Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects

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Decadal-scale observations of marine reserves suggest that indirect effects on taxa that occur through cascading trophic interactions take longer to develop than direct effects on target species. Combining and analyzing a unique set of long-term time series of ecologic data in and out of fisheries closures from disparate regions, we found that the time to initial detection of direct effects on target species (±SE) was 5.13 ± 1.9 years, whereas initial detection of indirect effects on other taxa, which were often trait mediated, took significantly longer (13.1 ± 2.0 years). Most target species showed initial direct effects, but their trajectories over time were highly variable. Many target species continued to increase, some leveled off, and others decreased. Decreases were due to natural fluctuations, fishing impacts from outside reserves, or indirect effects from target species at higher trophic levels. The average duration of stable periods for direct effects was 6.2 ± 1.2 years, even in studies of more than 15 years. For indirect effects, stable periods averaged 9.1 ± 1.6 years, although this was not significantly different from direct effects. Populations of directly targeted species were more stable in reserves than in fished areas, suggesting increased ecologic resilience. This is an important benefit of marine reserves with respect to their function as a tool for conservation and restoration.

fishing effects | interactions | time lags | trophic cascade | marine protected area

The current global trend to increase the number of no-take marine reserves is a phenomenon with complex ecologic, scientific, and socioeconomic dimensions (1–3). Stakeholders want to know how rapidly changes will occur after protection, even if natural variability can be large and difficult to predict. Patterns of variation in recovery rates of harvested species determined from long-term empirical studies can provide these important ecologic insights. Studies that have quantified the rate at which recovery of targeted species may take place have found the main factors affecting the recovery rates of populations in reserves to be the following: initial population size, intrinsic rate of increase (r), stock recruitment relationships, size of reserve, metapopulation structure, relationships with source locations, annual variations in success of individual recruitment events, the success of reducing fishing mortality (F) in the reserve (4–6), and the degree to which fishing has affected populations. Most of these factors relate to population growth, suggesting that recovery is a cumulative process. In addition, the design of reserves and rates of movement across reserve boundaries frequently play a strong role (4). All of these processes are likely to be mediated by environmental factors, such as habitat and disturbance.

Most studies on reserve effects have focused on reporting increases in abundance over time for fished species (7), with little change reported for nontargeted groups of fish, invertebrates, or basal trophic groups such as algae and corals (8–10). The few changes observed in populations of nontargeted species in reserves are thought to result from indirect effects that develop after the restoration of populations of higher predators (11–14). For example, in tropical systems, the recovery of herbivorous fish in reserves can lead to a decrease in macroalgal biomass and the release of space, resulting in enhanced recruitment of corals (15). In temperate reef ecosystems, the recovery of lobsters and large fish in marine reserves in New Zealand has led to higher predation and the decline of sea urchin populations, and in turn a reduction of grazing and the recovery of kelp forests (11, 13). Indirect trophic interactions resulting from changes at trophic levels two or more trophic levels higher are often termed *trophic cascades* (16). Indirect trophic interactions have the potential to lead to significant changes in ecosystem structure and function. Consequently, marine reserves have the potential to provide important insights into the indirect effects of fishing on marine ecosystems. Species assemblages in older reserves have also been shown to differ from both reference (fished) areas and recently created reserves, suggesting that indirect effects may take time to develop (9).

Delays in indirect effects after reserve protection may be due either to delays in direct effects (8) or to characteristics of the indirect responses themselves. Understanding these delays is important because ecologic theory predicts that lag factors are an important component of species interactions that determine whether population numbers stabilize or cycle and whether cycles are stable or chaotic (17). For indirect changes to occur in marine reserves, there must be direct effects that produce an absolute increase in abundance, mean size of individuals, or biomass of targeted species (i.e., restoration to some former level, not just a relative change compared with fished areas). This is because ecologic interactions are determined by absolute values, not relative differences between reserves and fished areas, such as might occur if the reserve protects communities while targeted species decline over time in fished areas.

Critical questions relating to the time course and temporal variation of direct and indirect effects on abundance of organisms in marine reserves include the following. (*i*) What is the rate of change, and has enough time elapsed for change to occur? (*ii*) Will indirect changes due to species interactions or effects on habitat always occur, and will they track those for directly targeted species or lag behind them? (*iii*) How stable are direct and

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indirect effects? (*iv*) Do levels of variation through time differ for direct and indirect effects, or for fished and unfished areas?

One limitation to our understanding of temporal variation in direct and indirect effects of marine reserve protection is the scarcity of long-term (decadal-scale) studies. As a result, there has been a heavy reliance in the literature on marine reserve efficacy on metaanalyses that use data from many reserves of different ages and locations to provide a space-for-time substitution. This approach provides fewer insights into the temporal dynamics and associated variation in reserve effects than continuous time series after closure. For example, continuous time series can inform assessments of ecologic resilience (18) that space-for-time substitution cannot. Furthermore, the reliance on reserve-fished response ratios is also problematic because of changing fishing effort outside reserves, which makes it difficult to understand the nature of any response.

Here we use a unique set of data collected on decadal time scales from multiple marine reserves in both tropical and temperate reef habitats to estimate how long it takes for direct and indirect effects to be detected initially, how stable such initial effects are through time, and to assess the causes of variation in timing and stability of direct and indirect reserve effects. Data included in this study comprise the full set of marine protected area (MPA) ecologic monitoring studies described in the published literature that we are aware of that (*i*) began before or within 5 years of MPA declaration, (*ii*) extend over more than 10 years, with at least 10 sampling events, and (*iii*) include data from both inside and outside MPAs. Our approach differs from previous temporal comparisons of marine reserves because we did not use ratios of reserve to nonreserve values, which can potentially imply changed density in reserves when this is not necessarily the case. In addition, we used continuous or near-continuous time series at each reserve to provide insights into the temporal dynamics and mechanisms that produce changes in marine reserves and analyze multiple long-term sets of raw data rather than apply a metaanalysis, thereby avoiding potential biases that can arise when data are filtered through the publication process (19).

Results

Direct Effects on Targeted Species. In 78% of the cases examined ($n = 15$), populations of directly exploited species increased over time in reserves (Figs. 1 and 2). The direct effects of protection on target species occurred relatively rapidly, first appearing within 5 years on average (5.13 ± 1.9 years; Fig. 3), indicating that the initial effects of protection often occur quickly. The

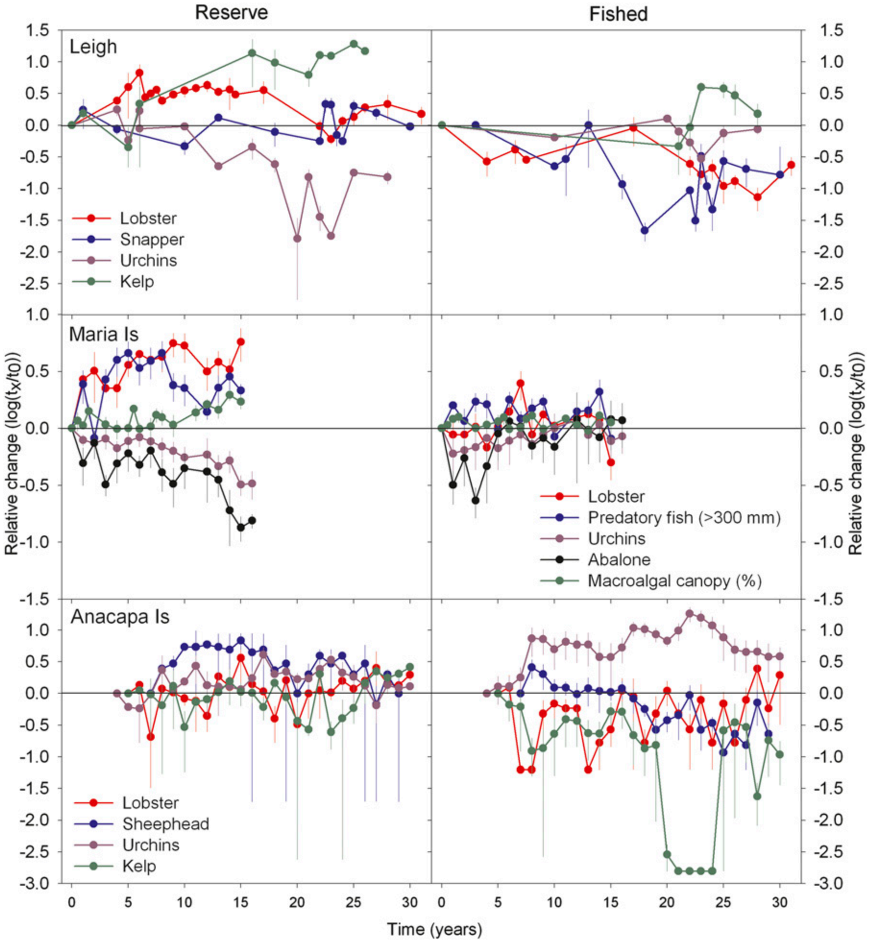

Fig. 1. Long-term changes in key populations at temperate no-take marine reserve locations and reference (fished) areas. Data are means (±SE), expressed as a ratio of the observed (t = x) vs. initial values at the time reserves were implemented (t = 0) and were log transformed for presentation and comparison. Temperate species: Leigh; lobster *Jasus edwardsii*, snapper *Pagrus auratus*, urchin *Evechinus chloroticus*, and kelp *Ecklonia radiata.* Maria; lobster *J. edwardsii*, predatory fish (species complex >300 mm fork length and excluding highly mobile species), urchin *Heliocidaris erythrogramma*, abalone *Haliotis rubrum*, and macroalgal canopy cover (species complex of large brown algae). Anacapa; lobster *Panulirus interruptus*, sheephead *Semicossyphus pulcher*, urchin *Strongylocentrotus purpuratus*, and kelp (Laminarian species complex). All values based on density estimates except for kelp canopy at Maria Island (percentage).

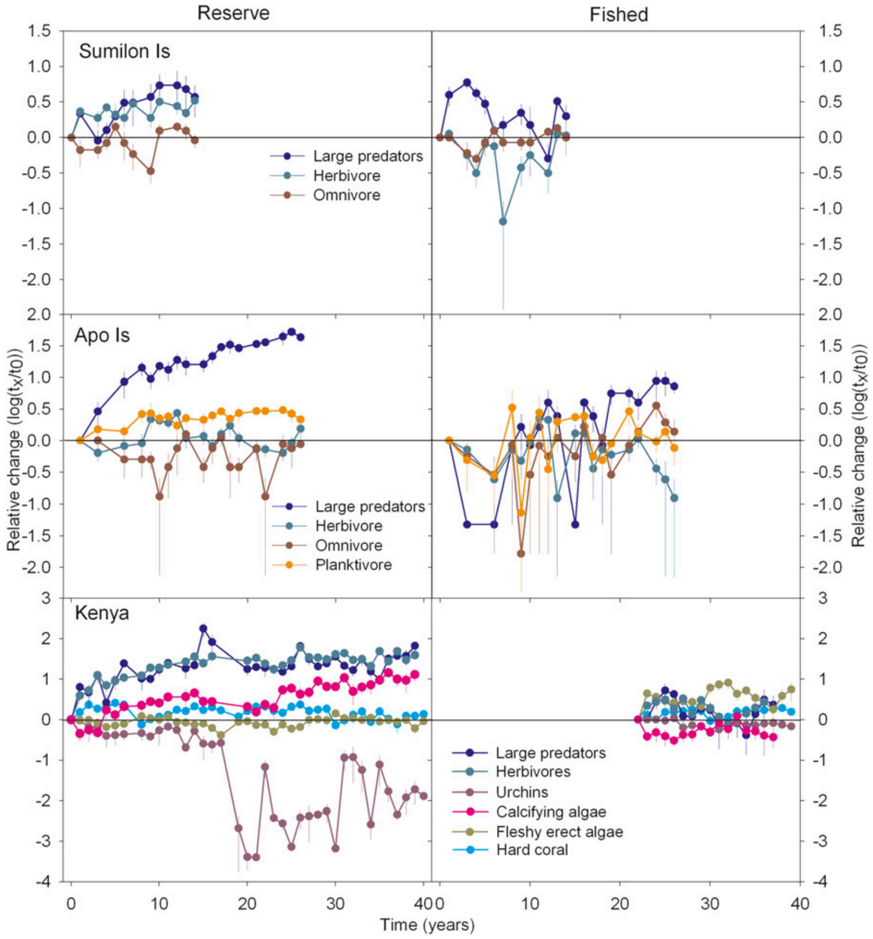

Fig. 2. Long-term changes in key populations at tropical no-take marine reserve locations and reference (fished) areas. Data are means (±SE), expressed as a ratio of the observed (t = x) vs. initial values at the time reserves were implemented (t = 0) and were log transformed for presentation and comparison. Tropical species: Sumilon; large predators Serranidae and Lutjanidae, omnivore *Hemigymnus melapterus*, herbivore *Scarus tricolor*. Apo; large predators Serranidae and Lutjanidae, omnivore *Hemigymnus melapterus*, herbivore *Scarus tricolor,* planktivore *Naso vlamingi.* Kenya; large predators including triggerfish Balistidae and wrasses, herbivores (species complex), and urchin *Echinometra mathaei*. All values based on density estimates, except for Kenyan case study, in which biomass (fish and urchins) and percentage cover (corals and algae) are used.

remaining groups that did not increase inside reserves (22% of outcomes) include both invertebrates and vertebrates from a range of trophic levels (e.g., lobster *Panulirus interruptus* at Anacapa Island and the omnivorous wrasse *Hemigymnus melapterus* at Apo and Sumilon Islands in the Philippines) (Figs. 1 and 2). For target species or taxa for which clear increases were observed, the effect was rarely static. Taxa commonly continued to increase over the entire period (e.g., large predators at Apo Island and lobster at Maria Island), others stabilized (e.g., predatory and herbivorous fish at Sumilon Island and the planktivore *Naso vlamingi* at Apo Island), whereas others declined after their initial increase (e.g., sheephead at Anacapa Island and lobster at Leigh) (Figs. 1 and 2).

Several different trends were apparent in the stability of direct effects on targeted species. The direct effects of reserve protection on target species, once established, tended to be stable for relatively short periods, with an average length of stability (period after initial recovery over which no further change, either positive or negative, was observed) of only 6.2 ± 1.2 years ($n = 14$) before trending either up or down. If changes were stable over time, we would expect that, after the initial recovery, the longer a reserve was in existence the longer stable periods would be, yet there was no relationship between the number of years a reserve had been in existence and the duration of stable periods (no significant change) after the initial recovery. Population stability in taxa for which direct effects were observed, expressed as coefficients of variation, was significantly greater in fished areas than in reserves (paired t test $t = -3.16$, $P < 0.05$, $n = 30$; Figs. 1 and 2).

Indirect Effects. Indirect effects were documented in most of the case studies, though not all (Figs. 1 and 2), with significant changes in just over 70% of the cases (71%, $n = 13$). The direction (positive or negative) of these effects varied depending on trophic level (Figs. 1 and 2). The majority of these were trophic effects and involved the recovery of exploited species at higher trophic levels, causing a decline in prey species. In most cases these prey were grazing invertebrates (sea urchins or abalone). Urchin populations in temperate systems declined as a result of lobster predation at Leigh and Maria Island. Declines in urchin numbers were also observed in tropical systems in Kenya after their triggerfish and wrasse predators increased in abundance (Fig. 2).

Trophic cascades led to an increase in basal groups such as macroalgae and calcifying algae in three of the six case studies. Declining densities of grazing urchins at Leigh and Maria Island resulted in an increase in kelp and macroalgal canopy, respectively (Fig. 1). In Kenya, relatively minor although significant declines in urchin densities occurred several years after predator

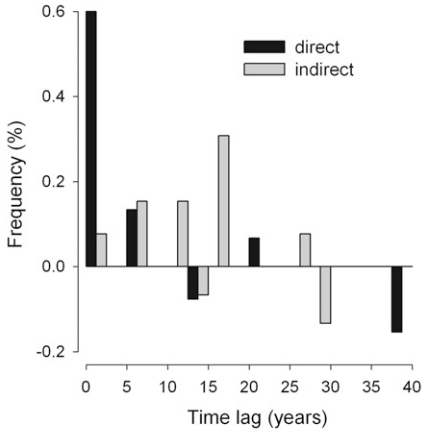

Fig. 3. Time to first detection of direct and indirect responses to marine reserve protection. Positive data indicate the proportion of observed species displaying direct and indirect effects, negative values indicate taxa for which no effect was observed. *n* = 28.

recovery was first noted, with a simultaneous increase in the cover of red and green calcareous algae. A much larger decline in urchin abundance took place after 16 years, although this was not accompanied by changes in cover of algal groups or corals (Fig. 2).

Indirect effects took 13.1 ± 2.0 years to appear, significantly longer than it took for direct effects to appear [$t_{(\text{two-tailed})} = 2.0$, df = 19, $P < 0.001$]. In all cases there were significant time lags between the appearance of direct effects on predators and corresponding indirect effects on prey, with indirect effects taking 36% ± 5% ($n = 10$) longer to appear than direct effects (Fig. 3), and the frequency distribution of time to effect was significantly different for direct and indirect effects (Kolmogorov-Smirnov $P < 0.05$). These time lags often represent a substantial proportion of the time over which observations were made, occurring well after the first direct effects of protection were noted.

On average, the duration of stable periods for indirect effects was approximately 10 years (9.1 ± 1.6 years, $n = 10$), which was not significantly different from the stable period for direct effects (6.2 ± 1.2 years, $n = 11$) Duration of stability did not vary as a function of reserve age ($F_{1,9} = 2.2, P = 0.17, n = 12$). Where indirect effects were observed, population variability did not differ significantly between reserves and fished areas (paired *t* test, $t = -0.87$, $P = 0.39$, $n = 13$; Figs. 1 and 2).

Discussion

Generality of Direct and Indirect Effects. The case studies described here support the findings of recent metaanalyses on the efficacy of marine reserves (7–10) but demonstrate the value of time series data in providing a longer-term perspective necessary to understand how target and nontarget populations will respond to protection, how these effects are manifested, how long they take to occur, and how stable they can be.

In general, direct effects on target species were rapid, initially occurring within 5 years, and relatively ubiquitous, and in all of the reserves examined populations of upper trophic level species, such as predatory fish and/or lobster, increased. However, despite these general initial patterns, the time series revealed a large amount of variation in the magnitude, direction, and stability of direct effects on target species. Although in most cases exploited species increased in reserves, numerous species showed little to no recovery. In one case an exploited species (abalone at Maria Island) actually declined with reserve protection, as an indirect effect of protecting the predators (lobster) of juvenile abalone (Fig. 1). In some cases increases in exploited species were not as strong as expected on the basis of studies that have compared reserve and fished sites (e.g., snapper at Leigh and sheephead at Anacapa) (Figs. 1 and 2). In these cases, the time series revealed that the effects of reserves seem to have been related to declines in populations at fished sites. In other cases, relatively high abundances of exploited species at reserve sites at the start of the time series may have limited the scope for populations to increase in reserves (e.g., lobster at Anacapa Island).

Indirect effects were just as common and of similar magnitude to direct effects in most of the case studies examined (Figs. 1 and 2). Indirect effects were particularly clear in two of the temperate reserves (Leigh and Maria Island), where a recovery of predators inside reserves has been followed by a decline in sea urchins and an increase in macroalgae (Fig. 1). These trophic changes are corroborated by a lack of changes in urchins and macroalgae at fished sites, as well as experimental manipulations (*SI Text*). In contrast to these examples, urchin and kelp abundance have remained relatively stable inside the Anacapa Island reserve, and indirect effects of predators are evident from changes at fished sites, where densities of the purple sea urchin *Strongylocentrotus purpuratus* have increased substantially over time and kelp has declined (Fig. 1). Persistent populations of predators in the Anacapa reserve are thought to have prevented similar increases in abundance of sea urchins and deforestation of kelp (14, 20). Indirect effects were only strongly evident in one of the tropical case studies: sea urchins declined in response to increased predators in Kenyan reserves, and the cover of calcifying algae increased (Fig. 2).

Stability. Direct effects of marine reserve protection, although commonly observed, did not result in static populations. Although there were examples of populations that stabilized and seemed to reach an asymptote in abundance, such as *N. vlamingi* at Apo (21) (Fig. 2), direct effects more commonly seemed to continue to increase, albeit at a slower rate, rather than stabilize (e.g., predatory and herbivorous fish in Kenyan reserves). This increasing trend may be the result of insufficient time for a single species to reach a maximum abundance (local carrying capacity), as in the case of lobsters at Maria Island. In the case of trends describing abundance of multiple taxa, prolonged increases may be due to the successive recovery of a series of species. For example, some trigger fish in Kenyan reserves have taken decades to recover (5) and have continued to increase after up to 40 years of protection. Large predatory reef fish (Serranidae, Lutjanidae) have continued to increase in density at Apo reserve for 25 years (Fig. 2). Similarly, among herbivorous fishes in Kenya, acanthurids increased rapidly at first and more slowly after 20 years (Fig. 2), whereas scarids peaked after approximately 10–15 years of protection (*SI Text*) and declined slightly after that, similar to trends reported here for Apo Island (Fig. 2).

We were surprised to see several instances in which abundances of targeted species rose initially, then declined (Figs. 1 and 2). At least three potential processes seemed to contribute to this pattern. First, initial changes did not always solely reflect reserve effects. For example, a significant component of the increase in fish >300 mm at Maria Island was due to localized recruitment pulses of trumpeter *Latridopsis forsteri* (22), and subsequent declines may be attributed to attrition of these cohorts and irregular recruitment events. The second reason for an unexpected decline was the possible indirect effect of increased predation by recovered predator populations in reserves. One clear-cut example is that of abalone in the Maria Island reserve. This species is commercially fished but declined in the reserve owing to predation by lobster (23) (Fig. 1). We suggest that declines in herbivorous fish at Apo Island are a likely example of this process because juvenile scarids are one of the preferred prey of serranid piscivores (24) (Fig. 2). The third process involved intensified fishing outside the reserves. At Leigh, lobster abundances increased rapidly in the first 8 years, stabilized for a further 10 years, and then fell to levels similar to those recorded at the time of the reserve's creation. The reason for the decline in numbers was probably increased fishing around the boundary of the reserve that targeted seasonal offshore movements of this species (25, 26).

Targeted populations seemed to be more stable through time in reserves than in fished areas. This is most likely because of the buffering afforded to populations in protected areas where the accumulation of age/size classes in populations will tend to smooth out fluctuations such as those caused by recruitment variability. Higher stability in unfished areas is consistent with the expectation of reduced ecologic resilience in disturbed systems (18). Despite the relative stability of reserves, there was change in most populations over time, consequently the duration of effects, whether direct or indirect, did not increase significantly as the age of the reserve increased. The lack of statistically significant variation in the stability of indirect effects between fished and reserve areas may be due to significant time lags in the development of indirect effects inside reserves. These time lags would tend to dampen the response of prey populations to changes in abundance of species in higher trophic levels that are directly affected by reserves or changes in fishing effort.

Time Lags and Trait-Mediated Effects. Marked differences were evident in the initial timing of direct and indirect effects. The relatively rapid occurrence of direct effects (mean, 5 years to first detected effect) was somewhat unexpected given the life-history characteristics of most of the targeted species, which are potentially long-lived and relatively slow growing. Colonization may be occurring through cross-boundary movements of individuals into some reserves. Such colonization has been found at some reserves where rapid recovery has been observed through large mature-sized animals taking up residence (4, 27), as well as through rapid larval recruitment directly into reserves (22, 28, 29), although few if any studies have been explicitly able to partition the major sources of recovery in reserves. Such colonization by adults is impossible for sedentary species (algae and corals) and unlikely for species with limited movement (e.g., urchins). Such groups (e.g., sea urchins, algae, and corals) could, however, recruit rapidly into reserves and are taxa known to be indirectly affected by marine reserve protection (Figs. 1 and 2). Nevertheless, this is not the most likely explanation for time lags seen in the development of indirect effects.

The most conspicuous time lags in indirect responses to protection involved sea urchins. Urchins at Leigh did not decline significantly in density until approximately 13 years of reserve protection, even though lobster densities increased after only 4 years, or one third as long. At Maria Island, urchins declined significantly after 7 years, whereas lobsters increased in abundance after only 1 year. A similar pattern was seen in the coral reef ecosystems of Kenya, where predatory fish increased significantly after only 1 or 2 years, but major declines in urchins did not occur for at least another 15 years.

The probable explanation for these time lags lies in the behavior of urchins and their predators. Urchin behavior can reduce the risk of predation. For example *Heliocidaris erythrogramma* at Maria Island is characteristically cryptic, remaining in crevices or burrows, rarely venturing out to feed, and surviving on drift algae (30). In northeastern New Zealand, the urchin *Evechinus chloroticus* is often conspicuous at depths between 6–12 m and creates barren grounds by openly grazing on kelp forests (11). However, in reserves *Evechinus* changes its behavior, becoming cryptic (13) and surviving on drift algae (31), most likely a response to increased densities of predators, as has been experimentally confirmed in other urchins (32). These behavioral traits mediate the effects of predation, reducing mortality rates in the urchin populations but presumably not eliminating predation mortality altogether.

Another factor potentially responsible for time lags in the response of urchin populations is size-specific predation on urchins. At Leigh and in Tasmania, smaller urchins are the preferred prey of lobsters and other predators (30, 31), and for *E. chloroticus* this size class of urchins is the most likely to be cryptic (31). Larger urchins are less likely to be cryptic, but they are also significantly less likely to suffer predation (30, 31). In Kenya, the eventual decline of a large sea urchin (*Echinothrix diadema*), which had persisted for many years, may be associated with the senescence of the large and predator-resistant adults and poor recruitment due to high predation on the less predator-resistant juveniles or low settlement. Consequently, larger urchins may continue to survive and graze openly for some time after predator numbers increase.

Furthermore, predators may take time to grow to sizes large enough to be effective predators of large urchins. *Jasus edwardsii* can take between 7 (males) and 15 (females) years to grow from immature size (85–89 mm carapace length) to 130 mm carapace length (33). Predator size can be as important as prey size for the predation effects described above, because until enough individual predators reach this critical size they will be unlikely to significantly affect prey populations (30, 34). Time lags in the response of herbivorous fish populations in the Philippines may be due to similar processes. Predatory fish (serranids) prefer juvenile scarids as prey (24), and because they will take 5–10 years (35) to mature there will be a lag before reduced recruitment begins to affect adult abundances.

These trait-mediated interactions involving urchin feeding behavior and predation may be the main reason for the large difference in the timing of indirect effects in the systems that we have observed and those described in intertidal systems where direct and indirect effects generally appear at the same time (36).

Implications for Management. We have shown that ecosystems in marine reserves have changed substantially after the removal of fishing pressure, but indirect effects are usually seen only after substantial time lags. The average time for indirect effects in our studies to first appear was more than 13 years and sometimes much longer. Marine managers will have to sustain confidence in the potential for restoration outcomes for considerable lengths of time before they can expect evidence of success in the form of indirect effects and the recovery of the broader ecosystem as well as target species. It is clear from the level of variability and ongoing change in abundance of targeted species, as well as from the time lags for indirect responses, that adaptive or evidence-based management (37) needs to be supported by long-term data collection at fairly high frequencies (<5 years). A case in point is the decline of lobsters at Leigh in the late 1990s. There was no lobster monitoring during this period, but if there had been, it might have been possible to modify the impacts of fishing on the reserve population.

Marine reserves demonstrate that varying fishing intensity can result in varying community states in marine ecosystems (38). Studies of these reserves have also shown that disturbance through fishing can affect resilience of such systems. Marine reserves can be a valuable research tool in their own right, as well as an essential part of adaptive management, because they constitute large-scale manipulations that can provide unique insights into the function of marine ecosystems and the effects of human activities on them (39). Even when they contain very similar components, not all ecosystems respond in the same way to human interventions, whether these are fishing or conservation. By studying these variations and understanding the reasons behind them, we will increase our ability to manage not only marine reserves but also to implement effective ecosystem-based management in a broader context (40). This will not be an easy task, and the evidence we have presented here suggests that it will take decades to observe, predict, and validate the full implications of marine reserves, because many of the processes we need to understand operate on these time scales.

Methods

The data presented here were collected from five marine reserves in coastal waters of New Zealand, Australia, California, and the Philippines, as well as aggregate data from a group of reserves in Kenyan coastal waters. These are analyzed as six case studies, three temperate and three tropical subtidal reserves in place for 10 years or more, in which observations exist from before or within 5 years of the time of reserve establishment and occur on average at least once every 2 years (with at least 10 sampling periods). The level of compliance with reserve regulations was high at all of these sites. Details of the time series from each of the reserves are given in *SI Text*.

Standardization and Presentation. We calculate metrics of abundance, biomass, or percentage cover using published and unpublished field survey data from a range of studies, sometimes conducted by a series of different investigators. To standardize the time series data, we have presented each data point as the log of the ratio of observed vs. initial value [log (N_{tx}/ N_{t0})]. Initial values were based on sampling carried out before reserve establishment or the starting value of monitoring programs (in most cases within 1 year of reserve establishment; *SI Text*). Where multiple samples were available from before establishment, means of these were used as the initial value. This approach meant that the starting point for all taxa in the reserve was zero [log (N_{t0}/N_{t0}) = 0], and the direction and deviation away from the starting value could be assessed over time.

Different metrics potentially compromise comparisons of effect size among the data; consequently, given that the main purpose of the study was to address the initial timing of change, we do not attempt to compare effect size among case studies. Variation is reported as SE throughout the text. This provided a standardized metric of relative change over time at reserve and nonreserve sites for a variety of target and nontarget taxa. We avoided ratios of reserve/nonreserve values because these might potentially imply changes in density in reserves when this was not necessarily the case.

Trends were assessed as two or more consecutive sampling periods in which there were either increases or decreases relative to initial levels at the time of reserve establishment. Significance of trends was identified from published analyses or assessed by graphic analysis (i.e., where 95% confidence intervals did not overlap with zero) because for some of the studies only means and error estimates were available. Stability of effects was defined as the proportion of the experiment after initial recovery over which no additional significant changes (either positive or negative) were observed (22). This metric summarizes the stability of a population. That is, whether it remains constant or exhibits some form of cyclic variation or continuing upward or downward trends. Another way we examined stability of populations was to calculate the coefficient of variation (SD/mean) over time for populations displaying direct and indirect effects both inside and outside reserves.

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Supporting Information

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SI Text

Case Studies: Temperate Systems

New Zealand. ***Context.*** The oldest marine reserve in New Zealand (Cape Rodney to Okakari Point, or Leigh Marine Reserve) was established in 1976 and extends roughly 800 m offshore along 5 km of coastal reef (518 ha). Fishing in the coastal area is predominantly recreational hook and line angling for *Pagrus auratus* (snapper), with commercial demersal long-lining concentrated further offshore. A substantial commercial and recreational pot fishery for spiny lobsters focuses on rocky reefs in this region. The only other invertebrate fisheries consist of minor recreational or traditional gathering of sea urchins and abalone. All marine reserves in New Zealand are fully "no-take," with no fishing or extraction of marine organisms. Data from several independent research or monitoring programs were compiled to assess long-term changes in the Leigh marine reserve (Fig. 1 in main text; see refs. 1–13 for sampling details).

Initial state. At the time of protection the temperate reef ecosystem in the Leigh Marine Reserve was characterized by a shallow algal zone, with crustose coralline algal barrens virtually devoid of macro algae present between depths of approximately 7–15 m (1). These barrens were maintained by the grazing of the urchin *Evechinus chloroticus*, which was present in densities of more than 4 m^{-2} and below this the reef was dominated by the kelp *Ecklonia radiata* (1).

After protection, abundances of snapper (*Pagrus auratus*) and spiny lobster (*Jasus edwardsii*) stabilized within 5–8 years of protection (2, 3). Spiny lobster populations increased by approximately 8-fold (3), and although density decreased after the mid-1990s, probably owing to an increase in fishing targeting the reserve boundaries during annual offshore movements (4), numbers have remained at around this mark up to the present time (Fig. 1 in main text). Although it does undertake seasonal offshore movements in northeast New Zealand, individual *J. edwardsii* are strongly site-attached (5), and recovery of protected populations is likely to have been due to recruitment into the reserve or adjacent reefs.

Snapper populations within the reserve were regularly studied initially. They showed an initial increase in density, then declined, a pattern likely to have been the result of a general increase in snapper numbers at that time, because a similar pattern was also seen in fished areas at Tawharanui.[*][†][‡] Densities since then have fluctuated, but sizes of snapper have probably been larger within the reserve since 1988, and certainly since 1996 (6, 7). By 1996 the density of snapper may have been similar to the levels of 1976; however, by this time the density of snapper was approximately 19 times greater inside the reserve than in nearby fished areas (7), and potentially the decline in snapper biomass outside the reserve has been greater than the increase within it. Relative abundance of snapper has remained at approximately this level or greater up to at least 2003 (8), and absolute biomasses are probably at levels of up to 10 times those of 1978.

Both snapper and spiny lobster are significant urchin predators of the urchin *E. chloroticus* (9). However, even after the populations of predators had increased and stabilized, populations of urchins maintained high densities in many parts of the reserve for at least a further 10 years (Fig. 1 in main text). Clear evidence of changes in urchin density were documented in the mid-1990s, and some areas were still in transition to kelp forest as late as 2001, 25 years after full protection. Once urchin densities fall below $\approx 1\ \text{m}^{-2}$ kelp populations can reestablish, and habitat state changes from urchin dominated barrens to kelp forest (10). These changes appeared at approximately the same time as the declines in urchin densities. Changes in the density of herbivorous molluscs associated with particular algal assemblages are also likely to have occurred around this time (10).

The time lag between the recovery of predator populations and the indirect effects on algal community structure was much longer than those commonly described in intertidal manipulations. This is likely to be related to the feeding behavior of urchin predators and to the behavioral response of urchins to these predators. Urchins adopt a more cryptic lifestyle to avoid predators, and both snapper and lobster prefer small urchins (9). It is important to understand such relatively complex interactions to predict the response of kelp forest communities to varying levels of predation. Further longitudinal studies of marine reserves are necessary to assess whether such time lags are common in subtidal rocky reef ecosystems.

Tasmania. ***Context.*** Four no-take marine reserves were declared in Tasmania in 1991 to conserve representative and unique Tasmanian marine habitats, to provide reference locations where the dynamics of marine communities could be observed independently of fishing effects, and to create fish propagation areas (11). Regular monitoring of reef communities inside and outside these reserves since 1991 has provided valuable insights into the direct and indirect effects of fishing and how the effects of reserves vary in relation to reserve size (12–14). Furthermore, experimental studies within these marine reserves have also provided empirical assessments of the proposed mechanisms responsible for changes in reserves (15, 16). In this synthesis we present trends from the largest of the four reserves at Maria Island, which protects 7 km of moderately exposed coastline. We do not present data from the other reserves where the effects of protection have been less evident, most likely owing to poaching and boundary effects associated with the small size of these reserves (1 to 2 km of coastline) (14). Key taxa have been monitored on an annual basis at six sites inside and six sites outside the Maria Island reserve since 1992 (13, 14).

Initial state. A long history of commercial and recreational fishing in Tasmania has led to the depletion of many fished stocks, including lobster, abalone, and a number of reef fish species (17). However, unlike other temperate systems there is no evidence that the removal of predators from reefs had resulted in an increase in sea urchins and deforestation of macroalgae habitats (12). In the Maria Island reserve the most common sea urchin, *Heliocidaris erythrogramma*, is relatively cryptic, occurs at relatively low densities ($\approx 2\ \text{m}^{-2}$), and there was no difference in algal assemblages between reserve and fished sites when the reserve was established (14).

Trends over time. Lobster and large reef fish (>300 mm) have increased in abundance and biomass in the Maria Island reserve after protection, whereas their abundances have remained relatively stable at nonreserve sites (Fig. 1 in main text) (13, 14). The abundance of lobster increased rapidly for the first 7 years after protection and seems to have leveled out since. In contrast, another heavily exploited species, the abalone *Haliotis rubra*, has

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[*] Grace RV (1981) Tawharanui marine monitoring programme. Report on progress. Unpublished report prepared for the Auckland Regional Authority, p 32.

[†] Grace RV (1989) Tawharanui marine monitoring programme. Report on progress. Unpublished report prepared for the Auckland Regional Authority, p 29.

[‡] Grace RV (1991) Tawharanui marine monitoring programme. Report on progress. Unpublished report prepared for the Auckland Regional Authority, p 26.

declined in the reserve (14). Manipulative studies and circumstantial evidence suggest that this decline is due in part to an indirect effect of protection, whereby the increased size and abundance of lobster has led to increased predation on small and intermediate size classes of abalone in the reserve (14, 16).

The abundance of sea urchins *H. erythrogramma* also declined in the reserve over time (Fig. 1 in main text). This decline was not evident at nonreserve sites, and experimental studies found higher predation rates on tagged urchins in the reserve (15). This indirect effect of protection was not evident in the first 7 years during which *H. erythrogramma* abundance was stable, but over the following 4 years urchin abundance declined by ≈30% (14). This lag in response is most likely related to the time taken for lobster to increase in abundance in the reserve and to reach a size that is sufficient to consume adult urchins (120 mm carapace length; ref. 15).

Macroalgal canopy cover has remained relatively stable at both reserve and fished sites over the 11 years of monitoring (Fig. 1 in main text), and there is no evidence that the decline in urchins in the reserve at Maria Island has resulted in changes in macroalgal assemblages. It is suggested that the changes in algal species composition seem to be due to natural variability within the system rather than being fishing related (14). Given that *H. erythrogramma* does not seem to have a structuring influence on algal assemblages, strong indirect effects of protection on macroalgae via trophic cascades are not likely in this system. However, the recent range expansion of another urchin, *Centrostephanus rodgersii*, into the region has resulted in the deforestation of kelp and an increase in the cover of urchin barrens in many areas (17, 18). Given the effects of this strong interactor on reef assemblages (19), longer-term monitoring is needed to assess how the effects of this species will transpire between reserve and fished areas.

Southern California. ***Context.*** The oldest marine reserve in the Channel Islands National Park is the Anacapa Island State Marine Reserve. This small (12 ha) no-take reserve was established alongshore Anacapa Island in 1978. Monitoring of fishes, invertebrates, and algae at the Channel Islands began in 1982 (20), and the data are available from the National Park in the form of a database and annual reports. The Park's monitoring effort includes 2 sites in the reserve and 14 other sites, 5 of which are suitable comparisons for the reserve. In 2003 the reserve was expanded in size (both along shore and into deeper water), and 10 other no-take reserves were added as a network of reserves in the Channel Islands. Fishing in the coastal area is predominantly recreational hook-and-line angling, and sport diving for fishes (spearfishing), spiny lobster, rock scallops, and, formerly, abalone. Near-shore commercial fishing primarily targets spiny lobster, squid, and red sea urchins.

Initial state. Because monitoring began a few years after protection, little information on the initial fished state is available. To complicate matters, in the winter of 1982–1983, the region experienced a massive El Nino Southern Oscillation (ENSO) event, and the associated large storms and warm water led to dramatic regional changes in the near-shore communities, including complete loss of kelp from many areas (21). Because of a lack of before–after comparison, the effects of fishing have been inferred primarily from comparison of the Anacapa Reserve with other monitoring sites within the same biogeographic area (some sites in the monitoring program are in colder areas with marine communities too different for suitable comparison with the two reserve monitoring sites). For the purpose of this study, we include five reference sites: four on Santa Cruz Island (Fry's Harbor, Pelican Bay, Yellow Banks, and Scorpion Anchorage) and one at Anacapa Island (Admiral's Reef).

Direct effects of fishing. Intensive fishing outside the reserve has led to differences in fished species inside and outside the small reserve. Compared with fished sites, the monitoring data indicate much higher abundances of spiny lobsters (*Panulirus interruptus*), rock scallops (*Crassedoma giganteum*), and pink abalone (*Haliotis corrugata*) (22, 23). Size measurements of red urchins (*Strongylocentrotus franciscanus*) taken by the monitoring program indicate larger size classes in the reserve, leading to a bimodal size distribution (in comparison with a single mode of smaller individuals outside the reserve) (23). The monitoring data indicate less-clear differences in fish density between reserve and fished sites, although this is likely because the comparisons do not take fish size into account (23). An independent study (24) found that two sport fish, sheephead (*Semicossyphus pulcher*) and kelp bass (*Paralabrax clathratus*), had orders of magnitude higher biomass in the reserve than immediately outside. One fishing effect has changed over time: although abalone species declined throughout the study region to near undetectable levels, the decline was much less rapid in the reserve than elsewhere (25). Preliminary assessments of new reserves added to the area in 2003 indicate that similar changes in the abundance and size of fished species occurred in the 5 years after protection (26).

Indirect effects of fishing. Fishing has potential for numerous indirect effects in this system. Spiny lobster (27) and sheephead (28) are important predators of strongylocentrotid urchins in Southern California, which are, in turn, important grazers on kelp (29). Consistent with a fishing-driven trophic cascade, the Anacapa reserve has lower densities of purple urchins and higher density of edible algae (22, 23). These differences are not driven by variation in purple urchin recruitment (22), suggesting a true indirect effect of fishing. These effects correspond to a broader ecosystem shift from algal dominated forests to crustose coralline algae and invertebrate dominated barrens (23). Furthermore, the increased abundance in purple urchins outside of the reserve seems to increase bacterial epidemics in the urchin population (22). The indirect effects of fishing are strongly region dependent. For instance, in the cooler western region of the channel Islands, spiny lobsters are less important predators, and a nonfished sea star exerts more control of urchin populations, suggesting that fishing will have much less of an indirect negative effect on kelp as one moves north and west (22, 23, 29).

Trends over time. Although most studies have considered spatial comparisons between the reserve and fished sites, there is considerable temporal variation in the system. In particular, oceanographic variation in temperature, storms, and nutrient availability alter conditions for giant kelp (which prefers cooler, calmer "La Nina" conditions) (29). Similarly, oceanographic variation associated with ENSO can lead to large-scale temporal variation in sea urchin recruitment (30). Lafferty and Behrens (31) compared the temporal variation in the kelp forest ecosystem inside and outside the reserve. They found that the reserve was always forested (according to a multivariate index), compared with a much more dynamic fluctuation between forests and barrens outside the reserve. They speculated that the higher abundance of urchin predators inside the reserve made it easier for kelp to recover after disturbances such as large storms associated with warm (nutrient-poor) water.

The temporal dynamics of predators, urchins, and kelp have varied considerably between reserve and analogous fished sites at the Channel Islands since monitoring began in 1982. At reserve sites, sheephead exhibited an initial increase and have generally been found at greater abundances since sampling began, whereas the abundance of lobster, urchins, and kelp has fluctuated around the initial value. In contrast, fished sites show much greater variation over time and large divergence away from the initial abundances, with lobster and sheephead tending to be lower than the initial value, urchins higher, and kelp lower. Although monitoring began 4 years after the reserve was established, these long-term patterns demonstrate that the contemporary contrasting states between reserve and fished sites have resulted from changes at fished sites over time, rather than changes in the reserve after protection. The large increase in urchins at fished sites was not evident in the reserve, and subsequently kelp declined at fished sites but remained stable at reserve sites. The increase in urchins may be related to regional-scale environmental factors (e.g., ENSO) promoting greater urchin recruitment in the early 1980s. This did not, however, result in a large increase in urchins in the reserve, most likely owing to the greater abundance and biomass of lobster (22) and sheephead (24). In the absence of predators at fished sites, urchins were able to increase in numbers and overgraze kelp forests, a state that persists at these sites today.

Case Studies: Tropical Systems

Philippines. ***Context.*** Sumilon and Apo Islands, Philippines, have produced evidence over nearly 3 to 4 decades that no-take marine reserves, protected and managed by local communities, can play a key role in biodiversity conservation and fisheries management (32). These reserves were established in 1974 (Sumilon) and 1982 (Apo). Sumilon Island has no permanent residents but is fished regularly (hook and line, traps, gill nets, and spears) by approximately 100 municipal fishers from the nearby island of Cebu. Apo Island has approximately 700 permanent residents, with approximately 100 municipal fishers, using the same types of fishing gear used at Sumilon. Sumilon reserve is 0.75 km long and 37.5 ha (≈25% of the coral reef area of the island). Apo reserve is 0.45 km long and 22.5 ha (≈10% of the coral reef area of the island). Sumilon reserve has had a complex history of management over the period 1974–2009 (32). In contrast, the no-take status of the Apo marine reserve has been maintained successfully from 1982 to 2009 owing to strong, highly successful, support from the organized and empowered local community.

Initial state. These two reserves and two adjacent fished areas have been monitored by underwater visual census by the same observer (G.R.R.) almost annually for 25 years (1983–2008) (32). Six replicate 1,000-m^2 areas are censused within each reserve and nonreserve area each year. More than 200 species of reef fish in 19 Families, together with major benthic categories, are surveyed. Fig. 2 in the main text shows trajectories of fish density relative to baseline levels at these four sites over 25 years at Apo Island (1983–2008 = 26 years of continuous no-take reserve protection) and over 14 years at Sumilon Island (1994–2008 = 14 years of continuous protection from all fishing gears except hook and line). Data collected at Sumilon from 1983 to 1993 are omitted here, because the reserve was opened to fishing on two occasions during this period (32, 33). Data are presented for representatives of four trophic groups of reef fish. All representative species were subject to fishing pressure. The first group, "large predators," consisted of three species of large-bodied *Cephalopholis* (a grouper) and five species of large-bodied *Lutjanus* (a tropical snapper). The second group, "herbivores" (more accurately "grazers and browsers"), was represented by *Scarus tricolor* (a large-bodied parrotfish). A third group, "omnivores," was represented by *Hemigymnus melapterus* (a large-bodied wrasse). The fourth group, "planktivores," was represented by *Naso vlamingii* (a large-bodied surgeonfish). (Data for planktivores presented only for Apo Island.)

Direct effects. Large predators, heavily targeted by fishers, displayed very strong positive responses to reserve protection, relative to both baseline levels in reserves and to fished controls (Fig. 2 in main text). There were 50-fold and 5-fold increases in density of these predators in the Apo and Sumilon reserves over periods of protection of 26 and 14 years, respectively. Build-up of large predators in these reserves was exponential over 9–18 years of reserve protection (33, 34). This exponential pattern continued at both reserves for up to 25 years (Apo) and 10–11 years (Sumilon) of reserve protection (Fig. 2 in main text). In contrast, the recovery trajectory of the large-bodied surgeonfish *N. vlamingii* in Apo reserve had an inflection point at 8–10 years and a distinct asymptote of density after 15–20 years of protection (35) (Fig. 2 in main text).

Distinct increases in relative density of large predators were noted in the two fished control areas (Fig. 2 in main text), for two different reasons. At Apo nonreserve, predator density showed a clear increase after a decade of protection of the nearby reserve (33), with this increase being very clear beyond 18 years of protection of the reserve (Fig. 2 in main text). This increase has been shown to be more pronounced closer to (200–250 m) than further from (250–500 m) the reserve boundary and provides evidence for spillover of fish from the Apo reserve to nearby fished areas (35–38). At Sumilon nonreseve (Fig. 2 in main text), predators initially increased in density markedly, owing to a very successful recruitment pulse of *Cephalopholis* in 1995 (33). However, the density of these predatory fish was subsequently reduced over time in the Sumilon nonreserve, whereas it continued to show a steady increase in the Sumilon reserve over the same period (Fig. 2 in main text). Recruitment pulses are known to have substantial effects on fish abundance both inside and outside reserves (33). A general observation from both islands is that relative density of reef fish was much more variable in the fished than in the reserve areas (Fig. 2 in main text). This may be partly due to the fact that in fished areas any gains from recruitment may be fished down relatively rapidly.

Indirect effects. The herbivorous parrotfish displayed a clear positive response to reserve protection at Sumilon reserve over periods of protection of 3–14 years (Fig. 2 in main text) and tended to decline in density in the Sumilon nonreserve (Fig. 2 in main text). The parrotfish also showed a positive response to 8–12 years of reserve protection at Apo (Fig. 2 in main text), with little clear pattern of change over time in the Apo nonreserve (Fig. 2 in main text). The increase in parrotfish density inside Apo reserve was lost from 13 to 26 years of protection. This may have been due to increased predation on juvenile parrotfish due to the buildup of predatory fish in Apo reserve. Other studies have noted increases followed by decreases in parrotfish density inside no-take reserves in both the Philippines (39) and Kenya (40).

The omnivorous wrasse displayed little response to reserve protection over time at Sumilon reserve and had very stable density at Sumilon nonreserve (Fig. 2 in main text). The wrasse declined in density at Apo reserve, and this reduced density persisted for 25 years (Fig. 2 in main text). This may have been due to increased predation on juvenile wrasses due to the buildup of predatory fish in Apo reserve. However, a similar long-term decline in density of the wrasse was recorded at Apo nonreserve over the same period (Fig. 2 in main text).

Trends over time. Despite the suggestion of trophic responses of reef fish communities to reserve protection (possible decreases in density of the parrotfish and wrasse coinciding with increases in predator density), such effects seem somewhat equivocal (similar patterns often noted in fished controls over the same time periods) and relatively weak. Furthermore, there was no evidence from the long-term studies of Sumilon and Apo islands that reserve protection has affected the benthos, particularly coral cover (see figure 3 in ref. 41). A recent study has detected very clear trophic and benthic responses to reserve protection in the southern Philippines (39). Distinct increases in density and biomass of both parrotfish and herbivorous surgeonfish coincided with significant but moderate declines in macroalgal cover in coastal reserves up to 11 years old in the southern Philippines (39). However, there was no evidence that fishing of herbivores on southern Philippine coral reefs has resulted in trophic cascades and subsequent "benthic phase shifts" (shifts from coral to algal dominance).

Kenya. ***Context.*** Fisheries closures in Kenya have been established over a period from 1972 to 2005, and this has created the potential to use a space-for-time substitution that spans nearly 40 years. The response to protection has been monitored over this period in four marine parks and at four unmanaged sites. The cessation of fishing results in fairly predictable changes for a variety of functional groups (40, 42). Fishing is very intense, diverse, and unselective in the areas around the fisheries closures. The general developing model arising from these studies is that the there is a pivotal role of the predators of sea urchins, largely some triggerfish species and large wrasses, which can change the ecology of these reefs from a sea urchin to a fish grazing ecosystems and associated ecology (43). The most effective predator, the red-lined triggerfish (*Balistapus undulatus*) is slow to recover, and consequently there can be a lag of more than a decade for ecologic processes to change.

Initial state. Two of the closures were studied before the elimination of fishing, and the initial states are typified by an abundance of herbivorous sea urchins feeding on turf algae, low to moderate hard coral, calcareous red and green algae, and fleshy erect algal cover, and small-bodied damselfishes, parrotfish, surgeonfish, and wrasses as the dominant fish. Erect algae can be abundant in places that are difficult for sea urchins to access, such as the top of coral heads with dead surfaces, which are often colonized by large brown algae, such as *Sargassum*.

Direct effects. Closure is associated with an increase in many of the fisheries target species, and the triggerfish and larger wrasses show a slow but steady increase after closures as well as the herbivorous fishes, which can be slower than the carnivorous fishes. Densities of these groups approximately double in a 10-year period, but the largest increases are in the biomass, associated with an increase in the sizes of fish, such that biomass of most fish groups experiences a >10-fold increase after 20 years of closure.

Indirect effects. Losses of sea urchins can be very species specific because there are approximately eight common species and they differ considerably in their body sizes, behaviors, and defenses against predation (44). Species living openly (*Tripneustes gratilla* and *Diadema setosum*) or small-bodied species (*Echinometra mathaei*) are expected to decline most rapidly with the increase in predators. Cryptic species and large-bodied species (*Echinostrephus molaris*, *D. savignyi*, and *Echinothrix diadema*) are expected to decline slower, and the largest species, *E. diadema*, can persist for many years before declining in numbers. Their loss may be due to senescence of old individuals and slow recruitment because of predation on the recruits as well as an eventual increase in predator sizes that can prey on the largest individuals. The switch from sea urchin to fish grazing is also expected to change the benthic cover. Calcareous algae (red and green species) and possibly hard corals are expected to increase after sea urchin grazing declines, and there may also be changes in the types of fleshy erect algae associated with the different selectivity of fish vs. urchins (45). These changes are expected to produce changes in ecologic functions of production and calcification, as well as a series of other poorly studied and understood indirect effects on various small and cryptic species.

Trends over time. There are a series of changes on different time scales, the quickest response being the increase in size of targeted species during the first few years of closure. At slightly longer time scales of 5–10 years more recruitment of individuals and species occurs, such that the numbers of species increase and eventually do not increase appreciably after approximately 10 years of closure. Slow-growing and colonizing species still require greater periods of time to approach equilibrium, and it is clear that even many moderate-sized species, such as in the surgeonfish and triggerfish families, have not reached their full biomass after 40 years of closures (40). The largest species with the largest space requirements, such as sharks and other top-level predators, may never colonize these small closures and maintain viable populations. Consequently, the full succession to pristine conditions is very unlikely to occur in these small to moderate-sized closures.

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