The Ecological and Evolutionary Consequences of Marine Reserves

Marissa L. Baskett[1] and Lewis A.K. Barnett[2,3]

[1]Department of Environmental Science and Policy, University of California, Davis, California 95616-5270; email: mlbaskett@ucdavis.edu

[2]Joint Institute for the Study of the Atmosphere and Oceans, under contract to Fisheries Resource Assessment and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, Seattle, Washington 98110; email: lewis.barnett@noaa.gov

[3]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195

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Abstract

Here we review the population, community, and evolutionary consequences of marine reserves. Responses at each level depend on the tendency of fisheries to target larger body sizes and the tendency for greater reserve protection with less movement within and across populations. The primary population response to reserves is survival to greater ages and sizes plus increases in the population size for harvested species, with greater response to reserves that are large relative to species' movement rates. The primary community response to reserves is an increase in total biomass and diversity, with the potential for trophic cascades and altered spatial patterning of metacommunities. The primary evolutionary response to reserves is increased genetic diversity, with the theoretical potential for protection against fisheries-induced evolution and selection for reduced movement. The potential for the combined outcome of these responses to buffer marine populations and communities against temporal environmental heterogeneity has preliminary theoretical and empirical support.

1. INTRODUCTION

Human activities such as fishing, coastal development, and nutrient runoff have caused declines in marine populations and altered marine communities (Kappel 2005). Recognition of the potential for these human activities to affect ecosystem-level properties and the sustainable delivery of marine ecosystem services has led to a more holistic, ecosystem-based approach to marine resource management (Arkema et al. 2006). One tool for implementing marine ecosystem-based management (EBM) is the establishment of marine protected areas (MPAs) with restricted human activities, which include no-take marine reserves (Lubchenco et al. 2003). The area covered by MPAs and marine reserves has increased steadily since the 1980s, especially in coastal systems (Wood et al. 2008). Because the protection of ecological and evolutionary processes is central to the goals of EBM and marine reserves (Francis et al. 2007, Lubchenco et al. 2003), an understanding of the ecological and evolutionary responses to marine reserves is central to evaluating the efficacy of these management tools.

Three differences between marine and terrestrial systems alter the expectations for and analysis of the ecological and evolutionary consequences of reserves. First, marine and terrestrial reserves can differ in their goals: The goal of terrestrial reserves is typically protection within the reserve boundaries, whereas marine reserves, in their role as a component of EBM, often have the additional goal of promoting the sustainability of fisheries outside the reserve boundaries (Carr et al. 2003, Guénette et al. 1998, Leslie 2005). Therefore, a consideration of the ecological and evolutionary consequences of marine reserves includes the consequences for harvested areas as well. Second, the primary anthropogenic impact on biodiversity outside terrestrial reserves is habitat degradation, whereas the primary anthropogenic impact outside marine reserves is fishing (Kappel 2005). This difference in the human role alters which individuals, populations, and guilds increase within and outside reserve boundaries following their establishment (Carr et al. 2003). Third, marine organisms typically realize greater scales of dispersal compared with their terrestrial taxonomic counterparts (Kinlan & Gaines 2003), in part because the physical differences between air and water cause a greater capacity for passive transport in marine systems than in terrestrial systems (Strathmann 1990). Therefore, marine systems have a greater potential for connectivity, both between protected and harvested areas and between individual reserves in a reserve network, especially given planktonic larval dispersal that can connect reserves without corridors (Carr et al. 2003, Stobutzki 2001). Essentially, marine reserves impose spatial heterogeneity in harvest across interconnected populations and communities.

The capacity for both dispersal in marine systems and harvest outside reserves introduces variation in how different individuals within populations—and populations within communities—respond to marine reserves. Specifically, fisheries often target larger-bodied fish within and across populations; this selectivity can result from the use of minimum size limits in management, the properties of the fishing gear used (e.g., mesh size), or catch value dependent on body size (Millar 1992, Shin et al. 2005, Tsikliras & Polymeros 2014). In addition, individuals and populations with less movement receive greater protection because of their greater retention within reserve boundaries (Botsford et al. 2001). The size selectivity of fisheries and movement selectivity of reserve protection inevitably interact through the connectivity of harvested and protected populations.

Here we review the ecological and evolutionary consequences of marine reserves. We integrate theoretical expectations of and empirical findings on responses to marine reserves on the population, community, and evolutionary levels. We use the selectivity of harvest and protection, as well as their expected combined effect in terms of response to heterogeneity in space and time, within and across populations to frame our understanding of the responses on each level (**Supplemental Figure 1**; follow the **Supplemental Materials link** from the Annual Reviews home

page at **http://www.annualreviews.org**). With this approach, we look to integrate topics that have received separate synthetic treatments: theoretical (Gerber et al. 2003) and empirical (Lester et al. 2009) marine reserve studies and population (Jennings 2000) and community (Baskett et al. 2007a) dynamics in marine reserves. Previous reviews and special issues on marine reserves have also focused on principles of reserve design (Lubchenco et al. 2003), the role of reserves in fisheries management (Guénette et al. 1998), and the role of reserve networks (Gaines et al. 2010a). Therefore, we refer the reader to these syntheses for questions of reserve network design and the effect of reserves on fisheries, while we draw from these varied topics in our distinct focus on ecological and evolutionary responses to reserve establishment.

Filling in: an increasing proportion of older, larger individuals as a population approaches stable age distribution after fishing mortality ceases

2. POPULATION CONSEQUENCES OF MARINE RESERVES

Because the immediate effect of marine reserves is to eliminate harvest, the primary expected (Jennings 2000, Polacheck 1990) and observed (Lester et al. 2009) response to reserve establishment is increased abundance and biomass of harvested species. In this section, we detail how the biomass and abundance responses of harvested species to marine reserves depend on an interaction among fishing intensity, fishing selectivity, and the target species' movement relative to reserve size.

2.1. Harvest Selectivity

One driver of increased biomass in reserves is larger body sizes for harvested populations (Lester et al. 2009), which arise from lower mortality and therefore greater survival to larger sizes, especially if a fishery targets larger individuals (both theoretically expected and empirically verified; see Taylor & McIlwain 2010, White et al. 2013). Therefore, both the age and size structure in reserves will fill in with older ages and larger sizes, eventually approaching a stable age and size distribution (White et al. 2013). As the age and size structure fill in, reproductive output increases because of the increased number of mature individuals and because fecundity increases with maternal age and size [e.g., modeled by White et al. (2013) and verified within reserves by Diaz et al. (2011); see also the sidebar, Long-Term Field Study: A Temperate Example]. Increases in offspring survival might also occur if maternal age or size increases offspring size or energy reserves (Hixon et al.

LONG-TERM FIELD STUDY: A TEMPERATE EXAMPLE

The Leigh reserve in New Zealand (est. 1976) provides a long-term temperate rocky reef case study. Snapper (*Pagrus auratus*), with size-selective harvest given a minimum size limit, exemplifies the filling in of size structure [14.3-fold higher density of harvested sizes (95% confidence interval: 10.0–20.5)] and greater overall biomass [9.9-fold (6.8–14.7)], which lead to greater reproductive output [18.1-fold (10.7–30.6)] inside reserves compared with harvested areas (Willis et al. 2003; see Section 2.1). Resident snapper have smaller average home ranges inside reserves (903 m, single core usage areas) than outside reserves (2,127 m, cases with multiple core usage areas) (Parsons et al. 2010), possibly due to density-dependent movement (Section 2.3) or selection for reduced movement (Section 4.2). Exemplifying cascading responses to increased harvested predator abundance [snapper, spiny lobsters (*Jasus edwardsii*); see Section 3.1], urchin (*Evechinus chloroticus*) density decreased [1.84(1.18–2.87):1 outside:inside] and crypsis increased [2.21(1.32–3.71):1 density of cryptic urchins inside:outside] (Shears & Babcock 2003), with a benthic habitat–type shift from urchin barrens (from 27–87% to 0% cover since reserve establishment) to kelp forests (*Ecklonia radiata*; from 0–5% to 17–50% cover) in regions <8 m (Parsons et al. 2004). Kelp forest stasis or decrease at greater depths, likely due to increased turbidity (Parsons et al. 2004), illustrates weakened cascades with disturbance.

2014); however, models predict that heavy exploitation is necessary for these effects to cause a noticeable difference in population productivity (Barnett et al. 2015 and references therein). If somatic growth is density dependent, body size at a given age might be smaller in reserves than in harvested areas (observed in Taylor & McIlwain 2010), and smaller body size can reduce the expected amount of increased reproductive capacity [modeled by Gårdmark et al. (2006)]. Overall, increases in abundance can arise from both decreased mortality and increased reproductive output as body size increases, whereas increases in biomass can arise from both increased body size and increased abundance. The expected increase in biomass and abundance is greater for higher harvest rates outside the reserves and before reserve establishment (Guénette & Pitcher 1999; White et al. 2010b, 2013).

The timescale of biomass and abundance responses inevitably depends on life history and fishing history (intensity and duration; see Gerber et al. 2003, Jennings 2000; see also the sidebar, Long-Term Field Study: A Tropical Example). Initial increases in biomass after reserve establishment typically precede increases in abundance because increases in body size depend on the within-generation process of somatic growth, whereas increases in abundance depend on the multigenerational process of increased reproduction (Halpern & Warner 2002, Molloy et al. 2009). The timescale of the age and size structure filling in response increases with increasing age at maturation and longevity (White et al. 2013). Initial, short-term (transient) responses in abundances can, theoretically, include declines or oscillations at a period of the generation time, especially for species with greater age at maturity, longevity, and intensity and duration of harvest (White et al. 2013). Environmentally driven stochastic recruitment can interact with these transient responses to further increase the amount of variability and time to longer-term increases (particularly for populations with intermediate age at maturity; see White et al. 2013, White & Rogers-Bennett 2010). Empirical observations include such variation in initial population response to reserve establishment (e.g., Freeman et al. 2012). Another possible source of population decline after reserve establishment is increased parasite or disease prevalence associated with increased population density, depending on the drivers of disease susceptibility and transmission (**Table 1**).

In addition to body size, fishing mortality can vary with sex, either from fisheries directly targeting a particular sex (Grüss et al. 2014b) or because of sexual size dimorphism; in extreme cases, such as for sequential hermaphrodites, fishing-skewed sex ratios can reduce reproductive success

LONG-TERM FIELD STUDY: A TROPICAL EXAMPLE

The Apo reserve in the Philippines (est. 1982) provides a long-term coral reef case study. Quantifying the timescale of biomass increases for harvested species (Section 2.1), the biomass of large, predatory fishes [47 species in the Serranidae (Epinephelinae), Lutjanidae, and Lethrinidae families] increased logistically with an expected time-to-carrying capacity of 40 years (Russ & Alcala 2010). Statistically significant increases in biomass adjacent to the reserve, ascribed to both reserve spillover and fishing effort reduction during the study period (Russ & Alcala 2010), illustrates the coupled responses across protected and unprotected areas (Section 2.3). Linear increases in species richness for large, predatory fishes, with an 11-fold increase over 25 years in the reserve (Russ & Alcala 2011), illustrate a diversity response in harvested guilds (Section 3). Outside the reserve, statistically significant linear increases in species richness occurred at a slower rate and decreased with distance from the reserve (Russ & Alcala 2011). This change in diversity and a 9% decrease in prey abundance and 3% increase in habitat complexity (coral cover, rugosity, and steepness) adjacent to the reserve (Russ & Alcala 2011) exemplify the potential for coupled community-level responses inside and outside reserves (Section 3.3).

Table 1 Context-dependent responses to marine reserves

Response	Context or hypothesized reason(s)	Citation(s)[a]
Disease prevalence in protected populations		
Higher	Transmission is density dependent	T: (McCallum et al. 2005) E: (Wootton et al. 2012)
Lower	Fishing facilitates disease spread via injuries in trapping and handling	E: (Freeman & MacDiarmid 2009)
No effect	Disease susceptibility depends on environmental factors (e.g., temperature)	E: (Coelho & Manfrino 2007, Page et al. 2009)
Effect of density-dependent movement		
Greater movement for protected populations	Competitive displacement, decreased fear of predation with crowding, or decreased fear of fishing in reserves	E: (Abesamis & Russ, 2005, Amargos et al. 2010, Ballantine 2014, Topping et al. 2006) T: (Kellner et al. 2008)
Less movement out of reserves	Increased residency to avoid negative interspecific interactions with increased crowding	E: (Parsons et al. 2010)
Greater movement into reserves	Conspecific attraction	E: (Eggleston & Parsons 2008) T: (Gerber et al. 2005, Langebrake et al. 2012)
Strength of trophic cascades within reserves[b]		
Weakened	Harvest (or bycatch) of both predators and prey, such that harvest release can outweigh predation increase in prey	T: (Baskett 2006, Kellner et al. 2010, Micheli et al. 2004a, Savina et al. 2013, Takashina et al. 2012) E: (Mumby et al. 2006, Shears et al. 2012)
Weakened	High levels of abiotic disturbance, such that disturbance can outweigh predation effects on prey	E: (Micheli et al. 2005)
Strengthened	Increased piscivore recruitment with increased sheltering algae	T: (Baskett 2007) E: (Sponaugle et al. 2012)
Weakened	Prey size refugia, where invulnerable prey sizes buffer response to predators. Note that increase in body size for harvested predators in response to reserves (Section 2.1) can dampen this effect.	T: (Baskett 2006) E: (Andrew & MacDiarmid 1991, Ballantine 2014, Mumby et al. 2006)
Weakened	Prey refugia in space given protection of refuge habitat	T: (Mangel & Levin 2005)
Strengthened	Alternative prey, which can increase apparent competition with predator increases	T: (Kellner et al. 2010, Takashina et al. 2012) E: (Berriman et al. 2015)
Both weakened and strengthened	Reduced movement or increased time in shelter for prey with predator increases (i.e., behaviorally mediated indirect interactions), which reduce predation effects on prey density but enhance declines in herbivory rates	E: (Babcock et al. 2010, Hereu 2005, O'Sullivan & Emmerson 2011)

[a]E, empirical; T, theoretical.

[b]See Polis et al. (2000) for a comprehensive list of factors that can strengthen or weaken cascades in ecological systems; here we focus on factors studied in marine reserves. Note that some references demonstrate the context or mechanism rather than the overall response.

(Hawkins & Roberts 2004). In such cases, harvested areas may have a skewed sex ratio, whereas the sex ratio inside reserves may be more even (Grüss et al. 2014b). For sequential hermaphrodites, male-first (protandrous) hermaphrodites can theoretically have increased reproductive success and output after reserve establishment because of the protection of larger, more fecund females (Alonzo & Mangel 2004; Grüss et al. 2014a,b). In the more common case of female-first (protogynous) hermaphrodites, a larger skew in sex ratio in harvested areas can occur after reserve establishment if reserves lead to displaced harvest, which can reduce reproduction if fertilization success depends on sex ratio (Chan et al. 2012). For sequential hermaphrodites with spawning migrations, the spatial segregation of sexes might allow fishing to target the larger sex more than expected by size selectivity alone, and reserve placement in spawning aggregation sites can lead to a more even sex ratio (Grüss et al. 2014b). Overall, the effect of reserves on a population's sex ratio depends on the target and intensity of sex-selective harvest, and any consequences for reproductive success—and therefore abundance and biomass response—depend on the connection between sex ratio and reproductive success.

2.2. Protection Selectivity

The potential for increased biomass and abundance within reserves increases with increased within-reserve retention and therefore decreased movement at all stages, from larval dispersal to postsettlement home ranges and any postsettlement migrations among habitats (Botsford et al. 2001, Grüss et al. 2011, Moffitt et al. 2009). For example, within–life span protection in an individual reserve, and therefore the filling in of the age and size structure, requires postsettlement home ranges to be smaller than approximately twice the reserve size; the amount of protection further increases with decreased home range size and therefore decreased likelihood of moving outside reserve boundaries (Babcock et al. 2012, Moffitt et al. 2009). Furthermore, within-reserve retention of reproductive output requires mean larval dispersal distances smaller than the reserve size or a reserve network connected by larval dispersal (detailed below) (Botsford et al. 2001, Lockwood et al. 2002, White et al. 2010a). In addition to decreased larval dispersal distance and therefore increased retention of reproductive output (Gaines et al. 2003), this population response is greater in places where oceanographic and habitat features entrain larvae and promote settlement [demonstrated both theoretically (White et al. 2010a) and empirically (Wen et al. 2013)].

Although the capacity for long-distance larval dispersal in many coastal marine organisms reduces the retention of reproductive output within individual reserves (Jennings 2000), it creates the opportunity for population connectivity among individual reserves in a reserve network (Botsford et al. 2001). Such connectivity retains reproductive output within a reserve network, which contributes to increased abundance and population persistence. In particular, although enough retention of locally produced offspring for self-replacement is unlikely within individual reserves for many marine species, network persistence (i.e., self-persistence for the connected populations in a network) can, theoretically, occur if the exchange of offspring among locations compensates for the shortfall in local retention of offspring (Hastings & Botsford 2006). This potential for network persistence depends on the distribution of reproduction throughout a seascape and the realized connectivity among subpopulations (Burgess et al. 2014, Gaines et al. 2003, Hastings & Botsford 2006). Direct empirical evidence of reserves enabling network persistence is lacking given the comprehensive data on fecundity, survivorship, and dispersal necessary for its assessment (Burgess et al. 2014), but a recent study suggests that the effect of a reserve network on abundance is greater than that expected from the sum of the individual reserves (Grorud-Colvert et al. 2014).

In some species, movement further depends on postsettlement migration between juvenile and adult habitats or spawning and feeding grounds. If ontogenetic migrations occur and both adult

Home range: the area that encompasses typical postsettlement movement patterns driven by daily activities (e.g., foraging)

Network persistence: long-term maintenance of a metapopulation achieved through replacement by connectivity among locations over multiple generations

and juvenile habitats are fished, increased abundance requires connected patches of both habitats within reserve boundaries [modeled by St. Mary et al. (2000) and White (2015)], and the strength of coupling between juvenile and adult habitats correlates with the effect of reserves on abundance [empirically demonstrated by Olds et al. (2013)]. For species with migrations beyond the scale of individual reserves, harvest at unprotected life history stages can lead to a lack of a reserve effect on population sizes (Grüss et al. 2014b). Therefore, protection of such species might require reserves in migratory corridors as well as essential habitats (Pendoley et al. 2014). Given the large-scale movement patterns common to harvested pelagic (open ocean) marine species, the potential response to pelagic marine reserves is debatable: Very large closures (White & Costello 2014) or a mix of static and dynamic reserves (Game et al. 2009) might lead to increased abundances but entail implementation and enforcement challenges (Kaplan et al. 2010).

Spillover: export of biomass or individuals from reserves to harvested areas

2.3. Response to Heterogeneity in Space and Time

The overall population response to the heterogeneity in harvest imposed by a reserve network depends on connectivity between protected and harvested areas. As detailed below, this connectivity depends on the interaction between harvest selectivity on size and protection selectivity on movement, especially if movement depends on size or density, and can alter population response to environmental variability in time.

The combination of abundance and biomass buildup inside reserves and decreasing within-reserve retention as movement increases leads to the potential for spillover from reserves to harvested areas. Spillover can, theoretically, lead to increased recruitment and biomass outside reserves if reserves are large enough for population response to occur but small enough for some movement over reserve boundaries (Moffitt et al. 2009, White et al. 2010a), especially if post-dispersal density-dependent recruitment occurs (as opposed to predispersal density dependence; see Gaylord et al. 2005). Empirical studies indicate that reserves can increase larval supply (reviewed in Pelc et al. 2010) and the abundance of postsettlement individuals in adjacent harvested areas (reviewed in Gell & Roberts 2003; see also the sidebar, Long-Term Field Study: A Tropical Example), depending on the physical and ecological features of the seascape (Grüss et al. 2011, Tupper 2007). However, declines can occur if the fishing effort displaced by reserves leads to increased mortality that outweighs the amount of spillover (Karnauskas et al. 2011, Rassweiler et al. 2012). Overall, the typical expected (Kellner et al. 2008, Pelc et al. 2010, White et al. 2011) and observed (e.g., Hackradt et al. 2014, Willis et al. 2003) spatial distribution of abundance peaks within reserves and declines toward the reserve boundaries, depending on the spatial pattern of fishing in harvested areas (e.g., concentration of fishing effort near reserve boundaries; see Kellner et al. 2007). The current standard for empirical inference of reserve-driven population responses is a before-after control-impact design—in other words, measurement of populations both inside and outside a reserve and before and after reserve establishment, which can control for the effect of environmental variability on population changes in time and the effect of habitat quality on population differences in space (Guidetti 2002, Jennings 2000). However, the interconnected response across reserves and harvested areas means that comparing data with theoretical expectations provides the greatest potential to quantify the influence of reserves on population dynamics over space and time (White et al. 2011).

Increases in abundance and biomass within reserves can further affect the amount of exchange between protected and harvested areas if movement depends on body size or population density. Empirical observations of density-dependent movement range from increased to decreased movement in reserves compared with harvested populations; these different outcomes likely depend on the behavior of the analyzed fish and the accuracy of the tagging method used to assess

movement (e.g., acoustic versus mark-recapture) (**Table 1**; see also the sidebar, Long-Term Field Study: A Temperate Example). Increased movement out of reserves with increased density can, theoretically, lead to increased spillover with increased reserve size (Kellner et al. 2008), as opposed to the typical expectation of decreased spillover with increased reserve size because of greater retention. Conversely, increased movement into reserves can lead to greater within-reserve abundance and less spillover with greater movement rates (Gerber et al. 2005, Langebrake et al. 2012), as opposed to smaller movement rates as typically expected. If movement depends on habitat quality and if fishing gear degrades the habitat, then reserve protection of habitat quality can lead to greater within-reserve population densities because of both greater population growth rates and increased retention (Rodwell et al. 2003). Finally, the filling in of the size structure within reserves can result in increased movement if home ranges increase with body size (as observed across species in coral reef fishes; see Nash et al. 2015).

Overall, reserve networks lead to spatial heterogeneity in size structure and population density across connected populations, which can buffer population response to temporal heterogeneity and directional change. Protection within reserves can, theoretically, reduce population variability in response to environmental stochasticity (Grafton et al. 2005, Mangel 2000a, Sladek Nowlis & Roberts 1999) and catastrophic disturbances (Allison et al. 2003), depending on the fisheries management outside reserves (McGilliard et al. 2011). In addition to faster recovery rates because of reduced mortality and increased reproduction, this buffering can arise from the greater role of density dependence with increased abundance, which decreases sensitivity to variation in mortality and reproduction (Botsford et al. 2014). Empirical observations are suggestive of reduced population variability in reserves compared with harvested areas (Babcock et al. 2010, Micheli et al. 2012), and experimental microbial microcosms indicate that reserves have the potential to reduce extinction risk by buffering against environmental stochasticity (Fryxell et al. 2006). Maintenance of larger populations within reserves can also decrease the likelihood of population collapse for species with Allee effects (Chan & Kim 2014, Quinn et al. 1993, Takashina & Mougi 2014). Empirical investigation extends this theoretical expectation to indicate that, in addition to supporting larger populations that are farther from the Allee effect threshold for population decline, reserves can also lower the population density at which this threshold occurs if mating success increases with body size as well as density (Stoner et al. 2012). Finally, models indicate that both the biomass buildup within reserves and connectivity with harvested areas can allow reserves to protect source populations that buffer against overfishing and management uncertainty (Apostolaki et al. 2002; Lauck et al. 1998; Mangel 2000b,c) and to reduce the risk of population collapse due to the interactive effects of fisheries and climate change (especially if larval energy reserves increase with maternal age and size; see Barnett et al. 2015).

3. COMMUNITY CONSEQUENCES OF MARINE RESERVES

Greater biomass and abundance for harvested populations within reserves shift the relative abundances of different species in a community, with the potential for greater diversity (Palumbi 2001) if abundance increases affect the local persistence likelihood. Species richness is greater in reserves than in harvested areas in many cases (Lester et al. 2009) and is realized at varying timescales (Anticamara et al. 2010, Claudet et al. 2008, Micheli et al. 2004b; see also the sidebar, Long-Term Field Study: A Tropical Example). However, increases in richness and other metrics of diversity (**Table 2**) occur less consistently and to a lesser degree than increased body size, abundance, and biomass (Lester et al. 2009, Soykan & Lewison 2015). One reason for weaker and mixed outcomes in diversity is that not all species increase—and some decline—after reserve establishment (Micheli et al. 2004b). As detailed in this section, community-level responses

Table 2 Observed response of community-level properties to reserves

Property	Response[a]	Citation(s)[b]
Diversity and structure		
Total abundance and biomass	Increase	M: (Soykan & Lewison 2015)
Species richness	Increase	M: (Côté et al. 2001, Lester et al. 2009)
Functional diversity	Increase	S: (Stelzenmüller et al. 2009, Villamor & Becerro 2012)
Rarity	Increase	M: (Soykan & Lewison 2015)
Evenness	Decrease	M: (Soykan & Lewison 2015)
Trophic level	Increase	S: (Stobart et al. 2009)
Stability[c]		
Variability in fish biomass	Decrease	M: (Worm et al. 2006)
Variability in species diversity	Decrease	S: (Bates et al. 2014)
Variability/turnover in community assemblage/structure	Lower	S: (Fraschetti et al. 2013, Mellin et al. 2014, Wing & Jack 2013)
Occurrence of nuisance species outbreaks	Lower	S: (McCook et al. 2010)
Resistance to disturbance	Inconsistent or unaffected	M: (Selig et al. 2012, Worm et al. 2006)
Recovery rate	Inconsistent or lower	M: (Graham et al. 2011, Worm et al. 2006)
Invasiveness	Unaffected	M: (Burfeind et al. 2013, Guidetti et al. 2014)

[a]Increase can refer to a greater value (and decrease a smaller value) inside compared with outside reserves (more common) or after compared with before reserve establishment, depending on the study.
[b]S, single study; M, meta-analysis, in which the response indicated is the cross-study average response, which might vary among studies. See Section 3.3 for possible explanations of variation in responses among studies.
[c]Note that a decrease in variability indicates an increase in stability.

depend on which species are harvested before reserve establishment, which harvested species have life history characteristics that lead to greater responses to reserves, and how interactions between harvested and nonharvested species across connected protected and harvested areas drive cascading responses throughout the entire community.

3.1. Harvest Selectivity

Because reserves reduce mortality for species targeted by fisheries, targeted species show more frequent and greater increases in biomass and density than nontarget species (Claudet et al. 2008, Hamilton et al. 2010, Micheli et al. 2004b, Molloy et al. 2009). Reserves can reduce mortality of nontarget species if they are caught as bycatch (Murawski et al. 2000). In addition, in areas fished with habitat-destructive fishing gear, reserves can lead to increases in habitat-forming organisms that benefit the entire community (Lindholm et al. 2004), which can lead to particularly strong responses in diversity (Sheehan et al. 2013). More generally, however, lack of exploitation can explain why some species do not respond to reserve establishment (Molloy et al. 2009). Furthermore, nontarget species can decline if their predators or competitors were previously harvested (Micheli et al. 2004b), as detailed below.

Among guilds in a community, species at high trophic levels (e.g., piscivores) experience larger increases in reserves (Edgar et al. 2014, Hamilton et al. 2010, Micheli et al. 2004a). This observed response might arise from increased body size with trophic level (a general relationship with exceptions; see Jennings et al. 2001) if large body size leads to more intensive fishing (Shin et al.

2005, Tsikliras & Polymeros 2014) or greater vulnerability to harvest, such that larger declines occur for higher trophic-level species given analogous levels of harvest (Reynolds et al. 2005). More intensive fishing at higher trophic levels might arise if yield or value per individual increases with body size across species (Shin et al. 2005). Greater vulnerability to harvest at higher trophic levels might arise if longevity or age at maturity, which can determine population productivity and extinction risk (Hutchings et al. 2012), increase with body size (Charnov 1993). Although increased fishing intensity or vulnerability with body size might increase the magnitude of response to reserves, slower population growth rates with increased body size (Blueweiss et al. 1978) might increase the timescale of such responses.

Greater increases at higher trophic levels have the potential to cause trophic cascades in marine reserves [supported by both theory (Walters et al. 1999) and data (Babcock et al. 2010)] with decreased abundance of some midtrophic species. Decreases in midtrophic species can further cause increases at the base of food webs, such as kelp in temperate reef systems (and therefore primary productivity); this increase occurs in some cases (e.g., Babcock et al. 1999) but not consistently (reviewed in Gilby & Stevens 2014; for examples of drivers of differential responses, see **Table 1** and the sidebar, Long-Term Field Study: A Temperate Example). Additional secondary effects of trophic cascades in reserves can include increases in small invertebrates (and therefore secondary productivity) that use macroalgae as shelter and increases in, or diet changes for, organisms that feed on macroalgae and any harbored invertebrates (and therefore tertiary productivity; reviewed in Ballantine 2014). Because trophic cascades involve a secondary response of prey to the initial response of predators, they occur on longer timescales than direct responses of targeted species do (Babcock et al. 2010). The strength and secondary effects of cascades further depend on a variety of biotic and abiotic processes (e.g., disturbance level, prey refugia, recruitment facilitation) as well as whether or not harvesting occurs for both predators and prey (**Table 1**). For example, in coral reef systems, which often have intensive fisheries for both herbivores and piscivores, decreases—rather than increases—in algal biomass can occur (reviewed in Gilby & Stevens 2014).

Beyond cascading effects of previously harvested predators on prey, cascading effects through marine communities can occur because of the protection of previously harvested competitors, prey, or facilitators of nontarget species (Baskett et al. 2007a). For example, the responses of red abalone (*Haliotis rufescens*, recreationally harvested in shallow areas) and red sea urchins (*Strongylocentrotus franciscanus*, commercially harvested at a wider range of depths) to reserves in northern California depend on a mix of facilitation and competition. Specifically, juvenile abalone had greater population densities in reserves than in harvested areas, most likely because of recruitment facilitation by urchin spines (Rogers-Bennett & Pearse 2001), whereas total abalone abundance decreased in a protected site but increased in a harvested site, most likely because of competition with the more intensively harvested urchins (Karpov et al. 2001). Increases in harvested prey in reserves can, theoretically, lead to increases in nontarget predators (Takashina et al. 2012) and greater increases in harvested predators than expected from elimination of predator fishing alone (Baskett et al. 2007a). Many seabirds and marine mammals exemplify nontarget predators with harvested prey, and the potential for their increase because of increased prey and reduced bycatch can be among the conservation goals of reserves (e.g., Ronconi et al. 2012). However, food web simulations indicate that whether such increases occur depends on food web complexities such as whether these predators share prey with harvested piscivores (with declines theoretically possible; see Pinnegar & Polunin 2004, Salomon et al. 2002). Finally, interactions with nontarget species might alter responses of harvested species to reserves. For example, if nontarget prey of harvested predators compete with or prey on those predators' juveniles, then historical increases in prey following predator release because of fishing can, theoretically, impede predator recovery in reserves (Baskett et al. 2006). Overall, the complexity of interactions between harvested and nontarget species across guilds in

marine communities means that trophic level might not provide a clear indication of community-level response to reserves, analogous to community-level response to harvest (Branch et al. 2010).

3.2. Protection Selectivity

Although decreased protection with increased movement (Section 2.2) might be expected to lead to an increased response to reserves for species with less movement (Botsford et al. 2001), harvest effects counter and outweigh movement effects in determining responses across species in a community. Specifically, species with greater movement tend to be more heavily harvested, such that the release from harvest typically outweighs the effect of reduced retention and leads to greater response with increasing movement across species (Micheli et al. 2004a, Palumbi 2004). However, density increases with increasing reserve size for species with larger-scale movement but not smaller-scale movement (Claudet et al. 2010) indicate that relative movement scale can affect differential response across species in a community; specifically, reserves protect low-movement species regardless of size but protection of high-movement species depends on reserve size. If the magnitude of population response affects local persistence, this increase in protection with increased reserve size might then lead to increasing species richness with reserve size, which has occurred in some cases (McClanahan et al. 2009) but is not evident in cross-system syntheses (Lester et al. 2009).

Although movement-dependent protection plays a secondary role in the community-level response to reserve establishment on average, theory indicates that it can play a larger role in cases in which dispersal affects the composition and spatial patterning of metacommunities. For example, decreased protection with increased movement can particularly affect species that require long-distance dispersal to coexist with superior competitors in communities with competition–colonization trade-offs (Baskett et al. 2007a). In addition, species interactions can alter how responses depend on reserve size and spacing relative to dispersal distance. Specifically, in a predator–prey metacommunity, despite less network connectivity, reserve spacing that matches the spatial scale of patchiness in metacommunity composition leads to greater increases in abundances than reserve spacing on the smaller scale of dispersal (Gouhier et al. 2013). More generally, because they negatively affect population growth rates, accounting for predation and competition typically increases the reserve size predicted to lead to a response in a harvested species (Baskett et al. 2007a).

3.3. Response to Heterogeneity in Space and Time

The spatial heterogeneity in harvest imposed by reserves can lead to spatial heterogeneity in community structure, such that the overall community-level response depends on exchange between protected and harvested areas. Below we detail how harvest selectivity and connectivity between protected and harvested areas interact to determine the overall community-level consequences in terms of structure across space and response to temporal heterogeneity.

In addition to larger populations of harvested species in reserves, populations of nontarget prey and competitors might be larger in harvested areas if fishing selectivity drives cascading effects in a marine community, such that the direction of spillover depends on harvested status and species interactions. Empirical studies suggest that spillover from reserves can alter community structure at adjacent sites, such as cascading effects leading to algal increases in temperate systems (Guidetti 2007) and slight coral increases in tropical systems (Russ & Alcala 2011; see also the sidebar, Long-Term Field Study: A Tropical Example). Theory indicates the potential for spill-in from harvested areas by nontarget species that experience competitive release; this dispersal into reserves can decrease the expected abundance of the harvested species compared with their

expected abundance when considering reserves in isolation (Baskett et al. 2007a). Note that changes in movement behavior in response to density changes (see **Table 1**) can further affect the amount of exchange between protected and harvested areas for different interacting species and therefore the overall community-level response [modeled by Takashina et al. (2012)].

Community stability:
the tendency for a community to have the same structure and composition over time

Ecological resilience:
likelihood of remaining in a particular state as opposed to shifting to a different state following a disturbance

One potential consequence of spatial heterogeneity in diversity and community structure across reserves and harvested areas is altered community stability under temporal environmental variability. Community stability has many overlapping definitions, components, and metrics that describe the tendency for a community to remain in or return to a particular state (reviewed in Ives & Carpenter 2007), including a decreased amount of change following disturbance (resistance), an increased rate of return to a given state (recovery rate), a decreased amount of variability in a state over time (temporal variability), a decreased likelihood of new species invasions (invasiveness), and an increased likelihood of remaining in a particular state if alternative stable states are part of the system structure (ecological resilience). Empirical investigations across ecological systems, including marine systems (Worm et al. 2006), generally support increased stability with diversity, which is typically measured as decreased temporal variability or invasiveness (Ives & Carpenter 2007). In addition to diversity, stability depends on redundancy, modularity, and the strength of feedback loops, and these four drivers of stability can trade off with each other (Levin & Lubchenco 2008). Reserves influence all of these factors through their effects on community composition and the connectivity between protected and harvested areas in a reserve network. The interactive effect of these factors therefore drives the overall effect of reserves on community-level stability in response to both natural and anthropogenic disturbances.

The primary observed effect of marine reserves on stability is decreased variability in fish biomass; increased resistance to or recovery from disturbance has been observed in some cases but not consistently (Worm et al. 2006; **Table 2**). One possible reason for this variation in response across diversity metrics is that reduced population variability in harvested species can be a direct population response to reserves (Section 2.3), whereas any increased resistance to and recovery from disturbance might be a secondary effect arising from interactive multispecies responses. For example, in addition to the potential for increased diversity to buffer trophic cascades (Polis et al. 2000), increased predator abundance in reserves might lead to increased top-down control and therefore weaker bottom-up effects (e.g., environmental disturbance-driven effects). However, any such secondary effects depend on food web structure and the degree of environmental variability (**Table 1**). In general, observations support this potential for increased stability in community composition and structure in reserves (see **Table 2**, in which the decreased variability in diversity and decrease in nuisance species outbreaks are hypothesized to be due to increased predator abundances). Beyond temporal variability in community structure, coral reefs exemplify the expectation for reserve-driven cascades to increase resistance to and recovery from disturbance—specifically, increases in herbivore abundance and diversity in reserves, and therefore decreased macroalgae competition with corals, are expected to buffer coral response to disturbance (Bellwood et al. 2004). However, observations of reserve effects on disturbance response in coral reefs vary: Increases in resistance (e.g., Olds et al. 2014) and recovery rates (e.g., Mumby & Harborne 2010) occur in some cases, but meta-analyses indicate no average effect of reserves on resistance (Selig et al. 2012) and slower rates of recovery on average in reserves compared with harvested areas (Graham et al. 2011). In addition to dependence on complex, diffuse interactions, potential reasons for mixed resistance and recovery responses include dependence of recovery effects on reserve age (Selig & Bruno 2010), greater representation of stress-susceptible corals in more diverse systems (Graham et al. 2011), and coupled responses across protected and harvested areas (as described for ecological resilience below).

Reduced invasiveness also represents a potential secondary effect of reserves on community stability through protection of native competitors and predators (reviewed in Burfeind et al. 2013). However, reserves might protect invasive species as well when targeted or susceptible to bycatch, harvested areas might provide source populations for nontarget invasive species that interact negatively with harvested native species [modeled by Kellner & Hastings (2009)], and increased tourism in reserves might enhance introductions of invasive species (Burfeind et al. 2013). Although the balance of these factors that promote or impede invasiveness varies across locations, such that invasive species increase in some cases and decrease in others (Burfeind et al. 2013), reserves typically have no effect on the presence of invasive species (Burfeind et al. 2013, Guidetti et al. 2014).

Reserve effects on ecological resilience are relevant only if alternative stable states (i.e., multiple initial-condition-dependent outcomes for a given set of environmental conditions) are part of the community structure, which is often debated and difficult to demonstrate empirically (Petraitis & Dudgeon 2004). The mechanisms that can, theoretically, lead to alternative stable states range from size-dependent or stage-dependent predator–prey interactions in temperate systems (e.g., Baskett et al. 2006; see Section 3.1) to macroalgal inhibition of coral recruitment and dilution of grazing in tropical reefs (e.g., Mumby et al. 2007). Therefore, in temperate reefs, observed increases in predator size and biomass in reserves might increase the resilience of kelp forests to shifts to urchin barrens (e.g., Ling et al. 2009), and in tropical reefs, observed increases in herbivores in reserves might increase the resilience of coral-dominated states to shifts to macroalgal-dominated states (e.g., Olds et al. 2014). However, direct empirical tests remain elusive. Theory indicates that increased predator biomass in reserves can increase resilience in a system with stage-dependent predator–prey interactions (i.e., prey suppression of the harvested predator's juveniles), in which connectivity between protected and harvested areas leads to increased resilience in harvested areas as well (Barnett & Baskett 2015). Therefore, a before-after comparison, if possible, is more likely to provide direct empirical insight into the effect of reserves on resilience than an inside-outside comparison. The potential for coupled reserve–harvested area responses for both resilience and invasiveness highlights a need for greater development of theoretical expectations of how harvest selectivity and connectivity between protected and harvested areas will interact to affect multiple aspects of community stability.

4. EVOLUTIONARY CONSEQUENCES OF MARINE RESERVES

Analogous to species diversity within communities, a potential consequence of reserves is increased genetic diversity in harvested populations. Loss of genetic diversity has occurred following intensive harvesting, including harvesting by marine fisheries, because of genetic bottlenecks due to population size declines (Allendorf et al. 2008, Pinsky & Palumbi 2014). Greater genetic diversity has been observed in reserves compared with harvested areas for a metric that did not naturally exhibit spatial structure in genetic variation (Pérez-Ruzafa et al. 2006). For organisms with spatial genetic structure on the scale of reserve size, theory indicates that the heterogeneity in population size imposed by reserves can alter patterns of genetic connectivity and allele distributions in space and, therefore, genetic diversity on the metapopulation level (Munroe et al. 2014). In addition to spatial patterns of genetic diversity, fisheries and marine reserves have the potential to alter the genetics and evolution of marine populations through changes in the selective pressures acting on heritable traits. Specifically, as detailed in this section, harvest selectivity can alter selection on body size–related traits, and protection selectivity can alter selection on movement.

4.1. Harvest Selectivity

Both elevated mortality and size selectivity from intensive fishing can select for earlier maturity, smaller size at maturity, smaller body size overall, and slower growth, which increase fitness by decreasing the likelihood of harvest mortality and increasing the reproductive output before harvest mortality occurs (Hutchings & Fraser 2008). Such fisheries-induced evolution can reduce the rate of recovery subsequent to fishery closure or reserve establishment (Walsh et al. 2005), depending on life history trade-offs and density-dependent interactions [causing theoretical predictions for the effect of observed life history changes on recovery rate to range from negligible (Kuparinen & Hutchings 2012) to substantial (Hutchings 2005)]. The effect on recovery rate further depends on the possibility and rate of reversal in evolution in reserves. In the case of full fisheries closures (i.e., no fishing in the entire population range), theory indicates that reversal of fisheries-induced evolution can occur on very long timescales (Enberg et al. 2009) and depends on the seasonality of reproduction and the existence of a life history trade-off between growth and reproduction (de Roos et al. 2006). Experiments support the possibility of reversal of fisheries-induced evolution on multigenerational timescales (Conover et al. 2009).

For reserves, theory indicates that protection against fisheries-induced evolution further depends on the amount of exchange between protected and harvested areas. For populations with sessile adults and dispersive larvae, if short-distance dispersal occurs, reserves can protect against fisheries-induced evolution within reserves boundaries with little effect on fisheries-induced evolution outside reserves (Baskett et al. 2005). However, if long-distance dispersal occurs, the greater exchange between protected and harvested areas leads to an averaging of selection across locations, such that less protection against fisheries-induced evolution occurs within reserves but some protection carries over to harvested areas (Baskett et al. 2005). Similarly, increasing adult movement reduces the potential for protection against fisheries-based selection within reserves (Miethe et al. 2010, 2011). For the case with a high level of larval exchange between protected and harvested areas, strong density-dependent recruitment can decrease the capacity for reserves to protect against fisheries-based selection by decreasing the relative contribution of the protected population to the total larval pool (Trexler & Travis 2000). If migration between feeding and spawning grounds occurs, reserves in feeding grounds are more likely to protect against fisheries-induced evolution than reserves in spawning grounds because they protect the full life cycle, including immature stages (Dunlop et al. 2009, Miethe et al. 2011). Empirically, increased body size in response to reserve establishment (Section 2.1) indicates the potential for reserves to protect against the size-selective pressures that drive fisheries-induced evolution (Fidler et al. 2014, Stoner et al. 2012). However, a direct empirical test of whether protection against fisheries-induced evolution occurs would need to disentangle the genetic and plastic (e.g., density- or environment-dependent) contributions to any changes in life history traits, such as through the use of tagged individuals or genetic markers (Kuparinen & Merilä 2007).

4.2. Protection Selectivity

If increased within-reserve retention with decreased dispersal distance (Section 3.2) results in greater protection of shorter-distance dispersing individuals in a population (and if variation in dispersal among individuals has a heritable basis), reserves might select for reduced dispersal. The theory of the evolution of dispersal indicates that, whereas heterogeneity in both space and time increases selection for dispersal as a bet-hedging strategy, heterogeneity in space that is static in time (e.g., heterogeneity in harvest mortality given marine reserves) decreases selection

for dispersal because dispersal increases the likelihood of moving from favorable to unfavorable habitats on average (Johnson & Gaines 1990). Accordingly, marine reserves can shift selection toward reduced dispersal if natural selection for dispersal occurs as a by-product of selection for a planktonic larval stage with increased feeding opportunities or reduced predation risk (hypothesized to be the case for many coastal marine organisms; see Strathmann et al. 2002) and if mortality outside reserves is high [modeled by Baskett et al. (2007b)]. However, if natural selection for dispersal arises from spatiotemporal heterogeneity, reserves can increase selection for dispersal, or for variability in dispersal, by increasing the degree of heterogeneity (depending on the cost of dispersal) (Baskett et al. 2007b).

Analogously, for postsettlement movement, theory indicates that marine reserves can select for increased site fidelity (i.e., decreased likelihood of an individual moving between protected and harvested patches) (Miethe et al. 2011). For species with spawning or feeding migrations outside reserves, the strength of selection for increased site fidelity decreases with the amount of the life cycle protected by reserves (Miethe et al. 2011). Providing circumstantial empirical support for this theory, increased site fidelity in Atlantic cod (*Gadus morhua*) can explain the observed increases in density and body size in reserves compared with harvested areas despite expectations for a high degree of connectivity across locations (Moland et al. 2013). More directly, some tagging studies have shown decreased movement in reserves (e.g., see the sidebar, Long-Term Field Study: A Temperate Example). However, plastic (e.g., density-dependent or size-dependent movement) as well as genetic responses can explain decreased movement, and other studies have observed increased movement (Section 2.3; **Table 1**). Therefore, incorporation of the array of potential plastic responses of movement rates to reserves into evolutionary models, as well as empirical evaluation of the genetic component of movement across protected and harvested areas, is necessary to further elucidate the capacity for reserves to select for reduced movement.

4.3. Response to Heterogeneity in Space and Time

If both protection against fisheries-induced evolution and evolutionary changes in movement were to occur in response to reserve establishment, they would inevitably interact to affect overall population dynamics across a network of reserves and harvested areas. Any reserve-based selection for reduced movement would reduce exchange between protected and harvested areas (Baskett et al. 2007b, Miethe et al. 2011, Parsons et al. 2010), which would increase protection against fisheries-induced evolution within reserve boundaries and lead to less carryover of that protection to harvested areas (and lead to greater genetic heterogeneity in space). Conversely, fisheries-induced evolution might alter movement patterns and therefore expectations for evolutionary responses in movement in reserves. For example, if migration depends on energetic state and increases with increased body size, fisheries-based selection on body size can, theoretically, lead to reduced movement (Jørgensen et al. 2008). Furthermore, fisheries-induced evolution can affect behavioral traits such as boldness (Biro & Post 2008); thus, reserve protection can lead to greater boldness within reserves compared with harvested areas (empirically observed in Farthing 2014, potentially either a genetic response to selection or a plastic response to differences in density and therefore competition). In both cases, any reserve protection against fisheries-induced evolution would result in greater movement in reserves compared with harvested areas, contrary to the expectation of selection for reduced movement in reserves described in Section 4.2. Therefore, a comprehensive understanding of the evolutionary consequences of marine reserves requires consideration of the combined effect of both fisheries and the spatial heterogeneity imposed by reserves on the coevolution of body size–related traits and movement traits. Given the complexity

of possible outcomes, model system experiments, which have proven successful in determining the genetic component of life history responses to harvest (e.g., Conover et al. 2009), might help to test theoretical expectations for fisheries-induced evolution in coupled reserve–harvested populations.

The evolutionary consequences of marine reserves might enhance the above-described potential for reserves to buffer populations against environmental variability and change (Section 2.3). Specifically, if reserves protect against fisheries-induced evolution on life history traits, increases in body size and reproductive output beyond those expected from the filling in of age and size structure could further contribute to increased recovery rates, reduced temporal variability in population size, and increased buffering of size-dependent Allee effects in stochastic environments. Furthermore, increased genetic diversity typically leads to increased fitness because of reduced inbreeding and increased adaptive capacity to environmental change (Lande 1988), and subpopulation structure in diversity can increase metapopulation robustness to environmental variability (Hilborn et al. 2003).

5. CONCLUSIONS

Overall, the variation in harvest and reserve protection within and across species influences the consequences of reserves at each ecological level (**Supplemental Figure 1**). The combined effect on all levels includes the potential for buffered response to temporal environmental heterogeneity, which has preliminary theoretical and empirical evidence but remains speculative in many cases (Sections 2.3, 3.3, and 4.3). Although we separately described the consequences of marine reserves at the population, community, and evolutionary levels in marine systems to provide structure for our review, these responses inevitably interact (**Figure 1**). For example, any protection against fisheries-induced evolution of smaller body sizes as an evolutionary consequence (Section 4.1) increases the amount of size-structure filling in that occurs at the population level (Section 2.1) and therefore increases any size-dependent and biomass-dependent responses, such as size-dependent cascading effects on nontarget species in the community (Section 3.1).

Although we have left the complex topic of reserve network design and monitoring to other reviews (Gaines et al. 2010b, Gerber et al. 2003, White et al. 2011), the ecological and evolutionary consequences reviewed here naturally connect to management decisions. For example, the dependence of population response on movement rates for harvested species (Section 2.2) informs the reserve network size necessary for effective protection of a focal harvested population, whereas the optimal network configuration depends on the conservation and fisheries goals of a given reserve network (reviewed in Gaines et al. 2010b). In addition, the relative strength of evidence for the different reserve consequences reviewed here can inform the degree of certainty for different reserve goals, such as the potential for reserves to serve as a management tool to protect the capacity for populations and communities to respond to climate change (Bernhardt & Leslie 2013) as reflected in the effect of reserves on population and community stability (Sections 2.3, 3.3, and 4.3). Finally, the direction and timescale of responses to reserves described here can inform expectations for monitoring, including the potential for short-term declines arising from natural population fluctuations (Section 2.1) and long-term declines in some species because of increases in their predators or competitors (Section 3.1). Overall, the complex interaction of the population, community, and evolutionary consequences of marine reserves reinforces the need for careful consideration of metrics and comparison of theoretical expectations with observations in order to determine the ability of reserves to achieve biodiversity and/or fisheries goals (White et al. 2011).
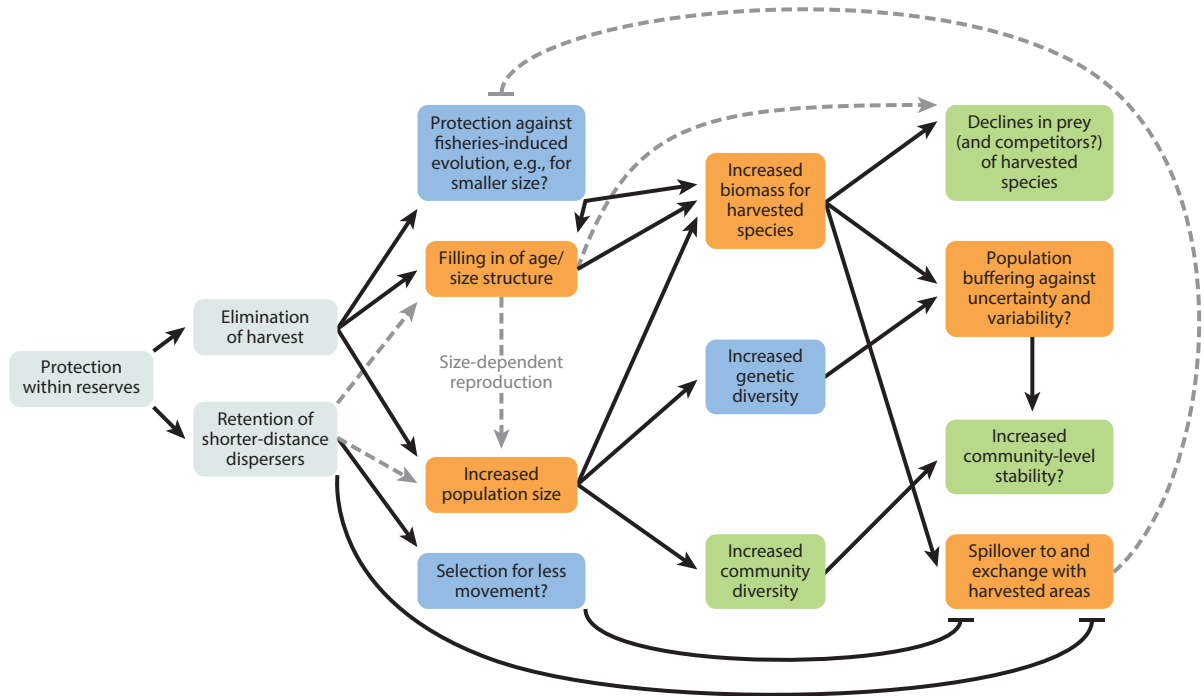
Figure 1

Flow diagram of the interaction between population (*orange*), community (*green*), and evolutionary (*blue*) consequences of marine reserves. Black solid lines indicate direct connections, and gray dashed lines indicate modulating influences (i.e., influences on the amount of the indicated change that occurs); arrows indicate drivers, and flatheads indicate interference or disruption of a given consequence. Questions marks indicate hypothesized, but not conclusively verified, consequences.

DISCLOSURE STATEMENT

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