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Review

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The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts

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Climate-driven changes in biotic interactions can profoundly alter ecological communities, particularly when they impact foundation species. In marine systems, changes in herbivory and the consequent loss of dominant habitat forming species can result in dramatic community phase shifts, such as from coral to macroalgal dominance when tropical fish herbivory decreases, and from algal forests to 'barrens' when temperate urchin grazing increases. Here, we propose a novel phase-shift away from macroalgal dominance caused by tropical herbivores extending their range into temperate regions. We argue that this phase shift is facilitated by poleward-flowing boundary currents that are creating ocean warming hotspots around the globe, enabling the range expansion of tropical species and increasing their grazing rates in temperate areas. Overgrazing of temperate macroalgae by tropical herbivorous fishes has already occurred in Japan and the Mediterranean. Emerging evidence suggests similar phenomena are occurring in other temperate regions, with increasing occurrence of tropical fishes on temperate reefs.

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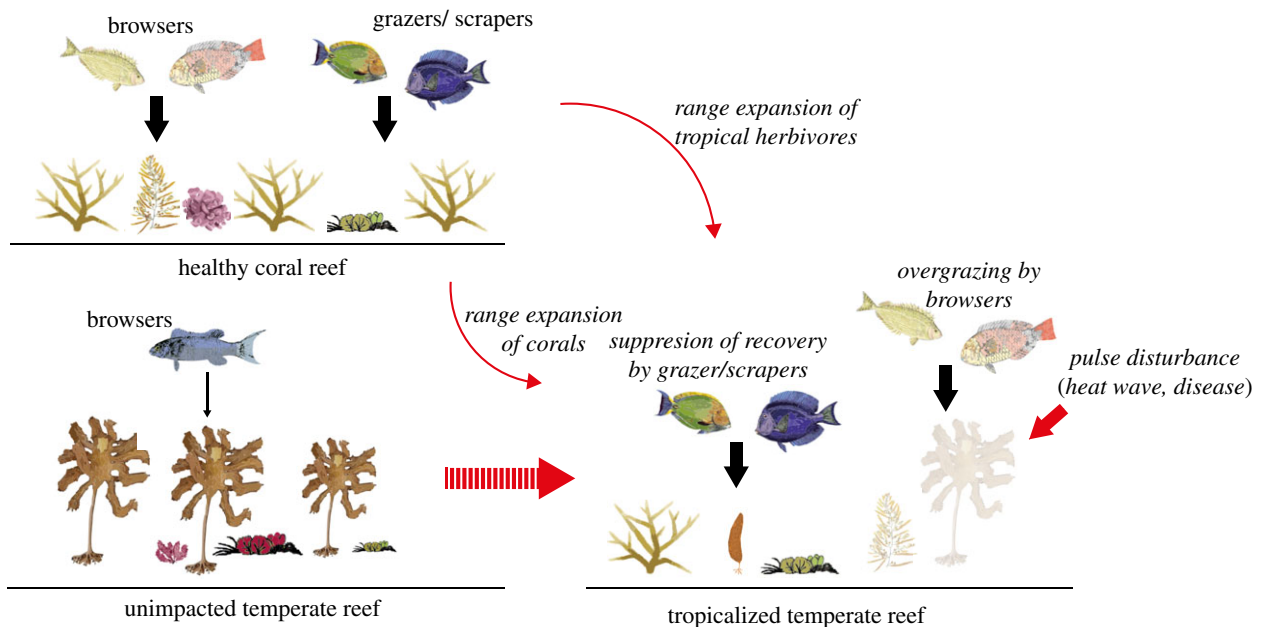
Figure 1. Conceptual model of fish control of macroalgal biomass on coral reefs, unimpacted and 'tropicalized' temperate reefs. *Proposed mechanisms shifting macroalgal-dominated temperate reefs to 'tropicalized' systems are in italics.* Black arrows of different widths symbolize dissimilar levels of herbivory. Faded macroalgae represent their decline in tropicalized systems owing to: (i) direct overgrazing by browsers, or (ii) prevention of recovery by grazers and scrapers when other sources of stress first initiate macroalgal decline.

1. Introduction

Understanding and predicting the impacts of climate change is now a central theme in ecology. Climate-related changes in temperature, rainfall patterns, frequency of extreme weather events and, in marine systems, altered ocean circulation and acidification, can all affect the physiology, distribution and phenology of organisms [1]. Such direct effects of climate change are well documented in both terrestrial and marine systems [2,3].

Climate change can also indirectly affect organisms by altering biotic interactions, which can have profound consequences for populations, community composition and ecosystem functions [4]. Indirect effects may occur: (i) via generation of new biotic interactions, as range-shifted species appear for the first time in naive communities [5]; (ii) by removing existing interactions when species shift out of their existing range [6]; or (iii) by modulating key behavioural, physiological or other traits that mediate species interactions [3]. When climate-driven changes in biotic interactions involve keystone or foundation species, impacts can cascade through the associated community [4].

Marine communities are thought to be more strongly regulated by top-down forces (consumers) than terrestrial communities [7], and climate-driven modulation of biotic interactions between consumers and their prey could therefore strongly impact marine systems. Herbivory is especially intense in marine environments, with approximately 70% of benthic primary production being consumed by herbivores globally [8]. Changes in herbivory in marine systems can cause community phase shifts in which the dominant habitat-forming organisms are eliminated, or replaced by a completely different group. Classic examples are found in tropical coral reefs, where a *decrease* in herbivory leads to a shift from coral- to algal-dominated reefs [9], and in temperate algal forests, where an *increase* in herbivory by sea urchins leads to deforested barrens [10]. Ocean warming has been implicated as a factor for both of these phase shifts [5,10].

Here, we propose a novel phase shift in coastal marine systems, driven by changes to herbivory linked to worldwide ocean warming: the potential deforestation of temperate algal forests and decline in temperate seagrass beds as tropical herbivores expand their ranges polewards (figure 1). This expansion exposes temperate macrophytes to high densities and diversity of tropical vertebrate herbivores that are capable of removing 100% of algal primary production on tropical coral reefs [11]. We first consider the oceanographic conditions that create ocean warming hotspots around the globe, highlighting the role of western boundary currents (WBCs) that transport warm tropical water into temperate regions. We then review range shifts of tropical herbivorous fishes and their effects on temperate macroalgal forests and seagrass meadows at these hotspots. Potential mechanisms for this novel herbivore-mediated phase shift are discussed, focusing on the functional diversity of consumers and primary producers, novelty effects and chemical defences. We then consider how changes in marine herbivory interact with other climate-mediated stressors to facilitate macrophyte declines and the tropicalization of temperate communities. Finally, the broader implications and societal impacts of this novel phase shift are examined in relation to food security, conservation and management.

2. Poleward boundary currents, other ocean warming hotspots and their consequences to species distribution and abundance

A large portion of the ocean has undergone significant warming over the past century that has been attributed to anthropogenic climate change [12]. There are however considerable regional differences in the rate of warming, with localized areas of enhanced warming commonly referred to as hotspots [13]. A common feature across many ocean temperature datasets is that during the twentieth century, temperate regions

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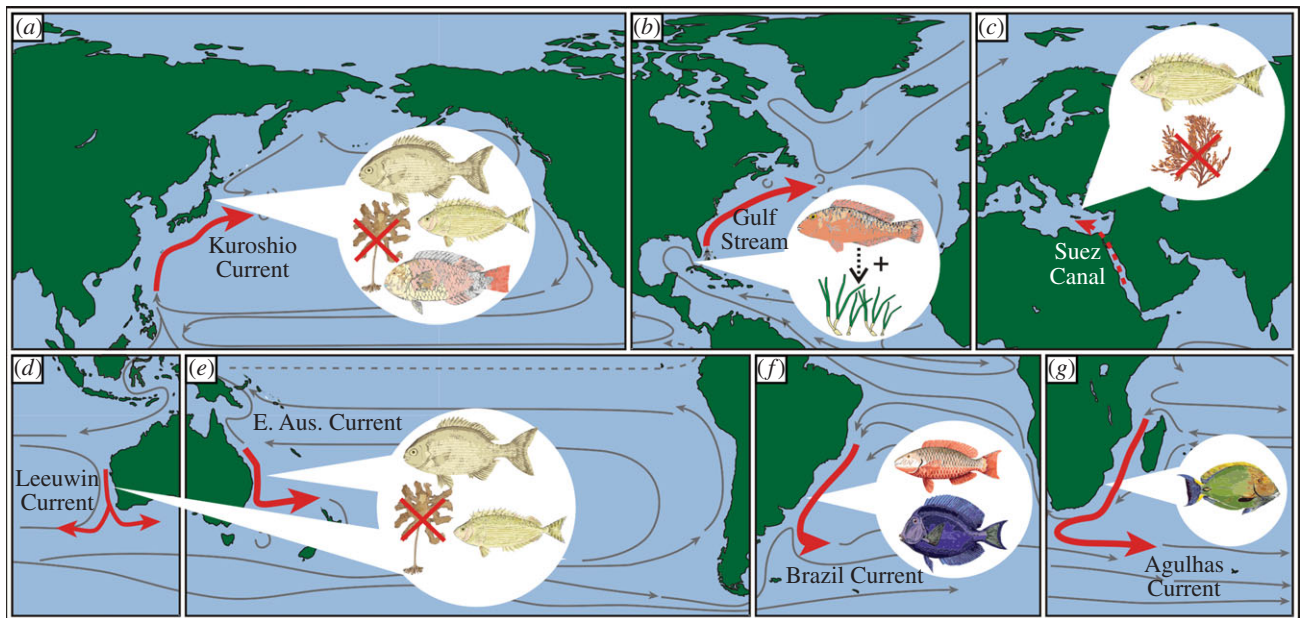
Figure 2. World map showing schematic of large-scale circulation, shifts in herbivorous fishes and ecological impacts in broad regions where emerging signs of the tropicalization of temperate marine communities have been recorded. Panels (*a,b*) and (*e*–*g*) highlight western (and eastern; *d*) boundary currents (depicted as arrows) that have been associated with ocean warming hotspots. Panel (*c*) shows the eastern Mediterranean region and the Suez Canal (dashed arrow). Loss of macrophytes is depicted with crosses symbolizing overgrazing of *Ecklonia* spp. by *Kyphosus* spp., *Siganus* spp. and *C. japonicus* in Japan (*a*); decline of *Ecklonia radiata* and potential overgrazing by *Kyphosus* spp. and *Siganus* spp. in western (*d*) and eastern (*e*) Australia, and loss of *Cystoseira* spp. in the Mediterranean owing to overgrazing by *Siganus* spp. (*c*). Increased herbivory by range-shifting parrotfish in the Gulf of Mexico is symbolized with a 'plus' symbol and a dashed black arrow (*b*). Tropical herbivorous fishes have been observed shifting their distribution in southeastern America (*f*) and southeastern Africa (*g*). See the electronic supplementary material, table S1 for a full list of range-shifting species and documented impacts. (Online version in colour.)

along poleward-flowing WBCs (figure 2) have warmed two to three times faster than the global mean (figure 3*a*) [14]. Regions with continuous tropical–temperate coastlines that are strongly influenced by WBCs—Japan, eastern USA, eastern Australia, northern Brazil and southeastern Africa—are thus potential hotspots for biological change as organisms respond to the warming of these coastal waters (electronic supplementary material, table S1).

Enhanced warming of temperate coastlines by WBCs is associated with a stronger poleward transport of warm low-latitude water driven by changes in the basin-wide wind field. In the Southern Hemisphere in particular, these wind changes have been tied to stratospheric ozone depletion and increased greenhouse gas concentrations [15]. Most state-of-the-art climate models incorporating these drivers (which form the Coupled Model Intercomparison Project v. 5, CMIP5; [16]) are able to reproduce many of the observed features for these trends in sea surface temperature (figure 3*b*). Model projections for the twenty-first century suggest that certain western boundary regions will continue to warm faster than the global average (figure 3*c*) probably forcing significant biological change.

In addition to WBCs, other oceanographic features also transport tropical water towards temperate regions. The poleward-flowing Leeuwin current along the coast of western Australia is a prime example (figure 2*d*). In 2011, a strengthening of this current caused a marine 'heat wave' in which the coastal waters along much of west Australia increased by 2–4°C for approximately two months [17]. Connectivity can also be altered substantially by humans, as with the opening of the Suez Canal that now allows connections between the previously isolated tropical Indo-Pacific waters and the Mediterranean Sea.

Changes in ocean circulation influence the distribution of marine species not only by shifting thermal zones [13], but also by affecting dispersal patterns [5]. Most coastal species have pelagic life-history stages (e.g. larvae, spores), whose abundance and distribution patterns are strongly influenced by coastal boundary currents such as WBCs [18]. This strongly influences recruitment and connectivity of fishes, macroalgae and other organisms [18]. Given the relatively low (or no) motility of many benthic organisms as adults and the restricted home ranges of most coastal fishes [19], the effects of altered circulation on larval dispersal can be considerable. There is now strong evidence for enhanced dispersal and range expansions of species from several intensifying WBCs, such as the East Australian Current and the Kuroshio Current (electronic supplementary material, table S1) [5,20]. Nevertheless, other factors such as warmer background temperatures may also affect growth rates and settlement times of tropical larvae, and consequently may also modulate future dispersal trajectories.

3. Intrusion of tropical herbivorous fishes into temperate systems and impacts on temperate algal and seagrass beds

The distributions of many marine fishes are shifting poleward [2,20], impacting world fisheries and causing a global 'tropicalization' of catch [21]. An increase in seawater temperatures and/or the poleward intensification of ocean currents has been linked to the intrusion of tropical fishes into temperate waters in all regions influenced by poleward boundary currents (electronic supplementary material, table S1): Japan (figure 2*a*; [22,23]), southeastern USA (figure 2*b*; [24,25]),
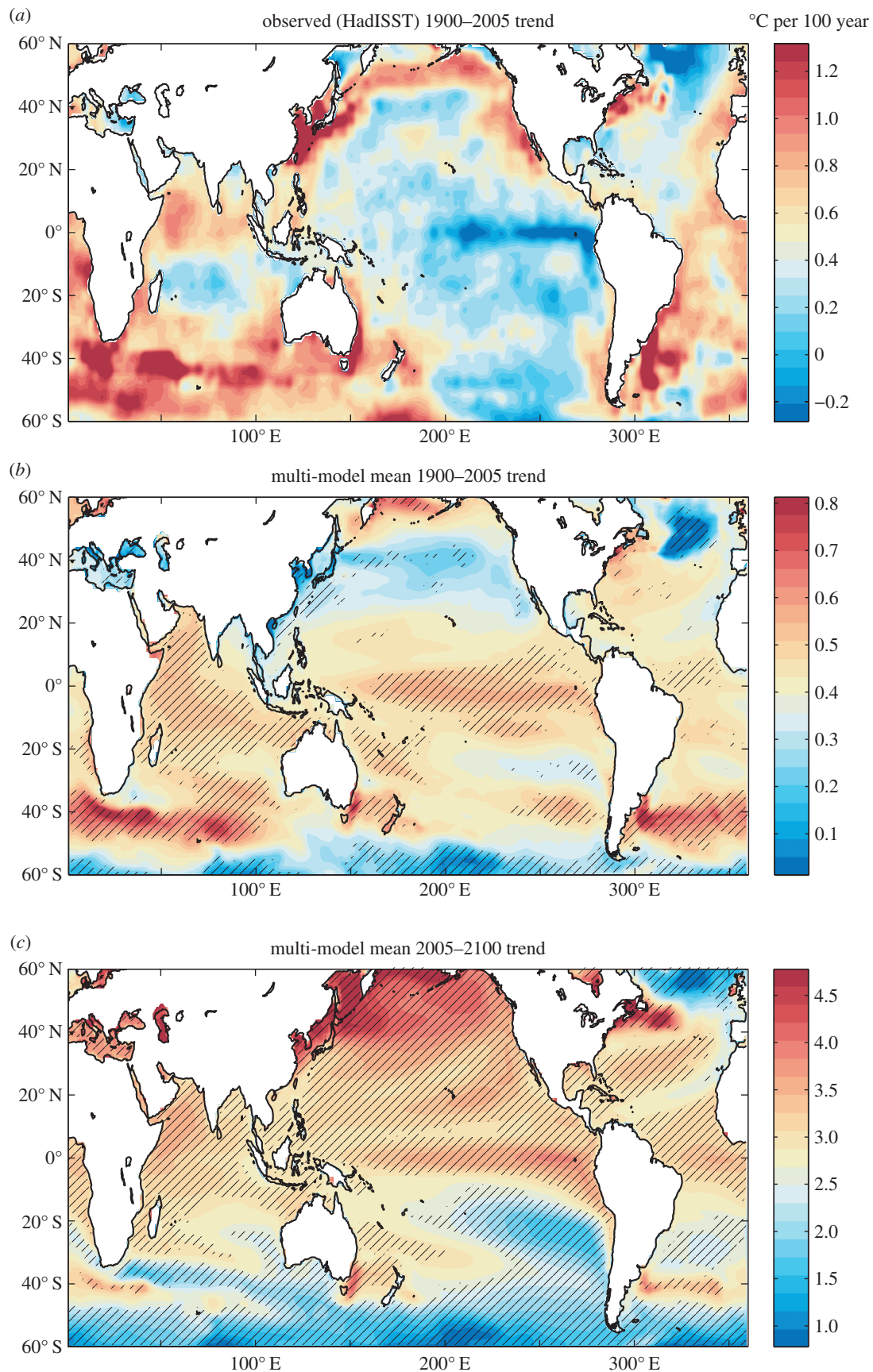
Figure 3. Trends in global sea surface temperatures (SST). (a) 1900–2005 trend in observed (HadISST) SST, (b) multi-model mean SST trend for the same period based on 34 CMIP5 models, (c) multi-model mean SST trend for 2005–2100 based on 28 CMIP5 models under the 'business as usual' RCP8.5 scenario. Mottling in (b) and (c) indicates regions where at least 75% of models agree that warming will be faster or slower than the globally averaged rate of warming. (Units °C per century) Note colour scales differ.

western (figure 2d; [17,26]) and eastern Australia (figure 2e; [27]), northeastern South America (figure 2f; [28,29]) and South Africa (figure 2g; [30]). Intrusions include key herbivores

from coral reef systems (see the electronic supplementary material, table S1 for a detailed species list), such as the unicorn-fish *Naso unicornis* [22,27], numerous species of *Acanthurus*

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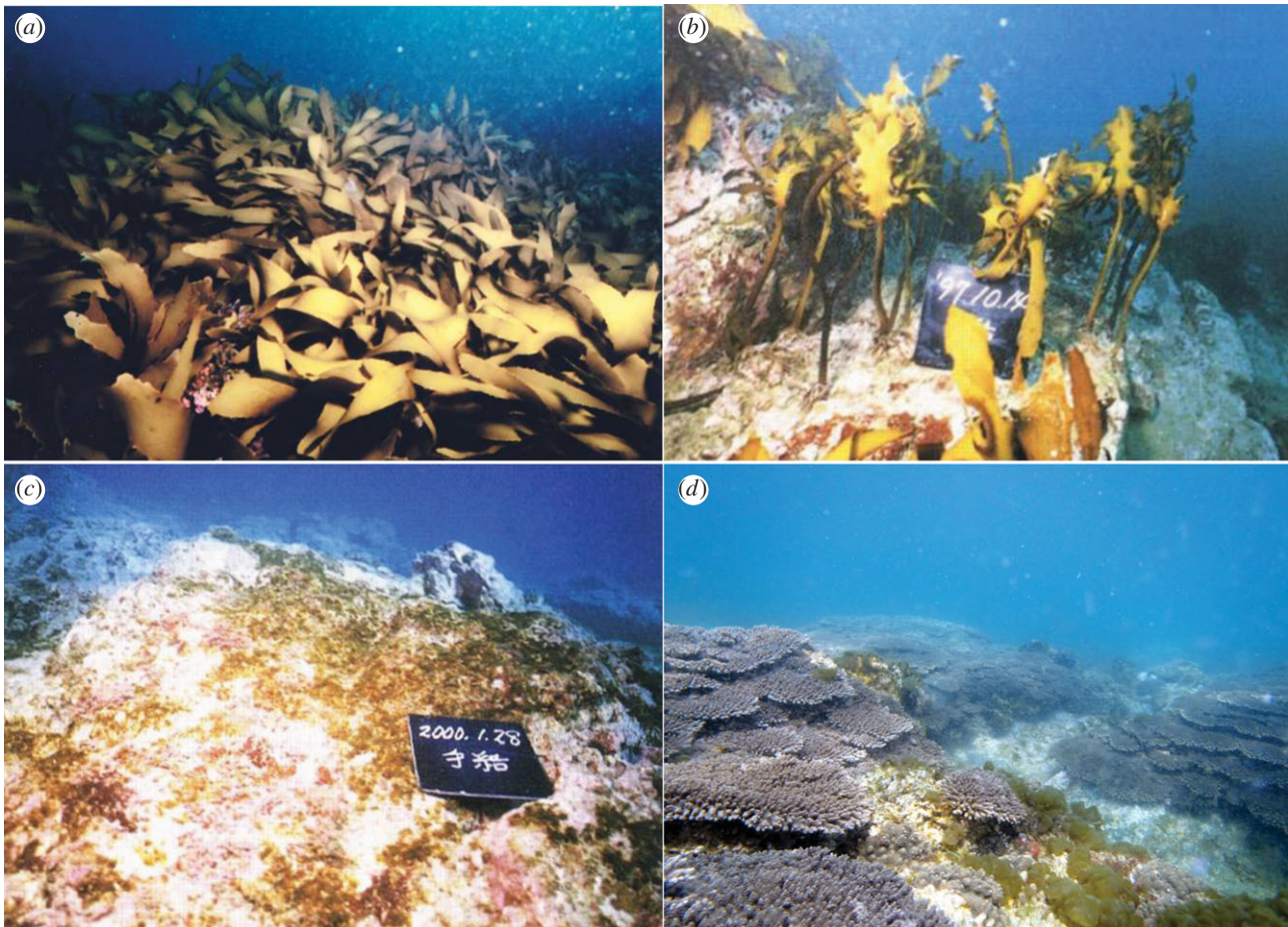
Figure 4. Underwater photographs from Tosa Bay (Southern Japan) showing: (*a*) well-developed *Ecklonia cava* bed in the early 1990s; (*b*) overgrazed *E. cava* bed ('isoyake') in October 1997; (*c*) rocky barren area in January 2000; (*d*) coral communities present in January 2013. Photographs (*a,d*) and (*b,c*) were taken from sites <50 m apart; the distance between sites (*a–d*) and (*b,c*) is approximately 400 m. The full original distribution of *E. cava* and its decline in Tosa Bay are reported by Serisawa *et al.* [34]. Photograph credits: (*a–c*) Zenji Imoto and (*d*) Yohei Nakamura.

[23–25,30] as well as many parrotfishes [23–25,28,29] and rabbitfishes [23,26]. In addition, tropical herbivorous rabbitfishes have colonized the Mediterranean Sea via the Suez Canal and established large populations (figure 2*c*; [31]).

Grazing by warm-water herbivorous fishes has had the greatest ecological impacts to date in southern Japan and the Mediterranean (electronic supplementary material, table S1), whereas evidence is growing in Australia and the USA (figure 1).

(a) Southern Japan and the 'isoyake' phenomenon

Increases in ocean temperature and a rise in the abundance of tropical fishes have coincided with a dramatic decline in macroalgal beds in southern Japan over the past three decades (figure 2*a* and the electronic supplementary material, table S1) [32,33]. It is estimated that the mass disappearance of kelp (*Ecklonia* spp.) and fucoid (*Sargassum* spp.) beds in southern Japan totals several thousand hectares, representing a loss of more than 40% of the cover of macroalgal beds since the 1990s [32]. This replacement of algal forests by deforested barrens is known in Japan as 'isoyake' (figure 4).

Tosa Bay in southern Japan (33° N) provides a dramatic example of a phase shift where a temperate kelp ecosystem has been tropicalized (figure 4) [23]. In the 1980s, benthic communities in Tosa Bay were dominated by forests of the kelp *Ecklonia cava* [34] (figure 4*a*). These algal beds declined following persistently warm conditions caused by the 1997 El Niño southern oscillation event [35]. Remaining populations

showed clear signs of intense herbivory by fishes by the end of the decade (figure 4*b*), resulting in denuded substrate, or isoyake, by the early 2000s (figure 4*c*). Over time, kelp forests have been replaced by reef building corals which now dominate the benthos (figure 4*d*) [36].

While multiple mechanisms may interact to produce isoyake, increased herbivory combined with the direct effects of changes in temperature are consistently cited as critical factors [33,37]. The rabbitfish *Siganus fuscescens*, the parrotfish *Calotomus japonicus* and various kyphosids appear to be the most responsible for the overgrazing of kelp beds and the creation of isoyake in southern Japan [33,37]. These tropical and subtropical species have been present in southern Japan for more than a century, but their annual grazing rates have increased dramatically as winter ocean temperatures have risen [33]. Warmer waters increase grazing rates of tropical fishes [38], and it is this temperature-mediated increase in grazing that has been linked to the regional disappearance of kelp forests in southern Japan [33].

The importance of temperature-mediated fish herbivory in limiting the development of kelp populations in southern Japan is confirmed by the habitual use of herbivore-exclusion cages or nets in management efforts to restore kelp populations. Using a caging experiment in an isoyake area, Masuda *et al.* [39] showed that transplanted kelps only survive throughout the year when protected from fish grazing, and uncaged kelp recruits quickly disappear owing to grazing during the warmer months when herbivory rates are highest, as evidenced

by bite marks on the fronds and by the persistence of recruits in cages.

(b) Eastern Mediterranean: a warming sea connected to the Indo-Pacific via the Suez Canal

The opening of the Suez Canal in 1869 connected the tropical Indo-Pacific with the temperate Mediterranean Sea, regions that had been separated since the Oligocene (i.e. 20 Ma) [40]. The canal allowed the Mediterranean Sea to be colonized by species from the Red Sea (figure 2c) [41]. Following this artificial introduction, the subsequent range expansion of tropical species has been strongly influenced by rising temperatures in the Mediterranean [39,42].

In recent decades, two herbivorous rabbitfishes, *Siganus rivulatus* and *Siganus luridus* have become abundant along the eastern part of the Mediterranean (electronic supplementary material, table S1). Experimental evidence shows that these rabbitfishes have profoundly transformed shallow rocky reefs, removing all canopy-forming macroalgae and preventing the establishment of new algae, shifting the system towards deforested areas covered by a thin layer of epilithic algae and detritus [31,43]. This shift from productive algal forests to largely denuded areas has occurred across of hundreds of kilometres, and has led to a 60% reduction in overall benthic biomass and 40% decrease in species richness [43].

In accordance with thermal tolerance limits of rabbitfish, the geographical distribution of areas deforested by rabbitfish is restricted to the southeastern Mediterranean Sea [43]. However, the Mediterranean basin is warming fast [44], and rabbitfish are responding by expanding their distribution westwards [41]. This continuing range expansion of tropical rabbitfishes poses a major threat to shallow water Mediterranean ecosystems, and demonstrates how the intrusion of tropical herbivores can dramatically affect temperate algal ecosystems.

(c) Emerging evidence of tropicalization from the USA and Australia

While the impacts of the intrusion of tropical herbivorous fishes in other regions are not yet as clear as it is in southern Japan or the Mediterranean, evidence is building. Warming has been linked to large increases in the abundance of some herbivorous fishes in the northern Gulf of Mexico (southeastern USA; electronic supplementary material, table S1), including a 22-fold increase in abundance of the parrotfish *Nicholsina usta* [25], which consumes seagrass at five times the rate of native grazers (figure 2b) [45]. Warming has also been linked to increases in the abundance of other tropical vertebrate herbivores in southeastern USA, including juvenile green turtles and manatees (electronic supplementary material, table S1) [46]. Herbivory by these species reduces the standing crop of seagrass, increasing energy flux through the grazing food web and reducing the nursery role of seagrasses for finfish and shellfish (K. L. Heck 2014, unpublished data).

There is evidence for a decline in kelp forests in tropical–temperate transition zones in eastern and western Australia, and some of this appears to be mediated by tropical or subtropical herbivorous fishes (figure 1d,e). In western Australia, macroalgal foundation species collapsed following an extreme heat wave event during 2011 [6,17]. Since then, macroalgal forests have not recovered, and emerging evidence suggests increases in the abundance of tropical and subtropical herbivorous fishes

are preventing their recovery (T. Wernberg 2014, unpublished data). In eastern Australia, kelp has disappeared from numerous warm-edge reefs in the past 5 years even though no discrete warming events have been recorded, and video footage shows unequivocal signs of intense fish herbivory in the years previous to kelp disappearance (A. Verges 2014, unpublished data). The role and ecological impact of tropical herbivores in these two temperate regions is currently being quantified.

4. Mechanisms facilitating the tropicalization of temperate systems by herbivorous fishes

(a) Functional differences between tropical and temperate herbivorous fishes

The diversity and composition of herbivore communities determines how well herbivores control tropical macroalgae [47,48]; this should also hold true for tropical herbivores invading temperate systems. On tropical reefs, a critical functional mix of herbivores is needed for suppression of macroalgae which facilitates coral dominance [47,48]. This includes 'browsers' that feed directly upon macroalgae, 'grazers' that feed on algal turfs and prevent the establishment of macroalgae, 'detritivores' that remove detritus from associated turfs and facilitate feeding by grazers, and 'scrapers' or 'excavators' that remove the turf and underlying substrate and can also influence macroalgae by removing recruits [49]. Changes in the relative abundance of these functional groups alter benthic community structure. For example, field manipulations of browsers and grazers in the Florida Keys showed that macroalgae suppressed corals in treatments with single herbivore species, but that mixed species removed a broader range of macroalgae and facilitated corals [48].

Variation in feeding within functional groups of herbivores also plays a key role in mediating macroalgal control. For example, Rasher *et al.* [47] showed that different species of macroalgal 'browsers' varied in their resistance to macroalgal chemical defences and that multiple species within a functional group are necessary to control algal assemblages. Thus, increased herbivore diversity increases suppression of macroalgae on reefs.

Because the taxonomic and functional diversity of herbivorous fishes in temperate systems is low [50], the addition of a diverse group of tropical fishes to temperate systems should also more strongly impact temperate macroalgae. The trajectory and magnitude of this effect is likely to depend on the mix of invading herbivores. For example, it is unlikely that the addition of grazers, detritivores or scrapers alone would remove mature kelp forests. However, if kelp forests are lost owing to direct grazing by browsers or by other means such as disease or a heat wave, then these functional groups of herbivores should prevent recovery. Tropical herbivores can thus strongly influence temperate macroalgae in a dual manner, by both removing adult thalli (browsers) and by preventing their re-establishment (grazers, scrapers and excavators).

An increase in the abundance of functionally diverse tropical and subtropical herbivorous fishes in temperate systems may therefore decrease the resilience of kelp forests (i.e. their ability to recover following perturbations). This contrasts markedly with what occurs in tropical systems, where increased functional diversity of herbivorous fishes increases the ability of coral reefs to recover from disturbance events [48].

(b) Functional differences between tropical and temperate macrophytes

Plant traits strongly influence the impact of herbivory on macrophytes in marine ecosystems [8]. Thus, the diversity and composition of primary producers in the recipient temperate systems will mediate the impacts of expanding tropical herbivores. Studies on the palatability of seaweeds [51] from temperate versus tropical locations indicate that lower latitude plants are better defended chemically and less palatable than higher latitude plants, although exceptions occur [52]. Additionally, as new herbivores invade, they encounter plants that have not been selected to resist these herbivores [53]. In the few experiments where tropical fishes and temperate seaweeds or their tissues have been mixed, the temperate seaweeds have generally been readily consumed [54].

Kelps and fucoids, the main foundation species of temperate rocky reefs, commonly produce phlorotannins, some of which deter herbivory [55]. However, levels of phlorotannins in tropical and temperate brown algae vary substantially, with variation more a function of taxonomy and the specifics of geography than latitude *per se* [56]. Herbivores vary substantially in their response to phlorotannins, with some herbivores avoiding high concentrations [52], whereas others are unaffected [57]. Regardless of this variability in the response of tropical or temperate herbivores to phlorotannins, the virtual elimination of kelps from areas of temperate Japan and fucoids from areas of the Mediterranean by tropical fishes suggests that phlorotannins were ineffective against these tropical herbivores.

Impacts of expanding tropical herbivores on seagrass meadows, the main foundation species in temperate soft-bottom ecosystems, may differ from those on macroalgae, because up to 50% of seagrass biomass is below the sediment–water interface and unavailable to herbivorous fishes. Additionally, exposed blades may be less digestible owing to their high cellulose content. Thus, tropical herbivorous fishes may suppress leaf length and above-ground biomass, but not seagrass survivorship. Additionally, moderate grazing can stimulate seagrass production [58], suggesting that seagrasses may be more grazing tolerant than many macroalgae. Nevertheless, prolonged, intense herbivory can deplete below-ground reserves and cause mortality, as evidenced by tropical herbivores limiting tropical seagrass distribution [59].

(c) Latitudinal- and temperature-mediated changes in nutritional quality of food sources

Globally, carbon : nitrogen ratios of plants predict the proportion of primary production consumed by herbivores [60] and macrophytes with higher nitrogen concentrations are frequently preferred by tropical herbivores [45]. Nitrogen content of plants consistently increases with latitude [61], thus, nitrogen-rich, temperate macrophytes may enhance the fitness of tropical herbivores and exacerbate herbivore persistence and influence in temperate locations.

Algal-derived detritus is nutritious and targeted by many tropical herbivorous fishes [62]. Temperature-mediated increases in dissolved organic matter [63] and bacterial activity [64] should increase production of particulate organic matter, resulting in more amorphous and highly nutritious detritus on temperate reefs. The movement and persistence of tropical herbivores into temperate reefs may therefore be facilitated by enhanced nutritional quality of detritus in these systems.

5. How will other effects of climate change modulate the interaction between temperate macroalgae and range-shifting tropical herbivores?

Macroalgae in temperate systems are already subjected to biotic and abiotic stressors owing to warming and other anthropogenic disturbances. These can affect interactions among species [65,66], complicating the impacts of intruding tropical herbivores. Here, we examine how other effects of climate change may influence macroalgae–herbivore interactions.

(a) Temperature

Increasing temperatures typically have negative impacts on canopy-forming macroalgae [reviewed in 65], and multiple lines of evidence suggest that the distribution of cool-water, habitat-forming macroalgae is already retracting poleward in response to warming [6,17,66]. In addition to these direct effects, temperature stress can affect the intensity of top-down control by herbivores owing to changes in the rates of both algal growth and consumption [38,67] and/or changes to macrophyte palatability [65].

Temperate algal abundance and structure may be compromised at their more tropical borders by increased herbivory, but the global impact of this may be limited by their potential to expand or increase their abundance at higher latitudes [68]. Indeed, emerging evidence suggests increasing temperatures may be inhibiting recruitment of some high latitude populations of herbivorous sea urchins, and this has been linked to the recent recovery of kelp forests in Norway [69]. However, this will not be a global effect, as the potential for high latitude escapes or refugia are limited by the end of continents in many mid-temperate latitudes [70].

(b) Increased coral – algal interactions

Increased water temperatures are strongly influencing the distribution of habitat-forming species other than algae, most notably corals. Although projections of coral species' distributions in a warmer world are compounded by uncertainties regarding ocean chemistry and local stressors [71], there is now evidence of poleward range extensions of corals in several systems influenced by poleward boundary currents, including Japan, western Australia and eastern Australia (electronic supplementary material, table S1).

The intrusion of corals into higher latitudes increases the prevalence of coral–algal interactions in temperate regions and a shift from algal to coral dominance has been observed in restricted areas in southern Japan ([36]; figure 4). In tropical regions, in the absence of herbivores, macroalgae generally outcompete corals [72]. Herbivores are therefore crucial in mediating the effects of algae on coral, as the ability of algae to compete depends on accumulating sufficient biomass to overgrow corals on tropical reefs [72]. An increase in total levels of herbivory via the arrival of new consumers is likely to enhance the establishment of corals in temperate systems, at the expense of macroalgae.

(c) Macroalgal disease and microbes

A consistent prediction of ocean warming is that higher temperatures alter the abundance, behaviour and distribution of

pathogens increasing the impact of diseases in marine systems [73]. Grazing can also facilitate disease by creating infection sites or otherwise compromising host resistance to consumers [74,75]. Furthermore, diseased hosts can be more susceptible to attack by herbivores [74], creating a potential positive feedback loop between these two groups of natural enemies. Consumers are also often vectors of disease [75], so shifts in the distribution of grazers owing to tropicalization may lead to greater exposure of hosts to vector-borne pathogens.

6. Socio-ecological consequences of climate-mediated changes in herbivory

Emerging theory predicts that increased physical stress and consumer pressure can interact to strongly determine impacts on the total ecosystem, leading to the local collapse of foundation species [75]. This has already been observed in multiple ecosystems, where consumer fronts develop in the areas of highest physical stress, spreading further subsequently [75]. Here, we propose a similar phenomenon, whereby climate change acts as a stressor that increases top-down control of temperate reef communities, eventually leading to the collapse of macroalgal foundation species and consequent decline in the diversity of associated biota.

If macroalgae are lost and not replaced, then biodiversity is likely to decline dramatically. However, if canopy-forming macroalgae are replaced by corals, then biodiversity may be retained or increase [76]. In the eastern Mediterranean, a shift away from macroalgae has led to a loss of over 60% of benthic biomass and species richness [43]. The ecosystem services provided by a new suite of species will change, and management practices will need to adapt to shifts in resource use by humans [77]. For example, in southern Japan, the disappearance of kelp habitat has led to the complete collapse of the abalone fishery, which went from generating 11 million yen in 1996 to extinction of the fishery by 2000 [34].

A shift towards vertebrate, herbivore-dominated systems in tropicalized systems may direct a greater proportion of production into food-based pathways that serve humans. Herbivorous fishes are a prominent component of tropical marine systems and are often targeted in a number of tropical fisheries even when alternative trophic groups remain available [78]. Range-expanding rabbitfishes are already an important component of fisheries catches in the eastern Mediterranean [79]. As tropicalization continues and the diversity of herbivores in temperate areas increases, it is likely that an even higher proportion of benthic production will be transferred to higher trophic levels owing to subtle resource partitioning among tropical herbivores [47,48]. Such changes in the distribution of species are likely to alter fishing patterns and behaviour.

Marine reserves may serve as areas that are more resistant to species range shifts and tropicalization (e.g. overgrazing by tropical herbivorous fishes) by building resilience in key temperate communities such as kelp forests and seagrass beds. For example, no-take marine reserves have already buffered fluctuations in biodiversity and provided resistance to the initial stages of tropicalization (i.e. the colonization by subtropical vagrants) in a warming hotspot off southeastern Australia [80]. This may be owing to increased predation inside the reserve, or to differences in biogenic habitat resulting from cascading effects of protection, which may provide different settlement cues for warm-affinity fishes outside reserves [80].

7. Conclusion

Climate change influences biotic interactions, leading to cascading ecosystem-scale effects as species from formerly separated communities interact. Here, we suggest that a novel, ocean warming driven phase shift in coastal kelp and macrophyte habitats has now begun, owing to range-shifting tropical herbivores and overgrazing of macrophyte forests. In two regions—Japan and the Mediterranean—there is experimental evidence that the intrusion of tropical herbivorous fishes has contributed to such a phase shift, resulting in widespread loss of canopy-forming macroalgae. In other temperate regions, oceanographic, distributional, ecological and fisheries data (electronic supplementary material, table S1) suggest that similar phenomena are also starting to occur, implying that tropicalization of temperate marine communities could become a global phenomenon. Such climate-mediated changes in herbivory have the potential to profoundly alter temperate communities, with cascading effects for the biodiversity and function of coastal ecosystems, and significant socio-economic and management implications.

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