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Implications for ecosystem functions and management actions

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Tropicalisation of temperate reefs: implications for ecosystem functions and management actions

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ABSTRACT

1. Temperate reefs from around the world are becoming tropicalised, as warm-water species shift their distribution towards the poles in response to warming. This is already causing profound shifts in dominant foundation species and associated ecological communities as canopy seaweeds such as kelp are replaced by tropical species.
2. Here, we argue that the cascading consequences of tropicalisation for the ecosystem properties and functions of warming temperate reefs depend largely on the taxa that end up dominating the seafloor. We put forward three potential tropicalisation trajectories, that differ in whether seaweeds, turf or corals become dominant. We highlight potential gains to certain ecosystem functions for some tropicalisation end-points. For example, local benthic fish productivity may increase in some tropicalised reefs as a higher proportion of primary

production is directly consumed, but this will be at the expense of other functions such as carbon export. We argue that understanding these changes in flows of energy and materials is essential to formulate new conservation strategies and management approaches that minimise risks as well as capture potential opportunities.

3. Regardless of which trajectory is followed, tropicalised systems represent largely novel ecosystem configurations. This poses major challenges to traditional conservation and environmental management approaches, which typically focus on maintaining or returning species to particular locations. We outline management practices that may either mitigate predicted structural and functional changes or make the most of potential new opportunities in tropicalised reefs. These include marine protected areas to increase resilience and connectivity, the development of new fisheries that target range-expanding invaders, and assisted evolution and migration strategies to facilitate the dominance of large habitat formers like corals or seaweeds.
4. We highlight important ecological and ethical challenges associated with developing novel approaches to manage tropicalised reefs, which may need to become increasingly interventionist. As technological innovations continue to emerge, having clear goals and considering the ethics surrounding interventions among the broader community are essential steps to successfully develop novel management approaches.

INTRODUCTION

Worldwide, species are responding to climate change through geographic range shifts (Pecl *et al.* 2017), changes in demographic processes (Selwood, McGeoch & Mac Nally 2015), physiological acclimatisation (Pörtner & Farrell 2008) and evolutionary adaptation (Hoffmann & Sgrò 2011). These changes are leading to profound alterations in species composition with impacts on our economies, food supply and health (Pecl *et al.* 2017).

A recent analysis of more than 35,000 plant, mammal, bird, fish, and invertebrate species revealed profound changes in global biodiversity, but contrary to expectations there was not a systematic loss of biodiversity (Dornelas *et al.* 2014). Instead, communities are undergoing a massive turnover in their constituent species, resulting in the global emergence of communities with novel species configurations (Hobbs *et al.* 2006). Changes in species distributions and altered biological assemblages in response to historical changes in the abiotic environment are well known from paleoecological studies (Blois *et al.* 2013), but in recent decades the rate at which species are moving has greatly accelerated in response to anthropogenic environmental change (Chen *et al.* 2011).

Species redistributions and the resulting emergence of novel biological assemblages pose major challenges to traditional conservation and environmental management approaches, which typically focus on maintaining or returning species to particular locations (Hobbs *et al.* 2017). As we are increasingly unable to protect or conserve historical conditions, new management approaches require understanding the mechanisms driving novel ecosystem configurations and how these changes impact the benefits that humans derive from our natural systems, so that we can secure ecosystem services into the future.

In marine systems, biological assemblages sitting just outside tropical latitudes are becoming re-organised or "tropicalised", as warm-affinity species become increasingly dominant and cool water species recede (Vergés *et al.* 2014a). These changes are linked to gradual warming coupled with intensifying poleward flowing boundary currents (Wu *et al.* 2012), which warm temperate waters and transport larvae from the tropics to temperate reefs (Vergés *et al.* 2014a). These new arrivals colonise warming temperate systems, and result in significant change in the system when new interactions among previously separated taxa emerge, for example tropical herbivores overgrazing temperate foundation seaweed species (Vergés *et al.* 2014b; Vergés *et al.* 2016). Rapid warming, such as during marine heatwaves, can also result in mass die-offs of kelp (Wernberg *et al.* 2016). These phenomena have led to extensive losses of seaweed forests and the species they support over hundreds of kilometres of coastlines, with declines now documented from eastern and

western Australia to Japan, Korea and the Mediterranean (Denis *et al.* 2013; Vergés *et al.* 2014b; Wernberg *et al.* 2016; Kumagai *et al.* 2018).

Although tropicalisation is a global and increasingly visible phenomenon (Vergés *et al.* 2014a), the overall consequences of these changes for ecosystem functions or services like primary production, nutrient cycling or fisheries production are poorly understood. As well as the loss of temperate species, tropicalisation also entails the range expansion of tropical habitat-forming species like corals (Tuckett *et al.* 2017) and the development of novel coral reef ecosystems (Graham *et al.* 2014). Thus a key question for understanding and managing these systems is: Will the functioning of novel tropicalised systems in time become similar to tropical habitats, such as coral reefs, or should entirely new ecosystem functions be expected?

Here, we discuss the potential consequences of tropicalisation for the properties and ecosystem functions (sensu Bellwood *et al.* In press) that underpin the goods and services that humans derive from temperate reefs, and its consequences for the management of our marine environment. Although recent studies show that range shifts in temperate species (e.g. from dominance of cold to warm-affinity kelp) is already impacting important ecosystem functions relating to benthic biomass, energy flow and nutrient cycling (Pessarrodona, Foggo & Smale 2018), here we focus on tropicalised shallow reefs in mid-latitudes (23-35 °N or S). In these regions, species are shifting across major biogeographic boundaries. These regions also represent both a potential refugia for corals as tropical temperatures rise beyond their physiological limits (Beger *et al.* 2014) and the contracting edge of economically important kelp forests that are the biogenic engine of temperate reefs (Bennett *et al.* 2016).

TRAJECTORIES FOR WARMING TROPICALISED REEFS

Habitat-forming organisms or foundation species mediate important ecosystem functions including nutrient cycling and provision of refuge, nursery, foraging and breeding areas for species. As a consequence, changes in the identity and relative abundance of habitat-formers in tropicalised

temperate reefs can cause dramatic changes in the physical structure and functioning of these systems, with significant knock-on effects for associated biodiversity (Terazono et al. 2012; Vergés et al. 2016; Wernberg et al., 2016).

Globally, tropicalised shallow reefs share two key phenomena: a loss of temperate seaweed forests as the dominant habitat-formers, and increases in tropical/ subtropical species. Different regions, however, differ in which taxa end up dominating the seafloor, with three potential trajectories identified for warming temperate reefs globally (Fig. 1):

(a) Seaweed-dominated reefs (e.g. Japan) – these systems may emerge if tropical seaweed species (Fig. 2b) replace temperate canopy-formers, as in some southern Japan reefs (Tanaka *et al.* 2012; Terazono *et al.* 2012) or, hypothetically, such a system may develop if some temperate seaweeds adapt to their new environment and persist into the future.

(b) Turf dominated reefs (e.g. eastern Mediterranean) – these systems are characterised by low structural complexity and simplified food webs, as canopy seaweeds become replaced by low-biomass turfing algae (Fig. 2c; Vergés *et al.* 2014b; Filbee-Dexter & Wernberg 2018)

(c) Turf and coral dominated reefs (e.g. Japan, Australia, Korea) – in these systems warm-temperate corals and/ or range expanding tropical corals coexist with turf algae (Fig. 2d), which have replaced seaweeds as the dominant primary producers (Yamano, Sugihara & Nomura 2011; Vergés *et al.* 2016; Wernberg *et al.* 2016; Tuckett *et al.* 2017).

PREDICTED IMPACTS TO BIODIVERSITY, ECOSYSTEM FUNCTIONS & SERVICES

Changes to biodiversity

The extent of biodiversity changes to temperate reef systems undergoing tropicalisation will depend on several factors: how fast temperate species contract and tropical ones expand; the degree of functional redundancy between habitat forming species lost and gained; changes in species interactions; and changes in beta diversity. To date, range shift observations suggest that tropical

species are expanding their ranges faster than temperate ones are retracting, leading to an overall increase in the total number of species present in tropicalised reefs (Vergés *et al.* 2016; Wernberg *et al.* 2016). This could be due to differences in mechanisms underpinning range extensions and contractions (Bates *et al.* 2014b); extensions only require the dispersal and establishment of a few new individuals whereas contractions require the death and disappearance of all individuals. This implies the inflated biodiversity could be based on an extinction debt and therefore potentially temporary.

Tropicalisation is unlikely to be the cause of species extinctions at a global scale at least in the short term (e.g. within 50 years), partly because many temperate species are habitat generalists (Taylor & Cole 1994) and partly because most temperate coastlines extend across broad latitudinal ranges where poleward retreat is possible. Exceptions to this include the Great Southern Reef (GSR) in Australia (Bennett *et al.* 2016), which runs across the entire southern edge of the continent (including Tasmania), but ends at 39 ^{o}S and has few stepping stones or connections further south towards Antarctica. The GSR has high levels of endemism; for example, up to 77% of seaweeds, and 56% of invertebrates are found nowhere else globally (Bennett *et al.* 2016). Many of these species could disappear given currently predicted poleward shifts in seaweed forests beyond the continent by 2100 (Martínez *et al.* 2018), posing a critical threat and substaintal management challenge for this region in the immediate future.

Seaweed forests support a broad range of organisms through provision of habitat or food, either directly or as detritus (Krumhansl & Scheibling 2012; Teagle *et al.* 2017; Fulton *et al.* 2019). Observational and experimental studies have shown substantial declines in α diversity through loss of overall abundance and number of species when seaweed forests disappear (Graham 2004; Ling 2008). Loss of species caused by the replacement of kelp forests by other seaweeds may be offset if these provide similar microhabitats (Coleman & Wernberg 2017), though species identity is likely to change. For example, co-occurring cool-water laminarian kelps and more warm-tolerant *Sargassum* species support significantly different associated communities (Coleman & Wernberg 2017) and a shift from kelp to *Sargassum* (Tanaka *et al.* 2012; Wernberg *et al.* 2016) will likely reflect these

changes. In contrast, where the seaweed forest is replaced by tightly packed low-lying turf species (Fig. 1c) biodiversity is likely to decline (Vergés *et al.* 2014b).

Changes in biodiversity can also be strongly influenced by the range expansion of coral as alternative habitat-formers, a process already occurring along the coasts of Japan (Yamano, Sugihara & Nomura 2011; Kumagai *et al.* 2018), Korea (Denis *et al.* 2014), the western Mediterranean (Serrano, Coma & Ribes 2012) and Australia (Baird, Sommer & Madin 2012; Tuckett *et al.* 2017). The range expansion of structurally complex corals is likely to result in increases in biodiversity as new ecological niches become available in temperate latitudes, and in some instances the associated fauna are already expanding their range along with coral organisms (Yamano *et al.* 2012). The scope for latitudinal expansion of corals is however species-specific (Madin *et al.* 2016), and increases in coral cover are not being recorded in all tropical-temperate transition zones. This suggests changes in biodiversity associated with corals are also likely to be highly region-specific and dependent on abiotic conditions such as light (Sommer *et al.* 2018).

Climate change is also making the ocean more acidic, especially in higher latitudes sitting just outside the tropics (Hooidonk *et al.* 2014), and this may impact range expanding corals and associated biodiversity. In particular, acidification tends to increase coral reef bioerosion, preventing effective reef accretion (Barkley *et al.* 2015), and this may be further accentuated by higher nutrients (e.g. due to increases in current-driven upwelling; Schaeffer, Roughan & Wood 2014), which can impair coral skeletal density and limit reef construction (Manzello *et al.* 2014). This suggests that high latitude coral-dominated reefs of the future may not form accreting reef frameworks (Perry & Alvarez-Filip In press), which may limit associated biodiversity. Ocean acidification may also limit corals by enhancing the competitive strength of turf and seaweeds generally (Connell & Russell 2010; Diaz- Pulido *et al.* 2011) and of kelp in particular (Linares *et al.* 2015).

Provision of habitat and nursery functions and implications for fisheries

A core function of habitat-forming species is the creation of physically complex living space and shelter on reefs for a variety of flora and fauna. Where tropicalisation causes shifts in benthic composition (e.g. by shifting from kelp to turf algae as the dominant taxa), refuges will be modified, which may lead to mortality of some species (O'Brien *et al.* 2018) or even declines of whole trophic groups that rely on specific refuges (Rogers *et al.* 2018).

Juvenile fishes, for instance, are particularly vulnerable to predation, and the shelter provided by nursery habitats such as kelp forests, can positively impact recruitment and success of fish populations (Carr 1991). Fish recruits and juveniles are often habitat-specialists and may have strong selectivity for specific microhabitats as nursery grounds (Tolimieri 1995), while settlement success may depend on availability of habitat settlement cues (Dixson, Abrego & Hay 2014) or settlement substrate.

Tropical coral reefs are generally considered more complex than seaweed forests (Gratwicke & Speight 2005), which in turn are more complex than turf-dominated reefs (Filbee-Dexter & Wernberg 2018). The replacement of seaweed forests with animal 'forests' on tropicalised reefs may have beneficial effects for some species, facilitating survivorship through protection from predators by offering new refuge spaces and camouflage (Wilson *et al.* 2010). Importantly, however, losses of temperate seaweed forests will have negative consequences for many economically important temperate species such as abalone (Serisawa *et al.* 2004), lobster (Johnson *et al.* 2011), and fish (Yamasaki *et al.* 2014).

On tropicalised temperate reefs, the time needed for slow growing species such as coral to establish will have a pronounced effect on fish recruitment (Coker, Wilson & Pratchett 2014). Further, on many tropical coral reefs, juveniles of reef fishes rely substantially on non-reef habitats such as seagrasses, mangroves and tropical seaweed forests as nurseries prior to ontogenetic migration to coral reefs as adults (Nagelkerken *et al.* 2002; Wilson *et al.* 2010; Fulton *et al.* 2019). Hence, the distribution of these habitats relative to tropicalised temperate reefs, as well as the presence of

connectivity corridors to facilitate ontogenetic movements that promote survivorship of juvenile fish (Berkström *et al.* 2013), may be limiting factors in the success of many tropical reef fishes on tropicalised reefs.

The consequences of potential substitution of kelps by tropical seaweeds will depend not only on the morphology of these 'new' habitat-formers, but also on their phenology. Many temperate laminarian kelp species are perennial with persistently high levels of cover/biomass, whereas tropical seaweeds such as *Sargassum* spp. have shorter periods of high vegetation cover (Fulton *et al.* 2014). Seasonal declines in seaweed cover as well as potential mismatches in timing between seaweed cover and recruitment events could affect fish population replenishment on tropicalised reefs (Terazono *et al.* 2012; Yamasaki *et al.* 2014).

In contrast to corals, kelps and other habitat forming seaweeds, turf algae provide minimal structure and habitat functions (Filbee-Dexter & Wernberg 2018). Nevertheless, some structurally-simple habitats, including turf algae dominated habitats, can be functionally important as juvenile fish nurseries for some species (Galaiduk *et al.* 2013), including many range shifting tropical species (Beck *et al.* 2017). This suggests that the replacement of kelp forests by turf algae may create a positive feedback loop that facilitates tropicalisation of temperate reefs, especially in areas where boulders may also offer abiotic refuge spaces.

Food webs and energy fluxes in temperate vs. tropical reefs and implications for tropicalised systems

Although benthic productivity is extremely high in both temperate and tropical reefs, the overall patterns of energy and organic carbon flow differ markedly between these systems. In temperate reefs (Fig. 1a), primary productivity of species like kelp is typically very high but also very seasonal (Wernberg *et al.* 2019), and only a small proportion of this productivity (<20%) is consumed by

herbivores, with over 80% ending up as detritus/ dissolved organic matter (Krumhansl & Scheibling 2012). Kelp detritus can be exported across distances ranging from meters to hundreds of kilometres (Filbee-Dexter *et al.* 2018). This constitutes an important trophic subsidy sustaining high secondary production in habitats with no or low primary production, including reefs with no canopy seaweeds, sandy beaches and the deep sea (Filbee-Dexter *et al.* 2018). Alternatively, kelp detritus may become sequestered in adjacent 'carbon sink habitats' such as seagrass meadows (Hill *et al.* 2015).

This situation is reversed in tropical coral-dominated reefs (Fig. 1d), where low biomass 'turfs' and associated microbes sustain highly productive habitats. Here, herbivorous fish consume 50-100% of turf primary production (Carpenter 1986; Hay 1991), including microbes and detritus (Wilson *et al.* 2003; Clements *et al.* 2017). These striking differences between tropical and temperate reefs in herbivory and detritivory are reflected in food web studies, which show that seaweeds support only a small proportion of total fish biomass in shallow temperate reefs (Truong *et al.* 2017), while turf algae and detritus are major contributors to fish biomass in coral reefs (McMahon *et al.* 2016).

We know little about how energy flow and food webs are changing in warming temperate reefs. A meta-analysis of more than 600 experiments showed that ocean warming typically increases metabolic rates as well as primary production and consumption (Nagelkerken & Connell 2015). Mesocosm experiments suggest that this can lead to ecosystem collapse and simplified food webs if increases in primary production are converted to unpalatable detritus and not consumed (Ullah *et al.* 2018). These mesocosm studies, however, typically do not incorporate the effects of 'species on the move' that characterise tropicalisation and which can have important effects on altered food web dynamics.

Importantly one of the most consistent observations on tropicalised temperate reefs globally has been the increased abundance and functional diversity of herbivorous fishes (Vergés *et al.* 2014a), and turf-feeding invertivores and detritivores (Bennett *et al.* 2015). Recent studies suggest these species can play a significant role in the remineralisation of turf algae, small-particulate POM and invertebrate biomass and may also be increasing the bioavailability of nutrients and impacting local redistribution and recycling patterns (Shantz *et al.* 2015). The increased availability of easily

accessible nutrients could fuel additional growth of turf algae and provide a feedback to strengthen the dominance of turf (Filbee-Dexter & Wernberg 2018). This suggests that some tropicalised reefs may start to resemble coral-dominated systems, with a higher proportion of primary production being consumed and recycled locally (Fig. 1c, 1d). This, in turn, may result in increased flow of energy to higher trophic levels, potentially leading to increases in the biomass of benthic species, but reducing the strength of cross-habitat trophic subsidies and impacting habitats that are currently subsidised by kelp detritus.

Changes in the pattern of energy and material flows brought about by shifts in habitat-formers in tropicalised temperate reefs will also impact the potential for carbon sequestration. Although the role of temperate kelp forests as effective long-term carbon sinks is still under investigation (Howard *et al.* 2017), recent studies suggest that kelp that reaches adjacent depositional areas can be sequestered in sediments and contribute meanginfully to the world's 'blue carbon' budget (Hill *et al.* 2015; Krause-Jensen *et al.* 2018). The replacement of low latitude kelps by corals or turf (Fig. 1c and 1d) would reduce this source of blue carbon, whereas a replacement with tropical seaweeds would mostly change detritus supply pathways.

Consequences for tourism activities

Tourism is a major component of the economy of many coastal areas (Kragt, Roebeling & Ruijs 2009; Bennett *et al.* 2016) and benefits society more broadly through its contribution to human well-being. Nature-based marine tourism, e.g. scuba diving, snorkelling, eco-filming and underwater photography, is highly dependent on healthy marine environments and a major source of revenue at coastal tourist destinations (Biggs *et al.* 2015; Bennett *et al.* 2016). Hence, tropicalisation of temperate reefs may redistribute tourism flows (Weatherdon *et al.* 2016) and create both winners and losers in the marine tourism industry, depending on the type and location of tourism activities (Moreno & Amelung 2009; Marshall *et al.* 2011). Such changes will require an adaptive response

from marine tourism markets to adjust existing tourism modes and take advantage of emerging opportunities (Graham *et al.* 2014; Weatherdon *et al.* 2016).

Kelp forest ecosystems support a range of marine tourism activities along temperate zone coastlines around the world. In Australia, tourism, recreational and commercial fisheries from the temperate Great Southern Reef is a major contributor to coastal economies with an estimated value of AUD$10 billion/year (Bennett *et al.* 2016). Ecotourism activities such as recreational scuba diving and eco-filming in the southern Benguela generates an estimated USD$22.4 million/year in tourism revenue for the region (Blamey & Bolton 2018). Similarly, recreational scuba diving in kelp forests and sport fishing are highly profitable sources of income for tourist enterprises in temperate reefs (Beaumont *et al.* 2007), with diving activity levels correlated with kelp persistence (Menzel *et al.* 2013). Both the economic and ecological value of temperate reefs may be impacted if kelp forests are lost from these ecosystems.

Warmer waters and shifts in temperate reef ecosystems towards communities more similar to tropical reefs, such as a high diversity of corals and reef fishes, may deliver an underwater scenery that is highly valued by reef-viewers (Williams & Polunin 2000), potentially increasing the tourism value of these reefs (Nakamura *et al.* 2013). For example, species range shifts associated with tropicalisation may create new opportunities for recreational fishing tourism (Champion *et al.* 2018), while warmer conditions may enhance fitness and thus yields of some native temperate species (Nelson *et al.* 2013). Conversely, the significance of catching increasingly rare and highly prized species of temperate fishes and organisms such as abalone and lobster, may be enhanced for recreational fishers. Cascading effects induced by tropicalisation may also alter the distribution pattern of higher trophic groups, with impacts on tourism activities that are based on encounters with these marine fauna, such as shark diving and whale watching.

Attraction to reef viewing activities by tourists has strong links to ecosystem condition, which is influenced by attributes such as healthy habitats, abundance of living marine life, diversity of fish and reef complexity (Biggs *et al.* 2015). While coral-dominated tropicalised temperate reefs (Fig. 1d)

may enhance the attractiveness of temperate reefs to tourists, thereby compensating for any tourism revenue losses associated with declines in healthy natural temperate reefs, a shift to turf-dominated reefs (Fig. 1c) is likely to reduce tourism and its benefits

APPROACHES TO MANAGING TROPICALISED REEFS

Even with rapid reductions in carbon dioxide emissions, the world's oceans will continue to warm for many decades, and continued impacts on coastal ecosystems are expected globally (Gattuso *et al.* 2015). Fundamental to our understanding of tropicalised temperate systems is that regardless of which trajectories are followed, these systems will represent novel ecosystem configurations. This poses major challenges, practically, legally and philosophically, to traditional approaches to conservation and environmental management, which typically focus on maintaining or returning species to particular locations (Hobbs *et al.* 2017; McDonald *et al.* 2019). Below we consider both more traditional (MPAs) and emerging ('assisted evolution') approaches to conservation of these ecosystems, and briefly discuss some of the ethical considerations underlying choices of management approaches.

Marine Protected Areas to increase resilience and connectivity

Marine protected areas (MPAs) generally limit or ban extractive activities either within individual reserves or within entire marine parks (e.g., networks of reserves spanning 100s of km). For kelp ecosystems, this protects not only the kelp themselves, but can also lead to restoration of trophic functions (Babcock *et al.* 2010). Cessation of extractive activities within MPAs generally results in greater abundance and size of higher order predators (Lester *et al.* 2009; Edgar *et al.* 2014). These effects can cascade through food webs by limiting urchin grazing and facilitating kelp recolonisation (Babcock *et al.* 2010). Whether increases in predators can also limit grazing by range-expanding herbivorous fish that maintain tropicalisaed reefs in kelp-free states is, however, largely unknown. In higher latitude reefs, MPAs appear to limit the spread of range-extending species and buffer climate-

related biological variability (Bates *et al.* 2014a; Bates *et al.* 2017), but whether this applies to lower latitude systems remains to be established.

A goal of many MPAs globally is to maintain connectivity in landscapes of habitat loss, fragmentation and degradation and to act as a source for recolonisation in non-protected areas (Palumbi 2003; Coleman *et al.* 2011). However, the strategy of reversing tropicalisation at low latitudes via facilitation of connectivity and recolonization of kelp may be challenging. The approach relies on three assumptions: (i) healthy kelp forests persist in MPAs within a landscape of degraded reefs, (ii) the initial stressor is not permanent and conditions will become favourable for recolonization and (iii) dispersal mechanisms are favourable for kelp dispersal into denuded areas. Such assumptions are rarely met. Direct climate stressors such as warming are often gradual and long term, and even when stressors are temporary (e.g. marine heatwaves) persistence of tropical biota such as herbivores will be an enduring indirect climate stressor that limits kelp recolonization (Wernberg *et al.* 2016). Moreover, oceanographic conditions that are required for dispersal and recolonisation of kelp into areas where it has been lost are often unfavourable (Coleman *et al.* 2017; Wernberg *et al.* 2018).

MPAs may play a greater role in mediating tropicalisation if scientists and managers begin to anticipate future change and manage beyond extant conditions to 'future-proof' the ecological systems and functions that we value (Coleman *et al.* 2017; Bruno *et al.* 2018). For example, there may be benefit in identifying potential thermal refugia (Ban *et al.* 2016). Similarly, areas with oceanographic conditions that allow kelp to thrive (Lourenço *et al.* 2016) could be prioritised for protection to prolong persistence in landscapes of degradation and tropicalisation. Nonetheless, projections of climate impacts within MPAs across the globe suggest that even with such consideration, climatic impacts within MPAs will continue to dramatically change marine ecosystems (Bruno *et al.* 2018).

Capturing new opportunities as a management action

A potential management approach to limit tropicalisation may be to target range-expanding invaders, for example by developing a new fishery or culling programs for specific species. This approach is already used with many invasive species. For example, invasive alien crabs are being used in the marine aquaria trade, turning a threat into a profit (Calado 2012), and similar strategies are being considered for other invasives like the Atlantic blue crab, which has substantial potential as a new fishery (Mancinelli *et al.* 2017). Targeted removals of the invasive lionfish are also being implemented worldwide and can be effective at minimising impacts (Frazer *et al.* 2012).

The development of new fisheries as species shift their distributions is emerging as an important adaptation strategy to climate change, albeit one with intrinsic major challenges as species shift across local, national, and international boundaries (Gaines *et al.* 2018; Pinsky *et al.* 2018). Although shifts in the distribution of commercially important fish stocks has already led to new fishery opportunities and positive economic impacts in some high latitude regions (Jansen *et al.* 2016), the socio-economic consequences of range-shifting species are still largely under-explored (Madin *et al.* 2012).

In the Eastern Mediterranean, range expanding rabbifishes have become an important component of fisheries catches (El-Haweet 2001; Bariche 2005) and are increasingly being targeted in Australia (Gilby, Tibbetts & Stevens 2017; Lenanton *et al.* 2017). However, whether targeting rabbitfish could effectively control the population and decrease grazing pressure on kelp forests remains hypothetical, given that rabbitfish have fast life histories and can sustain high fishery yields despite intense exploitation rates (Robinson *et al.* 2018). Further, any management action that depends on increased fishing effort will have by-catch implications that will also need to be considered.

Assisted evolution and migration

Assisted evolution is the acceleration of evolutionary processes to enhance certain traits (Jones & Monaco 2009; van Oppen *et al.* 2015). Conceptually, the idea includes one or both of (a) enhancing genetic adaptation (resilience) of a species to current or future environmental stressors such as climate change and (b) assisted (enhanced) gene flow (Aitken & Whitlock 2013) by which superior genes or genotypes are introduced and propagated through the target population. For the former, possibilities range from selective breeding of more resilient individuals to the creation of genetically modified organisms via direct genetic manipulations (van Oppen *et al.* 2015), which has recently been piloted using CRISPR/Cas9-genome editing (Cleves *et al.* 2018). For the later, transplanting adapted individuals (assisted migration) or 'seeding' challenged populations with propagules from enhanced individuals have both been contemplated.

Of the three broad possible community configurations for tropicalised temperate reefs (Fig. 1), we argue that systems with large habitat-formers - corals or seaweeds - are more desirable than systems dominated by turf alone (Fig. 1c). This implies three possible strategies for assisted evolution in these systems: (1) enhance the persistence and resilience of the resident, dominant temperate seaweeds (e.g. kelp), (2) enhance other canopy forming seaweeds, either those which themselves are moving polewards (tropical range expanders), or temperate residents which may be more resilient to change (e.g. more thermally tolerant), or (3) accelerate the movement or adaptation of corals to their new higher latitude habitats, for example if it is decided that coral functioning or provision of ecosystem services is preferable to other potential system configurations.

Trying to slow down or halt tropicalisation by genetically enhancing the resilience of kelp communities is largely unexplored. This could potentially be done at the low latitude margins of their ranges, which are already experiencing tropicalisation, or in more central, "core" populations that are yet to undergo change. Both have significant challenges linked to the complex biphasic life history of many seaweeds and our limited understanding of the genes and heritability underlying thermal tolerance in kelps (Wernberg *et al.* 2018). Moreover, kelp life histories often result in limited

dispersal (Durrant *et al.* 2014). Thus the second stage of assisted evolution – gene flow and uptake within the target population – is likely to be slow for most kelps. It is also clear that the loss of kelp is affected by both the direct physiological effects as well as the indirect effects of ocean warming, such as increased herbivory due to the poleward movement of tropical herbivorous fishes (Vergés *et al.* 2014a; Vergés *et al.* 2016). Thus enhancing kelp forests in the face of tropicalisation may require enhancing their resistance to biotic effects such as herbivory in parallel to temperature.

For kelp, an alternative option may be to "future-proof" core populations by moving thermally tolerant genotypes from low latitude populations to central populations, potentially enhancing resilience as warming advances poleward. However, this strategy relies on the assumption that low latitude kelps are better adapted and have been selected for thermal tolerance, which may not be the case (Wernberg *et al.* 2018; Donelson *et al.* 2019). Potential increases in thermal tolerance may also come at the cost of other important traits, such as growth (McAfee, O'Connor & Bishop 2017).

Laminarian kelp often occur mixed with other temperate canopy forming seaweeds that play similar functional roles (Steneck & Johnson 2013) and may present alternative targets for assisted adaptation. However, most canopy algae that co-occur with kelp at lower latitudes (particularly fucoids) are also of temperate affinity, and may actually be even more susceptible to warming and herbivory than kelps (Smale & Wernberg 2013; Martínez *et al.* 2018), presenting poorer targets for assisted adaptation. A more realistic scenario may be to consider assisting colonisation of range expanding tropical canopy forming algae (primarily *Sargassum* spp.) that could maintain relatively similar functional roles to those of kelp canopies in tropicalised systems (Fulton *et al.* 2019). Species of *Sargassum* are generally morphologically plastic and resilient to a wide range of abiotic and physical conditions (Loffler & Hoey 2018). Although tropical *Sargassum* species are generally susceptible to herbivores, they can nevertheless form extensive forests in some habitats during periods of maximum seaweed growth (Doropoulos *et al.* 2013; Fulton *et al.* 2019). Fucoids like *Sargassum* also have simple life histories and some species that float once dislodged have good dispersal capabilities (Deysher & Norton 1981). Hence, assisted gene flow or dispersal may be sufficient to

promote colonisation of canopies of tropical *Sargassum* spp. in areas undergoing climate-mediated tropicalisation, rather than assisted evolution per se.

The third option for maintaining more desirable ecosystem states than turf is to accelerate adaptation/movement of corals into cooler waters. Naturally recruited corals inhabiting high latitude reefs areas appear tolerant to cooler waters including cold spells (Tuckett & Wernberg 2018), but can still be susceptible to bleaching during warm thermal events (Hughes *et al.* 2017). Assisting the migration of more thermally tolerant corals may be beneficial to coral persistence at higher latitudes, however, there are still major knowledge gaps including the heritability of traits in corals and/or symbionts (van Oppen *et al.* 2015).

Ethical considerations

The traditional focus of conservation and management of marine ecosystems has been on maintaining or restoring systems to some presumed 'natural' or historical state. However, we argue that many if not most systems in terrestrial and marine environments have moved beyond historical limits of variability and represent novel ecosystems (sensu Hobbs *et al.* 2006). This includes tropicalising coastlines, and if we accept that these systems are novel, and the potential for restoring them to a historical state is low, the underlying logic for managing these systems changes (Barnosky *et al.* 2017). What, then, are our ethical obligations regarding the management of these new ecosystems?

Given that humans have played a major role in creating these novel ecosystems, it is in our view ethically appropriate to consider active ecological interventions when considering how to mitigate and manage tropicalising marine ecosystems. This view is gaining traction in the scientific literature generally, including the development of logical structures for where/when/how to implement interventions – 'decision trees' (Barnosky *et al.* 2017) – for terrestrial as well as marine systems (van Oppen *et al.* 2017; Filbee-Dexter & Smajdor 2019). Such studies indicate that the ethics

of more interventionist approaches depend on factors such as the degree of confidence that the system is outside of historical limits and/or is unlikely to return to a historical state in the future, and the type of intervention and associated risks of unknown consequences (Barnosky *et al.* 2017; van Oppen *et al.* 2017).

Another important consideration is how to settle on desired management goals. If we are not returning ecosystems to historical states, we must have some other target criteria for managing ecosystems. Maximising biodiversity, maximising ecosystem services or mimicking historical ecosystem structure and function are reasonable targets, but these three goals are also unlikely to be equally achieved by any given intervention (Barnosky *et al.* 2017).

Who then decides what these targets should be? Attitudes to the desirability and ethics of intervention are likely to differ both among scientists and practitioners (McLachlan, Hellmann & Schwartz 2007), and these differences are likely to be even greater once one includes the broader context of the general community, managers and politicians (Filbee-Dexter & Smajdor 2019). It will be critical for scientists and managers to focus on the community's acceptance of more interventionist approaches, and work towards building the social license necessary for implementation of these approaches. This needs to be done in a timely fashion, given the time-lag between experimental adoption of new approaches by specialists and community acceptance of these innovations. As an example, the science and technology development of stem cell therapies or more recently, CRISPER based approaches, is happening well in advance of community understanding or acceptance of the desirability or ethics of these technologies (Baltimore *et al.* 2015), contributing to disruption in uptake and community anxiety.

Tropicalising marine coastlines are a particularly interesting and challenging case for these ethical considerations. In most instances where ecological interventions are considered, they are aimed at rehabilitating a degraded system, even if it is not to a historical state. For tropicalised systems choices may need to be made between two highly valuable and valued ecosystems – kelp beds and coral reefs. That is, do we use the techniques described above to try and enhance the

persistence of kelp forests at their warm edges, do we do nothing, anticipating the gradual encroachment of tropical communities including corals into at least some systems, or do we – given the decline of corals in the core parts of their distributions – even try and enhance the polewards spread of corals into former kelp systems? These are questions that we believe few scientists or managers have yet confronted, and thus in many ways, the management and ethical considerations that arise from tropicalisation are novel, like the ecosystems themselves.

CONCLUSIONS

Temperate reefs and their diverse ecological communities have long supported human use, and there is strong economic and cultural reliance on these coastlines (Bennett *et al.* 2016; Blamey & Bolton 2018). Like coral reefs, temperate reefs are however becoming increasingly shaped by human-induced drivers instead of long-term natural biophysical gradients (Williams *et al.* 2019). Adapting to warming and tropicalised temperate reefs depends on our capacity to accurately understand changes to the functioning of these systems, and to devise adequate responses. Here we have presented three potential trajectories of tropicalisation for warming temperate reefs worldwide that differ in the taxa that end up dominating the seafloor (seaweeds, turf or corals; Fig. 1). We speculate that some tropicalisation end-points may result in gains to some ecosystem functions (e.g. local fish productivity), but at the expense of other functions (e.g. carbon export). Understanding these changes in flows of energy and materials is essential to formulate new conservation strategies and management approaches that minimise risks as well as capture potential opportunities. As technological innovations continue to emerge, having clear goals and considering the ethics surrounding interventionist approaches among the broader community are also essential steps to develop novel management approaches.

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AUTHORS CONTRIBUTIONS

AV led the overall conceptualization of the paper and all authors contributed critically to the writing of the manuscript and gave final approval for publication

DATA ACCESSIBILITY

This is a conceptual review article and includes no data to archive.

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FIGURES

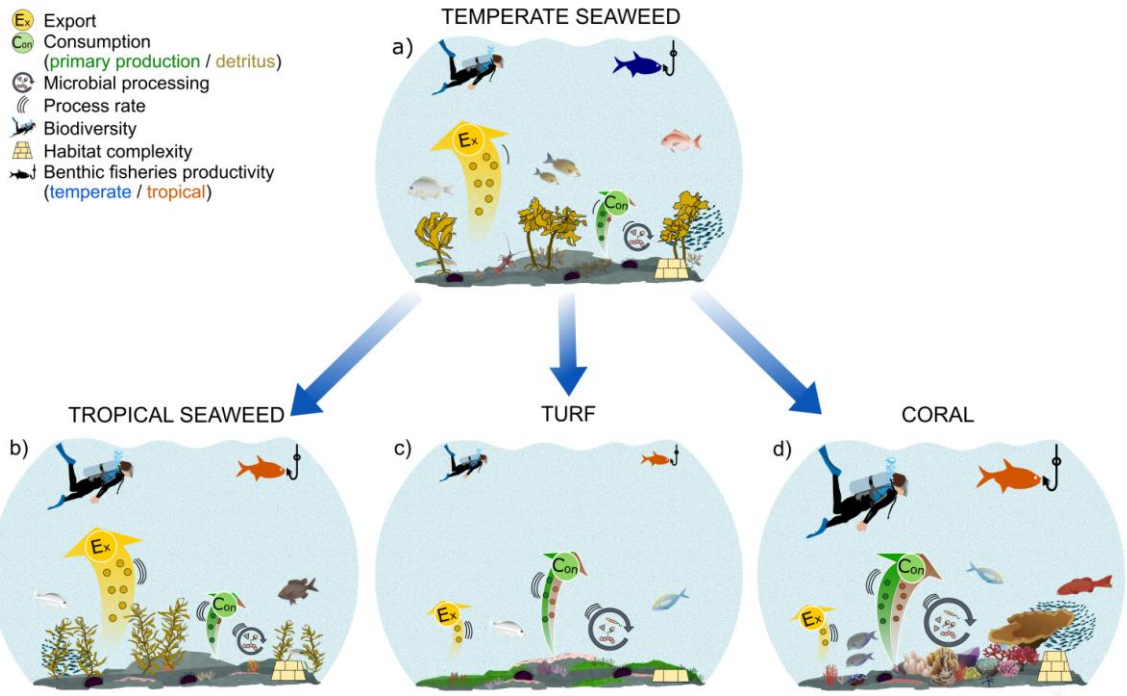

Figure 1. *Representation of key ecosystem functions in (a) current state seaweed-dominated temperate reefs, and three potential scenarios for future-state tropicalised temperate reefs dominated by (b) tropical seaweed, (c) turf algae, or (d) coral. We illustrate here extreme projections, however transitional phases between the various scenarios are also likely to occur. The size of legend icons indicates the relative importance of ecosystem processes.*

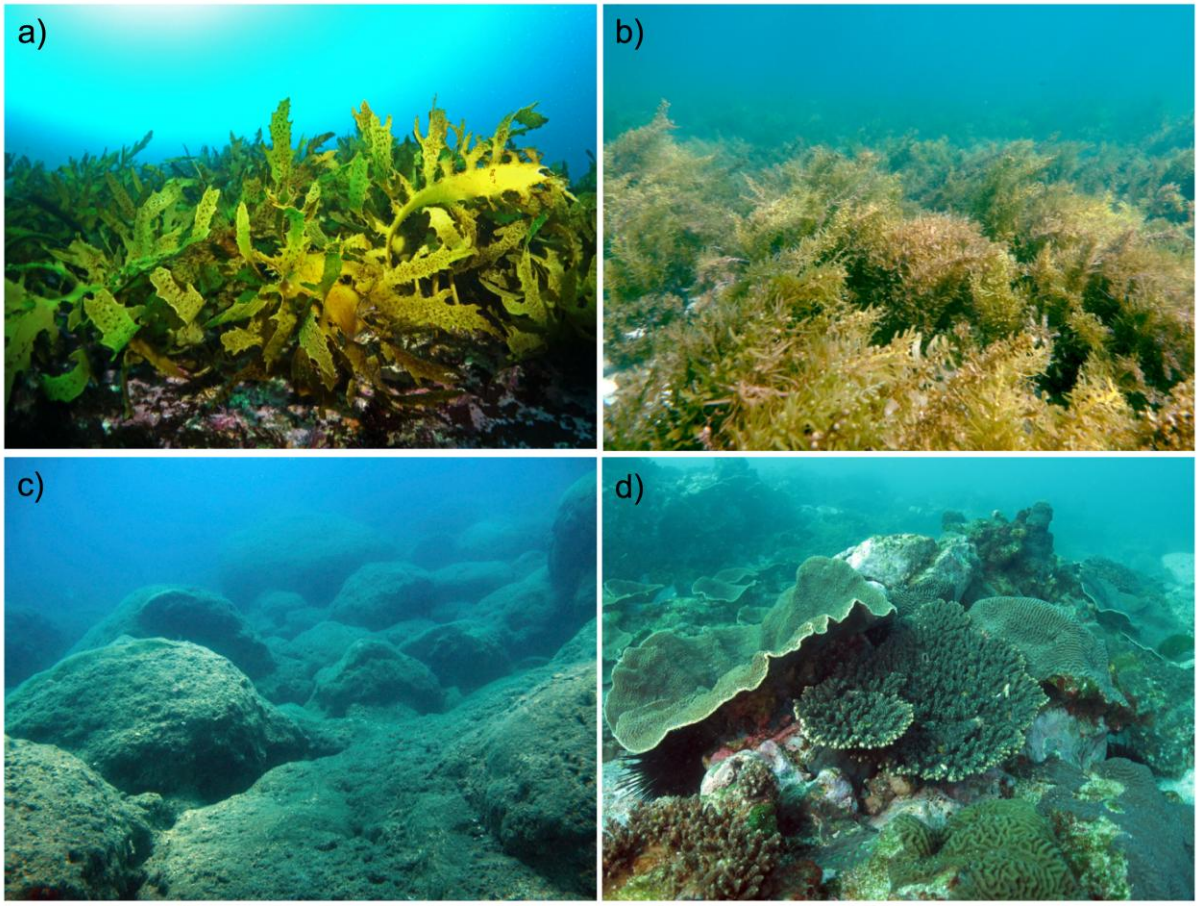

Figure 2. *Photographs depicting (a) Warming temperate reef in Sydney, eastern Australia, dominated by kelp; (b) Tropical fucoid seaweed forest in Ningaloo, western Australia; (c) Turf-dominated system in Aksaki, Turkey; and (d) coral-dominated system in the Solitary Islands tropical-temperate transition zone, eastern Australia. Photo credits: (a) John Turnbull, (b) Chris Fulton, (c) Adriana Vergés, (d) Brigitte Sommer.*