



CrossMark  
click for updates

## Review

**Cite this article:** Vergés A *et al.* 2014

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

*Proc. R. Soc. B* **281**: 20140846.

<http://dx.doi.org/10.1098/rspb.2014.0846>

Received: 13 April 2014

Accepted: 13 June 2014

### Subject Areas:

ecology

### Keywords:

climate change, ecosystem impacts, functional diversity, macroalgae, range shift, western boundary currents

### Author for correspondence:

Adriana Vergés

e-mail: [a.verges@unsw.edu.au](mailto:a.verges@unsw.edu.au)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.0846> or via <http://rspb.royalsocietypublishing.org>.

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

Adriana Vergés<sup>1,2,5</sup>, Peter D. Steinberg<sup>1,5,6</sup>, Mark E. Hay<sup>7</sup>, Alistair G. B. Poore<sup>2,5</sup>, Alexandra H. Campbell<sup>1,2,5</sup>, Enric Ballesteros<sup>8</sup>, Kenneth L. Heck Jr<sup>9</sup>, David J. Booth<sup>5,10</sup>, Melinda A. Coleman<sup>11</sup>, David A. Feary<sup>5,10</sup>, Will Figueira<sup>5,12</sup>, Tim Langlois<sup>13</sup>, Ezequiel M. Marzinelli<sup>1,5</sup>, Toni Mizerek<sup>5,14</sup>, Peter J. Mumby<sup>15</sup>, Yohei Nakamura<sup>16</sup>, Moninya Roughan<sup>3,5</sup>, Erik van Sebille<sup>4</sup>, Alex Sen Gupta<sup>4</sup>, Dan A. Smale<sup>13,17</sup>, Fiona Tomas<sup>18,19</sup>, Thomas Wernberg<sup>13</sup> and Shaun K. Wilson<sup>13,20</sup>

<sup>1</sup>Centre for Marine Bio-Innovation, School of Biological, Earth and Environmental Sciences, <sup>2</sup>Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, <sup>3</sup>School of Mathematics, and <sup>4</sup>Climate Change Research Centre and ARC Centre of Excellence for Climate, University of New South Wales, Sydney, New South Wales 2052, Australia

<sup>5</sup>Sydney Institute of Marine Sciences, Chowder Bay Road, Mosman, New South Wales 2088, Australia

<sup>6</sup>Advanced Environmental Biotechnology Centre, Nanyang Technical University, Singapore 637551, Republic of Singapore

<sup>7</sup>School of Biology and Aquatic Chemical Ecology Center, Georgia Institute of Technology, Atlanta, GA 30332, USA

<sup>8</sup>Centre d'Estudis Avançats de Blanes—CSIC, Blanes, Girona 17300, Spain

<sup>9</sup>Dauphin Island Sea Laboratory and University of South Alabama, Mobile, AL 36688-0002, USA

<sup>10</sup>School of the Environment, University of Technology Sydney, Broadway, New South Wales 2007, Australia

<sup>11</sup>Department of Primary Industries, NSW Fisheries, PO Box 4321, Coffs Harbour, New South Wales 2450, Australia

<sup>12</sup>School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia

<sup>13</sup>UWA Oceans Institute and School of Plant Biology, University of Western Australia, Crawley, Western Australia 6009, Australia

<sup>14</sup>Department of Biological Sciences, Macquarie University, North Ryde, New South Wales 2109, Australia

<sup>15</sup>Marine Spatial Ecology Laboratory, School of Biological Sciences, University of Queensland, St Lucia, Queensland 4072, Australia

<sup>16</sup>Graduate School of Kuroshio Science, Kochi University, Kochi 783-8502, Japan

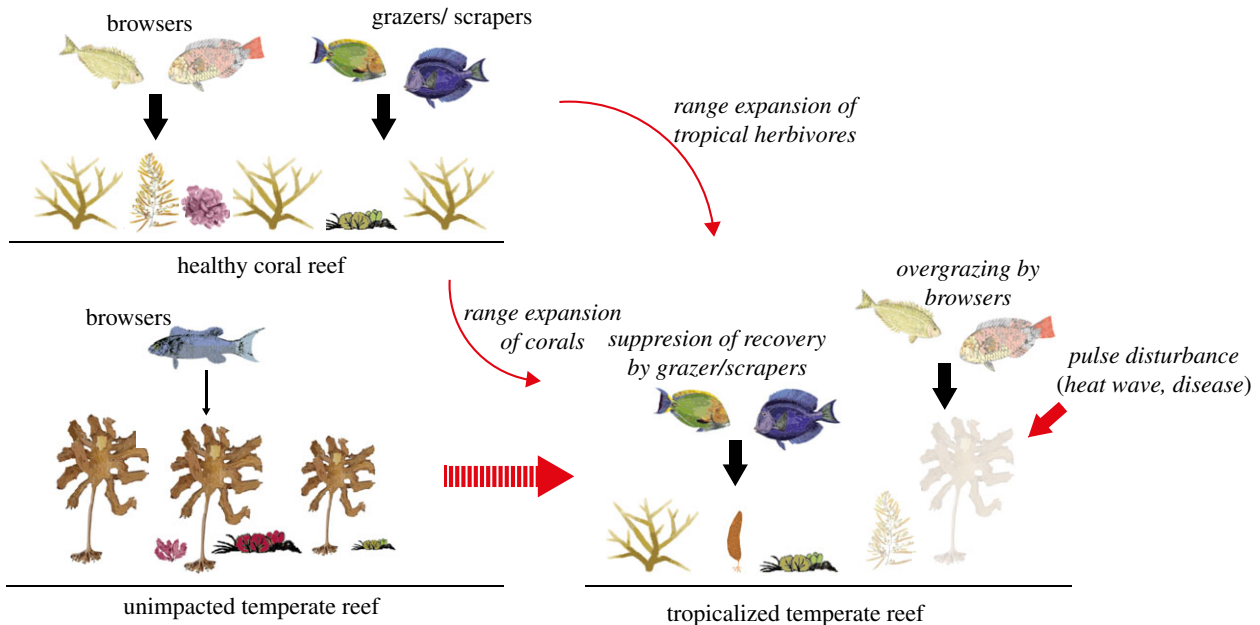
<sup>17</sup>Marine Biological Association of the United Kingdom, Citadel Hill, Plymouth PL1 2PB, UK

<sup>18</sup>Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), Esporles, Illes Balears 07190, Spain

<sup>19</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803, USA

<sup>20</sup>Department of Parks and Wildlife, Kensington, Western Australia 6151, Australia

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.



**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].

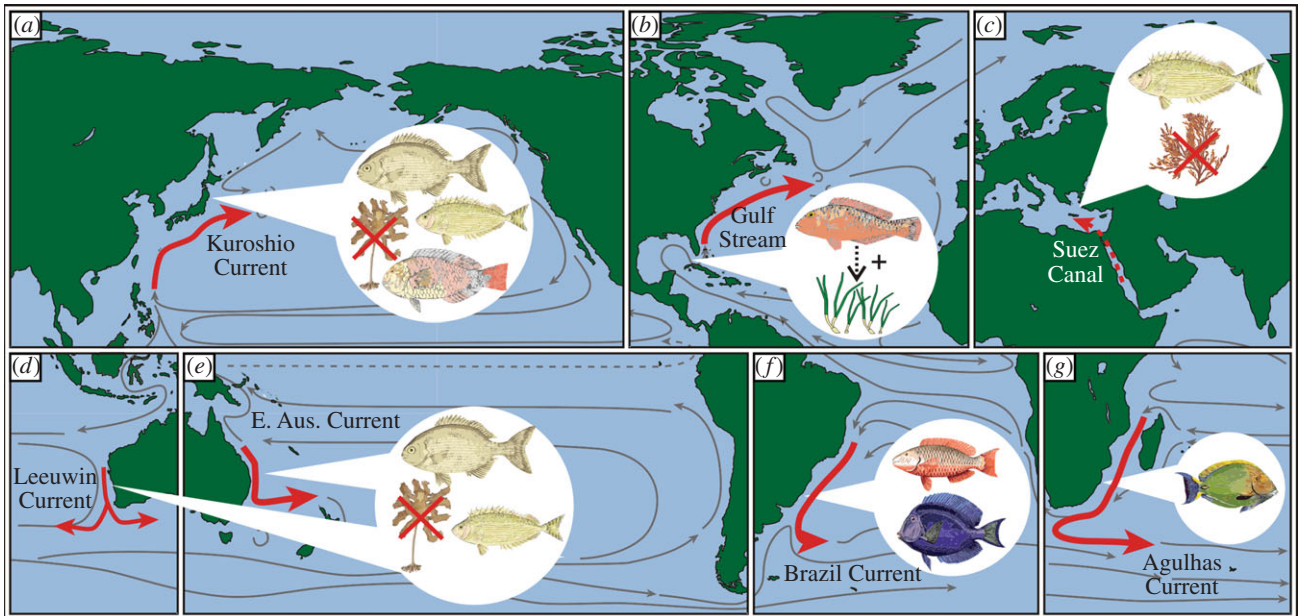
Climate change can also indirectly affect organisms by altering biotic interactions, which can have profound consequences for populations, community composition and ecosystem functions [4]. Indirect effects may occur: (i) via generation of new biotic interactions, as range-shifted species appear for 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



**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 3a) [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 3b). Model projections for the twenty-first century suggest that certain western boundary regions will continue to warm faster than the global average (figure 3c) probably forcing significant biological change.

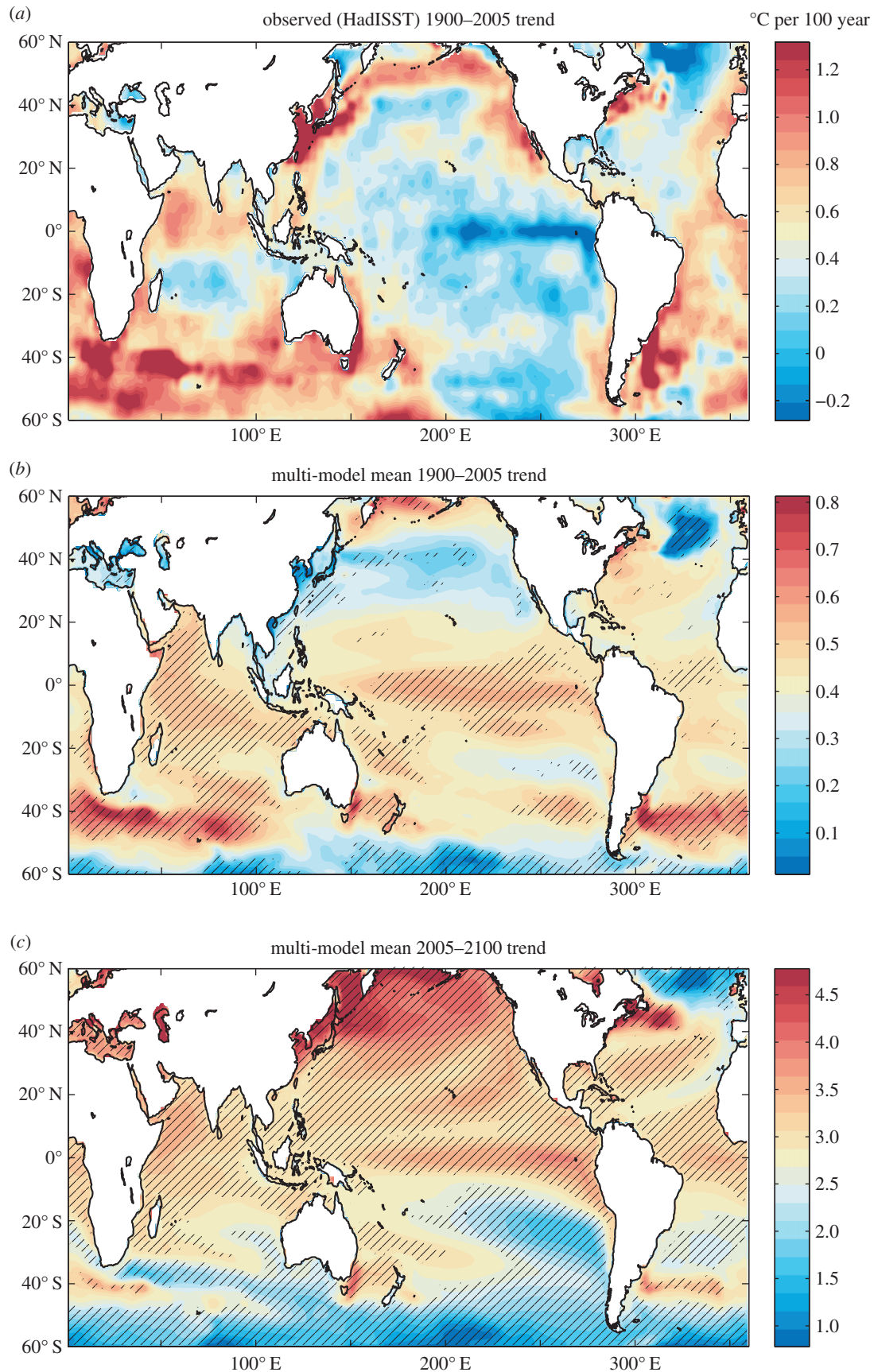
In addition to WBCs, other oceanographic features also transport tropical water towards temperate regions. The poleward-flowing Leeuwin current along the coast of western Australia is a prime example (figure 2d). In 2011, a strengthening of this current caused a marine ‘heat wave’ in which the coastal 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 2a; [22,23]), southeastern USA (figure 2b; [24,25]),

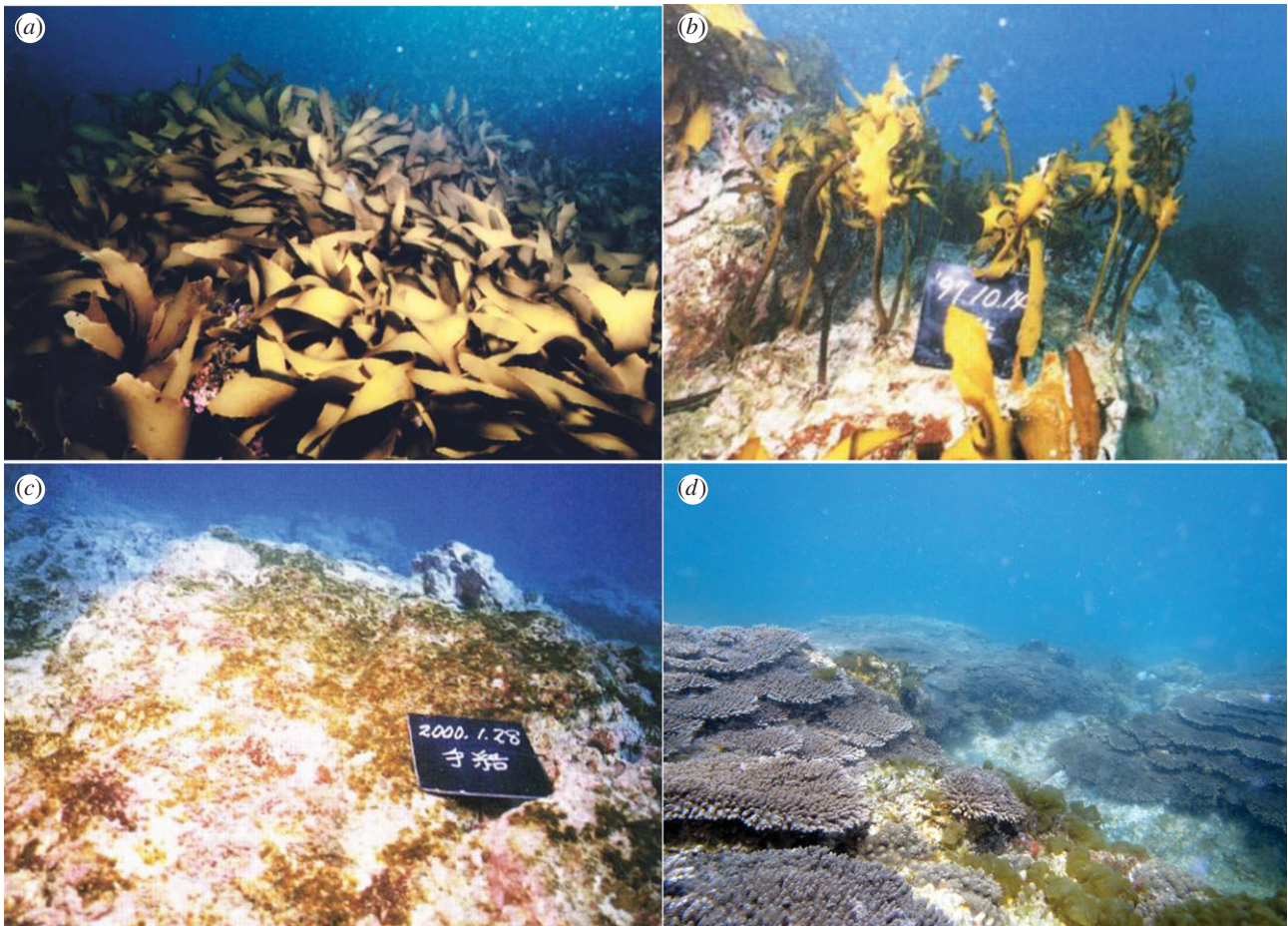




**Figure 3.** Trends in global sea surface temperatures (SST). (a) 1900–2005 trend in observed (HadISST) SST, (b) multi-model mean SST trend for the same period based on 34 CMIP5 models, (c) multi-model mean SST trend for 2005–2100 based on 28 CMIP5 models under the 'business as usual' RCP8.5 scenario. 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 2*d*; [17,26]) and eastern Australia (figure 2*e*; [27]), northeastern South America (figure 2*f*; [28,29]) and South Africa (figure 2*g*; [30]). Intrusions include key herbivores

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



**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 2c; [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 2a and the electronic supplementary material, table S1) [32,33]. It is estimated that the mass disappearance of kelp (*Ecklonia* spp.) and furoid (*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 4a). 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 4b), resulting in denuded substrate, or isoyake, by the early 2000s (figure 4c). Over time, kelp forests have been replaced by reef building corals which now dominate the benthos (figure 4d) [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 out-compete 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.

## References

1. IPCC 2014 *Climate change 2014: impacts, adaptation and vulnerability. Part A. Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (eds CB Field *et al.*). Cambridge, UK: Cambridge University Press.
2. Poloczanska ES *et al.* 2013 Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919–925. (doi:10.1038/nclimate1958)
3. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012 Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377. (doi:10.1111/j.1461-0248.2011.01736.x)
4. Zarnetske PL, Skelly DK, Urban MC. 2012 Biotic multipliers of climate change. *Science* **336**, 1516–1518. (doi:10.1126/science.1222732)
5. Ling SD. 2008 Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state.

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.

**Acknowledgements.** We thank the Evolution and Ecology Research Centre (UNSW) for funding the workshop on the tropicalization of temperate marine ecosystems that resulted in this review. Students and volunteers from the Centre for Marine Bio-Innovation (UNSW) helped to organize the event. F. E. Oliver provided substantial stimulus during the preparation of this review. Two anonymous reviewers offered constructive criticisms that significantly improved the final manuscript. This study resulted from a workshop convened by A.V., P.D.S. and A.G.P. entitled ‘Shifting species interactions and the tropicalization of temperate marine ecosystems’, held at the Sydney Institute of Marine Science (Australia) in November 2011. All authors contributed to the workshop and to sections of the manuscript. A.V. wrote the final manuscript and all authors contributed to revisions.

**Funding statement.** This study was funded by the Evolution and Ecology Research Centre, UNSW. Additional funding was provided by a UNSW Faculty of Science Visiting Research Fellowship to K.H. This is contribution 133 by the Sydney Institute of Marine Science.



- Oecologia* **156**, 883–894. (doi:10.1007/s00442-008-1043-9)
6. Smale DA, Wernberg T. 2013 Extreme climatic event drives range contraction of a habitat-forming species. *Proc. R. Soc. B* **280**, 20122829. (doi:10.1098/rspb.2012.2829)
  7. Shurin JB, Gruner DS, Hillebrand H. 2006 All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. B* **273**, 1–9. (doi:10.1098/rspb.2005.3377)
  8. Poore AGB *et al.* 2012 Global patterns in the impact of marine herbivores on benthic primary producers. *Ecol. Lett.* **15**, 912–922. (doi:10.1111/j.1461-0248.2012.01804.x)
  9. Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. 2010 Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* **25**, 633–642. (doi:10.1016/j.tree.2010.07.011)
  10. Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002 Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* **29**, 436–459. (doi:10.1017/S0376892902000322)
  11. Carpenter RC. 1986 Partitioning herbivory and its effects on coral-reef algal communities. *Ecol. Monogr.* **56**, 345–363. (doi:10.2307/1942551)
  12. IPCC. 2013 Climate change 2013: the physical science basis. In *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
  13. Sen Gupta A, Brown JN, Jourdain NC, van Sebille E, Ganachaud A, Vergés A. In press. Episodic and non-uniform migration of thermal habitats in a warming ocean. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* (doi:10.1016/j.dsr2.2013.12.002)
  14. Wu L *et al.* 2012 Enhanced warming over the global subtropical western boundary currents. *Nat. Clim. Change* **2**, 161–166. (doi:10.1038/nclimate1353)
  15. Arblaster JM, Meehl GA. 2006 Contributions of external forcings to southern annular mode trends. *J. Clim.* **19**, 2896–2905. (doi:10.1175/jcli3774.1)
  16. Taylor KE, Stouffer RJ, Meehl GA. 2012 An overview of CMIP5 and the experiment design. *Bull. Am. Meteorol. Soc.* **93**, 485–498. (doi:10.1175/bams-d-11-00094.1)
  17. Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS. 2013 An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Change* **3**, 78–82. (doi:10.1038/nclimate1627)
  18. Coleman MA, Roughan M, Macdonald HS, Connell SD, Gillanders BM, Kelaher BP, Steinberg PD. 2011 Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. *J. Ecol.* **99**, 1026–1032. (doi:10.1111/j.1365-2745.2011.01822.x)
  19. Chapman M, Kramer D. 2000 Movements of fishes within and among fringing coral reefs in Barbados. *Environ. Biol. Fish.* **57**, 11–24. (doi:10.1023/a:1004545724503)
  20. Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G. 2011 Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Glob. Ecol. Biogeogr.* **20**, 58–72. (doi:10.1111/j.1466-8238.2010.00575.x)
  21. Cheung WWL, Watson R, Pauly D. 2013 Signature of ocean warming in global fisheries catch. *Nature* **497**, 365–368. (doi:10.1038/nature12156)
  22. Soeparno ED, Nakamura Y, Shibuno T, Yamaoka K. 2012 Relationship between pelagic larval duration and abundance of tropical fishes on temperate coasts of Japan. *J. Fish Biol.* **80**, 346–357. (doi:10.1111/j.1095-8649.2011.03175.x)
  23. Nakamura Y, Feary DA, Kanda M, Yamaoka K. 2013 Tropical fishes dominate temperate reef fish communities within western Japan. *PLoS ONE* **8**, e81107. (doi:10.1371/journal.pone.0081107)
  24. Parker RO, Dixon RL. 1998 Changes in a North Carolina reef fish community after 15 years of intense fishing: global warming implications. *Trans. Am. Fish Soc.* **127**, 908–920. (doi:10.1577/1548-8659(1998)127<0908:ciancr>2.0.co;2)
  25. Fodrie FJ, Heck Jr KL, Powers SP, Graham WM, Robinson KL. 2010 Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Glob. Change Biol.* **16**, 48–59. (doi:10.1111/j.1365-2486.2009.01889.x)
  26. Hutchins JB. 1991 Dispersal of tropical fishes to temperate seas in the southern hemisphere. *J. R. Soc. West Aust.* **74**, 79–84.
  27. Booth DJ, Figueira WF, Gregson MA, Brown L, Beretta G. 2007 Occurrence of tropical fishes in temperate southeastern Australia: role of the East Australian Current. *Estuarine, Coastal Shelf Sci.* **72**, 102–114. (doi:10.1016/j.eess.2006.10.003)
  28. Barneche DR, Anderson AB, Floeter SR, Silveira M, Dinslaken DF, Carvalho-Filho A. 2009 Ten new records of reef fish on the coast of Santa Catarina State, Brazil. *Mar. Biodivers. Rec.* **2**, e143. (doi:10.1017/s1755267209990613)
  29. Luiz OJ, Carvalho-Filho A, Ferreira CEL, Floeter SR, Gasparini JL, Sazim I. 2008 The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation. *Zootaxa* **1807**, 1–25.
  30. Lloyd P, Plaganyi EE, Weeks SJ, Magno-Canto M, Plaganyi G. 2012 Ocean warming alters species abundance patterns and increases species diversity in an African sub-tropical reef-fish community. *Fish Oceanogr.* **21**, 78–94. (doi:10.1111/j.1365-2419.2011.00610.x)
  31. Sala E, Kizilkaya Z, Yildirim D, Ballesteros E. 2011 Alien marine fishes deplete algal biomass in the eastern Mediterranean. *PLoS ONE* **6**, e17356. (doi:10.1371/journal.pone.0017356)
  32. Nagai S, Yoshida G, Tarutani K. 2011 Change in species composition and distribution of algae in the coastal waters of Western Japan. In *Global warming impacts: case studies on the economy, human health, and on urban and natural environments* (ed. S Casalegno). Rijeka, Croatia: Intech.
  33. Yamaguchi A. 2010 Biological aspects of herbivorous fishes in the coastal areas of western Japan. *Bull. Fish. Res. Agen.* **32**, 89–94.
  34. Serisawa Y, Imoto Z, Ishikawa T, Ohno M. 2004 Decline of the *Ecklonia cava* population associated with increased seawater temperatures in Tosa Bay, southern Japan. *Fish Sci.* **70**, 189–191. (doi:10.1111/j.0919-9268.2004.00788.x)
  35. Tanaka K, Taino S, Haraguchi H, Prendergast G, Hiraoka M. 2012 Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecol. Evol.* **2**, 2854–2865. (doi:10.1002/ece3.391)
  36. Mezaki T, Kubota S. 2012 Changes of hermatypic coral community in coastal sea area of Kochi, high-latitude, Japan. *Aquabiology* **201**, 332–337.
  37. Fujita D. 2010 Current status and problems of isoyake in Japan. *Bull. Fish. Res. Agen.* **32**, 89–94.
  38. Smith TB. 2008 Temperature effects on herbivory for an Indo-Pacific parrotfish in Panama: implications for coral-algal competition. *Coral Reefs* **27**, 397–405. (doi:10.1007/s00338-007-0343-6)
  39. Raitos DE, Beaugrand G, Georgopoulos D, Zenetos A, Pancucci-Papadopoulou AM, Theocharis A, Papanthassiou E. 2010 Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. *Limnol. Oceanogr.* **55**, 1478–1484. (doi:10.4319/lo.2010.55.4.1478)
  40. Dercourt J *et al.* 1986 Geological evolution of the Tethys Belt from the Atlantic to the Pamirs since the LIAS. *Tectonophysics* **123**, 241–315. (doi:10.1016/0040-1951)
  41. Rilov G, Galil BS. 2009 Marine bioinvasions in the Mediterranean Sea: history, distribution and ecology. In *Biological invasions in marine ecosystems* (eds G Rilov, JA Crooks), pp. 549–575. Berlin, Germany: Springer.
  42. Pancucci-Papadopoulou MA, Raitos DE, Corsini-Foka M. 2012 Biological invasions and climatic warming: implications for south-eastern Aegean ecosystem functioning. *J. Mar. Biol. Assoc. UK* **92**, 777–789. (doi:10.1017/s0025315411000981)
  43. Vergés A, Tomas F, Cebrian E, Ballesteros E, Kizilkaya Z, Dendrinos P, Karamanlidis AA, Spiegel D, Sala E. In press. Tropical rabbitfish and the deforestation of a warming temperate sea. *J. Ecol.*
  44. Nykjaer L. 2009 Mediterranean Sea surface warming 1985–2006. *Clim. Res.* **39**, 11–17. (doi:10.3354/cr00794)
  45. Prado P, Heck KL. 2011 Seagrass selection by omnivorous and herbivorous consumers: determining factors. *Mar. Ecol. Prog. Ser.* **429**, 45–55. (doi:10.3354/meps09076)
  46. Avens L *et al.* 2012 Population characteristics, age structure, and growth dynamics of neritic juvenile green turtles in the northeastern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* **458**, 213–229. (doi:10.3354/meps09720)
  47. Rasher DB, Hoey A, Hay ME. 2013 Consumer diversity interacts with prey defences to drive ecosystem function. *Ecology* **94**, 1347–1358. (doi:10.1890/12-0389.1)

48. Burkepile DE, Hay ME. 2008 Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc. Natl Acad. Sci. USA* **105**, 16 201–16 206. (doi:10.1073/pnas.0801946105)
49. Choat JH, Robbins WD, Clements KD. 2004 The trophic status of herbivorous fishes on coral reefs II. Food processing modes and trophodynamics. *Mar. Biol.* **145**, 445–454. (doi:10.1007/s00227-004-1341-7)
50. Floeter SR, Behrens MD, Ferreira CEL, Paddock MJ, Horn MH. 2005 Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar. Biol.* **147**, 1435–1447. (doi:10.1007/s00227-005-0027-0)
51. Bolser R, Hay M. 1996 Are tropical plants better defended? Palatability and defenses of temperate vs tropical seaweeds. *Ecology* **77**, 2269–2286. (doi:10.2307/2265730)
52. Van Alstyne KL, Paul VJ. 1990 The biogeography of polyphenolic compounds in marine macroalgae: temperate brown algal defenses deter feeding by tropical herbivorous fishes. *Oecologia* **84**, 158–163.
53. Parker JD, Burkepile DE, Hay ME. 2006 Opposing effects of native and exotic herbivores on plant invasions. *Science* **311**, 1459–1461. (doi:10.1126/science.1121407)
54. Steinberg PD, Edyvane K, Denys R, Birdsey R, Vanaltena IA. 1991 Lack of avoidance of phenolic-rich brown algae by tropical herbivorous fishes. *Mar. Biol.* **109**, 335–343. (doi:10.1007/BF01319401)
55. Steinberg PD, Van Alstena I. 1992 Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. *Ecol. Monogr.* **62**, 189–222. (doi:10.2307/2937093)
56. Targett NM, Coen LD, Boettcher AA, Tanner CE. 1992 Biogeographic comparisons of marine algal polyphenolics: evidence against a latitudinal trend. *Oecologia* **89**, 464–470.
57. Targett NM, Boettcher AA, Targett TE, Vrolijk NH. 1995 Tropical marine herbivore assimilation of phenolic-rich plants. *Oecologia* **103**, 170–179. (doi:10.1007/BF00329077)
58. Vergés A, Perez M, Alcoverro T, Romero J. 2008 Compensation and resistance to herbivory in seagrasses: induced responses to simulated consumption by fish. *Oecologia* **155**, 751–760. (doi:10.1007/s00442-007-0943-4)
59. Ogden J, Brown R, Salesky N. 1973 Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* **182**, 715–717. (doi:10.1126/science.182.4113.715)
60. Cebrian J. 1999 Patterns in the fate of production in plant communities. *Am. Nat.* **154**, 449–468. (doi:10.1086/303244)
61. Borer ET *et al.* 2013 Global biogeography of autotroph chemistry: is insolation a driving force? *Oikos* **122**, 1121–1130. (doi:10.1111/j.1600-0706.2013.00465.x)
62. Wilson SK, Bellwood DR, Choat JH, Furnas MJ. 2003 Detritus in the epilithic algal matrix and its use by coral reef fishes. In *Oceanography and marine biology: an annual review* (eds RJA Atkinson, RN Gibson), pp. 279–309. Boca Raton, FL: CRC Press.
63. Wada S, Aoki MN, Tsuchiya Y, Sato T, Shinagawa H, Hama T. 2007 Quantitative and qualitative analyses of dissolved organic matter released from *Ecklonia cava* Kjellman, in Oura Bay, Shimoda, Izu Peninsula, Japan. *J. Exp. Mar. Biol. Ecol.* **349**, 344–358. (doi:10.1016/j.jembe.2007.05.024)
64. White P, Kalff J, Rasmussen J, Gasol J. 1991 The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microb. Ecol.* **21**, 99–118. (doi:10.1007/bf02539147)
65. Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, Graham MH. 2012 Effects of climate change on global seaweed communities. *J. Phycol.* **48**, 1064–1078. (doi:10.1111/j.1529-8817.2012.01224.x)
66. Wernberg T *et al.* 2011 Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *J. Exp. Mar. Biol. Ecol.* **400**, 7–16. (doi:10.1016/j.jembe.2011.02.021)
67. O'Connor MI. 2009 Warming strengthens an herbivore-plant interaction. *Ecology* **90**, 388–398. (doi:10.1890/08-0034.1)
68. Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM. 2007 Do distributional shifts of northern and southern species of algae match the warming pattern? *Glob. Change Biol.* **13**, 2592–2604. (doi:10.1111/j.1365-2486.2007.01451.x)
69. Fagerli C, Norderhaug K, Christie H. 2013 Lack of sea urchin settlement may explain kelp forest recovery in overgrazed areas in Norway. *Mar. Ecol. Prog. Ser.* **488**, 119–132. (doi:10.3354/meps10413)
70. Wernberg T, Russell BD, Thomsen MS, Gurgel CFD, Bradshaw CJA, Poloczanska ES, Connell SD. 2011 Seaweed communities in retreat from ocean warming. *Curr. Biol.* **21**, 1828–1832. (doi:10.1016/j.cub.2011.09.028)
71. Greenstein BJ, Pandolfi JM. 2008 Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. *Glob. Change Biol.* **14**, 513–528. (doi:10.1111/j.1365-2486.2007.01506.x)
72. McCook LJ, Jompa J, Diaz-Pulido G. 2001 Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* **19**, 400–417. (doi:10.1007/s003380000129)
73. Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD. 2002 Climate warming and disease risks for terrestrial and marine biota. *Science* **296**, 2158–2162. (doi:10.1126/science.1063699)
74. Campbell AH, Vergés A, Steinberg PD. 2014 Demographic consequences of disease in a habitat-forming seaweed and impacts on interactions between natural enemies. *Ecology* **95**, 142–152. (doi:10.1890/13-0213.1)
75. Silliman BR, McCoy MW, Angelini C, Holt RD, Griffin JN, van de Koppel J. 2013 Consumer fronts, global change, and runaway collapse in ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **44**, 503–538. (doi:10.1146/annurev-ecolsys-110512-135753)
76. 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.
77. Hobbs RJ *et al.* 2006 Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob. Ecol. Biogeogr.* **15**, 1–7. (doi:10.1111/j.1466-822X.2006.00212.x)
78. Edwards CB *et al.* 2014 Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B* **281**, 20131835. (doi:10.1098/rspb.2013.1835)
79. El-Hawet A. 2001 Catch composition and management of daytime purse seine fishery on the Southern Mediterranean Sea coast, Abu Qir Bay, Egypt. *Mediterr. Mar. Sci.* **2**, 119–126. (doi:10.12681/mms.270)
80. Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ. 2014 Resilience and signatures of tropicalization in protected reef fish communities. *Nat. Clim. Change* **4**, 62–67. (doi:10.1038/nclimate2062)