

Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes

Short running title: Tropical macroalgal fish and fisheries

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2 **ABSTRACT**

Canopy-forming macroalgae can construct extensive meadow habitats in tropical seascapes
4 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,
6 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
8 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
10 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
12 macroalgal and seagrass or coral reef habitats suggest macroalgal meadows may provide
habitat refuges, particularly for macrophyte-associated taxa. Moreover, the prominence of
14 juvenile fishes suggests macroalgal meadows facilitate the triphasic life cycle of many fishes
occupying diverse tropical seascapes. Correlations between macroalgal canopy structure and
16 juvenile abundance suggest changes in macroalgal habitat condition can influence the
replenishment of tropical fish populations, including the majority of macroalgal-associated
18 fishes that are targeted by commercial, subsistence, or recreational fisheries. While many
macroalgal-associated fishery species are of minor commercial value, their local importance
20 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,
22 there is a high likelihood that climate change will impact macroalgal-associated fish and
fisheries.

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

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ACKNOWLEDGEMENTS

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1. INTRODUCTION

26 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
28 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
30 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
32 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
34 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
36 (Brown et al., 2018; Olds et al. 2018; Sambrook et al., 2019).

38 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
40 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),
42 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
44 (Bertocci et al., 2015), comparatively little attention has been directed to how tropical
macroalgal habitats may influence patterns of fish diversity, replenishment and fisheries
46 production (Fig. 1).

48 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.
50 Typically, these meadows are dominated by canopy-forming macroalgae (e.g., *Sargassum*,
Sargassopsis, *Sirophysalis*, *Turbinaria*) with various understory genera (e.g., *Lobophora*,
52 *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.,
54 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
56 & 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
58 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
60 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;
62 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
64 and replenishment.

66 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
68 coral and seagrass habitats (Section 2), (ii) macroalgal habitats provide fish nurseries in
tropical seascapes (Section 3), and (iii) macroalgal-associated species support tropical
70 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

72 (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
74 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
76 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
78 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
80 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.

82

2. TROPICAL MACROALGAL FISHES: A DISTINCT ASSEMBLAGE?

84 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
86 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
88 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
90 assemblages in macroalgal meadows co-occurring alongside patches of coral reef and
seagrass provide a different seascape perspective. Drawing on results from 14 independent
92 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
94 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
96 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
98 are unique to macroalgal meadows, and that seagrass and macroalgae are not
interchangeable habitats for the ecological connectivity of many macrophyte-associated
100 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
102 (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
104 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
106 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
108 particular habitat type (e.g., mass-bleaching of corals).

110 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
112 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
114 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
116 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-
118 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
120 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*
122 spp.) and omnivores (*Chrysiptera* spp.) to benthic invertivores (e.g., *Coris*, *Choerodon*,
Halichoeres and *Stethojulis* species, *Lethrinus* spp., *Pseudojuloides elongatus*, *Pteragogus*
124 *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
126 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
128 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,
130 where these fishes could be exploiting a range of trophic resources, given they span
herbivores (*Acanthurus*, *Chlorurus*, *Scarus*, and *Siganus* species) to omnivores (*Gerres*
132 *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*,
134 *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
136 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
138 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
140 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
142 macroalgal and other habitat types by species operating across several trophic levels

suggests these fishes are functioning as mobile links that consume productivity within
144 macroalgal meadows and then disperse this across tropical seascapes during foraging and/or
ontogenetic migrations (Berkström et al., 2013). Accordingly, macroalgal meadows should
146 be considered one of several key habitats within a diverse and productive seascape that is
needed to sustain healthy tropical fish populations and communities.

148

An important limitation of our analyses is that by only considering species with data across
150 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
152 leopard grouper, *Mycteroperca rosacea*, is reliably predicted by *Sargassum* cover (Aburto-
Oropeza et al., 2007), but this species only occurs in the Eastern Central Pacific and there
154 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
156 visual census (Ackerman & Bellwood, 2000), the prominent method for surveying fish
(Murphy & Jenkins, 2010) and are not recorded frequently enough for inclusion in analyses.
158 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
160 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-
162 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-
164 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
166 of nutrients and energy (Depczynski et al., 2007; Brandl et al., 2019).

168 3. TROPICAL MACROALGAL MEADOWS AS FISH NURSERIES

170 While the presence of a high number of juveniles seems an obvious requirement for a
172 nursery habitat, this abundance of juveniles is irrelevant to future adult breeding
174 populations unless they grow and survive to reproductive age (i.e., recruitment success). As
176 such, the identification of a fish nursery habitat requires various lines of evidence, including
178 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.

184 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
186 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
188 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

190 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*
192 *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
194 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
196 tropical marine ecosystems (e.g., mesopredator *C. boenak*), and many are targeted by
commercial and/or recreational fisheries (e.g., *Lethrinus* and *Lutjanus* species).

198

Juvenile survivorship rates are a key quantum for identifying a fish nursery habitat, with
200 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.,
202 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
204 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
206 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
208 abundance in macroalgal meadows (Holmes et al., 2012). Indeed, several species we
identified as generalists/transients (Section 2) are piscivores that could periodically increase
210 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
212 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

214 requires investigation of relative rates of predator mortality imposed on juveniles occupying
a range of subtidal habitats within tropical seascapes.

216

218 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
220 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
222 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
224 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
226 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.,
228 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
230 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
232 recruitment success of the Pacific Ocean leopard grouper *Mycteroperca rosacea* in the
eastern Pacific (Aburto-Oropeza et al., 2007). Changes in canopy complexity could also
234 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
236 success was either affected greatly by differences in canopy structural complexity, or not at
all (e.g., Horinouchi, 2007; Perez-Matus et al., 2016).

238

Seascape context could also play a key role in determining the nursery quality of macroalgal
240 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
242 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
244 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
246 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
248 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
250 connected macroalgal patches should be a priority to ensure protection of key sources of
fish population replenishment.

252

Published and emerging evidence lends support to two criteria for tropical macroalgal
254 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
256 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-
258 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
260 macroalgal habitat availability and future fish population sizes, only evidence of patterns of
occupation and proportional abundance. Nonetheless, for species whose juveniles are

262 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
264 (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
266 targets for testing whether macroalgal habitats facilitate increased fish growth, survivorship
and recruitment success (*sensu* Beck et al., 2001; Dahlgren et al., 2006).

268

4. MACROALGAE-ASSOCIATED TROPICAL FISHERIES

270 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
272 production may enhance fishable biomass through direct consumption by browsing
herbivores (e.g., *Siganus* species, *L. vaigiensis* and *Calotomus spinidens*; Unsworth et al.,
274 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)
276 among targeted reef fishes, enabling them to withstand high fishing pressure (Hicks &
McClanahan, 2012; Morais & Bellwood, 2018). Secondly, macroalgae-derived detrital
278 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
280 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
282 (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
284 carnivorous fishes, thereby facilitating multiple routes for higher-order production involving

resident and transient carnivorous fishes, in addition to predation on herbivorous fishes
286 (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
288 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
290 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
292 have direct implications for recruitment and future fishery yields (Lim et al., 2016; Wilson et
al., 2017).

294

Over half of the 44 fish species most strongly associated with tropical macroalgal meadows
296 (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
298 Scarinae), as well as larger-bodied (>30 cm maximum length) generalist carnivores
(Lethrinidae, Serranidae) and invertivores (Labridae). While many of these species are of
300 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.
302 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
304 (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;
306 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
308 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 km² 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
334 (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*
336 *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
338 & 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
340 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
342 high (Jumawan-Nanual & Metillo, 2008; Soliman & Yamaoka, 2010). Since these macroalgae-
associated rabbitfish can form large transient spawning aggregations targeted by fishers
344 (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
346 fecundity, along with variable catchability are thought to limit the vulnerability of this fishery
to overexploitation (Robinson et al., 2017).

348

Tropical macroalgal habitats may appear to make a minor contribution to global fisheries
350 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
352 wealthy countries, the indirect contribution of macroalgal habitats to recreational fisheries
and local economies may be substantial. For example, at Ningaloo in Western Australia,
354 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
356 macroalgal habitats (Table 1). The potential for tropical macroalgal habitat to be fish

nurseries, trophic facilitators, and corridors for fish movement between habitats suggest
358 they warrant the same recognition as mangroves, seagrass beds and coral reefs in
ecosystem-based fisheries management. Spatial management and monitoring of tropical
360 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
362 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
364 how these habitat traits respond to climatic cycles and disturbance events (Aburto-Oropeza
et al., 2007; Wilson et al., 2017, 2018).

366

Apart from overexploitation, the other major threat to the sustainability of tropical fisheries
368 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
370 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
372 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
374 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
376 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
378 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,
380 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
382 fishing trip has become less certain (Robinson et al., 2018).

384 **5. VULNERABILITY OF MACROALGAL FISHES TO HABITAT LOSS**

Macroalgal meadows are sensitive to environmental fluctuations and local disturbances
386 (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
388 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
390 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
392 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
394 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
396 composition and ecosystem function (Diaz-Pulido et al., 2007). Over finer spatial scales,
experimental manipulation of nutrient concentrations (Schaffelke & Klumpp, 1998) and
398 sediment loads (Umar et al., 1998) demonstrate that environmental conditions can have a
direct effect on macroalgae canopy phenology. Nutrient pulses and increased sediment
400 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
402 cover and structure within macroalgal habitats.

404 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
406 species most severely affected by disturbances will be those that feed or shelter exclusively
within macroalgal habitats (Vázquez & Simberloff, 2002). Such macroalgal specialists might
408 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
410 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
412 (herbivorous) and indirect (carnivorous) food sources (Fulton et al. 2019). However, studies
that have explicitly assessed the influence of disturbances on tropical macroalgal meadows
414 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
416 undergone regime shifts from coral to macroalgal-dominated states (Graham et al., 2015).

418 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
420 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-
422 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
424 relationships between the abundance of macroalgal-associated fishes and percent
macroalgal cover (Fig. 6). Some species had a significant positive relationship with
426 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

428 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
430 general relationship differed in direction or significance among life history stages, suggesting
ontogenetic shifts in macroalgal habitat dependence. For example, abundance of juvenile
432 *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.,
434 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
436 increased dependence on macroalgal habitats as fish become older. There were also several
species that consistently declined in abundance as macroalgal canopy cover increased
438 (*Pomacentrus trilineatus*, *Canthigaster solandri*, *Plectrorhincus chaetodonoides* and *Fistularia*
commersonii), implying that these macroalgal-associated fishes, which were predominantly
440 found in macroalgal meadows rather than coral reef, may prefer macroalgal habitats with
low cover.

442

Our meta-analysis suggests that the extent of macroalgal dependence in tropical fishes
444 varies both interspecifically and ontogenically when considering only percent cover of
canopy-forming macroalgae. The within-meadow canopy structure of macroalgal meadows
446 is, however, a conglomerate of multiple factors and fishes may associate with specific
architectural components of the three-dimensional macroalgal canopy habitat. Previous
448 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-
450 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

452 compared annual patterns of fish abundance with canopy cover, height, and density to
identify which macroalgal structural elements consistently predict fish abundance (Fig. 7).
454 Some species, like *Leptoscarus vaigiensis* and *Lethrinus nebulosus*, clearly have strong
positive correlations with multiple facets of macroalgal canopy structure, whilst the
456 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
458 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 &
460 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
462 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
464 consequences for the replenishment of adult populations. However, experimental
manipulations of habitat structure and reciprocal removal of competitive fishes are required
466 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
468 aspects of canopy condition while keeping others constant (e.g., reducing height while
maintaining cover) in order to tease apart specific habitat effects.

470

Different levels of dependence upon particular canopy structural features may allow
472 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-
474 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

476 increasing canopy density in experimental patches of macroalgal habitat (Hoey & Bellwood,
2011), we found the overall abundance of macroalgae-associated herbivorous and
478 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
480 while we found some evidence for negative correlations between canopy density and the
abundance of two common macroalgal-associated herbivorous fishes (*Scarus ghobban* and
482 *Siganus fuscescens*; Fig. S3), the most abundant macroalgal meadow herbivore in our
dataset, *Leptoscarus vaigiensis*, responded positively to increases in canopy cover, height
484 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
486 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,
488 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
490 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
492 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
494 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
496 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
498 measures of canopy height and density (alongside percent cover) to resolve which aspects
best predict fish community structure and function in tropical macroalgal meadows.

500

502 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
504 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
506 susceptible to disturbances that affect specific macroalgae. Moreover, habitat features other
than the composition and soft habitat structure afforded by the macroalgae could influence
508 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
510 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
512 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
514 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
516 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
518 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
520 exclusively found in macroalgal habitats, however, displayed a mixed relationship with hard
substratum complexity (Fig. S5). For instance, abundance of the herbivorous browser
522 *Leptoscarus vaigiensis* was not unduly related to hard substratum complexity, while a
predatory serranid (*Epinephelus rivulatus*) tended to occupy meadows with greater hard

524 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
526 structures influence macroalgal fish communities across a greater range of tropical settings.

528 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.,
530 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
532 seascapes. Functional linkages among habitat patches support the persistence of marine
populations and communities and are pivotal for enabling ecosystems to persist and recover
534 from disturbances (Cumming, 2011; Olds et al., 2018). Consequently, disturbances that
disrupt connectivity among habitats are expected to have the greatest effect on those
536 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
538 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
540 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
542 and other habitat types within diverse tropical seascapes. Clearly, more seascape studies
that incorporate macroalgal habitats are required to improve our understanding of the
544 consequences of habitat destruction and fragmentation within tropical seascapes.

546 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

548 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.,
550 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.,
552 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
554 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
556 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
558 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
560 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
562 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
564 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
566 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
568 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.,
570 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
572 specialist fishes.

574 **6. CONCLUSIONS**

Macroalgal habitats can be a substantial component of tropical seascapes around the world.
576 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
578 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
580 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
582 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
584 considerable overlap between fish assemblages within macroalgal habitats and two other
common subtidal habitats - seagrass and coral reefs - which suggests macroalgal meadows
586 could also be important foraging habitats and/or stepping stones in the triphasic life cycles
of fishes in diverse tropical seascapes.

588

Juvenile fishes appear to be prominent in macroalgal habitats across the tropics, where the
590 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
592 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.,

594 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
596 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
598 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
600 fisheries.

602 Compared to other prominent tropical habitats like coral reef, macroalgal meadows are
spatially and seasonally dynamic in structure, which has major consequences for the
604 abundance and distribution of many macroalgal-associated fishes. Environmental conditions
such as sea temperature are important drivers of this dynamism, which suggests climate
606 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
608 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,
610 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
612 other tropical habitats. This will require long-term monitoring of fish abundance across
tropical seascapes, and assessments of how seasonal changes to macroalgal-canopy
614 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
616 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

618 becoming increasingly important as the extent of macroalgal habitat may change according
to climate-related coral mortality and regime shifts.

620

ACKNOWLEDGEMENTS

622 We thank participants to our special session on tropical macroalgal fishes at the 2017
Australian Society for Fish Biology and 10th Indo-Pacific Fish Conference for helpful
624 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
626 of Biodiversity, Conservation & Attractions, Australian Institute of Marine Science, the
Environment Conservation Fund of the Government of Hong Kong SAR (ECF15/2015 to PLYL
628 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
630 (UF140691 fellowship to NAJG), and the Swedish Research Council (2015-01257, E0344801).
We thank Sofia Wikström and three anonymous peer reviewers for constructive comments
632 on earlier drafts.

DATA AVAILABILITY

634 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:

950 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,
 952 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
 954 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	<i>Lethrinus atkinsoni</i>	50	WP	GC	Comm; Rec	Juv
	<i>L. genivittatus</i>	25	IO,WP	GC	Comm*	Both
	<i>L. nebulosus</i>	87	IO,WP,RS	GC	Comm; Rec	Juv
	<i>L. semicinctus</i>	35	IO,WP	GC	Comm*	Adult
	<i>L. variegatus</i>	20	IO,WP	GC	Comm*	Both
Siganidae	<i>Siganus fuscescens</i> ¹	40	WP	H	Comm	Adult
	<i>S. spinus</i>	28	IO,WP	H	Comm*	Both
	<i>S. sutor</i>	45	IO	H	Comm	Both
Labridae	<i>Cheilio inermis</i>	50	IO,WP,RS	I	Comm*	Both
	<i>Choerodon schoenleinii</i>	100	IO,WP	I	Comm ² ; Rec	Both
	<i>Oxycheilinus bimaculatus</i>	15	IO,WP	I	Subs	Adult
Serranidae (Epinephelinae)	<i>Cephalopholis boenak</i>	30	IO,WP	GC	Subs	Juv
	<i>Epinephelus</i> <i>coeruleopunctatus</i>	76	IO,WP	GC	Comm*	Adult
	<i>Epinephelus rivulatus</i>	45	IO,WP	GC	Comm*; Rec	Both
Labridae (Scarinae)	<i>Calotomus spinidens</i>	30	IO,WP	H	Comm	Adult
	<i>Leptoscarus vaigiensis</i>	35	IO,WP	H	Comm; Subs	Both
Lutjanidae	<i>Lutjanus carponotatus</i>	40	IO,WP	GC	Comm*; Rec	Juv
	<i>L. fulviflamma</i>	35	IO,WP,RS	GC	Comm; Rec	Juv
Carangidae	<i>Gnathanodon speciosus</i>	120	IO,WP,EP	GC	Comm*; Rec	Adult
Fistularidae	<i>Fistularia commersonii</i>	160	IO,WP,RS, EP,M	GC	Comm*	Adult
Mullidae	<i>Upeneus tragula</i>	25	IO,WP	I	Comm	Juv

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

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

960 **FIGURE LEGENDS**

Figure 1. Cumulative number of published studies on fish community structure within
962 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
964 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
966 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
968 different aspects of our data syntheses and meta-analysis of macroalgal-associated tropical
fishes (see Table S1 in Supporting Information).

970 **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
972 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,
974 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
976 (underlying data in Table S2).

Figure 4. Proportional abundance of juveniles and adults for 350 fish species within
978 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
980 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
982 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
984 (i.e., fall on the boundary lines of the quadrants).

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

988 **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
990 scores indicate species with positive (increased abundance) or negative (decreased
abundance) relationships with macroalgal cover (replication per species and life history
992 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
994 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
996 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
998 correlation indicate species with positive (increased abundance) or negative (decreased
abundance) relationships with macroalgal canopy structure. Hatching denote scores with
1000 95% confidence limits that fail to intersect zero, which indicates a consistent response
among years.

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