

Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes

Short running title: Tropical macroalgal fish and fisheries

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ABSTRACT

Canopy-forming macroalgae can construct extensive meadow habitats in tropical seascapes occupied by fishes that span a diversity of taxa, life history stages and ecological roles. Our synthesis assessed whether these tropical macroalgal habitats have unique fish assemblages, provide fish nurseries, and support local fisheries. We also applied a meta-analysis of independent surveys across 23 tropical reef locations in 11 countries to examine how macroalgal canopy condition is related to the abundance of macroalgal-associated fishes. Over 627 fish species were documented in tropical macroalgal meadows, with 218 of these taxa exhibiting higher local abundance within this habitat (cf. nearby coral reef) during at least one life history stage. Major overlap (40-43%) in local fish species richness among macroalgal and seagrass or coral reef habitats suggest macroalgal meadows may provide an important habitat refuge. Moreover, the prominence of juvenile fishes suggests macroalgal meadows facilitate the triphasic life cycle of many fishes occupying diverse tropical seascapes. Correlations between macroalgal canopy structure and juvenile abundance suggest macroalgal habitat condition can influence levels of replenishment in tropical fish populations, including the majority of macroalgal-associated fishes that are targeted by commercial, subsistence, or recreational fisheries. While many macroalgal-associated fishery species are of minor commercial value, their local importance for food and livelihood security can be substantial (e.g., up to 60% of landings in Kenyan reef fisheries). Given macroalgal canopy condition can vary substantially with sea temperature, there is a high likelihood that climate change will impact macroalgal-associated fish and fisheries.

Keywords: coral reef, nursery, ontogenetic migration, recruitment, *Sargassum*, seagrass

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1. INTRODUCTION

Conservation and management of fish biodiversity requires an understanding of the habitats needed to support and replenish all of the species in a region of interest. While some species may be uniquely linked to a certain habitat type, many fish taxa follow a triphasic life cycle, where planktonic larvae settle into an initial habitat before migrating to different habitats as juveniles and/or adults. Moreover, adult fishes often move among habitats over daily or longer time-scales to fulfil foraging or reproductive activities. Characterisation of a fauna according to surveys within a single habitat type, therefore, can lead to a conclusion that a collection of species are dependent on that habitat type. A wider seascape perspective that tracks the abundance and activities of fishes across different patch habitat types is needed to reveal the full suite of connected habitats that sustain fish populations and communities (Brown et al., 2018; Olds et al. 2018; Sambrook et al., 2019).

Tropical seascapes often comprise a mosaic of patch habitats created by corals, seagrass, sponges, mangroves, and canopy-forming macroalgae, any of which may be utilised by fishes. Considerable effort has been devoted to understanding the fish-habitat functions performed by some of these patch types, particularly corals (e.g., Coker, Wilson, & Pratchett, 2014), seagrass (e.g., Gillanders, 2006), and mangroves (e.g., Faunce & Serafy, 2006). Despite the long-recognised importance of macroalgae for fish and fisheries in temperate waters (Bertocci, Araújo, Oliveira, & Sousa-Pinto, 2015), comparatively little attention has been directed to how tropical macroalgal habitats may influence patterns of fish diversity, replenishment and fisheries production (Fig. 1).

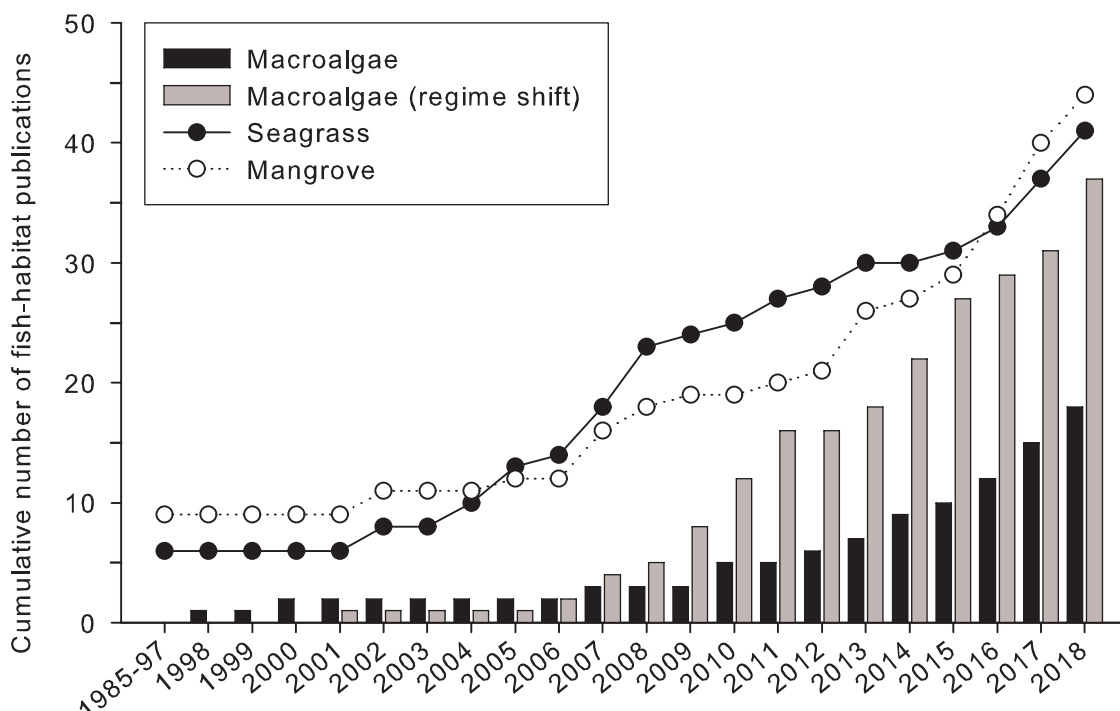


Figure 1. Cumulative number of published studies on fish community structure within tropical macroalgae meadows (dark bars), and within macroalgae-dominated habitat that

arose from a coral–macroalgal regime shift (grey bars). Published research effort on tropical fish communities within two other major macrophyte habitats - seagrass beds (solid line) and mangrove forests (dotted line) - are provided for comparison. Results are for 1985 to 2018 inclusive, based on a Scopus search conducted on 17 March 2019.

Macroalgal meadows can cover large areas of tropical seascapes (16–46% of shallow waters; Fulton et al., 2019) to provide food and shelter for shallow-water tropical fishes. Typically, these meadows are dominated by canopy-forming macroalgae (e.g., *Sargassum*, *Sargassopsis*, *Sirophysalis*, *Turbinaria*) with various understory genera (e.g., *Lobophora*, *Dictyota*, *Padina*) and an abundant epifaunal community, which provides a diverse prey base for higher-order consumers such as fish (Bittick, Clausing, Fong, Scoma, & Fong, 2019; Fulton et al., 2019; Tano et al., 2016). Indeed, current evidence suggests these complex macroalgal meadows are occupied by diverse assemblages of tropical fishes at various life history stages (e.g., Chaves, Pereira, & Feitosa, 2013; Eggertsen, Chacin, Halling & Berkström, 2019; Ornellas & Coutinho, 1998; Rossier & Kulbicki, 2000), some of which may support local fisheries (e.g., Campos, del Norte-Campos, & McManus, 1994; Hicks & McClanahan, 2012; Robinson et al., 2018). Tropical macroalgal meadows, however, are dynamic habitats that can vary dramatically in canopy structure across seasons and years (Fulton et al. 2019). Although individual studies have documented how changes in canopy condition can influence the abundance of certain macroalgae-associated fishes (e.g., Aburto-Oropeza, Sala, Paredes, Mendoza, & Ballesteros, 2007; Ornellas & Coutinho, 1998; Wilson et al., 2017), large-scale assessments are needed to understand the generality and nature of these macroalgal habitat effects on patterns of tropical fish diversity, abundance and replenishment.

In this synthesis we assess whether: (i) tropical macroalgal meadows have unique fish assemblages based on overlap in species occurrence and relative abundance with adjacent coral and seagrass habitats (Section 2), (ii) macroalgal habitats provide fish nurseries in tropical seascapes (Section 3), and (iii) macroalgal-associated species support tropical fisheries (Section 4). We also used a meta-analysis to assess (iv) the relationship between macroalgae habitat condition and the abundance of macroalgal-associated tropical fishes (Section 5). To do this we collated data from 23 independent studies in 11 countries (Fig. 2) that conducted underwater visual surveys across at least two adjacent habitat types within a tropical seascape (see Methods in Supporting Information for full details). We define habitats as areas dominated by the biogenic components of canopy-forming macroalgae (macroalgal meadows), live hard corals (coral reef), or seagrass (seagrass beds). Due to data availability the majority of our analyses focused on independent surveys that recorded the relative abundance of tropical fishes across adjacent areas of macroalgal meadow and coral reef (Table S1). In doing so, we identify how and why macroalgal habitats should be considered in the conservation and management of tropical fish and fisheries, and the emerging research fronts that are needed to bridge key knowledge gaps.



Figure 2. Location of the 24 independent studies (with some geographic overlap) included in different aspects of our data syntheses and meta-analysis of macroalgal-associated tropical fishes (see Table S1 in Supporting Information).

2. TROPICAL MACROALGAL FISHES: A DISTINCT ASSEMBLAGE?

Studies exploring fish community structure in tropical macroalgal habitats have steadily increased over the past two decades, yet the majority of such studies have been directed towards the consequences of coral-algal regime shifts (Fig. 1). In some respects, this has skewed perspectives towards tropical macroalgae as a ‘degraded’ reef state for fishes in areas where a loss of live coral cover has led to substantial losses of biodiversity (e.g., Feary, Almany, McCormick, & Jones, 2007; Graham et al., 2006). However, studies that have documented tropical fish assemblages in macroalgal meadows co-occurring alongside patches of coral reef and seagrass provide a different seascape perspective. Drawing on results from 14 independent studies that deployed comparable levels of visual survey effort across macroalgal meadows and two other tropical habitats (coral and/or seagrass, Table S2), we found the average proportion of local fish species richness that was only found within tropical macroalgal habitats was low (18%) relative to nearby coral reef (39%). However, we found the reverse for fish species found only in macroalgal meadows (40%) versus only in seagrass beds (20%). This suggests a sizeable portion of tropical fish biodiversity occupying macrophyte habitats are unique to macroalgal meadows, and that seagrass and macroalgae are not interchangeable habitats for the ecological connectivity of many macrophyte-associated fishes. Moreover, we found an average of 43% and 40% among-habitat overlap in local fish species among tropical macroalgae-coral and macroalgae-seagrass habitats, respectively (Fig. 3). In some locations this overlap was as high as 60–80% (e.g., Ningaloo, Seychelles; Table S2). Since over a third of fish species within a region can occupy both macroalgal and coral habitats, macroalgal meadows could provide stepping-stones or refuge habitats for fishes occupying a diverse tropical seascape subject to disturbance events. Depending on the trophic diversity of these macroalgal-associated fishes, such overlaps in habitat occupation could help stabilise ecosystem structure and function in the face of disturbances affecting a particular habitat type (e.g., mass-bleaching of corals).

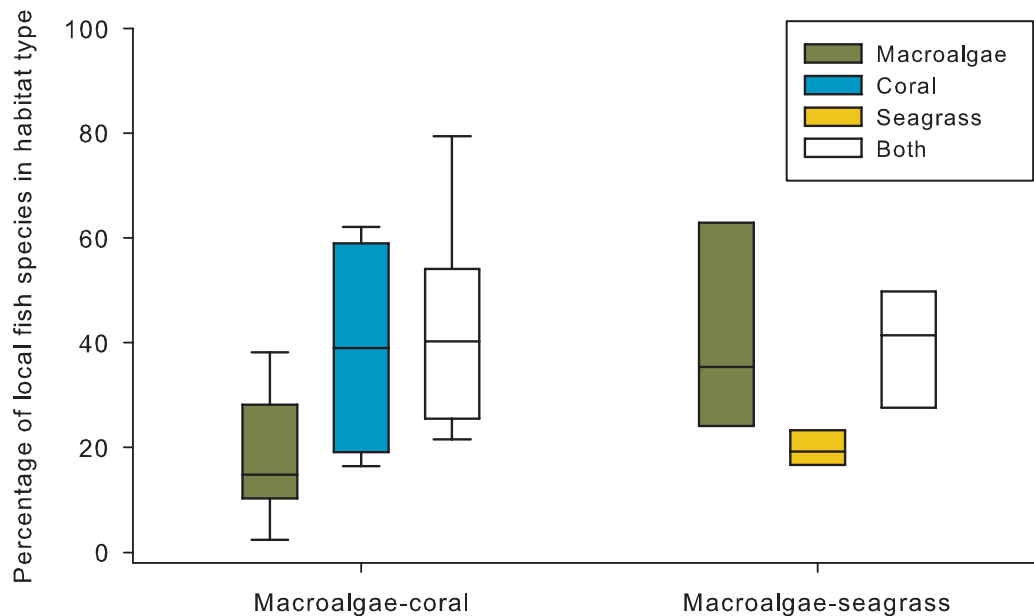


Figure 3. Percentage of conspicuous fish species (readily detected by visual surveys) occupying only tropical macroalgae, coral reef, or seagrass habitats, or occurring in both habitat types based on studies that explored pairwise (macroalgae vs coral/seagrass) occupation patterns. Boxplots indicate number of fish species that fall into each category, expressed as a percentage of the total fish species recorded in each of 12 (macroalgae-coral) and 7 (macroalgae-seagrass) independent studies encompassing 7 or more tropical locations (underlying data in Table S2).

Our compilation of fishes detected in tropical macroalgal meadows by 23 independent surveys (Table S1) found a broad range of taxonomic diversity, with 627 bony fish species from 75 families occurring as a juvenile and/or adult at some level of abundance (Table S3). At least some evidence suggests that a third of these macroalgal-associated fishes (218 species) had most (more than half) of their local abundance within macroalgal habitats, either as juveniles (147 species) or adults (130 species; Table S3). Taking a smaller subset of species for which we had replicated surveys (at least $n = 2$ for both life history stages) of relative abundance, we identified 44 fish species as being most strongly macroalgae-associated because one or both life history stages were predominantly abundant in macroalgal meadows compared to nearby coral reef (Fig. 4). Focusing on the 35 species with more than half of their adults within macroalgae, which we call macroalgal residents, we find a diversity of trophic levels and groups, from herbivores and detritivores (e.g., Marbled parrotfish, *Leptoscarus vaigiensis*, Labridae; and some *Siganus* species), to omnivores (*Chrysiptera* species) and benthic invertivores (e.g., some *Coris*, *Choerodon*, *Halichoeres*, *Pseudojuloides*, *Pteragogus*, *Stethojulis*, and *Lethrinus* species). A relatively small component of this macroalgal resident fish fauna (9%) are higher trophic-level carnivores that are known to consume other fishes (e.g., Cigar wrasse, *Cheilodactylus inermis*, Labridae; Starry moray, *Echidna nebulosa*, Muraenidae; Halfmoon grouper, *Epinephelus rivulatus*, Serranidae; Bluespotted cornetfish, *Fistularia commersonii*, Fistulariidae). A larger group of fishes (78 species) also had a substantial proportion (between a quarter to a half) of their relative adult abundance

within tropical macroalgal habitats. This lower relative abundance may reflect a more opportunistic or transient occupation of macroalgae, where these fishes could be exploiting a range of trophic resources, given they span herbivores and detritivores (*Acanthurus*, *Chlorurus*, *Scarus*, and *Siganus* species), to omnivores (*Gerres oyena*, Gerreidae), generalist carnivores (e.g., some *Lethrinus*, *Lutjanus*, *Thalassoma*, and Mullidae species), and fishes (8% of 77 species) known to consume other fishes (e.g., some *Caranx*, *Gymnothorax*, *Pterois*, *Saurida* and *Synodus* species; Fig. 4, Table S3). Notably, the mean trophic level of these resident (3.21, 35 species) and opportunistic (3.18, 78 species) fish groups are relatively similar. A typical adult fish found in tropical macroalgal habitat appears to be targeting invertebrate prey, such as the diverse and abundant epifauna found in macroalgal canopies (Martin-Smith, 1993; Tano et al., 2016; Wenger, van Lier, & Fulton, 2018). While there is a relatively small component of tropical fish diversity that we may consider dependent on macroalgal habitat, our results point to a larger role of macroalgal-associated fishes in the functioning of marine ecosystems. Strong overlap in the occupation of macroalgal and other habitat types by species operating across several trophic levels suggests these fishes are functioning as mobile links that consume productivity within macroalgal meadows and then disperse this across tropical seascapes during foraging and/or ontogenetic migrations (Berkström, Lindborg, Thyresson, & Gullström, 2013). Accordingly, macroalgal meadows should be considered one of several key habitats within a diverse and productive seascape that is needed to sustain healthy tropical fish populations and communities.

An important limitation of our analyses is that by only considering species with data across multiple independent studies, we are likely to exclude endemic species whose limited range inhibits the number of studies of their habitat ecology. For example, recruitment of the Leopard grouper (*Mycteroperca rosacea*, Serranidae) is reliably predicted by *Sargassum* cover (Aburto-Oropeza et al., 2007), but this species only occurs in the Eastern Central Pacific and there were insufficient independent empirical studies for this species to be highlighted in the trends discussed above. Similarly, cryptic species are not easily detected using underwater visual census, which is the prominent method for surveying fish (Murphy & Jenkins, 2010). For example, abundance of the Finspot wrasse (*Xenojulis margaritaceus*, Labridae) is known to respond to canopy cover and composition (Wenger et al., 2018), but small body size and cryptic colouration means this species is often not recorded in multi-taxa visual surveys. Accordingly, we see the above as a conservative estimate of the number of macroalgal-associated fish species across tropical reef locations, with a bias towards diurnally-active, conspicuous fish species of relatively large body size. Further research to identify small-bodied cryptic macroalgal-associated fishes is warranted, as these could be a considerable component of the overall tropical fish diversity with important implications for trophic flows of nutrients and energy (Brandl et al., 2019; Depczynski, Fulton, Marnane, & Bellwood, 2007).

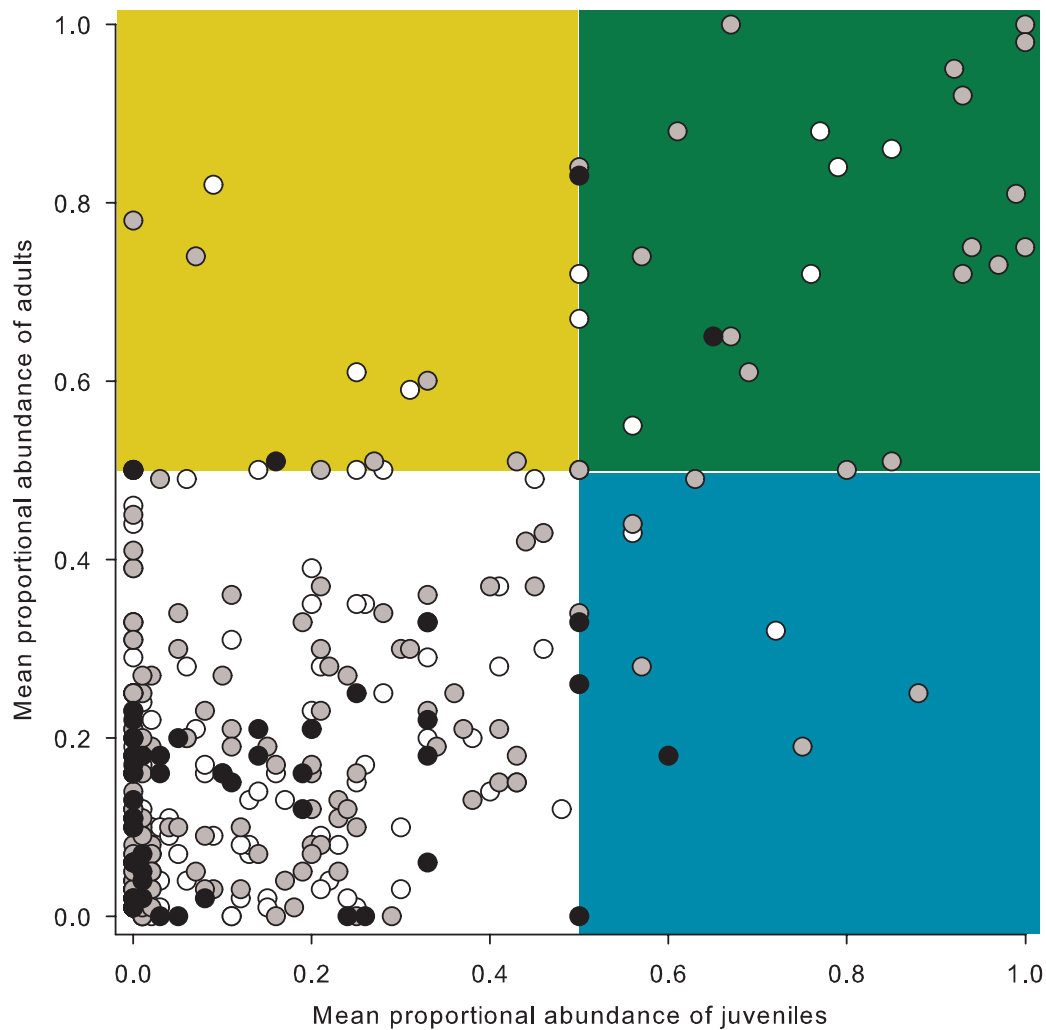


Figure 4. Proportional abundance of juveniles and adults for 350 fish species within macroalgal habitat relative to nearby coral reef, classified according to their adult trophic level (2.00-2.99 = white circles; 3.00-3.99 = grey; 4.00 or greater = black). Outer quadrants indicate species with higher macroalgal dependency due to majority (over half) of their juveniles (blue, 9 species, median trophic level = 3.68), adults (yellow, 13 species, 3.50), or both stages (green, 22 species, 3.50) occupying macroalgal habitats (Table S3). An additional 13 species had an equal proportion (0.5) of one or both life history stages among habitats (i.e., fall on the boundary lines of the quadrants).

3. TROPICAL MACROALGAL MEADOWS AS FISH NURSERIES

While the presence of a high number of juveniles seems an obvious requirement for a nursery habitat, this abundance of juveniles is irrelevant to future adult breeding populations unless they grow and survive to reproductive age (i.e., recruitment success). As such, the identification of a fish nursery habitat requires various lines of evidence, including the relative density, growth and survival rates of juveniles (Beck et al., 2001; Dahlgren et al., 2006; Gillanders, Able, Brown, Eggleston, & Sheridan, 2003). This means the connectivity of habitats within a seascape is also of key importance for nurseries to be effective in replenishing adult fish populations (Beck et al., 2001; Berkström et al., 2012; Whitfield,

2017). Marine macrophyte habitats such as seagrass and mangroves have long been thought to provide this seascape nursery function (e.g., Beck et al., 2001; Gillanders et al., 2003; Whitfield, 2017). However, the comparative importance and ecological significance of tropical macroalgae as fish nursery habitats have yet to be fully assessed (Adams et al., 2006; Mellin, Kulbicki, & Ponton, 2007). Here we synthesise the evidence for macroalgal habitats to work alongside other common marine subtidal habitats to support the life cycles of tropical fishes.

Our compilation of relative fish abundance across 23 tropical locations confirms that macroalgal habitat use by juveniles is globally widespread and includes a remarkably wide range of tropical fish taxa. Of the 627 fish species found within macroalgal habitats across these locations, 64% (399 species) were present as juveniles (Table S3). Over a third (147) of the 399 species present as juveniles in macroalgal habitats had their highest proportional abundance within macroalgal versus coral reef habitat (Table S3). Notably, several species with a high proportion of their juveniles within macroalgal habitat had the majority of their adults occupying nearby coral-dominated reef (e.g., Chocolate hind, *Cephalopholis boenak*, Serranidae; Yellowtail emperor, *Lethrinus atkinsoni*, Lethrinidae; Spangled emperor, *Lethrinus nebulosus*, Lethrinidae; Spanish flag snapper, *Lutjanus carponotatus*, Lutjanidae; Dory snapper, *Lutjanus fulvivflamma*, Lutjanidae; and Three-ribbon wrasse, *Stethojulis strigiventer*, Labridae; Table S3). As such, macroalgal habitats seem to provide a key middle step in the triphasic life cycle of some tropical “coral reef” fishes (Mellin et al., 2007; Sambrook et al., 2019; Wilson et al., 2010). Importantly, these macroalgal-coral reef species play vital functional roles in tropical marine ecosystems (e.g., mesopredatory species of *Cephalopholis* and *Epinephelus*), and many are targeted by commercial and/or recreational fisheries (e.g., *Epinephelus*, *Lethrinus* and *Lutjanus* species).

Juvenile survivorship rates are a key quantum for identifying a fish nursery habitat, with piscivory a major driver of early life history mortality (Beck et al., 2001). We found generally fewer piscivorous fish species within macroalgal meadows relative to nearby coral reef (e.g., fishes of highest trophic level in Fig 4; Fulton et al., 2019). While this suggests juvenile fish are subject to fewer types of piscivores in macroalgal habitats, more information is required to determine if this translates to lower predation risk. Chief among these requirements is whether the local density of the relatively few resident piscivorous fish species is low relative to alternative habitats like coral reef or seagrass. There is the potential that some other resident fish species become facultative fish-feeders during seasonal periods of high juvenile abundance in macroalgal meadows (Holmes, Wilson, Vanderklift, Babcock, & Fraser, 2012). Indeed, several species we identified as generalists/transients (Section 2) are piscivores that could periodically increase their abundance and foraging time within macroalgal meadows during periods of peak fish settlement. While it is possible that juvenile fish are subject to a relatively low diversity of piscivores relative to coral reef habitats, we have little evidence to conclude that macroalgal habitats confer higher rates of juvenile survival. We see this as a

key research front that requires investigation of relative rates of predator mortality imposed on juveniles occupying a range of subtidal habitats within tropical seascapes.

Within a given habitat type there is potential for a certain combination of optimum local conditions to create patches that are particularly effective fish nurseries that contribute to future adult populations (Dahlgren et al., 2006; Nagelkerken, Sheaves, Baker, & Connolly, 2015). Macroalgal habitats can vary considerably in canopy condition in ways that help explain differences in juvenile fish abundance over space and time. Percent macroalgal canopy cover, canopy height and/or density, as well as underlying attributes such as understory macroalgal cover, live coral and/or degree of underlying reef complexity have been linked to spatial and temporal variation in juvenile fish abundance (e.g., Eggertsen et al., 2019; van Lier, Wilson, Depczynski, Wenger, & Fulton, 2018; Wenger et al., 2018). Besides direct selection by juvenile fish for certain microhabitat shelters, these variations in canopy condition are likely to influence the availability of preferred prey (either the macroalgae or their epibionts; Lim, Wilson, Holmes, Noble, & Fulton, 2016; Wenger et al., 2018), with direct consequences for fish growth and survival. Indeed, a combination of macroalgal meadow condition and juvenile abundance were key predictors for the future abundance of *Lethrinus* sub-adults in the eastern Indian Ocean (Wilson et al., 2017); a finding that is consistent with an earlier study linking *Sargassum* condition to the recruitment success of the Pacific Ocean Leopard grouper in the eastern Pacific (Aburto-Oropeza et al., 2007). Changes in canopy complexity could also influence the success of piscivores to capture juvenile fish. However, the evidence for the latter remains equivocal, with studies in marine macrophyte habitats finding fish predator success was either affected greatly by differences in canopy structural complexity, or not at all (e.g., Horinouchi, 2007; Pérez-Matus, Sánchez, González-But, & Lamb, 2016).

Seascape context could also play a key role in determining the nursery quality of patchy habitats (Nagelkerken et al., 2015). Structural connectivity, measured as the proximity of a meadow patch to other viable habitats within the seascape, is emerging as an important predictor of juvenile abundance and diversity in macroalgal habitats (e.g., Bradley, Baker, Nagelkerken, & Sheaves, 2019; Mellin et al., 2007; van Lier et al., 2018). This is likely to be particularly important for ontogenetic migrations, such as the movement of key fishery target species (e.g., some *Lethrinus* species) from macroalgal to adjacent coral reef habitat as they increase in body size from juveniles to sub-adults (Wilson et al., 2017). In such species, both the canopy quality (e.g., composition, percent cover, height, density) and proximity of macroalgal habitats are likely to shape the magnitude of fish recruitment across diverse tropical seascapes (Nagelkerken et al., 2015; Wilson et al., 2017). From a management perspective, identifying these high quality and connected macroalgal patches should be a priority to ensure protection of key sources of fish population replenishment.

Published and emerging evidence lends support to two criteria for tropical macroalgal meadows functioning as fish nurseries: (i) they are widely used by juveniles of tropical reef fishes, many of which have the majority of their juvenile abundance within macroalgal habitats but are later found on coral reefs as adults; and (ii) juvenile macroalgal habitat quality can influence the future abundance of sub-adult and adult populations (e.g., Aburto-Oropeza et al., 2007; Wilson et al., 2017). Evidence for the former is much stronger and widespread than for the latter. Our analyses do not provide evidence of the link between macroalgal habitat availability and future fish population sizes, only evidence of patterns of occupation and proportional abundance. Nonetheless, for species whose juveniles are exclusively found within macroalgal habitats, it is likely this habitat type provides a nursery function, as long as all available habitats in the seascape have been adequately surveyed (Beck et al., 2001; Dahlgren et al., 2006). For future work, we suggest fish taxa with juveniles that utilise a range of purported nursery habitats (Fig. 3 – “both” category) could be prime targets for testing whether macroalgal habitats facilitate increased fish growth, survivorship and recruitment success (*sensu* Beck et al., 2001; Dahlgren et al., 2006).

4. MACROALGAE-ASSOCIATED TROPICAL FISHERIES

Tropical macroalgal habitats likely play several roles in supporting local fisheries production. First, as with kelp forests (see Bertocci et al., 2015; Brown et al., 2018), macroalgal production may enhance fishable biomass through direct consumption by browsing herbivores (e.g., Spinytooth parrotfish, *Calotomus spinidens*, Labridae; Marbled parrotfish; and some *Siganus* species; Fox & Bellwood, 2008; Hoey et al., 2013; Unsworth et al., 2007; Table 1). These herbivorous taxa have some of the highest rates of secondary production (i.e., rapid somatic growth and short longevity) among targeted reef fishes, enabling them to withstand high fishing pressure (Hicks & McClanahan, 2012; Morais & Bellwood, 2018). Secondly, macroalgae-derived detrital subsidies may be substantial in regions with extensive *Sargassum* beds because of the annual canopy loss in these habitats (Fulton et al., 2019). Macroalgal detritus may then be consumed by a wide range of invertebrates and grazing fishes across macroalgal and other habitat types that receive biomass subsidies through the drift of algal rafts and wrack (Stimson, 2013; Wilson, Bellwood, Choat, & Furnas, 2003; Zubia, Andréfouët, & Payri, 2015). Thirdly, canopy-forming macroalgae promote the production of epifaunal invertebrates that are preyed upon by smaller carnivorous fishes, thereby facilitating multiple routes for higher-order production involving resident and transient carnivorous fishes, in addition to predation on herbivorous fishes (Edgar & Aoki, 1993; Rossier & Kulbicki, 2000; Wenger et al., 2018). The importance of macroalgal habitats as foraging areas for some guilds of carnivorous fish may even exceed that of seagrass beds due to higher diversity, abundance and biomass of epifauna (Tano et al., 2016). Aside from these trophic pathways, structurally complex macroalgal communities may also serve as nursery habitats for the juveniles of targeted reef fish (Section 3). This means strong seasonal and interannual fluctuations in macroalgal habitat quality are likely to have direct implications for recruitment and future fishery yields (Lim et al., 2016; Wilson et al., 2017).

Table 1. List of 25 tropical macroalgal-associated fish species targeted for food fisheries. Max TL: maximum total length in cm. Range: IO – Indian Ocean, WP – West Pacific, EP – East Pacific; RS – Red Sea, M – Mediterranean, AO – Atlantic Ocean. Trophic groups: GC – generalist carnivore, I – invertivore, H – herbivore, O – omnivore. Fishery type: C – commercial, R – recreational, S – subsistence. Life history stage mostly found in macroalgal habitat (Table S3): Both - juveniles and adults. Data on size, distribution, trophic group and fisheries from Froese & Pauly (2018).

Family (Subfam.)	Species	Common name	Max TL	Range	Trophic group	Fishery	Life history
Carangidae	<i>Gnathanodon speciosus</i>	Golden trevally	120	IO,WP,EP	GC	C*; R	Adult
Fistulariidae	<i>Fistularia commersonii</i>	Bluespotted cornetfish	160	IO,WP,RS,EP,M	GC	C*	Adult
Labridae	<i>Cheilio inermis</i>	Cigar wrasse	50	IO,WP,RS	I	C*	Both
	<i>Choerodon schoenleinii</i>	Blackspot tuskfish	100	IO,WP	I	C ² ; R	Both
	<i>Oxycheilinus bimaculatus</i>	Two-spot wrasse	15	IO,WP	I	S	Adult
Labridae	<i>Calotomus spinidens</i>	Spinytooth parrotfish	30	IO,WP	H	C	Adult
(Scarinae)	<i>Leptoscarus vaigiensis</i>	Marbled parrotfish	35	IO,WP	H	C; S	Both
Lethrinidae	<i>Lethrinus atkinsoni</i>	Yellowtail emperor	50	WP	GC	C; R	Juvenile
	<i>L. genivittatus</i>	Longspine emperor	25	IO,WP	GC	C*	Both
	<i>L. nebulosus</i>	Spangled emperor	87	IO,WP,RS	GC	C; R	Juvenile
	<i>L. semicinctus</i>	Black-blotch emperor	35	IO,WP	GC	C*	Adult
	<i>L. variegatus</i>	Slender emperor	20	IO,WP	GC	C*	Both
Lutjanidae	<i>Lutjanus carponotatus</i>	Spanish flag snapper	40	IO,WP	GC	C*; R	Juvenile
	<i>L. fulvivflamma</i>	Dory snapper	35	IO,WP,RS	GC	C; R	Juvenile
Mullidae	<i>Upeneus tragula</i>	Freckled goatfish	25	IO,WP	I	C	Juvenile
Muraenidae	<i>Echidna nebulosa</i>	Starry moray	100	IO,WP,RS,EP,AO	GC	C*	Adult
Nemipteridae	<i>Scolopsis ghanam</i>	Arabian monocle bream	30	IO	GC	S	Both
Pomacentridae	<i>Abudefduf vaigiensis</i>	Indo-Pacific sergeant	20	IO,WP,RS	O	S	Juvenile
Serranidae	<i>Cephalopholis boenak</i>	Chocolate hind	30	IO,WP	GC	S	Juvenile
(Epinephelinae)	<i>Epinephelus coeruleopunctatus</i>	Whitespotted grouper	76	IO,WP	GC	C*	Adult
	<i>Epinephelus rivulatus</i>	Halfmoon grouper	45	IO,WP	GC	C*; R	Both
Siganidae	<i>Siganus fuscescens</i> ¹	Mottled spinefoot	40	WP	H	C	Adult
	<i>S. spinus</i>	Little spinefoot	28	IO,WP	H	C*	Both
	<i>S. sutor</i>	Shoemaker spinefoot	45	IO	H	C	Both
Tetraodontidae	<i>Arothron hispidus</i>	White-spotted puffer	50	IO,WP,EP	O	C* ³	Both

¹May be synonymous with *Siganus canaliculatus* (Hsu, Adiputra, Burridge, & Gwo, 2011); *Minor commercial status; ²Near threatened globally (Fairclough & Nakazono, 2004);

³Poisonous but traded in some countries

Over half of the 44 fish species most strongly associated with tropical macroalgal meadows (Section 2, Table S3) are targeted by commercial, subsistence or recreational fisheries (Table 1). Targeted species include herbivores in the families Siganidae and Labridae (subfamily Scarinae), as well as larger-bodied (>30 cm maximum length) generalist carnivores (Lethrinidae, Serranidae) and invertivores (Labridae). While many of these species are of minor commercial importance for industrial-scale fishing, they collectively represent a major component of production in small-scale fisheries that are significant for local communities. Estimating the contribution of macroalgal habitats to tropical fisheries is, however, problematic due to the lack of species- or habitat-specific data in global fisheries statistics (FAO, 2018). Furthermore, global data are likely to under-represent or completely exclude small-scale fisheries that target macroalgae-associated species (McManus, Nañola, Reyes, & Kesner, 1992; McClanahan, Hicks, & Darling, 2008; Pauly & Zeller, 2016). Taking one family of herbivorous and detritivorous fishes as a model, the rabbitfishes (Siganidae; FAO, 2018), we may get some indication of the importance of tropical macroalgal habitats to food security on a global scale (Table S5). Catch data for this family is mainly for herbivorous rabbitfish that school in large numbers and utilise macroalgal habitats, rather than the coral reef-associated pair-forming rabbitfish species (Campos et al., 1994; Hicks & McClanahan, 2012; Hoey et al., 2013; Robinson et al., 2018). Rabbitfishes are targeted in at least 23 countries where they typically account for a small proportion (median = 1.3%) of national aggregated marine fish landings, although their contribution can be more substantial in some countries (17% in Kenya; 32% in Bahrain; Table S5). Importantly, 77% of the reported global rabbitfish catch occurs in Indonesia and the Philippines, two low-income countries, with high human populations and extensive coral reefs threatened by overfishing (Burke, Reynter, Spalding, & Perry, 2012), and where the importance of rabbitfishes as a food source is increasing (Fig. 5). In the Philippines, annual rabbitfish catch has grown gradually over the past half-century, surpassing snapper (Lutjanidae) landings within the last two decades. In contrast, the trend in Indonesia suggests a more recent and rapid increase, with rabbitfish approaching emperor (Lethrinidae) landings in the past decade (Fig. 5). Some of this growth in herbivorous fish catches may have been linked to the expansion of seaweed farming in these countries, which has increased the macroalgal habitat and trophic resources available to fishes in shallow reef habitats (Hehre & Meeuwig, 2016).

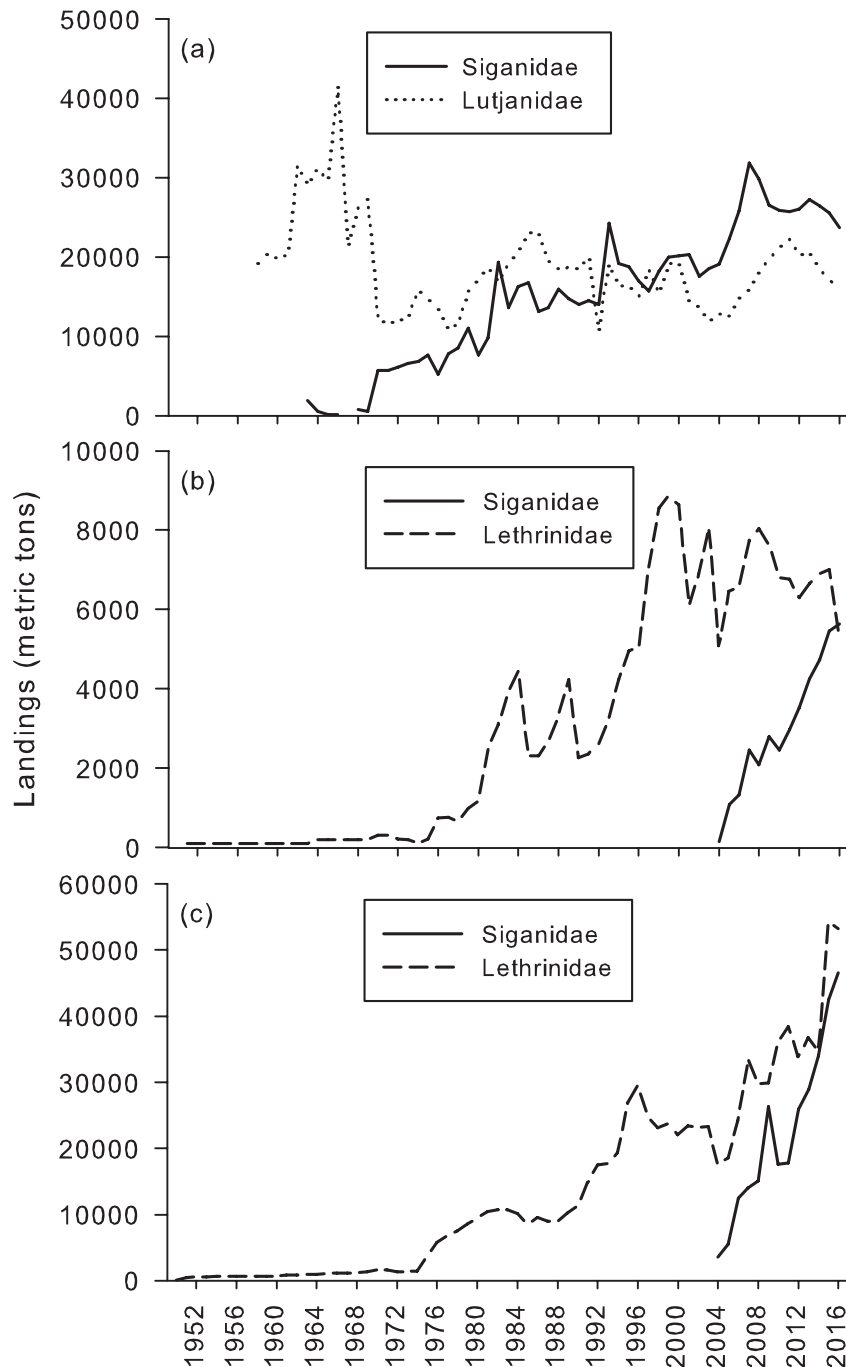


Figure 5. Landings of rabbitfish (Siganidae), snapper (Lutjanidae) and emperor (Lethrinidae) in the Philippines (a) and Indonesia (b – Pacific Ocean; c – Indian Ocean) from 1950 to 2016 (FAO, 2018).

Case studies of small-scale fisheries operating in shallow reef areas often dominated by macroalgal habitat suggest high yields of macroalgae-associated fishes at high levels of fishing effort (Campos et al., 1994; McManus et al., 1992). Total fish yields of 12 to 16 metric tons $\text{km}^2 \text{yr}^{-1}$ from back reefs have been reported in the Philippines and Kenya, respectively (McClanahan et al., 2008; McManus et al., 1992). These yields exceed mean reported annual fish yields from coral reefs in the Pacific and Indian Ocean (McClanahan, 2006) and are more

than 2 to 3 times the global maximum sustainable yield from coral reefs (Newton, Côté, Pilling, Jennings, & Dulvy, 2007). However, macroalgae-associated fishes that dominate yields may be at a high risk of overfishing in some localities. In Kenya, two herbivorous species, Marbled parrotfish and Shoemaker spinefoot (*Siganus sutor*, Siganidae), which together constitute over 60% of the total catch of small-scale reef fisheries by weight, have shown symptoms of growth and recruitment overfishing (Hicks & McClanahan, 2012). Similarly, in the Philippines, stocks of Mottled spinefoot (*Siganus fuscescens*, Siganidae) and Little spinefoot (*Siganus spinus*, Siganidae) are at severe risk of recruitment overfishing because both the adults and very young juveniles are targeted (McManus et al., 1992; Soliman & Yamaoka, 2010). As a consequence, smaller size-at-maturity and lower fecundity have been observed where fishing pressure is high (Jumawan-Nanual & Metillo, 2008; Soliman & Yamaoka, 2010). Since these macroalgae-associated rabbitfish can form large transient spawning aggregations targeted by fishers (Bijoux et al., 2013; McManus et al., 1992; Robinson et al., 2011; Robinson, Graham, Grüss, Gerry, & Bijoux, 2017), they are particularly susceptible to overfishing. However, fast somatic growth, early maturation and high fecundity, along with variable catchability are thought to limit the vulnerability of this fishery to overexploitation (Campos et al., 1994; Robinson et al., 2017).

Tropical macroalgal habitats may appear to make a minor contribution to global fisheries production, but like coral reefs, macroalgae can underpin and enhance the food security and livelihoods of coastal communities that have few other sources of income (Cabral & Geronimo, 2018). Even in wealthy countries, the indirect contribution of macroalgal habitats to recreational fisheries and local economies may be substantial. For example, at Ningaloo in Western Australia, recreational fishing is a major driver of tourism (Smallwood, Beckley, & Moore, 2013) and two commonly caught species, Halfmoon grouper and Spangled emperor (Ryan et al., 2017), utilise macroalgal habitats (Table 1). The potential for tropical macroalgal habitat to be fish nurseries, trophic facilitators, and corridors for fish movement between habitats suggest they warrant the same recognition as mangroves, seagrass beds and coral reefs in ecosystem-based fisheries management. Spatial management and monitoring of tropical macroalgal habitats could then provide capacity for the adaptive management of habitat-based fluctuations in fishable biomass of coastal target species (Brown et al., 2018; Green et al., 2014). This will require more quantitative information on the key aspects of macroalgal habitat quality and connectivity that affect both standing fish biomass and recruitment, and how these habitat traits respond to climatic cycles and disturbance events (Aburto-Oropeza et al., 2007; Wilson et al., 2017, 2018).

Apart from overexploitation, the other major threat to the sustainability of tropical fisheries is habitat loss, especially the loss of hard corals due to climate change (Bell et al., 2013; Newton et al., 2007). One of the responses of coral reefs to live coral loss is a regime shift from a coral-dominated to a macroalgal-dominated state (e.g., Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015). The implications of such a shift in habitat are anticipated to be

detrimental to the yield of coral reef fisheries (Graham et al., 2007; MacNeil et al., 2010; Pratchett et al., 2008; Pratchett, Hoey, & Wilson, 2014). However, data to assess long-term implications of regime shifts on tropical fisheries are scant. An exception is in the Seychelles, where long-term assessments of the inshore trap fishery found that yield and CPUE have been maintained or even increased following widespread bleaching and a shift to macroalgal-dominated habitat on some reefs (Robinson et al., 2018). Variability of the catch, however, has increased, and on reefs that underwent a regime shift the trophic structure of the fish assemblage was altered to shortened food chains with increases in biomass of low-trophic level herbivores and mid-level carnivores, such as emperors (Hempson, Graham, MacNeil, Hoey & Wilson, 2018). Therefore, while the catch has been maintained with a shift towards macroalgae-associated herbivorous fish, the predictability of catch per fishing trip has become less certain (Robinson et al., 2018).

5. VULNERABILITY OF MACROALGAL FISHES TO HABITAT LOSS

Macroalgal meadows are sensitive to environmental fluctuations and local disturbances (Olsen et al., 2019). Annual productivity of canopy-forming macroalgae is closely related to seasonal shifts in water temperature, although the range and optimal temperature for growth varies among taxa and regions (Fulton et al., 2019). As such, both local seasonal and large-scale climatic oscillations in sea temperature, such as those associated with the El Niño Southern Oscillation, can alter the structure of tropical macroalgal habitats (Fulton et al., 2019; Wilson et al., 2014, 2018). Similarly, extreme climatic events like heatwaves and cyclones can cause extensive loss of macroalgal habitat, with reduced macroalgal canopy cover often persisting for several years after the event (McCourt, 1984; Rogers, 1997; but see Loffler & Hoey, 2018). Long-term shifts in climate are also expected to alter the distribution and abundance of macroalgal species, leading to changes in community composition and ecosystem function (Diaz-Pulido et al., 2007). Over finer spatial scales, experimental manipulation of nutrient concentrations (Schaffelke & Klumpp, 1998) and sediment loads (Umar, McCook, & Price, 1998) demonstrate that environmental conditions can have a direct effect on macroalgae canopy phenology. Nutrient pulses and increased sediment loads associated with natural disturbances such as flooding, or human activities such as dredging and coastal development, are therefore expected to have a local impact on canopy cover and structure within macroalgal habitats.

Acute and continuous stressors that affect the structure of tropical macroalgal habitats are also expected to have an impact on the associated fishes. Ecological theory suggests that species most severely affected by disturbances will be those that feed or shelter exclusively within macroalgal habitats (Vázquez & Simberloff, 2002). Such macroalgal specialists might be especially vulnerable during the early life history stages when juvenile fishes are highly susceptible to predation and take shelter within particular aspects of macroalgal habitat microstructure. Changes in availability of dietary resources within macroalgal meadows may

also influence fish growth and abundance, given the role they play in supporting direct (herbivorous) and indirect (carnivorous) food sources (Fulton et al. 2019). However, studies that have explicitly assessed the influence of disturbances on tropical macroalgal meadows and their associated fish fauna have been limited to fine-scale macroalgal removal experiments (e.g., McClanahan, Hendrick, Rodrigues, & Polunin, 1999), or long-term comparisons of reefs that have undergone regime shifts from coral to macroalgal-dominated states (Graham et al., 2015).

Our meta-analysis of the correlation between fish abundance and varying macroalgal cover across a range of tropical locations around the world (Table S1) identified fish species and life history stages that are likely to be macroalgal-dependent and most affected by macroalgal habitat loss. Using Pearson's correlation adjusted for survey area in a weighted z-score, averaged across a minimum of three independent surveys per life history stage of each species (see section 4 of Methods in Supporting Information), we found a spectrum of relationships between the abundance of macroalgal-associated fishes and percent macroalgal cover (Fig. 6). Some species had a significant positive relationship with macroalgal canopy cover (i.e., a positive mean z-score with confidence interval above zero, indicated by hashed bars above the centre line, Fig. 6), increasing in abundance when cover was high and declining when it was low. For Marbled parrotfish (*Leptoscarus vaigiensis*, Labridae) and Cigar wrasse (*Cheilio inermis*, Labridae) this positive relationship was strong for both adults and juveniles (Fig. 6), while for other species the general relationship differed in direction or significance among life history stages, suggesting ontogenetic shifts in macroalgal habitat dependence. For example, the abundance of juvenile Spangled emperor (*Lethrinus atkinsoni*, Lethrinidae) was strongly correlated with canopy cover, but this relationship was not apparent for larger conspecifics (Fig. 6), which are typically found on nearby coral reef (Wilson et al., 2017). Conversely, the abundance of adult Halfmoon grouper (*Epinephelus rivulatus*, Serranidae) positively correlated with macroalgal canopy cover, while the abundance of their juveniles did not (Fig. 6), which suggests an increased dependence on macroalgal habitats with ontogeny. There were also several species that consistently declined in abundance as macroalgal canopy cover increased (Threeline damsel, *Pomacentrus trilineatus*, Pomacentridae; Spotted sharpnose, *Canthigaster solandri*, Tetraodontidae; Harlequin sweetlip, *Plectrorhincus chaetodonoides*, Haemulidae; and Bluespotted cornetfish; Fig. 6), implying that these macroalgal-associated fishes, which were predominantly found in macroalgal meadows rather than coral reef, may prefer macroalgal habitats with low cover.

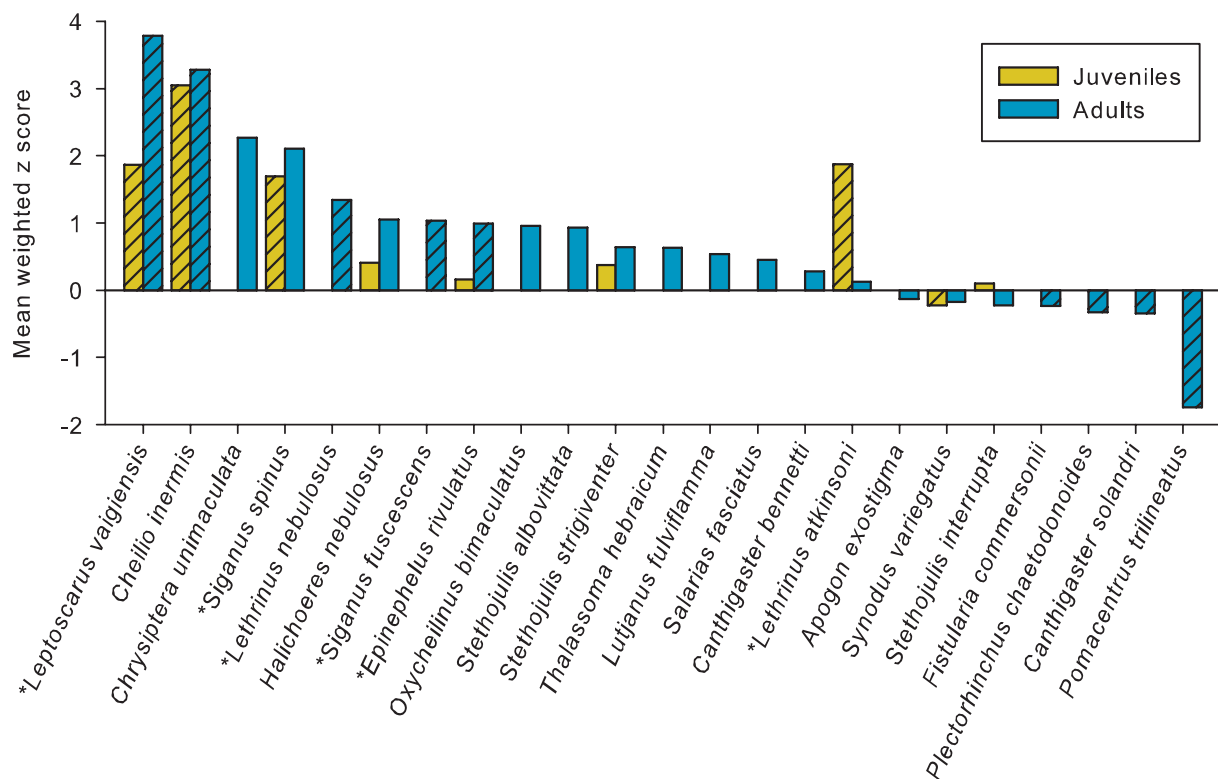


Figure 6. Relationship between the abundance of 23 fish species and macroalgal habitat cover across geographic locations encompassed by our meta-analysis. Mean weighted z scores indicate species with positive (increased abundance) or negative (decreased abundance) relationships with macroalgal cover (replication per species and life history stage are provided in Table S3). Hatching denote scores with 95% confidence limits that fail to intersect zero, which indicates a consistent response across locations. An asterisk indicates a species is targeted for fishing in one or more of the survey locations (Table 1).

Our meta-analysis suggests that the extent of macroalgal dependence in tropical fishes varies both interspecifically and ontogenically when considering only percent cover of canopy-forming macroalgae. The within-meadow canopy structure of macroalgal meadows, however, are often a conglomerate of multiple factors and fishes may associate with specific architectural components of the three-dimensional macroalgal canopy habitat. Previous studies have, for example, identified that abundance of fishes can also correlate with canopy height (Eggertsen et al., 2019; Evans, Wilson, Field, & Moore, 2014; Lim et al., 2016) or the density of canopy-forming macroalgae holdfasts (Wilson et al., 2014, 2017). Using six years of fish and habitat surveys at 19 sites spread across the Ningaloo lagoon in the eastern Indian Ocean, we compared annual patterns of fish abundance with canopy cover, height, and density to identify which macroalgal structural elements consistently predict fish abundance (Fig. 7). Some species, like Marbled parrotfish and Spangled emperor, clearly have strong positive correlations with multiple facets of macroalgal canopy structure, whilst the abundance of others (e.g. juvenile Three-ribbon wrasse, *Stethojulis strigiventer*, Labridae) primarily correlate with a single canopy feature such as height (Fig. 7b).

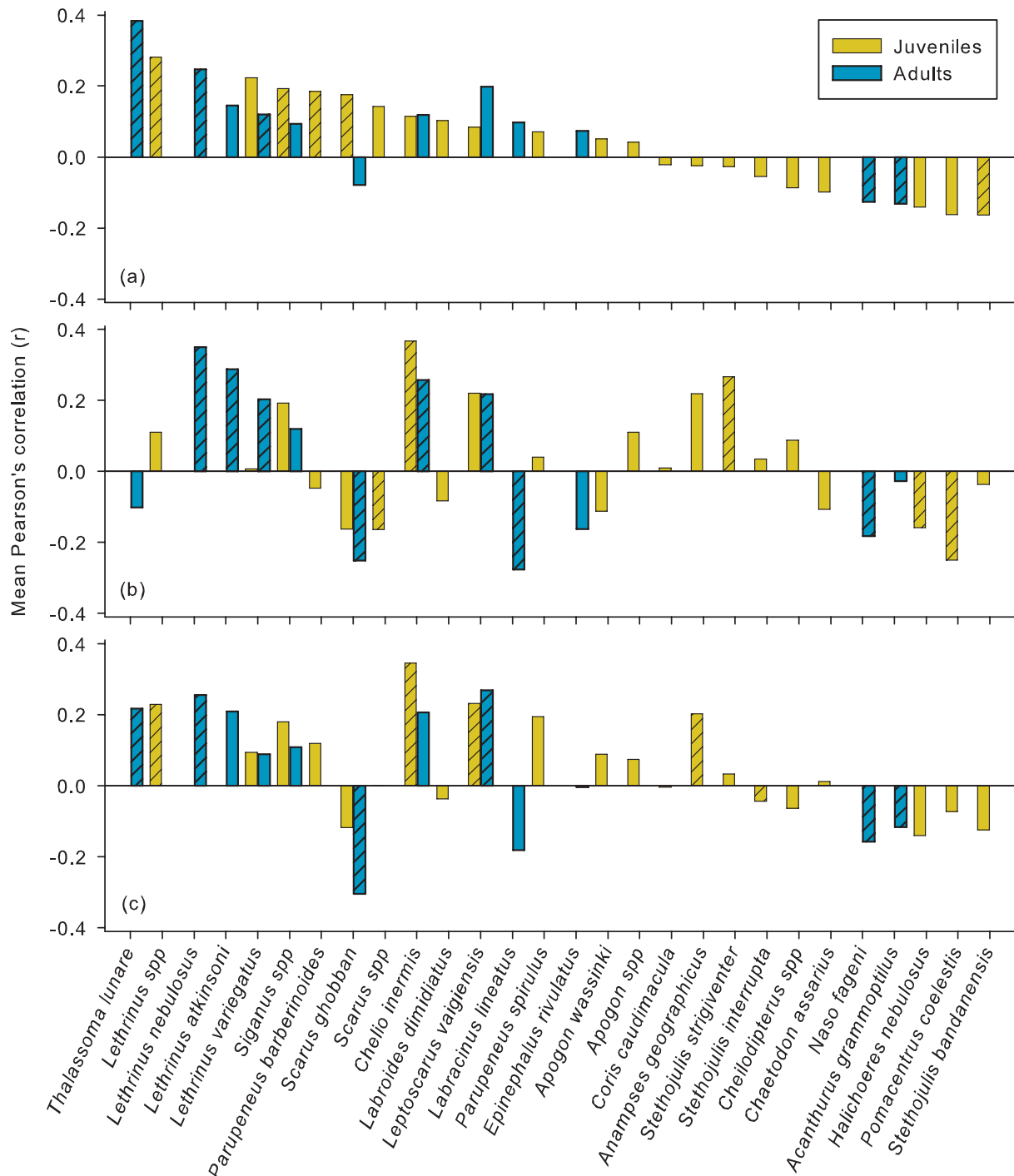


Figure 7. Correlations between the abundance of 28 fish species and mean annual ($n = 6$ years) macroalgal canopy habitat structure in terms of (a) percent cover, (b) height, and (c) density of holdfasts across 19 study sites at Ningaloo, Western Australia. Pearson's correlation indicate species with positive (increased abundance) or negative (decreased abundance) relationships with macroalgal canopy structure. Hatching denote scores with 95% confidence limits that fail to intersect zero, which indicates a consistent response among years.

Interestingly, the abundance of adults and juveniles of the same fish species often correlate with the same elements of macroalgal canopy structure, but juveniles typically have stronger canopy-abundance relationships (Figures 6 & 7). This suggests the early life history stages of most species may be more habitat dependent and vulnerable to environmental disturbances acting on macroalgal meadows. Temporal mismatches that arise between peak macroalgal habitat availability and seasonal pulses of larval fish settlement may, therefore, directly affect the survival of juveniles with long-term consequences for the replenishment of adult populations. However, experimental manipulations of habitat structure and reciprocal removal of competitive fishes are required to understand the true extent of habitat limitation, competition and recruitment facilitation in macroalgal meadows. A key challenge in these experiments will be manipulating certain aspects of canopy condition while keeping others constant (e.g., reducing height while maintaining cover) in order to tease apart specific habitat effects.

Different levels of dependence upon particular canopy structural features may allow partitioning of resources and co-existence of species (Wilson et al., 2014, 2017), which could explain the spectrum of relationships in the diversity and abundance of macroalgal-associated fishes across 19 meadows of varying canopy structure at Ningaloo (see Figures S1-S4). Although herbivorous fishes on coral-dominated reefs can respond negatively to increasing canopy density in experimental patches of macroalgal habitat (Hoey & Bellwood, 2011), we found the overall abundance of macroalgae-associated herbivorous and carnivorous fishes generally increased with macroalgal canopy density, height and cover at Ningaloo (Figures S1 & S2). Species-specific relationships are less clear (Figures S3 & S4), and while we found some evidence for negative correlations between canopy density and the abundance of two common macroalgal-associated herbivorous fishes (Blue-barred parrotfish, *Scarus ghobban*, Labridae; and Mottled spinefoot, *Siganus fuscescens*, Siganidae; Fig. S3), the most abundant macroalgal meadow herbivore in our dataset (Marbled parrotfish) responded positively to increases in canopy cover, height and density (Fig. S3). We are prevented from making generalisations on the nature and drivers of these relationships by a lack of diversity in the types of macroalgal habitat data collected by studies – the majority to date have been focused on percent cover. Macroalgal percent cover is unlikely to be a good predictor for other measures of canopy structure, given the disparity between the two metrics (Wilson et al., 2014; Lim et al., 2016). Indeed, studies at various locations around the world report that neighbouring macroalgal meadows within a tropical seascape can vary considerably in canopy cover, height and/or density, and that taxonomic and trophic groups of macroalgal fishes respond in different ways to this canopy complexity over space and time (e.g., Eggertsen et al., 2017, 2019; Wilson et al., 2017). Based on the evidence to date, canopy height and cover could arise as some of the best habitat-based predictors for temporal trends in macroalgal fish-habitat relationships, as these aspects often vary the most over time, while canopy density is relatively stable within meadows but can vary considerably among sites (e.g., Lim et al., 2016; Umar et al., 1998;

Wilson et al., 2014). To test these general hypotheses, we need more studies to include measures of canopy height and density (alongside percent cover) to resolve which aspects best predict fish community structure and function in tropical macroalgal meadows.

Limited evidence suggests fishes may also associate with certain macroalgal species or genera (e.g., *Sargassum*; Lim et al. 2016, Wenger et al. 2018). While we lack the information needed to assess macroalgal-specificity in a wider suite of tropical fishes, this should be an important line of research because this lack of ecological versatility can render fishes more susceptible to disturbances that affect specific macroalgae. Moreover, habitat features other than the composition and soft habitat structure afforded by the macroalgae could influence fish abundance. For instance, the structural complexity of the underlying hard substratum or availability of shelter holes may be a better predictor of abundance for some macroalgal fish species (Eggleston, 1995). The influence of hard substratum complexity (e.g., presence of live/dead corals, holes, crevices and/or general topographic variation) on fish communities has been well documented in coral-dominated systems (Graham & Nash, 2013), but has received minimal attention in macrophyte systems. Recent surveys in the western Indian Ocean found the abundance of juvenile fishes was greater in macroalgal meadows with more structurally complex hard substrate (Eggertsen et al., 2019). Hard habitat complexity has also emerged as an important predictor of macroalgae-associated adult fish communities at Ningaloo (van Lier et al., 2018). A more in-depth analysis of data from van Lier et al. (2018) revealed macroalgal meadows with high hard substratum complexity were often characterised by species typical of coral reefs (e.g., Moon wrasse, *Thalassoma lunare*, Labridae; Fig. S5). Fishes exclusively found in macroalgal habitats, however, displayed a mixed relationship with hard substratum complexity (Fig. S5). For instance, abundance of the herbivorous browser Marbled parrotfish was not unduly related to hard substratum complexity, while a predatory fish (Halfmoon grouper) tended to occupy meadows with greater hard substratum complexity (Fig. S5). Before any generalities can be drawn we need more assessments of how fine-scale changes in both soft macroalgal and hard substratum habitat structures influence macroalgal fish communities across a greater range of tropical settings.

Spatial arrangement and proximity of macroalgal meadows to other tropical habitat-forming taxa may also have an important bearing on fish diversity and abundance (Berkström et al., 2012; Bradley et al., 2019; Martin et al., 2018). Macroalgal meadows are often located in the vicinity of other habitats, forming a mosaic of interlinked patches in diverse tropical seascapes. Functional linkages among habitat patches support the persistence of marine populations and communities and are pivotal for enabling ecosystems to persist and recover from disturbances (Cumming, 2011; Olds et al., 2018). Consequently, disturbances that disrupt connectivity among habitats are expected to have the greatest effect on those species that migrate among habitats within the seascape (Dahlgren & Eggleston, 2000), such as the many fish species that appear to migrate from macroalgal to other habitats during

their ontogeny (Section 3). Adult fishes may also regularly move among different patches or habitats types to forage. For example, some of the strongest and most consistent relationships between canopy cover and abundance occur with adult Moon wrasse and Spangled emperor (Figures 6 & 7), highly mobile species that may move among meadows and other habitat types within diverse tropical seascapes. Clearly, more seascape studies that incorporate macroalgal habitats are required to improve our understanding of the consequences of habitat destruction and fragmentation within tropical seascapes.

Disturbances that alter the structure and composition of macroalgal communities can also result in ecologically novel situations for fish. Ecological novelty can be difficult to navigate for animals that lack relevant evolutionary experience (Sih, Ferrari, & Harris, 2011), and individuals that incorrectly assess habitat quality may fail to make the most of available habitat options (i.e., fall into ecological traps; Hale & Swearer, 2016). As a result, fish populations could be affected disproportionately to the level of changes in overall habitat condition (Hale, Treml, & Swearer, 2015). Numerous ecological traps have been revealed in terrestrial habitats (Hale & Swearer, 2016), and analogous cases are likely to arise in macroalgal systems. For example, via habitat fragmentation and subsequent failure of individuals to avoid risky patch edges (*sensu* Weldon & Haddad, 2005), or via fishes utilising non-native or range-expanding macrophytes that offer superficially similar habitat but lower quantity of resource provision throughout the relevant season (e.g., Hempson, Graham, MacNeil, Bodin, & Wilson, 2018; Rodewald, Shustack, & Hitchcock, 2010). Small-bodied juveniles, as well cryptic and endemic fishes with limited capacity to move to alternate habitats may be the most vulnerable to changes in macroalgal habitat. Conversely, larger bodied species that have a generalist carnivore diet and generalist habitat associations (e.g., ‘transient’ fish taxa identified in Section 2) may have the capacity to readily move among patches and adapt to macroalgal habitat loss (Berkström et al., 2013). Fish species that overlap in their habitat occupation of macroalgal meadows and seagrass beds (Fig. 3) may be particularly resilient to habitat disturbances affecting one habitat-forming organism in a diverse tropical seascape. However, even among these species, our meta-analysis of macroalgal-associated fishes and published studies on seagrass fish faunas (e.g., Eggertsen et al., 2017; Tano et al., 2017) suggest strong preferences for certain types and quality of macrophyte habitat. The negative effects of changes in coral canopy condition have been well documented in reef fishes that prefer certain hard coral species and growth forms (e.g., Pratchett et al., 2008, 2014; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Accordingly, shifts in the availability of preferred macrophyte canopy habitats are likely to have a detrimental impact on the abundance and/or condition of macrophyte specialist fishes.

6. CONCLUSIONS

Macroalgal habitats can be a substantial component of tropical seascapes around the world. Our synthesis has revealed that macroalgal meadows can support a unique component of tropical fish species richness, may be an important factor in shaping fish recruitment across diverse tropical seascapes, and provide a key habitat for productive species that support local fisheries. While over 600 species of bony fishes have been recorded in tropical macroalgal meadows around the world, at present there is only evidence to suggest a quarter to a third of those species have the majority of their juvenile and/or adult abundance within macroalgal habitat. Using the relatively few studies for which there are balanced visual surveys of fish species richness across different habitat types, we found considerable overlap between fish assemblages within macroalgal habitats and two other common subtidal habitats - seagrass and coral reefs - which suggests macroalgal meadows could also be important foraging habitats and/or stepping stones in the triphasic life cycles of fishes in diverse tropical seascapes.

Juvenile fishes appear to be prominent in macroalgal habitats across the tropics, where the quality of macroalgal canopy (percent cover, height and/or density) can be positively correlated to the abundance of juveniles. Evidence from two studies (in the Eastern Pacific and Western Indian oceans) suggests these habitat effects during the juvenile phase could influence the future abundance of fish in larger/older size classes (Aburto-Oropeza et al., 2007; Wilson et al., 2017). While this is suggestive that canopy-forming macroalgal habitats may serve as fish nurseries, we lack key lines of evidence to make a general conclusion. More information on rates of juvenile growth, survival and movement is needed before we can establish the potential nursery function of macroalgal meadows for tropical fish and fisheries. Similarly, we need greater resolution on the catch of macroalgal-associated fishes to fully understand the contribution of macroalgal habitats to tropical fisheries.

Compared to other prominent tropical habitats like coral reefs, macroalgal meadows are spatially and seasonally dynamic in structure, which has major consequences for the abundance and distribution of many macroalgal-associated fishes. Environmental conditions such as sea temperature are important drivers of this dynamism, which suggests climate change may affect tropical canopy-forming macroalgae and the associated fish communities and fisheries. Significantly, not all tropical macroalgal patches respond in the same way to seasonal and inter-annual changes in climate, with some patches in the seascape retaining canopy and providing a key habitat refuge (Lim et al., 2016; Wilson et al., 2017). Accordingly, we need to identify what makes certain macroalgal patches resilient to disturbance, and at what scale this needs to be maintained in order to facilitate functional connectivity with other tropical habitats. This will require long-term monitoring of fish abundance across tropical seascapes, and assessments of how seasonal changes to macroalgal-canopy structure affect patterns of fish distribution and replenishment across a suite of habitat types within tropical seascapes. Indeed, a lack of information on macroalgal fish

assemblages over prolonged periods has restricted our understanding of how these fish contribute to key ecological processes and ecosystem services. Filling this knowledge gap is becoming increasingly important as the extent of macroalgal habitat may change according to climate-related coral mortality and regime shifts.

ACKNOWLEDGEMENTS

We thank participants to our special session on tropical macroalgal fishes at the 2017 Australian Society for Fish Biology Conference and 10th Indo-Pacific Fish Conference for helpful discussions in the early phase of this project. Support was provided by The Australian National University (National Institutes Grant – Research School of Biology), WA Department of Biodiversity, Conservation & Attractions, Australian Institute of Marine Science, the Environment Conservation Fund of the Government of Hong Kong SAR (ECF15/2015 to PTYL and PKSL), the Philippine Department of Science and Technology Grants-in-Aid Program (to RAA and AAB), the Australian Research Council (DE130100688 to ASH), the Royal Society (UF140691 fellowship to NAJG), and the Swedish Research Council (2015-01257, E0344801). We thank Sofia Wikström and three anonymous peer reviewers for constructive comments on earlier drafts.

DATA AVAILABILITY

Metadata used in the analyses are provided in online Supporting Information.

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SUPPORTING INFORMATION

Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes

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METHODS

(a) Literature survey and metadata collation (Section 1)

The literature search (updated and finalised in March 2019) was conducted using the Scopus database, via the following search term structure: fish AND habitat AND tropical AND macroalga* OR seaweed OR alga* AND fish [within 15 words of] habitat AND habitat [within 50 words of] macroalga* OR seaweed OR alga* AND NOT subtropical OR sub-tropical AND NOT climate change AND NOT phase-shift AND NOT degrad* AND NOT herbivory. This structure was repeated for the alternative marine macrophyte habitats of seagrass and mangrove (replacing macroalga*/alga*/seaweed/ alga* in above). An additional search to yield studies of fish communities in sites that have undergone a coral-macroalgal phase shift was then made with the search term structure: fish AND coral AND macroalga* OR seaweed OR alga* AND fish [within 15 words of] coral AND coral [within 50 words of] macroalga* OR seaweed OR alga* AND phase-shift OR phase shift OR regime-shift OR regime shift OR alternate state OR alternate states AND NOT subtropical OR sub-tropical. All of the search results were scrutinised for relevance by reading the abstract and methods of each reference before compiling the final tally of relevant studies conducted per year, and plotting these as a cumulative frequency over time (Fig. 1).

Independent sources of data on fish community structure and abundance within macroalgal meadow habitats at tropical reef locations (i.e., being a place where the latitude falls between the tropics of Cancer to the north and Capricorn to the south) around the world were identified via two systematic approaches: (1) a targeted literature search (details above) to identify and contact the corresponding authors of relevant papers, and (2) an open call to ichthyologists via a special session on our meta-analysis topic at national (2017 Australian Society for Fish Biology) and international (10th Indo-Pacific Fish Conference 2017) scientific meetings. The latter approach included pre-conference broadcasts made online and via e-mail to international fish and fisheries society members, as well as past conference participants from around the world, and a live call for contributions during the special sessions. We also actively approached colleagues within our network of ichthyologists to help locate information in the grey literature, and otherwise unpublished data. We consulted closely with the data owners/managers to ensure there were no duplications among the independent datasets. This yielded a total of 24 independent datasets from 23 tropical locations encompassing all three major ocean basins and the Red Sea (Table S1), which fitted the general criteria of being independent underwater visual surveys (encompassing both manual diver-based and video-based techniques, but not baited video) of fishes within naturally occurring macroalgal habitats (i.e. we excluded experimental patch habitat studies) at three or more sites per location. Surveys that encompassed a broad suite of taxa (either whole families or multi-family surveys)

within macroalgal meadows and at least one other habitat type of coral reef or seagrass were included in the first part of our review and synthesis to characterise the tropical macroalgal fish fauna (see details in Methods section b below). Surveys that recorded the relative abundance of fish (either as single species or more) inside macroalgal meadows and adjacent coral reef areas in the same location were used to compile a list of macroalgal fishes (Table S3). This list was the basis for subsequent parts of our data syntheses (Table S1) by defining macroalgal-associated fishes on the basis of majority abundance in macroalgal meadows (as per Methods section b below). These macroalgal-associated taxa (indicated in bold font in Table S3) were the focus of the review of macroalgal habitats for fish nurseries (Methods section b) and tropical fisheries (Methods in section c), and a meta-analysis of habitat effects on fish abundance (Methods section d). All of these non-manipulative field surveys of fish abundance were conducted in accordance with the relevant institutional and national guidelines for animal research in each country.

(b) Characterising the tropical macroalgal fish fauna (Sections 2 & 3)

Overlap in tropical fish species richness among canopy-forming macroalgal habitats and either coral reef or seagrass was explored using studies that had conducted multi-family surveys of the presence-absence of conspicuous fish species (readily detected by visual surveys) via a balanced sampling effort (i.e., substantial percentage of replicated survey effort across each habitat type – see Table S2) across naturally occurring patches of at least two of these different habitat types at a given location. A total of 14 independent studies ($n = 12$ for macroalgae-coral, and $n = 7$ for macroalgae-seagrass; Table S2) fitted these criteria, which encompassed locations across the Atlantic, Indian and Pacific Oceans and the Red Sea (Table S2).

Patterns of relative abundance in macroalgal habitats were explored using a subset of the independent datasets that had estimated the density of juveniles ($n = 20$ studies) and/or adults ($n = 22$ studies) of each fish species with a relatively balanced survey effort inside and outside tropical macroalgal habitat adjacent to coral reef (Fig. 4 column in Table S1). Macroalgal habitat in these survey areas (and for analyses below) were characterised by a benthic cover of 10% or more canopy-forming macroalgae of the Family Sargassaceae (*Sargassum*, *Sargassopsis*, *Sirophysalis*, *Turbinaria*) and less than 3% live coral (*sensu* natural meadows described in Lim et al., 2016; Wilson et al., 2017; Wenger et al., 2018), while coral reef was characterised by 10% or more of live coral and less than 3% macroalgal cover (Table S4). We then created a biplot of mean proportional abundance of 350 fish species in macroalgal habitat (from a total pool of 627 species, Table S3), which were the taxa with paired abundances for juveniles and adults of each species across two or more independent surveys for both life history stages. To explore trophic structure, fish species were categorised into three trophic levels spanning lower order consumers such as herbivores and detritivores (2.00-2.99), mid-level carnivores (3.00-3.99), and higher order predators such as piscivores (4.00 or greater), using values provided by Froese and Pauly (2018; Table S3).

(c) Macroalgal-associated fisheries (Section 4)

The list of macroalgal-dependent fish species (i.e., proportional abundance >0.5 in macroalgae for at least one life history stage (indicated in bold font in Table S3) was used to explore which taxa may support tropical fisheries (Table 1), based on fishery status in Froese and Pauly (2018) and published information for our study locations (e.g., Hicks & McClanahan, 2012). Due to a lack of fine-scale spatial and taxonomic resolution in reported fisheries catch data, we chose to explore trends in catch for three macroalgal-associated fish families (Fig. 5) for reef fisheries in the Philippines and Indonesia (FAO, 2018).

(d) Habitat effects on macroalgae-associated fish abundance (Section 5)

To explore the size and significance of an effect from differences in macroalgae percent cover on the abundance of macroalgae-associated fishes, we conducted a meta-analysis of 21 independent sources (Fig. 6 column in Table S1) that recorded the relevant fish and habitat data in macroalgal meadow habitats for macroalgal-dependent species identified in Section 2 (i.e. those with the majority of their juveniles or

adults within macroalgal habitats, indicated with bold font in Table S3). For each independent source survey data, we calculated Pearson's correlation (r) for the relationship between abundance of each macroalgal-dependent fish species and percent cover of canopy-forming macroalgae across the replicate surveys conducted by that source. This was done for each of two life history stages (juvenile, adult) of fish species recorded by each independent source, where more than 20 individuals of a species life history stage were recorded across all replicate surveys. We then accounted for differences in relative survey effort across the independent sources by weighting the correlation by total survey area for each source dataset (see further details below) by converting Pearson's r values into a z score, calculated as $z = 0.5 \cdot [\ln(1+r)/\ln(1-r)]$ following Borenstein et al. (2009), and weighted by the natural log of total reef area surveyed by each survey (mean = 72,739 m², range 60 – 194,400 m²). Mean weighted z scores and 95% confidence intervals were then calculated where three or more values (i.e., three or more independent survey sources) were available for each life history stage per macroalgal-associated fish species. Significant z -scores (with values and confidence limits entirely above/below zero) were indicated with hashed bars (Fig. 6, Section 5 of main text), and the extent of macroalgal dependence was inferred from the magnitude and direction of the z -scores.

There was a general lack of data for other measures of macroalgal canopy structure (e.g. height, density) across the 21 survey locations used in the above analysis. However, a 6-year dataset collected by the same survey team at Ningaloo (underwater visual survey details in Wilson et al., 2018) allowed us to explore relationships between the abundance of 28 fish species recorded in macroalgal meadows at Ningaloo with annual macroalgal habitat conditions in terms of three different aspects of canopy structure: percent cover, canopy height, and canopy density. Since these data were collected with the same technique and amount of survey area effort over time, we simply calculated Pearson's r values annually for each life history stage per species across the 19 study sites (each were separated by a minimum of 600 metres and were spread across a 180km length of the fringing reef lagoon on the central Western Australian coast), and then averaged these across the 6 consecutive years to explore how the abundance of juveniles and adults of each species relate to annual conditions for each of the three aspects of macroalgal canopy structure (presented in Fig. 7, Section 5 of main text). Using this same 6-year Ningaloo dataset we also explored the nature of the relationships between time-averaged means (across 6 annual surveys covering a total area of 1350m² at each of 19 study sites) for three aspects of macroalgal canopy condition (percent cover, canopy height and canopy density) and the time-averaged means of fish species richness (S) and Pielou's evenness (J') for communities of herbivorous (Fig. S1) and carnivorous (Fig. S2) fishes, as well as time-averaged abundance per site (fish 1350m⁻²) for the three most abundant species in each of these two trophic groups (Figures S3 & S4). To capture the potential for non-linear relationships (such as may arise with optima at intermediate levels of habitat condition), we fitted second-order polynomials between the different measures of the fish community and each of the canopy habitat metrics (described above) using the 19 macroalgal meadow sites as replicates. The coefficient of determination (R^2) was also provided to indicate the adequacy of the fitted models.

Similarly, the lack of data availability for a consistently-quantified measure of hard substratum complexity underlying the macroalgal meadows across the full suite of independent surveys necessitated an analysis focused on underwater visual surveys of labrid fishes conducted across six point surveys (20m²) in each of 29 macroalgal meadow sites within the Ningaloo lagoon ($n = 174$ surveys; full details in van Lier et al. 2018). This took two forms: (1) optimising a multivariate ordination (Principal Coordinates) with hard substratum complexity categories (following van Lier et al., 2018), where low complexity = no or < 10cm vertical relief, medium complexity = 11-60cm vertical relief, high complexity = >61 cm vertical relief (Fig. S5a); and (2) calculation of odds ratios ($\pm$ 95% confidence intervals) from a logistic regression of hard substratum complexity versus adult and juvenile fish abundance (Fig. S5b), where a significant response >1

indicates increased odds of finding that species in an area with higher hard complexity, while a significant response <1 indicates increased odds of finding a species in an area with lower hard complexity. Non-significant responses (95% CL overlaps 1.0) indicate species with equal odds of being found in either high or low hard complexity areas. All species considered in these analyses were those present in $> 20\%$ of transects.

Table S1. List of independent surveys included in each aspect of the data syntheses and meta-analysis of tropical macroalgal-associated fishes.

Country	Location(s)	Source	Tables		Figures					
			S2	S3	3	4	6	7	S1-S4	S5
Australia	Orpheus Island, Great Barrier Reef	M. Bradley et al., 2019	*	*	*	*	*			
Australia	Turtle Group, Great Barrier Reef	A. Hoey unpubl. data		*		*	*			
Australia	Kimberley	C. Piggott unpubl. data	*	*	*	*	*			
Australia	Montebello Islands	Evans et al., 2014	*	*	*	*	*			
Australia	Ningaloo	D. Ellis unpubl. data		*		*	*			
Australia	Ningaloo	Lim et al., 2016		*		*	*			
Australia	Ningaloo	van Lier et al., 2018	*	*	*	*	*			*
Australia	Ningaloo	Wenger et al., 2018		*		*	*			
Australia	Ningaloo	Wilson et al., 2010	*	*	*					
Australia	Ningaloo	Wilson et al., 2018		*		*	*	*	*	
Brazil	Bahia	Eggertsen et al., 2017	*	*	*	*	*			
China	Hong Kong	P. Leung unpubl. data		*						
Fiji	Viti Levu	Rasher et al., 2013		*		*	*			
Fiji	Lakeba, Vanua-Levu & Viti Levu	M. Kulbicki & G. M. Tham unpubl. data		*		*	*			
French Polynesia	Society & Tuamotu islands	M. Kulbicki, R. Galzin, M. Harmelin-Vivien & G. M. Tham unpubl. data		*		*	*			
New Caledonia	Grand Terre	Rossier & Kulbicki, 2000	*		*					
New Caledonia	Grand, Loyalty & Chesterfield islands	M. Kulbicki, G. M. Tham & O. Rossier unpubl. data	*	*	*	*	*			
Philippines	Siquijor	R. Abesamis & A. Bucol unpubl. data	*	*	*	*	*			
Saudi Arabia	Red Sea	D. Coker unpubl. data	*	*	*	*	*			
Seychelles	Inner Seychelles	Chong-Seng et al., 2012 and unpubl. data	*	*	*	*	*			
Seychelles	Inner Seychelles	Graham et al., 2015	*	*	*	*	*			
Tanzania	Mafia Island	Eggertsen et al., 2019	*	*	*	*	*			
Tanzania	Zanzibar	Tano et al., 2017	*	*	*		*			
Tonga	Haapai, Tongatapu & Vavau islands	M. Kulbicki & G. M. Tham unpubl. data		*		*	*			

Table S2. Proportional distribution of local fish species richness among pairs of tropical subtidal habitat (presented in Fig. 3) at multiple tropical locations around the world. Species richness is indicated for each pairwise comparison of fish species surveyed within tropical macroalgal habitat and either (a) coral reef or (b) seagrass beds, at each study location. Species present in both habitat types (per pair) are tallied in the “Both” column. Values in terms of the percentage of total species richness in each location are provided in parentheses for the macroalgae and both categories. An average ($\pm$ standard error) of $49 \pm 4\%$ and $50 \pm 2\%$ of visual samples were deployed within macroalgal meadows for each of these pairwise groups (macroalgae-coral, macroalgae-seagrass, respectively). Relative sampling effort per source is provided in second-last column.

(a) Location	Macroalgae	Coral	Both	Total	% samples in macroalgae	Source
Brazil	2 (4%)	23	24 (49%)	49	50%	Eggertsen et al., 2017
Great Barrier Reef	11 (14%)	46	19 (25%)	76	33%	M. Bradley et al., 2019
Kimberley	27 (29%)	31	35 (38%)	93	66%	C. Piggott unpubl. data
Montebello Islands	16 (15%)	57	32 (30%)	105	35%	Evans et al., 2014
New Caledonia	64 (26%)	48	138 (55%)	250	50%	Rossier & Kulbicki, 2000
Ningaloo	11 (17%)	12	41 (64%)	64	86%	van Lier et al., 2018
Ningaloo	7 (13%)	25	24 (49%)	56	38%	Wilson et al., 2010
Philippines	46 (17%)	167	55 (21%)	268	38%	R. Abesamis & A. Bucol unpubl. data
Red Sea	12 (14%)	51	20 (24%)	83	57%	D. Coker unpubl. data
Seychelles	16 (10%)	28	123 (74%)	167	47%	Chong-Seng et al., 2012
Seychelles	2 (2%)	19	95 (82%)	116	43%	Graham et al., 2015
Tanzania	71 (42%)	54	46 (27%)	171	50%	Eggertsen et al., 2019
(b) Location	Macroalgae	Seagrass	Both	Total		Source
Brazil	17 (63%)	5	5 (19%)	27	50%	Eggertsen et al., 2017
Great Barrier Reef	7 (19%)	6	23 (64%)	36	42%	M. Bradley et al., 2019
Kimberley	27 (24%)	43	42 (38%)	112	53%	C. Piggott unpubl. data
New Caledonia	68 (31%)	44	111 (50%)	223	46%	M. Kulbicki, G. M. Tham & O. Rossier unpubl. data
Philippines	49 (39%)	24	52 (42%)	125	58%	R. Abesamis & A. Bucol unpubl. data
Tanzania	83 (68%)	6	34 (28%)	123	50%	Eggertsen et al., 2019
Tanzania	35 (35%)	23	41 (41%)	99	50%	Tano et al., 2017

Table S3. Mean proportional abundances ($\pm$ standard errors) of 627 bony fish species recorded within tropical macroalgal habitat relative to nearby coral reef. Number of replicate studies (n) underlying each mean proportion are indicated next to each life history column. Zero values indicate zero detection of that life history stage during studies that actively searched for the species within macroalgal habitat; blanks indicate no active searches for that life history stage of a species were made across the 22 independent studies (Table S1). Species (n = 218) marked with an asterisk are those with some evidence of higher proportional abundance of juveniles, adults or both life history stages within macroalgal versus coral reef habitat; a subset of these species (n = 44) for which we have at least 2 or more independent studies for both life history stages are indicated in bold font (i.e., macroalgal-dependent species identified in Fig. 4). Trophic level of the adult diet for the 350 species included in Figure 4 are sourced from Froese and Pauly (2018); a genus-level mean was applied to a species when a specific trophic level was unavailable.

Species	Juveniles	n	Adults	n	Trophic Level
<i>Abudefduf bengalensis</i>			0.49 $\pm$ 0.22	2	
<i>Abudefduf lorentzi</i> *			1	1	
<i>Abudefduf saxatilis</i>	0.29	1	0.11 $\pm$ 0.09	2	
<i>Abudefduf septemfasciatus</i>	0 $\pm$ 0	4	0.07 $\pm$ 0.07	4	3.09
<i>Abudefduf sexfasciatus</i>	0.38 $\pm$ 0.17	7	0.2 $\pm$ 0.12	8	2.40
<i>Abudefduf sordidus</i>	0 $\pm$ 0	3	0.46 $\pm$ 0.29	3	2.88
<i>Abudefduf sparoides</i> *	0.79	1	0.51 $\pm$ 0.26	2	
<i>Abudefduf vaigiensis</i>*	0.72 $\pm$ 0.24	4	0.32 $\pm$ 0.2	6	2.57
<i>Abudefduf whitleyi</i>	0	1	0.24 $\pm$ 0.24	2	
<i>Acanthochromis polyacanthus</i> *			0.59	1	
<i>Acanthopagrus schlegelii schlegelii</i>	0.03	1			
<i>Acanthurus achilles</i>	0.13	1	0	1	
<i>Acanthurus auranticavus</i>	0	1	0.02 $\pm$ 0.02	3	
<i>Acanthurus bahianus</i> *	0.9	1	0.05	1	
<i>Acanthurus blochii</i>	0.23 $\pm$ 0.19	5	0.08 $\pm$ 0.05	9	2.00
<i>Acanthurus chirurgus</i> *	0.9	1	0	1	
<i>Acanthurus coeruleus</i>	0.17	1	0.06	1	
<i>Acanthurus dussumieri</i>	0.26 $\pm$ 0.25	4	0.35 $\pm$ 0.16	6	2.00
<i>Acanthurus gahhm</i> *	1	1	1	1	
<i>Acanthurus grammoptilus</i> *	0.94 $\pm$ 0.06	2	0.73	1	
<i>Acanthurus leucosternon</i>			0.28 $\pm$ 0	2	
<i>Acanthurus lineatus</i>	0 $\pm$ 0	4	0.06 $\pm$ 0.04	6	2.00
<i>Acanthurus nigricans</i>	0 $\pm$ 0	4	0.02 $\pm$ 0.02	4	2.00
<i>Acanthurus nigricauda</i>	0.02 $\pm$ 0.01	4	0.04 $\pm$ 0.02	6	2.00
<i>Acanthurus nigrofasciatus</i>	0.07 $\pm$ 0.04	7	0.21 $\pm$ 0.09	11	2.00
<i>Acanthurus nigroris</i>	0 $\pm$ 0	2	0.06 $\pm$ 0.06	2	2.00
<i>Acanthurus olivaceus</i>	0.11 $\pm$ 0.11	4	0 $\pm$ 0	5	2.00
<i>Acanthurus pyroferus</i>	0.11 $\pm$ 0.07	5	0 $\pm$ 0	5	2.00
<i>Acanthurus sohal</i> *	0.93	1	0.04	1	
<i>Acanthurus tennentii</i> *			0.62 $\pm$ 0.1	2	
<i>Acanthurus triostegus</i>	0.2 $\pm$ 0.13	5	0.35 $\pm$ 0.15	8	2.00
<i>Acanthurus xanthopterus</i>	0 $\pm$ 0	4	0.18 $\pm$ 0.11	5	2.00

<i>Acentrogobius nebulosus</i> *			1	1	
<i>Aeoliscus strigatus</i>	0	1	0.01	1	
<i>Aethaloperca rogaa</i>			0.13 ± 0.03	2	
<i>Albula vulpes</i> *	1	1			
<i>Alectis ciliaris</i> *	0	1	1	1	
<i>Aluterus monoceros</i> *			1	1	
<i>Amanses scopas</i>	0 ± 0	4	0.02 ± 0.02	5	2.66
<i>Ambassis gymnocephalus</i> *	0.91	1			
<i>Amblyglyphidodon curacao</i>	0 ± 0	3	0.01 ± 0.01	4	2.63
<i>Amblyglyphidodon leucogaster</i>	0 ± 0	4	0.03 ± 0.02	6	2.63
<i>Amblyglyphidodon orbicularis</i>	0 ± 0	3	0.02 ± 0.02	3	2.63
<i>Amblygobius albimaculatus</i> *	1	1	1	1	
<i>Amblygobius bynoensis</i> *			1	1	
<i>Amblygobius phalaena</i>	0.05 ± 0.03	4	0.34 ± 0.18	5	3.60
<i>Amblygobius sphynx</i>	0.06 ± 0.06	2	0.28 ± 0.28	2	2.60
<i>Amphiprion akallopisos</i>	0.5 ± 0.5	2	0.5 ± 0.5	2	2.46
<i>Amphiprion akindynos</i>	0.08 ± 0.08	3	0.17 ± 0.16	3	2.46
<i>Amphiprion allardi</i>*	0.56 ± 0.44	2	0.43 ± 0.4	2	2.46
<i>Amphiprion chrysopterus</i>	0 ± 0	3	0.33 ± 0.33	3	2.17
<i>Amphiprion clarkii</i>	0.15 ± 0.15	4	0.01 ± 0.01	5	2.87
<i>Amphiprion frenatus</i> *	0.62	1	0.25	1	
<i>Amphiprion melanopus</i>	0 ± 0	3	0.01 ± 0.01	3	2.34
<i>Amphiprion ocellaris</i>	0.24	1	0.31 ± 0.31	2	
<i>Amphiprion rubrocinctus</i> *			1	1	
<i>Anampses caeruleopunctatus</i>	0.06 ± 0.04	6	0.2 ± 0.16	6	3.40
<i>Anampses geographicus</i>	0.41 ± 0.17	6	0.15 ± 0.07	6	3.50
<i>Anampses meleagrides</i>	0.2 ± 0.2	5	0.08 ± 0.06	7	3.50
<i>Anampses neoguinaicus</i>	0.01 ± 0.01	4	0.02 ± 0.02	4	3.50
<i>Anisotremus moricandi</i> *	1	1	0	1	
<i>Anyperodon leucogrammicus</i>	0.08 ± 0.08	3	0.03 ± 0.03	5	3.90
<i>Apogonichthyoides taeniatus</i> *	1	1	1	1	
<i>Apolemichthys trimaculatus</i>			0.07 ± 0.07	2	
<i>Aprion virescens</i>	0 ± 0	3	0.2 ± 0.16	5	4.28
<i>Arothron caeruleopunctatus</i> *			1	1	
<i>Arothron hispidus</i>*	0.67 ± 0.33	3	0.65 ± 0.15	2	3.24
<i>Arothron immaculatus</i> *	0	1	0.6	1	
<i>Arothron manilensis</i>	0 ± 0	2	0.39 ± 0.39	2	3.83
<i>Arothron meleagris</i>	0 ± 0	3	0.06 ± 0.06	4	3.62
<i>Arothron nigropunctatus</i>	0 ± 0	3	0.12 ± 0.08	4	3.37
<i>Assiculus punctatus</i> *			1	1	
<i>Asterropteryx ensifera</i> *			1	1	
<i>Asterropteryx semipunctata</i>			0.01	1	
<i>Atherinomorus lacunosus</i>	0.71	1			
<i>Atrosalarias fuscus holomelas</i>	0 ± 0	3	0.06 ± 0.03	3	2.00
<i>Aulostomus chinensis</i>	0 ± 0	4	0.11 ± 0.09	7	4.30

<i>Balistapus undulatus</i>	0.01 ± 0	4	0.04 ± 0.03	7	3.40
<i>Balistoides viridescens</i>	0.01 ± 0.01	4	0.25 ± 0.16	6	3.30
<i>Bodianus axillaris</i>	0 ± 0	4	0.16 ± 0.07	6	3.40
<i>Bodianus loxozonus</i>	0.01 ± 0.01	4	0.01 ± 0.01	4	3.60
<i>Bolbometopon muricatum</i>	0 ± 0	3	0.19 ± 0.19	5	2.70
<i>Caesio cuning</i>	0.08 ± 0.08	2	0.23 ± 0.22	3	3.40
<i>Calotomus carolinus</i>	0.21 ± 0.14	5	0.28 ± 0.14	8	2.00
<i>Calotomus spinidens</i>*	0.5 ± 0.5	2	0.67 ± 0.33	3	2.00
<i>Cantherhines pardalis</i>	0	1	0.06 ± 0.05	4	
<i>Canthigaster bennetti</i>	0.28 ± 0.18	6	0.5 ± 0.19	7	2.50
<i>Canthigaster compressa</i>	0	1	0.5 ± 0.5	2	
<i>Canthigaster solandri</i>	0.21 ± 0.2	5	0.5 ± 0.18	6	3.00
<i>Canthigaster valentini</i>	0.2 ± 0.2	5	0.23 ± 0.11	6	2.80
<i>Carangoides bartholomaei</i> *	0.7	1	0	1	
<i>Carangoides chrysophrys</i>	0.5 ± 0.5	2	0	1	
<i>Carangoides ferdau</i>	0 ± 0	3	0.22 ± 0.15	4	4.31
<i>Carangoides fulvoguttatus</i>	0.5 ± 0.5	2	0	1	
<i>Caranx ignobilis</i>	0.5 ± 0.5	2	0.26 ± 0.26	2	4.22
<i>Caranx melampygus</i>	0.08 ± 0.08	4	0.02 ± 0.02	5	4.50
<i>Centrogenys vaigiensis</i> *			1	1	
<i>Centropyge bicolor</i>	0 ± 0	3	0.01 ± 0	4	3.00
<i>Centropyge bispinosa</i>	0 ± 0	3	0.01 ± 0.01	3	2.80
<i>Centropyge flavissima</i>	0 ± 0	4	0.03 ± 0.02	4	2.80
<i>Centropyge multispinis</i> *	0.75	1	0.06 ± 0.05	5	
<i>Centropyge tibicen</i>	0 ± 0	2	0.01 ± 0.01	2	2.80
<i>Centropyge vroliki</i>	0	1	0.35	1	
<i>Cephalopholis argus</i>	0.01 ± 0.01	4	0.05 ± 0.03	10	4.48
<i>Cephalopholis boenak</i>*	0.6 ± 0.25	4	0.18 ± 0.18	4	4.07
<i>Cephalopholis cyanostigma</i>			0.13 ± 0.13	2	
<i>Cephalopholis sexmaculata</i> *	1	1	0.5 ± 0.5	2	
<i>Cephalopholis urodeta</i>	0 ± 0	4	0.01 ± 0.01	6	4.00
<i>Cetoscarus bicolor</i>	0.3 ± 0.2	5	0.03 ± 0.03	6	2.00
<i>Chaetodon assarius</i> *	0.97	1			
<i>Chaetodon aureofasciatus</i>	0.23 ± 0.21	3	0.13 ± 0.11	3	3.30
<i>Chaetodon auriga</i>	0.3 ± 0.14	8	0.3 ± 0.1	12	3.69
<i>Chaetodon bennetti</i>	0 ± 0	4	0.01 ± 0.01	5	3.10
<i>Chaetodon citrinellus</i>	0.2 ± 0.2	5	0.07 ± 0.02	4	3.52
<i>Chaetodon ephippium</i>	0 ± 0	5	0.04 ± 0.03	5	3.43
<i>Chaetodon fasciatus</i> *	1	1	0.14	1	
<i>Chaetodon flavirostris</i>	0.01 ± 0.01	3	0.06 ± 0.06	3	3.00
<i>Chaetodon guttatissimus</i>			0.04 ± 0.04	2	
<i>Chaetodon kleinii</i>	0.24 ± 0.19	5	0.02 ± 0.02	7	2.93
<i>Chaetodon lineolatus</i>	0 ± 0	5	0.16 ± 0.11	10	3.40
<i>Chaetodon lunula</i>	0 ± 0	4	0.12 ± 0.06	6	3.70
<i>Chaetodon lunulatus</i>	0 ± 0	6	0.01 ± 0	7	3.30

<i>Chaetodon melannotus</i>	0.19 ± 0.19	5	0.16 ± 0.1	9	4.35
<i>Chaetodon mertensii</i>	0.01 ± 0.01	5	0.1 ± 0.07	5	3.00
<i>Chaetodon pelewensis</i>	0 ± 0	4	0.01 ± 0	4	2.90
<i>Chaetodon semeion</i>	0 ± 0	3	0.33 ± 0.33	3	2.70
<i>Chaetodon speculum</i>	0.01 ± 0.01	2	0 ± 0	2	3.63
<i>Chaetodon striatus*</i>	1	1	0.31	1	
<i>Chaetodon trifascialis</i>	0.14 ± 0.14	7	0.07 ± 0.06	10	3.34
<i>Chaetodon trifasciatus</i>	0.11 ± 0.11	3	0.21 ± 0.07	4	3.34
<i>Chaetodon ulietensis</i>	0 ± 0	4	0.04 ± 0.03	4	2.70
<i>Chaetodon unimaculatus</i>	0.01 ± 0.01	4	0.01 ± 0.01	5	3.28
<i>Chaetodon vagabundus</i>	0.26 ± 0.16	6	0.17 ± 0.1	7	2.90
<i>Chaetodon xanthocephalus*</i>	1	1	0.36 ± 0.36	2	
<i>Chaetodon zanzibarensis</i>			0.37 ± 0.32	3	
<i>Chaetodontoplus duboulayi*</i>			0.56	1	
<i>Chaetodontoplus mesoleucus</i>			0.22 ± 0.22	2	
<i>Chanos chanos</i>	0 ± 0	2	0.13 ± 0.13	2	2.00
<i>Cheilinus abudjubbe*</i>	1	1	0.43	1	
<i>Cheilinus chlorourus</i>	0.31 ± 0.13	7	0.3 ± 0.1	8	3.90
<i>Cheilinus fasciatus</i>	0.25 ± 0.25	4	0 ± 0	7	3.40
<i>Cheilinus oxycephalus</i>	0.2 ± 0.2	5	0.12 ± 0.12	5	3.50
<i>Cheilinus trilobatus</i>	0.4 ± 0.15	9	0.37 ± 0.13	9	3.88
<i>Cheilinus undulatus</i>	0.19 ± 0.14	5	0.12 ± 0.12	6	4.00
<i>Cheilio inermis*</i>	0.65 ± 0.14	7	0.65 ± 0.1	10	4.10
<i>Cheilodipterus arabicus</i>	0	1	0.24	1	
<i>Cheilodipterus artus</i>	0 ± 0	4	0.17 ± 0.17	4	4.10
<i>Cheilodipterus macrodon</i>	0.33 ± 0.33	3	0.18 ± 0.16	6	4.00
<i>Cheilodipterus quinquelineatus</i>	0.45 ± 0.19	7	0.37 ± 0.13	10	3.89
<i>Chelmon marginalis*</i>	0.02 ± 0.02	2	0.63	1	
<i>Chiloscyllium punctatum*</i>			1	1	
<i>Chirocentrus dorab*</i>	0	1	1	1	
<i>Chlorurus atrilunula</i>			0.42 ± 0.28	2	
<i>Chlorurus bleekeri</i>	0 ± 0	4	0.04 ± 0.04	6	2.00
<i>Chlorurus capistratoides</i>			0.35	1	
<i>Chlorurus frontalis</i>	0.02 ± 0.02	3	0.1 ± 0.1	3	2.00
<i>Chlorurus gibbus*</i>	1	1	0.44	1	
<i>Chlorurus microrhinos</i>	0.15 ± 0.12	8	0.02 ± 0.02	5	2.00
<i>Chlorurus sordidus</i>	0.41 ± 0.13	7	0.28 ± 0.08	7	2.60
<i>Chlorurus spilurus</i>	0.22 ± 0.16	6	0.04 ± 0.03	7	2.00
<i>Chlorurus strongylocephalus</i>			0.18	1	
<i>Choerodon anchorago</i>			0.22 ± 0.22	2	
<i>Choerodon cauteroma*</i>	0.99	1	1	1	
<i>Choerodon cyanodus*</i>	0.69 ± 0.22	2	0.61 ± 0.19	2	3.60
<i>Choerodon graphicus</i>	0.28	1	0.03	1	
<i>Choerodon monostigma*</i>	0.92	1			
<i>Choerodon rubescens*</i>	1	1			

<i>Choerodon schoenleinii</i>*	0.93 ± 0.05	2	0.72 ± 0.14	3	3.40
<i>Chromis acares</i> *	0	1	1	1	
<i>Chromis atripectoralis</i>	0.01 ± 0.01	4	0.01 ± 0.01	7	3.06
<i>Chromis fieldi</i>	0	1	0.01 ± 0.01	2	
<i>Chromis iomelas</i>	0 ± 0	4	0.01 ± 0.01	4	2.70
<i>Chromis nigrura</i>			0.08 ± 0.08	2	
<i>Chromis notata</i>	0.5 ± 0.5	2	0	1	
<i>Chromis ternatensis</i>	0.01 ± 0.01	4	0 ± 0	8	3.40
<i>Chromis viridis</i>	0.12 ± 0.11	9	0.08 ± 0.06	8	2.92
<i>Chromis weberi</i>	0 ± 0	3	0.03 ± 0.02	7	3.40
<i>Chrysiptera annulata</i>*	0.85 ± 0.15	2	0.86 ± 0.14	3	2.80
<i>Chrysiptera biocellata</i>	0.45 ± 0.23	5	0.49 ± 0.22	5	2.00
<i>Chrysiptera brownriggii</i>	0.06 ± 0.02	5	0.49 ± 0.19	5	2.70
<i>Chrysiptera glauca</i>*	0.09 ± 0.09	2	0.82 ± 0.18	2	2.39
<i>Chrysiptera rollandi</i>	0 ± 0	4	0.01 ± 0.01	5	2.70
<i>Chrysiptera taupou</i>	0.03 ± 0.02	4	0.04 ± 0.02	4	2.60
<i>Chrysiptera unimaculata</i>*	0.77 ± 0.18	3	0.88 ± 0.1	4	2.08
<i>Cirrhilabrus exquisitus</i>	0 ± 0	2	0.33 ± 0.33	3	3.40
<i>Cirrhilabrus punctatus</i>	0.01 ± 0.01	4	0 ± 0	4	3.40
<i>Cirrhichthys falco</i>	0 ± 0	3	0.02 ± 0.02	3	4.00
<i>Cirrhichthys oxycephalus</i> *			1	1	
<i>Cirrhitis pinnulatus</i> *			1	1	
<i>Coris auricularis</i> *	1	1	1	1	
<i>Coris aygula</i>	0.01 ± 0.01	5	0.01 ± 0.01	6	3.70
<i>Coris batuensis</i>	0.07 ± 0.02	3	0.05 ± 0.02	4	3.57
<i>Coris caudimacula</i>*	0.97 ± 0.03	4	0.73 ± 0.24	4	3.40
<i>Coris cuvieri</i> *	1	1			
<i>Coris dorsomacula</i>	0 ± 0	3	0.06 ± 0.06	3	3.50
<i>Coris formosa</i>	0.5 ± 0.5	2	0.34 ± 0.18	3	3.30
<i>Coris gaimard</i>	0.24 ± 0.16	5	0.12 ± 0.05	5	3.53
<i>Corythoichthys intestinalis</i>	0.33 ± 0.33	3	0.33 ± 0.33	3	3.17
<i>Crossosalarias macrospilus</i> *	0	1	1	1	
<i>Cryptocentrus fasciatus</i>	0.5 ± 0.5	2	0.5 ± 0.5	2	3.00
<i>Cryptocentrus leucostictus</i> *	0	1	1	1	
<i>Cryptocentrus lutheri</i>	0	1	0.5 ± 0.5	2	
<i>Ctenochaetus binotatus</i>	0.02 ± 0.01	5	0.07 ± 0.03	8	2.00
<i>Ctenochaetus striatus</i>	0.01 ± 0.01	5	0.17 ± 0.09	11	2.00
<i>Ctenochaetus strigosus</i>	0.03 ± 0.03	4	0.01 ± 0.01	4	2.20
<i>Ctenochaetus truncatus</i>	0	1	0.11 ± 0.06	3	
<i>Ctenogobiops feroculus</i> *	0	1	1	1	
<i>Cymolutes praetextatus</i> *	0	1	0.83	1	
<i>Cypho purpurascens</i>	0 ± 0	2	0.21 ± 0.21	2	3.50
<i>Dascyllus aruanus</i>	0.21 ± 0.14	8	0.23 ± 0.12	8	3.30
<i>Dascyllus flavicaudus</i>	0	1	0.01	1	
<i>Dascyllus reticulatus</i>	0.16 ± 0.14	7	0.17 ± 0.17	6	3.10

<i>Dascyllus trimaculatus</i>	0.28 ± 0.13	8	0.25 ± 0.11	9	2.80
<i>Decapterus russelli</i> *	1	1			
<i>Diagramma pictum</i>	0	1	0.25 ± 0.25	4	
<i>Diodon hystrix</i>	0 ± 0	2	0.07 ± 0.07	3	3.67
<i>Diodon liturosus</i>	0	1	0.33 ± 0.33	3	
<i>Dischistodus chrysopoecilus</i> *	1	1	1	1	
<i>Dischistodus darwiniensis</i> *	0.9	1	0.97	1	
<i>Dischistodus perspicillatus</i> *			1	1	
<i>Dischistodus prosopotaenia</i>			0.33 ± 0.33	2	
<i>Doryrhamphus excisus excisus</i> *	0	1	0.7 ± 0.15	2	
<i>Echeneis naucrates</i>	0 ± 0	4	0.2 ± 0.12	4	3.68
<i>Echidna nebulosa</i>*	0.5 ± 0.5	2	0.83 ± 0.17	3	4.00
<i>Ecsenius midas</i>	0 ± 0	2	0.18 ± 0.18	3	2.60
<i>Ellochelon vaigiensis</i>	0 ± 0	2	0.44 ± 0.44	2	2.00
<i>Enneapterygius etheostomus</i> *	0.94	1			
<i>Epibulus insidiator</i>	0.11 ± 0.08	7	0.15 ± 0.08	11	4.00
<i>Epinephelus awoara</i> *	0.62	1			
<i>Epinephelus bilobatus</i> *	0.99	1	0.82 ± 0.18	2	
<i>Epinephelus bleekeri</i> *	1	1			
<i>Epinephelus caeruleopunctatus</i>*	0.43 ± 0.3	3	0.51 ± 0.22	5	3.70
<i>Epinephelus coioides</i>			0.34	1	
<i>Epinephelus cyanopodus</i>	0.26	1	0	1	
<i>Epinephelus fasciatus</i>	0.11 ± 0.06	3	0.19 ± 0.10	9	3.72
<i>Epinephelus hexagonatus</i>	0 ± 0	4	0.1 ± 0.1	5	4.00
<i>Epinephelus howlandi</i>	0.14 ± 0.07	3	0.18 ± 0.16	3	4.00
<i>Epinephelus maculatus</i>	0.03 ± 0.03	2	0 ± 0	2	4.00
<i>Epinephelus merra</i>	0.21 ± 0.2	5	0.37 ± 0.13	9	3.82
<i>Epinephelus polyphekadion</i>	0.01 ± 0.01	4	0.18 ± 0.11	4	4.00
<i>Epinephelus quoyanus</i> *	1	1			
<i>Epinephelus rivulatus</i>*	1 ± 0	2	0.98 ± 0.02	3	3.60
<i>Epinephelus tauvina</i>	0	1	0.5 ± 0.5	2	
<i>Evynnis cardinalis</i> *	0.68	1			
<i>Fistularia commersonii</i>*	0.16 ± 0.1	5	0.51 ± 0.15	8	4.26
<i>Fistularia petimba</i>	0 ± 0	3	0.11 ± 0.07	3	4.43
<i>Forcipiger longirostris</i>	0 ± 0	5	0.02 ± 0.02	5	3.50
<i>Fusigobius neophytus</i>	0 ± 0	2	0.25 ± 0.25	2	2.90
<i>Fusigobius pallidus</i> *			1	1	
<i>Gazza minuta</i>	0.5 ± 0.5	2	0	1	
<i>Gerres oyena</i>	0.25 ± 0.25	4	0.5 ± 0.29	4	2.70
<i>Girella punctata</i> *	0.99	1			
<i>Gnathanodon speciosus</i>*	0.33 ± 0.33	3	0.6 ± 0.24	4	3.80
<i>Gnatholepis anjerensis</i> *			1	1	
<i>Gnatholepis cauerensis</i> *	1	1	1 ± 0	2	
<i>Gomphosus caeruleus</i>	0.41 ± 0.01	2	0.21 ± 0.04	5	3.50
<i>Gomphosus varius</i>	0.01 ± 0.01	6	0.02 ± 0.01	6	3.68

<i>Grammatorcynus bilineatus</i>	0.33 ± 0.33	3	0.33 ± 0.33	3	4.20
<i>Grammistes sexlineatus</i> *	1	1	0.2	1	
<i>Gymnomuraena zebra</i> *	1	1	1 ± 0	2	
<i>Gymnothorax favagineus</i> *	1	1	1 ± 0	2	
<i>Gymnothorax flavimarginatus</i>	0.5 ± 0.5	2	0.33 ± 0.33	3	4.20
<i>Gymnothorax javanicus</i>	0 ± 0	2	0.39 ± 0.31	3	3.90
<i>Haemulon parra</i> *	0.89	1	0	1	
<i>Haemulon plumieri</i>	0.47	1	0	1	
<i>Halichoeres argus</i>	0.44 ± 0.21	4	0.42 ± 0.21	4	3.50
<i>Halichoeres biocellatus</i>	0 ± 0	4	0.01 ± 0.01	4	3.50
<i>Halichoeres brasiliensis</i>	0	1	0.5	1	
<i>Halichoeres brownfieldi</i> *	1	1	1	1	
<i>Halichoeres cosmetus</i>			0.46 ± 0.23	2	
<i>Halichoeres hortulanus</i>	0.37 ± 0.14	8	0.21 ± 0.07	9	3.40
<i>Halichoeres margaritaceus</i>	0.21 ± 0.16	6	0.3 ± 0.16	6	3.70
<i>Halichoeres marginatus</i>	0.36 ± 0.2	6	0.25 ± 0.1	8	3.19
<i>Halichoeres melanochir</i> *			0.75	1	
<i>Halichoeres miniatus</i> *			0.81	1	
<i>Halichoeres nebulosus</i>*	0.57 ± 0.16	8	0.74 ± 0.12	9	3.34
<i>Halichoeres nigrescens</i>*	0.92 ± 0.06	4	0.95 ± 0.04	3	3.50
<i>Halichoeres papilionaceus</i> *	1	1	1	1	
<i>Halichoeres podostigma</i> *	1	1	0.87	1	
<i>Halichoeres poeyi</i> *	1	1	0.72	1	
<i>Halichoeres prosopion</i>	0 ± 0	3	0.03 ± 0.03	4	3.50
<i>Halichoeres scapularis</i>*	0.99 ± 0.01	4	0.81 ± 0.13	6	3.50
<i>Halichoeres trimaculatus</i>	0.21 ± 0.11	4	0.08 ± 0.02	5	3.50
<i>Halophryne diemensis</i> *			1	1	
<i>Hemigymnus fasciatus</i>	0.43 ± 0.2	7	0.15 ± 0.08	9	3.50
<i>Hemigymnus melapterus</i>	0.1 ± 0.07	8	0.16 ± 0.07	10	3.60
<i>Hemipristis elongata</i> *			1	1	
<i>Hemiramphus far</i>	0	1	0.02	1	
<i>Heniochus acuminatus</i>	0.02 ± 0.02	5	0.08 ± 0.06	6	3.40
<i>Heniochus chrysostomus</i>	0 ± 0	4	0.06 ± 0.04	4	3.75
<i>Heniochus monoceros</i>	0 ± 0	4	0.03 ± 0.02	5	3.50
<i>Heteroclinus roseus</i>	0.05	1	0.11	1	
<i>Hipposcarus harid</i>			0.29 ± 0.14	3	
<i>Hipposcarus longiceps</i>	0.02 ± 0.02	5	0.05 ± 0.05	7	2.00
<i>Hologymnosus annulatus</i>	0.14 ± 0.13	5	0.21 ± 0.09	6	4.20
<i>Hypoatherina barnesi</i> *			1	1	
<i>Hypoatherina valenciennesi</i> *	1	1			
<i>Hyporhamphus dussumieri</i>	0.16 ± 0.16	3	0 ± 0	3	3.40
<i>Inimicus didactylus</i>	0	1	0.33	1	
<i>Istigobius decoratus</i> *	0.02	1	0.52 ± 0.48	2	
<i>Istigobius ornatus</i>	0	1	0.02	1	
<i>Labracinus cyclophthalmus</i>			0.21	1	

<i>Labracinus lineatus</i> *			0.91 ± 0.09	2	
<i>Labrichthys unilineatus</i>	0.18 ± 0.16	6	0.01 ± 0.01	9	3.34
<i>Labrisomus nuchipinnis</i> *	1	1	0.15	1	
<i>Labroides bicolor</i>	0.01 ± 0.01	6	0.11 ± 0.06	9	3.46
<i>Labroides dimidiatus</i>	0.24 ± 0.09	9	0.27 ± 0.08	11	3.46
<i>Labroides rubrolabiatu</i> s	0	1	0.33	1	
<i>Labropsis australis</i>	0.02 ± 0.02	3	0.01 ± 0.01	4	3.90
<i>Larabicus quadrilineatus</i>	0	1	0.04	1	
<i>Lateolabrax japonicus</i> *	1	1			
<i>Leptojulius cyanopleura</i> *	1	1	1	1	
<i>Liptoscarus vaigiensis</i>*	0.79 ± 0.12	10	0.84 ± 0.07	13	2.00
<i>Lethrinus atkinsoni</i>*	0.75 ± 0.12	9	0.19 ± 0.08	6	3.79
<i>Lethrinus enigmaticus</i>			0.5 ± 0.27	2	
<i>Lethrinus genivittatus</i>*	0.61 ± 0.39	2	0.88 ± 0.12	2	3.67
<i>Lethrinus harak</i>	0.46 ± 0.22	5	0.43 ± 0.11	8	3.59
<i>Lethrinus laticaudis</i> *	0.98	1	0.96 ± 0.04	2	
<i>Lethrinus lentjan</i>	0 ± 0	3	0.41 ± 0.19	6	3.94
<i>Lethrinus mahsena</i>			0.22 ± 0.22	2	
<i>Lethrinus nebulosus</i>*	0.8 ± 0.1	4	0.5 ± 0.21	5	3.76
<i>Lethrinus obsoletus</i>	0.19 ± 0.17	4	0.05 ± 0.03	5	3.89
<i>Lethrinus olivaceus</i>	0.34 ± 0.24	4	0.19 ± 0.16	6	3.95
<i>Lethrinus ornatus</i> *	1	1	0	1	
<i>Lethrinus punctulatus</i> *	1	1	1	1	
<i>Lethrinus rubrioperculatus</i>	0 ± 0	2	0.25 ± 0.25	3	3.75
<i>Lethrinus semicinctus</i>*	0.07 ± 0.07	2	0.74 ± 0.26	2	3.80
<i>Lethrinus variegatus</i>*	1 ± 0	2	0.75 ± 0.23	2	3.84
<i>Lethrinus xanthochilus</i>	0 ± 0	4	0.06 ± 0.06	4	3.78
<i>Luciogobius guttatus</i> *	1	1			
<i>Lutjanus bohar</i>	0.01 ± 0.01	5	0.02 ± 0.02	7	4.27
<i>Lutjanus carponotatus</i>*	0.88 ± 0.06	3	0.25 ± 0.21	3	3.89
<i>Lutjanus ehrenbergii</i>	0.33 ± 0.33	2	0.06 ± 0.04	3	4.40
<i>Lutjanus fulviflamma</i>*	0.57 ± 0.2	7	0.28 ± 0.12	8	3.79
<i>Lutjanus fulvus</i>	0.2 ± 0.2	5	0.16 ± 0.14	4	3.61
<i>Lutjanus gibbus</i>	0.03 ± 0.02	4	0.18 ± 0.12	7	4.12
<i>Lutjanus monostigma</i>	0.01 ± 0.01	4	0.04 ± 0.02	6	4.01
<i>Lutjanus semicinctus</i>	0	1	0.01	1	
<i>Macolor niger</i>	0 ± 0	3	0.02 ± 0.02	6	4.00
<i>Macropharyngodon bipartitus</i> *	1	1	0.29 ± 0.29	2	
<i>Macropharyngodon meleagris</i>	0.12 ± 0.12	5	0.03 ± 0.03	5	3.09
<i>Macropharyngodon negrosensis</i> *	0.54	1			
<i>Macropharyngodon ornatus</i>	0.16 ± 0.03	2	0.3	1	
<i>Malacoctenus delalandii</i>	0	1	0.35	1	
<i>Malacoctenus triangulatus</i>	0	1	0.25	1	
<i>Meiacanthus atrodorsalis</i>	0 ± 0	3	0.16 ± 0.12	4	2.70
<i>Meiacanthus grammistes</i>	0	1	0.47 ± 0.29	3	

<i>Meiacanthus mossambicus</i>*	0.5 ± 0.5	2	0.72 ± 0.28	2	2.70
<i>Meiacanthus tongaensis</i>	0 ± 0	2	0.03 ± 0.03	2	2.70
<i>Microcanthus strigatus</i>	0.5 ± 0.5	2	0	1	
<i>Microspathodon chrysurus</i>	0.35	1	0	1	
<i>Monacanthus chinensis</i> *	1	1			
<i>Monotaxis grandoculis</i>	0.23 ± 0.19	5	0.05 ± 0.04	7	3.37
<i>Mugil cephalus</i>	0.32 ± 0.32	2	0	1	
<i>Mulloidichthys flavolineatus</i>	0.2 ± 0.2	5	0.17 ± 0.13	8	3.84
<i>Mulloidichthys vanicolensis</i>	0.01 ± 0.01	4	0.09 ± 0.09	5	3.84
<i>Myripristis adusta</i> *	0	1	1	1	
<i>Myripristis kuntee</i>	0 ± 0	4	0.11 ± 0.1	4	3.36
<i>Myripristis murdjan</i>	0 ± 0	4	0.14 ± 0.14	4	3.39
<i>Myripristis violacea</i>	0.01 ± 0.01	4	0.09 ± 0.09	4	3.39
<i>Naso annulatus</i>	0.02 ± 0.02	4	0 ± 0	4	2.00
<i>Naso brevirostris</i>	0.01 ± 0.01	5	0.05 ± 0.05	7	2.20
<i>Naso elegans</i>			0.32 ± 0.32	2	
<i>Naso lituratus</i>	0.02 ± 0.02	4	0.07 ± 0.06	8	2.30
<i>Naso tonganus</i>	0	1	0.11 ± 0.11	2	
<i>Naso unicornis</i>	0.03 ± 0.03	5	0.1 ± 0.1	10	2.20
<i>Naso vlamingii</i>	0.01 ± 0.01	3	0 ± 0	4	2.20
<i>Nematalosa japonica</i>	0.01	1			
<i>Neoglyphidodon melas</i>	0 ± 0	5	0.1 ± 0.08	7	3.43
<i>Neoglyphidodon nigroris</i>	0	1	0.01 ± 0.01	2	
<i>Neoglyphidodon polyacanthus</i>	0.04 ± 0.04	2	0.09 ± 0.09	2	2.70
<i>Neoniphon argenteus</i>	0.33 ± 0.33	3	0.22 ± 0.22	3	4.00
<i>Neoniphon opercularis</i>	0 ± 0	3	0.25 ± 0.25	3	3.76
<i>Neoniphon sammara</i>	0.09 ± 0.07	4	0.03 ± 0.03	7	3.62
<i>Neopomacentrus cyanomos</i> *	0.79	1			
<i>Neopomacentrus filamentosus</i>	0.07	1	0	1	
<i>Neotrygon kuhlii</i>	0 ± 0	3	0.31 ± 0.24	4	3.26
<i>Novaculichthys macrolepidotus</i> *	0.14	1	0.93 ± 0.07	2	
<i>Novaculichthys taeniourus</i>	0.11 ± 0.11	4	0.36 ± 0.11	8	3.20
<i>Nuchequula nuchalis</i>	0.35	1			
<i>Ogilbyina salvati</i> *	0	1	0.61	1	
<i>Ophioblennius trinitatis</i>	0	1	0.01	1	
<i>Osteomugil cunnesius</i>	0.06	1			
<i>Osteomugil perusii</i> *	1	1			
<i>Ostorhinchus angustatus</i> *	0.19	1	0.63	1	
<i>Ostorhinchus aureus</i>	0 ± 0	2	0.03 ± 0.03	2	3.40
<i>Ostorhinchus cavitiensis</i>	0.4	1			
<i>Ostorhinchus compressus</i>	0.25 ± 0.25	2	0.1 ± 0.1	3	3.40
<i>Ostorhinchus cookii</i>*	0.96 ± 0.04	2	0.66 ± 0.17	3	3.34
<i>Ostorhinchus cyanosoma</i> *			1 ± 0	2	
<i>Ostorhinchus doederleini</i> *	0.74 ± 0.26	2	0.04	1	
<i>Ostorhinchus hoevenii</i> *			1	1	

<i>Ostorhinchus multilineatus</i> *			1	1	
<i>Ostorhinchus norfolcensis</i>	0.03	1	0	1	
<i>Ostorhinchus novemfasciatus</i> *	0	1	0.53 ± 0.47	2	
<i>Ostorhinchus rueppellii</i> *	1	1			
<i>Ostorhinchus semilineatus</i> *	1	1			
<i>Ostorhinchus taeniophorus</i> *	1	1			
<i>Ostorhinchus wassinki</i>	0.49	1			
<i>Ostracion cubicus</i>	0.15 ± 0.12	5	0.19 ± 0.15	4	3.40
<i>Oxycheilinus arenatus</i> *	0	1	1	1	
<i>Oxycheilinus bimaculatus</i>*	0.33 ± 0.33	3	0.78 ± 0.2	5	3.50
<i>Oxycheilinus celebicus</i> *	1	1	1	1	
<i>Oxycheilinus digramma</i>	0.02 ± 0.01	6	0.03 ± 0.02	9	3.69
<i>Oxycheilinus orientalis</i>	0 ± 0	2	0.5 ± 0.5	2	3.80
<i>Oxycheilinus unifasciatus</i>	0 ± 0	4	0.13 ± 0.13	4	4.10
<i>Oxymonacanthus longirostris</i>	0 ± 0	3	0.11 ± 0.09	7	3.30
<i>Pagrus major</i> *	0.97	1			
<i>Papilloculiceps longiceps</i>			1 ± 0	2	
<i>Parachaetodon ocellatus</i>			1	1	
<i>Paracirrhites arcatus</i>	0 ± 0	4	0.2 ± 0.2	5	3.63
<i>Paracirrhites forsteri</i>	0.01 ± 0.01	4	0.07 ± 0.06	5	4.30
<i>Paraluteres prionurus</i> *			1	1	
<i>Paramonacanthus pusillus</i> *	1	1			
<i>Paramonacanthus sulcatus</i> *	1	1			
<i>Parapercis cylindrica</i>	0.2 ± 0.2	5	0.39 ± 0.17	6	2.99
<i>Parapercis hexophthalma</i>	0.01 ± 0.01	3	0.2 ± 0.16	6	3.28
<i>Parapercis millepunctata</i>	0 ± 0	4	0.25 ± 0.25	4	3.54
<i>Parapercis schauinslandii</i> *	0	1	1	1	
<i>Parapristipoma trilineatum</i> *	1	1			
<i>Pareques acuminatus</i> *	0.54	1	0	1	
<i>Parma polylepis</i> *	0.13	1	0.88	1	
<i>Parupeneus barberinoides</i>	0.19 ± 0.16	6	0.33 ± 0.13	5	3.40
<i>Parupeneus barberinus</i>	0.33 ± 0.2	6	0.23 ± 0.09	8	3.40
<i>Parupeneus biaculeatus</i> *	0.63	1			
<i>Parupeneus ciliatus</i>	0.02 ± 0.01	3	0.19 ± 0.11	5	3.53
<i>Parupeneus crassilabris</i>	0.02 ± 0.01	4	0.03 ± 0.02	4	3.64
<i>Parupeneus cyclostomus</i>	0.03 ± 0.02	4	0.16 ± 0.08	6	4.20
<i>Parupeneus forsskali</i> *	0.92	1	0.88	1	
<i>Parupeneus indicus</i>	0.43 ± 0.2	6	0.18 ± 0.16	6	3.50
<i>Parupeneus macronema</i> *	0.82	1	0.55 ± 0.12	3	
<i>Parupeneus multifasciatus</i>	0.23 ± 0.19	5	0.11 ± 0.03	5	3.50
<i>Parupeneus pleurostigma</i>	0.02 ± 0.02	4	0.07 ± 0.05	4	3.41
<i>Parupeneus rubescens</i>			0.48	1	
<i>Parupeneus spilurus</i>	0.43 ± 0.3	3	0.15 ± 0.15	2	3.51
<i>Parupeneus trifasciatus</i> *	1	1	0.78 ± 0.22	3	
<i>Pelates quadrilineatus</i> *	1 ± 0	2	1	1	

<i>Pempheris oualensis</i>	0 ± 0	2	0.05 ± 0.05	2	3.60
<i>Pempheris schwenkii</i>	0.5 ± 0.5	2	0	1	
<i>Pentapodus emeryii</i> *	1	1	0.5 ± 0.5	2	
<i>Pentapodus porosus</i> *	1	1			
<i>Pentapodus vitta</i> *	1	1			
<i>Pervagor janthinosoma</i>	0 ± 0	2	0.18 ± 0.1	3	2.90
<i>Petroscirtes breviceps</i>	0.38	1			
<i>Petroscirtes lupus</i>	0.33	1	0.11	1	
<i>Petroscirtes mitratus</i> *	0	1	1	1	
<i>Plagiotremus laudandus laudandus</i>	0 ± 0	3	0.01 ± 0.01	3	4.40
<i>Plagiotremus rhinorhynchos</i>	0 ± 0	2	0.1 ± 0.1	2	4.50
<i>Plagiotremus tapeinosoma</i>	0.05 ± 0.05	4	0.1 ± 0.06	4	3.80
<i>Planiliza affinis</i> *	0.96	1			
<i>Planiliza macrolepis</i> *	0.99	1			
<i>Platax batavianus</i>			0.5	1	
<i>Platax boersii</i>			0.5	1	
<i>Platax pinnatus</i>	0	1	0.33 ± 0.33	3	
<i>Plectorhinchus chaetodonoides</i> *	0 ± 0	3	0.8	1	
<i>Plectorhinchus chrysotaenia</i> *			1	1	
<i>Plectorhinchus flavomaculatus</i>	0	1	0.5 ± 0.5	2	
<i>Plectorhinchus gibbosus</i>	0	1	0.33 ± 0.33	3	
<i>Plectorhinchus schotaf</i> *			0.68 ± 0.1	2	
<i>Plectorhinchus vittatus</i>	0.29 ± 0.29	2	0.16 ± 0.10	4	3.90
<i>Plectroglyphidodon dickii</i>	0 ± 0	5	0.01 ± 0.01	8	3.68
<i>Plectroglyphidodon johnstonianus</i>	0 ± 0	5	0.02 ± 0.01	7	3.35
<i>Plectroglyphidodon lacrymatus</i>	0.14 ± 0.09	7	0.14 ± 0.07	10	2.22
<i>Plectropomus laevis</i>	0 ± 0	4	0.06 ± 0.06	5	4.40
<i>Plectropomus leopardus</i>	0.2 ± 0.2	5	0.21 ± 0.16	6	4.42
<i>Plectropomus maculatus</i>	0.24 ± 0.19	5	0 ± 0	5	4.10
<i>Plotosus lineatus</i>	0.38 ± 0.24	4	0.13 ± 0.13	3	3.57
<i>Pomacanthus imperator</i>	0.13 ± 0.13	4	0.07 ± 0.05	7	2.70
<i>Pomacanthus paru</i> *	1	1	0	1	
<i>Pomacanthus semicirculatus</i>	0 ± 0	2	0.25 ± 0.15	4	2.70
<i>Pomacanthus sexstriatus</i>	0.16 ± 0.16	4	0.16 ± 0.11	5	2.60
<i>Pomacentrus adelus</i>	0.09 ± 0.09	3	0.09 ± 0.08	4	2.70
<i>Pomacentrus amboinensis</i>	0.06 ± 0.06	4	0.04 ± 0.04	4	2.40
<i>Pomacentrus baenschii</i> *			1	1	
<i>Pomacentrus bankanensis</i>	0.21 ± 0.21	3	0.03 ± 0.03	3	2.60
<i>Pomacentrus caeruleus</i> *	0.92	1	0.5 ± 0.5	2	
<i>Pomacentrus chrysurus</i>	0.41 ± 0.24	4	0.37 ± 0.21	4	2.60
<i>Pomacentrus coelestis</i>	0.1 ± 0.06	6	0.27 ± 0.16	6	3.20
<i>Pomacentrus grammorhynchus</i>	0.13 ± 0.13	2	0.08 ± 0.08	2	2.70
<i>Pomacentrus imitator</i>	0 ± 0	3	0.01 ± 0.01	3	2.70
<i>Pomacentrus limosus</i>	0.38	1			
<i>Pomacentrus milleri</i> *	0.18 ± 0.16	2	0.71	1	

<i>Pomacentrus moluccensis</i>	0.05 ± 0.05	5	0.07 ± 0.07	6	2.44
<i>Pomacentrus pavo</i>	0.05 ± 0.05	4	0.3 ± 0.2	5	3.00
<i>Pomacentrus philippinus</i>	0 ± 0	3	0.29 ± 0	4	2.70
<i>Pomacentrus sulfureus</i>			0.12 ± 0.08	4	
<i>Pomacentrus trilineatus*</i>	1	1	0.62 ± 0.15	5	
<i>Pomacentrus tripunctatus*</i>	0.87	1	0.53 ± 0.47	2	
<i>Pomacentrus vaiuli</i>	0.01 ± 0	4	0.01 ± 0.01	4	3.10
<i>Pomacentrus wardi</i>	0.13 ± 0.13	3	0.13 ± 0.11	3	2.00
<i>Priacanthus hamrur</i>	0.01 ± 0.01	4	0.02 ± 0.02	5	3.64
<i>Pristiapogon exostigma</i>	0 ± 0	2	0.5 ± 0.5	2	3.40
<i>Pristicon trimaculatus</i>	0	1	0.07	1	
<i>Psammoperca waigiensis*</i>	0.51 ± 0.49	2	0.5	1	
<i>Pseudechidna brummeri*</i>			1	1	
<i>Pseudobalistes fuscus</i>	0.05 ± 0.05	3	0 ± 0	3	4.04
<i>Pseudocheilinus evanidus</i>	0 ± 0	3	0.31 ± 0.24	4	3.50
<i>Pseudocheilinus hexataenia</i>	0.12 ± 0.08	6	0.1 ± 0.05	8	3.15
<i>Pseudochromis fuscus*</i>	1	1	0.04 ± 0.02	3	
<i>Pseudojuloides elongatus*</i>	0.67 ± 0.33	3	1 ± 0	3	3.50
<i>Pseudupeneus maculatus*</i>	1	1	0.87	1	
<i>Pteragogus flagellifera*</i>	0.93 ± 0.07	2	0.92 ± 0.08	4	3.50
<i>Ptereleotris evides</i>	0.08 ± 0.08	4	0.09 ± 0.09	5	3.40
<i>Ptereleotris hanae</i>	0 ± 0	3	0.21 ± 0.2	3	3.40
<i>Ptereleotris microlepis</i>	0 ± 0	2	0.45 ± 0.45	2	3.40
<i>Pterocaesio tile</i>	0 ± 0	4	0.01 ± 0.01	5	3.30
<i>Pterois volitans</i>	0 ± 0	2	0.5 ± 0.5	2	4.35
<i>Pygoplites diacanthus</i>	0 ± 0	4	0.1 ± 0.1	6	2.70
<i>Rhabdosargus sarba*</i>	0.89	1			
<i>Rhinecanthus aculeatus</i>	0.03 ± 0.02	4	0.49 ± 0.18	5	3.21
<i>Rhinecanthus assai*</i>			0.95	1	
<i>Rhinecanthus rectangulus</i>	0 ± 0	2	0.08 ± 0.08	2	3.52
<i>Rhinecanthus verrucosus*</i>	1	1	1	1	
<i>Salarias fasciatus*</i>	0.25 ± 0.25	4	0.61 ± 0.24	4	2.00
<i>Sardinella lemuru*</i>	0.97	1			
<i>Sargocentron diadema</i>	0 ± 0	4	0.12 ± 0.1	5	3.37
<i>Sargocentron rubrum</i>	0 ± 0	3	0.1 ± 0.1	3	3.58
<i>Sargocentron spiniferum</i>	0.02 ± 0.02	4	0.05 ± 0.04	5	3.60
<i>Saurida gracilis</i>	0.25 ± 0.25	4	0.25 ± 0.25	4	4.19
<i>Scaevius milii*</i>	0.6 ± 0.39	2	0.98	1	
<i>Scarus altipinnis</i>	0.12 ± 0.09	5	0.02 ± 0.02	7	2.00
<i>Scarus caudofasciatus</i>			0.25	1	
<i>Scarus chameleon</i>	0.33 ± 0.21	6	0.29 ± 0.15	7	2.00
<i>Scarus dimidiatus</i>	0.01 ± 0.01	4	0.07 ± 0.06	5	2.00
<i>Scarus flavipectoralis</i>	0.25 ± 0.25	4	0.01 ± 0.01	4	2.00
<i>Scarus frenatus</i>	0.21 ± 0.13	9	0.09 ± 0.06	10	2.00
<i>Scarus ghobban</i>	0.46 ± 0.14	10	0.3 ± 0.09	14	2.00

<i>Scarus globiceps</i>	0.08 ± 0.08	5	0.16 ± 0.08	7	2.00
<i>Scarus hutchinsi</i> *	0.71	1	0.81	1	
<i>Scarus hypselopterus</i> *	0.99	1	0.75	1	
<i>Scarus longipinnis</i>	0 ± 0	3	0.01 ± 0.01	3	2.00
<i>Scarus niger</i>	0.04 ± 0.03	6	0.11 ± 0.07	11	2.00
<i>Scarus oviceps</i>	0 ± 0	3	0.01 ± 0	4	2.00
<i>Scarus prasiognathus</i>	0.02 ± 0.02	2	0.22 ± 0.16	3	2.00
<i>Scarus psittacus</i>	0.25 ± 0.14	7	0.35 ± 0.09	10	2.00
<i>Scarus rivulatus</i>	0.25 ± 0.12	9	0.15 ± 0.09	9	2.00
<i>Scarus rubroviolaceus</i>	0.17 ± 0.17	6	0.13 ± 0.08	7	2.00
<i>Scarus russelii</i> *			0.81	1	
<i>Scarus scaber</i> *	0.53	1	0.2 ± 0.1	3	
<i>Scarus schlegeli</i>	0.4 ± 0.2	6	0.14 ± 0.1	8	2.00
<i>Scarus spinus</i>	0.01 ± 0.01	3	0.05 ± 0.05	3	2.00
<i>Scarus tricolor</i>			0.12 ± 0.12	3	
<i>Scarus viridifucatus</i>			0.25 ± 0.25	2	
<i>Scolopsis bilineata</i>	0.01 ± 0.01	4	0.16 ± 0.1	6	3.60
<i>Scolopsis frenatus</i>			0.24 ± 0.2	2	
<i>Scolopsis ghanam</i>*	0.5 ± 0.25	2	0.84 ± 0.16	2	3.60
<i>Scolopsis lineata</i> *	0.84 ± 0.16	2	0	1	
<i>Scolopsis monogramma</i> *	1	1	0.55	1	
<i>Scolopsis trilineata</i>	0.04 ± 0.03	3	0.1 ± 0.07	3	3.50
<i>Scomberoides commersonnianus</i> *	0	1	1	1	
<i>Scomberoides lysan</i>	0.26 ± 0.26	2	0 ± 0	2	4.00
<i>Scomberoides tol</i>	0 ± 0	5	0.23 ± 0.23	4	4.11
<i>Scombrops boops</i> *	0.79	1			
<i>Scorpaenopsis venosa</i> *	1	1	1	1	
<i>Sebastiscus marmoratus</i> *	0.75	1			
<i>Selar crumenophthalmus</i> *	0	1	1	1	
<i>Siganus argenteus</i>	0.11 ± 0.1	4	0.31 ± 0.15	8	2.00
<i>Siganus canaliculatus</i> *	0.99 ± 0.01	2	1	1	
<i>Siganus corallinus</i>	0.02 ± 0.02	2	0.1 ± 0.1	3	2.00
<i>Siganus doliatus</i>	0.48 ± 0.2	6	0.12 ± 0.06	8	2.00
<i>Siganus fuscescens</i>*	0.31 ± 0.16	3	0.59 ± 0.24	4	2.03
<i>Siganus lineatus</i>	0.33 ± 0.33	3	0.2 ± 0.2	4	2.00
<i>Siganus luridus</i>			0.28 ± 0.28	2	
<i>Siganus puelloides</i>			0.31 ± 0.05	2	
<i>Siganus punctatus</i>	0.01 ± 0.01	4	0.07 ± 0.04	6	2.00
<i>Siganus rivulatus</i> *	1	1	1	1	
<i>Siganus spinus</i>*	0.56 ± 0.19	5	0.55 ± 0.18	5	2.03
<i>Siganus stellatus</i>			0.27 ± 0.13	3	
<i>Siganus sutor</i>*	0.76 ± 0.24	2	0.72 ± 0.23	3	2.25
<i>Siganus virgatus</i>	0.14 ± 0.14	2	0.5 ± 0.5	2	2.70
<i>Sillago aeolus</i> *	1	1			
<i>Sillago sihama</i> *	1	1			

<i>Sparisoma amplum</i> *	1	1	0	1	
<i>Sparisoma axillare</i>	0.47	1	0.03	1	
<i>Sparisoma frondosum</i>	0.41	1	0	1	
<i>Sparisoma radians</i> *	1	1	0.5	1	
<i>Sphaeramia nematoptera</i>	0 ± 0	2	0.01 ± 0.01	2	3.20
<i>Sphoeroides spengleri</i> *	1	1	0	1	
<i>Sphyraena flavicauda</i>	0.05 ± 0.04	5	0.2 ± 0.2	5	4.50
<i>Sphyraena japonica</i> *	0.69	1			
<i>Sphyraena pinguis</i>	0.27 ± 0.27	2	0	1	
<i>Sphyraena putnamae</i>	0.46 ± 0.46	2	0	1	
<i>Spratelloides gracilis</i>	0.16	1			
<i>Stegastes albifasciatus</i>	0 ± 0	3	0.05 ± 0.05	3	2.00
<i>Stegastes fasciolatus</i>	0.01 ± 0.01	4	0.24 ± 0.16	6	2.16
<i>Stegastes fuscus</i>	0.13	1	0.08	1	
<i>Stegastes lividus</i>	0 ± 0	3	0.23 ± 0.19	5	2.20
<i>Stegastes nigricans</i>	0.3 ± 0.19	6	0.1 ± 0.07	7	2.24
<i>Stegastes obreptus</i>	0.18	1	0.5	1	
<i>Stegastes variabilis</i> *	0.95	1	0.73	1	
<i>Stephanolepis cirrhifer</i> *	0.53	1			
<i>Stethojulis albobittata</i>*	0.94 ± 0.01	2	0.75 ± 0.12	5	3.60
<i>Stethojulis bandanensis</i>	0.28 ± 0.11	8	0.34 ± 0.15	6	3.21
<i>Stethojulis interrupta</i>*	0.27 ± 0.13	6	0.51 ± 0.22	5	3.37
<i>Stethojulis strigiventer</i>*	0.63 ± 0.13	10	0.49 ± 0.18	7	3.14
<i>Stethojulis terina</i> *	1	1			
<i>Stethojulis trilineata</i>	0.33 ± 0.33	3	0.36 ± 0.32	3	3.21
<i>Sufflamen bursa</i>	0 ± 0	5	0.01 ± 0.01	5	2.91
<i>Sufflamen chrysopteron</i>	0.01 ± 0.01	4	0.27 ± 0.13	7	3.40
<i>Symphorus nematophorus</i> *			0.74	1	
<i>Syngnathus schlegeli</i> *	0.66	1			
<i>Synodus binotatus</i>	0 ± 0	2	0.5 ± 0.29	4	4.20
<i>Synodus dermatogenys</i>	0 ± 0	2	0.16 ± 0.16	3	4.20
<i>Synodus hoshinonis</i>	0.5 ± 0.5	2	0 ± 0	2	4.20
<i>Synodus variegatus</i>	0 ± 0	5	0.16 ± 0.08	8	4.20
<i>Takifugu ocellatus</i> *	1	1			
<i>Takifugu poecilonotus</i> *	0.91	1			
<i>Teixeirichthys jordani</i> *	1	1			
<i>Thalassoma amblycephalum</i>	0.17 ± 0.14	7	0.04 ± 0.04	5	3.10
<i>Thalassoma hardwicke</i>	0.06 ± 0.04	7	0.2 ± 0.07	10	3.50
<i>Thalassoma hebraicum</i>*	0.85 ± 0.12	2	0.51 ± 0.08	4	3.50
<i>Thalassoma janseni</i>	0.02 ± 0.02	3	0.27 ± 0.24	4	3.05
<i>Thalassoma lunare</i>	0.22 ± 0.13	10	0.28 ± 0.09	12	3.87
<i>Thalassoma lutescens</i>	0.02 ± 0.02	5	0.05 ± 0.03	5	3.72
<i>Thalassoma purpureum</i>	0.25 ± 0.19	5	0.16 ± 0.11	6	3.77
<i>Thalassoma quinquevittatum</i>	0 ± 0	4	0.06 ± 0.04	4	3.51
<i>Trachinotus bailloni</i> *	1	1			

<i>Trachurus japonicus</i> *	1	1			
<i>Upeneus tragula</i>*	0.56 ± 0.26	4	0.44 ± 0.39	2	3.59
<i>Valenciennea longipinnis</i>	0.06	1	0.03	1	
<i>Valenciennea puellaris</i>	0 ± 0	2	0.25 ± 0.25	2	3.80
<i>Valenciennea strigata</i>	0.1 ± 0.06	3	0.16 ± 0.07	3	4.00
<i>Variola louti</i>	0 ± 0	4	0.18 ± 0.16	6	4.33
<i>Xenajulis margaritaceus</i>*	1 ± 0	2	1 ± 0	2	3.50
<i>Zanclus cornutus</i>	0.01 ± 0.01	4	0.12 ± 0.06	8	2.50
<i>Zebrasoma desjardini</i>	0	1	0.08 ± 0.05	3	
<i>Zebrasoma scopas</i>	0 ± 0	6	0.03 ± 0.01	9	2.00

Table S4. Availability of two prominent habitat-forming organisms (coral and macroalgae), expressed as mean percent cover ($\pm$ standard error of the mean) across all study sites per location (minimum of $n = 3$ per source study), at locations where fish surveys were conducted within macroalgae-dominated and coral-dominated reef and included in Figure 4. Global means (across all surveys) are provided in bold font on the final row.

Location(s)	Source	Coral-dominated		Macroalgae-dominated	
		% live coral	% macroalgae	% live coral	% macroalgae
Orpheus Island, Great Barrier Reef	M. Bradley et al., 2019	58 $\pm$ 3.0	1 $\pm$ 0.5	0.4 $\pm$ 0.2	71 $\pm$ 4.9
Turtle Group, Great Barrier Reef	A. Hoey unpubl. data	37 $\pm$ 4.9	5 $\pm$ 2.6	8 $\pm$ 1.9	78 $\pm$ 2.0
Kimberley	C. Piggott unpubl. data	87 $\pm$ 7.2	5 $\pm$ 2.2	1 $\pm$ 0.6	95 $\pm$ 1.5
Montebello Islands	Evans et al., 2014	52 $\pm$ 3.6	2 $\pm$ 1.1	0.6 $\pm$ 0.2	45 $\pm$ 6.3
Ningaloo	D. Ellis unpubl. data	17 $\pm$ 2.6	12 $\pm$ 2.8	0.2 $\pm$ 0.1	31 $\pm$ 3.7
Ningaloo	Lim et al., 2016	20 $\pm$ 4.1	6 $\pm$ 1.6	0	47 $\pm$ 3.6
Ningaloo	van Lier et al., 2018	66 $\pm$ 7.5	1 $\pm$ 0.5	1 $\pm$ 0.5	58 $\pm$ 2.3
Ningaloo	Wenger et al., 2018	66 $\pm$ 7.5	1 $\pm$ 0.5	1 $\pm$ 0.4	58 $\pm$ 2.4
Ningaloo	Wilson et al., 2018	25 $\pm$ 3.4	6 $\pm$ 1.5	0.2 $\pm$ 0.1	38 $\pm$ 2.6
Bahia	Eggertsen et al., 2017	22 $\pm$ 2.6	5 $\pm$ 0.8	0	75 $\pm$ 2.2
Viti Levu	Rasher et al., 2013	49 $\pm$ 5.8	2 $\pm$ 0.4	7 $\pm$ 3.4	64 $\pm$ 13.7
Lakeba, Vanua-Levu & Viti Levu	M. Kulbicki & G. M. Tham unpubl. data	22 $\pm$ 6.2	0.1 $\pm$ 0.3	0.6 $\pm$ 0.5	51 $\pm$ 13.7
Society & Tuamotu islands	M. Kulbicki, R. Galzin, M. Harmelin-Vivien & G. M. Tham unpubl. data	28 $\pm$ 7.9	0.5 $\pm$ 0.5	1 $\pm$ 0.7	19 $\pm$ 5.3
Grand, Loyalty & Chesterfield islands	M. Kulbicki, G. M. Tham & O. Rossier unpubl. data	51 $\pm$ 8.1	0.5 $\pm$ 0.6	1 $\pm$ 0.6	44 $\pm$ 8.6
Siquijor	R. Abesamis & A. Bucol unpubl. data	58 $\pm$ 2.0	5 $\pm$ 0.9	0	79 $\pm$ 2.5
Red Sea	D. Coker unpubl. data	36 $\pm$ 4.1	1 $\pm$ 0.5	4 $\pm$ 0.2	57 $\pm$ 4.3
Inner Seychelles	Chong-Seng et al., 2012 and unpubl. data	26 $\pm$ 4.8	0.6 $\pm$ 0.4	3 $\pm$ 1.0	32 $\pm$ 7.1
Inner Seychelles	Graham et al., 2015	27 $\pm$ 3.6	1 $\pm$ 1.2	5 $\pm$ 1.5	31 $\pm$ 5.9
Mafia Island	Eggertsen et al., 2019	48 $\pm$ 5.3	4 $\pm$ 1.0	2 $\pm$ 0.4	29 $\pm$ 2.8
Haapai, Tongatapu & Vavau islands	M. Kulbicki & G. M. Tham unpubl. data	24 $\pm$ 6.0	0.6 $\pm$ 0.6	0.9 $\pm$ 0.6	39 $\pm$ 16.9
		41 $\pm$ 4.4	3 $\pm$ 0.7	2 $\pm$ 0.5	52 $\pm$ 4.5

Table S5. Rabbitfish (Family Siganidae) capture fisheries production, human population, gross national income (GNI) per capita, and coral reef area per country or territory.

Country/Territory	Rabbitfish production (m. tons) ¹	Percent of total rabbitfish production	Percent rabbitfish in total fish production	Human population ²	Per capita GNI (rank out of 183) ³	Percent of world's coral reef area ⁴
Indonesia	52,180	53.10	1.0	266,794,980	115	17.95
Philippines	23,674	24.09	1.4	106,512,074	112	8.81
Tanzania	3,741	3.81	4.4	59,091,392	159	1.26
Oman	3,476	3.54	1.3	4,829,946	46	0.19
Kenya	2,294	2.33	17.3	50,950,879	147	0.22
Bahrain	2,280	2.32	32.3	1,566,993	33	0.20
United Arab Emirates	2,200	2.24	3.0	9,541,615	19	0.42
Saudi Arabia	2,077	2.11	3.8	33,554,343	34	2.34
Malaysia	1,572	1.60	0.1	32,042,458	61	1.27
Egypt	1,515	1.54	1.3	99,375,741	121	1.34
Iran	1,295	1.32	0.2	82,011,735	87	0.25
Qatar	710	0.72	5.0	2,694,849	4	0.25
Libya	310	0.32	1.1	6,470,956	80	no data
Seychelles	301	0.31	0.2	95,235	47	0.59
Lebanon	233	0.24	5.5	6,093,509	69	no data
Fiji	220	0.22	0.5	912,241	90	3.52
Mauritius	145	0.15	0.8	912,241	59	0.31
Jordan	13	0.01	4.7	9,903,802	106	<0.01
Cyprus	9	0.01	0.6	1,189,085	31	no data
Singapore	9	0.01	1.1	5,791,901	8	<0.01
Palau	5	0.01	0.6	21,964	9	0.40
Guam	4	<0.01	0.3	165,718	no data	<0.01
Northern Mariana Islands	1	<0.01	0.1	55,194	no data	0.40

Data sources: ¹FAO (2018); ²United Nations Department of Economic and Social Affairs, Population Division, Population Estimates and Projections Section (2017) World Population Prospects, the 2017 Revision; ³World Bank GNI per capita, Atlas Method, 2017; ⁴Spalding et al. (2001).

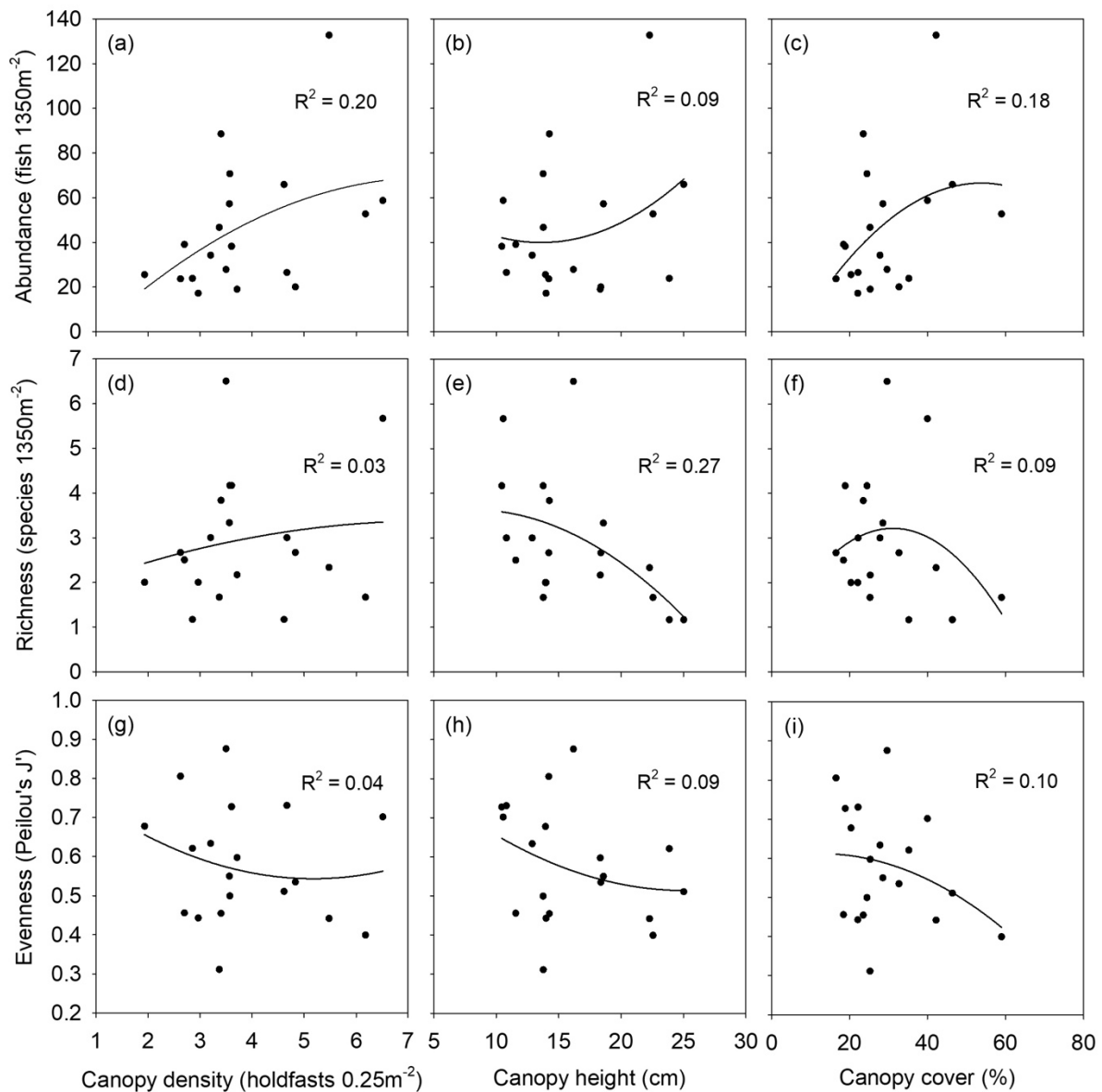


Figure S1. Second-order polynomial relationships between the annualised means for three aspects of macroalgal canopy condition (percent cover, canopy height, and canopy density) and the abundance (a-c), species richness (d-f) and evenness (g-i) of herbivorous fishes in 19 macroalgal meadow sites of the Ningaloo lagoon.

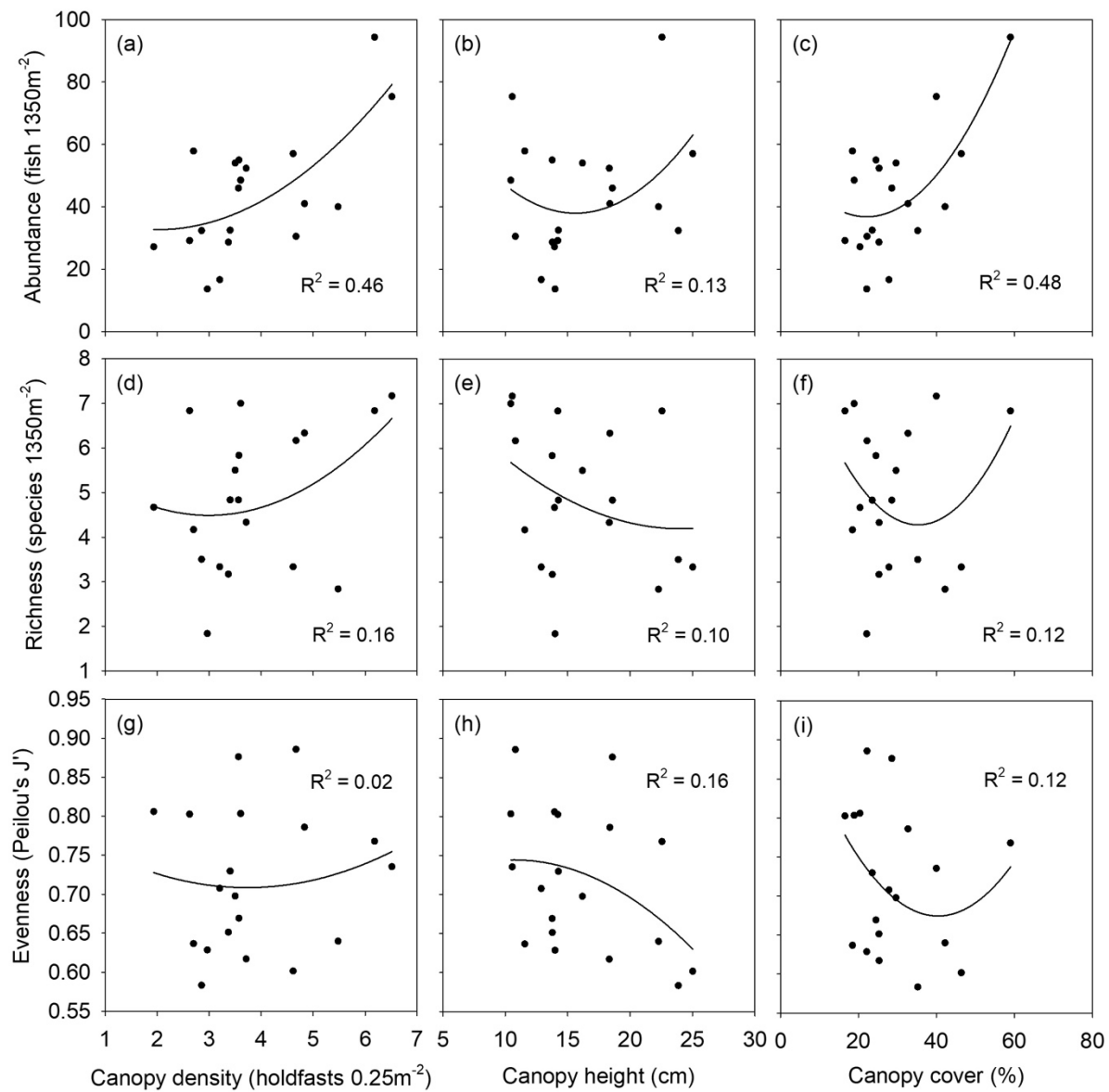


Figure S2. Second-order polynomial relationships between the annualised means for three aspects of macroalgal canopy condition (percent cover, canopy height, and canopy density) and the abundance (a-c), species richness (d-f) and evenness (g-i) of carnivorous fishes in 19 macroalgal meadow sites of the Ningaloo lagoon.

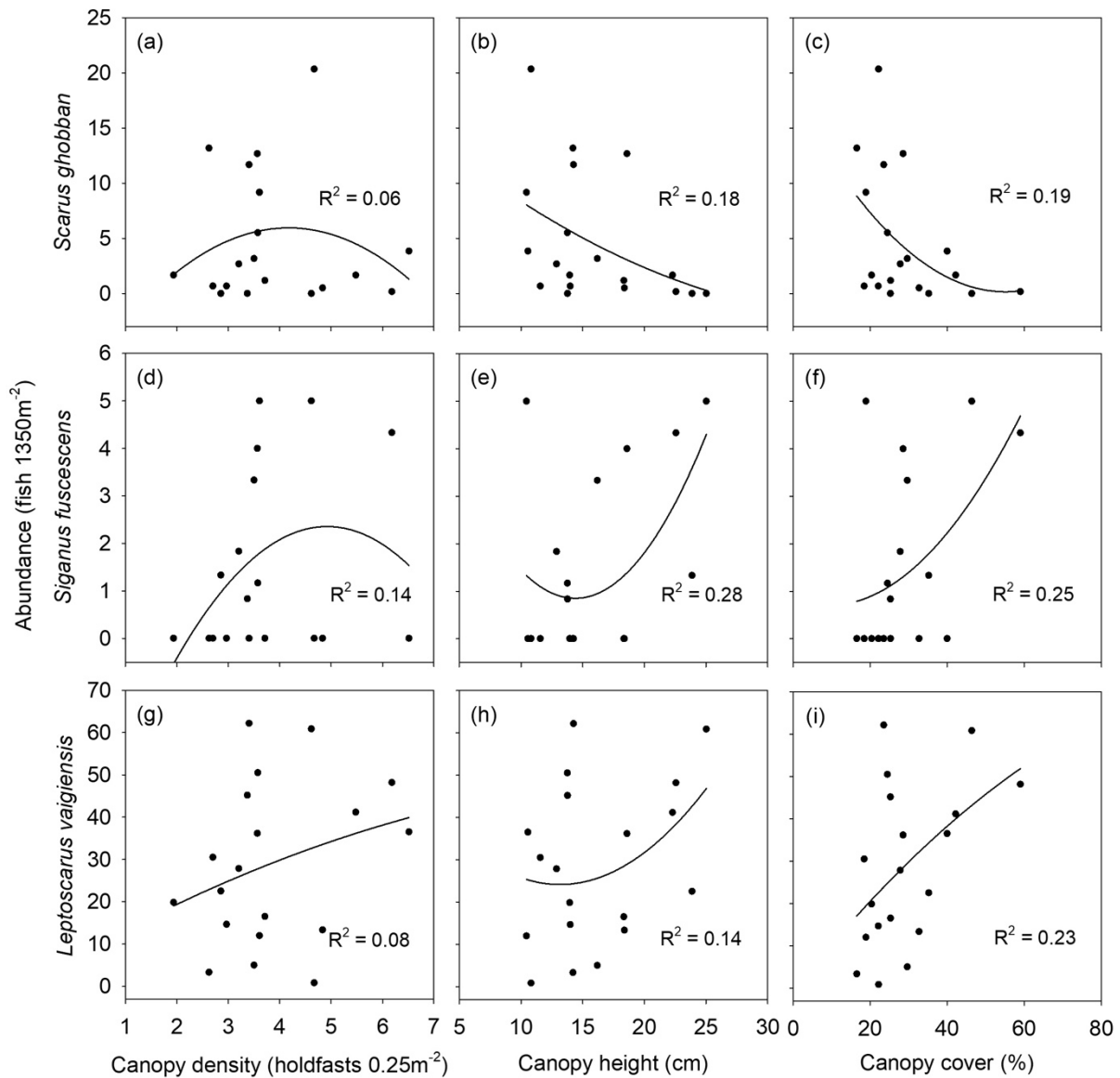


Figure S3. Second-order polynomial relationships between the annualised means for three aspects of macroalgal canopy condition (percent cover, canopy height, and canopy density) and the abundance of three common species of herbivorous fishes across 19 macroalgal meadow sites of the Ningaloo lagoon: Blue-barred parrotfish (*Scarus ghobban*, Labridae; a-c), Mottled spinefoot (*Siganus fuscescens*, Siganidae; d-f) and Marbled parrotfish (*Leptoscarus vaigiensis*, Labridae; g-i).

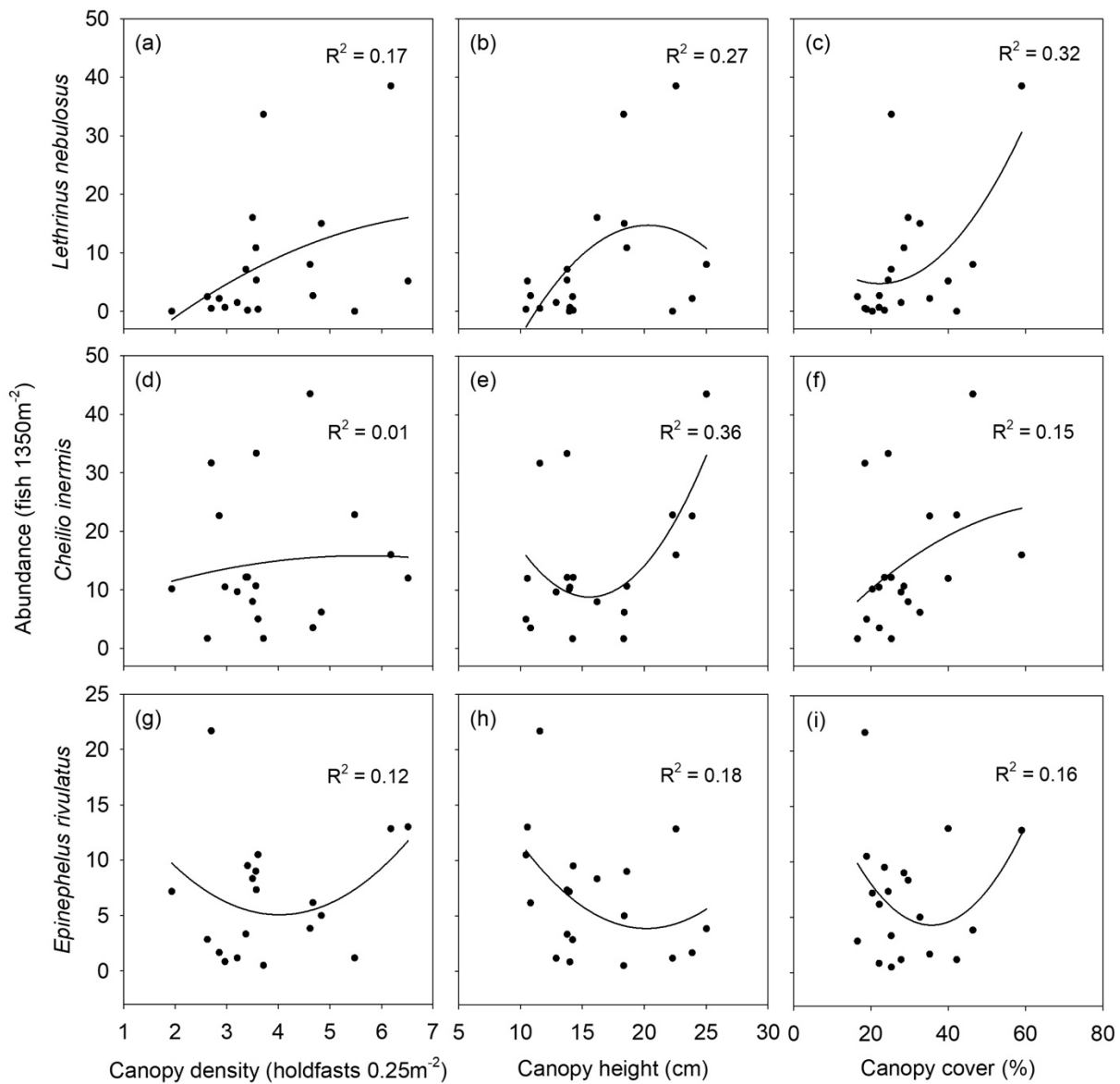


Figure S4. Second-order polynomial relationships between the annualised means for three aspects of macroalgal canopy condition (percent cover, canopy height, and canopy density) and the abundance of three common species of carnivorous fishes across 19 macroalgal meadow sites of the Ningaloo lagoon: Spangled emperor (*Lethrinus nebulosus*, Lethrinidae; a-c), Cigar wrasse (*Cheilio inermis*, Labridae; d-f) and Halfmoon grouper (*Epinephelus rivulatus*, Serranidae; g-i).

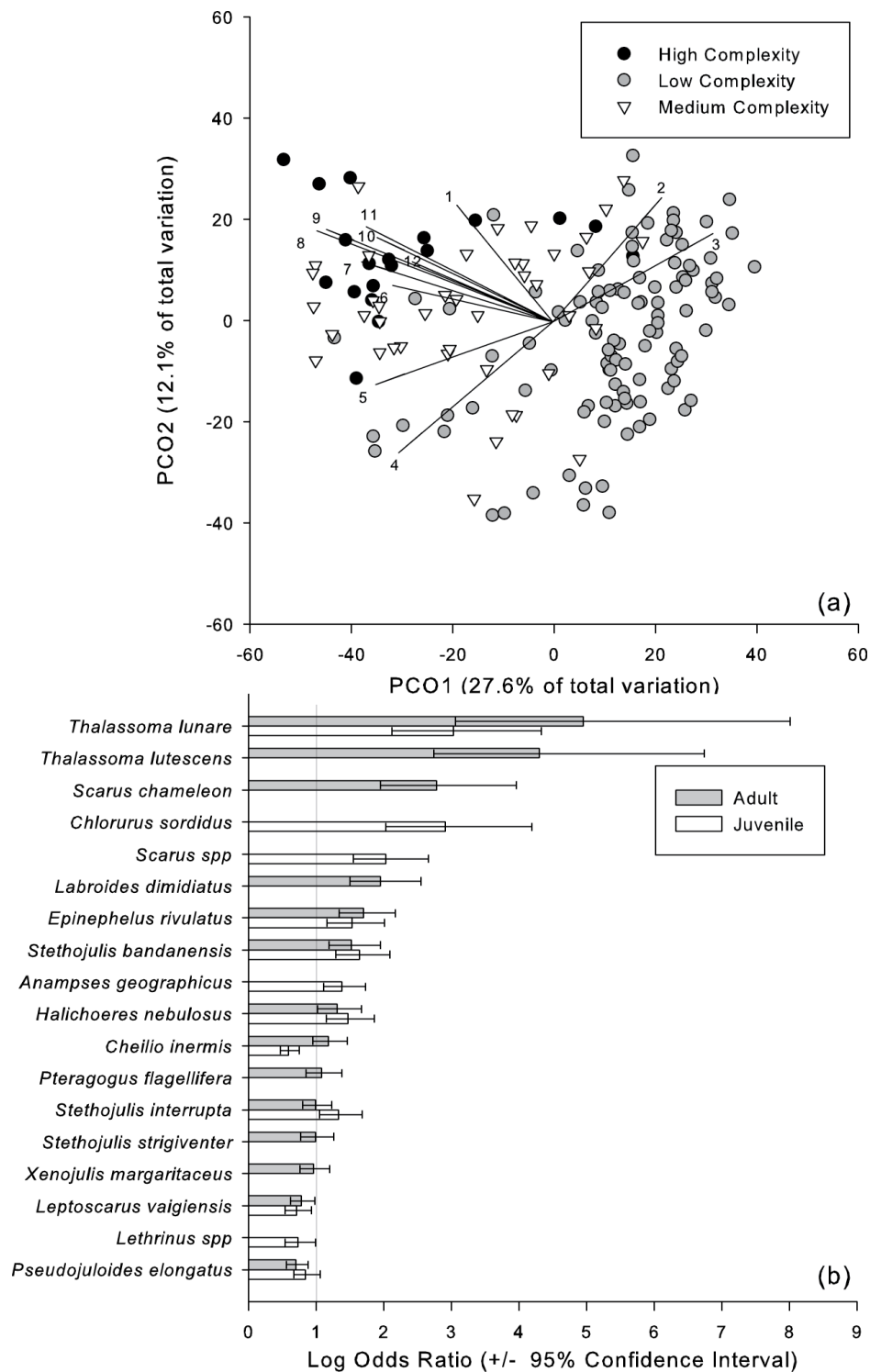


Figure S5. Assemblages of labrid fishes (f. Labridae) in macroalgal meadows with differing levels of underlying hard substratum complexity indicated via: (a) Principal Coordinates ordination of macroalgal fish community structure across transects of varying habitat complexity category (low complexity = no or < 10cm vertical relief, medium complexity = 11-60cm vertical relief, high complexity = >61 cm vertical relief), with vector overlays for species correlated (Pearson's $r > 0.5$) with the ordination structure; and (b) Odds ratios ($\pm$ 95% confidence intervals) from a logistic regression of hard complexity versus adult and juvenile fish abundance across 174 macroalgal meadow surveys, where a significant positive response (>1 , including 95% CI) indicates increased odds of finding that species in an area with higher hard complexity, while a significant negative response (<1) indicates increased odds of finding a species in an area with lower hard complexity. Species codes (panel a): 1 – Bluestreak cleaner wrasse (*Labroides dimidiatus*), 2 - Marbled

parrotfish (*Leptoscarus vaigiensis*), 3 – Long green wrasse (*Pseudojuloides elongatus*), 4 – Nebulous wrasse (*Halichoeres nebulosus*), 5 – Red shoulder wrasse (*Stethojulis bandanensis*), 6 – False leopard wrasse (*Macropharyngodon ornatus*), 7 - Pacific bullethead parrotfish (*Chlorurus spilurus*), 8 - Moon wrasse (*Thalassoma lunare*), 9 - Yellow-brown wrasse (*Thalssoma lutescens*), 10 - Chameleon parrotfish (*Scarus chameleon*), 11 – unidentified juvenile parrotfish (*Scarus* species), and 12 - Tripletail wrasse (*Cheilinus trilobatus*).

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