are abundant in the lagoon (Wilson et al. 2010, Depczynski et al. 2013, Wilson et al. 2017). Fish recruitment is probably lower in shallow depths on the reef slope (Depczynski et al. 2013), while little is known about recruitment processes in slope habitats deeper than 20 m.

Some settlement of fish larvae can occur all year (Wilson et al. 2014), but most settlement at Ningaloo is coincident with increasing seawater temperatures during the austral summer (McIlwain 2002, 2003). Much of this occurs between November and January (Meekan et al. 2001, McIlwain 2003), but spawning and settlement of some reef-associated species have also been recorded in February (McIlwain 2002, Wilson et al. 2016), indicating that recruitment may continue through to March or even April (Wilson et al. 2018b). The temporal differences in settlement intensity probably reflect variation in reproductive strategies among taxa, as well as environmental influences.

Spatial and temporal patterns in fish settlement at Ningaloo are influenced by variation in regional oceanography. Wilson et al. (2016) found differences in recruitment patterns between Bundegi, the western coast north of Point Cloates, and the western coast south of Point Cloates. This is probably because the southward-flowing Leeuwin Current, the northward-flowing Ningaloo Current and the tidally influenced local currents of the Exmouth Gulf shape the strength and timing of larval supply. Temporal variability in the strength of these currents can have a major influence on supply of fish larvae, with recruitment along the west coast of Ningaloo closely correlated with the

Southern Oscillation Index (SOI) and strength of the Leeuwin Current during the summer months (Wilson et al. 2017, Wilson et al. 2018a).

Large invertebrates are also conspicuous at Ningaloo, but knowledge about them is limited. Small giant clams *Tridacna maxima* can be abundant on intertidal platforms and some parts of the reef and likely experience considerable variation in recruitment and mortality (Black et al. 2011). Sea urchins, especially the burrowing urchin *Echinometra mathaei*, can be abundant in some habitats (Johansson et al. 2010), but unlike many other coral reefs, there is little evidence that sea urchins are a major influence on the abundance of macroalgae.

Connectivity among the various habitats facilitates the use of a broad array of resources by fish at Ningaloo and includes diurnal (Pillans et al. 2017), seasonal (Lim et al. 2016, Babcock et al. 2017) and ontogenetic movements (Wilson et al. 2010, Fitzpatrick et al. 2012) by individuals among habitats. In the early 1990s, 66% (of 1,781) of tagged individual *Lethrinus nebulosus* and *L. atkinsoni* were recaptured within 5.5 km of where they were tagged after ∼2.5 years (Moran et al. 1993). A few individuals had moved 110 km within three months of the release, and none were recaptured more than 148 km away. Recent research has used arrays of acoustic receivers (Pillans et al. 2009) and showed that although both juvenile and adult *L. nebulosus* had relatively small home ranges (mean 95% Kernel Utilisation Distribution [KUD] = 8.5 km^2), more than 60% of the 84 individuals tagged moved beyond the boundary of the 28 km^2 array of acoustic receivers (Pillans et al. 2014, Babcock et al. 2017). These studies provided strong evidence for long-distance spawning movements (>130 km) by *L. nebulosus,* which are among the farthest recorded for any species of coral reef fish. Movements of individuals tagged during spawning aggregations suggested that spawning aggregations occur adjacent to reef passages and the reef slope and occur after quarter moons between October and December. The study provided strong evidence that only large fish (>50 cm FL) participate in these movements during the spawning season, implying that a large proportion of fish above the minimum legal size (41 cm) do not spawn. A significant proportion of individual *L. nebulosus* also exhibit patterns of movement associated with time of day and tide (Babcock et al. 2017).

The unique megafauna of Ningaloo

Ningaloo is home to a large suite of marine megafauna, including sharks, turtles, whales, dolphins, dugongs and manta rays (Preen et al. 1997). The diversity and abundance of Ningaloo's megafauna was an important contributor to its inscription as a World Heritage Area. Whale sharks have predictable seasonal aggregations at Ningaloo (Wilson et al. 2001, Meekan et al. 2006), and together with manta rays and humpback whales form the basis of an economically important ecotourism industry at Ningaloo (Davis et al. 1997, Catlin & Jones 2010, Venables et al. 2016, Huveneers et al. 2017).

Two species of dolphins are resident at Ningaloo, the Indo-Pacific bottlenose dolphin *Tursiops aduncus* and the Australian humpback dolphin *Sousa sahulensis* (Allen et al. 2012, Jefferson & Rosenbaum 2014). Both species are relatively commonly seen in the coastal waters of Ningaloo, often in mixed-species groups (Hunt 2018). The density of *S. sahulensis* is the highest recorded, and it exhibits site fidelity and residency (Hunt et al. 2017, Hunt et al. 2019).

Humpback whales *Megaptera novaeangliae* and pygmy blue whales *Balaenoptera musculus brevicauda* migrate past Ningaloo each year on their way to breeding grounds further north, and back again (Chittleborough 1965, Jenner et al. 2001, Double et al. 2014). Like elsewhere in the world, the number of humpback whales was significantly reduced by whaling, which continued in Western Australia until 1963 (including at Ningaloo until 1957). The population has recovered rapidly since the species was protected (Bejder et al. 2015), and humpback whales have now been downgraded from vulnerable to conservation dependent in Western Australia. Exmouth Gulf is a resting area, particularly for females and their calves on their journey back to the Antarctic (Chittleborough 1965,

Jenner et al. 2001). While the Kimberley has been recognised as the main calving and breeding area for this population of humpback whales (Jenner et al. 2001), calving areas have become less well defined in Western Australia with the recovery of this population, and an increasing number of calves are being born at or near Ningaloo each year (Irvine et al. 2018). Killer whales *Orcinus orca* prey on humpback whale calves and are regularly present during the southern migration of humpback whales each year (Chittleborough 1953, Pitman et al. 2014).

White sharks *Carcharodon carcharias* are another potential predator of humpback whales. Although Ningaloo is near the northern range limit of white sharks for the coast, tagged individuals have been sporadically detected by acoustic receivers at Ningaloo during most of the year. The reasons white sharks travel to Ningaloo remain largely unknown, but migration for reproduction is unlikely because all acoustic detections in this area have been of juvenile or subadult individuals, nor do patterns in direction and timing of movement suggest that they follow migrating humpback whales (McAuley et al. 2017).

White sharks are just one of a diverse suite of elasmobranchs known to occur at Ningaloo, which supports among the most abundant and diverse shark and ray fauna found anywhere (Stevens et al. 2009, Vanderklift et al. 2014). Stevens et al. (2009) documented 47 species of elasmobranchs (30 sharks and 17 rays) in the state-managed Ningaloo Marine Park alone but estimated that there could be up to 118 species, based on the distribution of Australian elasmobranchs (Last & Stevens 2009).

The abundance and distribution of elasmobranchs at Ningaloo seems to be influenced by human activities. Commercial shark fishing is not permitted at Ningaloo west of 114°06E (the longitude of North West Cape), so Ningaloo is potentially an important refuge for species that are captured by this fishery, especially dusky shark *C. obscurus* and sandbar shark *C. plumbeus*. Sharks also interact with fishers frequently, with more than 10% of fish captured by fishers on the western side of North West Cape depredated by sharks and depredation occurring on more than a third of fishing trips across Ningaloo (Mitchell et al. 2018).

Individual dusky sharks tagged between Perth and Ningaloo moved freely between 21.7°S and 35.4°S, undertaking movements of up to 2,000–3,000 km per migratory event. The probability of these individuals being detected at Ningaloo was high in the austral winter–spring and low (males) to moderate (females) during the austral summer–autumn (Braccini et al. 2017). Indeed, the majority of detections were from Ningaloo (Braccini et al. 2017).

Some species move even further: one tiger shark tagged with a satellite tag at Ningaloo moved as far north as Sumba, Indonesia, and as far south as Esperance, on the south coast of Australia (Stevens et al. 2009). Acoustically tagged tiger sharks have demonstrated that some individuals appear to be nomadic, because they are only detected for a few months each year as they pass through Ningaloo, while others stay at Ningaloo for up to five years (Stevens et al. 2009, R. Pillans, unpublished data).

The lagoon provides an important nursery habitat for several species, including giant shovelnose ray *Glaucostegus typus*, blacktip reef shark *Carcharhinus melanopterus,* grey reef shark *C. amblyrhynchos,* nervous shark *C. cautus* and sicklefin lemon shark *Negaprion acutidens*. Acoustic tagging of neonates and juveniles of multiple species of sharks and rays showed that *N. acutidens* was the only species that displayed consistent use of shallow lagoon as a nursery (Oh et al. 2017a). Of the rays tagged, some juvenile *G. typus*, cowtail stingray *Pastinachus atrus* and porcupine ray *Urogymnus asperrimus* remained within the shallow lagoon, but others departed within a few months of tagging (Cerutti-Pereyra et al. 2014). However, the majority of these findings are based on few individuals, limiting their ability to conclusively determine the importance of habitats as nursery areas.

At Mangrove Bay, most (10 out of 13) tagged neonate blacktip reef sharks departed a 28 km^2 array of acoustic receivers within 16 days and had relatively large ranges (mean 95% Kernel Utilisation Distribution of 11.2 ± 12.5 km^2). In contrast, most (17 out of 23) tagged neonate sicklefin lemon sharks remained within the array for more than 30 days and had smaller ranges located close to where they were captured (mean 95% KUD = 4.8 ± 6.1 km^2) (Oh et al. 2017b). Both species

showed strong preference for inshore sandflats but also spent time in mangroves, macroalgae-covered limestone pavement and shoreline reefs; they actively avoided reef slope and sandy lagoon habitats. A similar study of juvenile and adult nervous sharks revealed a small home range (50% and 95% KUD of 0.66 and 3.64 km², respectively) with a strong preference for mangrove habitats, but, again, few individuals were used ($n = 12$), and most ($n = 7$) were resident for less than 40 days (Escalle et al. 2015).

Differences in residence and home range of grey reef sharks between Mangrove Bay and Coral Bay suggest habitat may influence movement (Speed et al. 2012, Speed et al. 2016). Speed et al. (2012) reported that five adult female blacktip reef sharks showed a preference for shallow inshore water during the warmest parts of the day which resulted in their body temperature being ∼1°C warmer than mean water temperature and suggested this was evidence of behavioural thermoregulation, with grey and blacktip reef sharks detected more frequently in shallow inshore waters in the afternoon. Vanderklift et al. (2014) found that more frequent observations of blacktip reef sharks on the reef flat at dusk (from camera deployments and an agent-based model) were corroborated with more detections of acoustically tagged animals on the reef flat at dusk. The maximum density of blacktip reef sharks estimated by Vanderklift et al. (2014) was 20–90 ind km⁻², which is amongst the highest densities recorded for this species and further highlights the importance of Ningaloo for elasmobranchs.

Overall, the diet of elasmobranchs at Ningaloo is poorly known. Many species of rays forage in soft sediments for invertebrates, and their diet overlaps, with annelids dominating the diets of the majority of species (*Pastinachus atrus*, *Taeniura lymma*, *Neotrygon kuhlii*, *Urogymnus asperrimus*), while crustaceans dominate the diet of *Himantura uarnak* (O'Shea et al. 2013). The foraging activities of rays result in significant bioturbation, with an estimated ∼42% of the shallow (mean depth of 5.6 cm) intertidal soft-sediment area turned over by stingrays annually (O'Shea et al. 2012).

One elasmobranch for which Ningaloo has become renowned is the whale shark *Rhincodon typus*, the only member of the family Rhincodontidae and the largest fish in the world, attaining lengths exceeding 16 m (Borrell et al. 2011). Distributed throughout tropical and warm temperate seas, but rare everywhere, large numbers of whale sharks aggregate at Ningaloo each year between March and July (Mau & Wilson 2007, Holmberg et al. 2008, Sleeman, Meekan, Wilson et al. 2010), although some whale sharks are present all year (Norman et al. 2016, Reynolds et al. 2017).

The aggregations of whale sharks at Ningaloo coincides with the period when the Leeuwin Current is strongest, and there tend to be more whale sharks in La Niña years when the Leeuwin Current is particularly strong (Sleeman, Meekan, Fitzpatrick et al. 2010, Taylor & Pearce 1999, Wilson et al. 2001). Concentrations of dissolved nutrients (and therefore phytoplankton abundance) are also highest at this time of year, and during La Niña years, observations imply that whale shark aggregations are linked to periods of enhanced primary production (Wyatt et al. 2010, Rousseaux et al. 2012). Rousseaux et al. (2012) also inferred that rates of consumption of phytoplankton by zooplankton were probably high, providing a plausible link to the taxa that whale sharks feed on. The inference is supported by frequent observations of whale sharks near reef passes (Anderson et al. 2014), which are places where primary production tends to be high (Wilson et al. 2002). Nevertheless, our broader understanding of the mechanisms through which oceanographic conditions and phytoplankton production influence whale shark abundance remains poor.

The regularity and predictability of whale shark aggregations at Ningaloo led to it becoming one of the first places where ecotourism focused on in-water interactions with this species. Established in 1989, the industry grew swiftly, and the number of people swimming with whale sharks each year increased to nearly 30,000 by 2017 (Rob & Barnes 2017). The total direct expenditure by tourists in the whale shark industry in 2014 was estimated to be over $AUD11.5 million per year, with an additional $AUD12.5 million spent in the region by tourists for whom the opportunity to snorkel with whale sharks was the primary motivation for their trip (Huveneers et al. 2017).

The whale sharks that visit Ningaloo are mostly males (74%–85%), the majority of which are immature – there are no records of neonates or individuals <3 m (Arzoumanian et al. 2005, Meekan

et al. 2006, Norman & Stevens 2007, Sequeira et al. 2016). Sexually mature males make up less than 10% of individuals, and mature females (at or exceeding published size at maturity) constitute <1% of individuals encountered (R. Pillans, unpublished data). Sex- and age-specific philopatry by whale sharks is also observed in other regions (Graham & Roberts 2007, Rowat & Gore 2007). To date, there has been no evidence of whale sharks mating at Ningaloo (Holmberg et al. 2008).

Four studies have estimated temporal trends in abundance for whale sharks at Ningaloo, with varying conclusions reached from different approaches (Bradshaw et al. 2007, Bradshaw et al. 2008, Holmberg et al. 2008, 2009). Using a capture-mark-recapture framework on 159 individuals of known sex and size, Bradshaw et al. (2007) estimated that 10 of 16 models yielded declining abundance (estimated changes in relative abundance ranged from 0.87 to 1.26 yr^{-1}). In contrast, Holmberg et al. (2008), also applying a capture-mark-recapture framework but on a larger dataset (representing 355 individuals over a 13-year period between 1995 and 2008), estimated an increasing trend in relative abundance of 1.12 yr^{-1} (SE = 0.06).

The variation in estimates of trends in abundance are also found in published trends in size. Bradshaw et al. (2008) found that estimates of length from the ecotourism industry declined between 1995 and 2004, but Holmberg et al. (2009) suggested that the decline in size was due to increased recruitment of smaller animals. Estimates from these types of models provide information about the philopatric portion of the broader whale shark population but do not account for the remainder, which might not visit Ningaloo during their life. The discrepancy between studies that seek to answer an important question in conservation ecology (and for the regional economy) indicates that alternative methods are required.

More than 8% of whale sharks observed at Ningaloo had scars consistent with vessel strike (Speed et al. 2007). Combined with the severity of some wounds, this might suggest that vessels pose a threat, although the magnitude of this threat is not known. There are no direct threats from fishing in Australian waters, but targeted fisheries that operated in the northern Indian Ocean in the 1990s are likely to have influenced abundance. It is possible that observed declines in genetic diversity (Vignaud et al. 2014) resulted from high levels of historical harvest in the northern Indian Ocean (Anderson & Ahmed 1993, Fowler 2000, Pravin 2000). Despite protection, continued illegal harvest has been documented in parts of the eastern Indian Ocean (White & Cavanagh 2007, Riley et al. 2009).

Vignaud et al. (2014) suggested that whale sharks exist in two distinct populations with minimal connectivity – the Indo-Pacific and the Atlantic Ocean. Other studies have suggested that there is sufficient gene flow to prevent sub-populations occurring within the Indo-Pacific (Schmidt et al. 2009, Castro et al. 2007). However, there is limited evidence from records of individuals identified from photographs that animals move between aggregation sites within each population (Rowat & Gore 2007, Speed et al. 2007, Brooks et al. 2010).

The uncertainty in estimates of abundance and knowledge of threats highlights the usefulness of understanding whale shark movement patterns. Tagging studies can help resolve these movements. There have been ~49 published tracks of whale sharks tagged with satellite tags at Ningaloo (Wilson et al. 2006, Sleeman, Meekan, Wilson, et al. 2010, Sequeira et al. 2013, Norman et al. 2016, Reynolds et al. 2017), and there are an additional ~50 individuals for which data have not yet been published (zoatrack.org/projects, http://www.seaturtle.org/tracking/?project_id=1112). The longest published track is 261 days (Norman et al. 2016), but unpublished data include three tracks over 300 days (R. Pillans, unpublished data).

Whale sharks tagged at Ningaloo show long-distance movements, including to Indonesia and Timor Leste (R. Pillans unpublished data,), with the extent of movements between 12–35°S and 100.9–121.72°E (Wilson et al. 2006, Sleeman, Meekan, Wilson, et al. 2010, Norman et al. 2016, Reynolds et al. 2017). However, most satellite-tagged whale sharks have remained within 300–400 km of Ningaloo (Wilson et al. 2006, Sleeman, Meekan, Wilson, et al. 2010, Norman et al. 2016, Reynolds et al. 2017). Long-distance movements away from Ningaloo have been primarily

northwards, towards Christmas Island, Java and the Timor Sea (Wilson et al. 2005, Wilson et al. 2006, Sleeman, Meekan, Wilson et al. 2010, Norman et al. 2016), as well as west as far as the Arafura Sea and Gulf of Carpentaria (Sleeman, Meekan, Wilson et al. 2010, R. Pillans unpublished data). Norman et al. (2016) also reported that a whale shark photographed off Borneo in 2007 was positively identified at Ningaloo in 2011 and 2012. This may reflect immigration, as no images of this animal were present prior to 2007. Southwards movements are less common, but some have been detected off Perth (Norman et al. 2016, R. Pillans unpublished data). For all published records of animals tagged with satellite tags at Ningaloo, the extent spans 26.5 degrees of latitude (5.5° to 32°S; >4,000 km) and 55 degrees of longitude (85° to 145°E). The reasons individuals move in a particular direction or for a particular distance are very poorly understood. Sleeman, Meekan, Fitzpatrick, et al. (2010) (2010) found that movement of satellite-tagged individuals was independent of near-surface currents and weakly correlated with sea-surface chlorophyll-*a* concentrations.

Although movements away from Ningaloo are poorly understood, there seems little doubt that whale sharks visit Ningaloo to feed. At Ningaloo, whale sharks have been observed feeding on tropical krill *Pseudeuphausia latifrons* (Gunn et al. 1999, Wilson et al. 2001, Taylor 2007), and this species has been identified in faecal samples of three individuals (Jarman & Wilson 2004). Marcus et al. (2016) found differences in fatty acid composition between years, suggesting variability in the prey consumed, perhaps when travelling both to and from Ningaloo Reef and while resident at Ningaloo. Resolution of where and when they feed has been assisted by tags with the ability to record and transmit water temperature and the depth that individuals swim to. Although some studies have implied deep foraging (Meekan et al. 2015), recent high frequency depth and temperature records, combined with accurate GPS data from whale sharks tagged at Ningaloo, suggest limited foraging at depths >200 m (R. Pillans, unpublished data).

Gleiss et al. (2011) used tags with different types of sensors to demonstrate that ascents always showed significant lateral acceleration, while descents were largely passive (they glide down and swim up). Whale sharks dived deeper at night than during the day but exhibited ram filter feeding at the surface during sunset and the first few hours of night, with sharks spending approximately 8 min per day in this position. Observations indicated these individuals were also feeding on *P. latifrons*. Thums et al. (2013) analysed temperature and depth data from four sharks and demonstrated that prolonged dives into deep, cool water were followed by long surface times and hypothesised that this behaviour was in response to thermoregulation. Additional data from long-term tag deployments are required to better resolve fine-scale behaviour associated with feeding, migrating and resident animals.

The big herbivores: Dugongs and turtles

Ningaloo and Exmouth Gulf also host populations of dugong *Dugong dugon* and turtles. Preen et al. (1997) estimated that there were 7–9,000 turtles (primarily green turtles *Chelonia mydas* and almost certainly an underestimate) and 1,000 dugong at Ningaloo from aerial surveys, estimates comparable to the Great Barrier Reef (Marsh & Saalfeld 1989, Marsh et al. 1994, Preen et al. 1997). Dugong abundance is lower at Ningaloo than at Shark Bay (Preen et al. 1997, Gales et al. 2004), but the proximity of these two World Heritage Areas (∼400 km between North West Cape and Shark Bay) allows dugong to move between them in response to loss of seagrass habitat following catastrophic events (Gales et al. 2004, Holley et al. 2006).

Six of the world's seven species of turtles have been recorded at Ningaloo, and four of these (green turtles *Chelonia mydas*, loggerhead turtles *Caretta caretta,* hawksbill turtles *Eretmochelys imbricata,* flatback turtles *Natator depressus*) nest on the adjacent beaches. The population of green turtles in the North West Shelf stock is one of the largest in the world (Limpus 2007), and the beaches of the Ningaloo Marine Park contain a high percentage of the nests of the south-eastern Indian Ocean populations of loggerhead and green turtles (Baldwin et al. 2003, Casale et al. 2015).

Each year, nesting is dominated by green (∼17,000 tracks) and loggerhead turtles (∼2,000 tracks) (Whiting 2016). The sparse nesting by hawksbills (∼400 tracks) reflects that Ningaloo is located at the southern margins of their nesting distribution for Western Australia. The most concentrated area of green turtle nesting is along the northern beaches and Muiron Islands, while loggerhead nesting is concentrated along beaches further south (Bungelup, Jane's Bay, Gnaraloo) and on South Muiron Island. Yearly surveys of nesting turtle tracks and nests have occurred since 2001; there is no increasing or decreasing trend in the number of tracks during this time, but there is substantial inter-annual variation (Whiting 2016).

Although resident turtles at Ningaloo exhibit relatively restricted movements (certainly green turtles: M. Vanderklift & R. Pillans, unpublished data), nesting females can migrate hundreds or even thousands of kilometres (Waayers et al. 2019, Table 1). The post-nesting migrations of green turtles tagged at Ningaloo have ranged from Shark Bay to the south (25°40 S; 400 km) to Kimberley in the north (16°50 S; >1,000 km), while loggerhead turtles have ranged even further, as far as the tip of Cape York in eastern Australia (DBCA, unpublished data). In turn, a small number of tag returns (from thousands of individuals tagged at nesting beaches and from Exmouth Gulf) have indicated that turtles resident at Ningaloo nest elsewhere in the Pilbara (Prince 1993, Prince et al. 2012).

Turtles are particularly sensitive to a changing climate, both directly through the influence that temperature exerts on the probability of a hatchling being male or female and indirectly through impacts on food resources and erosion of nesting beaches. The pivotal temperature for Ningaloo green turtles is 29.2°C (obtained from *in vitro* incubations in a laboratory); both males and females were produced between 27.9 and 30.4°C, gradually transitioning to all males at lower temperatures and all females at higher temperatures (Stubbs & Mitchell 2018).

Turtles (primarily green and hawksbill) were commercially harvested at Ningaloo until 1973, when the practice was banned. Although tens of thousands of turtles were harvested in the years prior to closure, exploitation was relatively late compared to elsewhere in the world (Halkyard 2014). Nevertheless, it probably led to locally depleted abundances (Halkyard 2014).

Table 1   Satellite tracking deployments for sea turtles initiated within Ningaloo Marine Park

Year	Source	Species	Sex	N	Habitat (B, W)	Distance L	Distance G
2007–2008	Ningaloo http://www.seaturtle.org/tracking/?project_id=265	L	F	9	B	1,559	–
2013	Ningaloo http://www.seaturtle.org/tracking/?project_id=814	G	M, I	2	W	–	–
2015–2019	Ningaloo http://www.seaturtle.org/tracking/?project_id=1101	G	F, M, I	35	B, W		189 (B), 4 (W)
2016	Muiron Islands http://www.seaturtle.org/tracking/?project_id=1176	L	F	5	B	1,900	
2016, 2017	Gnaraloo (1149) http://www.seaturtle.org/tracking/?project_id=1149	L	F	12	B	300	
2018	Muiron Islands, Ningaloo (1341) http://www.seaturtle.org/tracking/?project_id=1341	L, G	F	25	B	596	101

Abbreviations: L, loggerhead turtle; G, green turtle; F, female; M, male; I, immature; N, individuals; B, beach; W, water.

Note: Distance is the median displacement distance (in km, straight line between start and end point) for individuals which transmitted for >100 d. Habitat is where turtles were captured for tagging (beach or water).

Human use

Although the resident human population at Ningaloo is low (a combined population of <3,000 people in Exmouth and Coral Bay: Figure 5.4f), more than 150,000 people visit each year, most of whom visit for tourism (Jones et al. 2011; Figure 5.4e). A large proportion of these tourists engage in activities that interact with the marine ecosystem, including fishing and snorkelling, as well as interactions with wildlife such as whale sharks (Smallwood et al. 2012). These activities are managed through a suite of measures. The Commonwealth and state marine parks include spatial zones that include IUCN Categories II, IV, V and VI. Places where recreational fishing can occur are controlled by these zones, and the number and size of fish that can be caught and retained is controlled by a suite of regulations which include species-specific boat, bag, possession and slot (size) limits. Tour operators involved in wildlife interactions are licensed and are required to follow codes of conduct (Department of Parks & Wildlife 2013).

Recreational fishing is a popular activity and includes fishing from the shore and from private and charter boats (Smallwood & Beckley 2012, Lynch et al. 2019). Commercial fishing has been restricted in this area since the 1970s and does not occur at present (Marriott et al. 2012, Gaughan & Santoro 2018). Recreational fishing is predominantly line fishing; effort is concentrated in a few areas and occurring mostly from April to October (Smallwood & Beckley 2012).

Although data on recreational fishing effort and catch have been collected periodically since the late 1990s, different survey objectives and methods make comparisons between surveys difficult, and so broad trends are challenging to identify. In addition, these surveys are designed to provide catch and effort estimates for large fishery management units, which makes the data difficult to interpret in the context of local patterns. The most commonly caught and retained species by recreational fishers are emperors (Lethrinidae) and cods (Serranidae), with spangled emperor *Lethrinus nebulosus* and Chinaman rockcod *Epinephelus rivulatus* – both of which tend to occur in shallow water – the most commonly recorded species (Marriott et al. 2012, Ryan et al. 2017). Demersal species that inhabit deeper habitats, such as goldband snapper *Pristipomoides multidens* and rankin cod *Epinephelus multinotatus*, have been consistently recorded in recreational catches since 2011–12 (Ryan et al. 2013, Ryan et al. 2017, 2015).

Estimated retained catches of *L. nebulosus* from boat-based recreational fishers in the Gascoyne Coast bioregion (within which Ningaloo is located) were similar in 1998–99 and 2007–08 (16,000 vs 15,000 individual fish: Marriott et al. 2012). Most *L. nebulosus* are caught north of Coral Bay, with an expansion into offshore areas evident from 1998–99 to 2007–08 (Marriott et al. 2012). It is not possible to directly compare these studies with Ryan et al. (2017) because survey methods were different, but retained catches of *E. rivulatus, P. multidens* and *E. multinotatus* were steady between 2011–12 and 2015–16 at Ningaloo, while the estimated retained catch of *L. nebulosus* at Ningaloo was lower in 2015–16 (2,887 individual fish; SE ± 686) than 2011–12 (7,973 individual fish; SE ± 1,328: Ryan et al. 2017).

Participation in whale shark tourism has steadily increased, with more than 30,000 attendees on tours to snorkel with whale sharks in 2018 (Figure 7). Management frameworks have so far proved effective. For example, analyses of the potential impacts of ecotourism activities yielded no evidence that people swimming with them affected the likelihood of a whale shark being re-encountered or the residence time of individual whale sharks at Ningaloo (Sanzogni et al. 2015). There is some evidence that whale sharks change direction more often in the presence of tours but little to suggest this has long-term effects on their behaviour (Raudino et al. 2016).

Ecotourism at Ningaloo also includes tours to observe and swim with manta rays and humpback whales. Tours to swim with manta rays began in the early 1990s; operators of these tours can choose to abide by a voluntary code of conduct, but Venables et al. (2016) suggested that a management approach similar to that applied to the whale shark tourism industry would be useful. Tours to swim with humpback whales began in 2016, with a trial to determine whether it could develop into an
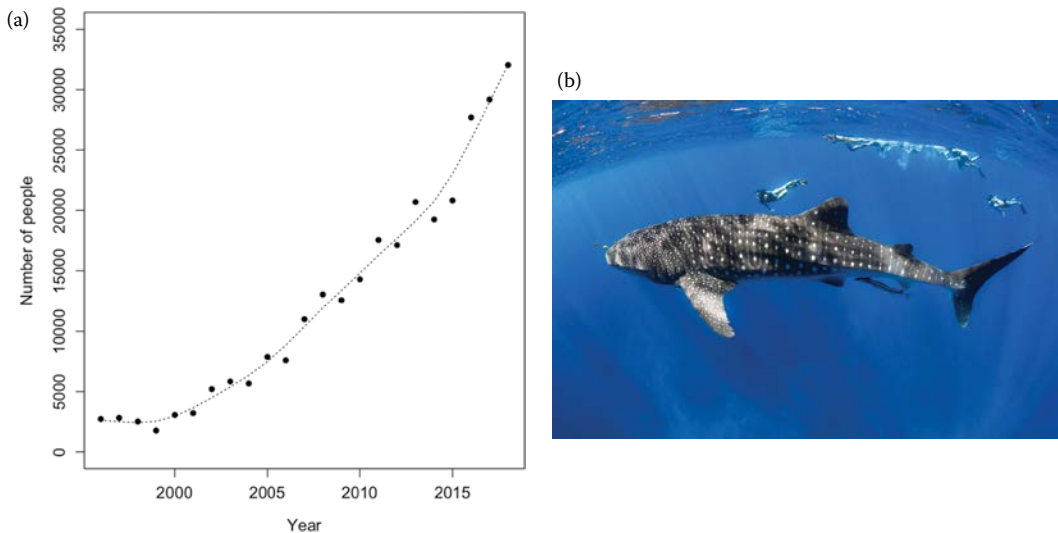
Figure 7 (a) Total numbers of passengers swimming with whale sharks on licensed tours in Ningaloo Marine Park. (Data from Wilson & Barnes. 2018.) (b) Tourists swimming a whale shark at Ningaloo Reef (photo credit: Violeta Brosig).

economically and ecologically sustainable industry; participation increased from approximately 2,300 passengers in 2016 to 3,185 passengers in 2018 (Department of Biodiversity Conservation and Attractions, unpublished data). Evidence suggests that application of best-practice principles can ensure minimal impacts to whales while enhancing safety and satisfaction of tour participants (Sprogis et al. 2020).

The future of Ningaloo

As with coral reefs globally, Ningaloo is facing increasing pressure from the combined effects of climate change and increasing human use (Fulton et al. 2011). Downscaled climate models tend to predict a weaker Leeuwin Current, especially in winter (resulting from a predicted reduction in the amount of water passing through the Indonesian Throughflow, which is in turn a result of a predicted weakening of winds in the tropical Pacific), with a deeper thermocline and more sporadic upwelling by the 2060s (Brinkman 2011, Sun et al. 2012). The downscaled models tend to predict larger changes than global climate models (Sun et al. 2012), a prediction which seems to be supported by empirical evidence using $\delta^{18}O$ in coral cores, which indicate a ~1.5°C increase in water temperature at Ningaloo over the last century, a rate of increase which is faster than the global average (Kuhnert et al. 2000).

Heron et al. (2017) used global climate models to predict that water at Ningaloo will reach temperatures warm enough to cause coral bleaching each year by 2049, and twice each decade by 2041 – a frequency that is almost certainly too high for corals to recover between warming events. The faster rates of warming yielded by downscaled models and evidence from coral cores mean that this might occur sooner. Exacerbating the likely increase in the frequency of bleaching is the potential for reduced supply of larvae from weaker currents, because the coral reefs to the north are likely to be sources of larvae for Ningaloo (Boschetti et al. 2019), and coral abundance on these reefs has already been significantly reduced (Gilmour et al. 2019, Haywood et al. 2019).

Warmer water will also generate effects beyond the direct influence on bleaching. Contemporary water temperatures at Ningaloo are not favourable for development of crown-of-thorns, a major

predator of corals on the Great Barrier Reef and some other places, including the Montebello Islands located just 100 km north of Ningaloo (Haywood et al. 2019, Keesing et al. 2019), but rare at Ningaloo. Water temperatures at Ningaloo are near the threshold above which larvae develop (∼28°C), but as temperatures warm, the probability of larvae surviving and developing will increase, in turn increasing the probability of an increase in abundance of adults (Henderson & Lucas 1971, Johnson & Babcock 1994).

If corals survive, their calcification rates should enable them to keep up with sea level rise (Perry et al. 2018), but this may be compromised if the abundance of bioeroders increases substantially. In parts of the western Indian Ocean, sea urchins such as *Echinometra mathaei* have become abundant, probably because the abundance of predatory fish that eat them has been reduced by unsustainable rates of fishing (McClanahan 1995, 2008). At Ningaloo, there is no obvious correlation between the abundance of *E. mathaei* and the abundance of its predators (Babcock et al. 2008), but the abundance of lethrinids (one of the predators of *E. mathaei*) is decreasing (Vanderklift et al. 2019).

Other primary producers will also likely be affected by increasing water temperatures. The abundance of seagrasses, primarily *Halophila* spp., has been reduced by extreme events in Exmouth Gulf (with marine heatwaves or cyclones the likely cause), but recovery has occurred within a few years (Loneragan et al. 2013, Vanderklift et al. 2016). Some seagrasses, such as *Amphibolis antarctica*, have their northernmost distribution limits at Ningaloo. *Amphibolis* experienced widespread mortality in 2011 at Shark Bay, south of Ningaloo, due to an extreme marine heatwave and impacts are still evident almost ten years later (Arias-Ortiz et al. 2018). The effects of this event on *A. antarctica* at Ningaloo are poorly known, but reports suggest it is vulnerable to climate extremes at Ningaloo as well (Van Keulen 2018).

Mangroves can adapt to sea level rise if there is sufficient space for them to expand, but over shorter timeframes they will also suffer from climate variability. For example, mangroves on the western Ningaloo coast experienced mortality during periods of very low sea level during which salinity in the underlying soil increased (Lovelock et al. 2017). The balance between long-term trends and short-term variability in sea level, and availability of space to expand into, will determine their future at Ningaloo, but which will be the primary influence is unknown. Some older trees have died at Mangrove Bay this century (Lovelock et al. 2017), but studies based on aerial imagery over a relatively short period (<10 years) indicate that the small stands at Mangrove Bay have increased in spatial extent, although they have experienced some canopy loss (Holmes et al. 2017).

Changes to upwelling might influence whale sharks and manta rays, but their reliance on food resources supported by upwelled nutrients is not well understood, and so predictions are necessarily speculative. Increasing air temperature will increase sand temperatures: the pivotal temperature in an *in vitro* laboratory incubation of green turtle hatchlings from Ningaloo was ∼29°C (Stubbs & Mitchell 2018), which was the mean sand temperature recorded by Trocini (2013) in 2006–2008 at Ningaloo, who also recorded temperatures exceeding 33°C in the last third of incubation periods for more than half of the nests surveyed. The nesting success of turtles can also be reduced by erosion of beaches during cyclones: predictions for cyclones are very uncertain, but most global models predict a greater proportion of stronger cyclones, although not necessarily a greater frequency (Walsh et al. 2016).

Ningaloo will also face increased pressure from growing human use (Fulton et al. 2011): most visitors to Ningaloo are from Western Australia, a state whose population will potentially more than double by 2066 (with a projected range of 3.6–5.9 million, http://www.abs.gov.au). A growing number of visitors will result in increasing need for coastal infrastructure, and decisions will need to be made about whether such infrastructure is consistent with ensuring the sustainable use of Ningaloo. At present, we know little about the ability of Ningaloo's ecosystems to absorb additional pressures. For example, trends in fish abundance indicate that some taxa might not readily absorb additional fishing effort, and understanding how to balance sustainable rates of effort with the aspirations of visitors to fish will require sound information about the ecology and biology of the species (Fulton et al. 2011).

While current estimates of growth of the resident population of Exmouth are not considered large (increasing from 2,536 residents in 2012 to an estimated 4,604 in 2051 under a 'high growth scenario'; Gascoyne Development Commission, 2015), the number of tourists that visit Ningaloo is likely to increase. It is difficult to accurately estimate rates of visitor use because there are multiple entry points along 300 km of coastline. However, long-term increases in the number of people participating in tourism activities suggest continued growth in visitation is likely. For example, tourists visiting Ningaloo to swim with whale sharks on licensed tours have increased steadily since 1996 (Wilson & Barnes 2019: Figure 7).

Predatory feral animals (red foxes *Vulpes vulpes*, and possibly cats *Felis catus*) have been a substantial source of mortality of turtle hatchlings in the past. Feral animal control programs (including baits) targeted at protecting turtle rookeries along the Ningaloo Coast have been effective in significantly reducing predation on nests and hatchlings by feral animals to levels approaching zero (Markovina 2017).

Ningaloo, in common with many of the world's coral reefs, is experiencing steadily increasing pressures, which are now manifesting in changes to some components of the ecosystem, including declining abundances of corals and fish. It experiences seasonal winds, upwelling and wave-driven currents, which tend to dampen the impacts of ocean warming. Well-enforced regulations provide some protection from the pressures of increasing human use. However, the presence of taxa at their northern range limits, and the possibility that even relatively small changes could breach thresholds (such as the thermal tolerance of corals and crown-of-thorns larvae), mean that even relatively small changes in temperature could generate unanticipated outcomes. The extensive effort to elucidate the ecology of Ningaloo in recent decades has provided much knowledge, but there are still key processes we do not understand. Generating better knowledge (including traditional ecological knowledge) about these processes and how they respond to the pressures of climate change and human use through well-coordinated research, and translating that knowledge into practical actions, will be critical for the future of Ningaloo.

Acknowledgements

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