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

R. C. Babcock[a,1], N. T. Shears[b], A. C. Alcala[c], N. S. Barrett[d], G. J. Edgar[d], K. D. Lafferty[e], T. R. McClanahan[f], and G. R. Russ[g]

[a]Commonwealth Scientific and Industrial Research Organization, Marine and Atmospheric Research, Cleveland, Queensland 4163, Australia; [b]Marine Science Institute, University of California, Santa Barbara, CA 93106; [c]Silliman University-Angelo King Center for Research and Environmental Management, Silliman University, Dumaguete City 6200, Philippines; [d]Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Hobart, Tasmania 7001, Australia; [e]Western Ecological Research Center, US Geological Survey, c/o Marine Science Institute, University of California, Santa Barbara, CA 93106; [f]Wildlife Conservation Society, Marine Programs, Bronx, NY 10460-1099; and [g]School of Marine and Tropical Biology and Australian Research Council Centre for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

Edited by Steven D. Gaines, University of California, Santa Barbara, CA, and accepted by the Editorial Board January 29, 2010 (received for review July 28, 2009)

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

Author contributions: R.C.B., N.T.S., A.C.A., N.S.B., G.J.E., K.D.L., T.R.M., and G.R.R. designed research; R.C.B., N.T.S., A.C.A., N.S.B., G.J.E., K.D.L., T.R.M., and G.R.R. performed research; R.C.B. and N.T.S. analyzed data; and R.C.B., N.T.S., N.S.B., G.J.E., K.D.L., T.R.M., and G.R.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. S.D.G. is a guest editor invited by the Editorial Board.

[1]To whom all correspondence should be addressed. E-mail: russ.babcock@csiro.au.

This article contains supporting information online at www.pnas.org/cgi/content/full/0908012107/DCSupplemental.

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

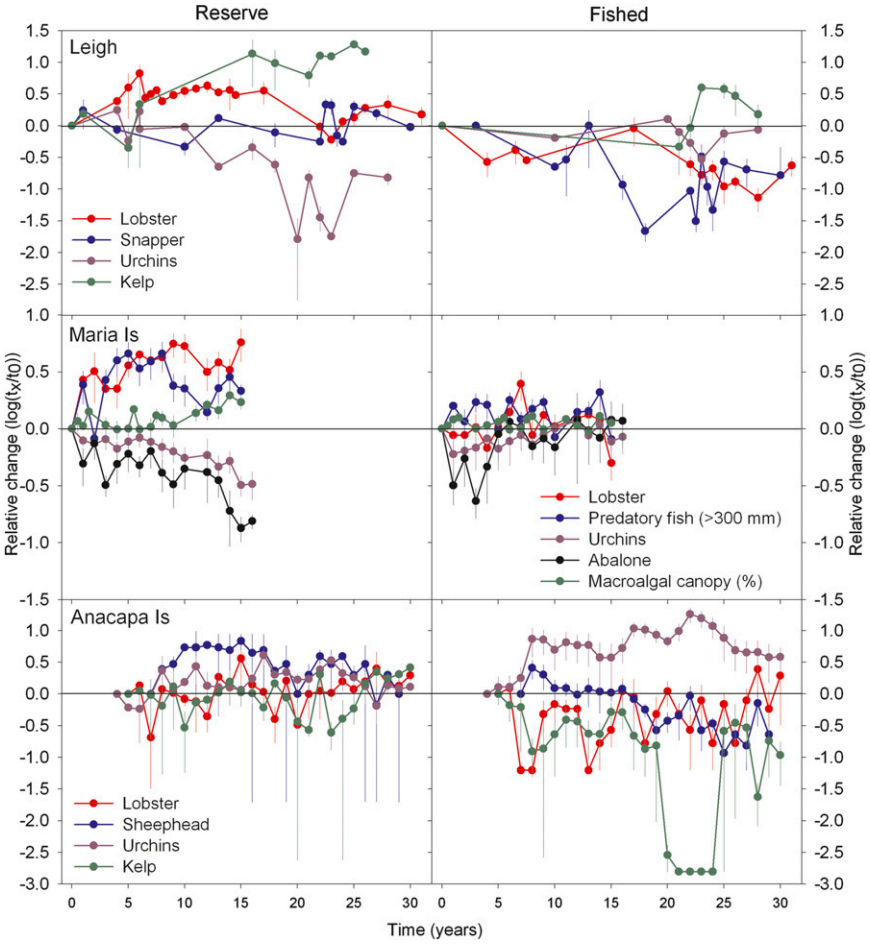

Fig. 1. Long-term changes in key populations at temperate no-take marine reserve locations and reference (fished) areas. Data are means (±SE), expressed as a ratio of the observed (t = x) vs. initial values at the time reserves were implemented (t = 0) and were log transformed for presentation and comparison. 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).

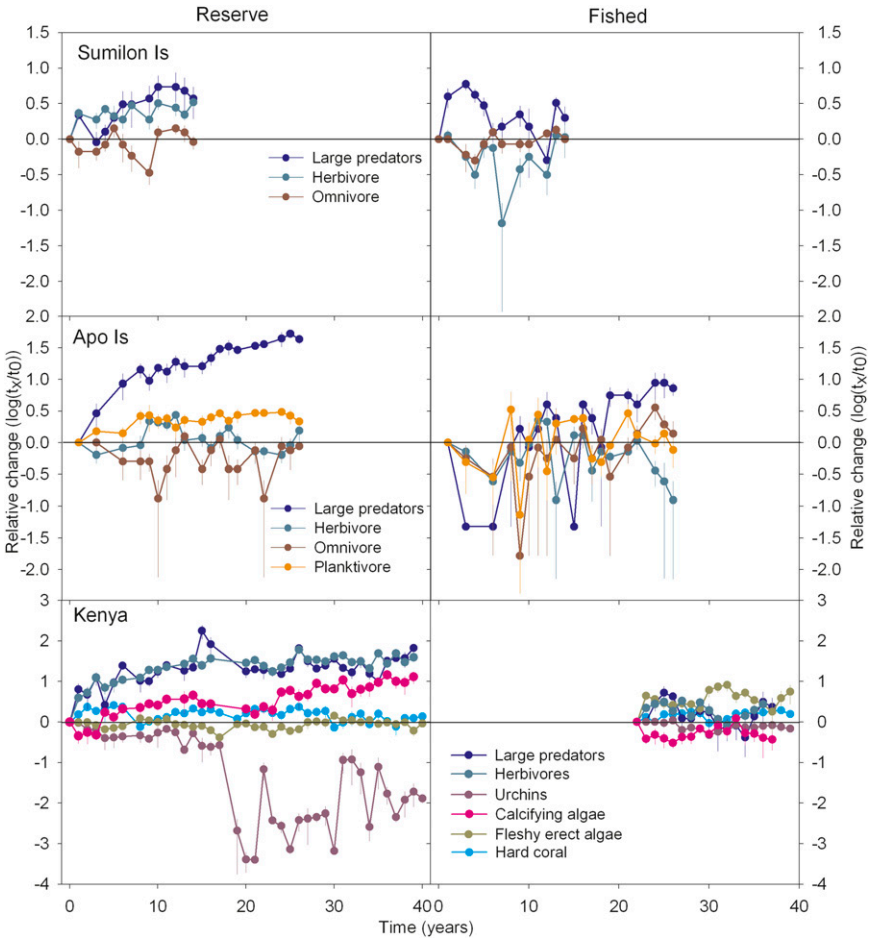

Fig. 2. Long-term changes in key populations at tropical no-take marine reserve locations and reference (fished) areas. Data are means (±SE), expressed as a ratio of the observed (t = x) vs. initial values at the time reserves were implemented (t = 0) and were log transformed for presentation and comparison. 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

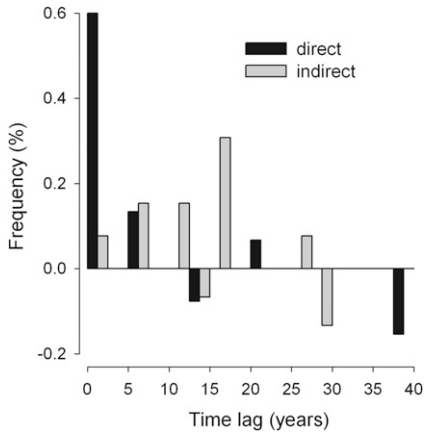

Fig. 3. Time to first detection of direct and indirect responses to marine reserve protection. Positive data indicate the proportion of observed species displaying direct and indirect effects, negative values indicate taxa for which no effect was observed. n = 28.

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.

ACKNOWLEDGMENTS. We thank C. Wood, M. Behrens, and two anonymous reviewers for providing comments on the paper; David Kushner of the National Park Service for providing data for the Anacapa reserve comparison; and Tim Haggitt and Kala Sivaguru for providing data for the Leigh Reserve time series.

1. Balmford A, Gravestock P, Hockley N, McClean CJ, Roberts CM (2004) The worldwide costs of marine protected areas. *Proc Natl Acad Sci USA* 101:9694–9697.
2. Cinner JE, et al. (2009) Linking social and ecological systems to sustain coral reef fisheries. *Curr Biol* 19:206–212.
3. Steneck RS, et al. (2009) Thinking and managing outside the box: Coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. *Coral Reefs* 28:367–368.
4. Denny CM, Willis TJ, Babcock RC (2004) Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Mar Ecol Prog Ser* 272:183–190.
5. McClanahan TR (2000) Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biol Conserv* 94:191–198.
6. Jennings S (2001) Patterns and prediction of population recovery in marine reserves. *Rev Fish Biol Fish* 10:209–231.
7. Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol Appl* 13:S117–S137.
8. Molloy PP, McLean IB, Cote IM (2009) Effects of marine reserve age on fish populations: A global meta-analysis. *J Appl Ecol* 46:743–751.
9. Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecol Appl* 14:1709–1723.
10. Lester SE, et al. (2009) Biological effects within no-take marine reserves: A global synthesis. *Mar Ecol Prog Ser* 384:33–46.
11. Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. *Mar Ecol Prog Ser* 189:125–134.
12. Castilla JC (1999) Coastal marine communities: Trends and perspectives from human exclusion experiments. *Trends Ecol Evol* 14:280–283.
13. Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Mar Ecol Prog Ser* 246:1–16.
14. Behrens MD, Lafferty KD (2004) Effects of marine reserves and urchin disease on southern California rocky reef communities. *Mar Ecol Prog Ser* 279:129–139.
15. Mumby PJ, et al. (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101.
16. Pinnegar JK, et al. (2000) Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. *Environ Conserv* 27:179–200.
17. May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269:471–477.
18. Gunderson LH (2000) Ecological resilience—in theory and application. *Annu Rev Ecol Syst* 31:425–439.
19. Tomkins JL, Kotiaho JS (2004) Publication bias in meta-analysis: Seeing the wood for the trees. *Oikos* 104:194–196.
20. Lafferty KD, Behrens MD (2005) Temporal variation in the state of rocky reefs: Does fishing increase the vulnerability of kelp forests to disturbance?. *Proceedings of the Sixth California Islands Symposium*, eds Garcelon DK, Schwemm CA (Institute for Wildlife Studies, Arcata, CA), pp 499–500.
21. Abesamis RA, Russ GR (2005) Density-dependent spillover from a marine reserve: Long-term evidence. *Ecol Appl* 15:1798–1812.
22. Barrett N, Edgar GJ, Buxton CD, Haddon M (2007) Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *J Exp Mar Biol Ecol* 345:141–157.
23. Barrett NS, Buxton CD, Edgar GJ (2009) Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *J Exp Mar Biol Ecol* 370:104–119.
24. St. John J, Russ GR, Brown I, Squire L (2001) The diet of the large coral reef serranid, *Plectropomus leopardus*, in two fishing zones on the Great Barrier Reef, Australia. *Fish Bull (Wash D C)* 99:180–192.
25. Kelly S, MacDiarmid AB (2003) Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *N Z J Mar Freshw Res* 37:149–158.
26. Kelly S, Scott D, MacDiarmid AB (2002) The value of a spillover fishery for spiny lobsters around a marine reserve in northern New Zealand. *Coast Manage* 30: 153–166.
27. Russ GR, Alcala AC (1989) Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar Ecol Prog Ser* 56:13–27.
28. Russ GR, Alcala AC (1996) Marine reserves: Rates and patterns of recovery and decline in abundance of large predatory fish. *Ecol Appl* 6:947–961.
29. Russ GR, Alcala AC (2003) Marine reserves: Rates and patterns of recovery and decline of predatory fish, 1983-2000. *Ecol Appl* 13:1553–1565.
30. Pederson HG, Johnson CR (2006) Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. *J Exp Mar Biol Ecol* 336: 120–134.
31. Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142.
32. Hagen NT, Andersen A, Stabell OB (2002) Alarm responses of the green sea urchin, *Strongylocentrotus droebachiensis*, induced by chemically labelled durophagous predators and simulated acts of predation. *Mar Biol* 140:365–374.
33. Annala JH, Bycroft BL (1988) Growth of rock lobsters *(Jasus edwardsii)* in Fiordland, New Zealand. *N Z J Mar Freshw Res* 2:29–41.
34. Andrew NL, MacDiarmid AB (1991) Interrelations between sea urchins and spiny lobsters in northern New Zealand. *Mar Ecol Prog Ser* 70:211–222.
35. Choat JH, Robertson DR (2002) Age-based studies on coral reef fishes. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, ed Sale PF (Academic Press, San Diego), pp 57–80.
36. Menge BA (1997) Detection of direct versus indirect effects: Were experiments long enough? *Am Nat* 149:801–823.
37. Hilborn R, Walters CJ (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty* (Chapman and Hall, New York).
38. Sutherland JP (1974) Multiple stable points in natural communities. *Am Nat* 108: 859–873.
39. Walters CJ, Holling CS (1990) Large-scale management experiments and learning by doing. *Ecology* 71:2060–2068.
40. Babcock EA, Pikitch EK, McAllister MK, Apostolaki P, Santora C (2005) A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. *ICES J Mar Sci* 62:469–476.