The capacity for marine protected areas to buffer climate change effects

Marissa L. Baskett
A report to NRDC

Greenhouse gas emissions and the associated climate change has a myriad of interacting impacts on marine systems [46]. Directional changes include increasing temperatures, which might reduce reproduction and survival in some marine organisms, and sea level rise, which might decrease habitat availability in areas with significant coastal development [46]. In addition, climate change is increasing the magnitude of extreme events such as storms and marine heat waves, which can cause large-scale mortality in some marine organisms, including taxa such as corals and kelp that provide the foundational habitat for coastal systems [38, 46, 85]. Finally, increased carbon dioxide drives ocean acidification (OA), which interferes with the ability for many marine organisms to build calcium structures (e.g., oyster shells, coral skeletons) and therefore can reduce their growth, survival, and reproduction [55]. Overall, the effects of climate change and OA can reduce the potential for marine systems to sustainably deliver a variety of ecosystem services, such as fisheries, tourism, and storm buffering [46].

One potential tool to buffer climate change effects on marine systems is marine protected areas [MPAs; 17]. MPAs are areas with restricted fishing, a subset of which are no-take marine reserves with no fishing [64]. The implementation of MPAs and marine reserves has been increasing since the 1980s [112], and their goals encompass protecting biodiversity, promoting the sustainability of fisheries, or both [59]. MPA establishment frequently leads to increases in the size and numbers of fished species within their boundaries, as previously fished species are more likely to survive to older, larger stages [11, 60]. Such increases can lead to increased reproduction, with potential spillover to areas outside reserves [11, 86] given the long-distance dispersal that occurs at early life stages for many marine species [54]. This spillover can provide a buffer against overfishing [67] and increase catch per unit effort [97]; increased total fisheries yield, i.e. spillover outweighing displaced fishery effort, is expected for overfished species but not sustainably fished species [47]. Another potential secondary effect of MPAs is cascading effects through ecological communities, such as (a) increases in herbivorous fish which then reduce the algae that might compete with corals, (b) increases in predatory fish and lobster which then reduce the sea urchins that graze kelp, or (c) when fishing practices damage habitat (e.g., bottom trawling), increases in habitat-forming organisms that benefit the remainder of the ecological community [5, 11, 62, 100]. Such secondary cascading effects can take 2-3 times as long to occur within MPAs than initial increases in previously harvested species [5].

Given these responses to MPA establishment, MPAs have the potential to serve a number of buffering roles to disturbance and change [11], including that from climate change [17]. First, MPAs might promote the capacity for genetic adaptation within vulnerable populations. Second, MPAs might promote resilience on both the population and community levels, where such resilience has three aspects (Fig. 1a): (a) the resistance to disturbance, i.e. amount by which a population or community changes following a disturbance, (b) the rate of recovery following disturbance[1], i.e. rate of population increase or community return

[1] Also known as "engineering resilience".

to its original composition, and (c) the likelihood of recovery following disturbance[2] if there is a threshold population size or community state beyond which recovery cannot occur [Fig. 1b,c; 48, 61]. On a population level, such thresholds[3] arise when a certain population density is necessary for successful reproduction, feeding, or predator avoidance [e.g., for species that form spawning or feeding aggregations; 28]. On a community level, such thresholds can arise if strong feedbacks maintain multiple possible states under the same conditions, such as kelp providing habit for predators of kelp-grazing urchins while urchins promote conditions that increase the settlement success of new urchins [63], or corals providing habitat for herbivorous fish while algae prevents coral settlement [16]. While such thresholds are possible in theory [e.g., 12, 78], establishing whether or not they occur in reality is difficult given the need to observe different communities under the same conditions over long time periods and large areas [89]. Therefore, the prevalence of thresholds on the community level is a subject of scientific debate and ongoing research [24, 79, 88, 101, 114]. If MPAs can lead to these buffering effects within their boundaries, then there is the possibility that they might also buffer outside areas, and therefore fisheries for harvested species, through spillover.

The remainder of this summary details each type of buffering capacity described above in terms of the mechanism by which it occurs and the current state of evidence for it occurring (summarized in Table 1). The realization of this buffering capacity relies on an effective MPA, which in turn depends on the level of protection, degree of enforcement, size, age, and degree of isolation [33]. In addition, as described in more detail below, MPAs are one of many possible management approaches that might increase marine population and ecosystem persistence under climate change, where implementing multiple approaches increases the likelihood of overall success.

Genetic adaptation

If OA and climate change exceed organisms' physiological limits, then genetic adaptation provides an avenue to persistence [along with movement to cooler locations, e.g. poleward or deeper; 30, 49, 68]. The capacity for and rate of genetic adaptation increases with genetic diversity [57]. Genetic diversity, in turn, increases with population size as larger populations are less likely to randomly lose rare genes [58]. Therefore, the mechanism by which MPAs might increase genetic adaptive capacity to climate change is by protecting larger populations that might otherwise occur, especially for harvested species. Accordingly, harvest can lead to a loss of genetic diversity [2, 90], and greater genetic diversity within reserves compared to outside areas has been observed in one case study [87]. Whether such greater genetic diversity within MPA boundaries translates to greater total genetic diversity throughout a population's range would likely on displaced effort [11]: if MPA establishment leads to intensified fisheries in outside areas, then the total population (and therefore expected genetic diversity) might remain the same, while if MPAs reduce rather than displace total effort, then the total population would be greater with MPAs. In addition, genetic diversity will only increase adaptive capacity if it is diversity underlying traits relevant to climate change adaptation, and protecting such diversity might require a targeted approach at locations with

[2] Also known as "ecological resilience".

[3] Also known as "Allee effects".

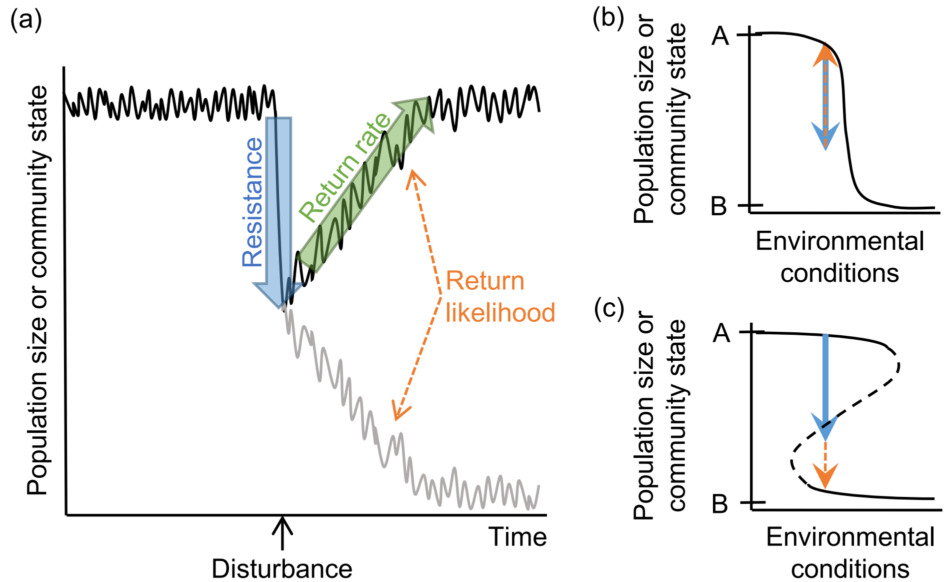

Figure 1: Three metrics of resilience: (a) example population size or community state over time that indicates each metric following a disturbance: resistance (blue) as the amount of change following disturbance, return rate (green) as the speed at which the population or ecological community recovers to its original state, and return likelihood (orange) as the probability that the population or community recovers as compared to continues to decline (gray line). (b) Return likelihood is not relevant when only one population or community state (black line) is relevant for a given set of environmental conditions, in which case recovery (orange dashed arrow) from a disturbance (blue arrow) can always eventually occur. Rather, (c) return likelihood is relevant when there is a threshold (black dashed line) necessary for recovery, such that any disturbance that crosses this threshold (blue arrow) leads to further decline (orange dashed arrow).

the relevant range of genotypes [99]. The genetic diversity that is relevant to adaptation to climate change will likely be diversity in temperature tolerance that occurs along a series of locations through local adaptation [e.g., along a latitudinal gradient; 17]. Protecting this functional genetic diversity therefore might rely on a network of MPAs across the relevant locations [17].

In addition to increased population sizes, the presence of more older, larger individuals in MPAs has the potential to increase genetic diversity, and therefore adaptive capacity, under environmental variability. Specifically, having older individuals means an overall reproductive population that has experienced different environmental histories with different selective pressures, which can increase genetic variance in theory [34]. Such greater genetic diversity, with a greater presence of rare alleles, due to greater presence of older individuals occurred in an MPA where an extreme low-oxygen event [the type of extreme event expected to be more common under climate change; 18] particularly affected the smaller, younger individuals of a fished abalone in Baja California [80]. Therefore, the greater survival of the older abalone within reserve boundaries maintained genetic diversity [80].

Another potential evolutionary outcome of MPAs for harvested species is to protect against the selection for earlier maturity and faster growth from fisheries [8, 32, 74, 75]. These expected fisheries-driven trait changes, due to reduced likelihood of living to older ages with fisheries, occur in a number of fished species [52]. If MPAs can reduce such selection [as suggested by models, which indicate that the capacity for such protection depends on factors such as the amount of dispersal and movement; 8, 32, 74, 75], then size, generation time, and reproduction would further increase [although such increases might take multiple generations; 25, 35], which would accentuate the the above two mechanisms (greater population sizes and age structure) that promote genetic diversity. This potential outcome of MPAs could also accentuate the population-level resilience mechanisms described below [depending on factors such as the degree of density-dependent interactions; 51, 56, 108].

Population-level resilience

Protection in MPAs can lead to greater population resistance to disturbance, including climate change-driven extreme events, if vulnerability to disturbance is age- or size-dependent. Such greater resistance occurred in the above-mentioned extreme low-oxygen event that affected abalone in Baja California, where older, larger abalone were more likely to survive the event [73]. Due to size-dependent survival and greater prevalence of larger individuals within MPA boundaries, abalone density was 3.7 times greater within MPA boundaries than outside following the low-oxygen disturbance [73].

Protection in MPAs can lead to faster population recovery from disturbance, and therefore lower overall population variability, through multiple mechanisms. First, larger population sizes with more older, larger individuals will have greater reproductive output and therefore faster overall population growth rates [31, 110]. In addition to faster recovery following disturbance, this response buffers populations against gradual, directional climate change effects that might reduce reproductive output [e.g., climate change-driven mismatches between the timing of reproduction and the ideal environmental conditions for eggs with the earlier onset of spring; 6]. Second, if population sizes are greater, then resource limitation will tend to play a greater role in driving population sizes, which can reduce the role of environmental impacts such as disturbance [Figure 2a; 19]. Third, if earlier life stages are more vulnerable to disturbance, then the increased resistance from more older individuals in MPAs will lead to an increase in the reproductive population following disturbance, as occurred in the above-mentioned abalone study [73]. For environmental variability and disturbances that affect reproductive success, which is common in marine systems where eggs and larvae are particularly vulnerable stages [in some cases, populations experience years of little to no reproduction followed by years of large reproduction; 22], having a truncated age structure with fishing leads to a population that is more vulnerable to a series of poor-reproductive years compared to population with more older, larger individuals in MPAs [Figure 2b; 19, 93]. Documenting lower population variability within MPAs, as can arise from all three mechanisms, requires long time series of data after MPAs have led to the build up of older, larger individuals for previously fished species; in cases where such data are available, lower variability in MPAs does occur [5, 73].

Lower variability within MPAs can, in theory, also translate into lower variability in fisheries yield through spillover [66]. In addition, the mechanisms behind lower variability inevitably rely on sufficient protection within MPA boundaries, which can depend on fisheries

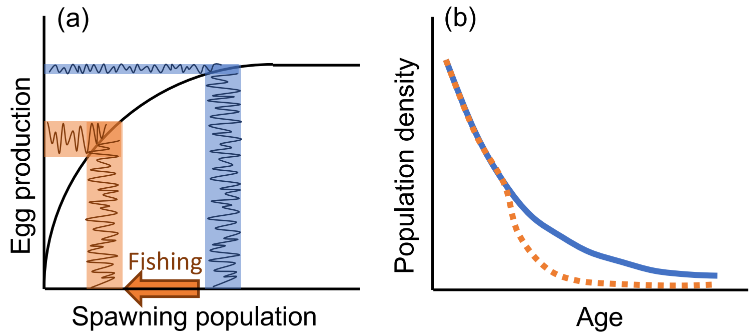

Figure 2: (a) Fishing can increase the role of environmental variability compared to density-dependence in driving population sizes [following 19]: the black line indicates the spanwer-egg production relationship, which saturates due to density dependence capping population size. Blue (no fishing) and orange (fishing) highlighted areas indicate the range of population sizes under a given amount of environmental variability, with solid lines within illustrating an example case of population variability. Under no fishing (blue), density dependence dampens the effect of environmental variability on egg production, which does not occur when fishing reduces spawner population size (orange). (b) Illustration of age structure without (blue solid line) and with (orange dotted line) fishing. As fewer individuals survive to older sizes with fishing, a shorter series of poor-recruitment year can affect the overall population. Note also that fishing causes both a smaller spawner population size overall (a) and fewer older, larger individuals (b) that typically have higher egg production, both of which reduce overall egg production and therefore rate of recovery from disturbance.

management outside, especially for species with high movement rates. For example, for a harvested species in New Zealand that has seasonal migration, a decline in protection within MPAs was likely due to intensified fishing outside MPA boundaries [5].

As noted above, whether MPAs might increase the likelihood of population recovery from disturbance is only relevant if there is a threshold below which a population cannot recover. In addition to occurring in species that rely on larger groups for successful reproduction, feeding, or predator avoidance as mentioned above, such thresholds can arise for particularly small populations through random processes [i.e., demographic stochasticity and genetic drift; 42, 58]. When recovery thresholds are relevant, larger population sizes in MPAs can reduce the likelihood of population sizes falling to susceptible sizes [1, 23, 94, 105]. In addition to population size, mating success can rely on having larger individuals, in which cases MPAs further decrease the likelihood of crossing threshold by protecting older, larger individuals in MPAs [104].

Also as noted above, when climate change exceeds a population's physiological limits in its historic location, then the avenues for persistence are either genetic adaptation or movement to new locations [30, 49, 68]. Shifts in the range of marine species, including harvested marine species, as expected from climate change have occurred [91, 92]. MPAs might promote this movement response to climate change by protecting larger populations and therefore greater realized dispersal [95]. However, models indicate that this potential relies on fisheries outside MPAs remaining unchanged following MPA establishment; if MPAs lead to displaced, intensified fishing in outside areas, then MPAs can actually reduce movement responses due to the non-MPA regions of particularly low population sizes [39].

Community-level resilience

Greater community-level resilience, as measured through both resistance to disturbance and the rate of return following disturbance, can arise from greater diversity for ecosystems in general [53, 113]. While MPAs typically lead to modest increases in diversity measured as the total number of species [27, 60], they lead to more consistent and measurable decreases in rarity [i.e., MPAs typically lead to a lower number of particularly small populations; 102]. Therefore, MPAs can increase the functionally realized diversity, i.e. the number of species effectively playing different functional roles such as different diets or different responses to disturbance [e.g., see 103, 107, for observations of increased functional diversity in Mediterranian MPAs]. For example, in an analysis of multiple MPAs protecting tropical coral reef systems, increased fish diversity and the associated increased consumption of algae (a key ecosystem function) arose through the presence of a few key species of herbivorous fish [106]. In addition, community-level changes within MPAs can spill over to lead to increased diversity and changes in community structure in adjacent fished areas [as occurred in a long-established coral reef reserve; 96].

When MPAs do protect greater diversity, they can also include a broader suite of vulnerable species, which can decrease resistance to disturbance. Such decreased resistance associated with greater diversity does occur in coral reef MPAs, where coral species that are vulnerable to disturbance from fishing activity are also vulnerable to storms and extreme temperatures (29, 43, 69, but see 84 for a case of increased coral reef resistance to flooding with MPA protection). However, in theory, the presence of a more diverse suite of coral species, including more vulnerable species, can increase return rate and recovery likelihood despite decreased resistance [13]. This increased return rate and likelihood arises from diversity in the response to disturbance: high stress tolerance (typically associated with slow growth) or fast post-disturbance re-growth (typically associated with low stress tolerance); the combined response decreases the prevalence of non-coral competitors (e.g., algae) following disturbance to the mutual benefit of both types [13]. The overall outcome of resistance and return rate is variability, and decreased variability (i.e., increased stability) in species diversity and the composition of the ecological community does occur with MPAs [14, 37, 71, 111].

Coral reefs represent the system where increased community-level resilience to climate change in MPAs is frequently discussed [109]. Corals, the species that provide the foundation for the system, are particularly vulnerable to marine heat waves [when coral bleaching occurs; 16, 50]. Potential benefits to corals from MPAs might be reduced disturbance from fishing activities as well as reduced competition from algae in areas with intensive fishing on herbivorous fish and invertebrates [16, 77]. MPA protection of herbivorous fish, in particular, is hypothesized as potentially protecting coral reef resilience by increasing the rate and likelihood of coral recovery following heat stress [77]. Observing this hypothesized outcome in reality relies on a number of factors: a well-regulated MPA established for a long enough period for cascading effects to occur and in a location with intensive enough fishing on herbivorous fish to alter total algal consumption (or involve habitat-damaging practices that affect corals directly), with a long enough time series after a disturbance to measure recovery rate and likelihood. While the large majority of the handful of studies that have investigated this outcome find no effect on coral resilience [20], the lack of MPA effect is typically due to missing one of these factors (fishing on herbivorous fish is not intensive in Carassou et al. 21, Graham et al. 45, Manfrino et al. 65, MPA protection is lacking in Muthiga 81, potential lack of time for recovery from pre-MPA degradation before disturbance in McClanahan et al. 70). In comparison, in one of the longest-established, well-enforced coral reef MPAs, the Great Barrier Reef Marine Park, the impact of disturbances (e.g., marine heat waves, storms) on the composition of the ecological community was 30% lower, with 20% faster recovery, in MPAs (72; see also Mumby and Harborne 76 for a case study with faster recovery in MPAs). That said, the mechanisms linking herbivory to coral performance are uncertain [20, 98] and continue to be a topic of scientific investigation. If MPA protection of herbivorous fish cascading to reduced algal competition with corals is relevant to coral reefs, then the increased community-level resilience can also, in theory, increase the chance that corals have the opportunity to genetically adapt to climate change [10].

More generally (beyond coral reefs), when community-level thresholds are relevant, another mechanism by which MPAs might increase recovery likelihood is through the protection of a more "pristine" (unfished) state that is further from any thresholds below which recovery might not occur. In one model, with domination by either larger-bodied fished species (that consume the competitors of their juveniles) or smaller-bodied unfished species (that, when prevalent, outcompete the juveniles of their predators), not only can greater recovery likelihood (of the state dominated by the larger-bodied species) within MPAs occur, but it also can spill over to areas outside. Specifically, protection of the target state (dominated by the larger-bodied species) in MPAs can provide a source population for recovery in fished areas under environmental disturbance and therefore enhanced the overall sustainability of the fishery given disturbance [7].

MPAs as one tool in a multi-faceted approach

MPAs are one of multiple possible management tools to that might increase the resilience of marine systems to climate change [4]. MPAs might not be effective in buffering against climate change effects for all species, and, for species they can affect, the implementation of additional management actions can increase the capacity for MPAs to promote adaptive capacity and resiliency by reducing additional stressors. For example, greenhouse gas mitigation can reduce the climate stress, while sustainable fisheries management and integrated land-sea management can further reduce local stressors, as described below.

The more severe the climate change, the more likely that the future climate will exceed the adaptive capacity and resilience of even the most pristine ecosystem. Therefore, any management actions to reduce greenhouse gas emissions inevitably increase the likelihood that marine ecosystems can keep up with the rate and amount of climate change [9, 10, 20]. A speculative outcome of MPAs is localized reduction in carbon dioxide and OA mitigation through increased primary production and fish seawater osmoregulation [95], which would further enhance their buffering effect, but the potential for and magnitude of such mitigation is highly uncertain and remains an area of active research. If disturbances from extreme climatic events cross thresholds that lead to population or community declines, then active restoration might be a part of management actions; here a possible role of MPAs is in lowering the threshold necessary for restoration to succeed [44], in the same way that they might increase the distance to the threshold for collapse as described above. The greater the climate change, the more likely that managers and stakeholders might consider riskier interventions that promote the stress-tolerance of vulnerable species such as tropical corals [e.g., captive breeding, potentially with directed selection for stress tolerance, or translocation of stress-tolerant genotypes or species; 82, 83]. The success of such interventions would rely on the survival and reproductive success of the stress-tolerant individuals, where MPAs and other actions to reduce local stress can increase the likelihood of that success [82, 83].

Many of the potential mechanisms for MPAs to buffer climate change effects described above (e.g., enhanced genetic diversity and movement potential) rely on sustainable fisheries management outside MPA boundaries. One approach to increasing the sustainability of fisheries is to address the "tragedy of the commons" incentives to overfish through rights-based fishing, i.e. promote ownership and stewardship by fishers through individual transferable quotas [ITQs; 26] and territorial user rights of fisheries [TURFs; 41]. Such approaches have led to outcomes analogous to the above-described mechanisms of MPA buffering, such as reduction of variability in fishing and harvested population sizes [36] and protection of a more diverse, natural community structure [40]. Another aspect of fisheries management that might increase buffering by protecting community structure is banning of fishing practices or gear with high habitat damage or bycatch [15], including practices that directly damage corals given the role of coral structural complexity in recovery from disturbance [45]. Similarly, integrated land-sea management can reduce stressors such as nutrient and sediment runoff both within and outside MPA boundaries [3], which can then increase the recovery from disturbance of vulnerable species such as corals [e.g., as observed in 45].

Summary

- MPAs might increase the capacity for genetic adaptation to climate change by protecting genetic diversity through two mechanisms: (1) protecting larger populations, and (2) protecting more older individuals and therefore diversity of environmental histories experienced. Such protection depends on (a) an increased total population across both MPAs and harvested areas, which would occur if MPAs reduced rather than displaced total fishing, and (b) the diversity protected is relevant to traits that affect persistence under climate change, such as in temperature tolerance, which might require protection along environmental gradients in temperature.

- MPAs can buffer populations against a changing environment and extreme events by increasing the number of older, larger, highly reproductive individuals, which reduces susceptibility to stressors and increases population growth rate and therefore recovery rate. MPA-driven increases in population size can also increase recovery likelihood if a population has a threshold beyond which recovery cannot occur.

- MPAs might buffer ecological communities against a changing environment and extreme events by protecting greater species diversity, species that play key roles in the community, and a more natural community state. This possibility is difficult to demonstrate given the longer time frame necessary for MPA effects to cascade through communities and to measure MPA effects on community-level variability.

- MPAs are one of multiple tools that can increase persistence under climate change. Other tools include rights-based fisheries management, regulation of destructive fishing gear, integrated land-see management with pollution reduction, and, most fundamentally, greenhouse gas reduction. The implementation of multiple tools, including MPAs, can interact to increase the likelihood of overall success.

Table 1: Potential ways by which MPAs might buffer responses to climate change and their mechanisms. All mechanisms have theoretical support as well as empirical support for individual linkages in the indicated mechanisms, but empirical support for the full suite of mechanisms and end buffering outcome is more difficult and rare.

Buffering outcome	Mechanism	Case study
↑ Genetic adaptation	↑ population size → ↑ genetic variation	[87]
	↑ older individuals → ↑ environmental histories → ↑ genetic variation	[80]
Population-level resistance	↑ older, larger individuals → ↓ vulnerability	[73]
Population-level return rate	↑ larger individuals, population size → ↑ reproduction	[5]
	↑ population size → resource limitation > disturbance effects	[5]
	↑ older individuals → ↑ averaging across environmental histories	[5]
Population-level recovery likelihood	↑ population size → ↓ distance from threshold	[104]
	↑ older, larger individuals → ↑ mating success → ↓ distance from threshold	[104]
Population-level tracking of climate change	↑ population size, reproduction → realized dispersal	[39]
Community-level recovery rate and likelihood	↑ population sizes, ↑ diversity, ↓ rarity → ↑ ecosystem function, response capacity to disturbance	[72]
Community-level recovery likelihood	↑ similarity to unfished community composition → ↑ distance from threshold	[72]

References

[1] E. A. Aalto, F. Micheli, C. A. Boch, J. A. Espinoza Montes, C. B. Woodson, and G. A. De Leo. Catastrophic mortality, allee effects, and marine protected areas. *Am. Nat.*, 193(3):391–408, 2019.

[2] F Allendorf, P England, G Luikart, P Ritchie, and N Ryman. Genetic effects of harvest on wild animal populations. *Trends Ecol. Evol.*, 23(6):327–337, 2008.

[3] J. G. Alvarez-Romero, R. L. Pressey, N. C. Ban, K. Vance-Borland, C. Willer, C. J. Klein, and S. D. Gaines. Integrated land-sea conservation planning: The missing links. *Annu. Rev. Ecol. Evol. Syst.*, 42:381–409, 2011.

[4] K. R. N. Anthony, P. A. Marshall, A. Abdulla, R. Beeden, C. Bergh, R. Black, C. M. Eakin, E. T. Game, M. Gooch, N. A. J. Graham, A. Green, S. F. Heron, R. van Hooidonk, C. Knowland, S. Mangubhai, N. Marshall, J. A. Maynard, P. McGinnity, E. McLeod, P. J. Mumby, M. Nystrom, D. Obura, J. Oliver, H. P. Possingham, R. L. Pressey, G. P. Rowlands, J. Tamelander, D. Wachenfeld, and S. Wear. Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob. Change Biol.*, 21(1):48–61, 2015.

[5] R. C. Babcock, N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl. Acad. Sci. U. S. A.*, 107 (43):18256–18261, 2010. ISSN 0027-8424. doi: 10.1073/pnas.0908012107.

[6] L. A. K. Barnett, M. L. Baskett, and L. W. Botsford. Quantifying the potential for marine reserves or harvest reductions to buffer temporal mismatches caused by climate change. *Can. J. Fish. Aquat. Sci.*, 72(3):376–389, 2015. ISSN 0706-652X. doi: 10.1139/cjfas-2014-0243.

[7] L.A.K. Barnett and M.L. Baskett. Marine reserves can enhance ecological resilience. *Ecol. Lett.*, 18(12):1301–1310, 2015.

[8] M. L. Baskett, S. A. Levin, S. D. Gaines, and J. Dushoff. Marine reserve design and the evolution of size at maturation in harvested fish. *Ecol. Appl.*, 15:882–901, 2005.

[9] M. L. Baskett, S. D. Gaines, and R. M. Nisbet. Symbiont diversity may help coral reefs survive moderate climate change. *Ecol. Appl.*, 19(1):3–17, 2009.

[10] M. L. Baskett, R. M. Nisbet, C. V. Kappel, P. J. Mumby, and S. D. Gaines. Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison. *Glob. Change Biol.*, 16(4):1229–1246, 2010.

[11] M.L. Baskett and L.A.K. Barnett. The ecological and evolutionary consequences of marine reserves. *Annu. Rev. Ecol. Evol. Syst.*, 46:49–73, 2015.

[12] M.L. Baskett and A.K. Salomon. Recruitment facilitation can drive alternative states on temperate reefs. *Ecology*, 91(6):1763–1773, 2010.

[13] M.L. Baskett, N.S. Fabina, and K. Gross. Response diversity can increase ecological resilience to disturbance in coral reefs. *Am. Nat.*, 184(2):E16–E31, 2014.

[14] A. E. Bates, N. S. Barrett, R. D. Stuart-Smith, N. J. Holbrook, P. A. Thompson, and G. J. Edgar. Resilience and signatures of tropicalization in protected reef fish communities. *Nat. Clim. Chang.*, 4(1):62–67, 2014.

[15] S. Bejarano, S. Pardede, S. J. Campbell, A. S. Hoey, and S. C. A. Ferse. Herbivorous fish rise as a destructive fishing practice falls in an indonesian marine national park, in press. e01981.

[16] D. R. Bellwood, T. P. Hughes, C. Folke, and M. Nyström. Confronting the coral reef crisis. *Nature*, 429(6994):827–833, 2004.

[17] J. R. Bernhardt and H. M. Leslie. Resilience to climate change in coastal marine ecosystems. *Annu. Rev. Mar. Sci.*, 5:371–392, 2013.

[18] J. Bijma, H.O. Pörtner, C. Yesson, and A.D. Rogers. Climate change and the oceans–what does the future hold? *Mar. Pollut. Bull.*, 74(2):495–505, 2013.

[19] L. W. Botsford, M. D. Holland, J. C. Field, and A. Hastings. Cohort resonance: A significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES J. Mar. Sci.*, 71(8):2158–2170, 2014. doi: 10.1093/icesjms/fsu063.

[20] J.F. Bruno, I.M. Côté, and L.T. Toth. Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? *Annu. Rev. Mar. Sci.*, 11:307–334, 2019.

[21] L. Carassou, M. Leopold, N. Guillemot, L. Wantiez, and M. Kulbicki. Does herbivorous fish protection really improve coral reef resilience? A case study from new Caledonia (South pacific). *PLoS One*, 8(4):e60564, 2013.

[22] M. H. Carr and C. Syms. Recruitment: the replishment of demersal fish populations. In L. G. Allen, D. J. Pondella II, and M. H. Horn, editors, *The Ecology of Marine Fishes: California and Adjacent Waters*, pages 411–427. University of California Press, 2006.

[23] M. H. Chan and P. S. Kim. Modelling the impact of marine reserves on a population with depensatory dynamics. *Bull. Math. Biol.*, 76(9):2122–2143, 2014. ISSN 0092-8240.

[24] J. H. Connell and W. P. Sousa. On the evidence needed to judge ecological stability or persistence. *Am. Nat.*, 121(6):789–824, 1983.

[25] D. O. Conover, S. B. Munch, and S. A. Arnott. Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 276 (1664):2015–2020, 2009.

[26] P. Copes. A critical-review of the individual quota as a device in fisheries management. *Land Econ.*, 62(3):278–291, 1986.

[27] I. M. Côté, I. Mosqueira, and J. D. Reynolds. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J. Fish Biol.*, 59(Suppl. A): 178–189, 2001.

[28] F. Courchamp, T. Clutton-Brock, and B. Grenfell. Inverse density dependence and the Allee effect. *Trends Ecol. Evol.*, 14(10):405–410, 1999.

[29] E. S. Darling, T. R. McClanahan, and I. M. Cote. Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conserv. Lett.*, 3 (2):122–130, 2010.

[30] M. B. Davis and R. G. Shaw. Range shifts and adaptive responses to Quaternary climate change. *Science*, 292(5517):673–679, 2001.

[31] D. Diaz, S. Mallol, A. M. Parma, and R. Goni. Decadal trend in lobster reproductive output from a temperate marine protected area. *Mar. Ecol. Prog. Ser.*, 433:149–157, 2011. ISSN 0171-8630. doi: 10.3354/meps09182.

[32] E. S. Dunlop, M. L. Baskett, M. Heino, and U. Dieckmann. Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. *Evol. Appl.*, 2(3):371–393, 2009.

[33] G. J. Edgar, R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, M. A. Becerro, A. T. F. Bernard, J. Berkhout, C. D. Buxton, S. J. Campbell, A. T. Cooper, M. Davey, S. C. Edgar, G. Forsterra, D. E. Galvan, A. J. Irigoyen, D. J. Kushner, R. Moura, P. E. Parnell, N. T. Shears, G. Soler, E. M. A. Strain, and R. J. Thomson. Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506(7487):216–220, 2014. ISSN 0028-0836. doi: 10.1038/nature13022.

[34] S. Ellner and N. G. Hairston. Role of overlapping generations in maintaining genetic-variation in a fluctuating environment. *Am. Nat.*, 143(3):403–417, 1994.

[35] K. Enberg, C. Jørgensen, E. S. Dunlop, M. Heino, and U. Dieckmann. Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evol. Appl.*, 2(3):394–414, 2009.

[36] T. E. Essington. Ecological indicators display reduced variation in North American catch share fisheries. *Proc. Natl. Acad. Sci. U. S. A.*, 107(2):754–759, 2010.

[37] S. Fraschetti, G. Guarnieri, S. Bevilacqua, A. Terlizzi, and F. Boero. Protection enhances community and habitat stability: Evidence from a Mediterranean marine protected area. *PLoS ONE*, 8(12):e81838, 2013.

[38] T.L. Frölicher and C. Laufkötter. Emerging risks from marine heat waves. *Nature Communications*, 9(1):650, 2018.

[39] E. Fuller, E. Brush, and M. L. Pinsky. The persistence of populations facing climate shifts and harvest. *Ecosphere*, 6(9):153, 2015.

[40] S. Gelcich, N. Godoy, L. Prado, and J. C. Castilla. Add-on conservation benefits of marine territorial user rights fishery policies in Central Chile. *Ecol. Appl.*, 18(1): 273–281, 2008.

[41] S. Gelcich, T. P. Hughes, P. Olsson, C. Folke, O. Defeo, M. Fernandez, S. Foale, L. H. Gunderson, C. Rodriguez-Sickert, M. Scheffer, R. S. Steneck, and J. C. Castilla. Navigating transformations in governance of Chilean marine coastal resources. *Proc. Natl. Acad. Sci. U. S. A.*, 107(39):16794–16799, 2010.

[42] M. E. Gilpin and M. E. Soulé. Minimum viable populations: processes of extinction. In M. E. Soulé, editor, *Conservation Biology: The Science of Scarcity and Diversity*, pages 19–34. Sinauer Associates, Sunderland, MA, 1986.

[43] N. A. J. Graham, T. R. McClanahan, M. A. MacNeil, S. K. Wilson, N. V. C. Polunin, S. Jennings, P. Chabanet, S. Clark, M. D. Spalding, Y. Letourneur, L. Bigot, R. Galzin, M. C. Ohman, K. C. Garpe, A. J. Edwards, and C. R. C. Sheppard. Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS One*, 3(8):e3039, 2008.

[44] N. A. J. Graham, D. R. Bellwood, J. E. Cinner, T. P. Hughes, A. V. Norstrom, and M. Nystrom. Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol. Environ.*, 11(10):541–548, 2013.

[45] N. A. J. Graham, S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518 (7537):94–97, 2015.

[46] C. D. G. Harley, A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. The impacts of climate change in coastal marine systems. *Ecol. Lett.*, 9(2):228–241, 2006.

[47] R. Hilborn, K. Stokes, J. J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, K. L. Cochrane, S. Garcia, S. J. Hall, G. P. Kirkwood, K. Sainsbury, G. Stefansson, and C. Walters. When can marine reserves improve fisheries management? *Ocean and Coastal Management*, 47(3-4):197–205, 2004.

[48] C. S. Holling. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, 4: 1–23, 1973.

[49] R. D. Holt. The microevolutionary consequences of climate change. *Trends Ecol. Evol.*, 5(9):311–315, 1990.

[50] T. P. Hughes, K. D. Anderson, S. R. Connolly, S. F. Heron, J. T. Kerry, J. M. Lough, A. H. Baird, J. K. Baum, M. L. Berumen, T. C. Bridge, D. C. Claar, C. M. Eakin, J. P. Gilmour, N. A. J. Graham, H. Harrison, J. P. A. Hobbs, A. S. Hoey, M. Hoogenboom, R. J. Lowe, M. T. McCulloch, J. M. Pandolfi, M. Pratchett, V. Schoepf, G. Torda, and S. K. Wilson. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, 359(6371):80–83, 2018.

[51] J. A. Hutchings. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.*, 62(4):824–832, April 2005.

[52] J. A. Hutchings and D. J. Fraser. The nature of fisheries- and farming-induced evolution. *Mol. Ecol.*, 17(1):294–313, 2008.

[53] A. R. Ives and S. R. Carpenter. Stability and diversity of ecosystems. *Science*, 317 (5834):58–62, 2007.

[54] B. P. Kinlan and S. D. Gaines. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology*, 84(8):2007–2020, 2003.

[55] K.J. Kroeker, R.L. Kordas, R.N. Crim, and G.G. Singh. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.*, 13(11): 1419–1434, 2010.

[56] A Kuparinen and J A Hutchings. Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 279(1738):2571–2579, 2012.

[57] R. Lande. Genetics and demography in biological conservation. *Science*, 241(4872): 1455–1460, 1988.

[58] R. Lande. Anthropogenic, ecological and genetic factors in extinction and conservation. *Researches on Population Ecology*, 40(3):259–269, 1998.

[59] H. M. Leslie. A synthesis of marine conservation planning approaches. *Conserv. Biol.*, 19(6):1701–1713, 2005.

[60] S. E. Lester, B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airame, and R. R. Warner. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.*, 384:33–46, 2009. ISSN 0171-8630. doi: 10.3354/meps08029.

[61] S. A. Levin and J. Lubchenco. Resilience, robustness, and marine ecosystem-based management. *Bioscience*, 58(1):27–32, 2008.

[62] J. Lindholm, P. Auster, and P. Valentine. Role of a large marine protected area for conserving landscape attributes of sand habitats on Georges Bank (NW Atlantic). *Mar. Ecol. Prog. Ser.*, 269:61–68, 2004. ISSN 0171-8630. doi: 10.3354/meps269061.

[63] S.D. Ling, R.E. Scheibling, A. Rassweiler, C.R. Johnson, N. Shears, S.D. Connell, A.K. Salomon, K.M. Norderhaug, A. Perez-Matus, J.C. Hernandez, and S. Clemente. Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.*, 370(1659):20130269, 2015.

[64] J. Lubchenco, S. R. Palumbi, S. D. Gaines, and S. Andelman. Plugging a hole in the ocean: The emerging science of marine reserves. *Ecol. Appl.*, 13:S3–S7, 2003.

[65] C. Manfrino, C. A. Jacoby, E. Camp, and T. K. Frazer. A positive trajectory for corals at Little Cayman Island. *PLoS One*, 8(10):e75432, 2013.

[66] M. Mangel. Irreducible uncertainties, sustainable fisheries and marine reserves. *Evol. Ecol. Res.*, 2:547–557, 2000.

[67] M. Mangel. Trade-offs between fish habitat and fishing mortality and the role of reserves. *Bull. Mar. Sci.*, 66:663–674, 2000.

[68] J. P. McCarty. Ecological consequences of recent climate change. *Conserv. Biol.*, 15 (2):320–331, 2001.

[69] T. R. McClanahan. Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia*, 155(1):169–177, 2008.

[70] T. R. McClanahan, N. A. Muthiga, and R. A. Coleman. Testing for top-down control: can post-disturbance fisheries closures reverse algal dominance? *Aquatic Conserv.: Mar. Freshw. Ecosyst.*, 21(7):658–675, 2011.

[71] C. Mellin, C. J. A. Bradshaw, D. A. Fordham, and M. J. Caley. Strong but opposing β-diversity–stability relationships in coral reef fish communities. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 281(1777):20131993, 2014.

[72] C. Mellin, M. A. MacNeil, A. J. Cheal, M. J. Emslie, and M. J. Caley. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.*, 19(6):629–637, 2016.

[73] F. Micheli, A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. E. Montes, M. Rossetto, and G. A. De Leo. Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One*, 7(7):e40832, 2012.

[74] T. Miethe, C. Dytham, U. Dieckmann, and J. W. Pitchford. Marine reserves and the evolutionary effects of fishing on size at maturation. *ICES J. Mar. Sci.*, 67(3):412–425, 2010.

[75] T. Miethe, J. W. Pitchford, and C. Dytham. Modelling the evolutionary effects of a coastal marine reserve on different ecological guilds of fish. *Journal of the Marine Biological Association of the United Kingdom*, 91(06):1369–1380, 2011.

[76] P. J. Mumby and A. R. Harborne. Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS One*, 5(1):e8657, 2010.

[77] P. J. Mumby and R. S. Steneck. Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.*, 23(10):555–563, 2008.

[78] P. J. Mumby, A. Hastings, and H. J. Edwards. Thresholds and the resilience of Caribbean coral reefs. *Nature*, 450(7166):98–101, 2007.

[79] P. J. Mumby, R. S. Steneck, and A. Hastings. Evidence for and against the existence of alternate attractors on coral reefs. *Oikos*, 122(4):481–491, 2013.

[80] A. Munguia-Vega, A. Saenz-Arroyo, A. P. Greenley, J. A. Espinoza-Montes, S. R. Palumbi, M. Rossetto, and F. Micheli. Marine reserves help preserve genetic diversity after impacts derived from climate variability: Lessons from the pink abalone in Baja California. *Glob. Ecol. Conserv.*, 4:264–276, 2015.

[81] N. A. Muthiga. Evaluating the effectiveness of management of the Malindi-Watamu marine protected area complex in Kenya. *Ocean Coastal Manage.*, 52(8):417–423, 2009.

[82] NASEM. *A Research Review of Interventions to Increase the Persistence and Resilience of Coral Reefs*. The National Academies Press, Washington, DC, 2019. National Academies of Sciences, Engineering, and Medicine; https://doi.org/10.17226/25279.

[83] NASEM. *A Decision Framework for Interventions to Increase the Persistence and Resilience of Coral Reefs*. The National Academies Press, Washington, DC, 2019. National Academies of Sciences, Engineering, and Medicine; https://doi.org/10.17226/25424.

[84] A. D. Olds, K. A. Pitt, P. S. Maxwell, R. C. Babcock, D. Rissik, and R. M. Connolly. Marine reserves help coastal ecosystems cope with extreme weather. *Glob. Change Biol.*, 20(10):3050–3058, 2014. ISSN 1365-2486. doi: 10.1111/gcb.12606.

[85] E.C. Oliver, M.G. Donat, M.T. Burrows, P.J. Moore, D.A. Smale, L.V. Alexander, J.A. Benthuysen, M. Feng, A.S. Gupta, A.J. Hobday, and N.J. Holbrook. Longer and more frequent marine heatwaves over the past century. *Nature Communications*, 9(1): 1324, 2018.

[86] R. A. Pelc, M. L. Baskett, T. Tanci, S. D. Gaines, and R. R. Warner. Quantifying larval export from South African marine reserves. *Mar. Ecol. Prog. Ser.*, 394:65–78, 2009. ISSN 0171-8630. doi: 10.3354/meps08326.

[87] A. Pérez-Ruzafa, M. González-Wangüemert, P. Lenfant, C. Marcos, and J. A. García-Charton. Effects of fishing protection on the genetic structure of fish populations. *Biol. Conserv.*, 129:244–255, 2006.

[88] C. H. Peterson. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points. *Am. Nat.*, 124(1):127–133, 1984.

[89] P. S. Petraitis and S. R. Dudgeon. Detection of alternative stable states in marine communities. *J. Exp. Mar. Biol. Ecol.*, 300(1–2):343–371, 2004.

[90] M. L. Pinsky and S. R. Palumbi. Meta-analysis reveals lower genetic diversity in overfished populations. *Mol. Ecol.*, 23(1):29–39, 2014.

[91] M.L. Pinsky and M. Fogarty. Lagged social-ecological responses to climate and range shifts in fisheries. *Climatic change*, 115(3-4):883–891, 2012.

[92] M.L. Pinsky, B. Worm, M.J. Fogarty, J.L. Sarmiento, and S.A. Levin. Marine taxa track local climate velocities. *Science*, 341(6151):1239–1242, 2013.

[93] B. Planque, J. M. Fromentin, P. Cury, K. F. Drinkwater, S. Jennings, R. I. Perry, and S. Kifani. How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.*, 79(3-4):403–417, 2010.

[94] J. F. Quinn, S. R. Wing, and L. W. Botsford. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Am. Zool.*, 33:537–550, 1993.

[95] C. M. Roberts, B. C. O'Leary, D. J. McCauley, P. M. Cury, C. M. Duarte, J. Lubchenco, D. Pauly, A. Saenz-Arroyo, U. R. Sumaila, R. W. Wilson, B. Worm, and J. C. Castilla. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci. U. S. A.*, 114(24):6167–6175, 2017.

[96] G. R. Russ and A. C. Alcala. Enhanced biodiversity beyond marine reserve boundaries: The cup spillith over. *Ecol. Appl.*, 21(1):241–250, 2011. ISSN 1051-0761. doi: 10.1890/09-1197.1.

[97] G. R. Russ, A. C. Alcala, A. P. Maypa, H. P. Calumpong, and A. T. White. Marine reserve benefits local fisheries. *Ecol. Appl.*, 14:597–606, 2004.

[98] G. R. Russ, S. L. A. Questel, J. R. Rizzari, and A. C. Alcala. The parrotfish-coral relationship: refuting the ubiquity of a prevailing paradigm. *Mar. Biol.*, 162(10): 2029–2045, 2015.

[99] C. M. Sgro, A. J. Lowe, and A. A. Hoffmann. Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.*, 4(2):326–337, 2011.

[100] E. V. Sheehan, T. F. Stevens, S. C. Gall, S. L. Cousens, and M. J. Attrill. Recovery of a temperate reef assemblage in a marine protected area following the exclusion of towed demersal fishing. *Plos One*, 8(12):e83883, 2013. ISSN 1932-6203. doi: 10.1371/journal.pone.0083883.

[101] W. P. Sousa and J. H. Connell. Further comments on the evidence for multiple stable points in natural communities. *Am. Nat.*, 125(4):612–615, 1985.

[102] C.U. Soykan and R.L. Lewison. Using community-level metrics to monitor the effects of marine protected areas on biodiversity. *Conserv. Biol.*, 29(3):775–783, 2015.

[103] V. Stelzenmüller, F. Maynou, and P. Martín. Patterns of species and functional diversity around a coastal marine reserve: A fisheries perspective. *Aquatic Conserv.: Mar. Freshw. Ecosyst.*, 19(5):554–565, 2009. ISSN 1099-0755.

[104] A. W. Stoner, M. H. Davis, and C. J. Booker. Negative consequences of Allee effect are compounded by fishing pressure: Comparison of queen conch reproduction in fishing grounds and a marine protected area. *Bull. Mar. Sci.*, 88(1):89–104, 2012.

[105] N. Takashina and A. Mougi. Effects of marine protected areas on overfished fishing stocks with multiple stable states. *J. Theor. Biol.*, 341:64–70, 2014. ISSN 0022-5193. doi: 10.1016/j.jtbi.2013.09.027.

[106] Z.M. Topor, D.B. Rasher, J.E. Duffy, and S.J. Brandl. Marine protected areas enhance coral reef functioning by promoting fish biodiversity. *Conserv. Lett.*, page e12638, 2019.

[107] A. Villamor and M. A. Becerro. Species, trophic, and functional diversity in marine protected and non-protected areas. *Journal of Sea Research*, 73:109–116, 2012. ISSN 1385-1101. doi: 10.1016/j.seares.2012.07.002.

[108] S. B. Walsh, M. R .and Munch, S. Chiba, and D. O. Conover. Maladaptive changes in multiple traits caused by fishing: Impediments to population recovery. *Ecol. Lett.*, 9(2):142–148, 2005.

[109] J. M. West and R. V. Salm. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv. Biol.*, 17(4):956–967, 2003.

[110] J. W. White, L. W. Botsford, A. Hastings, M. L. Baskett, D. M. Kaplan, and L. A. K. Barnett. Transient responses of fished populations to marine reserve establishment. *Conserv. Lett.*, 6(3):180–191, 2013. ISSN 1755-263X. doi: 10.1111/j.1755-263X.2012.00295.x.

[111] Stephen R Wing and Lucy Jack. Marine reserve networks conserve biodiversity by stabilizing communities and maintaining food web structure. *Ecosphere*, 4(11):art135, 2013.

[112] L.J. Wood, L. Fish, J. Laughren, and D. Pauly. Assessing progress towards global marine protection targets: Shortfalls in information and action. *Oryx*, 42(3):340–351, 2008.

[113] B. Worm, E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314 (5800):787–790, 2006.

[114] K. Zychaluk, J. F. Bruno, D. Clancy, T. R. McClanahan, and M. Spencer. Data-driven models for regional coral-reef dynamics. *Ecol. Lett.*, 15(2):151–158, 2012.