Form and function of tropical macroalgal reefs in the Anthropocene

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Abstract

1. Tropical reefs have been subjected to a range of anthropogenic pressures such as global climate change, overfishing and eutrophication that have raised questions about the prominence of macroalgae on tropical reefs, whether they pose a threat to biodiversity, and how they may influence the function of tropical marine ecosystems.
2. We synthesise current understanding of the structure and function of tropical macroalgal reefs, and how they may support various ecosystem goods and services. We then forecast how key stressors may alter the role of macroalgal reefs in tropical seascapes of the Anthropocene.
3. High levels of primary productivity from tropical canopy macroalgae, which rivals that of other key producers (e.g., corals, turfing algae), can be widely dispersed across tropical seascapes leading to a boost secondary productivity in a range of biomes that include coral reefs, and support periodic harvests of macroalgal biomass for industrial and agricultural uses. Complex macroalgal reefs that comprise a mixture of canopy and understory taxa can also provide key habitats for a diverse community of epifauna, as well as juvenile and adult fishes that are the basis for important tropical fisheries.
4. Key macroalgal taxa (e.g., *Sargassum*) that form complex macroalgal reefs are likely to be sensitive to future climate change. Increases in maximum sea temperature, in particular, could depress biomass production and/or drive phenological shifts in canopy formation that will affect their capacity to support tropical marine ecosystems.
5. Macroalgal reefs can support a suite of tropical marine ecosystem functions when embedded within an interconnected mosaic of habitat types. Habitat connectivity is, therefore, essential if we are to maintain tropical marine biodiversity alongside key ecosystem goods and services. Consequently, complex macroalgal reefs should be

treated as a key ecological asset in strategies for the conservation and management of diverse tropical seascapes.

Keywords nursery, productivity, *Sargassum*, seascape, seasonality, spatial subsidy

1. INTRODUCTION

Tropical macroalgal reefs, which we define as patches of carbonate reef with higher relative cover of fleshy macroalgae than live coral, have long been recorded alongside coral and other patch habitat types in a range of fringing, barrier and atoll reef settings (Stephenson, Stephenson, Tandy, & Spender, 1931; Littler & Littler, 1988; Bruno, Precht, Vroom, & Aronson, 2014). Some types of tropical macroalgae have been increasing in prevalence during the Anthropocene due to overfishing, coral bleaching and/or eutrophication removing some of the limitations to macroalgal growth on tropical reefs, which in some cases has triggered broad-scale coral-algal regime shifts (e.g., Hughes, 1994; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015). While this has increased awareness of macroalgae in tropical reef research and management, this has often been skewed towards the negative effects of macroalgae on coral reefs (e.g., Bellwood, Hughes, Folke, & Nyström, 2004; Hughes et al., 2017). However, macroalgae can be the dominant benthic organism on tropical reefs due to a range of environmental drivers (Bruno et al., 2014; Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015), and as primary producers that span a range of growth forms, macroalgae have the capacity to support many other species in tropical marine ecosystems (Fulton et al., 2014; Tano et al., 2016). Moreover, seascape-scale assessments, that include all shallow inshore substrates, indicate that areas dominated by macroalgae (e.g., 16%, 23% and 46% in Tanzania, New Caledonia and Ningaloo (western Australia), respectively) can be extensive relative to coral-dominated habitat (4-8%) (Garrigue, 1995; Kobryn, Wouters,

& Beckley, 2011; Tano et al., 2017). Depending on the spatial setting and extent, macroalgal reefs can be key components of interconnected tropical seascapes that complement the functions and services provided by other subtidal habitats, such as coral reefs and seagrass beds (Hyndes et al., 2014; Nagelkerken, Sheaves, Baker, & Connolly, 2015).

Macroalgal reefs vary immensely in composition and structure in response to a range of environmental and biotic conditions (Steneck & Dethier, 1994). In some settings, a tropical reef can become dominated by a few weedy macroalgae species of low stature, especially when grazing pressure is severely depressed by overfishing (e.g., Littler & Littler, 1988; Hughes, 1994; Mumby, 2009). However, macroalgae can also dominate tropical reefs where natural levels of wave energy, sedimentation, and nutrient supply facilitate macroalgal growth over that of benthic competitors such as corals and coralline algae (Bruno et al. 2014; Gove et al., 2015; Williams et al., 2015). Under these conditions, complex macroalgal reefs have developed across the Indo-Pacific and Red Sea, where they typically comprise a mixture of canopy-forming (e.g., *Sargassum, Turbinaria*) and/or understory taxa (e.g., *Dictyota*, *Lobophora*) that provide microhabitats for a diversity and abundance of epifauna and nekton (Rossier & Kulbicki, 2000; Ateweberhan, Bruggemann, & Breeman, 2006; Tano et al., 2016). Such macroalgae-associated fauna also take advantage of the local productivity to fulfil their trophic requirements - either directly as herbivores, or indirectly as carnivores exploiting secondary production (Edgar & Aoki, 1993; Lim, Wilson, Holmes, Noble, & Fulton, 2016; Wenger, van Lier, & Fulton, 2018). In this way, macroalgal reefs can facilitate biodiversity and flows of energy and biomass to underpin a range of tropical marine ecosystem goods and services (Fig. 1).

In this review we synthesise our current understanding of how the structure and function of macroalgal reefs can influence the services they support within tropical marine ecosystems. We then explore how environmental stressors interact with these macroalgal structure-function relationships, and what this means for the future of tropical reefs in the Anthropocene. In doing so, we challenge some emerging paradigms and reappraise how we should manage tropical macroalgal reefs as part of diverse and connected seascapes.

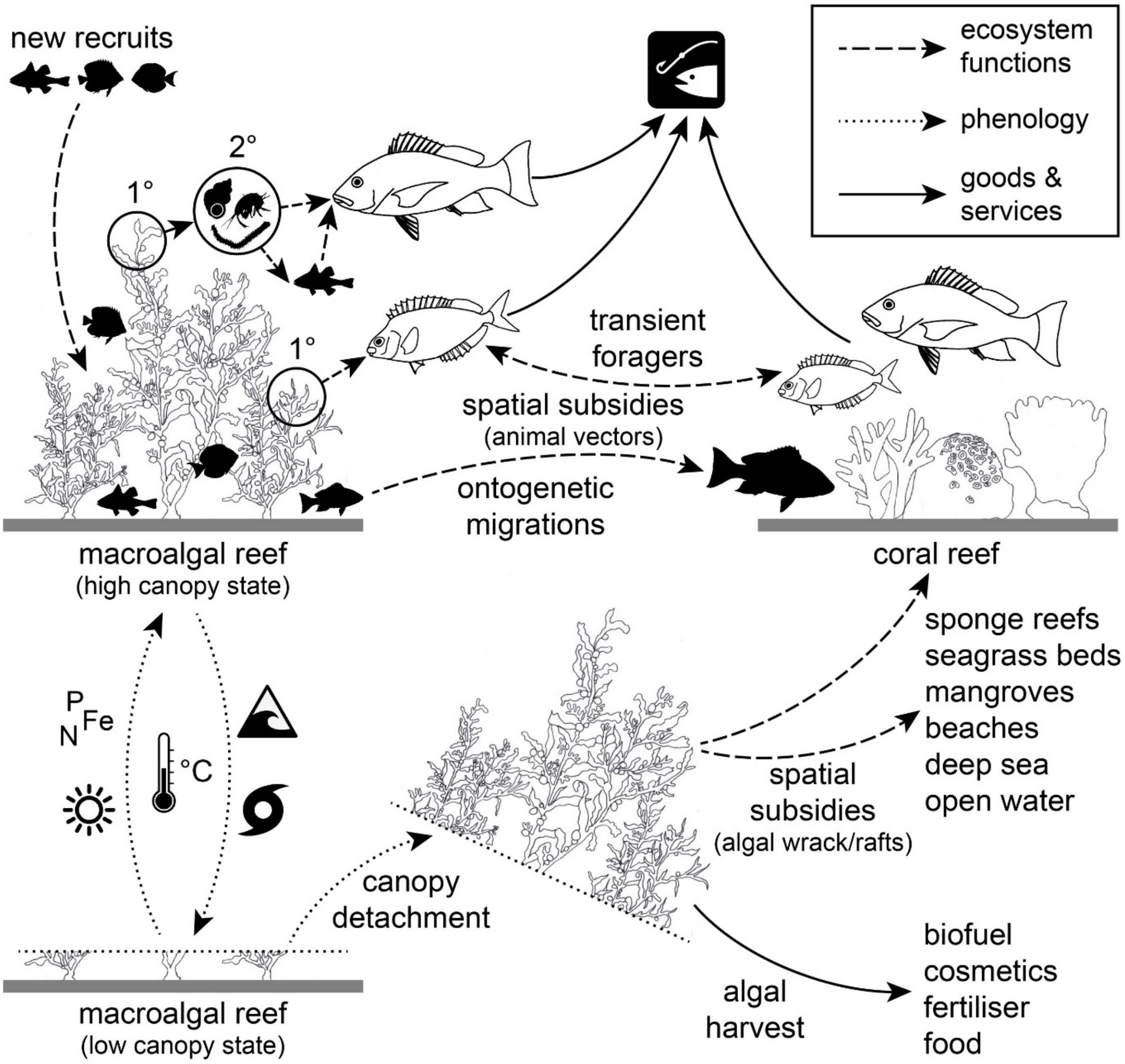

Figure 1 How complex tropical macroalgal reefs can support marine ecosystem functions, goods and services. Seasonal cycles in the phenology of canopy-forming macroalgae (e.g., *Sargassum*) provide primary (1°) and secondary (2°) production as well as habitat for resident and transient consumers, especially during high canopy states. Spatial subsidies of macroalgal

productivity to other biomes occurs via surface (rafts) and subsurface (wrack) dispersal of detached macroalgal canopy biomass and faunal migrations. The timing and extent of these phenological cycles in tropical macroalgal canopy biomass, which underpin food security and other harvest products, are dependent on several environmental drivers such as sea temperature, daylength, nutrient pulses and disturbance events (Fig. 2).

2. ECOSYSTEM FUNCTIONS AND SERVICES FROM MACROALGAL REEFS

2.1 Primary and secondary production

Productivity is a fundamental attribute of ecosystems that influences overall patterns of biodiversity, structure and function, and the extent of goods and services that can be sustained over space and time. Our meta-analysis of areal productivity across a range of common benthic producers (i.e., taxa that typically comprise 10% or more of the benthic cover on tropical reefs) indicated high rates of both gross and net areal primary production in two key groups - reef-building corals and canopy-forming *Sargassum* – both of which also provide habitat for other species (Fig. 2A). Net production from *Sargassum* is typically rapid and episodic, with an almost complete annual turnover of biomass across seasonal cycles of canopy growth and decay (Fig. 2B). Similar seasonal variation in the productivity of other reef producers are likely due to shifts in daylength and sea temperature (Kinsey, 1977), although the short time periods of most production estimates (hours/days) prevents a wider investigation of seasonal variation in tropical reef production. Once detached, macroalgal canopy biomass is widely dispersed by drifting rafts and wrack, which can be deposited across a range of subtidal and intertidal biomes (Fig. 1; section 2.3).

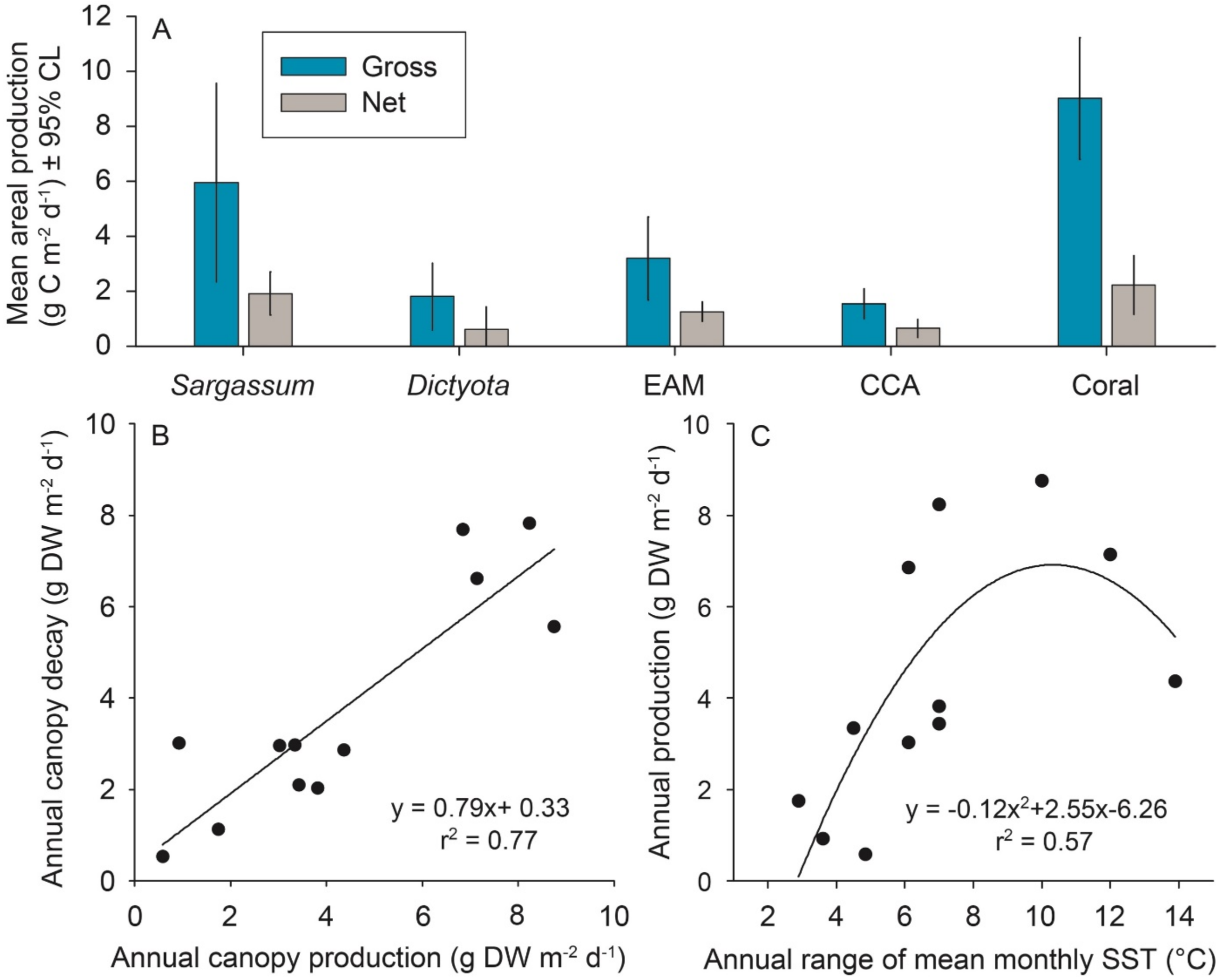

Figure 2 Comparison of A. mean gross and net areal production in sections of tropical reef dominated by one of five major primary producers – canopy-forming *Sargassum*, *Dictyota*, the epilithic algal matrix (EAM), crustose coralline algae (CCA) or scleractinian corals – based on 40 independent studies at tropical locations (Table S1). Means (± 95% confidence limits) are based on four or more studies per group (except *Dictyota* gross production where n = 2, Table S1). Note that net production for *Sargassum* were typically measured on uncaged biomass (i.e. subject to herbivory) during the seasonal growth phase (typically 4-6 months), which is followed by 3-4 months of canopy detachment when 80-90% of production is dispersed. As such, production values are likely to be conservative for macroalgae due to losses from herbivory (Poore et al., 2012). Meta-analysis of relationship between (B) *in situ* annual growth and decay of tropical *Sargassum* canopy biomass, and (C) *in situ* annual *Sargassum* canopy growth and the annual range in mean monthly sea surface temperatures (SST) recorded by 12 independent studies focused on *Sargassum*-dominated reef areas at seven tropical locations (Table S2).

Consumption and conversion of primary production into higher trophic levels is critical for many ecosystem goods provided by tropical reefs, such as fishable biomass. In corals, much of the relatively high net primary production from zooxanthellae is utilised by the host coral (Hatcher, 1990), with feeding by corallivores and coral exudates providing external trophic pathways for some of the coral primary production to enter the wider ecosystem (Wild et al., 2004; Cole, Lawton, Wilson, & Pratchett, 2011). Another key component of coral-dominated reefs, the epilithic algal matrix (EAM), is known to support high levels of net primary production that is readily converted into herbivorous fish biomass (Russ, 2003; Bellwood et al., 2018). A number of herbivorous fishes such as *Leptoscarus vaigiensis*, *Siganus sutor*, and *Naso unicornis* have co-evolved to target macroalgae (Choat, Robbins, & Clements, 2004; Hoey, Brandl, & Bellwood, 2013; Lim et al., 2016). These browsing herbivores may exhibit some of the highest known rates of secondary production (i.e., somatic growth) in tropical reef fishes (Morais & Bellwood, 2018), which can underpin important tropical fisheries (Hicks & McClanahan, 2012; Rogers, Blanchard, & Mumby, 2018; Robinson et al., 2018). Emerging evidence also suggests that microalgae, endolithic algae, and bacteria are targeted by some reef fishes (Clements et al., 2017), which quantitative productivity data may ultimately reveal as a major trophic resource alongside macroscopic producers like macroalgae and corals.

Canopy macroalgae can also facilitate secondary and higher order productivity through their epifauna. *Sargassum* and other macroalgae with complex canopies can host a wide diversity and abundance of invertebrate epifauna, which in turn support the growth and reproductive output of carnivorous fishes that target these epifaunal prey (Edgar & Aoki, 1993; Wenger et al., 2018). Indeed, macroalgal reefs appear to host a greater diversity and higher standing biomass of epifauna than either tropical seagrass (Tano et al., 2016) or the EAM (e.g., crustacea; Kramer et al., 2014), which is likely due to the higher (volumetric) capacity for canopy-forming macroalgae to support epifauna than other types of smaller macrophyte host (Wenger et al., 2018). This means canopy-forming macroalgae can support secondary productivity an order of magnitude higher than EAM or many other types of subtidal microhabitat, with the exception of dead coral heads that may also provide complex “canopy” habitat for epifauna (Edgar 1990; Edgar & Aoki, 1993; Kramer, Bellwood, & Bellwood, 2014). Consequently, tropical macroalgae can be both key primary producers and facilitators of secondary production that underpin major trophic flows of energy and biomass through tropical marine ecosystems.

2.2 Complex habitat for key species and processes

Habitat complexity is integral for maintaining the biodiversity of tropical reefs. The collapse of coral reef structural complexity is associated with a substantial loss of reef-associated species (Graham & Nash, 2013; Rogers, Blanchard, & Mumby, 2014). Macroalgal habitats have similar functional relationships with their associated biota, where changes in canopy structure (density, cover, height) and composition are strong predictors of the abundance and diversity of key epifauna and nekton (Tano et al., 2016; Wilson et al., 2014; Wenger et al., 2018). While there appear to be relatively few macroalgal reef specialist fishes (Rossier & Kulbicki, 2000), many tropical reef fish taxa are supported as transients across macroalgal and coral reef habitats during ontogeny or foraging migrations (Fig. 1). Notably, macroalgal-associated fishes span a diversity of trophic groups, albeit at a lower level of taxonomic diversity and redundancy than those found on coral reefs (Fig. 3). Nonetheless, many of the relatively abundant macroalgal-associated fish taxa are of ecological significance, such as browsing herbivores (e.g., *Leptoscarus vaigiensis*, *Siganus sutor*), generalist carnivores (e.g., *Lethrinus* spp.), and piscivores (e.g., *Epinephelus* spp.), many of which are also important fishery targets (Rossier & Kulbicki, 2000; Hicks & McClanahan, 2012; Wilson et al., 2017; Robinson et al., 2018).

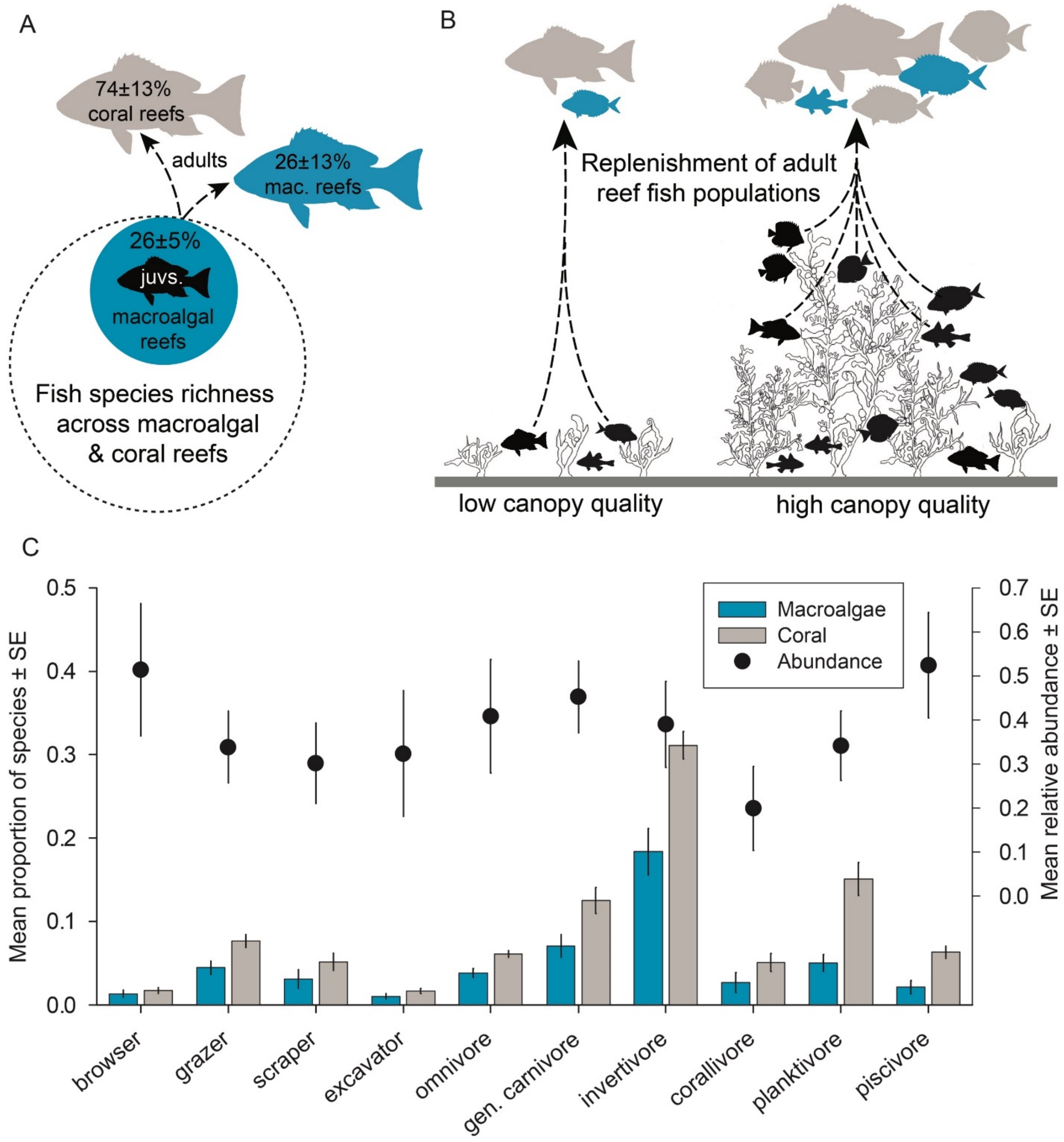

Figure 3 Role of complex macroalgal reefs in supporting tropical fishes via: A. Dominant habitat for the juvenile stages of 26 ± 5% (mean ± standard error) of local reef fish species occurring across macroalgal and/or coral reefs – the adults of most of these species (74 ± 13%) are predominantly found on coral reefs (underlying meta-data in Table S3); B. Complex macroalgal reefs can have a high concentration of juvenile reef fishes, although canopy habitat quality (percent cover, density, canopy height) can strongly influence the diversity and abundance of new fish recruits that survive to replenish adult populations in both coral (grey) and complex macroalgal (blue) reefs, including fishery target species; and C. Supporting a diverse community of adult reef fishes that is comparable to nearby coral reefs, yet at much lower levels of taxonomic redundancy (Table S4). Note the mean relative abundance of species (> 0.5 equates

to more individuals on macroalgal than coral reef) in these trophic groups (dots, right y-axis) is around 0.5 or below, which suggests most adult reef fishes are not specialised occupants of complex macroalgal reefs, and likely use such areas as transient foraging grounds (e.g., browsers and piscivores).

Habitat quality and complexity are also critical for supporting key ecosystem processes. Complex macroalgal reefs comprising canopy-forming genera like *Sargassum* can play a major role in supporting the replenishment of fish populations via the provision of seasonal nursery habitats for juveniles (Fig. 3A). Our meta-analysis revealed that 17-49% of the regional pool of reef fish species have the majority of their juveniles within complex macroalgal reef habitats (Table S3) - around three-quarters of those taxa later migrate to coral reefs where the majority of their adults are found (Fig. 3A). Importantly, variations in macroalgal canopy structure are closely linked to the diversity and abundance of juvenile fishes occupying a particular patch (Wilson et al., 2014), and the abundance of future life-history stages (Fig. 3B; Aburto-Oropeza, Sala, Paredes, Mendoza, & Ballesteros, 2007; Wilson et al., 2017). Consequently, local changes in macroalgae canopy habitat can influence the number of juveniles that recruit into future adult fish populations, including those which are prime fishery targets in coral reef habitats. Accordingly, macroalgal-dominated reefs can underpin both the replenishment and productivity of tropical reef fisheries.

2.3 Spatial subsidies across tropical seascapes

Spatial subsidies occur when there is a decoupling between the location of primary production, and where the biomass and energy is assimilated. The rapid seasonal accumulation and subsequent detachment of tropical *Sargassum* canopy biomass creates a pathway for this energy and nutrients to be widely dispersed to other marine ecosystem components via rafting (Zubia, Andréfouët, & Payri, 2015), underwater wrack, and movement of transient fauna (Polis, Anderson, & Holt, 1997; Hyndes et al., 2014). Direct transport of biomass can be considerable depending on the dispersal vector. On tropical reefs, drift biomass derived from tropical *Sargassum* has been recorded at a rate of 20.8 g C m^{-2} d^{-1} across Hawaiian coral reefs (Morrisey, 1985 in Stimson, 2013), whilst at depths of 40 metres macroalgal biomass arrives on reef slopes at rates of 2.5 g C m^{-2} d^{-1} (Stimson, 2013). Such spatial subsidies of macroalgal biomass are substantial, being more than double the *in situ* areal production of other common tropical benthic organisms (Fig. 2A). Macroalgal wrack and rafts are then likely to enter detrital pathways and fuel secondary production in areas where it is deposited (Wilson, Bellwood, Choat, & Furnas, 2003; Hyndes et al., 2014).

Macroalgae-derived energy and nutrients can flow throughout tropical marine ecosystems via various pathways. For instance, macroalgae exudates (dissolved organic carbon) are rapidly taken up by sponges and their associated bacteria, which is then passed to corals and higher trophic levels via the sponge-detritus loop (Rix et al., 2017; Mumby & Steneck, 2018). Mobile animals may also transport production that was consumed in macroalgal reefs over considerable areas and distances via predator-prey linkages and excretion of wastes across the seascape (Berkström et al., 2012). For instance, the diurnal foraging migrations of large-bodied carnivorous reef fishes can cover ranges of up to 1300 hectares that encompass both coral and macroalgal reefs (Taylor & Mills, 2013; Babcock, Pillans, & Rochester, 2017). Likewise, ontogenetic migrations of fish that live and feed on macroalgal reefs as juveniles can transfer macroalgal productivity across seascapes over much longer time scales. Through these mechanisms, the high primary production within macroalgal reefs becomes dispersed across habitats to support whole-ecosystem productivity that is critical for maintaining biodiversity and food security.

2.4 Industrial products and solutions

Wild and cultivated tropical macroalgae are currently harvested for industrial products that include food, biofuel, cosmetics, pharmaceutical compounds, agricultural products, and anti-fouling compounds (Prud'homme van Reine & Trono, 2001; Borines, McHenry, & de Leon, 2011; Song, Duc Pham, Seon, & Chul Woo, 2015). Much of this harvest of tropical macroalgae occurs in southeast Asia and east Africa, but it has the capacity to support coastal livelihoods throughout the Indo-Pacific (Prud'homme van Reine & Trono, 2001; Borines et al., 2011). The phenology and high productivity of tropical taxa such as *Sargassum* facilitates sustainable annual harvests of high areal yield (Zubia et al., 2015). Indeed, this potential for high productivity is a reason why tropical macroalgae have been suggested as a vector for carbon sequestration (Chung, Beardall, Mehta, Sahoo, & Stojkovic, 2011; Sondak et al., 2017). Emerging evidence indicates that macroalgal reefs have the capacity to store "blue" carbon via burial in adjacent sediment deposits and/or transport into the deep sea (Krause-Jensen & Duarte, 2016; Atwood et al., 2018). However, for carbon capture and storage to be of significant magnitude relative to global carbon emissions, rates of production need to be increased. Given nutrient availability is a key limitation (Littler et al., 1991; Roff & Mumby, 2012), the addition of micronutrients has been suggested as one way to boost carbon capture by marine primary producers such as phytoplankton (Bigg, Jickells, Liss, & Osborn, 2003). However, such micronutrient augmentation can have unintended effects, and may not produce negative carbon emissions after nutrient fabrication and transport is taken into account. Moreover, micronutrient additions (e.g. iron) can increase the prevalence of undesirable ecosystem components such as cyanobacterial mats (Kelly et al., 2012). Perhaps more feasible is the direct capture of carbon dioxide from industrial activities (e.g., ethanol production) to fuel tropical macroalgae mariculture that is converted into forms for long-term carbon storage (e.g., biochar; Roberts, Paul, Dworjanyn, Bird, & de Nys, 2015).

3. FUTURE SCENARIOS FOR MACROALGAE IN TROPICAL SEASCAPES

What will be the nature and function of macroalgae in tropical seascapes of the future? To answer this question, we must explore the proximate effects of global and local stressors on the composition of macroalgal reefs, their productivity, and their likely context within tropical seascapes. Marine climate change in the form of ocean warming, acidification and/or shifting storm regimes may impinge on tropical macroalgal reef structure and function. Of particular concern are thermal anomalies that are likely to intensify in tropical marine regions if we continue on “business-as-usual” scenarios (van Hooidonk et al., 2016; Oliver et al., 2018). Current evidence indicates that annual canopy production in a key taxon - *Sargassum* - is sensitive to thermal climate, both in terms of mean sea surface temperature (SST; Glenn, Smith, & Doty, 1990; Ateweberhan et al., 2006; Fulton et al., 2014), and the annual range in mean monthly SST (Fig. 2C). While intermediate levels of ocean warming might increase macroalgal growth and production in some understory taxa such as *Laurencia* and *Lobophora* (Gouvea et al., 2017; Hernández, Sangil, Fanai, & Hernández, 2018), this may not be the case for canopy-forming *Sargassum* that exhibit lower levels of canopy biomass at upper extremes of regional SST (Hwang, Tsai, & Lee, 2004; Ateweberhan et al., 2006; Fulton et al., 2014). This may be because these canopy-forming macroalgae, like many other tropical species, are already living close to their thermal limits (Koch, Bowes, Ross, & Zhang, 2013). Indeed, the available evidence suggests anomalies of 1-2°C above the highest mean monthly SST are likely to cause severe declines in *Sargassum* growth and canopy collapse (Prince, 1980; McCourt 1984). However, understory fleshy macroalgae may exhibit either resistance (no effect) or a modest increase in production under combinations of warming and acidification (Johnson, Price, & Smith, 2014; Gouvea et al., 2017; Hernández et al., 2018). Taken collectively, this suggests marine climate change will drive a loss of tropical canopy-forming taxa to effectively flatten macroalgal reefs down to low-complexity stands of short and/or unpalatable macroalgae (Littler & Littler, 1988; Littler et al., 1991).

In the near term, a shift in the composition and canopy structure of macroalgal reefs will have major consequences for tropical ecosystems. The implications for productivity are obvious in that less canopy growth will mean a decline in the annual turnover and dispersal of primary production across our tropical seascapes, followed by declines in secondary and higher-level production. The consequences of macroalgal habitat degradation could also be substantial for key biota such as fishes. This is because of the strong functional links between macroalgal habitat quality and reef fish abundance, particularly canopy height and density, which are sensitive to variations in sea temperature over annual and interannual (Fulton et al., 2014) and longer (Wilson et al., 2018) temporal cycles. In years of poor canopy growth, we tend to find a lower abundance and diversity of juvenile and adult fishes on macroalgal reefs (Aburto-Oropeza et al., 2007; Wilson et al., 2018), which can translate to smaller future fish populations on both macroalgal and coral reefs (Wilson et al., 2017). These effects are particularly severe for species that are macroalgal reef specialists (Lim et al., 2016; Wenger et al., 2018), but they can also impact the many species that predominantly settle into macroalgal reefs.

Fishes that recruit to macroalgal reefs may be particularly vulnerable to shifts in canopy phenology arising from climate change. On “hot reefs” with very high summer maximum SST (e.g., 35°C in Red Sea and southern Taiwan), peak *Sargassum* canopy biomass occurs in the cooler winter-spring period (Hwang et al., 2004; Ateweberhan et al., 2006), rather than the summer-autumn at most other tropical locations (Glenn et al., 1990; Vuki & Price, 1994; Fulton et al., 2014). Global increases in summer maximum SST due to climate change may drive a general shift in *Sargassum* canopy phenology towards the “hot reefs” condition (i.e., peak during cooler winter months), which would create a nursery habitat mismatch for the many fish species that exhibit summer peaks in recruitment (Williams, 1983; McIlwain, 2003; Abesamis & Russ, 2010). An adaptive shift in fish recruitment season is possible, with indications that reef fishes recruiting to “hot” macroalgal reefs mostly do so during the cooler months when *Sargassum* canopy biomass is highest (Isari et al., 2017). Such recruitment patterns can arise from seasonal shifts in the survival of juveniles, rather than shifts in spawning behaviour and reproductive output (Robertson, 1990), which means taxa with more serial recruitment patterns (e.g., some Acanthurids, Labrids, Haemulids, Pomacentrids; Doherty, 1991; Srinivasan & Jones, 2006; Sponaugle, Walter, Grorud-Colvert, & Paddack, 2012) may be more adaptable to shifts in macroalgal habitat phenology.

Many of the ecological functions of macroalgal reefs depend on connectivity across a mosaic of reef types, so seascape context is critically important for understanding future scenarios for tropical reefs. Catastrophic declines in coral cover have become prevalent in the Anthropocene and are predicted to accelerate during this century (Hughes et al., 2018). A substantive loss of either macroalgal or coral cover will break pathways of connectivity that are integral for sustaining biodiversity via ontogenetic and foraging migrations (Harborne et al., 2016; van Lier, Wilson, Depczynski, Wenger, & Fulton, 2018), and spatial subsidies that underpin productivity and harvestable biomass. A loss of reef-building corals and crustose coralline algae will also jeopardise the carbonate reef base required for all types of tropical reef (including macroalgal) and their associated biota. The spatial scales at which such seascape connectivity may be broken are alarmingly small. For one of the main vectors - reef fishes - van Lier et al. (2018) found marked reductions in fish diversity (taxonomic and functional) on macroalgal reefs when the distance between coral and macroalgal patches exceeded 500 metres. Similarly, Berkström, Lindborg, Thyresson, and Gullström (2013) found 750 metres to be a key threshold for the abundance of adult reef fishes that are transient foragers across a mosaic of tropical habitats (coral, seagrass, and macroalgae). These distance thresholds are likely to be much lower for juvenile fishes undertaking ontogenetic migrations (Grober-Dunsmore et al., 2008; Berkström et al., 2013). Moreover, key processes like grazing activity by transient herbivorous fishes may also be substantially affected at small spatial scales of patch separation (e.g., 75-100 metres; Vergés, Vanderklift, Doropoulos, & Hyndes, 2011; Downie, Babcock, Thomson, & Vanderklift, 2013). Seascapes must comprise a mix of coral and macroalgal reefs, as well as other habitat types, to support the complement of species that underpin the ecological processes and connections that maintain healthy and productive tropical ecosystems.

With mass coral bleaching and mortality increasing worldwide, we are entering an era of increasing dominance of tropical reefs by organisms other than coral. Many coral reefs comprise a mix of coral and algal cover (mostly as an epilithic algal matrix or EAM; Goatley & Bellwood, 2011; Bruno et al., 2014), which sustains a diverse and productive fish fauna of grazers, detritivores and carnivores (Russ, 2003; Wilson et al., 2003; Bellwood et al., 2018; Rogers et al., 2018). Reefs dominated by a mix of understory and canopy-forming macroalgae can have a similar diversity of fish trophic groups, although at a lower level of species richness (Fig. 3C). Indeed, fish communities on reefs that have undergone regime shifts from coral to canopy-forming macroalgae have shown such changes in functional structure, yet they are still diverse and abundant (Graham et al., 2015). Moreover, many of the fishes that utilise complex macroalgal reefs can support productive fisheries (Hicks & McClanahan, 2012; Robinson et al., 2018). However, it is conceivable that future coral-algal regime shifts may occur when environmental conditions are unsuitable for canopy-forming macroalgae like *Sargassum*. If the thermal anomalies that have triggered mass bleaching and mortality of corals worldwide (Hughes et al., 2018) continue to increase in severity and frequency (van Hooidonk et al., 2016; Oliver et al., 2018), then we may also see a collapse of canopy-forming macroalgae in many tropical regions. This means that with continuing ocean warming the future for an increasing number of tropical reefs may be one where two key habitat-forming groups - corals and canopy-forming macroalgae - are no longer able to sustain the productive and complex habitats that underpin key ecological functions and socio-economic benefits. Instead, we would see a greater dominance of macroalgae that have lower levels of structural complexity (e.g. EAM), lower areal productivity (e.g., *Dictyota*; Fig. 2A), and/or low palatability (e.g., *Turbinaria*; Bittick, Bilotti, Peterson, & Stewart, 2010). These types of macroalgal reef state will not support the same spectrum of ecosystem functions we have come to expect from diverse and productive tropical seascapes comprising coral, canopy-forming macroalgae and other complex reef habitats.

4. RESEARCH AND MANAGEMENT PRIORITIES

Tropical reefs are imperilled by a range of threats that have increased the risk and extent of coral-algal regime shifts around the world during the Anthropocene (Bellwood et al., 2004; Graham et al., 2015; Hughes et al., 2017). Wholesale shifts from coral to macroalgal-dominated states are an example of the negative effects of macroalgal overgrowth. However, macroalgae do have important roles to play in tropical marine ecosystems. Tropical macroalgal reefs are common in proximity to landmasses (Littler et al., 1991), where they can be one of the most prominent types of shallow-water habitat (Garrigue, 1995; Kobryn et al., 2011; Tano et al., 2017). This creates a risk of erroneously concluding that macroalgal-dominated areas are largely due to anthropogenic impacts such as eutrophication and overfishing. A key criterion for classifying a state of algal overgrowth should be evidence that a coral-algal regime shift has occurred, concomitant with feedback processes (e.g., reduced herbivory) that maintain a skew towards macroalgal reef states (Scheffer & Carpenter, 2003; Bellwood et al., 2004). In such circumstances, the key stressors should be identified and directly addressed in an attempt to promote recovery to a pre-regime shift state. However, if such evidence is lacking, then we cannot exclude the possibility that macroalgal-dominated habitats are a natural component of the tropical seascape (Bruno et al., 2014; Gove et al., 2015; Williams et al., 2015). Indeed, macroalgal reefs are found along coastlines and on remote reefs with relatively low anthropogenic impacts relevant to macroalgal growth (i.e., minimal land-use and catchment modifications, minimal harvest of herbivores), where they are part of an interconnected mosaic of coral and other patch habitat types (e.g., Kobryn et al., 2011; Gove et al., 2015; Williams et al., 2015). In such cases, macroalgal reefs may warrant protection to support their key roles in ecosystem productivity and function.

Macroalgal reefs can vary immensely in their capacity to support ecosystem functions, goods and services. High complexity macroalgal reefs comprising a mixture of canopy and understory taxa have the potential to support biodiversity and productivity at many levels, including key fisheries that underpin food security for tropical maritime nations. We suggest there is sufficient evidence to include complex macroalgal reefs as a key habitat within a mosaic of ‘seascape nurseries’ (Nagelkerken et al., 2015; Harborne et al., 2016) that warrant attention in conservation and spatial management strategies.

Evidence is also building that complex macroalgal reefs may be instrumental in supporting productivity across the tropical seascape via spatial subsidies, and in so doing, support a broad range of ecosystem goods that span direct algal harvests to enhanced levels of fishable biomass. Given the potential for wide variations in canopy quality and biomass turnover, and the functional consequences for the role of macroalgal reefs in tropical marine ecosystems, there is a need to identify and protect high quality patches from local threats. The latter include increases in turbidity, habitat destruction from anchoring, sediment smothering from poor catchment management and dredging (Umar, McCook, & Price, 1998), as well as overfishing-induced trophic cascades that drive the ecological release of herbivores (e.g., urchins; Wallner-Hahn et al., 2015).

Given the vast differences in the emergent ecosystem functions that can arise from different types of macroalgal reefs, identifying the environmental thresholds that may bound different macroalgal reef states is a high priority. Low complexity macroalgal reefs, such as those typical of the early stages of a coral-algal regime shift under high anthropogenic stress, are unlikely to support high levels of marine biodiversity and ecosystem function. Yet, there is a strong potential for these types of macroalgae to dominate tropical reefs of the Anthropocene. Since so many ecosystem functions flow from canopy structure and turnover, we also need to assess how environmental change may affect tropical macroalgal phenology (Koch et al., 2013). In part, this means a better understanding of the resilience of different macroalgal reef types to disturbance such as unseasonal canopy loss from storms and marine heatwaves, and their resistance to long-term stressors such as sedimentation and climate change. Indeed, more information on the thermal thresholds that will trigger shifts in the timing and extent of macroalgal canopy production and decay should be a priority. Equally important is understanding the scale at which functional connectivity occurs among macroalgal and other tropical reef habitats, which will require study of the distances, pathways and vectors of macroalgal biomass movement and utilisation across the seascape (Olds et al., 2018). In doing so, we can then understand how tropical macroalgae contribute to the abundance and productivity of tropical marine ecosystems that comprise a mosaic of connected habitats. This integrated view of ecosystem functions that connect multiple habitat types (coral or otherwise) will be critical in setting appropriate targets for the spatial conservation and management of diverse tropical seascapes.

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AUTHOR CONTRIBUTIONS

CF and SW conceived the ideas and led the writing of the manuscript; all authors contributed data to the meta-analysis, which CF collated and analysed; all authors contributed critically to the writing of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data are available in the Supporting Information and sources cited therein.

REFERENCES

Abesamis, R. A., & Russ, G. R. (2010). Patterns of recruitment of coral reef fishes in a monsoonal environment. *Coral Reefs*, 29, 911-921.

Aburto-Oropeza, O., Sala, E., Paredes, G., Mendoza, A., & Ballesteros, E. (2007). Predictability of reef fish recruitment in a highly variable nursery habitat. *Ecology*, 88, 2220–2228.

Ateweberhan, M., Bruggemann, J. H., & Breeman, A. M. (2006). Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). *Coral Reefs*, 25, 391–406.

Atwood, T. B., Madin, E. M. P., Harborne, A. R., Hammill, E., Luiz, O. J., Ollivier, Q. R., … Lovelock, C. E. (2018). Predators Shape Sedimentary Organic Carbon Storage in a Coral Reef Ecosystem. *Frontiers in Ecology and Evolution*, 6, 110.

Babcock, R. C., Pillans, R. D., & Rochester, W. A. (2017). Environmental and individual effects on the behaviour and spawning movements of *Lethrinus nebulosus* on a coral reef. *Marine and Freshwater Research*, 68, 1422–1437.

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, 429, 827–833.

Bellwood, D. R., Tebbett, S. B., Bellwood, O., Mihalitsis, M., Morais, R. A., Streit, R. P., & Fulton, C. J. (2018). The role of the reef flat in coral reef trophodynamics: Past, present, and future. *Ecology and Evolution*, 8, 4108–4119.

Berkström, C., Gullström, M., Lindborg, R., Mwandya, A. W., Yahya, S. A. S., Kautsky, N., & Nyström, M. (2012). Exploring ‘knowns’ and ‘unknowns’ in tropical seascape connectivity with insights from East African coral reefs. *Estuarine, Coastal and Shelf Science*, 107, 1-21.

Berkström, C., Lindborg, R., Thyresson, M., & Gullström, M. (2013). Assessing connectivity in a tropical embayment: Fish migrations and seascape ecology. *Biological Conservation*, 166, 43–53.

Bigg, G. R., Jickells, T. D., Liss, P. S., & Osborn, T. J. (2003). The role of the oceans in climate. *International Journal of Climatology*, 23, 1127–1159.

Bittick, S. J., Bilotti, N. D., Peterson, H. A., Stewart, H. L. (2010). *Turbinaria ornata* as an herbivory refuge for associate algae. *Marine Biology*, 157, 317–323.

Borines, M. G., McHenry, M. P., & de Leon, R. L. (2011). Integrated macroalgae production for sustainable bioethanol, aquaculture and agriculture in Pacific island nations. *Biofuels, Bioproducts and Biorefining*, 5, 599–608.

Bruno, J. F., Precht, W. F., Vroom, P. S., & Aronson, R. B. (2014). Coral reef baselines: how much macroalgae is natural? *Marine Pollution Bulletin*, 80, 24–9.

Choat, J. H., Robbins, W. D., & Clements, K. D. (2004). The trophic status of herbivorous fishes on coral reefs. II. Food processing modes and trophodynamics. *Marine Biology*, 145, 445-454.

Chung, I. K., Beardall, J., Mehta, S., Sahoo, D., & Stojkovic, S. (2011). Using marine macroalgae for carbon sequestration: A critical appraisal. *Journal of Applied Phycology*, 23, 877–886.

Cole, A. J., Lawton, R. J., Wilson, S. K., & Pratchett, M. S. (2012). Consumption of tabular acroporid corals by reef fishes: A comparison with plant-herbivore interactions. *Functional Ecology*, 26, 307–316.

Doherty, P. (1991). Spatial and temporal patterns in recruitment. pp. 261-293, in: Sale, P. F. (ed) *The Ecology of Fishes on Coral Reefs*. Academic Press, Sydney.

Downie, R., Babcock, R., Thomson, D., & Vanderklift, M. (2013). Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs. *Marine Ecology Progress Series*, 482, 217–225.

Edgar, G. J. (1990). The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. *Journal of Experimental Marine Biology and Ecology*, 137, 215–240.

Edgar, G. J., & Aoki, M. (1993). Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese Sargassum. *Oecologia*, 95, 122–133.

Fulton, C. J., Depczynski, M., Holmes, T. H., Noble, M. M., Radford, B., Wernberg, T., & Wilson, S. K. (2014). Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. *Limnology and Oceanography*, 59, 156–166.

Garrigue, C. (1995). Macrophyte associations on the soft bottoms of the south-west lagoon of New Caledonia: Description, structure and biomass. *Botanica Marina*, 38, 481–492.

Glenn, E., Smith, C., & Doty, M. (1990). Influence of antecedent water temperatures on standing crop of a *Sargassum* spp.-dominated reef flat in Hawaii. *Marine Biology*, 105, 323–328.

Goatley, C. H. R., & Bellwood, D. R. (2011). The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE*, 6, e27307.

Gove, J., Williams, G., McManus, M., Clark, S., Ehses, J., & Wedding, L. (2015). Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. *Marine Ecology Progress Series*, 522, 33–48.

Gouvea, L. P., Schubert, N., Martins, C. D. L., Sissini, M., Ramlov, F., Rodrigues, E. R. de O., … Horta, P. A. (2017). Interactive effects of marine heatwaves and eutrophication on the ecophysiology of a widespread and ecologically important macroalga. *Limnology and Oceanography*, 62, 2056–2075.

Graham, N. A., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, 32, 315-26.

Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518, 94–97.

Grober-Dunsmore, R., Frazer, T. K., Beets, J. P., Lindberg, W. J., Zwick, P., & Funicelli, N. A. (2008). Influence of landscape structure on reef fish assemblages. *Landscape Ecology*, 23, 37–53.

Harborne, A. R., Nagelkerken, I., Wolff, N. H., Bozec, Y.-M., Dorenbosch, M., Grol, M. G. G., & Mumby, P. J. (2016). Direct and indirect effects of nursery habitats on coral-reef fish assemblages, grazing pressure, and benthic dynamics. *Oikos*, 125, 957–967.

Hatcher, B. G. (1990). Coral reef primary productivity: a hierarchy of pattern and process. *Trends in Ecology & Evolution*, *5*, 149–155.

Hernández, C. A., Sangil, C., Fanai, A., & Hernández, J. C. (2018). Macroalgal response to a warmer ocean with higher CO_2 concentration. *Marine Environmental Research*, 136, 99–105.

Hicks, C. C., & McClanahan, T. R. (2012). Assessing gear modifications needed to optimize yields in a heavily exploited, multi-species, seagrass and coral reef fishery. *PLoS ONE*, 7, e36022.

Hoey, A. S., Brandl, S. J., & Bellwood, D. R. (2013). Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs*, 32, 973–984.

Hughes, T. P. (1994). Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science,* 265*,* 1547–1551.

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., … Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, 546, 82–90.

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, 359, 80–83.

Hwang, R.-L., Tsai, C.-C., & Lee, T.-M. (2004). Assessment of temperature and nutrient limitation on seasonal dynamics among species of *Sargassum* from a coral reef in southern Taiwan. *Journal of Phycology*, 40, 463–473.

Hyndes, G. A., Nagelkerken, I., Mcleod, R. J., Connolly, R. M., Lavery, P. S., & Vanderklift, M. A. (2014). Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biological Reviews*, 89, 232–254.

Isari, S., Pearman, J. K., Casas, L., Michell, C. T., Curdia, J., Berumen, M. L., & Irigoien, X. (2017). Exploring the larval fish community of the central Red Sea with an integrated morphological and molecular approach. *PLoS ONE*, 12, e0182503.

Johnson, M. D., Price, N. N., & Smith, J. E. (2014). Contrasting effects of ocean acidification on tropical fleshy and calcareous algae. *PeerJ*, 2, e411.

Kelly, L. W., Barott, K. L., Dinsdale, E., Friedlander, A. M., Nosrat, B., Obura, D., … Rohwer, F. (2012). Black reefs: Iron-induced phase shifts on coral reefs. *ISME Journal, 6*, 638–649.

Kinsey, D. W. (1977). Seasonality and zonation in coral reef productivity and calcification. In Proceedings of the Third International Coral Reef Symposium, 2, 383–388.

Kobryn, H. T., Wouters, K., & Beckley, L. E. (2011). *Habitats of the Ningaloo Reef and adjacent coastal areas determined through hyperspectral imagery*. Ningaloo Collaboration Cluster Final Report No. 1b, CSIRO National Research Flagships Wealth from Oceans, Canberra. https://research.csiro.au/ningaloo/ningaloo-collaboration-cluster/research-outputs-from-the-nrp/

Koch, M., Bowes, G., Ross, C., & Zhang, X. H. (2013). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology*, 19, 103–132.

Kramer, M. J., Bellwood, D. R., & Bellwood, O. (2014). Benthic crustacea on coral reefs: A quantitative survey. *Marine Ecology Progress Series*, 511, 105–116.

Krause-Jensen, D., & Duarte, C. M. (2016). Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience,* 9, 737-743.

Lim, I., Wilson, S. K., Holmes, T. H., Noble, M. M., & Fulton, C. J. (2016). Specialisation within a shifting habitat mosaic underpins the seasonal abundance of a tropical fish. *Ecosphere*, 7, e01212.

Littler, M.M., & Littler, D.S. (1988). Structure and role of algae in tropical reef communities. In: Lembi, C. A., & Waaland, J. R. (eds) *Algae and Human Affairs*, Cambridge University Press, Cambridge, pp. 29–56.

Littler, M. M., Littler, D. S., & Titlyanov, E. A. (1991). Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. *Coral Reefs*, 10, 199–209.

McCourt, R. (1984). Seasonal patterns of abundance, distributions, and phenology in relation to growth strategies of three *Sargassum* species. *Journal of Experimental Marine Biology and Ecology*, 74, 141–156.

McIlwain, J. L. (2003). Fine-scale temporal and spatial patterns of larval supply to a fringing reef in Western Australia. *Marine Ecology Progress Series*, 252, 207–222.

Morais, R. A., & Bellwood, D. R. (2018). Global drivers of reef fish growth. *Fish and Fisheries*, doi:10.1111/faf.12297

Mumby, P. J. (2009). Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs*, 28, 761–773.

Mumby, P. J., & Steneck, R. S. (2018). Paradigm lost: dynamic nutrients and missing detritus on coral reefs. *BioScience* doi:10.1093/biosci/biy055

Nagelkerken, I., Sheaves, M., Baker, R., & Connolly, R. M. (2015). The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*, 16, 362–371.

Olds, A. D., Nagelkerken, I., Huijbers, C. M., Gilby, B. L., Pittman, S. J., Schlacher, T. A. (2018). Connectivity in Coastal Seascapes. In: Pittman SJ (ed) *Seascape Ecology*. John Wiley & Sons, pp. 261-292.

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., … Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*, 1324.

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28, 289–316.

Poore, A. G. B., Campbell, A. H., Coleman, R. A., Edgar, G. J., Jormalainen, V., Reynolds, P. L., … Emmett Duffy, J. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, 15, 912–922.

Prince, J. S. (1980). The ecology of *Sargassum pteropleuron* Grunow (Phaeophyceae, Fucales) in the waters off South Florida II. Seasonal photosynthesis and respiraton of *S. pteropleuron* and comparison of its phenology with that of *S. polyceratium* Montagne. *Phycologia*, 19, 190–193.

Prud’homme van Reine, W. F., & Trono, G. C. (2001). *Plant Resources of South-East Asia No. 15 Cryptogams: Algae*. Backhuys Publishers, Leiden.

Rix, L., de Goeij, J. M., van Oevelen, D., Struck, U., Al-Horani, F. A., Wild, C., & Naumann, M. S. (2017). Differential recycling of coral and algal dissolved organic matter via the sponge loop. *Functional Ecology*, 31, 778–789.

Roberts, D. A., Paul, N. A., Dworjanyn, S. A., Bird, M. I., & De Nys, R. (2015). Biochar from commercially cultivated seaweed for soil amelioration. *Scientific Reports*, 5, 9665. doi:10.1038/srep09665

Robertson, D. R. (1990). Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. *Journal of Experimental Marine Biology and Ecology*, 144, 49–62.

Robinson, J. P. W., Wilson, S. K., Robinson, J., Gerry, C., Lucas, J., Assan, C., … Graham, N. A. J. (2018). Productive instability of coral reef fisheries after climate-driven regime shifts. *Nature Ecology and Evolution*. doi:10.1038/s41559-018-0715-z

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, 24, 1000-1005

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2018). Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology*, 55, 1041–1049.

Roff, G., & Mumby, P. J. (2012). Global disparity in the resilience of coral reefs. *Trends in Ecology and Evolution*, 27, 404–413.

Rossier, O., & Kulbicki, M. (2000). A comparison of fish assemblages from two types of algal beds and coral reefs in the south-west lagoon of New Caledonia. *Cybium*, 24, 3–26.

Russ, G. R. (2003). Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs*, 22, 63–67.

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, 18, 648-656.

Sondak, C. F. A., Ang, P. O., Beardall, J., Bellgrove, A., Boo, S. M., Gerung, G. S., … Chung, I. K. (2017). Carbon dioxide mitigation potential of seaweed aquaculture beds (SABs). *Journal of Applied Phycology*, 29, 2363–2373.

Song, M., Duc Pham, H., Seon, J., & Chul Woo, H. (2015). Marine brown algae: A conundrum answer for sustainable biofuels production. *Renewable and Sustainable Energy Reviews*, 50, 782–792.

Sponaugle, S., Walter, K. D., Grorud-Colvert, K., & Paddack, M. J. (2012). Influence of marine reserves on reef fish recruitment in the upper Florida Keys. *Coral Reefs*, 31, 641–652.

Srinivasan, M., & Jones, G. P. (2006). Extended breeding and recruitment periods of fishes on a low latitude coral reef. *Coral Reefs*, 25, 673–682.

Steneck, R. S., & Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos*, 69, 476-498.

Stephenson, T. A., Stephenson, A., Tandy, G., & Spender, M. (1931). The structure and ecology of low isles and other reefs. *Great Barrier Reef Expedition 1928-29 Scientific Reports*, 3, 17-112.

Stimson, J. (2013). Consumption by herbivorous fishes of macroalgae exported from coral reef flat refuges to the reef slope. *Marine Ecology Progress Series*, 472, 87–99.

Tano, S., Eggertsen, M., Wikström, S. A., Berkström, C., Buriyo, A. S., & Halling, C. (2016). Tropical seaweed beds are important habitats for mobile invertebrate epifauna. *Estuarine, Coastal and Shelf Science*, 183, 1–12.

Tano, S. A., Eggertsen, M., Wikstrom, S., Berkstrom, C., Buriyo, A., & Halling, C. (2017). Tropical seaweed beds as important habitats for juvenile fish. *Marine and Freshwater Research*, 68, 1921–1934.

Taylor, B. M., & Mills, J. S. (2013). Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperor fishes. *Coral Reefs*, 32, 1077–1087.

Umar, M. J., McCook, L. J., & Price, I. R. (1998). Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. *Coral Reefs*, 17, 169–177.

van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadia, G., Raymundo, L., … Planes, S. (2016). Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports*, 6, 39666.

van Lier, J. R., Wilson, S. K., Depczynski, M., Wenger, L. N., & Fulton, C. J. (2018). Habitat connectivity and complexity underpin fish community structure across a seascape of tropical macroalgae meadows. *Landscape Ecology*, 33, 1287-1300.

Vergés, A., Vanderklift, M. a, Doropoulos, C., & Hyndes, G. a. (2011). Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *PloS One*, 6, e17115.

Vuki, V. C., & Price, I. R. (1994). Seasonal changes in the *Sargassum* populations on a fringing coral reef, Magnetic Island, Great Barrier Reef region, Australia. *Aquatic Botany*, 48, 153–166.

Wallner-Hahn, S., de la Torre-Castro, M., Eklöf, J. S., Gullström, M., Muthiga, N. A., & Uku, J. (2015). Cascade effects and sea-urchin overgrazing: An analysis of drivers behind the exploitation of sea urchin predators for management improvement. *Ocean and Coastal Management*, 107, 16–27.

Wenger, L. N., Van Lier, J. R., & Fulton, C. J. (2018). Microhabitat selectivity shapes the seascape ecology of a carnivorous macroalgae-associated tropical fish. *Marine Ecology Progress Series*, 590, 187–200.

Wild, C., Huettel, M., Klueter, A., Kremb, S. G., Rasheed, M. Y. M., & Jorgensen, B. B. (2004). Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature*, 428, 66–70.

Williams, D. McB. (1983). Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. *Marine Ecology Progress Series*, 10, 231–237.

Williams, G. J., Gove, J. M., Eynaud, Y., Zgliczynski, B. J., & Sandin, S. A. (2015). Local human impacts decouple natural biophysical relationships on Pacific coral reefs. *Ecography*, 38, 751–761.

Wilson, S. K., Bellwood, D. R., Choat, J. H., & Furnas, M. J. (2003). Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology: An Annual Review*, 41, 279–309.

Wilson, S. K., Fulton, C. J., Depczynski, M., Holmes, T. H., Noble, M. M., Radford, B., & Tinkler, P. (2014). Seasonal changes in habitat structure underpin shifts in macroalgae-associated tropical fish communities. *Marine Biology*, 161, 2597–2607.

Wilson, S. K., Depczynski, M., Holmes, T. H., Noble, M. M., Radford, B. T., Tinkler, P., & Fulton, C. J. (2017). Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. *Limnology and Oceanography*, 62, 1868–1880.

Wilson, S. K., Depcyznski, M., Fisher, R., Holmes, T. H., Noble, M. M., Radford, B. T., … Fulton, C. J. (2018). Climatic forcing and larval dispersal capabilities shape the replenishment of fishes and their habitat-forming biota on a tropical coral reef. *Ecology and Evolution*, 8, 1918–1928.

Zubia, M., Andréfouët, S., & Payri, C. (2015). Distribution and biomass evaluation of drifting brown algae from Moorea lagoon (French Polynesia) for eco-friendly agricultural use. *Journal of Applied Phycology*, 27, 1277–1287.

SUPPORTING INFORMATION

Additional Supporting Information may be found online.