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Critical science gaps impede use of no-take fishery reserves

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As well as serving valuable biodiversity conservation roles, functioning no-take fishery reserves protect a portion of the fishery stock as insurance against future overfishing. So long as there is adequate compliance by the fishing community, it is likely that they will also sustain and even enhance fishery yields in the surrounding area. However, there are significant gaps in scientific knowledge that must be filled if no-take reserves are to be used effectively as fishery management tools. Unfortunately, these gaps are being glossed over by some uncritical advocacy. Here, we review the science, identify the most crucial gaps, and suggest ways to fill them, so that a promising management tool can help meet the growing challenges faced by coastal marine fisheries.

Introduction

Worldwide, coastal marine fisheries are under ever-increasing threat of collapse. Effort increases, yields remain stable or decline, and other anthropogenic impacts degrade habitats and ecological systems on which the fishery species depend [1–3].

Marine protected areas (MPAs) of various types are a form of resource management that regulates human activities in particular locations. Although there are many types of MPA, we are concerned here with no-take fishery reserves (see Glossary), also termed 'closed areas' or 'harvest refugia' [4], and we focus on fishery benefits while recognizing that no-take reserves also have important biodiversity conservation benefits. Such reserves commonly increase the density, biomass and average size of target species within their borders [5], and there are a few well documented cases where they supplement fished stocks in surrounding areas [6,7]. However, it is premature to assume that no-take reserves are invariably effective in fisheries management, because there are relatively few empirical studies, many of which are poorly

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Glossary

Adaptive management: a resource management program in which management actions are deliberately used as experimental manipulations of the managed system to test predictions of alternative models.
BACIP: 'before-after control-impact pairs'; a sampling design that enables the unambiguous testing of effects on an ecological system owing to a particular impact, such as creation of a no-take reserve.
Connectivity: the demographic linking of local populations through the dispersal among them of individuals as larvae, juveniles, or adults. Successful dispersal requires that individuals move between populations, and become successfully incorporated into the recipient population.
Dispersal envelope: the probability distribution of dispersal distances around a source location, such as a no-take reserve.
Groundfish: a broad array of demersal fishery species that are captured by towed gear, such as trawls, that travel across the substratum.
No-take fishery reserve: a marine protected area within which extractive fishing activities are regulated (usually not permitted).
Recruitment: the addition of a cohort of young animals to a population. Recruitment of marine species is measured at various stages in the lifetime: at the age or size at which individuals become susceptible to the fishery, or at a specific time of life such as when moving from the pelagic larval to the demersal phase.
Recruitment subsidy: the enhancement of production of a fishery species, within the fished locations surrounding one or more no-take reserves, owing to the net export from the reserve of pelagic larvae.
Spillover: the enhancement of production of a fishery species, within the fished locations surrounding one or more no-take reserves, owing to the net movement of juveniles and adults out of the reserve.
Stock-recruit relationship: the relationship between the size of a population (stock) and the rate of recruitment to it. In most marine organisms, these relationships show such high variance in space and time that it has proved difficult to determine the nature of the underlying dynamics.
Trophic cascade: a change in the relative abundances of species comprising an ecological community caused by changes in abundance at one trophic level leading to changes at other levels because of the feeding interactions that take place. In the context of no-take reserves, cessation of fishing large piscivores might lead to declines in the abundance of their prey species, and the release of still lower trophic groups that then become more abundant.

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designed, and even the reported increases in density within reserve borders can be slight. Empirical studies of no-take reserves published before 2002 were outnumbered by theoretical papers and reviews (44% versus 56% of 205 total), many of which were characterized as advocacy [8]. Halpern reviewed 89 empirical studies, and found that 63% reported increases in density whereas 7% reported declines [5]. Using more rigorous standards for sampling design and magnitude of reported density difference, Willis *et al*. report just five empirical studies that demonstrate this simple effect unambiguously [8]. Well documented effects outside reserve borders are even rarer [7].

Similar to others [2,6–13], we anticipate that no-take reserves can become an effective fishery management tool. However, we are concerned (as are some others [8,14]) that repeated, uncritical advocacy has the potential to: (i) diminish recognition of the remaining gaps in our knowledge and, therefore, diminish support for continued research and development of an important management tool; (ii) raise expectations in the fishing community and in conservation circles that might prove unachievable [15]; (iii) lead to neglect of other effective techniques for managing fishing effort [14]; and (iv) result in expenditure of scarce financial and other resources in the creation and management of no-take reserves that are inappropriately sized or sited. The overall result will be a continued decline in coastal fisheries, and the erosion of the credibility of marine science and scientists with respect to questions of resource management and conservation [16]. Here, we summarize the theory underlying the use of no-take reserves, identify gaps in knowledge and suggest ways in which to fill them.

Theory for design of no-take reserves

Reserves can insure against over-exploitation, and enhance surrounding fisheries

No-take reserves potentially achieve two things for fisheries management: they provide insurance against unsustainable declines of species owing to overfishing, and they supplement the production of fishery species in the surrounding fished area, thereby sustaining or enhancing yields. These functions derive primarily from the recruitment variation and connectivity that are characteristic of marine populations.

Recruitment to fishery populations is typically highly variable in both space and time [17,18]. Consequently, a strong recruitment event can persist for many years, and be particularly important in long-term replenishment. However, variable recruitment also means that small (e.g. overfished) populations will be especially susceptible to dramatic crashes, or even local extinction [19,20]. Therefore, no-take reserves, which tend to maintain population densities at higher levels, can provide an effective buffer against overexploitation [21].

Marine populations are interconnected, exchanging individuals mainly through larval dispersal and thereby influencing the dynamics of each population. This connectivity is key to the role of no-take reserves because it provides the mechanism for reserves to enhance fish production outside their borders [14,22,23]. By allowing individuals within their borders to grow larger and live longer, no-take reserves greatly enhance the fecundity of sedentary species; this increased fecundity tends to enhance fishery yields in surrounding populations through two processes: spillover and recruitment subsidy [14]. Spillover and recruitment subsidies are likely to act at different spatial scales, and the design of reserves will ideally use information about the rates and patterns of exchange for all life-history stages of the target organisms.

To be fully effective, no-take reserves should display sustained net export of target biomass that at least compensates for the loss of the fishing area used to set up the reserves [14]. Theoretical studies have focused on the mechanisms of spillover [24] and recruitment subsidy [25–30]; however, empirical tests of the theory are rare [8]. Effective no-take reserves, or networks of these, must be both net exporters of propagules to sustain surrounding fisheries, and largely self-sustaining systems [14,29]. Ideally, the level of sustained net export must be just right, because there must be sufficient self-recruitment (within a single reserve or a network of reserves) to ensure sustainability when surrounding unprotected populations are fished down. The design of a network should entail a delicate balancing act involving correct choice of size, number and placement of reserves. One might even expect that protection of a specific proportion of habitat is required for effectiveness (Box 1). One of the main scientific factors driving these design choices should be the extent of connectivity among local populations of the target species, a feature of marine populations about which we know relatively little.

Size, placement, and spacing rules for no-take reserves

For biodiversity conservation, there are sound biological reasons to expect that larger reserves will be more effective. Larger reserves hold larger populations of more species. These larger populations should be better protected from extinction, both because they are larger, and because individuals should be able to complete their life cycles within the reserve boundaries, making the populations largely self-sustaining [29,31,32].

However, no-take reserves also have a fisheries management role. As well as being large enough to contain and protect a population of adequate size, they need to be small enough to be able to supplement production effectively in surrounding fished populations [22,33]. Spillover alone, which is a function of perimeter length rather than area of the reserve, is likely to have only modest and local enhancing effects on fished populations, but recruitment subsidy, with the potential to supplement production of fished populations over much greater areas, is negatively dependent on reserve area [33–35]. We recognize that, because reserve sizes also will be dependent on the mobility and demography of the target fishery species they are intended to assist, reserves cannot be simultaneously of optimum size for all contained species, and widely ranging rare species might never be adequately conserved using reserves (Box 2).

Even the smallest no-take reserves ($\sim$1–5 km^2) usually provide conservation benefits in terms of enhanced biomass of sedentary target species within the boundaries [5].

Box 1. Amount of area to be protected

The proportion of a coastal area to be protected is usually determined through a compromise between the desire by some to protect all biodiversity and ecosystem function from human impact, and the socioeconomically valid goal of providing for continued use of the fishery and other resources in the area. Because no-take reserves have explicit fishery management goals, the question must be, what is the minimum proportion of area to place within reserves to sustain or enhance the fishery?

Unfortunately, the question of how much area is needed is not clarified by examining existing no-take reserves. These are predominantly small, comprising only a tiny proportion of the surrounding area, and increases in density and biomass, a sign that the reserve provides protection, appear not to be related to reserve size over the range of sizes available [5]. No-take reserves currently comprise 5% of Florida Keys National Marine Sanctuary and, until recently, <5% of the Great Barrier Reef Marine Park (GBRMP), the two largest managed areas in the world. A broader range of examples will be available soon: the GBRMP was rezoned to increase no-take reserves to 33.4% of its total area on July 1, 2004 [54], and the recently designated Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve will have 20% of area within no-take reserves [55].

Protecting 20% of the area has become a commonly cited target. This arbitrary target relies on the assumption that protecting 20% of the area protects 20% of the original spawning stock, and on the argument that protecting 20% of the stock would prevent recruitment overfishing [9,11]. More recent models suggest that >35% of the total area needs to be in no-take reserves to prevent recruitment overfishing of sedentary species, such as sea urchins or many reef fishes, and area requirements differ among species with differing biology [22,29,33]. If a demographic bottleneck in the form of limited essential habitat exists for a managed species (such as occurs for immediately post-settlement American lobster *Homarus americanus*) the total sea area protected becomes largely irrelevant for management [56]. Even details of hydrodynamics could affect how much of the area should be protected and in how many pieces [48]. For now, efforts to prescribe the correct percentage of sea area to protect to sustain a fishery have limited scientific support. Attempts to specify a universal proportion for protection seem naïve.

Small reserves might also provide some spillover [5,7,34–37], and can have an important fishery management role if situated at crucial locations, such as spawning aggregation sites [38] (Box 2). Theory suggests that fishery value is enhanced in a network of small no-take reserves rather than in few, widely spaced large reserves, because the many small reserves supplement production over a greater proportion of the surrounding fished area [22,33,39,40]. In addition, whereas establishing a few large reserves might have practical advantages in terms of designation and compliance, large marine reserves can be impractical because they disadvantage some local communities whose fishing grounds become closed to fishing, and benefit others whose fishing grounds remain open (Box 3).

The crucial gaps in scientific knowledge

The planning of MPA locations, sizes and spacing is currently decided, to a large degree, by the natural geography of habitats, compromises among different user groups, issues of compliance and governance, and much ‘educated’ guesswork concerning ecological aspects of the task [4,13,41]. Few attempts have been made to develop, and even fewer to test, ecological theory to help guide this process [29]. Clearly, there is scope to develop ecological criteria [32] to inform the decision-making

Box 2. Mobility of the target species

Most no-take reserves are small (1–20 km^2, median ~16 km^2) [13,57], and many coastal demersal fishes are relatively sedentary (living spaces of <1 km^2 suit many coral reef species [37]). However, many coastal fishery species, such as cod, snappers, or groupers, tend to be larger in size and often also more mobile. Such species also are usually long lived and slow to mature; these characteristics correlate with higher probability of depletion or extirpation owing to overfishing [13,58]. How well do reserves serve to sustain fisheries for these larger, economically more important species?

Some fishery species are known to travel many kilometers annually to specific spawning areas (e.g. certain snappers *Lutjanus* spp. and groupers *Epinephelus* spp. [13,14]), seasonally in response to temperature changes (e.g. sole *Solea solea* [59]), or while undergoing ontogenetic habitat shifts (e.g. American lobster *Homarus americanus* [60]). Considerable interspecific variation is evident among rocky- and coral reef fishery species in the timing and extent of spawning migrations, for example, and even within families trends might not be evident [61]. Among groupers, the coral trout *Plectropomus leopardus* is a ‘resident’ spawner, moving <2 km to spawning sites, and is well suited to current scales of typical no-take reserves [62], yet the Nassau grouper *Epinephelus striatus* and the Gag grouper *Mycteroperca microlepis* migrate yearly 10 to >100 km from home reefs to reproduce at specific spawning sites [63]. Aggregations occur at highly predictable times and sites, and are particularly vulnerable to fishing [64]. Yet although protection of aggregations can effectively enhance spawning success [38], few no-take reserves have explicitly incorporated spawning sites [61].

Mobility of continental shelf groundfish species is not well known. It is estimated, however, that the effectiveness of reserves for managing cod *Gadus morhua* or haddock *Melanogrammus aeglefinus* on Georges Bank would depend crucially on reserve location that is relative to seasonal movement patterns of the fish [65]. North Sea cod would require no-take areas >60 000 km^2 for effective management [45]. The scale of reserves currently in place appears insufficient to accommodate the mobility of many such valuable groundfish species.

In general, the larger economically valuable fish species do not necessarily mimic behavior of smaller species, and interspecific differences mean that no-take reserves must be designed for specific target species. There are many fishery species about which we need more basic ecological information before implementing no-take fishery reserves to help manage them.

process; however, significant gaps in our knowledge of the ecology of coastal marine systems make this a bigger challenge than some seem to suggest [42]. We identify five crucial gaps in the ecological science of no-take reserves.

(i) When designing no-take reserve networks, the distance and direction in which marine larvae disperse is a primary ecological issue because it directly determines three key things. These are whether: (i) the size of a planned reserve will ensure rates of self-recruitment that are adequate for persistence of its target populations; (ii) the placement and spacing of a network of reserves will promote persistence of their target populations through dispersal among them; and (iii) the sizes, spacing and placement of reserves will maximize potential fishery benefits on neighboring fishing grounds through recruitment subsidy [6,10,23,29,33,43]. Knowledge of average effective dispersal envelopes is limited, principally because patterns of larval dispersal are taxon-, site-, and probably also time-specific, and are driven by a complex of sensory capabilities, behavioral responses, and physical hydrodynamic processes [18]. Gaining information

Box 3. Socio-economic factors and the design of no-take reserves

Marine reserves are proposed, designed, legally codified, implemented and managed through socioeconomically complex and largely political processes. Too many of them fail to become effective management instruments. Ideally, no-take reserves should be designed using the best available science. Their effects should be evaluated, and the results integrated into improved management practice [14]. This iterative process of adaptive management can only happen within a close collaboration of scientists, managers, the fishing community and other stakeholders, such as occurred in the study of line-fishing effects on the Great Barrier Reef [66]. Building political will, developing effective collaborations and securing adequate funding for stakeholder incentives and policing are as vital for success of a science-based reserve program as are the identification of hypotheses and the planning of specific manipulations [16,51].

Without attention to the underlying socioeconomic issues, science-based reserve development will be significantly constrained, and is unlikely to serve scientific or other needs effectively [50]. Needed are a well-informed set of stakeholders, real capacity to enforce regulations and a design, management and monitoring program that suits the current state of the fishery, provides alternative livelihood options and deals with the need to maintain quality of life of the citizens [49]. Enforcement should be consistent, and the extent and pattern of noncompliance documented [40]. Otherwise, the honest resource users will be disenfranchised, community support for the reserve will whither and, concurrently, the controls needed for scientific evaluation of results will be compromised or lost. In rare places where communities traditionally have depended on local marine resources, customary marine tenure provides pre-existing capacity and incentive to enforce protection, and the concept of marine reserves is readily accepted [67]. Most reserves, however, are in sites that lack prior community-driven management structures, and capacity and incentive to enforce regulations must be built. Finally, it must be acknowledged that incentives and stakeholder buy-in are necessary, but not sufficient. Even with strong stakeholder buy-in, some no-take reserves are well managed [7,67], whereas others are not. Local management arrangements at the Soufriere Marine Management Area [68], at Sumilon Island [69] and in the Fijian qoliqoli [70] have proved neither politically stable, nor responsive to exploitation pressure [13]. The socioeconomics of no-take reserve introduction are not yet well understood [49,50], but they must be married with the science if adaptive management procedures are to be implemented.

about patterns of larval dispersal is a challenging multi-disciplinary task. This is true even for those species with the shortest larval lives, yet many of the important fishery species have relatively long larval lives (weeks to months), and are behaviorally competent pelagic creatures for much of this time. Although there is some localized recruitment in species with broad geographical ranges [43,44], it is also likely that the variance in dispersal distances is high both within and among locations, an important factor ecologically and evolutionarily.

(ii) We know more about the patterns of movement during the juvenile and adult phases of fishery species, but even here there are serious gaps in information (Box 2), and movement patterns at these life stages are crucially important in determining the extent of spillover from reserves. In addition, some species might be too mobile for management using reserves to be practical. It might not be politically possible to implement reserves of sufficient size to provide them with the level of protection required [13,45].

(iii) Knowledge of the ecosystem impacts of fishing is also limited, but this becomes an important need when implementing no-take reserves [3,46]. The lack of fishing inside the reserve might lead, through processes such as trophic cascades, to changes in community structure that cannot currently be predicted explicitly [5,13]. The rule that populations of fishery species will be more abundant, larger, older and, therefore more fecund inside a reserve might not hold if such shifts in community structure occur. If establishment of a reserve does not result in protected populations becoming more abundant and more fecund, there is no possibility of recruitment subsidy and spillover. Some reported failures to see increased density within reserves [5,8] might be due to such ecosystem impacts.

(iv) We lack adequate knowledge of the behavior of water masses in the vicinity of complex coastlines and, although our ability to model hydrodynamics is rapidly improving, there continue to be empirical reports that reveal ever greater complexity, particularly in the temporal variability of hydrodynamic patterns [47]. This limits our ability to site reserves effectively, because the pattern of water movement in a region might modify the effectiveness of any particular pattern of reserve size and spacing [48]. It is also theoretically logical and enticing to place no-take reserves at sites that function as sources of propagules, rather than at sites that serve as sinks for propagules from elsewhere [28]. However, current hydrodynamic knowledge does not enable us to identify source or sink locations without prior monitoring of hydrodynamics at each location. Neither do we know if there are likely to be locations that function as permanent sources, as opposed to locations that are sources on one occasion, but not on others.

(v) Finally, we have remarkably few well designed studies of no-take reserves that can rigorously demonstrate that they have sustained or enhanced fishery yield in the surrounding region. Solid evidence of recruitment subsidy does not yet exist, and much of the evidence of spillover is equivocal [13,14]. The long-term study of the Apo Island (Philippines) reserve by Alcala, Russ and colleagues provides the best example of a reserve-based management program that has enhanced catches over decadal timescales because of spillover [7]. More such studies are needed.

Taken together, these gaps in our scientific knowledge need to be addressed because they prevent development of an explicit science for reserve design, one that can generate quantitative criteria for use in planning of no-take reserve networks. This does not obviate the fact that criteria other than scientific ones are also important (Box 3), and we note that, in the socioeconomic arena, there are also gaps in understanding [49,50]. For example, what is the impact on a fishing community of the establishment of a reserve network of particular design, and how does that community's response change fishing effort in the remaining fishable area? These gaps are outside the scope of this article, but also need to be addressed.

How do we fill the gaps in our knowledge?

MPAs will only be successful if we set them up in the right way and for the right reasons. Only 31% of MPAs currently meet their management goals, because too many are set up in the wrong places or with unrealistic expectations [51]. We do not advocate delay in the efforts to improve the sustainability of fisheries, but we believe that we must recognize the serious gaps in our knowledge and take steps to fill them. The best way to do this is to use the existing science in deliberately adaptive management approaches for the design and implementation of networks of no-take reserves.

There is a need for targeted funding of research to gain the missing biological information for target species (e.g. mobility, life-history, rates and patterns of settlement and recruitment, connectivity among neighboring populations, and the status of these populations as either sources or sinks); as well as physical information about bathymetry, habitat and hydrodynamics at locations being considered for reserves. Research is also needed into effective ways of using no-take reserves in combination with established methods for controlling fishing effort. Particularly useful will be cost–benefit approaches to determine the situations under which particular management tools are most effective. Simultaneously, we need to identify information bottlenecks and weaknesses in foundation principles (if they exist). For example, reproduction is often assumed paramount in determining demographics of populations, yet stock–recruit relationships are uncertain in fish, and other ecological factors, such as limits on available nursery habitat, or patterns of connectivity, might be demographically limiting for particular populations [13,23]. Above all, there is a need for research manipulations that will empirically test the efficacy of no-take reserves as fishery management tools. Because these experiments must be performed at appropriate spatial and temporal scales, this research should be done in the context of adaptive management, where the management intervention is deliberately varied in space or time, so that the results can be used as an experimental test of stated hypotheses, and where the intervention is intended to be modified on the basis of the results obtained [52]. Such research should be carefully planned, using an appropriate BACIP design, so that the results are explicit and powerful tests of hypotheses [14]. This is not the time to waste opportunities with unreplicated, confounded, or other inadequate experimental designs.

We already know something of the scales of movement of adults of target species (Box 2), and can investigate how these lead to spillover from no-take reserves. The key issue needing attention is to specify the larval dispersal envelopes of target species, and how these determine connectivity among populations. New techniques to investigate this crucial issue are rapidly being developed [53]. With explicit data on larval dispersal, it should be possible to adjust reserve size, placement and spacing to achieve particular management objectives [22,29,33]. For example, if reserves are established at a scale that is larger than average dispersal distances, they should function as marine sanctuaries for biodiversity conservation (Figure 1a). No-take fishery reserves, however, should be sized and spaced within dispersal envelopes for selected fishery species as part of the management of surrounding fisheries (Figure 1b). It should eventually be possible to specify optimal number, sizes and specific locations of a network of no-take reserves to achieve enhancement of specific fisheries, while ensuring the sustainability of the network through self-recruitment [42]. This will require information about local geography, bathymetry and hydrodynamics in addition to the data on dispersal patterns [48]. We are not yet close to achieving this, and deliberate use of adaptive management approaches using networks of no-take reserves to test hypotheses will be essential if advances are to be made.

Adaptive management requires the building of a much stronger collaboration between scientists, fishery managers and the fishing community, with all three groups recognizing that an effective management intervention will be of benefit to all (Box 3). Research funding agencies, management agencies, and donor NGOs must recognize that adaptive management done to gain new scientific knowledge is a legitimate activity for funding [16].

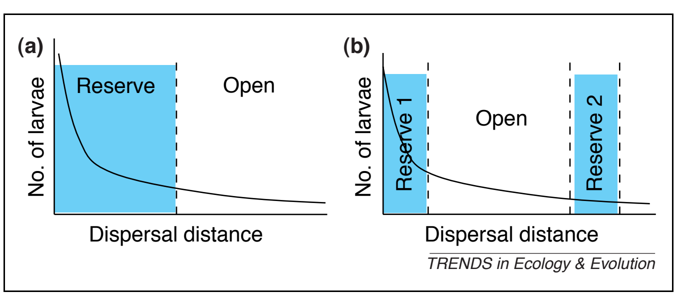

Figure 1. The size and spacing of no-take reserves with respect to dispersal distances of the species of interest. Reserves intended for conservation **(a)** should be large enough to retain a substantial portion of larval dispersal to ensure adequate self-recruitment. For fisheries enhancement **(b)**, they should be sized and spaced to enable a significant proportion of larvae to disperse to surrounding fished areas. Distance is measured from the center of the reserve (at the origin) and the dispersal curve is drawn with respect to larvae produced there. [Shaded areas are reserves; dotted lines, reserve boundaries. For simplicity in (b), the dispersal of larvae produced in reserve no. 2 is not included].

Conclusions

No-take reserves are potentially valuable fishery management tools, but there are significant gaps in our biological knowledge that currently preclude implementing them with full confidence that they will sustain surrounding fisheries. These gaps can be filled, but first they must be acknowledged. Filling them will require a significant investment in targeted research, chiefly in the context of adaptive management, and this will require the development of strong collaborations among the scientific, the management and the fishing communities. The most crucial questions concern connectivity and the anticipated recruitment subsidy that this should make possible. Answering these questions will enable the development of more explicit rules concerning size, placement and spacing of reserves, the amount of habitat that needs to be protected, and the most appropriate ways of combining no-take reserves with other management tools. There is risk in proceeding to implement no-take reserves without simultaneously seeking to fill the knowledge gaps, yet there exists a great urgency to develop more effective tools for the sustainable management of coastal fisheries. Building sustainable coastal fisheries has considerable benefits beyond those to the fishing community, but achieving these benefits will be difficult and will require that we explore possible tools carefully and rigorously, while using them to the best of our current capability. Acknowledging the gaps in knowledge is the first step in building a more effective science of no-take reserves.

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