

REVIEW PAPER

The ecology, behaviour and physiology of fishes on coral reef flats, and the potential impacts of climate change

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Reef flats, typically a low-relief carbonate and sand habitat in shallow water leeward of the reef crest, are one of the most extensive zones on Pacific coral reefs. This shallow zone often supports an abundant and diverse fish assemblage that is exposed to more significant variations in physical factors, such as water depth and movement, temperature and ultraviolet (UV) radiation levels, than most other reef fishes. This review examines the characteristics of reef flat fish assemblages, and then investigates what is known about how they respond to their biophysical environment. Because of the challenges of living in shallow, wave-exposed water, reef flats typically support a distinct fish assemblage compared to other reef habitats. This assemblage clearly changes across tidal cycles as some larger species migrate to deeper water at low tide and other species modify their behaviour, but quantitative data are generally lacking. At least some reef flat fish species are well-adapted to high temperatures, low oxygen concentrations and high levels of UV radiation. These behavioural and physiological adaptations suggest that there may be differences in the demographic processes between reef flat assemblages and those in deeper water. Indeed, there is some evidence that reef flats may act as nurseries for some species, but more research is required. Further studies are also required to predict the effects of climate change, which is likely to have multifaceted impacts on reef flats by increasing temperature, water motion and sediment load. Sea-level rise may also affect reef flat fish assemblages and food webs by increasing the amount of time that larger species are able to forage in this zone. The lack of data on reef flats is surprising given their size and relative ease of access, and a better understanding of their functional role within tropical marine seascapes is urgently required.

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Key words: ecosystem services; environmental variation; nursery habitat; sea-level rise; tides; water movement.

INTRODUCTION

The zonation of coral reefs is one of their characteristic features, driven by a range of biophysical factors such as wave exposure, light and antecedent topography (Done, 1983). Of this array of zones, reef flats are arguably the most conspicuous geomorphological features of modern reefs (Yamano, 2000). Reef flats are typically shallow



FIG. 1. Aerial photograph showing the extensive inner reef flat (a) and outer reef flat (b) at Green Island, Great Barrier Reef. The reef flat is shoreward of the reef crest (c) and reef slope (d). The eastern reef flat surrounds a lagoonal complex (e).

areas, frequently only a few metres deep, landward of a reef crest or ridge, and in some locations may be divided into an outer reef flat just behind the reef crest and an inner flat adjoining the land or lagoon (Fig. 1). Outer reef flats are often characterized by a high proportion of carbonate substratum with limited topographic complexity, patches of which are increasingly interspersed by patches of soft sediment during the transition to the inner reef flat. This mix of habitats supports a diverse and abundant fish fauna. In addition to the size of the reef flat zone within tropical seascapes, there are other reasons that make them of interest to fish biologists, ecologists and physiologists. As reef flats are in shallow water, any changes in water depths across tidal cycles can be biologically significant, in contrast to deeper habitats where abiotic conditions tend to change seasonally rather than diurnally. For example, low tides can cause corals and other benthic microhabitats to be aerially exposed (Chappell, 1980). Thus, many flats represent ‘semi-intertidal’ habitats on reefs; unlike true intertidal areas, aerial exposure is typically limited to conditions such as particularly large tidal cycles (Cubit, 1985). Changes in water depth also contribute to a range of environmental parameters, including water temperature, dissolved oxygen concentration and ultraviolet (UV) radiation, varying significantly on

short temporal scales. As a consequence of these alterations to the physical environment over tidal cycles, the fish community may undergo profound changes. For example, some large fish species may have to leave the flat at low tide because the water is too shallow (Vivien, 1973), and other species may be unable to cope with the high temperatures, low oxygen concentrations and high levels of UV radiation. Therefore, reef flats represent a natural laboratory to examine the physiological capacity of reef fishes, the impacts of rapid changes in biotic relationships (such as the implications of a reduction in predation pressure at low tide), and how the range of benefits and disadvantages of living in such a variable environment may lead to trade-offs in the ecology of shallow-water species and differences with conspecifics in deeper habitats.

Reef flats also represent the frontline for understanding the effects of climate change on tropical marine seascapes. Climate change, through the multiple effects of altering temperatures, acidity, sea level and storm and wave energy, is perhaps the most pervasive threat to the integrity of coral reefs (Hoegh-Guldberg, 1999; Hoegh-Guldberg *et al.*, 2007). Because of their position in shallow water, flats and their fish communities may be the most severely affected reef habitat. For example, the effects of coral bleaching typically decrease with increasing depth (Hoegh-Guldberg, 1999), and the focus of concerns about sea-level rise in the tropics has been shallow coastal habitats (Wilson *et al.*, 2010). In addition to being significantly affected, reef flats also provide clues about how marine species may adapt to climate change. For example, the extreme conditions in shallow reefs are the focus for how fishes cope with the physiological stresses of high temperatures, high UV radiation levels and low oxygen concentrations (Zamzow & Losey, 2002; Nilsson *et al.*, 2004).

Understanding the impacts of climate change on reef flats is critical because of the range of goods and services that they provide. Reef flats are important for shoreline protection by dissipating a significant fraction of the incoming wave energy (Sheppard *et al.*, 2005), and are key sites for coral mining in countries such as the Maldives (Dawson Shepherd *et al.*, 1992). Furthermore, ancient intertidal fish traps highlight how reef flat fishes have long been exploited by man (Gibson, 2003). Reef flats remain key fishing grounds in many areas, including south-west Madagascar, where the reef flat is the habitat most often visited by fishermen (Laroche & Ramananarivo, 1995). In addition to providing adult fishes to fisherfolk, the shallow water refuge hypothesis (Baker & Sheaves, 2007) suggests that reef flats may have a nursery function for a range of fishes, including commercially and ecologically important species. Finally, shallow, diverse reef flats are popular sites for snorkelling and reef walking by tourists (Leujak & Ormond, 2008; Hannak *et al.*, 2011).

This review draws together the disparate literature on reef flat fishes, and establishes the current state of knowledge about the composition, ecology, behaviour and physiology of these shallow water assemblages. The aim is that this summary will achieve a number of goals. First, it will provide a better understanding of the degree to which reef flat fish assemblages are distinct from those found in deeper water. As researchers move beyond considering coral reefs as homogenous entities, questions of variations in habitat-scale assemblages and their critical demographic traits provide important insights into how fish populations actually function (Figueira *et al.*, 2008). Second, the review assesses what is known about how reef flat fishes cope with the significant changes in their physical environment, a topic that has received relatively little attention on reefs. Although variables such as current flow and temperature

often vary to the greatest extent on flats, conditions are rarely totally stable in any reef habitat. A consideration of how physical factors can shape the identity, ecology and physiology of fish assemblages in shallow water may reinforce the need to consider abiotic variability more carefully in other parts of the seascape. Environmental variability is important in other marine seascapes, such as estuaries (Gibson *et al.*, 1998), and this review also aims to provide the ability for researchers to compare across ecosystems. Third, identifying the functional value of reef flats to fishes, such as acting as juvenile nurseries, being the preferred habitat of species throughout their lifecycle, or functioning as adult feeding grounds, will aid the design of marine conservation initiatives. Fourth, the review will highlight gaps in the current understanding of shallow water fish assemblages, with the aim of stimulating a diverse research agenda focused on this habitat. Finally, the text assesses the existing and potential future threats to reef flat fishes from the multiple impacts of climate change.

SCOPE OF THE REVIEW

For isostatic reasons, Atlantic Ocean reefs have experienced a continuous sea-level rise throughout the Holocene so that even their shallowest points are typically sub-tidal (Hopley, 2011). In contrast, sea level has been at its present level for *c.* 6000 years in most regions of the western Pacific Ocean (Yamano, 2000; Hopley, 2011). This relatively static sea level has led to shallow reefs filling the vertical accommodation space available and then expanding laterally, usually generating extensive reef flats (Yamano, 2000). The relative importance of reef flats in the geomorphology of Pacific Ocean reefs and their frequently large tidal ranges, compared to the more modest extent of Caribbean back reefs with their small tidal range (Adams *et al.*, 2006; Harborne *et al.*, 2006), means that this review focuses on Pacific Ocean reefs. Additional literature is drawn from the Indian Ocean and Red Sea where available. Although much of the literature in this review is generated from a few, relatively well-studied areas, such as the Great Barrier Reef and French Polynesia, it aims to be relevant throughout the region.

One of the challenges of a habitat- or zone-specific review is penetrating the nomenclature used by different researchers in the literature. 'Reef flat' is a relatively well-recognized geomorphological term, although it often spans a range of habitat types. Because the available literature is relatively modest the review incorporates studies on 'back reefs' where the description suggests a functionally equivalent area (shallow water, some hard-bottom substrata and tidally influenced). In contrast, lagoonal habitats, inshore sand and mud flats and shallow seagrass beds have generally been excluded. These habitats are functionally different to reef flats because they lack the abundant carbonate patches that are found on flats, although lagoons may contain geomorphologically distinct patch reefs.

A GEOMORPHOLOGICAL, PHYSICAL, AND BENTHIC OVERVIEW OF REEF FLATS

A full review of the formation, physical environment and coverage in recent reviews, and benthic communities on reef flats, and their significant variation across

the region, is beyond the scope of this review. An appreciation of the biophysical conditions experienced by fishes on flats, however, is important as a context for the subsequent text. While there are multiple environmental gradients across reef flats, it is generally recognized that wind-driven waves constitute the most important factor affecting benthic communities. This contrasts with deeper reef slopes, where wave energy typically co-varies with the major forcing function of light levels (Bradbury & Young, 1981). Water motion on reef flats is characterized as having higher velocities and stronger directional changes than reef slopes, and indeed the values can be comparable to reef crests (Fulton & Bellwood, 2005), although energy decreases away from the reef crest and towards the lagoon (Thornborough & Davies, 2011). Water motion varies spatially and temporally and consequently reef flats can be broadly grouped as coral-dominated or rubble-dominated (Thornborough & Davies, 2011). Coral-dominated reef flats are commonly found on high-energy reefs and are clearly zoned, from windward to leeward (Thornborough & Davies, 2011). In contrast, rubble-dominated reef flats are found in areas with more variable exposure regimes, and the allochthonous rubble originates on the reef front and is then moved onto the flat where it is sorted along a wave energy gradient (Thornborough & Davies, 2011). Additionally, in locations such as the areas around islands in the Torres Straits, reef flats consist of inert, sediment-covered, cemented platforms that are exposed at low tide, and corals are restricted to pools and the edges of the flat (Hopley, 2011).

Within over-arching exposure regimes, water motion also interacts with tidal state to influence benthic and fish assemblages. At low tide, wave energy is focused almost entirely on the reef front, but at high tide it is distributed across much of the reef profile (Thornborough & Davies, 2011). Furthermore, increased potential wave heights as water depths increase means that higher waves can occur during higher tides (Nelson, 1994). Tidal flow is a further source of water motion on reef flats, but perhaps more importantly it controls water depth, and tidal range is a key environmental variable affecting reef flat communities. Tidal ranges and cycles vary widely throughout the Pacific Ocean, but generally within the tropics, the tidal range peaks at the equator and then decreases towards *c.* 20° north and south, although there is a secondary peak at *c.* 15° south (Moore, 1972). The presence of oceanic islands close to the equator in the biodiverse area of Indonesia and the Philippines, however, causes a high diversity of tidal types and ranges, and much of this area has a limited tidal range of <2 m (Krumme, 2009). The variability in ranges from spring to neap tides is also an important consideration on reef flats, and the tropics are characterized by relatively large spring ranges compared to relatively small neap ranges (Moore, 1972).

Water transparency is a further important environmental variable that interacts with wave energy to influence the nature of reef flats. On the Great Barrier Reef, water clarity decreases from Coral Sea atolls to inner-shelf reefs because of riverine inputs, and is a key factor leading to limited flats on the inner shelf (Done, 1982). Parameterization of other physical conditions on reef flats has received relatively little attention, but oxygen levels vary significantly, particularly in some microhabitats. For example, the water within respiring coral colonies can become hypoxic on calm nights (minimum oxygen concentration can be 2–30% of air saturation) (Nilsson *et al.*, 2007a). Even away from coral colonies, oxygen levels can vary at least five-fold over a 24 h cycle (Kinsey & Kinsey, 1967), along with temperature

fluctuations of up to 12° C depending on the time of low water and wind speed (Potts & Swart, 1984). Furthermore, reef flat temperatures can be 3–4° C higher, and with a much greater range, than those at the base of reef slopes (Potts & Swart, 1984). Finally, compared to lagoons and oceanic water away from reefs, reef flats can have lower alkalinity and dissolved inorganic carbon (Ohde & van Woesik, 1999), and the carbonate chemistry of reef flats is extremely variable over tidal cycles (Shaw *et al.*, 2012).

Benthic communities are highly variable across reef flats (Done, 1982), but wave energy gradients often lead to zonation patterns, particularly on coral-dominated flats. Thus, robust, massive, encrusting and branching corals are located in windward areas, changing to diverse assemblages of primarily branching corals (especially from the genus *Acropora*) as energy decreases (Thornborough & Davies, 2011). Chappell (1980) provides a conceptual overview of how coral morphologies vary across reef flats in response to both changing wave and aerial exposure: highest coral diversities and tabular and branching corals are typically just inshore of the reef crest where wave stress is high, but exposure is low. There is then a transition to a lower diversity assemblage of microatolls and massive and encrusting growth forms on the inner flat where wave stress is lower, but aerial exposure is greater (Chappell, 1980). A diverse assemblage of macro, turf and coralline algae is also an important component of reef flat benthic communities. Algae occur on all carbonate patches not covered by corals and other sessile invertebrates, and some species inhabit soft-sediment areas, although their abundance can vary significantly with season (Rogers, 1997). The high water movement across reef flats, combined with an abundance of sunlight and diverse assemblage of primary producers, means that reef flats and crests typically have higher rates of primary productivity than other reef habitats (Hatcher, 1988).

FISH ASSEMBLAGES ON REEF FLATS

The zonation of fish assemblages across reef profiles, and the potential drivers, has long been recognized (Williams, 1991), and reef flat fish assemblages are typically distinct from other zones. For example, reef flats in the Ryukyu Islands, Japan, were dominated by the sapphire devil *Chrysiptera cyanea* (Quoy & Gaimard 1825) and the brown surgeonfish *Acanthurus nigrofusus* (Forsskål 1775), while the most abundant species on the reef slope were the scaly damsel *Pomacentrus lepidogenys* Fowler & Bean 1928, Richardson's reef-damsel *Pomacentrus richardsoni* (Snyder 1909) and the striated surgeonfish *Ctenochaetus striatus* (Quoy & Gaimard 1825) (Lecchini *et al.*, 2003). Furthermore, there is a considerable variation within reef flats. On the reef flats of Réunion Island, there were distinct fish assemblages, and different dominant feeding guilds, on back reefs, inner reef flats and outer reef flats (Letourneur, 1996; Letourneur *et al.*, 2008). Herbivores (mainly acanthurids) and omnivores (mainly pomacentrids) were the most abundant guilds on the inner and outer flats (Letourneur, 1996). The differences in these assemblages were much more significant than those for each individual habitat type among reefs. The patterns were also temporally consistent over a 6 year period, although the stochastic summer settlement of juveniles made the winter assemblages more similar to each other (Letourneur *et al.*, 2008).

Studies comparing reef fish assemblages among zones have frequently attempted to link the patterns to key biophysical factors. As for benthic communities, a major driver of fish assemblages is frequently wave energy. Perhaps, the clearest demonstrations of the link between water motion and fish assemblages on flats are the functional approaches considering swimming modes (Fulton & Bellwood, 2005; Fulton *et al.*, 2005). Different swimming modes (*e.g.* pectoral, pectoral-caudal and caudal swimming) have different biomechanical and energetic attributes, with pectoral swimming being highly efficient and providing a competitive advantage in wave-swept habitats (Fulton & Bellwood, 2005). Consequently, when examining 156 species across five habitats and four exposure regimes, pectoral swimmers predominated in locations with high levels of water motion, and the proportion of pectoral-caudal and caudal swimmers decreased with increasing flow velocity (Fulton & Bellwood, 2005). Furthermore, within the pectoral swimming families of Acanthuridae, Labridae and Pomacentridae, attributes of pectoral fin morphology correlate with swimming performance, and predict the distribution patterns of species in all three families across a range of reef habitats that included flats (Fulton *et al.*, 2005). Water motion has also been implicated as a major driver of reef flat fish assemblages in the Ryukyu Islands (Lecchini *et al.*, 2003) and Réunion Island (Letourneur, 1996).

The other major driver of reef flat fish assemblages is benthic community type. The abundance and diversity of Pacific Ocean fishes have long been linked to coral cover and complexity in a wide range of reef habitats (Bell & Galzin, 1984), and benthic structure is certainly important for reef flats. For example, distinct assemblages of fishes across reef flats and slopes in Vietnam were associated with variations in living coral cover and the cover of particular coral growth forms and genera, along with depth and distance from the coast (Van Nguyen & Phan, 2008). Therefore, as for other habitats, disturbances to coral cover and rugosity will often impact reef flat fish assemblages. For example, fish assemblages vary significantly among those on non-disturbed reef flats, on non-disturbed outer reef slopes, and on reef habitats perturbed by eutrophication at Réunion Island (Chabanet *et al.*, 1997). Furthermore, coral bleaching events can lead to an increased abundance of herbivores and a low abundance of browsers of sessile invertebrates, particularly chaetodontids that feed on coral tissue (Chabanet, 2002). Coral mining can also affect reef flat fish assemblages, with the major effects in the Maldives being a reduction in the abundance of planktivores, benthic herbivores and omnivores (Dawson Shepherd *et al.*, 1992). In addition to indirect effects that affect fish habitat, the direct effects of fishing on reef flats can be substantial. There is little evidence to suggest that different species are targeted on flats compared to deeper reef areas but, in one of the few quantitative assessments of fishing pressure by zone, the increased usage of reef flats led to catches in Madagascar being dominated by lethrinids and siganids (Laroche & Ramananarivo, 1995). Because of the effects of fishing, conservation initiatives such as marine protected areas can change reef flat assemblages significantly compared to unprotected areas by reducing direct and indirect impacts on fishes (Öhman *et al.*, 1997).

As for other reef habitats and zones, investigations of fish assemblages on reef flats has focused on species that can be visually surveyed, and less attention has been dedicated to cryptic species. Data demonstrate, however, that there are differences among reef zones and the effects of water motion are also pervasive in this component of the fish assemblage. For example, the exposed, wave-swept front flat reef zone at Lizard Island (Great Barrier Reef) was the most species-poor zone for cryptic

fishes, with the highest numbers of individuals and species found in calmer habitats such as lagoons and reef bases (Depczynski & Bellwood, 2005). Furthermore, larger individuals (heavier than the mean mass of 0.18 g) were more common in exposed, wave-swept reef zones and microhabitat availability was important in areas with low wave energy (Depczynski & Bellwood, 2005). Substratum composition and microhabitat availability were also identified as critical drivers of abundance patterns of gobies across a heterogeneous reef flat comprising four habitats around Orpheus Island, Great Barrier Reef (Hernaman & Probert, 2008). Cryptobenthic fishes are the major resident component of fish assemblages on sandy areas that comprise significant areas of some reef flats. At Lizard Island, significant differences were found among burrowing goby assemblages on different sandy habitats, with differences linked to factors such as depth, distance from consolidated reef, sediment composition and the level of disturbance (Syms & Jones, 2004).

In addition to the data on entire assemblages, there are a number of studies that focus on individual feeding guilds or families. Perhaps, the most studied group of fishes on reef flats is the herbivores, particularly parrotfishes, because of their functional importance in grazing algae and effects on coral demographics (Mumby, 2009). Reef flat herbivores are perhaps best studied across the Great Barrier Reef, with well-described cross-shelf and cross-zone patterns (Russ, 1984a,b; Hoey & Bellwood, 2008). It appears that assemblages on inner-shelf reefs are distinct from those on mid- and outer-shelf reefs, although the pattern is confused by the frequent lack of a clear reef flat on the inner shelf (Done, 1982). Consequently, Russ (1984a) reports significantly fewer numbers of surgeonfish and parrotfish species and individuals on inshore reefs, but surveys were carried out at depths of >3 m and therefore the data are difficult to compare with true reef flats further offshore. In contrast, working in shallower water on a better defined flat further north, and possibly with better visibility, Hoey & Bellwood (2008) document inner-shelf reef flat densities of parrotfishes that were comparable to, or greater than, those on mid- and outer-shelf reefs, and were dominated by species from the genus *Scarus*. Parrotfish biomasses, however, were lower on inner-shelf reef flats, especially compared to flats on the outer shelf that support schools of the large-bodied humphead parrotfish *Bolbometopon muricatum* (Valenciennes 1840) (Hoey & Bellwood, 2008). Reef zonation is clearer on mid- and outer-shelf reefs, and reef slopes, crests, flats and lagoons support distinct herbivore assemblages (Russ, 1984a, b). 'Cropping' and 'scraping' herbivores were particularly abundant in the shallow crest and flat zones (Russ, 1984b). Although there are differences among mid- and outer-shelf reefs, inter-zone differences are greater than those among shelf locations (Russ, 1984a, b). As for entire assemblages, the drivers of herbivore abundances across zones are varied. A major factor causing the biomass of herbivorous fishes to be greater on reef crests than slopes and flats, however, is the higher turf algal production rates on crests (Russ, 2003). Consequently, where seasonal changes in algal distributions are significant, this can drive changes in the distribution of herbivores. For example, in the Red Sea, the clear zonation of the herbivore community is lost in the summer as reef flat species exploit deeper zones and some reef crest species feed on the reef flat (Afeworki *et al.*, 2013).

Inter-location and inter-zone patterns in wrasses have also been studied because of their diversity and ubiquity within reef fish assemblages. As pectoral swimmers, wrasses are well-adapted to high levels of water motion, and this is a key variable

affecting inter-zone patterns (Bellwood & Wainwright, 2001; Fulton *et al.*, 2001). On the Great Barrier Reef, inter-habitat differences were greater than those across the shelf, and exposed reef flats and crests on mid- and outer-shelf reefs were characterized by a distinct assemblage (Bellwood & Wainwright, 2001). Furthermore, the fin morphologies of species in these exposed sites were consistent with characteristics that provided fishes with efficient lift-based swimming (Bellwood & Wainwright, 2001). Species with fin morphologies that are not well-adapted to high levels of water motion do occur on reef flats, but appear to forage close to the bottom and use refuges from water movement so that fin morphologies also predict the microhabitat use of wrasses (Fulton *et al.*, 2001). Although other benthic community variables may also shape wrasse assemblages, depth (a proxy for water motion) is more important than percentage of living substratum, substratum diversity, complexity or season (Green, 1996).

Some family-specific data are also available for damselfishes and butterflyfishes. For example, Meekan *et al.* (1995) describe the distribution of 15 species of damselfishes at Lizard Island (Great Barrier Reef), and highlight that herbivorous species dominate in shallow reef flats and crests, while planktivorous and omnivorous species were most abundant on the deeper reef slope. Reef flats were the preferred habitats of butterflyfishes such as the speckled butterflyfish *Chaetodon citrinellus* Cuvier 1831 and the chevron butterflyfish *Chaetodon trifascialis* Quoy & Gaimard 1825 in Moorea, where the number of species was relatively constant across zones but the number of individuals increased from the inner to the outer flat and was highest on the reef slope at 10 m (Bouchon-Navaro, 1981). Of the remaining taxa within reef flat assemblages, there are few examples of species that are obligate inhabitants of this zone, but the epaulette shark *Hemiscyllium ocellatum* (Bonnaterre 1788) is rarely found elsewhere and is an important benthic predator in the fish assemblage (Heupel & Bennett, 1998; Fig. 2). Given the challenges of life on reef flats, there are more species that avoid the habitat. For example, late larvae of the leopard grouper *Plectropomus leopardus* (Lacépède 1802) appear to actively avoid



FIG. 2. The epaulette shark *Hemiscyllium ocellatum* is one of the few species largely restricted to reef flats, and here is seen foraging in <50 cm of water on the outer flat at Heron Island, Great Barrier Reef.

settlement in shallow water, with no larvae observed settling at depths <4.2 m (Leis & Carson-Ewart, 1999).

Despite a number of papers dedicated to different aspects of reef flat fish assemblages, and clear changes with tidal state (Vivien, 1973), there are surprisingly few papers that discuss the dynamic nature of assemblages with changing water depth. This is at least partly caused by the difficulties of surveying fishes at low tide, meaning that many studies standardize their surveys by working at high tide (Russ, 1984a; Fox & Bellwood, 2007). Surveys in Indonesia, however, report a 30% reduction in fish abundance and a significant decrease in species richness as the tide dropped from *c.* 2 to <1 m across a range of shallow water habitats, including reef flats, but changes were less significant on reefs than seagrass beds (Unsworth *et al.*, 2007). Particularly noticeable was that large predatory species, such as jacks and snappers, were not seen at low tide and their abundances increased with increasing water depth (Unsworth *et al.*, (2007). This absence of some piscivores at low tide is important when considering shallow-water trophodynamics. In the Red Sea, surveys of habitats similar to those of Unsworth *et al.* (2007) indicated that state of the tide and time of day influenced the composition of fish assemblages, although the study concluded that substratum type was the strongest factor (Ashworth *et al.*, 2006).

FISH BEHAVIOUR ON REEF FLATS

Changes to the fish assemblage on reef flats over tidal cycles are the result of the combined behaviours of individuals, particularly moving to deeper water to avoid stranding at low tide. Tidal migrations by fishes are seen across a wide range of marine ecosystems, and have a range of functions. For example, fishes may use tidal currents for transport, access intertidal feeding grounds, avoid predators or maximize reproductive outputs (Gibson, 2003). Compared to the detailed studies of some species in other ecosystems, such as coastal and estuarine pleuronectids (Gibson *et al.*, 1998), the study of tidal movement of reef flat fishes is in its infancy. Consequently, there are surprisingly few studies of how and why fishes move to other parts of the seascape in response to changing water depth, or indeed other biophysical drivers. There are some relatively qualitative observations of fishes moving onto reef flats to feed as water depth increases, including the classification of fishes into temporary and permanent flat species in Madagascar (Vivien, 1973). There is also an observation from Indonesia that some fishes may move off reef flats to feed in very shallow seagrass beds at high tide (Unsworth *et al.*, 2007). Equally, some species may be moving onto or away from reef flats to avoid predators although, unlike individuals in deeper water, fishes on reef flats experience a constantly changing predator environment with marine predators at high tide and avian predators at low tide (Fig. 3). Avian predators, such as the reef egret *Egretta sacra*, can be a significant threat to reef flat fishes at low tide and can take $0.3\text{--}0.4$ g of fish min^{-1} of hunting time when the water is low enough (Recher & Recher, 1972). Presumably, birds are also a major reason for species that remain on reef flats choosing to hide in refuges at low tide (A. R. Harborne, pers. obs.). Furthermore, some species move from sand and coral flats to spawn in other habitats, such as the outer reef slope, presumably to maximize the dispersal of gametes (Johannes, 1978).

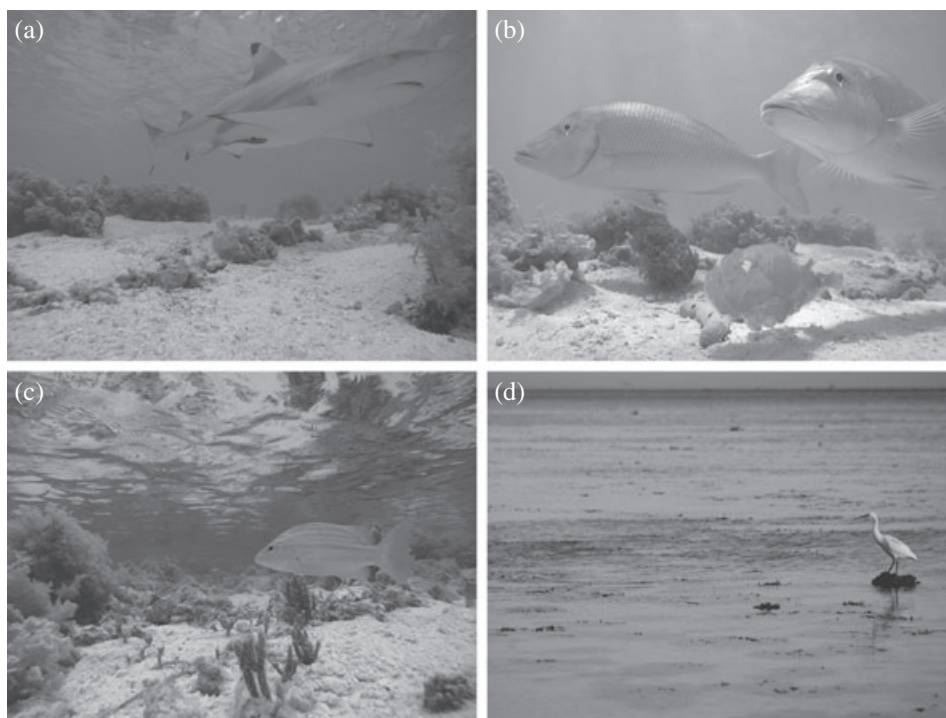


FIG. 3. Changes to the identity of predators across a tidal cycle at Heron Island, Great Barrier Reef: (a) *Carcharhinus melanopterus* and (b) *Lethrinus nebulosus* around high tide (water depths >150 cm), (c) a meso-predator, *Lutjanus carponotatus* still active in shallow water (water depth <50 cm) and (d) an *Egretta sacra* perched on an aerially exposed coral at low tide (water depth <30 cm).

More quantitative observations of how water depth affects fishes require detailed visual surveys or tracking technologies, and both have been used for reef fishes in shallow water. Using visual surveys, daily migrations of *A. nigrofasciatus* have been documented in Eilat. In the morning, groups of *A. nigrofasciatus* move up 1.5 km from nocturnal shelters to shoreline feeding sites, and then return to shelters in the late afternoon (Mazeroll & Montgomery, 1995). *Acanthurus nigrofasciatus* provides an opportunity to examine movement cues, which are poorly understood in many fishes, although the cues can be split into those that are exogenous (*e.g.* changing salinity) and those that are endogenous (*e.g.* a circatidal rhythm of activity) (Gibson, 2003). Migrations to feeding sites appeared to rely on sunrise and sunset cues, and to utilize specific landmarks for navigation rather than odour, sun compass or electromagnetic detection (Mazeroll & Montgomery, 1998). Surgeonfishes have also been tracked on reef flats in Guam with passive acoustic telemetry, but were less mobile and demonstrated strong site fidelity with only the largest fishes having home ranges extending onto the deeper reef slope (Marshall *et al.*, 2011). Similar results were found using acoustic transmitters for the surf parrotfish *Scarus rivulatus* Valenciennes 1840 on the Great Barrier Reef, where most records were from the reef flat and crest compared to the reef base (Welsh & Bellwood, 2012). Acoustic tracking is particularly useful for large, wide-ranging species, and has shown that blacktip

reef sharks *Carcharhinus melanopterus* (Quoy & Gaimard 1824) at Palmyra Atoll have strong site fidelity to sand-flat ledges and exhibit diel and tidal movements (Papastamatiou *et al.*, 2009). The development of optimal foraging and migration models, as available for some temperate species (Burrows, 1994), would significantly help understand the movement of reef fishes in shallow water.

The prevalence of parasites on fishes represents an additional, intriguing method of inferring fish movements among habitats. There are few data available, but two studies provide data from Heron Island on the Great Barrier Reef. The first study highlighted a significantly greater prevalence and number of an undescribed *Benedenia* parasite on the blackeye thicklip *Hemigymnus melapterus* (Bloch 1791) from the flat compared to those from the reef slope (Grutter, 1998). The natural history of the parasite, which does not leave its host, suggests that *H. melapterus* does not move between the reef flat and slope, even though these zones are only a few hundred metres apart (Grutter, 1998). Similarly, Spanish flag snapper *Lutjanus carponotatus* (Richardson 1842) from reef flats and nearby reef slopes were examined for the presence of *Pomphorhynchus heronensis*, and fishes from the slope had significantly fewer worms than fishes in shallower water (Cribb *et al.*, 2000). These data also suggest limited movement between zones, and that transmission of the parasite is concentrated locally (Cribb *et al.*, 2000). These two studies raise a range of questions, such as whether restricted water volumes or some other factor specific to reef flats is the cause of the higher abundances of parasites in fishes. In combination with the acoustic data, the parasite data also suggest that although some larger fishes must leave the flat at low tide, it is possible for medium-sized fishes to live exclusively on reef flats where at least some water remains over tidal cycles.

Irrespective of whether reef flat fishes are permanent residents or transient visitors, tidally driven behaviours interact with other factors to affect foraging and feeding activity. Time of day is an important variable affecting the feeding behaviour of fishes on flats, and has been most commonly studied in herbivores. For example, at sites in the Coral Sea that included reef flats, three species of damselfishes and two species of surgeonfishes had an afternoon peak in feeding activity (Polunin & Klumpp, 1989). Higher afternoon feeding has also been reported for six size classes of *S. rivulatus* on a Great Barrier Reef outer reef flat (Bonaldo & Bellwood, 2008), for seven species of parrotfishes on both flats and other zones in the Egyptian Red Sea (Alwany *et al.*, 2009) and for *C. striatus* (Montgomery *et al.*, 1989). The last study, however, reported more constant feeding rates throughout the morning and afternoon for *A. nigrofusus* and the yellowtail tang *Zebrasoma xanthurum* (Blyth 1852). Diel changes in feeding rates appear not to be correlated with tides, water movement, light or internal respiratory rhythms (Polunin & Klumpp, 1989), but are more likely caused by the build-up of photosynthates during the day and the better nutritional quality of algae in the afternoon (Polunin & Klumpp, 1989; Bonaldo & Bellwood, 2008). There are fewer data available for other trophic groups, but strikes by piscivores on juvenile fishes on a back reef in Western Australia were most frequent in the mid-afternoon (Holmes *et al.*, 2012). In contrast, the invertivore *H. ocellatum*, which is almost an obligate reef flat dweller, displayed no obvious pattern in the state of digested prey items when sampled at a range of times over the day and night, although tidal state is likely to be an important factor as the species prefers to forage at low tide (Heupel & Bennett, 1998). The height at which planktivores, such as the lemon damsel *Pomacentrus moluccensis* Bleeker 1853, feed

above reef flat corals is positively correlated to water depth rather than time of day (unpubl. data), perhaps because zooplankton in this zone are more abundant near the water surface where retention in the reef system is maximized and predation rates are lower (Alldredge & King, 2009). Reef flat planktivores may also rely on a greater range of foods including lower-quality, reef-derived and recycled production because of less access to higher-quality oceanic productivity (Wyatt *et al.*, 2012). This perhaps explains the lower abundances of this functional group on reef flats than on more exposed reef slopes (Meekan *et al.*, 1995).

Along with shaping fish assemblages, wave energy on reef flats has additional effects by altering the foraging behaviour of fishes. At Lizard Island, Great Barrier Reef, species could be grouped as either widely foraging or having restricted foraging behaviour, and this was correlated with locomotory ability as assessed by fin morphology (Fulton & Bellwood, 2002). Foraging in moving water can also be aided by rheotaxis (orientation with respect to water currents), and *H. ocellatum* faces upstream when resting in order to aid station-holding, but swimming was not correlated with water direction (Peach, 2002). Water movement has a less important role for species that forage in territories, where water depth appears most important. Many surgeonfishes are territorial, and in contrast to deeper water where territories can be constantly defended, species such as the lined surgeonfish *Acanthurus lineatus* (L. 1758) may be forced into deeper water at low tides where they cease feeding (Nursall, 1974; Craig, 1996). Intertidal fishes may also establish escape routes into deeper water when threatened by predators, leading to 'stampedes' for the refuges provided by the higher coral cover on the reef slope (Robertson *et al.*, 1979). Reef flat territories, however, are valuable feeding grounds because even though fishes may need to refuge or sleep in deeper water, intertidal territories are re-established each morning and there is high day-to-day site fidelity (Craig, 1996).

THE CONTRIBUTION OF REEF FLAT FISHES TO ECOLOGICAL PROCESSES

It is beyond the scope of this review to discuss the functional value of fishes to ecological processes, but it is instructive to consider whether their role appears to be more or less important on reef flats and if the identity of key species is similar. Of all the ecological processes on reefs, perhaps the best studied is herbivory because of its vital role in controlling macroalgal cover and facilitating demographic processes in corals (Mumby, 2009). Herbivory on reef flats has been particularly well-studied on the Great Barrier Reef, and grazing of algae is significantly lower than on crest and slope habitats, particularly on inshore reefs. On inshore Orpheus Island, there was a 240-fold decrease in grazing activity, dominated by two parrotfishes [*S. rivulatus* and the steephead parrotfish *Chlorurus microrhinos* (Bleeker 1854)] and a rabbitfish (the barred spinefoot *Siganus doliatus* Guérin-Méneville 1829–1838), on the reef flat compared to the crest (Fox & Bellwood, 2007). Consequently, *S. rivulatus* grazes a square metre of reef on the crest per month, while only 27 and 1.3% of a square metre would be grazed in the same time on the slope and inner reef flat (Fox & Bellwood, 2007). These values vary across the Great Barrier Reef, with a square metre of crest on other inshore reefs being grazed 8.5–11.0 times per year compared to 4.9 times per year on the reef flat, while grazing rates are more homogenous

on mid- and outer-shelf reefs (Hoey & Bellwood, 2008). Grazing rates are also lower on mid-shelf reefs, and lowest on outer-shelf reefs (Hoey & Bellwood, 2008), and lower on mid-shelf reef slopes and bases compared to shallow reef crests and flats (Hoey & Bellwood, 2010). The high grazing rates at reef crests suggest that grazers are able to deal with high wave energy and tidal fluctuations in water depth, but perhaps low algal productivity and the low topographic complexity (shelter) of reef flats limit the density of grazers (Fox & Bellwood, 2007). The typically higher topographic complexity of reef flats on mid- and outer-shelf reefs may explain why grazing rates on these reefs are more similar to those of crests. Irrespective of which habitat is most heavily grazed, patterns in grazing pressure are reflected in macroalgal distributions. For example, on Orpheus Island, grazing impacts were negatively correlated with macroalgal cover (Fox & Bellwood, 2007). High grazing pressure on crests can also reduce algal turf height, sediment loads and particulate content compared to turfs on reef flats with lower grazing rates (Bonaldo & Bellwood, 2011a).

Some herbivorous fishes are also significant bioeroders (biological eroders of hard substrata), either through the indirect removal of hard substrata during feeding (e.g. excavating parrotfishes; Bellwood & Choat, 1990) or direct predation of corals (Mumby, 2009). The key bioeroding parrotfishes may not necessarily be the most abundant, as bioerosion capacity depends on bite volumes and rates. In the Red Sea, the daisy parrotfish *Chlorurus sordidus* (Forsskål 1775) is most abundant on reef flats, but the less common blue-barred parrotfish *Scarus ghobban* Forsskål 1775 had a much higher bioerosion rate per individual, meaning that both were important contributors to overall bioerosion rates (Alwany *et al.*, 2009). On the Great Barrier Reef, bioerosion rates are highest ($>20 \text{ kg m}^{-2} \text{ year}^{-1}$) on the reef flats and crests of the outer-shelf reefs because of the contribution of the large-bodied *B. muricatum* that is uncommon on inner- and mid-shelf reefs (Bellwood *et al.*, 2003; Hoey & Bellwood, 2008). Rates across back reef, flat, crest and slope are more homogeneous on mid-shelf reefs and almost entirely driven by the abundance of *C. microrhinos*, and are negligible on the flats of inner-shelf reefs (Bellwood *et al.*, 2003). Coral predation by *B. muricatum* is also significant on outer-shelf reef flats and crests (12.7 and $15.0 \text{ kg m}^{-2} \text{ year}^{-1}$), and is at least two orders of magnitude higher than other habitats (Hoey & Bellwood, 2008). Even where *B. muricatum* is uncommon on the Great Barrier Reef, parrotfish grazing scars are most common on reef flat and crest habitats, and are focused on massive corals from the genus *Porites*, potentially affecting its distribution (Bonaldo & Bellwood, 2011b).

In addition to bioerosion, the large areas of sand on many reef flats mean that bioturbation (the physical disturbance of sediment associated with foraging or burrowing activities) by fishes can be important. Bioturbation by fishes is a key influence on microbial communities in sediments, altering the physical environment for benthic invertebrates, and releasing nutrients into the water column (Holmlund & Hammer, 1999). Many large species use sandy habitats in shallow reef zones for foraging (Jones *et al.*, 1991), and species such as the spangled emperor *Lethrinus nebulosus* (Forsskål 1775) and the cowtail ray *Pastinachus sephen* (Forsskål 1775) can be seen foraging in large numbers on sandy inner reef flats on the Great Barrier Reef (A. R. Harborne, pers. obs.). Rays may be a particularly important contributor to bioturbation rates, although data for tropical species are scarce. On sandy flats at Ningaloo Reef (Western Australia), however, stingrays excavated 1.08 m^3 (760.8 kg)

of sediment in 21 days, representing 2.4% of the area sampled (O'Shea *et al.*, 2012). Consequently, it is possible that 42% of the soft sediments in the study area were reworked by stingrays annually (O'Shea *et al.*, 2012), suggesting that bioturbation of soft-sediment patches on reef flats could be considerable. Smaller reef fishes, such as juvenile dash-and-dot goatfish *Parupeneus barberinus* (Lacépède 1801), can also dig vigorously on the reef flat (Lukoschek & McCormick, 2001), but the amount of sediment they rework is unknown.

THE PHYSIOLOGY OF FISHES ON REEF FLATS

Reef flats represent a challenging environment for fishes because of the relatively rapid changes in water depth, and the potential for extreme and fluctuating temperatures, oxygen concentrations and levels of UV radiation in shallow water. It is unclear whether reef flat species and individuals are physiological generalists compared to species and conspecific in deeper water, but it is possible to establish what adaptations may aid fishes permanently living in shallow water. Perhaps, the most critical requirement of reef flat species is the ability to withstand low oxygen concentrations. Coral reefs are typically not considered to be hypoxic environments (Nilsson *et al.*, 2004), but it is increasingly recognized that species taking refuge in respiring corals will frequently have to deal with hypoxic conditions where oxygen concentrations may be 2% of air saturation (Nilsson *et al.*, 2007a). Such conditions are not limited to reef flats, but they may be exacerbated on flats because of higher water temperatures and the potential for fishes to be trapped in tidal pools (Nilsson *et al.*, 2007b), and the need to hide during low tides. Interestingly, one of the earliest reported examples of a tropical species coping with hypoxic conditions was *H. ocellatum* (Fig. 2), a reef flat specialist that appears to be tolerant to both mild hypoxia and cyclic exposure to extreme hypoxia (Wise *et al.*, 1998). A more detailed study then demonstrated that falling oxygen concentrations cause *H. ocellatum* to increase its ventilatory rate, allowing it to maintain its normal metabolic rate down to very low oxygen concentrations; it is then able to enter a state of metabolic and ventilatory depression under severely hypoxic conditions (Routley *et al.*, 2002). The hypoxic response of individual *H. ocellatum* is also enhanced by pre-conditioning to low oxygen concentrations (Routley *et al.*, 2002).

Subsequently, it has been demonstrated that a range of reef teleosts also have a remarkable tolerance to hypoxia. For example, 31 teleost species (from seven families) that inhabit shallow water on the Great Barrier Reef can maintain their rate of oxygen consumption down to 20–30% of air saturation, and many appeared unaffected by hypoxia until levels fell below 10% of air saturation (Nilsson & Östlund-Nilsson, 2004; Nilsson *et al.*, 2007a). Indeed, it can be concluded that a well-developed tolerance to hypoxia is a necessity for fishes using coral as nocturnal refuges (Nilsson *et al.*, 2007b). In addition to this need for tolerance to hypoxia, reef flat fishes face the further challenge that their home coral may be aerially exposed during particularly low tides. Therefore, some gobies are able to tolerate air exposure for 3 h by circulating a small volume of water over the gills and obtaining oxygen through diffusion from air, and possibly taking up oxygen through the skin (Nilsson *et al.*, 2004). Among cryptobenthic species, air breathing abilities are particularly apparent in species that live in corals in shallow water where air exposure is most

likely (Nilsson *et al.*, 2007a). In contrast to the data on tolerance to hypoxia, there are few studies of hyperoxia. Photosynthesizing reef organisms can increase oxygen levels to >200% of air saturation, and such high concentrations can cause cellular damage in fishes (Nilsson *et al.*, 2007b).

Rates of oxygen consumption by fishes are compromised by elevated temperatures, and high temperatures are particularly likely in the shallow water on flats. A temperature increase of 2–4° C can reduce the aerobic capacity of cardinalfishes to less than half of that measured at a control temperature of 29° C (Nilsson *et al.*, 2009). Three damselfish species, however, retained more than half of their aerobic capacity at 33° C, suggesting a range of temperature tolerances among reef fishes (Nilsson *et al.*, 2009). Increased temperatures also reduce hypoxia tolerance, and may not be ameliorated by acclimation (Nilsson *et al.*, 2010). Furthermore, the metabolic consequences of increased temperature lead to severe reductions in fish swimming performance, so that fishes are less able to cope with the high levels of water motion on reef flats (Johansen & Jones, 2011). Temperature increases can also reduce the breeding rates, sperm production and somatic growth rates of reef fishes (Munday *et al.*, 2008; Donelson *et al.*, 2010), although there is no evidence that fishes on flats produce fewer larvae or grow slower than conspecifics in deeper water. Despite the effects of increased temperatures, how the ecological impacts on reef fish populations differ between a 2 and 4° C fluctuation (as experienced on a daily basis) compared to a 2 and 4° C mean increase (driven by climate change) is currently not clear.

The final major metabolic challenge to fishes in shallow water, compared to individuals in deeper water, is coping with high levels of UV radiation. UV is absorbed by sea water, especially when organic material is present, but transmission can be 50–80% m⁻¹ in clear tropical seas (Zamzow, 2007). A wide range of fish species produce both UVA- and UVB-absorbing compounds in their epithelial mucus, and can alter the absorbance properties of their mucus depending on the UV regime (Zamzow & Losey, 2002). It appears likely that reef flat species have particularly effective UV-screening mucus, and there is supporting evidence from individuals of the saddle wrasse *Thalassoma duperrey* (Quoy & Gaimard 1824); the mucus of individuals from deeper water blocked less of the UV portion of the spectrum than individuals from shallow water (Zamzow & Losey, 2002). Variations in UV absorption also occur with turbidity, as UV is attenuated more quickly in turbid water (Zamzow, 2007). Species in turbid water may either shift the spectral quality of their mucus when in clearer water or simply increase its overall UV absorbance (Zamzow, 2007).

The lack of data comparing physiological adaptations of shallow and deep water fishes means that it is difficult to establish how intraspecific body condition varies among reef zones, and ultimately what the implications are for population demographics. There is increasing interest in the scale and drivers of variation in key demographic rates, as the relative reproductive contributions of fishes in different habitat patches have important implications for population and metapopulation dynamics (Figueira & Crowder, 2006). Examples of changes in body condition and demographic rates with depth are scarce on Pacific reefs, but Rolland's demoiselle *Chrysiptera rollandi* (Whitley 1961) has slower initial growth rates and a larger mean asymptotic length with increasing depth on the Great Barrier Reef (Hoey *et al.*, 2007). Although larger individuals were found in deeper water, relative gonad mass and overall body condition were generally higher in shallower water (Hoey *et al.*,

2007). The drivers of these differences in *C. rollandi* were unclear, but the higher physiological condition of two butterflyfish species at reef front sites (compared to back reef sites) on the Great Barrier Reef can be a result of prey quality and quantity (Berumen *et al.*, 2005). Furthermore, food digestion is an energetically costly process in fishes, and increased water temperatures on reef flats may speed up the process, allowing fishes to feed again more quickly after each meal (Secor, 2009). Along with food availability and digestibility, other potential drivers of changes in key demographic traits with depth are competition, intraspecific density-dependent effects and predation risk (Figueira *et al.*, 2008). Demographic rates can also be affected by habitat context. For example, mortality of juvenile damselfishes and cardinalfishes was higher on isolated corals in a sand and coral matrix compared to a continuous rock reef flat in Japan (Nanami & Nishihira, 2003). These differential mortality rates were most likely caused by density-dependent effects, and affected the population stability in the two different habitat types (Nanami & Nishihira, 2003).

REEF FLATS AS FISH NURSERIES

The identification and importance of nursery habitats in the ecology of reef fishes have attracted considerable research attention (Beck *et al.*, 2001). Many species do not settle directly to their preferred adult habitats, but instead settle into nursery areas and undergo ontogenetic shifts to adult habitats over their lifetime. Shallow tropical marine habitats, such as mangroves and seagrass beds, are frequently identified as nursery habitats and are suggested to offer advantages to juvenile fishes, such as decreased predation pressure or increased food availability (Beck *et al.*, 2001). Compared to assemblages on reefs without nearby nurseries, these advantages may significantly alter the structure and composition of fish assemblages on reefs close to nursery habitats (Mumby *et al.*, 2004). Consequently, the identification of nursery habitats is important for understanding the ecology and conservation of reef fishes. Conclusively demonstrating that habitat is a nursery, however, is problematic, and there is a growing literature on the precise requirements that are needed for a habitat to be identified as a nursery (Beck *et al.*, 2001; Adams *et al.*, 2006; Dahlgren *et al.*, 2006). Although the majority of tropical marine data are related to mangrove and seagrass habitats, there is recognition that all 'back reef' habitats (habitats bound by the leeward side of the reef crest and the high-tide line) have the potential to be nurseries (Adams *et al.*, 2006). Comprehensive studies examining the nursery role of reef flats in the Pacific are scarce. In the absence of conclusive evidence, this section first examines the potential of reef flats to act as nurseries, and then summarizes data that are consistent with this functional role.

It is tempting to assign a nursery role to reef flats because of the shallow water refuge paradigm, which posits that small fishes in shallow water have a refuge from larger predators that cannot access habitats with insufficient water depths (Baker & Sheaves, 2007). Empirical evidence is mixed (Baker & Sheaves, 2007), however, and estimating potential predation pressure is problematic in many ecosystems because the full suite of predators is rarely known and many piscivores may be facultative (Sheaves, 2001). This is certainly true on reefs, where video studies continue to reveal the key piscivorous role of species previously thought to be of

minor importance (Holmes *et al.*, 2012). Furthermore, fishes in shallow water are susceptible to terrestrial predators such as birds that are abundant on many Pacific Ocean reef flats (Recher & Recher, 1972; Fig. 3), providing additional complexities when trying to assess the combined effects of multiple predators. The critical question is whether mortality rates decline in shallow water (Sheaves, 2001), and there are few studies comparing fish mortality rates among habitat types. At Lizard Island, Great Barrier Reef, newly settled damselfishes on the flat of a patch reef sustained higher mortality than those on the reef base (McCormick & Hoey, 2004). The mechanisms explaining this pattern were not clear, but it did not reflect surveys of potential predators, which suggested a greater abundance and diversity at the reef base. Other data for fishes settling to reef flats and back reefs suggest that *c.* 61% of settling bluespine unicornfish *Naso unicornis* (Forsskål 1775) in Moorea were lost in the first 12 h, and then between 9 and 20% per day (Doherty *et al.*, 2004). After 7 weeks, predation of a large pulse of honeycomb grouper *Epinephelus merra* Bloch 1793 onto reefs around Réunion Island was 85–88% in back reef areas and from 93 to 95% on reef flats (Letourneur *et al.*, 1998), and only 1% of *A. lineatus* recruits survived the first year after settling onto an outer reef flat in American Samoa (Craig *et al.*, 1997). Predation rates of settling reef fishes are recognized as being very high on reefs (Almany & Webster, 2006), and without comparative data from other habitats it is difficult to assess whether these rates will translate into higher contributions to adult populations, and hence a nursery function (Beck *et al.*, 2001).

In the absence of direct evidence of a nursery role for reef flats, there are data that indirectly suggest that flats are important to juvenile fishes. Perhaps, the most obvious indirect evidence is the high abundance of juveniles, which is often invoked as evidence of a nursery function but does not demonstrate the requisite above average contribution to adult populations per unit area. Butterflyfishes demonstrate some of the best documented patterns of juveniles favouring shallow water in contrast to more widely dispersed adults. This is particularly true for generalist species with wide diets, such as the threadfin butterflyfish *Chaetodon auriga* Forsskål 1775 and the vagabond butterflyfish *Chaetodon vagabundus* L. 1758, where the juveniles are most abundant on some reef flats and shallow patch reefs (Pratchett *et al.*, 2008; Clark & Russ, 2012). Species may also use reef flats as part of a complex ontogenetic migration, such as the blackfin dartfish *Ptereleotris evides* (Jordan & Hubbs 1925) that settles seaward of the reef crest and then moves onto the flat just behind the crest before moving onto the crest and finally onto the reef slope (McCormick & Makey, 1997). More generally, *c.* one-third of fishes recorded on shallow seagrass beds, coral patches, reef flats and sand in the Red Sea were juveniles, suggesting a nursery function for these habitats (Ashworth *et al.*, 2006). Despite high mortality rates, there is some evidence of high settlement rates of some fish recruits onto reef flats, which is consistent with fishes utilizing them as nursery habitats. For example, during a mass settlement of the grouper *E. merra* onto reefs around Reunion Island, mean densities were higher on reef flats than on back reef areas (Letourneur *et al.*, 1998), and a dense pulse of *A. lineatus* recruits onto the outer reef flat has been recorded in American Samoa (Craig *et al.*, 1997). Recruits of *L. carponotatus* were also mainly found on reef flats on the Great Barrier Reef, and were rarely found seaward of the reef crest (Wen *et al.*, 2013). Reef flats, however, may be less important nurseries than seagrass beds (Dorenbosch *et al.*, 2005), and only two of the eight abundant

wrasse species at Lizard Island, Great Barrier Reef, showed differential habitat use by adults and recruits (Green, 1996).

POTENTIAL IMPACTS OF CLIMATE CHANGE ON REEF FLAT FISHES

Global climate change is having a range of detrimental effects on marine ecosystems, including increasing temperatures, rising sea levels, ocean acidification and changed circulation patterns (Hoegh-Guldberg, 1999; Hoegh-Guldberg *et al.*, 2007). Although these effects are pervasive across reefs, reef flats may be particularly susceptible because of their position in shallow water. Under climate change scenarios, fishes in shallow water may be exposed to greater increases and fluctuations in temperature, and associated fluctuations in oxygen levels, than individuals in deeper water. For example, on Heron Island, Great Barrier Reef, the reef flat is in a shallow water mass that is greatly influenced by prevailing conditions, while the base of the reef slope is in a more oceanic water mass that is more thermally stable (Potts & Swart, 1984). Few studies have explicitly considered the effects of climate change on reef flats, but literature on interactions between climate change and reef organisms suggest how reef flat fish assemblages may be affected in the short- to medium-term

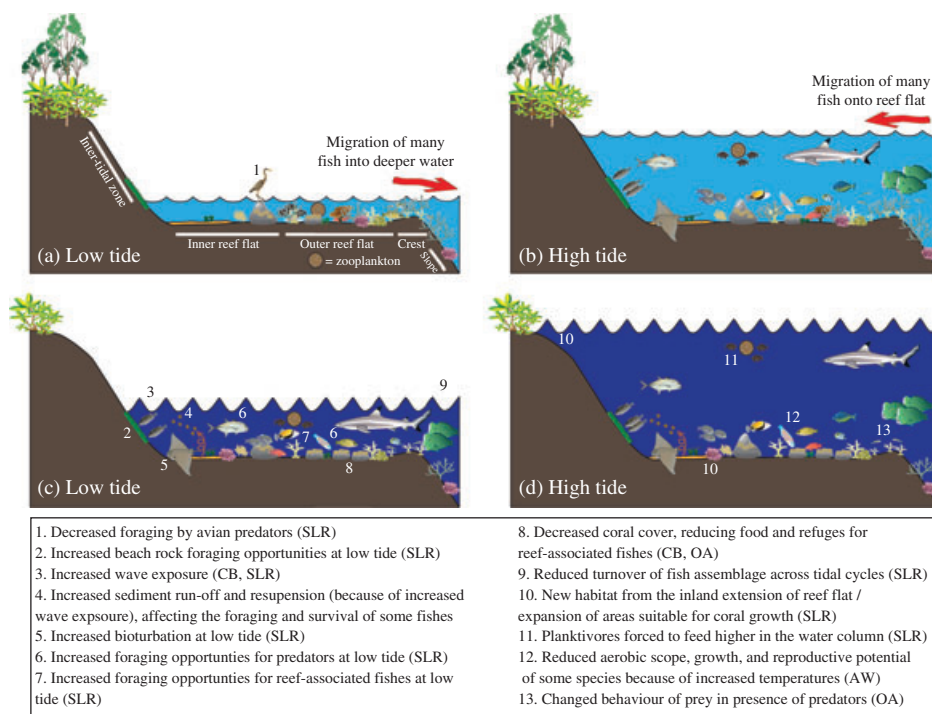


FIG. 4. (a, b) Schematic representation of a reef flat over a tidal cycle and (c, d) the potential direct and indirect effects of climate change on their fish assemblages. The major climate change impacts that will be the predominant driver of each potential effect are indicated: SLR, sea-level rise; CB, coral bleaching; OA, ocean acidification; AW, atmospheric warming.

(Fig. 4). These impacts will also act synergistically with the suite of other threats affecting reef health, including over-fishing, diseases and invasive species (Hoegh-Guldberg, 1999). In addition to these general threats to all reef habitats, some reef flats are subject to extensive coral breakages by snorkellers and reef walkers (Leujak & Ormond, 2008; Hannak *et al.*, 2011).

There is a growing literature on the effects of increasing seawater temperature and acidification on the physiology and behaviour of fishes, and much of it is highly relevant to reef flat species. Increasing temperatures are particularly important because it appears that at least some reef fishes are close to their thermal tolerance, so that at higher temperatures their circulatory and ventilatory systems are unable to supply oxygen to fulfil the extra demand in their tissues (Munday *et al.*, 2012). The impacts of increasing temperature on the oxygen consumption and aerobic scope of six different fish species have been demonstrated by physiological tests on individuals from the northern (Lizard Island) and southern (Heron Island) Great Barrier Reef (Gardiner *et al.*, 2010). Fishes from four of the Heron Island species had a much greater scope to increase their maximum oxygen intake rates, suggesting that they performed much better at 5°C above summer surface-water temperature. This work suggests that high-latitude populations may be less impacted by ocean warming than low-latitude populations, but there will be significant interspecies differences (Gardiner *et al.*, 2010). Consequently, there is the possibility of a shift to temperature-tolerant species as the climate changes (Nilsson *et al.*, 2009). Whether fishes on reef flats, which are exposed to more extreme and fluctuating temperatures, are better adapted to cope with climate change than individuals in deeper water is currently unknown, but back reef and nearshore corals are less vulnerable to changes in temperature than those on fore-reefs, possibly because the former routinely experience greater diurnal and seasonal thermal fluctuations (Castillo *et al.*, 2012). Equally, the capacity of fishes to adapt to increased temperatures is poorly understood, although there is a growing recognition that transgenerational acclimation may be more common than previously thought (Munday *et al.*, 2012). The problems of oxygen consumption may be further compounded by ocean acidification, because acidified water (pH 7.8 and *c.* 1000 ppm CO₂) can have metabolic effects similar to a 3°C increase in water temperature (Munday *et al.*, 2009). Acidification also has effects on fish growth and behaviour, with increasing CO₂ concentrations leading to fishes moving further from shelter and experiencing increased predation rates (Munday *et al.*, 2012). Increased temperatures can also affect the reproductive output of fishes, and potentially lead to population declines (Donelson *et al.*, 2010).

In contrast to the direct effects of temperature and CO₂ concentrations on fishes, the impacts of sea-level rise are rarely discussed. In a recent review of the impacts of climate change on reef fishes, sea-level rise was only highlighted in the context of effects on connected seagrass and mangrove habitats (Wilson *et al.*, 2010). While reef fishes will be able to cope with increased water depths across most reef habitats, there is the potential for sea-level rise to have important impacts on reef flat assemblages. This increased sensitivity is driven by low tides on many reef flats causing larger fishes to move into deeper water, and potentially offer fishes remaining on the flat a refuge from predation. For example, low tide (<50 cm deep) at Heron Island, Great Barrier Reef, leads to the biomass of carnivorous and piscivorous teleosts declining by up to 30-fold at some sites, and the absence of sharks and rays that are relatively abundant at high tide (unpubl. data). Predicted sea-level

risers of 50 and 140 cm above the 1990 level by 2100 because of thermal expansion of water, melting, glaciers and ice sheets, and changed water storage on land (Rahmstorf, 2007) could potentially lead to a 'permanent high tide'. Consequently, changes in fish assemblages over tidal cycles may be reduced on some reef flats. If larger fishes are able to remain on flats for longer periods, this may positively change their demographics by providing increased foraging opportunities. In contrast, a loss of a temporal refuge from predation may detrimentally affect the demographics of prey species, although the full implications of interacting factors such as their own increased foraging opportunities, reduced access by avian predators, and changes to food availability and water movement are difficult to predict. For example, planktivores may have to feed higher in the water column, and become more susceptible to predators, in order to reach the high densities of zooplankton at the surface (Alldredge & King, 2009). Surgeonfishes feeding on beach rock (Montgomery *et al.*, 1989), however, may have increased foraging opportunities as intertidal zones could be permanently inundated. Consequently, it appears that sea-level rise has the potential to fundamentally alter the trophodynamics on some reef flats, and perhaps any nursery functions. Such changes have presumably occurred previously as reefs have had to keep-up, catch-up or be drowned by Holocene variations in sea level (Woodroffe & Murray-Wallace, 2012), but the next 100 years are likely to provide an opportunity to document in detail the effects of changing sea level on fishes in shallow coral reef habitats.

The impacts of sea-level rise on reef flat fishes in some locations may be ameliorated by the creation of some new reef flat habitat following inundation of land areas. Perhaps, more importantly, the impacts of sea-level rise will be influenced by the ability of benthic habitats to 'keep-up'. Coral reef growth rates mean that they are unlikely to be 'drowned' as previously feared (Spencer, 1995), so water depths across reef profiles may not increase significantly. Large areas of some reef flats, however, consist of soft sediment, and these have limited accretion potential. Therefore, even if coral-rich areas track sea-level rise, soft-sediment habitat patches are likely to be found in deeper water and offer larger fishes a refuge at low tide. There is further potential for profound changes to reef flat fish communities in areas such as the Torres Straits, which currently consist of an in-filled, sediment-rich carbonate platform that is exposed at low tide and has very little coral growth (Yamano, 2000; Hopley, 2011). In such 'inert' areas, coral cover and reef growth may significantly increase under sea-level rise scenarios where sediment transport increases and aerial exposure is reduced (Hopley, 2011). There is empirical evidence of the potential for these changes in Thailand, where sea level increases over a 50 year period were positively correlated with coral cover (Brown *et al.*, 2011). Similarly, a 40 year history of engineering projects for an access channel at Heron Island, Great Barrier Reef, has led to changes in coral development on the reef flat, and rapid vertical development associated with periods of increased sea level (Scopéltis *et al.*, 2011). Future coral development may be limited by mortality events associated with coral bleaching (Hoegh-Guldberg, 1999) and decreasing growth rates caused by ocean acidification (Hoegh-Guldberg *et al.*, 2007). Irrespective of any new coral growth, bleaching and other sources of coral mortality and loss of topographic complexity, such as outbreaks of disease and crown-of-thorns starfish *Acanthaster planci*, may have significant effects on fish assemblages by degrading the quality of refuges and reducing food availability (Jones *et al.*, 2004). Climate change may also lead to future

cyclones being more intense (Knutson *et al.*, 2010), which will further degrade damaged benthic communities and the fishes that rely on them. The loss of coral refuges required for sheltering from predators and high water motion are well-recognized on reefs, but the loss of refuges may have an additional impact on reef flats by exposing fishes to more UV radiation.

Coral loss, combined with sea-level rise, may also dramatically alter the hydrodynamic regime experienced by reef flat fishes. For example, the 1998 bleaching event in the Seychelles reduced shallow water coral growth and has led to 75% more wave energy reaching shorelines (Sheppard *et al.*, 2005). The loss of protective reef crests might be exacerbated by projected increases in annual mean significant wave heights and changes in wave direction, which are associated with strengthening westerly winds, particularly in the Southern Ocean (Hemer *et al.*, 2013). Given the importance of wave energy for controlling the distribution of many fishes (Depczynski & Bellwood, 2005; Fulton & Bellwood, 2005), such increases in hydrodynamic conditions may have significant effects on reef flat fishes. Additionally, more water movement will move sediment from the inner to coral-rich outer reef flat zones and increase seabed shear stresses, sediment resuspension into the water column and periods of high turbidity, although it will reduce sediment residence times (Storzazzi *et al.*, 2011). For example, predictions for a reef flat in Hawaii suggest that suspended-sediment concentrations will increase from *c.* 11 to *c.* 20 mg l⁻¹ with a 20 cm sea-level rise (Ogston & Field, 2010). Sediment loads in coastal waters can be further increased by changes in coastal land use increasing terrestrial run-off, and these increased sediment loads can smother and reduce the light available to corals that provide important microhabitats to fishes (Fabricius, 2005). Recent work has also demonstrated more direct effects of sediment to some fishes. High sediment concentrations can inhibit the ability of damselfishes to select their preferred settlement habitat by disrupting chemical cues, and may reduce survival of recruiting fishes (Wenger *et al.*, 2011). Increased sediment also causes juveniles of the spiny chromis *Acanthochromis polyacanthus* (Bleeker 1855) to take longer to find and consume food, which decreases growth rates, body condition and survival (Wenger *et al.*, 2012). Survival of damselfishes may also be reduced after modest increases in sediment load because of increased predator-induced mortality (Wenger *et al.*, 2013). Furthermore, sediment on reefs suppresses the herbivory, so that increased sediment loads could directly affect resilience (Goatley & Bellwood, 2012).

CONCLUSIONS

Given the relative ease of working on shallow reef flats close to shore, and their spatial extent, there are surprisingly few data on the behaviour, ecology and physiology of their fish assemblages. For example, even though it is obvious to even the most occasional snorkeller or reef walker that the fish assemblage changes on reef flats with tidal state, there are few quantitative data describing the temporal turnover of species. Furthermore, there is currently very little understanding of how many of the tidally driven changes in the abundances of individual species are caused by fishes migrating to deeper water (the transient or temporary component) and how many are caused by fishes being hidden in and under corals at low tide (the resident

or permanent component). Vivien (1973) suggested reef flat fishes could be separated into a permanent community of species that do not migrate over tidal cycles, including those that are there throughout their life cycle and those that are only on flats during certain life phases, and a temporary community of species that migrates from reef slopes and seagrass beds over tidal cycles to feed and shelter on the flat, the identity of which may vary from day to night. Forty years later, however, the components of these different assemblages are still largely unquantified for many reefs. Furthermore, changes in fish assemblages over tidal cycles are not driven by water depth alone, but are caused by interactions between depth, water flow, time of day or night, the nature of benthic assemblages and seascape context. New insights into how physical drivers affect the behaviour of fishes, using techniques such as video observations and acoustic tracking, will provide a clearer picture of how ecological processes and trophodynamics change over tidal cycles. Such work will also identify key species that could be the focus of physiological studies of how fishes adapt to life on reef flats; interesting targets could be species that are resident on reef flats while congeners are transient.

Perhaps, a more challenging research agenda will be demonstrating the key factors that cause many species to value reef flats so highly. For example, *C. melanopterus* at Heron Island, Great Barrier Reef, leave the reef flat only when they are virtually stranded and re-enter the habitat as soon as the water becomes sufficiently deep (A. R. Harborne pers. obs.). Sharks and rays also congregate to rest in predictable areas along the shoreline during the day, but it is not known how their behaviours change at night. Presumably, the drivers of this behaviour are multi-faceted, but are likely to include prey availability, increased hunting efficiency in shallow water (Heithaus *et al.*, 2009), the metabolic benefits of increased temperatures in shallow water and avoidance of predators in deeper water (Mourier *et al.*, 2013). In temperate waters, leopard sharks *Triakis semifasciata* Girard 1855 seek the warmest areas of an embayment, and the higher body core temperatures are likely to aid digestion, somatic growth and possibly reproduction (Hight & Lowe, 2007). As many of the obvious transient species are carnivores, elucidating their behaviours will be an important factor in understanding changes in predation pressure and whether reef flats do indeed have a nursery function for some species. Many of these carnivores are also economically important species and elucidating their daily movement patterns will help establish effective conservation initiatives.

A greater knowledge of the fish assemblages and functional value of reef flats will be vital for understanding the impacts and effects of threats to reef health. In many respects, reef flats are among the most susceptible habitats to climate change. Investigations of changes in water temperature and acidity are rarely habitat specific, but combining empirical studies with observed gradients of the mean and variance of physical variables across a reef profile may be an important step forward as researchers attempt to predict the future of reefs under various climate change scenarios. Furthermore, the implications of sea-level rise on reef flats appear to warrant more research. Although the potential for complex changes to reef flat food webs with increasing sea levels has long been recognized (Cubit, 1985), there are few studies on the likely magnitude of the impacts. In summary, reef flats represent an extensive and diverse Pacific Ocean, Indian Ocean and Red Sea reef habitat with key ecological functions, a relatively important role of physical drivers compared to other reef habitats, provide a range of goods and services and are in the frontline

of tropical marine climate change research. It is well-established that inter-habitat differences on reefs are profound and important for the overall functioning of reefs (Hatcher, 1997); a better understanding of how reef flats function differently to habitats in deeper water will be critical to attempt to manage and maintain tropical marine seascapes through an uncertain future.

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