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The speeding up of marine ecosystems

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A B S T R A C T

Four drivers of global change are acting in concert to speed up the ecology of our coastal and open ocean ecosystems. Ocean warming, nutrient pollution, disturbance, and species additions increase biological and ecological rates, favoring weedy communities and causing pervasive human impacts. Ocean warming via greenhouse gas emissions is accelerating metabolic processes, with effects scaling up to populations and ecosystems. Likewise, supercharging primary production via increased resources (e.g., nutrients and light) is leading to faster, weedier communities in estuarine and coastal ecosystems. Disturbances like ocean heat waves are becoming more frequent, resetting succession, and creating permanently young assemblages, while species additions are transporting the quick-growing and the fecund. The speeding up of marine ecosystems will necessitate changes in the ways we do science, attempt conservation, and use ecosystem services.

Introduction

Human activities are causing countless changes to ocean and coastal ecosystems. Fishing has depleted predator populations [1], pollution has reduced local biodiversity [2], and ocean warming is shifting species poleward [3] and decimating populations of foundation species, such as kelps [4]. These dramatic changes are increasingly documented across great swathes of the ocean, yet they represent only the tip of the iceberg. Beneath the surface lies increased ecological process rates; driven by human activities and causing a pervasive 'speeding up' of marine ecosystems. This ecological acceleration requires a rapid shift in our scientific approach to understanding marine ecosystems, the reprioritization of our conservation strategies, and a transformation of the way we use the services of the sea.

Here we argue that the growing industrialization of the global economy is increasing many of the fundamental rates of marine ecosystems, such as how fast organisms grow, move, die, and consume each other, and how quickly energy transfers between trophic levels. We describe empirical evidence that four major drivers of global ecological change (warming, nutrient pollution, disturbance, and species additions) act in unison to increase the fundamental rates of organisms, populations, and communities (Fig. 1). The drivers collectively select for species of small size, short life-span, fast growth, and high recruitment ability [5–8] – all *r*-selected traits typical of weedy species. Species with these traits would also benefit from anthropogenically increased disturbance frequency and nutrients [8], reinforcing their presence in a community. We argue that these factors combined should move communities towards an ongoing state of early succession, comprised of predominantly weedy species suited to high disturbance environments. In principle, this concept may apply to any system where the balance of *r*- and *k*- selected species is regulated by heat, nutrients, or disturbance, or is susceptible to the introduction of weedy species. Any one of these factors may produce this effect, but together their synergies may create a self-reinforcing cycle of weediness (Fig. 2).

Heat

Ocean heating has the potential to act as a global-scale metabolic accelerator, almost universally increasing the metabolism of marine organisms [9]. Most marine organisms are ectotherms, meaning their metabolism is strongly influenced by temperature and should increase up to a point as the ocean warms (Fig. 2) [9–11]. The majority of marine research in this area is aimed at the effects of warming on fitness and survival (e.g. [12]), rather than on the downstream consequences of increased metabolisms for populations and food webs. Yet before warming exceeds the optimum environmental temperature of ectotherms, it increases countless physiological rates potentially with broad ecosystem consequences.

Sub-lethal metabolic rate increases may result in faster growth and shorter generation times, increased caloric demand, and even reductions in organism size [13]. The temperature change required to directly affect metabolism will, however, depend upon the species and environmental context [12]. While it is difficult to make community-level predictions, increased metabolism could lead to greater consumption and top-down control of prey populations [14]. Additionally, the carrying capacity of producer and consumer populations should shrink as temperature, metabolism, and caloric demand increase. If every individual needs more energy just to survive, the intensity of intra-specific competition will also increase due to fewer resources [15], until mortality or another event increases resource availability. This would also negatively affect homeothermic marine birds and mammals when their prey become food-limited and less abundant [16].

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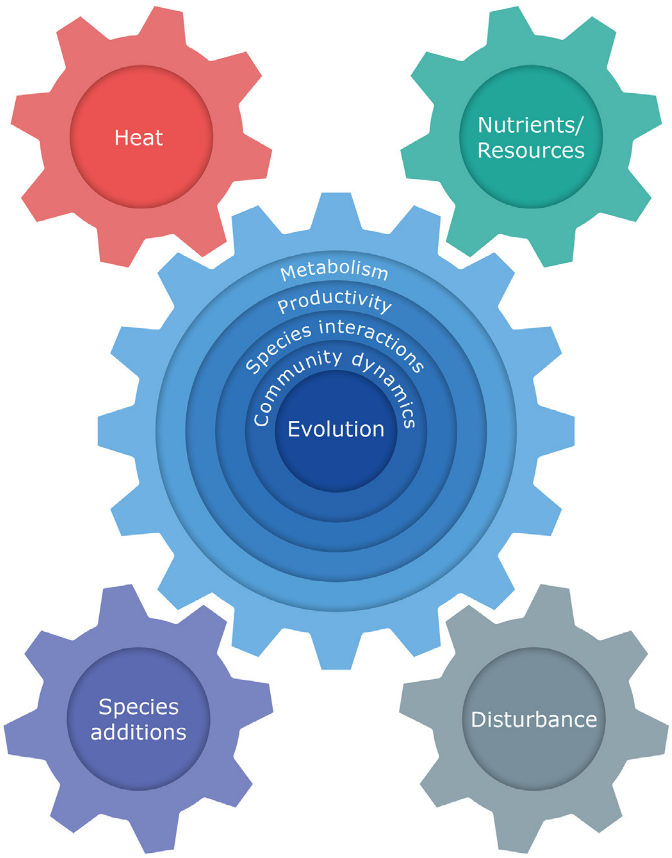

Fig. 1. Conceptual depiction of four drivers (external cogs) that are increasing biological process rates (internal rings) in the ocean.

By reducing population sizes, warming could interact with other rate drivers since smaller populations are at greater risk of local extinction [17]. Additionally, the availability of some resources is declining, just as metabolic acceleration is increasing demand for them. Oxygen levels, for example, are declining in the ocean due to ocean heating (via decreased oxygen solubility) and increased stratification that slows ocean mixing [18]. Warming is predicted to increase the susceptibility of coastal and ocean ecosystems to hypoxic disturbance events [18, 19]. Reduced oxygen environments will also generally lead to increasing metabolisms, reduced sizes, and changed ecological functions of numerous organisms [20, 21]. Such synergisms could amplify the negative effect of accelerating metabolisms on species- and functional-group standing biomass levels [22].

Via the acceleration of growth, ocean warming could also reduce genetic and demographic population connectivity, which has wide ranging implications for adaptation and stock management. Most marine fish and invertebrates have a life history stage in which small larvae are dispersed by ocean currents. Since larval developmental rates increase with temperature, warming should reduce the duration of the larval stage, such that larvae will settle more quickly and closer to home [23]. In some cases, regional management plans are taking these dispersal functions into account, such as in the design of networks of marine reserves [24].

Finally, ocean warming has the potential to increase rates of speciation and adaptive evolution. The 'evolutionary speed' hypothesis argues that warmer climates support greater mutation rates and reduced generation times of individuals, which in turn causes faster rates of genetic divergence among populations, higher rates of speciation, and/or lower rates of extinction [25, 26]. There is evidence for higher speciation rates in tropical climates [27] and Rohde [26] proposed that biodiversity peaks at the equator due to the kinetic effects of environmental temperature on rates of biological processes.

Nutrients and other resources

Growing human populations with increasing *per capita* consumption have accelerated agricultural and industrial activities that release nutrients such as nitrogen, phosphorus, and carbon to our waterways [28]. Much of the increase in nutrient discharges to coastal waters has resulted from the global 10-fold increase in synthetic fertilizer use since the 1950s, although sewage disposal, fossil fuel combustion, and organic enrichment from terrestrial runoff have also contributed [29]. Such enrichment has effectively "fertilized" coastal seas, leading in many cases to increased rates of primary productivity and oxygen consumption. Indeed, nutrient addition is so effective at increasing productivity it has been promoted as a means of geoengineering climate [30].

Although nutrient addition often creates stark headlines of eutrophic events such as "Dead Zones" and "Fish Kills", we contend that most coastal areas are not yet enriched to the point of ecosystem collapse. Nutrient addition can quickly lead to eutrophication in lakes and slow-moving rivers, but along coasts greater circulation and flushing can rapidly dilute effluents and run-off. What is rarely acknowledged, is that within these systems, nutrient addition often increases primary productivity, thereby fueling the acceleration of coastal food webs. As a result, even heavily enriched estuaries may only suffer algal blooms under a restricted set of environmental conditions. This can lead to counterintuitive relationships between nutrient pollution and biodiversity, as reported in our coastal research on fishes [31] and invertebrates [32–34]. Where oxygen "dead zones" do occur they tend to lead to a "smaller-faster" ecosystem, in which a greater proportion of energy is tied up in microorganisms, small fishes, and adjusted respiration rates [18]. And as with warming, there are feedbacks between nutrient addition and deoxygenation: nutrient addition itself can cause deoxygenation (or hypoxic conditions), but low oxygen conditions can directly influence nutrient cycling in a manner that further increases primary productivity and reinforces hypoxic conditions, even when anthropogenic inputs of nutrients have been reduced [18, 19].

While nutrient addition has been by far the most widespread resource addition to marine ecosystems in the 20th century, energy is also being added to some areas in the form of light [35]. At higher latitudes, polar coasts are typically covered by sea-ice for most of the year, such that their nearshore marine communities are light-limited. In areas where climate change is causing sea-ice to break out earlier in summer, much more light is entering the water column per year, thereby promoting primary production of algae and phytoplankton [36, 37]. This may cause slow-growing invertebrate-dominated communities to be replaced by fast-growing algal communities, speeding up production and subsequent ecological processes (e.g., herbivory, decomposition) across vast areas of polar marine habitat [36, 38].

Disturbance

The increasing frequency of human disturbances is shifting marine communities towards younger, early successional states, creating ecosystems dominated by fast-growing "weedy" species. Human use of the coastal zone introduces a plethora of local and regional scale disturbances including pollution [39], resource extraction [40], physical disturbance such as construction [41], and eutrophic or hypoxic episodes resulting in mass mortality events when nutrient concentrations exceed organismal or ecosystem thresholds [18]. The most frequent and impactful human use of the ocean is fishing, which disturbs benthic habitats via trawling and selectively removes larger species and those from higher trophic levels. This leads to "younger" assemblages dominated by smaller individuals with faster metabolisms and growth rates, and greater mass normalized energetic demands [40].

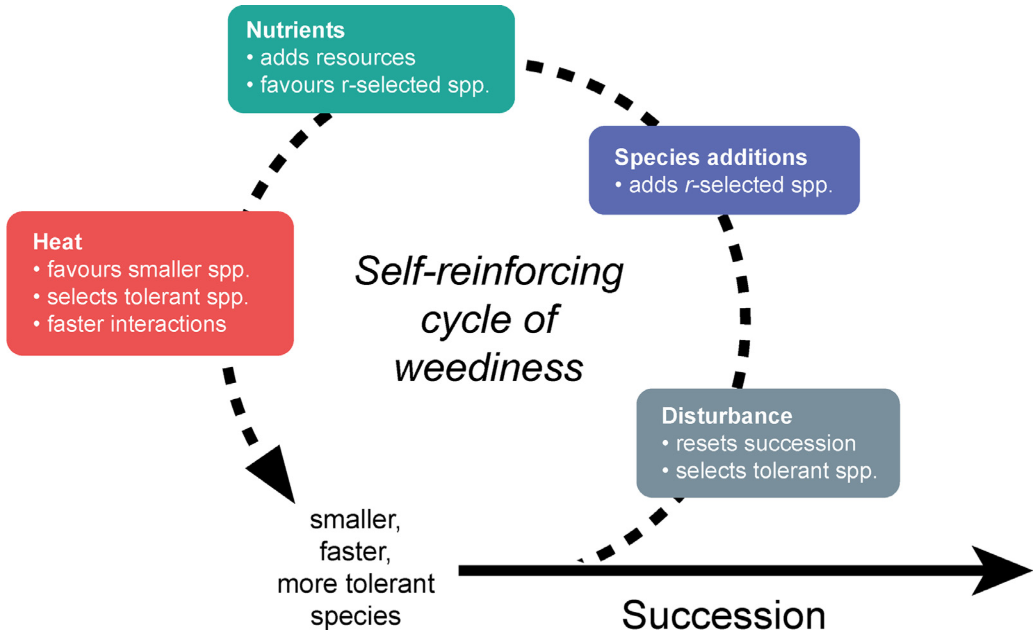

Fig. 2. The self-reinforcing cycles of weediness.

Anthropogenic heat waves are now adding to the mix at regional and global scales, in some cases inflicting unprecedented impacts on coastal and marine ecosystems [42, 43]. Global warming may increase metabolism and primary productivity (as described above), but past the temperature optimum for an organism it becomes a source of physiological stress. Eventually, past a threshold when thermal stress is lethal, it becomes a disturbance at the population- and community-levels (Fig. 2). Recent marine heat waves have increased short-term (weeks to months) temperatures in some regions by nearly 6 °C above seasonal norms. For example, in Australia, a marine heatwave in 2011 decimated kelp forests in Western Australia [44]. In 2016 and 2017, elevated ocean temperature caused mass coral bleaching on the Great Barrier Reef [45] and a heat wave combined with a drought in the Gulf of Carpentaria killed approximately 10% of Australia's mangroves [46]. High temperature anomalies have also been linked with numerous disease-driven rapid declines of keystone species such as sea stars [47], and foundation species including corals and sea grasses [48, 49].

Disturbances typically cause mortality and release resources, effectively re-setting or winding-back successional processes of community assembly [50]. Increasing the frequency or severity of disturbances therefore promotes early successional states, and, if frequent, can keep communities in long-term states of ongoing recolonization by weedy *r*-selected species (Fig. 2) [5, 6]. While this scenario can occur naturally in some high-energy environments, such as in polar coasts frequently disturbed by ice scour [51], we hypothesize that human disturbances are pushing an unnaturally high proportion of communities into early successional states.

Species invasions

The introduction of *r*-selected weedy species into systems that are high in disturbance, nutrients, and energy creates a self-reinforcing ecological feedback loop of weedy communities (Fig. 2). Humans continue to introduce new species into modified marine systems that are more connected than ever via shipping. Shipping accounts for 60–90% of marine bioinvasions and shipping trade is predicted to grow anywhere from 3 to 20 fold by 2050 [52]. A majority of invasive species are "weedy" or *r*-selected, characterized by relatively fast growth rates, short life spans, and the prolific production of poorly provisioned but environmentally-tolerant propagules [7]. There are, of course, exceptions, and it is often the highly competitive invaders that have the greatest impact and are therefore most well-known (e.g., lionfish). Nonetheless, meta-analyses indicate that most introduced marine species are macroplanktivores, deposit feeders, and detritivores [53], which generally exhibit *r*-selected weedy traits. By creating more weedy communities, we are inadvertently engineering communities that are more resilient to the challenges of the Anthropocene. Weedy communities should be more resilient to future disturbances, since their recovery rates are quicker and more likely to exceed the disturbance frequency [8]. For example, communities with high turnover and short lifespans, such as microbes, are capable of rapid and ongoing recovery [54].

Implications for conservation, management, and people

Widespread rate changes will result in novel species assemblages with unique biological traits and ecological characteristics. Adapting to these fast-paced communities will necessitate changes to the way we: (1) do science, namely what we pay attention to, (2) manage fisheries, and (3) obtain services from the ocean. Below, we provide recommendations for each required change.

1 *Ecologists and managers need to be thinking more about rates, and how the relative rates of processes alter emergent patterns.*

Ecology has traditionally focused on pattern and scale, producing theories that assume steady rates in ecological processes. Now, in the Anthropocene, by exacerbating drivers that increase rates of metabolism, productivity, disturbance and community re-assembly, species addition and evolution, we are changing how various ecological processes and their interactions play out. The relative rates of ecological processes affect both the theoretical predictions of pure ecology, such as mechanisms of coexistence [55], and the suitability of various management and conservation strategies. Numerous subdisciplines, such as pelagic ecology and biological oceanography, have long focused on rates but with little reference to ecosystem structure or biodiversity [56], and some community ecologists do measure rates of basic processes including primary production, herbivory, and per capita predation intensity [57]. Yet we believe a re-emphasis on rates — and importantly their cross-scale, functional interdependencies — could increase the applied relevance of much of marine ecological science.

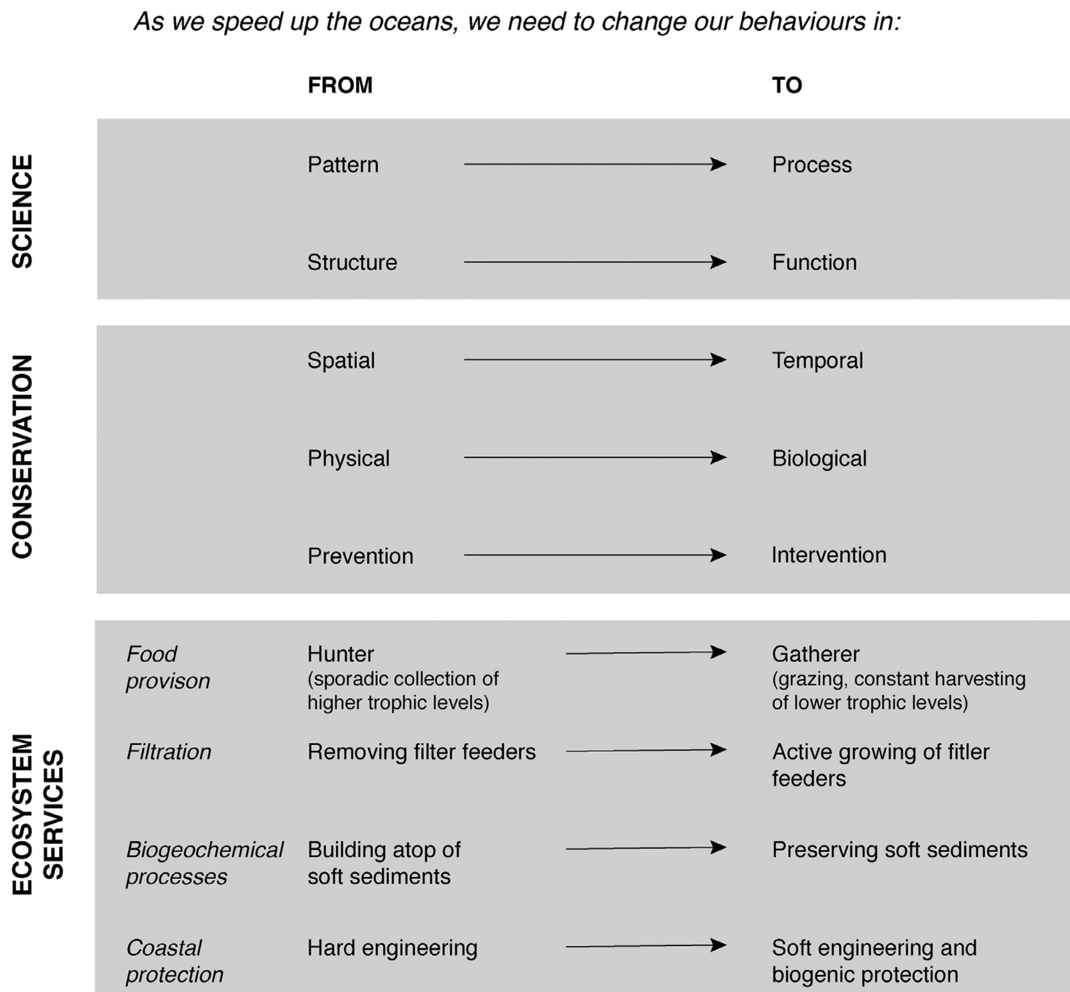

Fig. 3. Implication of the great speeding up for science, conservation, and ecosystem services.

Luckily, new technologies are increasing our ability to measure such rate changes. In addition to revealing responses to multiple interacting disturbances (e.g. [58]), next generation molecular tools can also detect real-time expression of genes for multiple metabolic functions [59]. Likewise, remote sensing can help establish historical disturbance frequencies (at least for the past 30 years) and allow us to monitor proxies of ocean surface water quality and productivity in real time at global scales [60, 61]). Such new sources of data on rates and processes will complement traditional physiological studies and help researchers develop more sophisticated ecological theory and models.

2 *Marine conservation has for decades focused on spatial management, restoration, and stressor mitigation. As ecological systems speed up we need to become more dynamic, adaptive, and interventionist in our approach to conservation.*

Marine conservation is often focused on reducing the impact of local drivers such as pollution and extractive industries. Spatial management tools have frequently been used to manage impacts; such as the point-source control of pollution, and the licensing or zoning of areas for fishing and mining. Most spatial management has assumed a static approach with fixed barriers while temporally dynamic (or adaptive) management has been less common. An exception is fisheries management which commonly uses seasonal closures and annual quotas.

The effect of any intervention is relative to the basal rate of recruitment, growth, resource acquisition, life histories, and community assembly. Since these are rapidly changing, our sense of "what works" needs to be constantly recalibrated. Moreover, managers will be faced with new categories of problems, such as mismatches in phenologies as species differ in their response to changing rate drivers. The scaling of rates such as metabolism and caloric demand with temperature varies considerably among species [62, 63], so metabolic acceleration and other aspects of speeding up can alter the outcomes of species interactions. In the future, to manage marine systems for multiple objectives (e.g., biodiversity and ecosystem function), we will need to employ dynamic conservation approaches and be looking to the effectiveness of interventions practiced at different latitudes [64]. Interventions have traditionally been avoided due to fear of unforeseen consequences, but if environmental change exceeds the potential for adaptation and range expansion, we may need to consider assisted migration [65] and other interventions to maintain ecosystem functions.

Overall, managers will have to adapt their targets, approaches, and mitigations to the accelerating dynamics of the system they conserve. This means some increased uncertainty — which managers understandably dislike. And although some of the specifics are unpredictable, the general rate changes we describe are theoretically based and quite widely empirically validated. What is more difficult to manage is the increasing uncertainty caused by an increasing frequency of extreme events that create unprecedented disturbances of both scale and type [66]. More work is needed to develop socio-ecological models and approaches to decision science that embrace this uncertainty within conservation and environmental management [67].

3 *Changing so many essential rates will have strong effects on the services people derive from the ocean.*

With so many variables changing so quickly, humans will need to be increasingly dynamic in their utilization of ecosystem services. For example, all things being equal, ocean warming will result in reduced productivity of the populations we have traditionally harvested for food and other resources. This will require changes in fisheries management (e.g., reduced MSY for some species in warming regions) and developing other food provisioning systems. In some cases, we can take advantage of many aspects of speeding up (e.g., faster growth and turnover of basal species) by harvesting at lower trophic levels and beginning to emphasize gathering rather than hunting. We can also exploit increased primary production in response to nutrient addition by actively farming fast growing filter feeders (e.g., bivalves and jellyfish) for direct consumption, but also for the service they provide in the form of water filtration that reduces the potential for eutrophication [68].

Conclusions

Multiple drivers are acting in concert to accelerate ecological dynamics in the ocean. Adding heat is accelerating the metabolism of ectotherms, nutrients are providing the limiting factor in primary production, disturbances are resetting systems, and species additions are distributing the fast and the fertile. These factors work together to create positive feedback loops of increasing speed and weediness.

As the ecology of the ocean speeds up, so too must ecologists. We need to determine what degree of warming is sufficient to cause ecologically meaningful metabolic acceleration and its many knock-on consequences. We must rapidly adopt new technologies (e.g., metatranscriptomics and remote sensing) that allow for the simultaneous monitoring of rate processes and the patterns they influence. And we need to create and test meaningful interventions to counter the loss of critical services such as food production and coastal protection. The great speeding up of our coasts and ocean demands that we change our approach to ecology and conservation and transform the way we use the ocean (Fig. 3).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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