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ORIGINAL ARTICLE

The contribution of macroalgae-associated fishes to small-scale tropical reef fisheries

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Abstract

Macroalgae-dominated reefs are a prominent habitat in tropical seascapes that support a diversity of fishes, including fishery target species. To what extent, then, do macroalgal habitats contribute to small-scale tropical reef fisheries? To address this question we: (1) Quantified the macroalgae-associated fish component in catches from 133 small-scale fisheries, (2) Compared life-history traits relevant to fishing (e.g. growth, longevity) in macroalgal and coral-associated fishes, (3) Examined how macroalgae-associated species can influence catch diversity, trophic level and vulnerability and (4) Explored how tropical fisheries change with the expansion of macroalgal habitats using a case study of fishery-independent data for Seychelles. Fish that utilised macroalgal habitats comprise 24% of the catch, but very few fished species relied entirely on macroalgal or coral habitats post-settlement. Macroalgal and coral-associated fishes had similar life-history traits, although vulnerability to fishing declined with increasing contribution of macroalgae association to the catch, whilst mean trophic level and diversity peaked when macroalgal-associated fish accounted for 20%–30% of catches. The Seychelles case study revealed similar total fish biomass on macroalgal and coral reefs, although the biomass of primary target species increased as macroalgae cover expanded. Our findings reinforce that multiple habitat types are needed to support tropical fishery stability and sustainability. Whilst coral habitats have been the focus of tropical fisheries management, we show the potential for macroalgae-associated fish to support catch size and diversity in ways that reduce vulnerability to overfishing. This is pertinent to seascapes where repeated disturbances are facilitating the replacement of coral reef with macroalgal habitats.

KEYWORDS
catch composition, coral reefs, ecosystem-based management, Regime shifts, *Sargassum*, seaweed habitats

1 | INTRODUCTION

Tropical seascapes typically comprise patch mosaics of multiple habitat types that collectively support diverse and productive marine ecosystems. The contribution of coral reefs (Moberg & Folke, 1999), seagrass meadows (Cullen-Unsworth & Unsworth, 2013; Mtwana Nordlund et al., 2016) and mangrove forests (Ewel et al., 1998) to ecosystem goods and services is well documented. Another ubiquitous component of shallow tropical marine ecosystems are macroalgae (Bruno et al., 2014), with canopy-forming genera (e.g. *Sargassum*) tending to aggregate in meadows with high rates of net primary productivity and standing biomass that provide both food and complex habitat for diverse fish and invertebrate assemblages (Fulton et al., 2019; Gouvêa et al., 2020). Whilst macroalgal meadows occur naturally in many locations, on some tropical reefs macroalgae has replaced corals after stressors and disturbances have caused extensive coral mortality (Graham et al., 2015; Hughes, 1994). Increased intensity and frequency of marine heatwaves are likely to place further stress on coral reefs (Hughes et al., 2018), leading to fundamental

changes to how patches of coral and macroalgal-dominated habitats are arranged and connected within tropical seascapes. Shifts in habitat composition and spatial arrangement, and the consequences of reconfiguring seascapes for key ecosystem services from tropical reefs, such as small-scale fisheries, requires urgent attention (Cinner et al., 2012; Pratchett et al., 2014; Woodhead et al., 2019). The contribution of macroalgal habitats to ecosystem services is especially relevant given it is a common, yet understudied component of the tropical seascape (Fulton et al., 2020).

Tropical reef fisheries make substantial contributions to local economies (Grafeld et al., 2017) and are a key source of nutrients for coastal communities (Hicks et al., 2019), supporting millions of people globally (Teh et al., 2013). Small-scale tropical fisheries utilise different gear types to catch a diverse range of fish species for recreational, subsistence, artisanal or commercial purposes (Humphries et al., 2019). Many small-scale tropical fisheries already experience levels of fishing that are unsustainable (Newton et al., 2007) and recovery of the most overfished assemblages will take decades to reach even half their expected pristine biomass (MacNeil et al., 2015). Problems associated with overfishing may be exacerbated by increasing seawater temperature that is expected to change fish species distributions, metabolism, activity, growth rates and body size (Cheung et al., 2009; Huss et al., 2019; Johansen et al., 2014; Jutfelt, 2020; Pauly & Cheung, 2018). Ecosystem shifts in benthic habitats from climate-related disturbances have also altered species communities on reefs (Pratchett et al., 2008), catch composition (Cheung et al., 2013; Robinson, Wilson, Robinson, et al., 2019) and productivity (Rogers et al., 2014). Information on catch composition may be especially relevant for assessing and adapting management actions for small-scale tropical fisheries (Hicks & McClanahan, 2012; Mbaru & McClanahan, 2013). However, a lack of species-specific catch composition data has limited our long-term prognosis of how these fisheries may change.

Catch composition of tropical reef fisheries is likely to be reliant on the habitats within local seascapes, with the stand-alone contribution of coral reefs, seagrass and mangroves to fisheries productivity already well recognised (Manson et al., 2005; Pratchett et al., 2011; Unsworth et al., 2019). Fleshy macroalgae are also common on tropical reefs, surveys of more than 1800 sites finding around 20% of reefs have an average benthic macroalgal cover of 25% or greater (Bruno et al., 2009). Moreover, at some locations macroalgal reefs are extensive and represent a major part of the shallow water seascape (e.g. Ningaloo Reef in Western Australia; Kobryn et al., 2013). On some reefs (e.g. Seychelles), macroalgae cover has also expanded into space vacated by corals following heat-induced mortality (Graham et al., 2015), suggesting this habitat may become more common within tropical seascapes in the future. In other settings, macroalgae represents a smaller component of an interconnected mosaic of habitats (Sievers et al., 2020; Tano et al., 2017). These macroalgal reefs are productive habitat for fish to forage and/or shelter at various life-history stages, with species dependence often shifting with ontogeny (Eggertsen et al., 2019; Fulton et al., 2020; Sambrook et al., 2019). More than 200 species of fish are predominantly found in macroalgal habitats relative to nearby coral reefs, either as adults or juveniles, whilst many more species periodically shelter and forage upon resources within macroalgal habitats (Fulton et al., 2020). The prominence of macroalgae-associated species in some catches suggests that macroalgal habitats can have a key role in supporting tropical fisheries (Fulton et al., 2020). Moreover, fisheries reliance on this habitat type may increase if macroalgae become more prominent following mass coral mortality (Robinson, Wilson, Robinson, et al., 2019).

As the composition and diversity of fish assemblages on macroalgal and coral-dominated reefs differ (Fulton et al., 2019, 2020; Robinson, Wilson, Jennings, et al., 2019), shifts in habitat or fishing locations are expected to alter catch composition. Accordingly, assessments of catch diversity, vulnerability and mean tropic level can provide an indicator of fishery stability, sustainability and impacts to ecosystem health associated with increased fisher reliance on macroalgal habitats. For example, over-reliance of a fishery on a single habitat can reduce catch diversity, leaving the fishery susceptible to inherent fluctuations in stocks of a few species (Robinson et al., 2020). Similarly, targeting species with life-history traits that make them susceptible to overfishing will undermine the sustainability of the fishery. An understanding of catch contributions from macroalgae-associated fishes, and how this relates to key fishery indicators, is needed to appreciate how shifts towards macroalgal-dominated reefs may influence the sustainability and stability of fishery harvests. This information can be supplemented with diver surveys of target species abundance, which provide fisheries-independent assessments of the contribution of macroalgal habitats to tropical reef fisheries. This may be especially useful at locations like the Seychelles, where the composition of fish assemblages has changed following extensive coral bleaching and regime shifts to macroalgal-dominance on some reefs (Graham et al., 2015, 2020).

Here we quantify the contribution of macroalgal habitats to small-scale tropical reef fisheries and examine how increased fishery reliance on macroalgae-associated species may affect stability and sustainability of the catch. To do this we utilised catch data in 133 small-scale fisheries from 49 studies spanning 28 countries (see Table S1 for details), in combination with fish habitat-use information from a recent global appraisal of tropical coral and macroalgal reefs (Fulton et al., 2020). These analyses recognise that many species undertake ontogenetic migrations and consider habitat associations at both adult and juvenile stages by focusing on the proportional occupation of habitat types throughout fish life histories. To explore vulnerability to overfishing, fishery stability and sustainability, we utilised two sets of data: (1) the life-history traits relevant to potential overfishing (growth, maturity, longevity, maximum size) in a suite of genera that contain both macroalgae and coral-associated species; and (2) overall catch diversity, mean trophic level and vulnerability to fishing as indicators of fishery stability and sustainability with increasing occurrence of macroalgae association. Finally, we used a case study in the Seychelles to examine temporal trends in fish assemblages where there has been either a gradual increase in macroalgal or live coral over a period of nine years (Graham et al.,

2015), a time-series, which allowed us to assess how fishery resources change with coral and macroalgal habitat availability.

2 | METHODS

2.1 | Contribution of macroalgae-associated fishes to catches

The contribution of macroalgal habitat to small-scale tropical reef fisheries was estimated by combining species-level reef fisheries catch data from the literature, with previously reported global estimates of the proportional abundance of fish species in macroalgal habitats (Fulton et al., 2020).

Catch data was sourced from the literature using Google Scholar and the search words 'tropical', 'reef', 'fishery', 'species' and 'catch' as dependent terms. The results were sorted by relevance to search words and the best matches were examined for species-specific fisheries catch data from tropical reefs. Combined, more than 500 studies were canvased for relevant data. We also asked authors that had provided information on fish habitat associations in Fulton et al. (2020) if they were aware of any relevant catch data from their study area. Only studies that provided quantitative species-level catch information were included in analyses. We found suitable data for 133 fisheries from 49 studies that spanned 28 countries and 91 locations (Figure 1, Table S1). This included catch information collected between 1986 and 2019, but excluded catch data collected from open (oceanic) water. Moreover, any deep water or pelagic species, and all sharks and rays were excluded from calculations. For each study, information on the fishing gear (trap, spear, net, line, mixed) and type of fishery (recreational, subsistence, commercial, artisanal or experimental) was recorded. The experimental fishery type referred to catch data that was collected for research purposes.

Fish associations with macroalgal and coral habitats were based on published survey data for 627 fish species from 23 locations across 11 countries (documented in Table S2, extracted from Fulton et al., 2020). At each location, underwater visual surveys by divers or video (unbaited) estimated the abundance of adult and juvenile fish on both macroalgal and coral reefs at three or more sites. Proportional abundance within each habitat was then calculated for adults and juveniles of each species. These data indicate that approximately a third of fishes (218 species) were predominantly found on macroalgal habitats (compared to nearby coral reef) during their juvenile and/or adult life-history stage, whilst many more were occasionally recorded on macroalgal reefs (Fulton et al., 2020). Here we refer to any fish that was observed on macroalgal reefs, during either life-history stage, as macroalgae-associated. This definition allows a comprehensive assessment of macroalgal habitat use by fish and the contribution of this habitat to fisheries. Our analyses include catch data from 8 of the 11 countries where fish habitat associations were assessed. However, we acknowledge that habitat associations were not available for all locations where catch data was recorded and the extent to which a species relies on macroalgal habitat may vary across their range (Bradley et al., 2020).

To calculate the extent to which each species within the catch associated with macroalgae (pS_i) we multiplied the contribution of species *i* to the catch (C_i) by the proportional abundance of that species occurring in macroalgal habitat (pM_i), which was based on habitat associations of adults, juveniles (Table S2) or an average of these two life-history stages:

$$pS_i = C_i \times pM_i$$

The proportion of the overall catch associated with macroalgal reefs for all fishes (pC_m) was then calculated as the sum of all species-level estimates of macroalgae association (pSi), divided by the total recorded catch (C_T):

$$pC_m = \sum_{i=1}^{n} pS_i \div C_T$$

In calculating species-level macroalgal contributions (pS_i), we used an average of the proportional abundance of that species in macroalgae habitat (pM_i) across the adult and juvenile life-history stages. To gauge the relative importance of macroalgal habitat during each life-history stage we carried out the same analysis using only adult or juvenile habitat association data. Where habitat data were not available for a given fish species the average value across all species in the relevant genus was used for the pM_i term above.

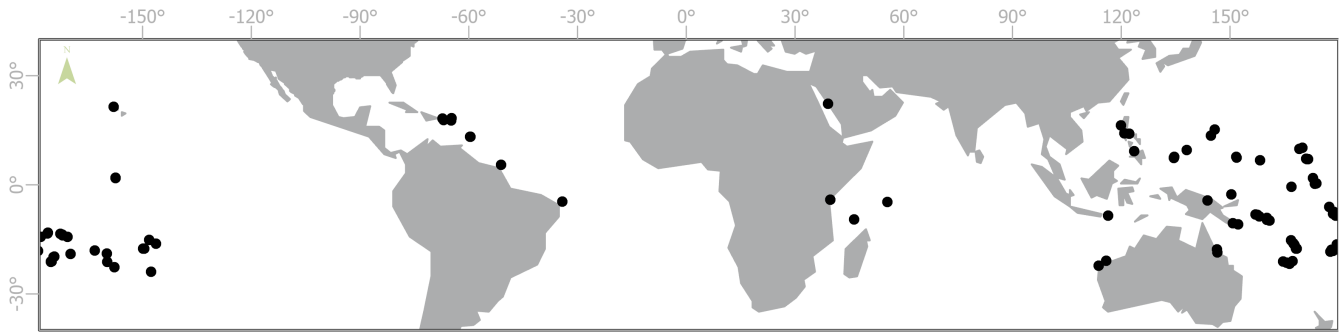

FIGURE 1 Locations with species-specific catch data used to calculate the contribution of macroalgae-associated fishes to small-scale reef fisheries

Where catch data was recorded as both count and weight of each species, only weight was used. The preference for weight data is unlikely to have influenced how much of the catch was associated with macroalgae, as a comparison of pC_m estimates based on both weight and count data from the same studies found that this did not unduly influence results (Paired T-test: $t = 0.60$, $df = 10$, $p = .56$). The influence of fishing gears and the type of fishery on estimates of the proportion of macroalgae-associated catch (pC_m) were assessed using generalised linear mixed models, where gear type (trap, spear, net, line, mixed) and fishery type (recreational/subsistence, commercial, artisanal, experimental) were fixed factors, and both country and location were random factors. Recreational and subsistence estimates were pooled to ensure there was adequate replication within a group that typically fish for personal consumption. Models were fitted using the beta family, with a log link function via the glmmTMB (Brooks et al., 2017) and INLA (Rue et al., 2009) packages in R. All INLA models were fit using the uninformative default INLA priors, which uses the Integrated Nested Laplace Approximation. The maximum likelihood estimates obtained through the glmmTMB fits provide a robust and well established method for assessing relative model support using AICc weights (Burnham & Anderson, 2002). Whilst we had no prior information to include in our Bayesian analysis the model fits obtained through INLA provides a robust means of quantifying parameter uncertainty and associated 95% confidence limits, which is non-trivial for generalised mixed models using frequentist approaches. In addition, the Bayesian approach allows the relative strength of each factor and the associated uncertainty to be examined using Bayesian posterior probability densities, which were obtained using the inla.posterior.sample function (Rue et al., 2009).

To assess the contribution of fish species to the catch that are more reliant on either macroalgal or coral habitats we repeated calculations only considering species with >50% abundance in either habitat type. These calculations were based on an average of juvenile and adult habitat associations across all catch data (Table S1). We also considered species with proportional occupation estimates of >75%, >90%, >95% and 100% in each habitat type to explore how species of increasing macroalgal or coral habitat dependence contributed to catches.

2.2 | Life-history traits

Sustainability of tropical reef fisheries relates to the life-history traits of captured species. Populations of faster-growing, small-bodied fish that mature rapidly and have short life spans are generally less vulnerable to overfishing than their larger, slow-growing counterparts (Abesamis et al., 2014). Growth rates, longevity, maturity and maximum size estimates can all be derived from size at age growth analyses and combined with ecological characteristics such as geographical range and spatial behaviour to provide an overall indicator of species vulnerability to fishing (Cheung et al., 2005). Species from higher trophic levels are also often targeted by fishers (Pauly et al., 1998), although this may not always be the case in tropical fisheries (Graham et al., 2017; Russ & Alcala, 1998). We examined the traits and ecology of species with varying levels of association to macroalgal-dominated reefs to assess the sustainability of fisheries reliant on species that strongly associate with this habitat.

Life-history traits (growth coefficient (k), asymptotic length (L infinity) and an index of vulnerability to fishing (Cheung et al., 2005)) for each species identified in the catch data were extracted from FishBase (Froese & Pauly, 2020) using the rfishbase package (Boettiger et al., 2012). As few fish exclusively associate with one habitat, our analysis assessed the strength of the relationship between a species trait value and the extent to which that species associates with macroalgae. The correlation between these variables indicated if species with strong macroalgae associations were characterised by the presence (positive correlation) or absence (negative correlation) of that trait. To minimise confounding life-history trends with taxonomic differences, we constrained these analyses to four relatively diverse genera, each of which contained species with strong and weak association to macroalgal habitats (*Epinephelus*, *Lethrinus*, *Parupeneus and Siganus*).

To further assess fishery stability, ecosystem impacts and sustainability with increasing reliance on macroalgal habitat we calculated the Simpson's index, mean trophic level and vulnerability to fishing for catch data, and regressed these values against the proportion of catch associated with macroalgae for that fishery (Table S1). Both mean trophic level and vulnerability to fishing were calculated as abundance-weighted catch averages, based on the relative abundance of each fish species in the catch (Graham et al., 2017). Trophic level and vulnerability to fishing were both extracted for each species using the rfishbase package (Boettiger et al., 2012). To allow for potential non-linear relationships we used generalised additive models, with a smoother fitted to the average (between juvenile and adult) proportions of the fishery associated with macroalgae (pC_m). As Simpson's index, mean trophic level and vulnerability all take positive values on a continuous scale, models were fitted using a Gamma distribution with a log link function via maximum likelihood using the packages gamm4 (Wood & Scheipl, 2014) and Bayesian MCMC methods via brms (Bürkner, 2017), with country and location included as intercept level random effects. This combined approach allows extraction of the AICc through maximum likelihood, with the Bayesian posterior sample providing a robust quantification of model uncertainty. The brms models were fit using the default priors, with 20,000 iterations and four chains, with model fits assessed using divergent transitions, rhat, and visual assessment of chain mixing.

2.3 | Fisheries-independent surveys: Seychelles case study

Diver surveys of fish assemblages provide fishery-independent assessments of target species abundance and potential contribution to the fishery. To consider how changing macroalgal and coral reef cover influences the availability of fish to small-scale reef fisheries, we examined temporal trends in fish assemblages on reefs in

Seychelles based on detailed benthic and fish data collected between 2005 and 2014. This location is ideal for examining habitat changes to reef fish as Seychelles reefs are typical of those throughout the western Indian Ocean that experienced extensive climate-driven coral bleaching in 1998 (Graham et al., 2015). Moreover, on Seychelles reefs this bleaching instigated a regime-shift from coral to macroalgae on some reefs, whilst coral cover on other nearby reefs gradually recovered to pre-bleaching levels (Graham et al., 2015). Prior to coral bleaching, average macroalgal cover on both regime-shifting and recovering reefs was <3% and coral cover was >25% (Graham et al., 2015). However, following the 1998 coral bleaching, average coral cover remained <10% on the nine regime-shifted macroalgal reefs between 2005 and 2014, whilst macroalgal cover increased from 21% to 31%. Over the same period, average coral cover on twelve recovering reefs increased from 11% in 2005 to 27% in 2014, whilst macroalgal cover remained negligible (Figure S1). Structural complexity of the underlying hard reef also declined on regime-shifted macroalgal reefs between 2005 and 2011 and was lower than structural complexity on recovering reefs, which remained stable over the same time period (Wilson et al., 2019).

At each of the 21 reefs, underwater visual census was used to estimate the size and abundance of diurnally active non-cryptic fishes (134 species) within eight 7m radius point count areas located at the base of the reef slope (depth 6.1 ± 0.3 m). The accuracy of size estimates (to the nearest cm) was assessed daily, before UVC commenced, by comparing visual estimates of PVC pipe to the actual pipe lengths. Estimates were consistently within 4% of actual lengths (Graham et al., 2007). Size estimates of fish were converted to weights based on length-weight relationships (Froese & Pauly, 2020) and assemblage biomass calculated by summing all fish weights within a count area. Fish were placed into fishery target groups (primary, important, occasional, non-target) based on their prominence within inshore trap and handline fisheries in the Seychelles (Grandcourt, 1999).

3 | RESULTS

3.1 | Macroalgal contributions to catches

A total of 412 fish species were identified within the 49 studies that documented catch data for small-scale tropical reef fisheries. Approximately a quarter of the catch (Mean pC_m = 24 ±1% SE) from these fisheries is associated with macroalgal reefs when considering habitat use of both adults and juvenile fishes. When considering only juvenile habitat associations, the contribution of macroalgae-associated fishes are similar (24% ± 1%) to when only adult habitat data is used (23% ± 1%). However, there was a considerable range in the catch composition amongst locations: >50% of catches at Bolinao in the Philippines, the Ningaloo region of Western Australia and Mombasa in Kenya were macroalgae-associated fishes, whilst <10% of fishes caught around some Micronesia, Fiji and Cook Islands were macroalgae-associated (Table 1). Heavy reliance on macroalgal fishes at a few locations meant the modelled median contribution of macroalgae-associated fishes to small-scale tropical fisheries (21%) was slightly lower than the estimated mean (Figure 2). Fish at locations with both high and low representations of macroalgal species were caught for a range of purposes, using several types of gear. However, the proportion of the catch associated with macroalgal habitats did not differ with respect to different fishing methods, nor the type of fishery (Figure 2, Table S3). Inconsistencies in

TABLE 1 Percent contribution of macroalgae-associated fishes to small-scale tropical fisheries

Country	N	Range	Average
Australia	12	16–81	41
GBR	5	16–24	20
Ningaloo	4	62–81	69
Pilbara	3	36–43	39
Barbados	2	26–34	30
Brazil	2	17–29	23
Cook Is	4	8–14	10
Fiji	8	8–31	20
French Polynesia	5	11–20	14
Indonesia	2	7–19	13
Kenya	5	30–63	52
Kiribati	7	11–31	18
Marshall Is	5	10–16	13
Micronesia	10	3–22	14
Nauru	1	31–31	31
New Caledonia	6	16–25	21
Niue	1	9–9	9
Palau	8	10–25	20
Philippines	11	23–88	46
Bolinao	6	37–88	51
Siquijor	4	28–74	43
PNG	5	15–25	20
Puerto Rico	2	17–24	21
Samoa	4	18–19	18
Saudi Arabia	3	18–43	27
Seychelles	3	19–30	23
Solomon Is	6	14–24	17
Tonga	6	20–39	27
Tuvalu	5	12–16	14
US Virgin Is	1	35–35	35
USA	2	16–17	17
Vanuatu	4	10–19	15
Wallis & Futuna (France)	3	13–18	16

Note: Averages calculated from *N* catch composition data in each country. Averages and range of macroalgae-associated contributions at locations within countries where *N* > 2 are also presented. See Table S1 for information on data sources, time of data collection, gear used and type of fishery at each location.

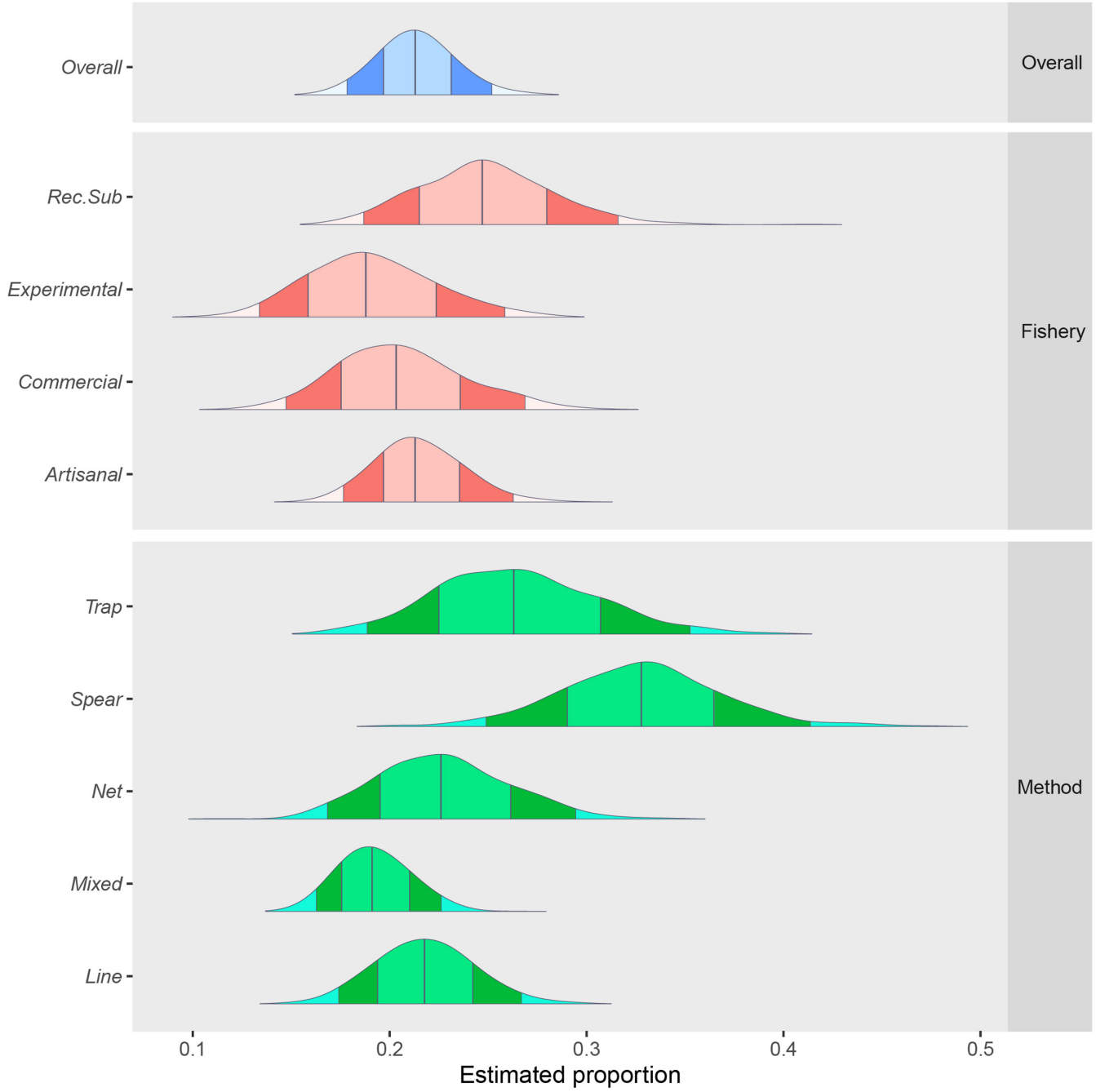

FIGURE 2 Posterior probability density for the proportion of small-scale tropical reef fishery catch associated with tropical macroalgal habitat. Solid vertical line within each distribution shows median value for overall catch data ($n = 133$), different fishing methods (trap [$n = 11$], spear [$n = 9$], net [$n = 10$], mixed [$n = 76$], line [$n = 27$]) and for different types of fisheries (recreation/subsistence [$n = 19$], experimental [$n = 17$], commercial [$n = 18$], artisanal [$n = 79$]). The pale central sections show the interquartile range, and the outer darker bands 95% credible intervals

environmental conditions and species distributions amongst locations make it inappropriate to assess temporal trends across all data. However, at Ningaloo, where we have extensive habitat association, and catch data collected on four separate occasions over almost 20 years (1998–2017), macroalgae-associated fishes consistently represented >50% of the recreational catch.

The contribution of macroalgae-associated fishes to small-scale tropical reef fisheries declined with increasing species dependence on macroalgal habitat (Figure 3). On average, species with >50% dependence on macroalgae comprised 14% ± 3% of the catch, whilst those that were exclusively recorded in macroalgal habitats accounted for <1% of the catch. Some notable exceptions were fisheries in the Philippines and along the Western Australian coast that had exceptionally high reliance on fishes with strong macroalgae associations (e.g. some siganids, scarids or lethrinids). In contrast, fishes with >50% dependence on coral reefs comprised 86% ± 3%

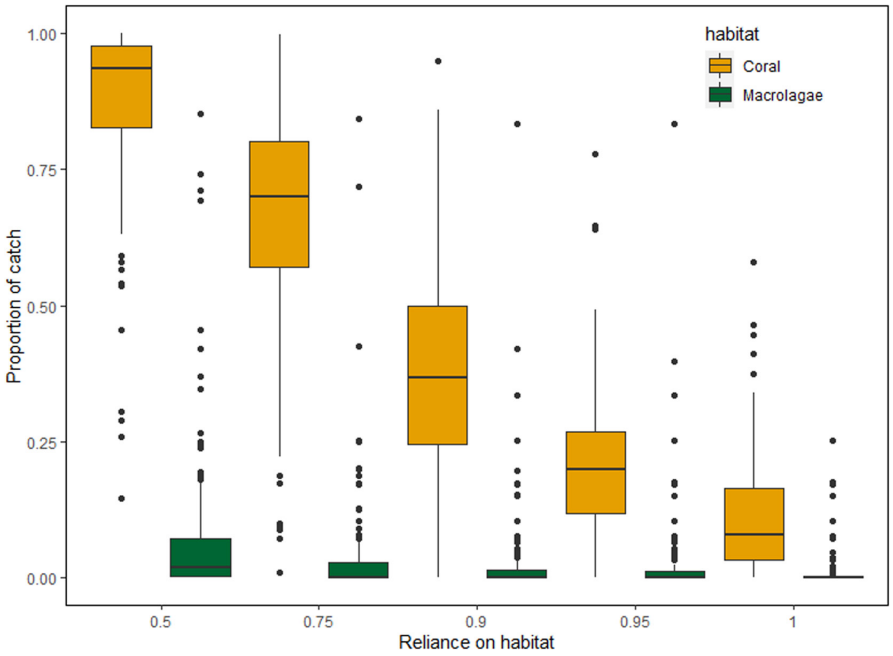

FIGURE 3 Contribution of fish that were recorded predominantly (either at >50%, 75%, 90%, 95% or 100% of their relative abundance) in macroalgal (green) or coral (yellow) habitats throughout their life history. Plot is based on 133 species-specific assessments of catch data from 49 studies. Reliance on habitat is based on proportional habitat occupation of both adult and juvenile fishes from 23 studies across 11 countries (see Fulton et al., 2020). Boxes represent 25–75 percentiles, divided by median values. Whiskers are 1.5 times the interquartile range and dots are outliers

Genera	#spp	Macroalgae association	Correlation (*p* value)		
			k	L_{inf}	Vulnerability
Epinephelus	16	0–0.98	−0.12 (.66)	0.00 (.99)	0.02 (.93)
Lethrinus	16	0–0.95	0.47 (.07)	−0.22 (.42)	−0.42 (.11)
Parupeneus	10	0–0.88	0.29 (.41)	−0.42 (.22)	−0.60 (.07)
Siganus	15	0–1.00	0.25 (.37)	−0.28 (.30)	0.09 (.46)

TABLE 2 Correlations between three life-history traits (growth k, maximum size L_{inf}, vulnerability to fishing index) and extent of macroalgae association for species within each of four genera that had a spread of habitat associations from almost exclusively coral to entirely macroalgal habitat occupation during their life history

Note: Species with a macroalgae association of 1 were only found in macroalgal habitats, whilst those with an association of 0 were only recorded in coral habitats.

of catches, although only 12% ± 2% were species that were exclusively observed within coral-dominated habitat. Thus, only a small proportion of tropical small-scale fisheries catches are supported by either macroalgal or coral habitat specialists.

3.2 | Vulnerability of the catch to overfishing

For those genera with species that exhibit a broad spectrum of habitat associations there were no consistently strong relationships between habitat-use and growth parameters or fishing vulnerability (Table 2). *Lethrinus*, *Parupeneus and Siganus* species with greater macroalgae associations tended to have higher growth parameters (k) and smaller maximum body sizes (L_{inf}). Whilst there was some statistical support for these relationships in *Lethrinus*, other relationships were weak, and all were non-significant (>0.05; Table 2). On balance, the current evidence suggests that the vulnerability to fishing of macroalgae- and coral-associated fishes from these genera was similar.

Trends were, however, detected when the diversity, mean trophic level and fishing vulnerability of the entire catch were compared to the proportion of macroalgae-associated fish within the catch (Table S4). Catch diversity, measured as Simpson's Index, peaked when the contribution of macroalgae-associated fish was ~20% (Figure 4). Similarly, the mean trophic level of the catch was highest when macroalgae-associated fishes represented 20% to 30% of the catch, although large errors about the model indicate this relationship is weak and mean trophic level can be high even when macroalgae-associated species represent >50% of the catch (Figure 4). The vulnerability of the catch to fishing was greatest when macroalgae-associated fish were absent from the catch and declined as the contribution of these fish increased (Figure 4).

3.3 | Fishery-independent surveys: Seychelles case study

Underwater surveys of fish assemblages on regime-shifted macroalgal and recovering coral reefs in 2014 provided insight into Seychelles fish resources available in these two habitats. On both reef types, fish assemblages were characterised by a high abundance of small-bodied fishes (<15 cm total length; Figure 5). We also observed a similar total biomass of fish on regime-shifted (506 ± 79 SE kg.Ha) and recovering (537 ± 59 SE kg.Ha) reefs. Total fish biomass on macroalgal regime-shifted reefs in the Seychelles may, however, be high compared to locations in the Pacific where biomass

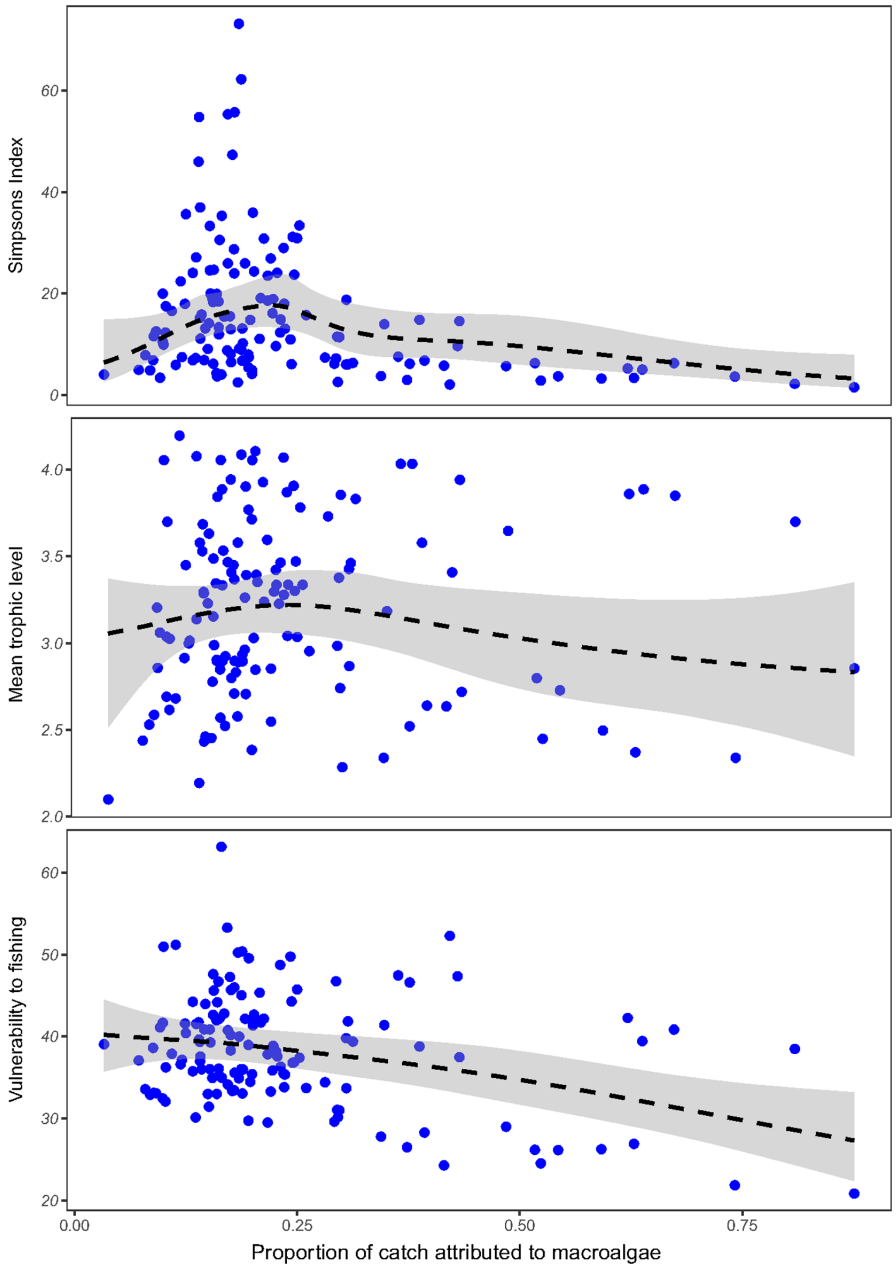

FIGURE 4 Variation in catch diversity (Simpson's index), mean trophic level and fishing vulnerability with respect to how much of the catch is represented by macroalgae-associated fish. Dashed line represents the median posterior predicted values of the generalised additive model with the shaded grey area showing the 95% credible intervals (Table S4)

on macroalgal habitats is ~20%–60% of what is recorded on nearby coral reefs (Table S5).

The biomass of primary fishery targets on regime-shifted macroalgal reefs increased between 2005 and 2014 (Figure 6), concurrent with an increase in macroalgae cover on these reefs over the same period (Figure S1). Consequently, biomass of primary targets was greater on regime-shifted than recovering reefs in 2014. Conversely, the biomass of important target species increased substantially on recovering reefs in 2011 and was almost twice that of primary target biomass on these reefs since 2011. The biomass of primary and important target species on regime-shifted reefs was similar in 2011 and 2014. On both reef types primary targets are mainly herbivorous rabbitfishes (Siganidae) and parrotfishes (Scarinae), whilst those in the important category tend to be from higher trophic levels. The biomass of occasional targets did not differ greatly over the survey period or amongst reef types, though non-target biomass increased on recovering reefs and was notably higher on these reefs than those that had undergone a regime-shift from 2011.

4 | DISCUSSION

Macroalgae-associated fishes typically represent a quarter of the tropical small-scale fishery catch, indicating that macroalgal reefs are important habitat for these fisheries. The catch contribution of macroalgae-associated fishes varied considerably amongst study locations, and this was not related to the fishing gear, or type of fishery, suggesting other factors such as resource access, market demands, habitat availability and fisher behaviour influence

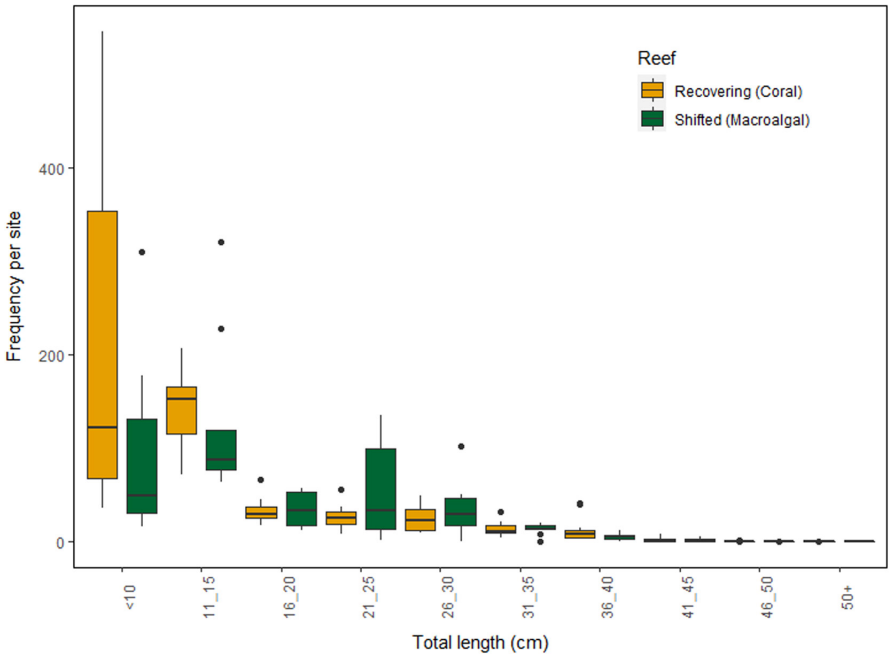

FIGURE 5 Size distribution of fishes on macroalgae-dominated ($n = 9$, shifted) and coral-dominated ($n = 12$, recovering) Seychelles reefs in 2014. Estimates based on 8 circular point counts with 7 m radius at each reef (total area 1232 m^2 per reef). Boxes represent 25–75 percentiles, divided by median values. Whiskers are 1.5x the interquartile range and dots are outliers

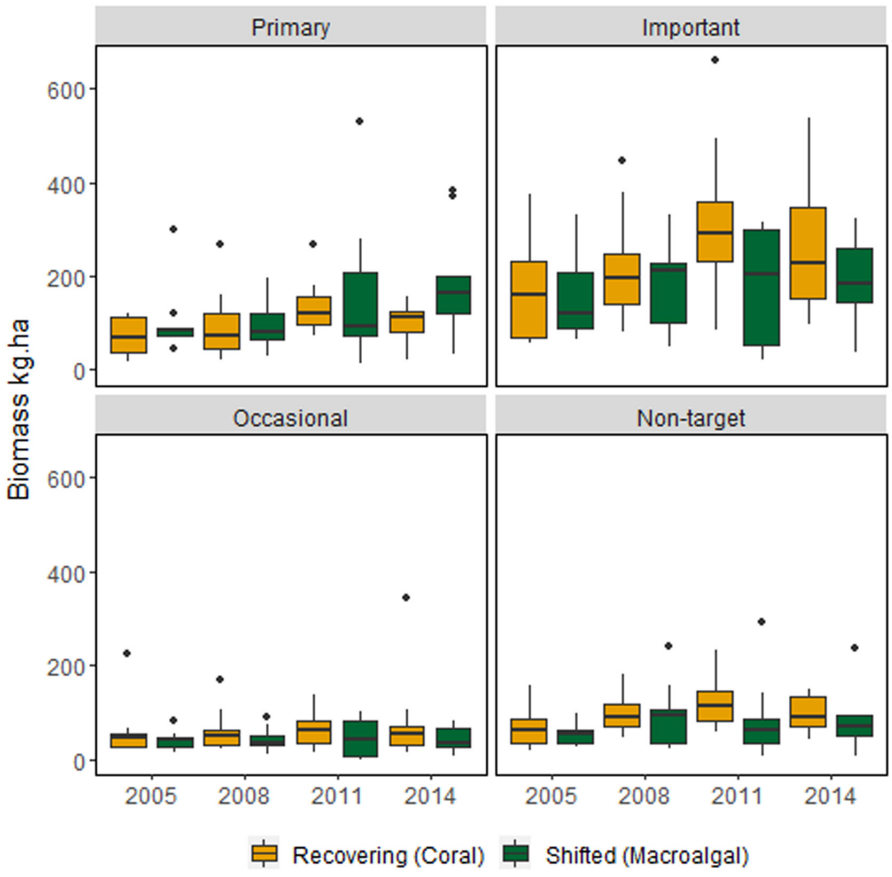

FIGURE 6 Biomass of fisheries target groups on 9 macroalgae-dominated (regime-shifted) and 12 coral-dominated (recovering) reefs in the Seychelles. Boxes represent 25–75 percentiles, divided by median values. Whiskers are 1.5X the interquartile range and dots are outliers

catch composition. Our results also indicate that species that are totally reliant on either macroalgae or coral habitat throughout post-settlement typically represent a small proportion of the total catch, suggesting small-scale tropical reef fisheries typically harvest species that utilise several habitats within diverse seascapes (Fulton et al., 2020; Sambrook et al., 2019; Sievers et al., 2020). Maintaining these habitats, and the links between them, allows species to undertake foraging, ontogenetic and breeding migrations necessary to support healthy populations (Berkström et al., 2013; van Lier et al., 2018; Olds et al., 2012). Degradation, reduction or fragmentation of habitats will have a detrimental impact on the abundance of many tropical fishes, with flow-on affects for sustainable harvests from tropical fisheries (Hoey et al., 2016; Pratchett et al., 2011; Wilson et al., 2006).

Our systematic review compiled and filtered data in a transparent and robust manner, allowing the inclusion of both published and grey literature to avoid publication bias (Hopewell et al., 2005). However, a dearth of species-level catch composition information hinders our temporal and spatial understanding of how habitat contributes to fisheries. Accordingly, detailed mapping of habitat and fisher behaviour should be coupled with catch data and monitored if we are to understand drivers of change in fisheries catch. Indeed, the quantity of different habitat types within a seascape may be a primary driver of source habitats for fisheries catches. We found that small-scale tropical reef fisheries are especially reliant on macroalgae-associated fishes where there are extensive lagoons or reefs that harbour macrophyte assemblages such as macroalgae and seagrass (Hicks & McClanahan, 2012). For example, extensive macroalgal meadows are common in the lagoon at Ningaloo reef on the west coast of Australia and represent 46% of the overall shallow water habitat (Kobryn et al., 2013). Accordingly, macroalgae-associated fish consistently represent the majority of the recreational catch at Ningaloo. At many other locations where macroalgae are a prominent feature of the seascape, catches were dominated by nominally herbivorous scarids and siganids, such as in the Seychelles (Shoemaker spinefoot, *Siganus sutor*, Siganidae: Robinson, Wilson, Robinson, et al., 2019) and Philippines (Spinytooth parrotfish, *Calotomus spinidens*, Labridae; Marbled parrotfish, *Leptoscarus vaigiensis*, Labridae; Black rabbitfish, *Siganus fuscescens*, Siganidae: Fulton et al., 2020). Catches of these fish have also increased following expansion of macroalgal habitats due to regime shifts (Robinson, Wilson, Robinson, et al., 2019) or farming of seaweed (Hehre & Meeuwig, 2016). This provides some insight into how fisheries may change in response to shifts in macroalgae cover in tropical seascapes—either expansion of macroalgae due to regime shifts following mass coral mortality, or contraction following macroalgae removal/mortality due to local and global pressures. In our assessment of Seychelles reefs, we find that the biomass of herbivorous species of primary importance to local fisheries can increase as macroalgae cover expands, especially when these species are protected from fishing (Graham et al., 2020). Further exploration of such seascape effects are warranted, which will require increased efforts towards seascape mapping using remote-sensing and other large-scale methods (Kobryn et al., 2013; van Lier et al., 2018).

Herbivorous fishes are clearly important to many tropical fisheries and are abundant within macroalgal habitats (Graham et al., 2020; Hempson et al., 2018). However, a diversity of carnivores is also common on macroalgal reefs (Fulton et al., 2019), and in some locations can account for the majority of the catch. For example, at Ningaloo reef, two carnivorous species that are closely associated with macroalgal reefs (Spangled emperor, *Lethrinus nebulosus*, Lethrinidae and Chinaman rockcod, *Epinephelus rivulatus*, Serranidae) represented 50%–70% of the recreational catches recorded over the past 20 years (Ryan et al., 2019; Sumner et al., 2002). These results infer that macroalgae-associated fishes from a diverse array of trophic levels can contribute to small-scale tropical reef fisheries.

Variation in the trophic composition of the catch may reflect differences in fishing pressure, consumer preferences, market value or cultural importance (Kittinger et al., 2015; Thyresson et al., 2013). Notably, both trophic level and diversity of catches peaked when macroalgae-associated species represented 20%–30% of the catch. A diverse catch portfolio can maintain catch rates, buffering the size and value of the catch against fluctuations in fish populations and habitat condition (Robinson et al., 2020), whilst a high trophic level of catch may be indicative of lower fishing pressure (Humphries et al., 2019; McClanahan et al., 2008). The correlation of high catch diversity and mean trophic level when macroalgae-associated fish represent approximately a quarter of the catch emphasises the significance of multiple habitats to sustainable fisheries in many locations.

Our results also suggest that life-history traits and vulnerability to fishing of macroalgae and coral-associated congenerics are similar. Indeed, species in both habitats had life-history traits that make them highly susceptible to overfishing. However, faster-growing siganid and scarid species were characteristic of many catches dominated by macroalgae-associated fish (Fulton et al., 2020) and, accordingly, we detected a negative correlation between fishing vulnerability and the proportion of macroalgae-associated fish in the catch. Although this relationship is weak, it may help explain the persistence of catch rates for some fisheries heavily reliant on macroalgae-associated species (McClanahan et al., 2008; Robinson, Wilson, Robinson, et al., 2019).

Fish that are habitat specialists as either adults and/or juveniles are highly vulnerable to disturbances that impact that habitat (Munday, 2004; Pratchett et al., 2012; Wilson et al., 2008), and this may adversely affect fisheries that target these species. However, we found a relatively low percentage of fish that are 100% coral or macroalgae-associated within the catch of small-scale tropical fisheries. The prominence of fishes that use multiple habitats throughout their life suggests that the immediate effects of habitat disturbances on catch rates may be buffered, a supposition supported by comparing catch data before and soon after mass bleaching in the Seychelles (Grandcourt & Cesar, 2003). However, many species require specific habitat types during certain life-history stages, and long-term declines in stock and catch may occur if essential habitat required by either adult or juvenile fish is increasingly unavailable in the seascape (Graham et al., 2007). Our analyses only consider macroalgal and coral reef habitats, with other habitats not assessed here, such as seagrass and mangroves (Sambrook et al., 2019; Sievers et al., 2020), also providing important fish habitat. The typical catch from small-scale tropical reef fisheries is, therefore, a conglomeration of species with different habitat associations and is not reliant on species that are dependent on a single habitat type.

Awareness of the need to protect and manage a more diverse seascape to support catches from tropical reef fisheries is increasing (Fulton et al., 2020; Sambrook et al., 2019; Sievers et al., 2020). Fish populations that appear to be coral-associated because adults are harvested from coral-dominated habitats, could in fact be replenished by recruitment and early growth of juveniles and subadults

in nearby macroalgal habitats (Aburto-Oropeza et al., 2007; Wilson et al., 2017). Seagrass habitats can also provide this role in recruitment, given considerable overlap in fish species richness across seagrass and macroalgal habitats within tropical seascapes (~40%, Fulton et al., 2020). An example of a macrophyte-associated species important in small-scale fisheries is the marbled parrotfish, which can inhabit either macroalgae or seagrass habitats, depending on habitat availability within the local seascape. In some locations (e.g. Ningaloo) this may not be possible due to the scarcity of suitable seagrass beds (Kobryn et al., 2013), and accordingly, the abundance of marbled parrotfish fluctuates with increases and decreases in the tropical *Sargassum* that provides both food and shelter for this species (Lim et al., 2016). Evidence that many reef fish species adopt this tripartite life cycle is increasing, and this points to why diverse seascapes can underpin the replenishment of fishery target species. As such, an informed approach to seascape-scale habitat management and protection should include monitoring of habitat condition in multiple habitat types so we capture all the important ecosystem elements supporting tropical fisheries sustainability.

The physical complexity of habitat structure may be especially relevant for supporting fisheries. The complexity of underlying hard reef structures provides shelter for a broad array of species and can underpin key processes, such as recruitment and predator-prey interactions on tropical reefs (Pratchett et al., 2008). Hard reef complexity is also important for the productivity of tropical fisheries (Rogers et al., 2014). Interestingly, fisheries productivity is highest on reefs where structure is at levels that provide shelter for prey whilst still allowing predation by fish (Rogers, Blanchard, & Mumby, 2018; Rogers, Blanchard, Newman et al., 2018). Productivity on macroalgal reefs can also be high where the structure of canopy-forming seaweeds and underlying reef create intermediate levels of complexity for invertebrates and small fish prey (Fulton et al., 2020). Indeed, the similarity of fish biomass on coral (with high hard complexity) and macroalgal reefs (dominated by *Sargassum* but with significantly lower underlying reef complexity) in the Seychelles suggests that canopy-forming macroalgae can compensate for the loss of hard complexity and support fisheries productivity. Canopy density and height are known to influence the suitability of macroalgal habitats for the juveniles of species important to fisheries (Evans et al., 2014; Tang et al., 2020; Wilson et al., 2017). This also suggests a vulnerability: if canopy-forming macroalgal taxa are replaced by low-stature understory macroalgae, we are likely to see reduced levels of fish recruitment (Fulton et al., 2019). In addition to canopy structure, other factors such as the taxonomic composition of macroalgae present, the availability of fish dietary items and the proximity of macroalgal patches to each other and other habitat types can be important (van Lier et al., 2018; Sambrook et al., 2020; Wenger et al., 2018).

Management of tropical reefs in the Anthropocene requires that we identify and protect the most important processes or functions (Bellwood et al., 2019). This will need a broad perspective: one that considers processes within reefs as well as habitat connectivity across seascapes (Sievers et al., 2020). Previous studies have highlighted the importance of seagrass (Jackson et al., 2015; Unsworth et al., 2019) and mangroves (Carrasquilla-Henao & Juanes, 2017) to fisheries. Our analyses synthesised a growing body of evidence that tropical macroalgae are an important habitat for supporting the diversity and productivity of small-scale tropical fisheries and the communities that rely on them. Maintaining connections between coral, macroalgal and other key habitat components in tropical seascapes, such as mangroves and seagrass, is critical for both marine conservation and sustaining tropical fisheries. The consistently high contribution of macroalgae-associated fishes to the catch on some reefs also suggests that yields may be maintained or increased under future increases in macroalgal habitat due to climate-driven coral mortality. Increased occurrence of some macroalgae-associated fishes within the catch may make these fisheries more resilient to high fishing pressure, though lower catch diversity may reduce catch stability and alter the economic value of the catch. Increased exploitation of species from lower trophic levels may also have flow-on effects for herbivory and resilience of coral reefs. The role of macroalgal habitats and associated fishes should, therefore, be incorporated into ecosystem-based management of small-scale tropical reef fisheries.

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DATA AVAILABILITY STATEMENT

Data used for calculations in this study are presented in Supplementary Information (Tables S1 and S2).

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