

Climate resilience in marine protected areas and the ‘Protection Paradox’

Amanda E. Bates^{a,b,*}, Robert S.C. Cooke^{c,d,e}, Murray I. Duncan^{b,f,g}, Graham J. Edgar^h,
John F. Brunoⁱ, Lisandro Benedetti-Cecchi^j, Isabelle M. Côté^k, Jonathan S. Lefcheck^l,
Mark John Costello^m, Neville Barrett^h, Tomas J. Bird^a, Phillip B. Fenberg^b, Rick D. Stuart-Smith^h

^a Department of Ocean Sciences, Memorial University of Newfoundland, St. John's A1C 5S7, Canada

^b Ocean and Earth Sciences, National Oceanography Centre Southampton, University of Southampton Waterfront Campus, Southampton, SO14 3ZH, United Kingdom

^c Biological Sciences, University of Southampton, Southampton SO17 1BJ, United Kingdom

^d Geography and Environment, University of Southampton, Southampton SO17 1BJ, United Kingdom

^e Marwell Wildlife, Thomson's Lane, Colden Common, Winchester SO21 1JH, United Kingdom

^f Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown 6140, South Africa

^g South African Institute of Aquatic Biodiversity, Grahamstown 6140, South Africa

^h Institute for Marine and Antarctic Studies, University of Tasmania, Hobart 7001, Tasmania, Australia

ⁱ Department of Biology, The University of North Carolina at Chapel Hill, Chapel Hill 27599-3280, USA

^j Department of Biology, University of Pisa, CoNISMa, Pisa, Italy

^k Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

^l Tennenbaum Marine Observatories Network, MarineGEO, Smithsonian Environmental Research Center, Edgewater, MD 21037 USA

^m Institute of Marine Science, University of Auckland, Auckland 1142, New Zealand

ABSTRACT

Restricting human activities through Marine Protected Areas (MPAs) is assumed to create more resilient biological communities with a greater capacity to resist and recover following climate events. Here we review the evidence linking protection from local pressures (e.g., fishing and habitat destruction) with increased resilience. Despite strong theoretical underpinnings, studies have only rarely attributed resilience responses to the recovery of food webs and habitats, and increases in the diversity of communities and populations. When detected, resistance to ocean warming and recovery after extreme events in MPAs have small effect sizes against a backdrop of natural variability. By contrast, large die-offs are well described from MPAs following climate stress events. This may be in part because protection from one set of pressures or drivers (such as fishing) can select for species that are highly sensitive to others (such as warming), creating a ‘Protection Paradox’. Given that climate change is overwhelming the resilience capacity of marine ecosystems, the only primary solution is to reduce carbon emissions. High-quality monitoring data in both space and time can also identify emergent resilience signals that do exist, in combination with adequate reference data to quantify the initial system state. This knowledge will allow networks of diverse protected areas to incorporate spatial refugia against climate change, and identify resilient biological components of natural systems. Sufficient spatial replication further offers insurance against losses in any given MPA, and the possibility for many weak signals of resilience to accumulate.

1. Introduction

A major challenge for conservation science is to maximize sustainability of natural resource use when human activities increasingly threaten ecosystems (Oliver et al., 2015a, 2015b). Improving sustainability outcomes requires multi-disciplinary, multi-scale, multi-taxon methods to quantify the capacity of ecosystems to cope with existing and future pressures (Williams et al., 2008; Foley et al., 2010; Edgar et al., 2016). Scientists and policy-makers are thinking both globally and locally to implement sustainability-based management objectives prescribed by international governance structures (Gill et al., 2017). Under the Convention on Biological Diversity Aichi Targets (6 and 11) and Sustainable Development Goal 14 (SDG14), all oceans are to be

sustainably used, and thus “protected” from over-exploitation, and 10% of coastal seas should be fully protected from human activities by 2020.

Protecting habitats and species from human pressures is assumed to promote communities that are more resilient (Carpenter et al., 2001). Here, we consider resilience as a function of two measures of disturbance-induced ecological change: *resistance* to and *recovery* from disturbance. Resistance is the capacity of a system to maintain function and structure in the face of an acute disturbance (Holling, 1973; Kerkhoff and Enquist, 2007; Hodgson et al., 2015; Nimmo et al., 2015). Recovery is the rate of return to a community structure and function similar to the pre-perturbation state (Hodgson et al., 2015; Oliver et al., 2015a), where a community is an assemblage of species characterised by particular dominant species that re-occurs in space and time.

* Corresponding author at: Department of Ocean Sciences, Memorial University of Newfoundland, St. John's A1C 5S7, Canada.

E-mail address: abates@mun.ca (A.E. Bates).

Resilience is an intrinsic property that depends on both the trajectory of disturbance events (the magnitude and rate of change) (Kerckhoff and Dunquist, 2007) and the initial state of the biological system (Beisner et al., 2003).

To support the overarching goal of maintaining ecosystem functions through resilience, fully protected areas in marine systems (i.e., no-take Marine Protected Areas (MPAs), marine reserves) are considered “important mechanisms for safeguarding ocean life” (SDG14). Yet, the capacity of MPAs to protect ocean ecosystems from climate change remains an open question (Roberts et al., 2017). While we can protect biodiversity from impacts related directly to local human activities, it is difficult to predict the indirect changes in food webs and ecological interactions. Protected areas have historically been designed to restrict activities that remove species and destroy habitats directly, but climate change drivers, such as ocean acidification, long-term warming, and extreme heat events (McLeod et al., 2009), operate over larger scales that do not necessarily respect MPA borders. Climate change drivers have not, until recently, been considered in designing MPAs.

Here, we consider whether protected areas offer greater resilience when exposed to extreme events because the biological communities they harbour are in a more natural condition. We focus on biological responses to decadal signals of ocean warming and extreme weather events in areas protected from fishing – because this research area is relatively data rich. Given that protection from human pressures is expected to increase resilience through a number of direct and indirect mechanisms, we consider these various mechanisms at the biological scales at which researchers measure resistance and recovery: food web, habitat, community and population. We then discuss why relatively little empirical support exists for many proposed resilience mechanisms, and present scenarios in which protection from local pressures is inadequate to sustain species exposed to multiple climate change drivers and disturbance events – or may even increase changes in the biological communities exposed to such events. Finally, we make recommendations for an effective, equitable and ecologically connected global conservation network.

2. Resilience mechanisms in MPAs

Much of what we know about the influence of protection on resilience comes from fisheries data. Fished stocks are typically monitored in time and space because fisheries have economic value and maintaining viable stocks is a key priority. When no-take MPAs are implemented, monitoring is conducted to determine if preventing exploitation of populations and restricting fishing gears that damage critical ecological habitat succeed in meeting conservation objectives. Monitoring has revealed fished populations can rebound and enhance food webs within years to decades following protection (Babcock et al., 2010; Costello, 2014; Coleman et al., 2015), and species forming biogenic habitats can often recover naturally when protected. Various facets of biodiversity are also expected to improve with protection, both at the level of communities (e.g., species diversity) and populations (e.g., genetic). Here we briefly discuss the mechanisms expected to promote resilience at four levels of biological organization.

2.1. Food web

2.1.1. Increase in predators

Given the importance of body size in structuring populations, ecological networks and food webs (Woodward et al., 2005), any change in average body size of individuals (particularly at higher trophic levels) can have profound cascading impacts on communities. Protection from fishing allows large species to recover and increases the relative numbers of large individuals, leading to higher overall biomass (Pauly et al., 1998; Fenberg and Roy, 2008; Lotze et al., 2011; Costello, 2014; Coleman et al., 2015) (Fig. 1). For instance, coral reefs with some form of fisheries restriction, in particular no-take areas, support (on average)

more carnivores, bigger individuals and higher fish biomass than comparable reefs open to fishing (Costello, 2014; MacNeil et al., 2015; Campbell et al., 2018).

More intact trophic food webs and greater trophic web complexity arising from protection influence the strength of ‘top-down’ trophic cascades (Heath et al., 2013; McCauley et al., 2015). Shifts in abundance at the highest trophic levels are transferred to lower trophic levels through connectivity between taxa in food webs. While the removal of top predators by fishing can drive cascading effects that completely restructure food webs (Frank et al., 2005), the same is true if predator populations recover. Abundant predators keep species such as herbivorous urchins in check, and allow kelp and other macroalgae to flourish where they were previously grazed bare (e.g., Leleu et al., 2012). However, there are also examples from coral reefs where higher abundances or biomass of predators have failed to trigger trophic cascades (e.g., Ruppert et al., 2013; Rizzari et al., 2014).

The presence of large individuals has also been linked to population and community stability in protected areas across a number of studies and locations (Fenberg and Roy, 2008). Long-term data from Australia’s tropical and temperate reefs demonstrate clearly that community composition is more stable (i.e., resists change under environmental variability) within protected areas where top predators are present, compared to adjacent habitats open to fishing, with relatively more rapid recovery following climate disturbances (Bates et al., 2013; Mellin et al., 2016).

Theory developed from the field of invasion ecology also predicts that the retention or recovery of top predators can help local communities resist colonization by invasive and range-shifting species. This ‘biotic resistance’ is due to stronger top-down control on community structure where invasive or range-shifting species are consumed (Worm et al., 2006; Byrnes et al., 2007). There is some evidence that larger predators in protected areas can limit initial colonization (Bates et al., 2017). For example, larger lobsters in protected areas feed on and limit populations of an urchin (*Centrostephanus rodgersii*), a pest species that has shifted its historical range to Tasmania (Ling et al., 2009; Johnson et al., 2011). By contrast, the abundance of invasive lionfish in the Caribbean is unrelated to predator densities (Hackerott et al., 2013). Given these species-specific results and the limited coverage of no-take MPAs (protected areas where fishing and other extractive activities are prohibited presently cover < 2% of the ocean: Boonzaier and Pauly, 2016), it is difficult to envision how MPAs can presently limit invasive and range-shifting species across seascapes. This is especially true where the average larval dispersal distance vastly exceeds the reach of most protected areas (Gaines et al., 2007).

2.1.2. Increase in herbivores

Retaining a greater biomass of herbivorous fishes has been strongly advocated as a mechanism to increase the resilience of coral reef systems (e.g., Roberts et al., 2017). When herbivores increase in biomass and graze down macroalgae, corals can colonize and grow (Graham et al., 2015; Mellin et al., 2016; Nash et al., 2016; Strain et al., 2019). Even so, the extent of increased herbivore biomass in protected areas, and how increased herbivory in turn relates to coral reef resilience depends on both the local and regional contexts - protection alone does not necessarily translate into herbivore recovery. Herbivorous fishes on coral reefs can increase or decrease depending on the type of coral system, the relative fishing pressures on herbivores, and which top predators occur in the region (e.g., Ogden and Lobel, 1978; Hughes et al., 2007; Stuart-Smith et al., 2018; Bruno et al., 2019). Herbivore responses also involve both fish and invertebrate players, especially in temperate systems (Bates et al., 2017). Thus while this topic has caused much debate in tropical systems, it is also unknown whether herbivore recovery plays any role in resilience in temperate systems, where food webs are simpler due to fewer species (e.g., Stuart-Smith et al., 2013).

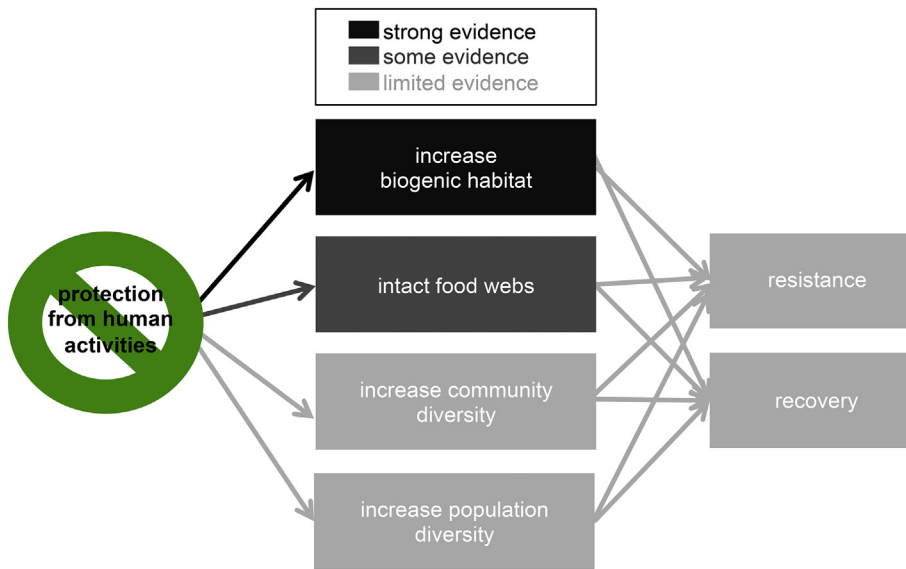


Fig. 1. Protection from human pressures has been shown to maintain or improve habitats, food webs and diversity of communities and populations through a number of mechanisms discussed in the main text. These different scales of biological organization are ranked based on the varying strengths of evidence for mechanisms leading to each outcome, which in turn supports increased ecological resilience. Accumulation of weak signals of resilience across many different biological scales should enhance the overall capacity of protected communities to resist and recover from climate drivers.

2.1.3. Increase in parasites

Given a strong focus of research on predation and herbivory, it is possible that trophic effects among less charismatic fauna may be going unrecognized. Parasites are a fundamental trophic guild that are understudied as a key driver of community patterns, yet theory predicts that healthy and diverse parasite communities can stabilize food webs (Lafferty et al., 2008). The increase in large fishes in protected areas should lead to increased parasite populations due to the additional biomass and higher host population abundances. In one case, higher overall abundances of parasites in protected areas have been documented, but fewer parasites per individual fish were recorded without a reduction in fish health (Wood et al., 2013). Focusing on the full components of food webs will help us to predict how less-studied trophic groups will respond to protection and extreme events.

2.2. Habitat

2.2.1. Increase in habitat complexity

Foundation taxa (i.e., those species responsible for the physical structure of an ecosystem by forming biogenic habitats) are impacted by human activities that cause physical damage such as benthic trawling and dredging (Sciberras et al., 2018). When these pressures are removed through management actions and benthic systems are protected from the physical damage such as arising from fishing gears (Lotze et al., 2011), the recovery of habitat-forming species is possible (Babcock et al., 2010) and sometimes rapid (Orth et al., 2017). Multiple indirect mechanisms may also promote species that form critical habitat (Babcock et al., 2010). For instance, coral and kelp cover can be higher and more stable through time in some areas protected from fishing (e.g., Bates et al., 2017; Castilla et al., 2007). The responses of these foundation species have been attributed to a reduction in grazing intensity through trophic shifts following protection (discussed in 2.1 Food Web) and declines in species that impede recruitment of habitat-forming species (Castilla et al., 2007; Ling et al., 2009; Selig and Bruno, 2010; Leleu et al., 2012; Sala et al., 2012; Bates et al., 2017).

2.2.2. Increase in ecosystem functions

The ecosystem benefits of foundation species that form habitat (e.g., corals and sponges form reefs, seagrasses form meadows, macroalgae form forests, oysters and mussels form beds) are well documented (Bruno and Bertness, 2001; Palumbi et al., 2009). These species provide habitat for diverse food webs through increased structural complexity (Beck et al., 2001) and increased productivity (Cebrian, 2002), and

support numerous ecosystem functions and services (Barbier et al., 2011). For instance, some species that form tubes and burrows can stabilize sediments, and others, such as kelps, can change water flows and temperature regimes (Palumbi et al., 2009). Regardless of the pathway (direct, indirect, or a combination of both), recovery of habitat-forming species can benefit not only dependent species and support higher abundances of more species that play diverse community roles, but also alter entire ecosystems. A future research direction is to identify the vulnerability of habitat-forming species to climate change and other drivers, and the potential role of these species in underpinning climate change resilience and other disturbances (e.g., as suggested by Roberts et al., 2017).

2.3. Community

2.3.1. Increase in species diversity

The existence of large, well-managed protected areas is associated with higher overall biodiversity, based on analyses across different systems and regions (Fenberg et al., 2012; Edgar et al., 2014). Increases in the richness and diversity of species in a community are predicted to lead to greater levels and stability of ecological functions, along with the capacity to resist and recover from disturbance events (Tilman et al., 1996; Figge, 2004).

This “portfolio effect” may be generated by the variation among taxa in their responses to disturbance, i.e., response diversity, leading to asynchrony between species’ population sizes and ultimately greater ecological stability (Wang and Loreau, 2014; Oliver et al., 2015a). Response diversity is thus predicted to provide insurance against changes in functioning due to loss of species, and is considered crucial for ecosystem renewal and reorganisation following disturbances (Mouillot et al., 2016). However, evidence for response diversity (at the community level) leading to resilience in natural systems is sparse (Fig. 1).

Manipulative experiments do suggest that more species should translate to greater functioning and resilience across a range of marine ecosystems (Maggi et al., 2011; Gamfeldt et al., 2014). In terms of real-world datasets, diverse rocky and coral reef fish communities appear (on average) more resistant to warming and variability in temperature (Duffy et al., 2016), and are more temporally stable (Bates et al., 2013; Mellin et al., 2014), with lower rates of collapse and extinction of commercially important fish and invertebrate taxa over time (Worm et al., 2006). However, the relationship between species richness and the portfolio of functional roles appears to be stronger in species-poor

communities than in species-rich ones (Duffy et al., 2016). Temperate communities tend to exhibit lower functional redundancy; consequently, removal of one species from a temperate area may generate larger negative consequences for the ecosystem than the removal of one species from a more diverse tropical assemblage (Micheli and Halpern, 2005). However, empirical evidence of relationships between species richness, functional diversity and resilience may be highly context dependent (Wahl et al., 2011; Zhang et al., 2014) and differ between temperate and tropical communities – highlighting important future research areas to be tested in quantitative frameworks.

2.4. Population

2.4.1. Increase in genetic diversity

Protected areas may play a role in facilitating both the resistance of individuals to disturbance events (such as due to climate extremes) and population recovery following high mortality. This is because fishing, through targeting individuals, can reduce genetic and trait specific diversity (Pinsky and Palumbi, 2014; McCauley et al., 2015). A reduction in genetic diversity likely represents a loss of adaptive potential that may impair the capacity of a population to resist or recover from a disturbance (Walsh et al., 2006), whereas management actions that lead to the opposite effect – enhancement of genetic diversity – should increase population-level resilience. However, we are unaware of data showing an MPA to have such an effect.

2.4.2. Increase in body size

The influence of fisheries exploitation on certain life-history traits (e.g., size, age and reproduction) can affect the temporal dynamics of recruitment (Anderson et al., 2008; Planque et al., 2010). Fish in exploited populations tend to be smaller, thinner, and less fecund, and reproduce at smaller sizes (Jørgensen et al., 2007). Size-based trait selection has important implications because trophic interactions and spatial dynamics in the ocean tend to be based on body size (Webb et al., 2011). Larger fish, for instance, tend to have longer spawning seasons (Hixon et al., 2014). Longer spawning windows mean unfavourable periods can be avoided, whereby the timing of spawning events can be delayed until the return of more favourable conditions, thereby promoting successful recruitment (Hixon et al., 2014). Indeed, following a hypoxic event in Baja California that caused widespread mortality in many benthic invertebrate species, pink abalone (*Haliotis corrugata*) were less affected in MPAs than in unprotected areas (Micheli et al., 2012). The relatively larger body size and egg production of the adults found within MPAs, and the related success in juvenile recruitment, conferred population stability and recovery following exposure to low oxygen.

2.4.3. Increase in body condition

A mechanism associated with resistance of large individuals is health. Large individuals protected from capture in MPAs, or that better maintain overall condition because of high food availability, should possess more energetic reserves to cope with environmental variability (although the reverse may be true if density dependence comes into play, Lizaso et al., 2000). If abundant ectothermic consumers are supported by greater food quantity or quality, they might be more resilient to environmental stressors. Enhanced energy requirements, due to temperature-dependency for example, will be more likely to be met by local resources during periods of elevated temperature (e.g., corals: Hoogenboom et al., 2009, fishes: Pörtner and Peck, 2010). Larger and more fecund animals can persist during unfavourable periods by utilising body reserves, and release greater numbers of eggs and larvae than small species once the unfavourable period has passed (Edgar, 1994). Such effects were observed during the prolonged 1983 El Niño event in the Galapagos where, during a period of little water column stratification and low primary and secondary production, small sea lions tended to die before large individuals because of energy

limitations (Trillmich and Limberger, 1985). On the other hand, higher abundance and metabolic demands with warmer temperatures may increase competition for food such that populations become food limited or are impacted by high predation or foraging. The role of protection in providing an “energetic buffer” during warmer seasons and years, and promoting individuals that are healthier and can survive and/or recover following extreme events, deserves investigation.

2.4.4. Increase in physiological performance

The extent to which fishing selectively removes traits other than those related to size (e.g., behavioural or physiological) has until recently received relatively little attention (Biro and Post, 2008), but these traits could be important in moderating population responses to climate drivers. Growing empirical and theoretical evidence suggests that, for passive-gear fisheries, the behavioural state of an individual plays an important role in determining vulnerability to capture (Lennox et al., 2017). For example, bold or aggressive individuals can out-compete conspecifics to a bait or encounter bait more often through higher activity levels, rendering them more vulnerable to capture, and ultimately resulting in timid and less behaviourally diverse populations (Uusi-Heikkilä et al., 2008; Rupia et al., 2016; Arlinghaus et al., 2017; Cooke et al., 2017). Such bold and aggressive behavioural types are often associated with particular metabolic phenotypes. Humans may therefore be applying directional selection pressures across seascapes, potentially leading to populations with smaller, more timid individuals, and thus fundamentally restructuring communities.

3. Factors contributing to limited evidence for resilience in protected areas

3.1. Variability in impacts and responses

Given the theoretical expectations for greater resilience in protected areas but the limited evidence for these mechanisms (Fig. 1), we ask: why aren't we detecting evidence of enhanced resistance and recovery in protected areas more generally? We explore four possible contributing factors here.

First, the systems in which we are testing for resilience might have already been heavily altered by climate change and human activities, and may therefore not follow theoretical expectations (Knowlton and Jackson, 2008; Lotze and Worm, 2009). For example, if temperature regimes are shifting rapidly, then recovery to undisturbed conditions will be attenuated or impossible. While MPAs are often monitored, most MPAs are young (Babcock et al., 2010; Edgar et al., 2014). Thus climate change and other human activities have likely already impacted MPAs before their implementation and subsequent monitoring (Shifting Baseline Syndrome: Papworth et al., 2009).

Second, resilience responses in real world communities are also complicated by the level of protection and enforcement afforded to an MPA, as well as MPA size and age. In fact, the effectiveness of most protected areas at limiting local human pressures is compromised. Many MPAs allow some fishing and are poorly enforced (Claudet et al., 2008; Costello, 2014; Edgar et al., 2014). Many MPAs are also small, with high edge to area ratios, and thus resilience responses will be attenuated by encroaching fishing activities, such as heavy boundary fishing pressure. Small MPAs also may have significant movement of individuals from exploited species outside protected boundaries, which may not be measured (Gell and Roberts, 2003). Most protected areas are also young, and the mechanisms facilitating resilience may take multiple decades to manifest as communities recover following protection (Babcock et al., 2010; Lotze et al., 2011; MacNeil et al., 2015).

Third, multiple resilience responses are expected and even depend on the particular response being measured (Bates et al., 2017). For example, two case studies found positive relationships between habitat complexity and resistance to disturbance: a Mediterranean algal system (long-term, over a decade, Fraschetti et al., 2013) and a tropical

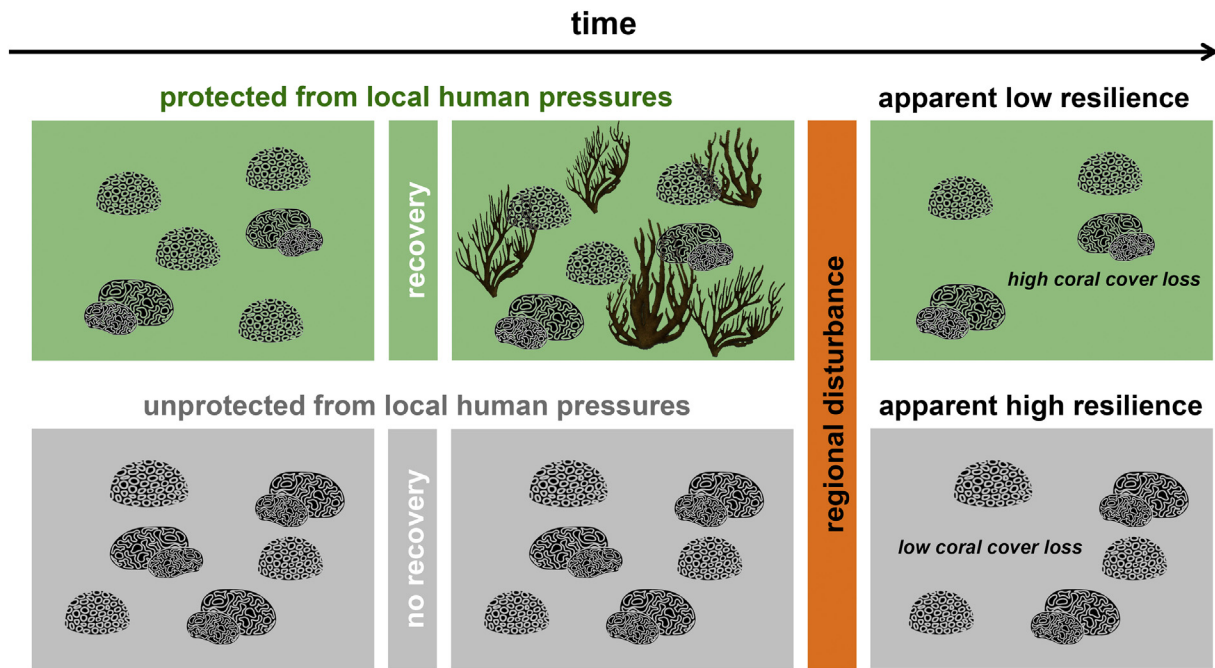


Fig. 2. Communities protected from local human pressures in Marine Protected Areas (MPAs) recover individuals and species. A “Protection Paradox” arises when an MPA is hit by a disturbance event and loses more individuals or species in comparison to areas outside the MPA. We illustrate this effect here with different coral morphotypes represented by massive and branching shapes. Branching corals that are reef-forming competitive dominants such as *Acropora* spp. are relatively sensitive to physical damage from local human activities, such as from boating anchors and fishing nets, and are more easily lost from unprotected communities. However, massive corals recover under local protection. Even so, extreme heat events cross MPA borders and it is branching morphotypes that are also the most thermally sensitive (e.g., Hughes et al., 2018), resulting in a relatively larger reduction in coral cover and complexity in the protected compared to the unprotected community and apparent low resilience to climate disturbances. By contrast, those species that are thermally resistant (e.g., mound-shaped corals) survive the disturbance and thus coral cover remains more stable through time, displaying apparent high resilience.

seagrass system (short-term, before and after a monsoon event, Alonso Aller et al., 2017). Resilience mechanisms may therefore be missed if the data required to quantify a specific mechanism were not included in a monitoring program. Yet it is challenging to imagine how to measure all possible combinations of biological responses in all species present with high-resolution data (from genes to communities). The biological rates and outcomes underlying responses such as physiological stress and increased survivorship are inherently difficult to measure in the field. Such processes are rarely observed or measured directly in field studies and may require proxies of biochemical processes (Dahlhoff, 2004), biomass (Caddy, 2004; Piatt et al., 2007), or resource-intensive tagging studies (Heupel and Simpfendorfer, 2002; Gormley et al., 2012) to approximate true values. Such data may be particularly important when indirect mechanisms such as behavioural selection underpin species responses following protection, but will require dedicated budgets for on-going monitoring.

Fourth, even when monitoring programs are designed to quantify resilience responses following protection, the magnitude of these dynamics may be highly variable, dampened by other signals, and difficult to detect (Ciannelli et al., 2004). Indeed, when resilience mechanisms have been reported the effect size is small in both temperate (e.g., Bates et al., 2013) and tropical systems (Mellin et al., 2016; Alonso Aller et al., 2017). Moreover, responses may be linear or weakly non-linear over time, or display strong thresholds. In many cases we may not have sufficient empirical evidence to detect these types of responses with small effect sizes, even though these signals may exist.

Given this set of challenges, measuring resilience likely requires quantitative data at different scales of biological organization. Biodiversity change can only be inferred from long-term (decadal) baselines and comparisons with reference areas. The only likely reference areas, or controls, are large and old protected areas, or locations otherwise not directly or indirectly impacted by human activities, such as military zones (Cizek et al., 2013). Any attempts to measure

resilience should take into account attributes that may shape the resistance profiles and recovery trajectories. These include MPA size and age of reserves, as well as any neighbouring impacts, baseline expectations of natural variability, historical exploitation levels, and the existing community composition. Such data are rare globally and fundamentally limited by sample size (Edgar et al., 2016). It therefore remains an open question if the observed effects sizes, which are small, integrate across seascapes to build resilience at a network scale that is greater than a sum of parts (Gao and Barabási, 2016). Moreover, it is possible that further monitoring will reveal stronger effects once confounding variables are identified and controlled for, and with the increasing information available on the recovery of protected areas following disturbance events.

3.2. The Protection Paradox

While detecting resilience outcomes in MPAs is difficult, mortality events can be conspicuous. Indeed, mass mortality events such as coral bleaching are well known from MPAs (Hughes et al., 2018). If the species and habitats that are protected from local human pressures are also more sensitive to climate-related environmental variability (i.e., vulnerability traits are linked), protected areas in which they are allowed to recover may stand to lose the most when other or more severe disturbances hit. For instance, coral species that are sensitive to physical disturbance because they are branching can also be sensitive to warming (Jackson and Hughes, 1985; Hughes et al., 2003; Darling et al., 2013). In fact, many habitat-forming species that are protected, for example, when coastal development is limited or human activities that damage the benthos are prevented, are also highly sensitive to increases in temperature, extreme weather and storms. Seagrass and kelp, for example, appear to be negatively affected by warming events (Wernberg et al., 2016) and shifts in nutrient regimes (Lefcheck et al., 2017). Recent losses of reef-building corals have been primarily driven

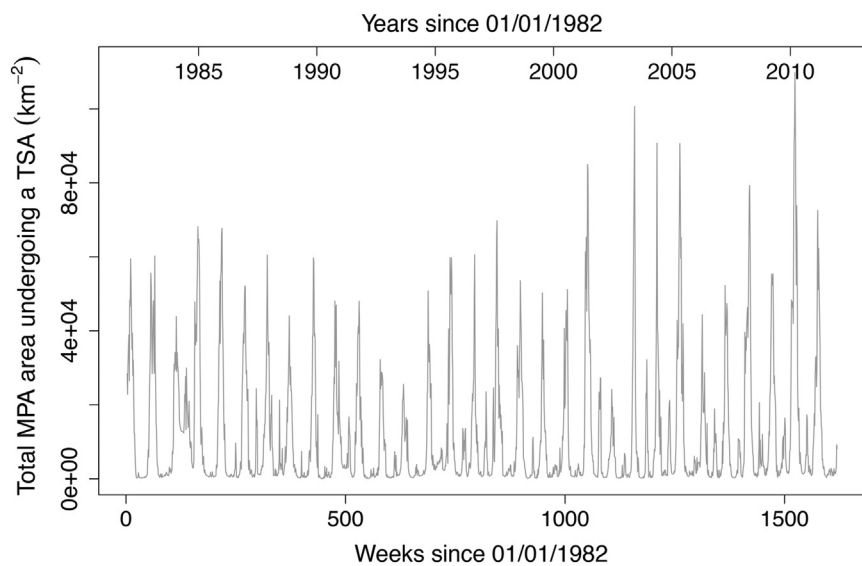


Fig. 3. Total area of no-take marine protected areas (MPAs) undergoing thermal stress anomalies (TSA) at weekly intervals, reported as weeks (bottom x-axis) and years (top x-axis) since 01/01/1982. The time-series ends 25/12/2012. Area totals through time are based on locations of current MPAs and do not take the date of declaration into account. The data series illustrates that the total area presently protected in our oceans is consistently exposed to thermal stress anomalies. Given that it is difficult to predict thermal stress events, it may not be possible to design MPAs so that they will remain untouched by thermal stress events.

by warming and extreme heat events, causing bleaching, disease and functional changes across coral reefs at a global scale (Hughes et al., 2018). By virtue of having promoted the recovery of these habitats, protected habitat-forming species are primed for losses in the event of extreme heat events or other climate-related impacts.

When protection from one pressure is implemented (e.g., fishing) and vulnerable species recover, these species may also be relatively more sensitive to other pressures that are not regulated (e.g., climate events) (Hughes et al., 2003). Here we describe this challenge as a “Protection Paradox” (Fig. 2). When the performance of protected areas are compared to areas open to fishing and other human activities, this paradox is emphasized. In these impacted sites, many sensitive species will have already been lost, i.e., ‘extinction filters’ (Balmford, 2006). Extinction filters have the potential to make the most disturbed communities appear the most resilient to extreme events by preselecting for fewer, hardier species. Conversely, there may be relatively greater losses in MPAs where there is equal or greater vulnerability to climate effects but many more species to lose (Fig. 2).

This issue is apparent in tropical reef systems where coral loss after thermal events can be markedly greater on reefs with higher coral cover (Selig et al., 2012; Zhang et al., 2014) (Fig. 2). For example, coral communities in Kenyan protected areas had higher coral cover than those on fished reefs before the 1998 temperature anomaly that caused a mass coral bleaching event, but lost a greater proportion of it during the event (Darling et al., 2010). In this instance, prior to bleaching, MPAs provided a refuge for coral species that were susceptible to the direct impacts of fishing gear and to low herbivory (owing to the absence of herbivorous fishes in fished areas). Protected areas harboured a rich set of hard coral species with varied forms, adding significant life-history diversity and functional complexity to the system, but some of these species also had low tolerance to warmer temperatures (Darling et al., 2013). This example highlights the challenge of protecting species with co-tolerances or co-susceptibilities to multiple climate stressors and disturbances.

3.3. Exposure of MPAs to extreme events highlights the Protection Paradox

A disparity thus exists between research promoting MPAs as a tool for increasing resilience and the many observations of mass mortality events in protected areas. The best examples come from coral reef systems. This is because a large global effort that has been placed on the management and research of coral reefs, combined with the vulnerability of corals to temperature-related bleaching and damage due to storms. Indeed, a ‘protection provides resilience’ paradigm now

underpins the management of coral reefs worldwide (Roberts et al., 2017; West and Salm, 2003). However, there is very little empirical evidence in support of this assumption (Bruno et al., 2019). On average, protection had no overall effect on the magnitude of resistance or recovery of coral communities to large-scale disturbances, including mass-bleaching events and storms, in 66 marine protected areas worldwide (Bruno et al., 2019). Likewise, Selig et al. (2012) found that the strong effect of warm sea surface temperature anomalies on corals was unaffected by local protection in 289 marine protected areas. Numerous other local and regional studies have reported similar results (Carassou et al., 2013; Coelho and Manfrino, 2007; Graham et al., 2008; Toth et al., 2014). The recent (from 2015 to 2017) mass bleaching and subsequent heavy coral mortality on some of the world’s most isolated and well-protected reefs, e.g., the Great Barrier Reef, the Chagos Archipelago, Jarvis and other equatorial Pacific atolls (Sheppard et al., 2017; Brainard et al., 2018; Hughes et al., 2018), support the broader inference that local protection, or the reduction of local anthropogenic stresses, does not boost resilience of corals to extreme exposure to strong temperature-related stressors.

These observations of coral ecosystems raise an expectation that can be extended beyond the tropics: extreme events are increasing (e.g., heat waves: Oliver et al., 2018). Extreme heat (and other climate) events will cross the borders of protected areas and may damage and alter the communities and habitats present. Our own analysis of the geographic extent of heat wave events in relation to MPA size supports this contention. Here, we define the incidence of heat waves as thermal stress anomalies, TSA (as in Selig et al., 2010). TSA are when temperatures exceed the climatologically warmest week of the year by 1 °C or more based on a 31-year historical baseline period from 1982 to 2012 at 4-km resolution (CoRTAD database, version V, available at <https://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>). We identified all no-take MPAs larger than 16 km² ($n = 368$, from the World Database on Protected Areas (IUCN and UNEP-WCMC (2018))), and matched the temperature data to these locations. We found that the median size of MPAs with some no-take area that were affected by at least one thermal stress anomaly was 1145 km², whereas the median size of a thermal stress anomaly falling within the boundaries of an MPA was 64 km². Overall, only 20% of thermal stress anomalies impacted the full extent of MPAs. However, from 1982 to 2012, there was an increasing trend for the total area being hit by thermal stress anomaly events to increase, reaching 1.5 million square kilometers (Fig. 3).

Mean sea-surface temperatures within protected areas will warm by an estimated 2.8 °C compared to present by 2100 (business-as-usual

scenario, representative concentration pathway 8.5 (RCP8.5); van Vuuren et al., 2011), with mean sea surface temperature and oxygen concentration exceeding their ranges of current natural variability by mid-century in 42% of MPAs (Bruno et al., 2018). Moreover, the estimated temperature limits for the average species within shallow rocky and coral reef species in protected areas will be exceeded by 2050 in the warmest tropical seas, and a century later for many protected communities at higher latitudes (Stuart-Smith et al., 2015; Bruno et al., 2018). Historical data, in combination with case studies, predict both high exposure and sensitivity to future change in species residing in protected areas. Mortality events can therefore be expected in protected areas given a scenario of unabated carbon emissions. Thus an important first step, given that most MPAs were not put in place with climate change as a design constraint, is to explicitly consider climate change when planning MPA networks. For instance, locations with low climate velocity or those with steep depth gradients (and thus temperature gradients) may offer refugia (Schloss et al., 2011).

Yet extreme temperature, low oxygen concentration and low pH have different spatial patterns of emergence that do not overlap (Bruno et al., 2018). Therefore planning to reduce exposure to one climate change driver may increase exposure to another (Bruno et al., 2018). Prediction of future climate events further comes with low accuracy (e.g., Dessai et al., 2009). No-take MPAs implemented within a spatial network may therefore be synergetic in terms of the resilience an individual MPA can provide, offering insurance against unexpected extreme events (e.g., McLeod et al., 2009). MPAs within a network may protect some populations, thereby maintaining the viability of species. MPAs may also function, as has been suggested for terrestrial parks, as migratory corridors, or stepping stones, for species tracking their climate niches (Thomas et al., 2012). Thus, no-take MPAs within a well-connected network might provide large-scale resilience that individual MPAs do not provide on a smaller scale, and thus provide insurance against climate events and other disturbances that are spatially patchy (e.g., Selig et al., 2010).

4. A global MPA network

Here, we have identified some of the theoretical reasons why individual MPAs, and MPA networks, can buffer ecological communities against climate change and preserve the suite of goods and services necessary for human well-being (Fig. 1). Fully protected networks of MPAs are expected to support resilience at all levels of biodiversity. Indeed, signals of resistance and recovery have been observed across different scales of biological organization where quality data and effective MPAs are in place. However, in many examples these signals are weak and require high-resolution monitoring and reference data to detect, or are inconsistent across different aspects of diversity, systems and regions. We therefore cannot assume that protection will provide sufficient buffering against climate change via enhanced resilience. Ultimately projected climate scenarios will overwhelm even the strongest resilience effects recorded to date, and mitigation of global warming is the most pressing management response to protect against adverse change.

In the interim, we suggest enhancing the global network of MPAs to provide the spatial and habitat refugia, such as cooler upwelling areas, from which impacted areas may be replenished through time. To help prioritize important reference areas for inclusion in a global MPA network, recognizing areas in which populations, species and functional groups are either extremely vulnerable or resistant to particular environmental disturbances is also key. We further suggest creating precautionary networks in areas where we simply don't know how species and communities will respond to climate drivers, including from deep ocean systems. MPAs, in being focal areas for long-term monitoring, will offer a framework for filling gaps in our biodiversity information and facilitate earlier detection of warning signals for shaping management actions.

Instead of debating whether individual MPAs increase particular components of biodiversity and resilience to climate change, based on arguably poor-resolution data in many cases (limited in space and time), a seascape approach may offer considerable insight in the mechanisms by which networks of MPAs can offer system-level resilience. Indeed, the failure of ecological resilience is often tested as a rapid decline following a particular perturbation event, but in nature, a large number of parameters interact to control resilience. Recent theoretical advances suggest that common network features can increase resilience (Gao and Barabási, 2016), and in terrestrial systems, defining and delivering resilience networks at the landscape scale has been prioritized (e.g., Isaac et al., 2018), suggesting that similar approaches may also be considered for seascapes. At a minimum, networks of MPAs will offer some insurance against indiscriminate climate and disturbance events that are spatially heterogeneous, and cross the borders of some MPAs but not others.

While the primary solution to reducing the impact of climate change on biodiversity is to reduce carbon emissions, we argue that fully protected areas need to be strategically expanded to represent biodiversity in its full scope, to take advantage of resilience mechanisms where they are known, and to include areas that can function as refugia from various stressors. An increase in the area protected within networks provides insurance to increase the probability that some areas will persist within a mosaic of disturbance types and magnitudes. Building insurance through protecting a diverse portfolio of natural systems is vital not only for the ecosystem functions protected systems offer, but also for the services that humans derive from protected areas.

Acknowledgements

A.E.B. was supported by the Canada Research Chairs programme. Scholarship salary to R.S.C.C was through a scholarship co-funded by the SPITFIRE Doctoral Training Partnership and the University of Southampton and M.I.D. through the Commonwealth Scholarship Commission and the National Research Foundation of South Africa. I.M.C. is supported by a Discovery grant of the Natural Sciences and Engineering Research Council of Canada.

References

- Alonso Aller, E., Jiddawi, N.S., Eklöf, J.S., 2017. Marine protected areas increase temporal stability of community structure, but not density or diversity, of tropical sea-grass fish communities. *PLoS One* 12, e0183999.
- Anderson, C.N.K., Hsieh, C.-h., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835.
- Arlinghaus, R., Laskowski, K.L., Alós, J., Klefoth, T., Monk, C.T., Nakayama, S., Schröder, A., 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *J. Fish Fish.* 18, 360–373.
- Babcock, R.C., Shears, N.T., Alcalá, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl. Acad. Sci.* 107, 18256–18261.
- Balmford, A., 2006. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol. Evol.* 11, 193–196.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169–193.
- Bates, A.E., Barrett, N.S., Stuart-Smith, R.D., Holbrook, N.J., Thompson, P.A., Edgar, G.J., 2013. Resilience and signatures of tropicalization in protected reef fish communities. *Nat. Clim. Chang.* 4, 62.
- Bates, A.E., Stuart-Smith, R.D., Barrett, N.S., Edgar, G.J., 2017. Biological interactions both facilitate and resist climate-related functional change in temperate reef communities. *Proc. R. Soc. B Biol. Sci.* 284, 20170484.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *BioScience* 51, 633–641.
- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* 1, 376–382.
- Biro, P.A., Post, J.R., 2008. Rapid depletion of genotypes with fast growth and bold

- personality traits from harvested fish populations. *Proc. Natl. Acad. Sci.* 105, 2919–2922.
- Boonzaier, L., Pauly, D., 2016. Marine protection targets: an updated assessment of global progress. *Oryx* 50, 27–35.
- Brainard, R.E., Oliver, T., McPhaden, M.J., Cohen, A., Venegas, R., Heenan, A., Vargas-Ángel, B., Rotjan, R., Mangubhai, S., Flint, E., Hunter, S.A., 2018. Ecological impacts of the 2015/16 El Niño in the Central Equatorial Pacific. *Bull. Am. Meteorol. Soc.* 99, S21–S26.
- Bruno, J.F., Bertness, M.D., 2001. Habitat modification and facilitation in benthic marine communities. *Marine community ecology:201-218*. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Sunderland, pp. 201–218.
- Bruno, J.F., Bates, A.E., Cacciapaglia, C., Pike, E.P., Amstrup, S.C., van Hoooidonk, R., Henson, S.A., Aronson, R.B., 2018. Climate change threatens the world's marine protected areas. *Nat. Clim. Chang.* 8, 499–503.
- Bruno, J.B., Côté, I.M., Toth, L.T., 2019. Climate change, coral loss, and the curious case of the porolith fish paradigm: why don't MPAs improve reef resilience? *Annu. Rev. Mar. Sci.* 11, 14.1–14.28.
- Byrnes, J.E., Reynolds, P.L., Stachowicz, J.J., 2007. Invasions and extinctions reshape coastal marine food webs. *PLoS One* 2, e295.
- Caddy, J.F., 2004. Current usage of fisheries indicators and reference points, and their potential application to management of fisheries for marine invertebrates. *Can. J. Fish. Aquat. Sci.* 61, 1307–1324.
- Campbell, S.J., Edgar, G.J., Stuart-Smith, R.D., Soler, G., Bates, A.E., 2018. Fishing-gear restrictions and biomass gains for coral reef fishes in marine protected areas. *Conserv. Biol.* 32, 401–410.
- Carassou, L., Léopold, M., Guillemot, N., Wantiez, L., Kulbicki, M., 2013. Does Herbivorous Fish Protection Really Improve Coral Reef Resilience? A Case Study from New Caledonia (South Pacific). *PLoS ONE* 8 (4), e60564. <https://doi.org/10.1371/journal.pone.0060564>.
- Carpenter, S., Walker, B., Anderies, M.J., Abel, N., 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4, 765–781.
- Castilla, J.C., Campo, M.A., Bustamante, R.H., 2007. Recovery of *Durvillaea antarctica* (Durvilleales) inside and outside Las Cruces Marine Reserve, Chile. *Ecol. Appl.* 17, 1511–1522.
- Cebrian, J., 2002. Variability and control of carbon consumption, export, and accumulation in marine communities. *Limnol. Oceanogr.* 47, 11–22.
- Ciannelli, L., Chan, K.-S., Bailey, K.M., Stensteth, N.C., 2004. Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology* 85, 3418–3427.
- Cizek, O., Vrba, P., Benes, J., Hrazsky, Z., Koptik, J., Kucera, T., Marhoul, P., Zamecnik, J., Konvicka, M., 2013. Conservation potential of abandoned military areas matches that of established reserves: plants and butterflies in the Czech Republic. *PLoS One* 8, e53124.
- Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., Garcia-Charton, J.A., Perez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.M., Dimech, M., Falcon, J.M., Guala, I., Milazzo, M., Sanchez-Meca, J., Somerfield, P.J., Stobart, B., Vandepierre, F., Valle, C., Planes, S., 2008. Marine reserves: size and age do matter. *Ecol. Lett.* 11, 481–489.
- Coelho, V.R., Manfrino, C., 2007. Coral community decline at a remote Caribbean island: marine no-take reserves are not enough. *Aquatic Conserv: Mar. Freshw. Ecosyst.* 17, 666–685. <https://doi.org/10.1002/aqc.822>.
- Coleman, M.A., Bates, A.E., Stuart-Smith, R.D., Malcolm, H.A., Harasti, D., Jordan, A., Knott, N.A., Edgar, G.J., Kelaher, B., 2015. Functional traits reveal early changes in marine reserves following protection from fishing. *Divers. Distrib.* 21, 876–887.
- Cooke, E.L.L., Wilson, A.D.M., Elvidge, C.K., Cooke, S.J., 2017. Does capture method or the presence of aquatic protected areas influence the selective harvest of behavioural types in largemouth bass? *Can. J. Fish. Aquat. Sci.* 74, 1151–1157.
- Costello, M.J., 2014. Long live marine reserves: a review of experiences and benefits. *Biol. Conserv.* 176, 289–296.
- Dahlhoff, E.P., 2004. Biochemical indicators of stress and metabolism: applications for marine ecological studies. *Annu. Rev. Physiol.* 66, 183–207.
- Darling, E.S., McClanahan, T.R., Côté, I.M., 2010. Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conserv. Lett.* 3, 122–130.
- Darling, E.S., McClanahan, T.R., Côté, I.M., 2013. Life histories predict coral community disassembly under multiple stressors. *Glob. Chang. Biol.* 19, 1930–1940.
- Dessai, S., Hulme, M., Lempert, R., Pielke, R., 2009. Do we need better predictions to adapt to a changing climate? *EOS Trans. Am. Geophys. Union* 90, 111–112.
- Duffy, J.E., Lefcheck, J.S., Stuart-Smith, R.D., Navarrete, S.A., Edgar, G.J., 2016. Biodiversity enhances reef fish biomass and resistance to climate change. *Proc. Natl. Acad. Sci. U. S. A.* 113, 6230–6235.
- Edgar, G.J., 1994. Observations on the size-structure of macrofaunal assemblages. *J. Exp. Mar. Biol. Ecol.* 176, 227–243.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Beger, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irgovien, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216.
- Edgar, G.J., Bates, A., Bird, T.J., Jones, A.H., Kininmonth, S., Stuart-Smith, R.D., Webb, T.J., 2016. New approaches to marine conservation through scaling up of ecological data. *Annu. Rev. Mar. Sci.* 8, 435–461.
- Fenberg, P.B., Roy, K., 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol. Ecol.* 17, 209–220.
- Fenberg, P.B., Caselle, J.E., Claudet, J., Clemence, M., Gaines, S.D., Antonio García-Charton, J., Gonçalves, E.J., Grorud-Colvert, K., Guidetti, P., Jenkins, S.R., Jones, P.J.S., Lester, S.E., McAllen, R., Moland, E., Planes, S., Sørensen, T.K., 2012. The science of European marine reserves: status, efficacy, and future needs. *Mar. Policy* 36, 1012–1021.
- Figge, F., 2004. Bio-folio: applying portfolio theory to biodiversity. *Biodivers. Conserv.* 13, 827–849.
- Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.M., Prahler, E., Rohrer, N., Sivas, D., Beck, M.W., Carr, M.H., Crowder, L.B., Duffy, J.E., Hacker, S.D., McLeod, K.L., Palumbi, S.R., Peterson, C.H., Regan, H.M., Ruckelshaus, M.H., Sandifer, P.A., Steneck, R.S., 2010. Guiding ecological principles for marine spatial planning. *Mar. Policy* 34, 955–966.
- Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623.
- Fraschetti, S., Guarnieri, G., Bevilacqua, S., Terlizzi, A., Boero, F., 2013. Protection enhances community and habitat stability: evidence from a Mediterranean marine protected area. *PLoS One* 8, e81838.
- Gaines, S.D., Gaylord, B., Gerber, L.R., Hastings, A., Kinlan, B.P., 2007. Connecting places the ecological consequences of dispersal in the sea. *Oceanography* 20, 90–99.
- Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2014. Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos* 124, 252–265.
- Gao, J.B., Barzel, Barabási, A.-L., 2016. Universal resilience patterns in complex networks. *Nature* 530, 307–312.
- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18, 448–455.
- Gill, D.A., Mascia, M.B., Ahmadi, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543, 665.
- Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., Fresne, S.d., Bräger, S., 2012. First evidence that marine protected areas can work for marine mammals. *J. Appl. Ecol.* 49, 474–480.
- Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., et al., 2008. Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. *PLoS ONE* 3 (8), e3039. <https://doi.org/10.1371/journal.pone.0003039>.
- Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D., Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518, 94.
- Hackerott, S., Valdivia, A., Green, S.J., Côté, I.M., Cox, C.E., Akins, L., Layman, C.A., Precht, W.F., Bruno, J.F., 2013. Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. *PLoS One* 8, e68259.
- Heath, M.R., Speirs, D.C., Steele, J.J., 2013. Understanding patterns and processes in models of trophic cascades. *Ecol. Lett.* 17, 101–114.
- Heupel, M.R., Simpfendorfer, C.A., 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Can. J. Fish. Aquat. Sci.* 59, 624–632.
- Hixon, M.A., Johnson, D.W., Sogard, S.M., 2014. BOFFFFS: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71, 2171–2185.
- Hodgson, D., McDonald, J.L., Hosken, D.J., 2015. What do you mean, 'resilient'? *Trends Ecol. Evol.* 30, 503–506.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hoogenboom, M.O., Connolly, S.R., Anthony, K.R.N., 2009. Effects of photoacclimation on the light niche of corals: a process-based approach. *Mar. Biol.* 156, 2493–2503.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301, 929.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanivsky, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365.
- Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G., McWilliam, M.J., Pears, R.J., Pratchett, M.S., Skirving, W.J., Stella, J.S., Torda, G., 2018. Global warming transforms coral reef assemblages. *Nature* 556, 492–496.
- Isaac, N.J.B., Brotherton, P.N.N., Bullock, J.M., Gregory, R.D., Boehning-Gaese, K., Connor, B., Crick, H.Q.P., Freckleton, J.P., Gill, J.A., Hails, R.S., Hartikainen, M., Hester, A.J., Milner-Gulland, E.J., Oliver, T.H., Pearson, R.G., Sutherland, W.J., Thomas, C.D., Travis, J.M.J., Turnbull, L.A., Willis, K., Woodward, G., Mace, G.M., 2018. Defining and delivering resilient ecological networks: nature conservation in England. *J. Appl. Ecol.* 55, 2537–2543.
- IUCN and UNEP-WCMC, 2018. The World Database on Protected Areas (WDPA) [online]. In: March/2018 of the Version Downloaded. UNEP-WCMC, Cambridge, UK Available at www.protectedplanet.net.
- Jackson, J.B.C., Hughes, T.P., 1985. Adaptive Strategies of Coral-reef Invertebrates: Coral-reef Environments that Are Regularly Disturbed by Storms and by Predation Often Favor the Very Organisms most Susceptible to Damage by these Processes. *vol.* 73. pp. 265–274.
- Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A., Swadling, K.M., Taw, N., 2011. Climate change cascades: shifts in

- oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J. Exp. Mar. Biol. Ecol.* 400, 17–32.
- Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A.G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Ecology: managing evolving fish stocks. *Science* 318, 1247–1248.
- Kerckhoff, A.J., Enquist, B.J., 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *BioScience* 57, 489–499.
- Knowlton, N., Jackson, J.B.C., 2008. Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol.* 6, e54.
- Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., De Leo, G., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.J., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R., Thielges, D.W., 2008. Parasites in food webs: the ultimate missing links. *Ecol. Lett.* 11, 533–546.
- Lefcheck, J.S., Wilcox, D.J., Murphy, R.R., Marion, S.R., Orth, R.J., 2017. Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Glob. Chang. Biol.* 23, 3474–3483.
- Leleu, K., Remy-Zephir, B., Grace, R., Costello, M.J., 2012. Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. *Biol. Conserv.* 155, 193–201.
- Lennox, R.J., Alós, J., Arlinghaus, R., Horodysky, A., Klefoth, T., Monk, C.T., Cooke, S.J., 2017. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish Fish.* 18, 986–1010.
- Ling, S.D., Johnson, C.R., Frusher, S.D., Ridgway, K.R., 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proc. Natl. Acad. Sci.* 106, 22341–22345.
- Lizaso, J., Goni, R., Renones, O., Charton, J., Galzin, R., Bayle, J., Sanchez Jerez, P., Perez Ruzafa, A., Ramos, A.A., 2000. Density dependence in marine protected populations: a review. *Environ. Conserv.* 27, 144–158.
- Lotze, H.K., Worm, B., 2009. Historical baselines for large marine animals. *Trends Ecol. Evol.* 24, 254–262.
- Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C., Airoidi, L., 2011. Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* 26, 595–605.
- MacNeil, M.A., Graham, N.A.J., Cinner, J.E., Wilson, S.K., Williams, I.D., Maina, J., Newman, S., Friedlander, A.M., Jupiter, S., Polunin, N.V.C., McClanahan, T.R., 2015. Recovery potential of the world's coral reef fishes. *Nature* 520, 341–344.
- Maggi, E., Bertocci, L., Vaselli, S., Benedetti-Cecchi, L., 2011. Connell and Slatyer's models of succession in the biodiversity era. *Ecology* 92, 1399–1406.
- McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. *Science* 347, 1255641.
- McLeod, E., Salm, R., Green, A., Almany, J., 2009. Designing marine protected area networks to address the impacts of climate change. *Front. Ecol. Environ.* 7, 362–370.
- Mellin, C., Bradshaw, C.J.A., Fordham, D.A., Caley, M.J., 2014. Strong but opposing beta-diversity-stability relationships in coral reef fish communities. *Proc. R. Soc. B Biol. Sci.* 281, 20131993.
- Mellin, C., Aaron MacNeil, M., Cheal, A.J., Emslie, M.J., Julian Caley, M., 2016. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* 19, 629–637.
- Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* 8, 391–400.
- Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J.A., Rossetto, M., De Leo, G.A., 2012. Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One* 7, e40832.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2016. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177.
- Nash, K.L., Graham, N.A.J., Jennings, S., Wilson, S.K., Bellwood, D.R., 2016. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *J. Appl. Ecol.* 53, 646–655.
- Nimmo, D.G., Mac Nally, R., Cunningham, S.C., Haslem, A., Bennett, A.F., 2015. Vive la resistance: reviving resistance for 21st century conservation. *Trends Ecol. Evol.* 30, 516–523.
- Ogden, J.C., Lobel, P.S., 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.* 3, 49–63.
- Oliver, T.H., Isaac, N.J., August, T.A., Woodcock, B.A., Roy, D.B., Bullock, J.M., 2015a. Declining resilience of ecosystem functions under biodiversity loss. *Nat. Commun.* 6, 10122.
- Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martín-López, B., Woodcock, B.A., Bullock, J.M., 2015b. Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* 30, 673–684.
- Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuyens, J.A., Peng, M., Sen Gupta, A., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Straub, S.C., Wernberg, T., 2018. Longer and more frequent marine heatwaves over the past century. *Nat. Commun.* 9, 1324.
- Orth, R.J., Lefcheck, J.S., Wilcox, D.J., 2017. Boat propeller scarring of seagrass beds in lower Chesapeake Bay, USA: patterns, causes, recovery, and management. *Estuar. Coasts* 40, 1666–1676.
- Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J., Halpern, B.S., Ince, L.S., Leong, J., Norse, E., Stachowicz, J.J., Wall, D.H., 2009. Managing for ocean biodiversity to sustain marine ecosystem services. *Front. Ecol. Environ.* 7, 204–211.
- Papworth, S., Rist, J., Coad, L., Milner-Gulland, E.J., 2009. Evidence for shifting baseline syndrome in conservation. *Conserv. Lett.* 2, 93–100.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Piatt, J.F., Harding, A.M.A., Shultz, M.T., Speckman, S.G., van Pelt, T.I., Drew, G.S., Kettle, A.B., 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Mar. Ecol. Prog. Ser.* 352, 221–234.
- Pinsky, M.L., Palumbi, S.R., 2014. Meta-analysis reveals lower genetic diversity in overfished populations. *Mol. Ecol.* 23, 29–39.
- Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I., Kifani, S., 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.* 79, 403–417.
- Pörtner, H.-O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish Biol.* 77, 1745–1779.
- Rizzari, J.R., Frisch, A.J., Hoey, A.S., McCormick, M.I., 2014. Not worth the risk: apex predators suppress herbivory on coral reefs. *Oikos* 123, 829–836.
- Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, U.R., Wilson, R.W., Worm, B., Castilla, J.C., 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci.* 114, 6167–6175.
- Rupia, E.J., Binning, S.A., Roche, D.G., Lu, W., 2016. Fight-flight or freeze-hide? Personality and metabolic phenotype mediate physiological defence responses in flatfish. *J. Anim. Ecol.* 85, 927–937.
- Ruppert, J.L.W., Travers, M.J., Smith, L.L., Fortin, M.J., Meekan, M.G., 2013. Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS One* 8, e74648.
- Sala, E., Ballesteros, E., Dendinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S., Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F., Zabala, M., 2012. The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. *PLoS One* 7, e32742.
- Schloss, C.A., Lawler, J.J., Papendick, H.L., Case, J.M., Evans, D.M., DeLap, J.H., Langdon, J.G.R., Hall, S.A., Larson, E.R., 2011. Systematic conservation planning in the face of climate change: bet-hedging on the Columbia Plateau. *PLoS One* 6, e28788.
- Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. *Fish Fish.* 0, 1–18.
- SDG14** <https://sustainabledevelopment.un.org/sdg14>.
- Selig, E.R., Bruno, J.F., 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS One* 5, e9278.
- Selig, E.R., Casey, K.S., Bruno, J.F., 2010. New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management. *Glob. Ecol. Biogeogr.* 19, 397–411.
- Selig, E.R., Casey, K.S., Bruno, J.F., 2012. Temperature-driven coral decline: the role of marine protected areas. *Glob. Chang. Biol.* 18, 1561–1570.
- Sheppard, C., Sheppard, A., Mogg, A., Bayley, D., Dempsey, A.C., Roche, R., et al., 2017. Coral bleaching and mortality in the Chagos Archipelago to 2017. *Atoll Res. Bull.* 613, 1.
- Strain, E.M., Edgar, G.J., Ceccarelli, D., Stuart-Smith, R.D., Hosack, G.R., Thomson, R.J., 2019. A global assessment of the direct and indirect benefits of marine protected areas for coral reef conservation. *Divers. Distrib.* 25, 9–20.
- Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, E.J., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoidi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G., Strain, E.M.A., Willis, T.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501, 539–542.
- Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J., Bates, A.E., 2015. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* 528, 88.
- Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M., Edgar, G.J., 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature* 560, 92–96.
- Thomas, C.D., Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A.D., Crick, H.Q.P., Findon, R.A., Fox, R., Hodgson, J.A., Holt, A.R., Morecroft, M.D., O'Hanlon, N.J., Oliver, T.H., Pearce-Higgins, J.W., Procter, D.A., Thomas, J.A., Walker, K.J., Walmsley, C.A., Wilson, R.J., Hill, J.K., 2012. Protected areas facilitate species' range expansions. *Proc. Natl. Acad. Sci.* 109, 14063.
- Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718.
- Toth, L.T., van Woessik, R., Murdoch, T.J.T., et al., 2014. Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. *Coral Reefs* 33, 565. <https://doi.org/10.1007/s00338-014-1158-x>.
- Trillmich, F., Limberger, D., 1985. Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia* 67, 19–22.
- Uusi-Heikkilä, S., Wolter, C., Klefoth, T., Arlinghaus, R., 2008. A behavioral perspective on fishing-induced evolution. *Trends Ecol. Evol.* 23, 419–421.
- van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. *Clim. Chang.* 109, 5.
- Wahl, M., Link, H., Alexandridis, N., Thomason, J.C., Cifuentes, M., Costello, M.J., da Gama, B.A.P., Hillock, K., Hobday, A.J., Kaufmann, M.J., Keller, S., Kraufvelin, P., Krüger, I., Lauterbach, L., Antunes, B.L., Molis, M., Nakaoka, M., Nyström, J., Radzi, Z.B., Stockhausen, B., Thiel, M., Vance, T., Weseloh, A., Whittle, M., Wiesmann, L., Wunderer, L., Yamakita, T., Lenz, M., 2011. Re-structuring of marine communities

- exposed to environmental change: a global study on the interactive effects of species and functional richness. *PLoS One* 6, e19514.
- Walsh, M.R., Munch, S.B., Chiba, S., Conover, D.O., 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol. Lett.* 9, 142–148.
- Wang, S., Loreau, M., 2014. Ecosystem stability in space: α , β and γ variability. *Ecol. Lett.* 17, 891–901.
- Webb, T.J., Dulvy, N.K., Jennings, S., Polunin, N.V.C., 2011. The birds and the seas: body size reconciles differences in the abundance–occupancy relationship across marine and terrestrial vertebrates. *Oikos* 120, 537–549.
- Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M.A., Wilson, S., 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353, 169–172.
- West, J.M., Salm, R.V., 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv. Biol.* 17, 956–967.
- Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* 6, e325.
- Wood, C.L., Micheli, F., Fernandez, M., Gelcich, S., Castilla, J.C., Carvajal, J., 2013. Marine protected areas facilitate parasite populations among four fished host species of central Chile. *J. Anim. Ecol.* 82, 1276–1287.
- Woodward, Guy, Bo, Ebenman, Emmerson, Mark, Montoya, Jose M., Olesen, Jens M., Valido, Alfredo, Warren, Philip H., 2005. Body size in ecological networks. *Trends Ecol. Evol.* 20 (7), 402–409. <https://doi.org/10.1016/j.tree.2005.04.005>.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790.
- Zhang, S.Y., Speare, K.E., Long, Z.T., McKeever, K.A., Gyoerko, M., Ramus, A.P., Mohorn, Z., Akins, K.L., Hambridge, S.M., Graham, N.A.J., Nash, K.L., Selig, E.R., Bruno, J.F., 2014. Is coral richness related to community resistance to and recovery from disturbance? *PeerJ* 2, e308.