Evolving science of marine reserves: New developments and emerging research frontiers

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The field of marine reserve science has matured greatly over the last decade, moving beyond studies of single reserves and beyond perspectives from single disciplines. This Special Feature exemplifies recent advances in marine reserve research, showing insights gained from synthetic studies of reserve networks, long-term changes within reserves, integration of social and ecological science research, and balance between reserve design for conservation as well as fishery and other commercial objectives. This rich body of research helps to inform conservation planning for marine ecosystems but also poses new challenges for further study, including how to best design integrated fisheries management and conservation systems, how to effectively evaluate the performance of entire reserve networks, and how to examine the complex coupling between ecological and socioeconomic responses to reserve networks.

conservation | ecosystem-based management | fisheries | marine protected areas | marine resource management

The ocean provides countless benefits, or ecosystem services, to people living both in coastal and landlocked areas (1). As ocean uses expand with emerging activities (e.g., wave energy farms) and growing human populations, oceans are burdened by an ever-increasing list of impacts—from overfishing to habitat degradation to climatic change (2). Attempts are underway to reform ocean management to better account for and balance the multitude of human uses and to more effectively address the cumulative impacts affecting the overall health of ecosystems. To this end, ecosystem-based management (EBM) and marine spatial planning (MSP) are gaining considerable traction around the world (3, 4). A key management tool for both EBM and MSP is no-take marine reserves, in which all harvesting and destructive activities are prohibited. There are a growing number of no-take marine reserves globally, although most are quite small. In aggregate, marine reserves constitute just 0.08% of the world's oceans (5). Nonetheless, there has been considerable scientific study focused on understanding the outcomes of reserve protection, with particular attention to the ecological effects that occur within reserve boundaries.

Marine reserves can be established to achieve goals of conservation (e.g., mitigating impacts to ecosystems) and/or fisheries management (e.g., sustaining fish harvests), while also providing scientists with a better sense of the community composition, dynamics, and functioning of intact marine systems. Studies indicate that closed areas typically lead to conservation benefits, notably increases in the abundance and size of the fish, invertebrates, and seaweeds living within their borders (6, 7). However, this may not always be true, depending on fisherman behavior in response to reserves, fishing regulations outside the reserve, and the regulations affecting other activities within and outside of closed areas. The effects of marine reserves on adjacent fisheries are far less clear than the potential conservation benefits, although some of the research in this Special Feature addresses this issue. The causes of variation in responses among species and trophic levels are also becoming increasingly well-understood (6, 8–10).

More recent research on marine reserves extends beyond a focus on single reserves and beyond considerations of solely ecological changes to consider perspectives from the social sciences. These research directions include examining the consequences of reserves for local communities, adapting reserve and reserve network design to consider socio-economic factors and impacts, and determining the effects of reserves on fishing yields and profits in unprotected waters (11, 12). This large body of research has set the stage for an evolving field of marine reserve science—one which addresses increasingly complex, multidisciplinary questions about the design and consequences of marine reserves and reserve networks—and provides a growing foundation to inform marine management efforts.

In this paper, we introduce the Special Feature, highlighting how this collection of contributions (*i*) exemplifies results and improved understanding that are emerging from recent marine reserve research, (*ii*) reveals innovative ways to apply this collective knowledge to reserve design and evaluation, and (*iii*) explores how to incorporate this wealth of information into continuing scientific research, management, and policy given our changing world. We then offer our perspective on some of the most exciting next research directions, suggesting that there is great potential for advances in (*i*) understanding complex ecological processes and dynamics inside reserves, (*ii*) evaluating the consequences of networks of reserves, (*iii*) incorporating reserves into an adaptive management framework, (*iv*) integrating the design of reserve networks with property rights-based fisheries management, (*v*) scaling the size of marine reserves to better achieve global conservation and fisheries goals, and (*vi*) cross-pollinating marine reserve science with fisheries science and accounting for fisherman behavior. The field of marine reserve science has made significant strides forward in recent years, but we assert that there is still much more to learn.

Developments in Marine Reserve Science

We begin the Special Feature with several pieces that illustrate the rigorous and interdisciplinary research that has emerged from the diverse community of scientists studying marine reserves. Babcock et al. (13) review time series data from decades-old marine reserves around the globe to reveal a synthetic picture about the time scales and variability in ecological responses to reserve protection. Their analyses show that direct ecological effects accumulate more quickly than indirect effects and suggest that targeted species may be more resilient inside reserves relative to fished areas. Second, Pollnac et al. (14) synthesize social and ecological data from multiple studies from the Philippines, Western Indian Ocean, and Caribbean to determine both social and

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ecological drivers of positive reserve effects. The authors (14) find that human population density and compliance with reserve regulations are the strongest predictors of fish biomass in reserves, but the nature of these social effects is regionally specific. Furthermore, they illustrate how compliance itself is complexly related to a number of other technological, social, and institutional variables. The strong integration of social and ecological data in this study provides a much richer understanding of reserve effects and mediating factors than were previously revealed from single-discipline approaches. Next, Pelc et al. (15) develop a spatially explicit model to quantify the magnitude, scale, and spatial and temporal signal of larval export (the movement of young beyond reserve borders), a critical process if reserves are to function as networks and benefit outside areas. Their modeling results suggest that given typical increases in production inside reserves, larval export can compensate for displaced fishing effort outside of reserves, although this effect will often be difficult to detect empirically because of the dilution of long-distance dispersers and the high recruitment variability in most systems. This piece suggests that future studies of larval export will be greatly advanced by applying a suite of methods and data from fields such as oceanography, larval biology, chemistry, and mathematical modeling.

The last two pieces present results from two networks of marine reserves in the United States and Australia. Although initial scientific studies of marine reserves focused on documenting the effects of single reserves, one potential way to scale up the benefits from small reserves, without excluding human uses over large areas, is to create networks of multiple marine reserves and other types of marine protected areas (MPAs). The Great Barrier Reef Marine Park in Australia and the Channel Islands National Marine Sanctuary in California offer two prominent examples of such networks of marine reserves where there are now adequate data to examine network effects. Hamilton et al. (16) document significant increases in the density and biomass of targeted fish populations inside the Channel Islands reserve network after 5 y of protection, a finding that only emerged when the authors took into account the major environmental and biogeographic gradient across the islands. McCook et al. (17) synthesize a vast amount of data and monitoring studies from the Great Barrier Reef, which show rapid effects of reserve protection for targeted fish and sharks, improvements to ecosystem health and resilience, and net economic benefits resulting from tourism revenues. These two studies provide an important starting point for our growing understanding of reserve networks and how to measure and assess whether a collection of reserves is truly functioning as a network along both ecological and socioeconomic dimensions.

Innovations in Reserve Network Design and Evaluation. The next three pieces in the Special Feature use the wealth of knowledge highlighted in the first section to inform innovative approaches to reserve design and evaluation. Gaines et al. (18) synthesize existing conservation and bioeconomic approaches to reserve design and provide design guidelines for reserve networks (size, spacing, location, and configuration) that reduce or eliminate the commonly presumed tradeoff between conservation and fisheries goals. Although tradeoffs are unavoidable for certain species and settings, their synthesis suggests that networks may frequently be beneficial, even if fishery prosperity is the primary goal. Similarly, Costello et al. (19) highlight the potential for well-designed reserve networks to simultaneously benefit biological conservation and fishery returns. Their study provides a modeling framework for assessing the value of information in spatial fisheries management, showing how improved spatial data on key features such as patterns of larval movement can improve reserve network design. They find that the use of improved scientific information during the marine reserve design process tends to lead to larger reserve areas, better conservation outcomes, and higher fishery profits. Finally, the study by Smith et al. (20) shows the importance of accounting for fisherman behavior with a modeling analysis that examines short-term and long-term opportunity costs of marine reserves to better understand stakeholder opposition to or support for marine reserves.

Applying Marine Reserve Science in a Changing World. The contributions highlighted thus far suggest that we have made important steps towards better understanding the effects of reserve protection, the social and ecological drivers of reserve failures and successes, the dynamics and functioning of marine ecosystems protected by marine reserves, and the application of this information for more effective reserve design. However, to achieve long-term protection and sustainability of marine ecosystem services, we must apply this knowledge to the pressing management and policy needs of a changing world. The final pieces in this feature suggest a path forward in which we respond dynamically to the changing social, cultural, and management seascapes.

Grorud-Colvert et al. (21) provide a perspective on how to communicate our scientific understanding of marine reserves given dramatic changes in how people acquire and perceive information and a need to reach diverse and changing audiences. The authors (21) argue that, through an understanding of the target audience, well-crafted main messages, audience- and topic-specific communication tactics, and an iterative evaluation of the impact of communication efforts, science can effectively inform management decision-making processes. Halpern et al. (22) examine how marine reserves can be integrated into EBM, a broader approach to sustaining ecosystems services. The authors (22) evaluate the extent to which fishing contributes to declining ocean health in marine ecosystems around the world, indicating where and when marine reserves can play a major role in improving ocean health and thus, in achieving EBM goals. This paper (22) provides an important framework for expanding the global array of reserves to better address the existing and predicted distribution of threats to marine ecosystems. Finally, Arrieta et al. (23) take a unique perspective on marine reserves by addressing the implications of preserving genetic diversity for commercial interests. Prospecting for biological resources has provided enormous social and commercial benefits, and the oceans harbor a rich pool of unexplored biological diversity. This paper posits that the preservation of such genetic resources suggests another need for marine reserves and poses the unanswered question of whether current network design approaches are adequate to meet this added challenge.

Emerging Research Frontiers

Reflecting on the current status of our scientific knowledge of marine reserves, including some of the most recent advances featured in this issue, we now turn to the future of marine reserve research. We focus on six promising research avenues below. Although this is not a comprehensive list, it reviews some of the leading horizons for marine reserve research, where scientific advances have the greatest potential to inform local and global management and conservation.

Ecological Processes and Dynamics. A vast body of ecological research has verified that marine reserves of varying sizes and across a wide range of locations can have a positive effect on species density, size, biomass, and diversity (6, 7). Initial positive effects often appear within 5 y, although older reserves typically show even greater positive responses (7, 13, 24). However, despite the large body of work focused on ecological effects within marine reserves, there still are open questions about some of the key ecological processes and dynamics. For example, given impending global change and the restoration potential of marine reserves, are ecosystems within reserves more resilient? Resilience can be crucial for determining whether or not reserves will provide population and community-level buffers in the face of disturbances, both large scale (e.g., climate change) and local (e.g., coral bleaching events). So far, empirical evidence both supports the concept of greater resilience in marine reserves (13, 25, 26) and refutes it (27), illustrating the need to approach this question more systematically in diverse situations and in the face of diverse ecosystem threats.

Marine reserve science and implementation increasingly focuses on networks of reserves rather than individual reserves. One of the key arguments for networks is their potential to reduce or eliminate the costs to fisheries if reserves are sited in ways that protect key sources of larvae (13). However, we know very little about marine reserves as sources and sinks of larvae, even after over a decade of attempts to quantify the origins of larval supply (15). More and more, coupled biophysical models are providing the opportunity to predict where sources and sinks may be located within a region (19, 28, 29), allowing for the targeted sampling of a discrete number of sites to ground-truth these predictions. Even in situations where larval source locations are well-understood, there remains the additional question of whether larvae from different sources have differential postsettlement survival at a given site.

Finally, whereas relatively sedentary species repeatedly show positive responses to reserve protection, the utility of marine reserves for highly mobile species, which may spend the majority of their time outside reserves, is often deemed negligible (30), although notable exceptions exist (17). Reserve protection of spawning grounds and other critical habitat could be beneficial, but it remains to be seen whether or not reserve protection of these key areas has demonstrable benefits to highly mobile stocks that are targeted by fisheries. Closing areas such as spawning grounds will likely increase fishing costs by removing opportunities to selectively harvest when fish are densely aggregated, suggesting the need for more research about the cost-benefit tradeoffs of managing these areas. For example, data may show that fishing costs could be reduced if harvest levels at spawning grounds are set sustainably and effectively enforced. Conversely, documentation of fishing adjacent to reserves and adult spillover indicate that marine reserves may provide inherent benefits for mobile species, also helping to sustain local fisheries (31) and resulting in greater profits for fishermen who concentrate their effort adjacent to the MPA (32). However, these results may be highly sensitive to the degree of overharvest before reserve implementation. Overall, protecting highly mobile species through marine reserves may require innovative research to design plans that combine strategically placed reserves with other management approaches in fished waters.

Network Evaluation. There have been increasing international commitments to implement MPA networks (5, 33), many of which include the stipulation to include highly protected (no-take) areas as an integral part of these networks. Networks offer the theoretical promise of achieving goals that single small protected areas cannot accomplish, such as protecting a broader variety of habitat types and facilitating connectivity among sites to sustain threatened populations. Processes to plan and implement networks of marine reserves have taken place in areas such as California (34, 35), the Great Barrier Reef, Australia (36, 37), and the Central Visayas Region in the Philippines (38, 39), the first two of which are the subject of contributions in this Special Feature. Additional networks are being implemented, planned, or discussed throughout the world. Although existing networks are still relatively new, early evidence has shown that fished species can exhibit relatively rapid increases in density and biomass inside reserve networks compared with fished areas outside (16, 17). However, we have a poor understanding of the additive and/or synergistic effects of reserves in these or other networks. Innovative monitoring and data analysis strategies are required to understand complex network effects. How do we determine if a network is truly operating as such, and will a reserve network function as more than the sum of its parts?

Although studies have documented key ecological (and to a lesser extent, socioeconomic) responses on a reserve-by-reserve basis, the protocols for analyzing responses for multiple, interacting reserves remain poorly explored. This partly reflects the obvious constraint that obtaining data from reserve networks requires that reserve networks actually exist. As noted above, this constraint has only recently diminished because of the establishment of a few large networks, from which empirical data are now emerging. The absence of empirical data, however, is not the only constraint. We lack clear conceptual frameworks for testing whether network effects actually occur. Reserve networks are not likely to be implemented in a configuration that allows for the effective testing of network benefits using a traditionally balanced statistical approach. Rather, we will have to tease the analysis of network benefits from designs that reflect scientific guidance modified by diverse public policy processes. For example, in the context of a theoretical model, one could test network effects by first implementing each reserve individually in simulations and examining ecological responses of species and socioeconomic effects on fisheries. Then, after implementing the entire network of reserves simultaneously, the ecological and socioeconomic effects of the network could be compared with the changes that occurred when each reserve was implemented singularly. Of course, this experiment cannot be done in practice, but advances in spatially explicit simulation models are allowing for increasingly reliable predictions of reserve effects (19). Such model experiments are likely to be a key tool for predicting population, ecosystem, and fisheries responses across a marine reserve network. Because implemented networks will undoubtedly include a diverse array of reserve sizes and configurations, such model experiments can forecast where larger responses driven by network benefits are most likely to occur. A coupling of bioeconomic models to strategic field monitoring provides a framework for predicting near- and long-term regional responses within reserve networks, informing cost-effective data collection, and evaluating overall network performance.

Adaptive Management. Inherently linked to the concept of evaluating reserves and reserve networks is the goal to adaptively manage these areas. Although many reserve management plans include a clause to evaluate whether reserves are meeting their intended goals and if not, to modify the design accordingly, we often lack a clear framework for determining what data and analyses are required to make these challenging decisions. In the Great Barrier Reef Marine Park, a review of the total area and habitat types that were protected in marine reserves illustrated that the network was likely inadequate to protect the full range of marine biodiversity found in the park (36). In one of the few global examples of adaptively managing marine reserves, the zoning of the park was subsequently modified to increase the total area protected in marine reserves from 4.5% to 33%, which encompassed a minimum of 20% of all identified bioregions in the park (17). Using only habitat representation analyses illustrated some of the inadequacies of management in the Marine Park, but more in-depth ecological and socioeconomic data are crucial for answering further questions about the adequacy of reserve size, maintenance of key ecological processes, protection of target species, costs and benefits to local communities, and enforcement success. What is the minimum information needed to adaptively manage these areas? A framework for implementing adaptive management is necessary to ensure that we are moving towards optimal networks (e.g., ones that collectively maximize a range of objectives including resource conservation and viable fisheries outside the reserves.) This may require increasing the number or size of protected areas, changing the spatial configuration of reserves, or strategically removing some reserves from a network.

Property Rights. Marine reserves cannot be expected to address all of the threats and human uses faced by ocean ecosystems (22) nor can reserves solve inherent economic inefficiencies associated with failed fisheries management. Even in areas where fishing is the predominant human impact and thus, reserves can serve a central role in achieving ocean health, reserves are likely to be most successful if they are integrated with an EBM approach that also promotes effective management strategies outside reserve borders (22). Fisheries management in the United States and around the world is increasingly looking to incentive-based approaches to ensure efficient, economically viable, and ecologically sustainable fisheries (40–43). Property rights-based fisheries management, or catch shares, can come in numerous forms, including individual transferable quotas (ITQs), fishing cooperatives, community quota systems, and territorial user rights fisheries (TURFs), where shares of a total allowable catch are allocated to fishermen, vessels, or communities or exclusive spatial access to resources is conferred to individuals or communities. As catch share programs become more commonplace, it will be critical that we better understand the interaction of marine reserves and property rights-based fisheries management. In particular, the marriage of these two management approaches has the potential to result in important synergies.

Despite theoretical and empirical evidence that catch shares can support more profitable and sustainable fisheries than traditional management approaches, property rights approaches are not without their challenges. Externalities, or economic side effects, often exist and can erode the security or exclusivity of property rights and thus, reduce their benefits. Although these take many forms, common examples include target species moving beyond a TURF or international boundary, the existence of an unregulated recreational sector, or unintentional harvest of juveniles or destruction of habitat that reduces the productivity of the stock. In the presence of such externalities, property rights approaches may suffer some of the same ecological and economic challenges as traditionally managed fisheries. Marine reserves may offer an opportunity to solve some of these externality problems. For example, by pairing TURFs with marine reserves, adult spillover and larval export from a protected area can benefit nearby TURF owners. The reserve compensates for overharvest by individual TURF owners; if a combined TURF–reserve system is designed properly, the collection of TURFs will realize optimal yields (44), and TURF owners may actually advocate for adjacent reserves. Capitalizing on these types of synergies and simultaneously promoting profitable fisheries and sustainable fish populations will require new research to investigate (*i*) when marine reserves can improve or eliminate the externality problems faced by property rights-based fisheries management and (*ii*) how to best design these integrated management systems. However, although the integration of catch share systems and reserves may be economically and environmentally more effective, we must also account for the social and psychological effects of displaced or reduced fishing effort (45, 46).

Large-Scale Marine Reserves. Marine reserves have historically been implemented as relatively small areas in coastal waters that are not effectively connected at a global scale. By themselves, small reserves cannot protect some of the world's most threatened fishery species (e.g., bluefin tuna) or ecosystems (e.g., coral reefs and the Arctic). Recent efforts to establish orders-of-magnitude larger individual reserves (e.g., Northwest Hawaiian Islands national monument) or large-scale reserve networks (e.g., Great Barrier Reef Marine Park), in addition to a recent synthesis of the science in support of pelagic MPAs (47), suggest that there is potential to reenvision the spatial scale and geographic extent over which marine reserves and other types of MPAs are implemented. Other than a few cases, the implementation of large marine reserves spanning 100 km or more has not been well-explored in practice or theory, particularly in international waters (the high seas) or across international boundaries. There has been some analysis of the legal implications of high-seas MPAs (48), but there is a need for ecological and economic modeling to explore the potential role of large-scale MPAs in protecting highly mobile species, limiting access to protect stocks and ecosystems in previously unchecked international waters, resolving territorial conflicts, and promoting more sustainable harvests of transboundary stocks. By providing the scientific underpinnings for the design of a large-scale connected network of marine reserves and other MPAs that expands beyond near-shore waters, we may be able to deliver a strategy for more effective global conservation, improved protection against climate change, and appropriate incentives for sustainable harvest of fisheries spanning international borders.

Integrating Marine Reserve and Fishery Science. The implementation of marine reserves and other types of MPAs is advancing in many regions around the world but is often focused solely on conservation goals and is decoupled from fisheries management. The result is that spatial management of the ocean often takes the form of conservation measures overlaid on previously nonspatial fisheries management regimes. These processes are often sequential rather than integrated; for example, MPAs are implemented without an explicit consideration of fisheries management outside the closures and the resulting influence on MPA performance. How fisheries management strategies should change in response to spatial closures and conversely, how marine reserve planning should better incorporate information about fisheries management in the surrounding waters are critical questions that warrant new thinking and research.

Textbook treatments of fisheries science, which focus on stock assessment in a nonspatial world, will require extensions and innovations to effectively inform the integration of marine reserve science and fisheries science. We need new models to inform the simultaneous (not sequential) redesign of fisheries management as networks of MPAs are implemented. Bioeconomic models can be used to optimize fishery management adjacent to closed areas, promoting both high fishery profits and sustainable fish stocks and enabling fishery closures with maximal positive impacts for minimal economic costs.

Similarly, marine reserve design needs to take into account fisheries management and the behavior of fishermen outside (and inside) reserve boundaries. For example, predictions from bioeconomic modeling for the Marine Life Protection Act process in California suggest that reserve network performance depends dramatically on assumptions about the management of fishing effort outside the protected areas (19). Just as the behavior of fishermen outside reserves is important to reserve design, so is the compliance of fishermen with MPA restrictions. Compliance data from the Great Barrier Reef Marine Park combined with ecological monitoring show a large difference between fish biomass in no-take vs. no-entry zones, indicating that poaching is likely occurring in no-take zones, and the behavior of fishermen is critical to reserve effectiveness (17). In general, fishermen as a stakeholder group remain largely uncharacterized in terms of behavior and cultural values across ecosystems and regions, which is primarily because of the lack of a standardized approach to data collection across anthropological studies in both developed and developing countries. Methods that are nontransferable, even across studies within the same region, severely limit our capability to detect patterns in fisherman behavior and connect these to common social measures of reserve success. Studies that then link social and ecological metrics across systems are even rarer (14). There is a real need for strictly comparable data, and achievement of this goal may necessitate changes in beliefs among involved researchers. Facilitated conversations within and among anthropologists, economists, and ecologists are crucial for developing these comparable data and consistent metrics.

Conclusion

Marine reserves are inherently a spatial form of ocean management. The global implementation of these spatial restrictions on human uses provides advances and insights that form an excellent foundation for a broader, more comprehensive approach to ecosystem-based management and marine spatial planning. With the rapid emergence of new ocean uses such as wave farms for renewable power and offshore aquaculture for enhanced food production, there is likely to be increasing pressure to spatially segregate different uses and stakeholders. As we look to the future, the successful transition to effective marine spatial planning will be far more efficient and far less confrontational if it draws on the scientific insight from marine reserves. The findings in this Special Feature provide an excellent synthesis for launching this discussion.

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