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 shifts in macroalgal canopy condition are 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 habitat refuges, particularly for macrophyte-associated taxa. 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 changes in macroalgal habitat condition can influence the replenishment of 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). Since 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 et al., 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 et al., 2015), comparatively little attention has been directed to how tropical macroalgal habitats may influence patterns of fish diversity, replenishment and fisheries production (Fig. 1).

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 et al., 2019; Tano et al., 2016; Fulton et al., 2019). Indeed, emerging evidence suggests these complex macroalgal meadows are occupied by diverse assemblages of tropical fishes at various life history stages (e.g., Ornellas & Coutinho, 1998; Rossier & Kulbicki, 2000; Eggertsen et al., 2019), some of which may support local fisheries (Hicks & McClanahan, 2012; Robinson et al., 2018). These 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., Ornellas & Coutinho, 1998; Aburto-Oropeza et al., 2007; 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). When referring to habitats, we mean 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 the 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.

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 et al., 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).

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 (e.g., *Leptoscarus vaigiensis, Siganus* spp.) and omnivores (*Chrysiptera* spp.) to benthic invertivores (e.g., *Coris, Choerodon, Halichoeres* and *Stethojulis* species, *Lethrinus* spp., *Pseudojuloides elongatus, Pteragogus flagellifera, Xenojulis margaritaceus*). 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., *Cheilio inermis*, *Echidna nebulosa, Epinephelus rivulatus*, *Fistularia commersonii*). 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 (*Acanthurus, Chlorurus, Scarus,* and *Siganus* species) to omnivores (*Gerres oyena*), generalist carnivores (e.g., some *Lethrinus*, *Lutjanus, Thalassoma,* and Mullidae species), and some (8% of 77 species) known to consume other fishes (e.g., *Caranx ignobilis, 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 is 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 et al., 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 et al., 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 roscacea*, 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 (Ackerman & Bellwood, 2000), the prominent method for surveying fish (Murphy & Jenkins, 2010) and are not recorded frequently enough for inclusion in analyses. For example, abundance of the wrasse, *Xenojulis margaritaceus*, 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 (Depczynski et al., 2007; Brandl et al., 2019).

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; Gillanders et al., 2003; Dahlgren et al., 2006). 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 et al., 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., *Cephalopholis boenak, Lethrinus atkinsoni* and *L. nebulosus, Lutjanus carponotatus and L. fluviflamma, Stethojulis strigiventer*; 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; Wilson et al., 2010; Sambrook et al., 2019). Importantly, these macroalgal-coral reef species play vital functional roles in tropical marine ecosystems (e.g., mesopredator *C. boenak*), and many are targeted by commercial and/or recreational fisheries (e.g., *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 et al., 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 et al., 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 et al., 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 et al., 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 *Mycteroperca roscacea* 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; Perez-Matus et al., 2016).

Seascape context could also play a key role in determining the nursery quality of macroalgal 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., Mellin et al., 2007; van Lier et al., 2018; Bradley et al., 2019). This is likely to be particularly important for ontogenetic migrations, such as the movement of key fishing target species (*Lethrinus* spp.) 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., *Siganus* species, *L. vaigiensis* and *Calotomus spinidens*; Unsworth et al., 2007; Fox & Bellwood, 2008; Hoey et al., 2013; 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 et al., 2003; Zubia et al., 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).

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 et al., 1992; McClanahan et al., 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 S4). 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 et al., 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).

Case studies of small-scale fisheries operating in back reef and lagoon areas often dominated by macroalgal habitat suggest high yields of macroalgae-associated fishes at high levels of fishing effort (McManus et al., 1992; Unsworth & Cullen, 2010). Total fish yields of 12 to 16 metric tons km^2 yr^{-1} from back reefs have been reported in the Philippines and Kenya, respectively (McManus et al., 1992; McClanahan et al., 2008). 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 et al., 2007). However, macroalgae-associated fishes that dominate yields may be at a high risk of overfishing in some localities. In Kenya, two herbivorous species (*Siganus sutor* and *Leptoscarus vaigiensis*), together making up >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 *Siganus fuscescens* and *S. spinus* 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 has 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), 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 (Robinson et al., 2017).

Tropical macroalgal habitats may appear to make a minor contribution to global fisheries production, but they 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 et al., 2013) and two commonly caught species, *Epinephelus rivulatus* and *Lethrinus nebulosus* (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 (Newton et al., 2007; Bell et al., 2013). One of the responses of coral reefs to live coral loss is a regime shift from a coral-dominated to a macroalgal-dominated state (Hughes, 1994; Graham et al., 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; Pratchett et al., 2008, 2014; MacNeil et al., 2010). 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 et al., 2018b). 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 (Wilson et al., 2014, 2018; Fulton et al., 2019). 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 et al., 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 (McClanahan et al., 1999, 2001), 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 *Leptoscarus vaigiensis* and *Cheilio inermis,* this positive relationship was strong for both adults and juveniles, 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, abundance of juvenile *Lethrinus atkinsoni* was strongly correlated with canopy cover, but this relationship was not apparent for larger conspecifics, which are typically found on nearby coral reef (Wilson et al., 2017). Conversely, the abundance of adult *Epinephelus rivulatus* positively correlated with macroalgal canopy cover, while the abundance of their juveniles did not, which suggests an increased dependence on macroalgal habitats as fish become older. There were also several species that consistently declined in abundance as macroalgal canopy cover increased (*Pomacentrus trilineatus*, *Canthigaster solandri, Plectrorhincus chaetodonoides* and *Fistularia commersonii*), implying that these macroalgal-associated fishes, which were predominantly found in macroalgal meadows rather than coral reef, may prefer macroalgal habitats with low cover.

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 is, however, 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 (Evans et al., 2014; Lim et al., 2016; Eggertsen et al., 2019) 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 *Leptoscarus vaigiensis* and *Lethrinus nebulosus*, clearly have strong positive correlations with multiple facets of macroalgal canopy structure, whilst the abundance of others (e.g. juvenile *Stethojulis strigiventer*) primarily correlate with a single canopy feature such as height (Fig. 7b). 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 (*Scarus ghobban* and *Siganus fuscescens*; Fig. S3), the most abundant macroalgal meadow herbivore in our dataset, *Leptoscarus vaigiensis*, 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. *Thalassoma lunare*; 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 *Leptoscarus vaigiensis* was not unduly related to hard substratum complexity, while a predatory serranid (*Epinephelus rivulatus*) 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; Martin et al., 2018; Bradley et al., 2019). 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 *Thalassoma lunare* and *Lethrinus nebulosus* (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 et al., 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 et al., 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., Rodewald et al., 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., 2004; Wilson et al., 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 house 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 needed to make that 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 reef, 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.

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DATA AVAILABILITY

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

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Table 1. List of 25 macroalgae-associated species targeted for food fisheries. Max TL: maximum total length. 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. Type of fishery: Comm – commercial, Rec – recreational, Subs – subsistence. MA-LH stage denotes which life history stage mostly found in macroalgal habitat (Table S3): Juv – juveniles, Both - juveniles and adults. Data on maximum size, distribution, trophic group and fisheries from Froese & Pauly (2018).

Family (Subfamily)	**Species**	**Max TL (cm)**	**Range**	**Trophic group**	**Type of fishery**	**MA-LH stage**
Lethrinidae	*Lethrinus atkinsoni*	50	WP	GC	Comm; Rec	Juv
	L. genivittatus	25	IO,WP	GC	Comm*	Both
	L. nebulosus	87	IO,WP,RS	GC	Comm; Rec	Juv
	L. semicinctus	35	IO,WP	GC	Comm*	Adult
	L. variegatus	20	IO,WP	GC	Comm*	Both
Siganidae	*Siganus fuscescens*[1]	40	WP	H	Comm	Adult
	S. spinus	28	IO,WP	H	Comm*	Both
	S. sutor	45	IO	H	Comm	Both
Labridae	*Cheilio inermis*	50	IO,WP,RS	I	Comm*	Both
	Choerodon schoenleinii	100	IO,WP	I	Comm[2]; Rec	Both
	Oxycheilinus bimaculatus	15	IO,WP	I	Subs	Adult
Serranidae (Epinephelinae)	*Cephalopholis boenak*	30	IO,WP	GC	Subs	Juv
	Epinephelus coeruleopunctatus	76	IO,WP	GC	Comm*	Adult
	Epinephelus rivulatus	45	IO,WP	GC	Comm*; Rec	Both
Labridae (Scarinae)	*Calotomus spinidens*	30	IO,WP	H	Comm	Adult
	Leptoscarus vaigiensis	35	IO,WP	H	Comm; Subs	Both
Lutjanidae	*Lutjanus carponotatus*	40	IO,WP	GC	Comm*; Rec	Juv
	L. fulviflamma	35	IO,WP,RS	GC	Comm; Rec	Juv
Carangidae	*Gnathanodon speciosus*	120	IO,WP,EP	GC	Comm*; Rec	Adult
Fistularidae	*Fistularia commersonii*	160	IO,WP,RS, EP,M	GC	Comm*	Adult
Mullidae	*Upeneus tragula*	25	IO,WP	I	Comm	Juv

Muraenidae	*Echidna nebulosa*	100	IO,WP,RS, EP,AO	GC	Comm*	Adult
Nemipteridae	*Scolopsis ghanam*	30	IO	GC	Subs	Both
Pomacentridae	*Abudefduf vaigiensis*	20	IO,WP,RS	O	Subs	Juv
Tetraodontidae	*Arothron hispidus*	50	IO,WP,EP	O	Comm*[3]	Both

[1] May be synonymous with *Siganus canaliculatus* (Hsu et al., 2011); *Minor commercial status; [2] Near threatened globally (Fairclough & Nakazono, 2004); [3] Poisonous but traded in some countries.

FIGURE LEGENDS

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.

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).

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).

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).

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).

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).

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.