TRAJECTORIES AND CORRELATES OF COMMUNITY CHANGE IN NO-TAKE MARINE RESERVES

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Abstract. Marine reserves are a spatial approach to marine management and conservation aimed at protecting and restoring multispecies assemblages and the structure and function of marine ecosystems. We used meta-analyses of published data to address the questions of how and over what time frames marine assemblages change within no-take marine reserves as they recover from fishing and other human uses. We used 20 studies of coastal fish assemblages from 31 temperate and tropical locations, reporting abundances, and in some cases biomass, of 10–134 species from reserve and reference conditions (i.e., conditions in nearby fished sites or before reserve establishment) spanning 1–25 years of protection. Synthesis of data from these diverse sets of assemblages showed that: (1) a species' level of exploitation, trophic level, and the duration of protection through the no-take reserve explain small but significant amounts of variation in individual species responses to protection, with only species that are targeted by fishing or by aquarium trade showing overall enhanced abundances in protected areas, and increasing positive effects of protection on abundances at top trophic levels through time; (2) up to a third of species in different studies (19% on average) appeared to be negatively affected by protection, indicating that indirect effects of protection through competitive or predatory interactions may be common; and (3) variation and lags in species responses to protection resulted in protected assemblages diverging from reference conditions, with greater proportions of total fish biomass at top trophic levels in protected compared to fished assemblages. These results indicate that marine reserves are effective in enhancing local abundances of exploited species and restoring the structure of whole communities, though these changes occur through a series of transient states and, for some communities, over long time frames (decades). In contrast with the more predictable increases of aggregate community variables such as total abundance and biomass, individual species and community structure exhibited broad variation in their responses to protection. Marine protected areas represent multiple human-exclusion ''experiments,'' replicated in a variety of ecosystem types and geographic locations, providing key insights on community-wide impacts of the removal of human extraction. Long-term monitoring of community trajectories in marine protected areas and modeling studies scaling up local effects to relevant spatial and temporal scales are needed to increase our ability to protect and restore whole marine systems and to set realistic targets for the conservation and restoration of specific assemblages.

Key words: coastal fish assemblages; community change; community structure; fishing impacts; human impacts; indirect effects; marine protected areas; marine reserves; meta-analysis; recovery; temporal trajectories; trophic cascades.

INTRODUCTION

Marine reserves, portions of the coastline or ocean set aside and protected from fishing and other extractive uses, have recently received great attention as a means of conserving marine biodiversity and restoring depleted fish stocks (Allison et al. 1998, NRC 2001, Palumbi 2001, 2002). In addition to protecting the populations directly targeted by fishing, reserves are established with the goals of protecting and restoring

habitat, whole assemblages, and ecological interactions among their components and to replenish depleted populations in adjacent areas through export of larvae, juveniles, and adults (NRC 2001, Palumbi 2002).

In recent years, a large number of studies have evaluated the performance of reserves with respect to these objectives. Increased abundances, biomass, organism sizes, and diversity have been documented for a variety of marine species and assemblages from many different locations (Boersma and Parrish 1999, Palumbi 2001, 2002, Halpern 2003). Changes in community composition have also been highlighted in a number of cases and have been attributed to both differential responses of species with different life histories and dispersal

abilities to fishing or to protection (e.g., Jennings et al. 1999, Jennings 2001, Fisher and Frank 2002) and to indirect effects of protection through trophic interactions (McClanahan et al. 1996, 1999, Sala and Zabala 1996, Sala et al. 1998, Steneck 1998, Babcock et al. 1999, Pinnegar et al. 2000, Micheli et al. *in press*). In addition to local responses within reserves, spillover into adjacent areas and increased catch per unit effort (CPUE) following reserve establishment have also been documented (Yamasaki and Kuwahara 1990, Russ and Alcala 1996, McClanahan and Mangi 2000, Roberts et al. 2001, Gell and Roberts 2003).

Key questions that have just begun to be addressed concern the temporal trajectories and the between-species variability of population and community responses to protection. How rapid are biological responses within and around marine protected areas (MPAs)? How persistent through time? How do responses vary depending on the species or assemblages considered? What are the characteristics of species exhibiting differential responses to protection? How common are indirect effects of protection, i.e., situations in which some species decline because of increased predation or competition within the protected areas? Answers to these questions are critical for predicting time frames of recovery of depleted populations and communities and for implementing management and monitoring of MPAs. A better understanding of the patterns and correlates of the variation in efficacy of protection and in the temporal trajectories of recovery in MPAs is needed. This understanding will help predict what species and community attributes are more likely to benefit from protection within no-take reserves. It also will help select focal species, species groups, and biological variables for monitoring reserve effectiveness (Goñi et al. 2000, Fraschetti et al. 2002). Finally, it will contribute to establishing realistic targets for reserve evaluation (e.g., a five-year time frame was proposed for initial evaluation of the efficacy of reserves in the Channel Islands Marine Sanctuary, California, USA; Gerber et al. 2003).

Empirical observations to date have indicated that some variables change relatively soon after the implementation of a reserve and remain near the new level. A recent synthesis of empirical data showed that density, biomass, average organism size, and diversity in reserves relative to controls reached mean levels within a typically short time (1–3 yr) and subsequently remained consistent across reserves up to 40 yr of age (Halpern and Warner 2002). Moreover, responses in these biological variables were independent of reserve size, indicating that even small reserves can enhance population and assemblages (Halpern 2003).

In contrast with persistent effects on total abundances, biomass, and numbers of species, long-term studies of MPAs indicate that continuous change in community composition and transient states in community structure can occur over decades following MPA establishment (e.g., McClanahan 2000, Shears and Babcock 2002). Thus, the distribution of the enhanced abundances and biomass among different components of the community may vary over long time frames. For example, establishment of the Mombasa Marine National Park in Kenya was followed by increases in a sea-urchin predator, the wrasse *Chelinus trilobatus*, during the first 3 yr (McClanahan 2000). However, sea urchin declines and recovery of corals occurred after more than 10 yr and coincided with later recovery of the triggerfish *Balistapus undulatus*, also a predator of sea urchins. Data from five fully protected Kenyan MPAs indicate that populations of *B. undulatus* showed positive trends in their abundances after over 30 yr of protection (McClanahan 2000).

Species may respond differently to protection depending on the intensity of exploitation to which they are subject outside the reserve and prior to its establishment, their life history characteristics, and their larval, juvenile, and adult dispersal ability. In a meta-analysis of studies of fish assemblages from marine reserves, Mosquera et al. (2000) found that differential responses of fish families to marine reserve establishment correlated with their level of exploitation and body size, with stronger positive responses for the taxa characterized by larger body sizes. Because maximum body size is usually correlated with life history parameters such as age at maturity, growth, and reproductive output, this variable may be a useful surrogate for predicting recovery rates from low population sizes (Jennings et al. 1999, Jennings 2001). Fisher and Frank (2002) examined changes in community composition from a 31-yr time series of abundances of over 70 fish species within a fishery closure and an adjacent reference area on the Scotian Shelf, Canada. A preliminary review of life history attributes for 16 species in this data set indicated that different trajectories may be related to dispersal ability of the species. In contrast to the results reported above (Jennings et al. 1999, Mosquera et al. 2000, Jennings 2001), species with benthic eggs, ovoviviparity, and small body size (i.e., species likely to have limited dispersal in the larval, juvenile, or adult stages) tended to benefit from the fishery closure more than those with pelagic eggs or larger body sizes (i.e., potentially greater dispersal abilities and home ranges; Fisher and Frank 2002).

The limited availability of long-term data series from MPAs prevents direct comparisons of the temporal trajectories in community structure and dominance by different species and trophic groups following the establishment of MPAs. However, MPAs with varying settings and histories of protection provide multiple human-exclusion ''experiments'' from which generalizations about community responses to protection can be drawn. To examine variation in community structure as a function of duration of protection and of the ecological characteristics of the species in the community, we synthesized published data of fish assemblages from re-

serves ranging 1–25 yr in age. We used this data set to address the following questions: (1) How do responses to protection vary among species and/or species groups? (2) What are the correlates of the different responses of species to protection? (3) Over what time frames (e.g., few years to decades) do communities respond to protection? Answers to these questions are critically important to predicting recovery following fishing disturbance and to the management and evaluation of reserves.

METHODS

The data set

We searched the literature for field studies that examined responses of multispecies assemblages to protection within no-take marine reserves. Because our goal was to examine change in community structure associated with reserve establishment, we included studies in which abundances or biomass within no-take reserves had been compared to reference conditions, determined from spatial reference sites or measurements before the reserve establishment (Appendix). Studies that focused on a few focal species (less than 10 species, as an arbitrary threshold) or that reported only total abundances or biomass instead of data for individual species were not included in the analyses. Because most studies meeting these requirements focused primarily on fish assemblages, we did not include the few studies that reported data on benthic algal and invertebrate assemblages (e.g., McClanahan 1997, Lasiak 1998, Edgar and Barrett 1999) and limited our analysis to examining variation in fish assemblages.

All studies had been conducted using visual census techniques (belt transects or point counts) with only one exception. Johnson et al. (1999) compared fish abundances between unfished and fished sites within the Merritt Island National Wildlife Refuge, Florida, USA, using trammel-net samples. CPUE data were used for this study. Ultimately data from 20 studies, conducted at 31 different locations, were included in these analyses (Appendix). Only three studies compared fish assemblages before and after reserve establishment. In a majority of studies, fish assemblages within no-take reserves were compared to assemblages at fished reference sites. Between 10 and 134 fish species were censused in each study (Appendix). The final data set comprised a total of 376 species, belonging to 62 families. Because only five studies reported biomass data (Appendix), most analyses were conducted only on density or abundance data. From each study we noted the following variables describing the characteristics of protection and of the sampling intensity: (1) the duration of protection (ranging 1–25 yr); (2) the reserve size (i.e., its surface area, ranging 11–32 388 ha); (3) the type(s) of habitat sampled (e.g., coral reef, temperate rocky reef, seagrass beds, or estuary); (4) the number of species censused (ranging 10–134 spe-

cies); and (5) the number of replicate belt transects or point counts conducted in the censuses (ranging 5–130; see Appendix).

One of our goals was to establish how patterns of change in community composition varied depending on the level of resolution used to describe community composition. Weak responses of multiple species to protection may sum and result in overall greater effect sizes when species are pooled into broader groups (e.g., broader taxonomic or functional groups). Conversely, strong individual responses may be obscured when species are grouped into broader categories. We chose trophic groups as the functional categories within which species were pooled because fishing typically disproportionately targets species at high trophic levels and this can influence the overall trophic structure of marine communities (e.g., Pauly et al. 1998); thus, we expected recovery from fishing to include increased abundances or biomass of top predators and shifts in trophic structure. Halpern's (2003) analysis of published data indicated that different trophic groups show similar responses to protection. However, in that analysis species were assigned to trophic groups based on their family. Because there is considerable variation in species diets within each family, lumping of species into family-level trophic groups might have obscured differential responses of trophic groups.

Each species was assigned to one of six trophic groups using the diet information reported in R. Froese's and D. Pauly's database "FishBase" (*available online*):[6] herbivores, detritivores, omnivores, invertebrate-feeders, planktivores, and piscivores. Piscivores included both species that tend to feed exclusively on other fishes and species feeding on both fishes and benthic or pelagic invertebrates (i.e., at trophic level ≥ 3.5). We extracted additional information about potentially important correlates of the responses of individual species to protection from FishBase. These variables included: (1) exploitation level (i.e., whether the species is a major fishing target, a minor target, is targeted by aquarium trade, or is not targeted by any fishery); (2) trophic level (ranging 2.0–4.5 for the species in this data set); (3) maximum body size (i.e., maximum length reported, ranging 5.5–300 cm for the species in this data set); and (4) adult mobility (sedentary or territorial, mobile, and highly mobile or migratory species). Information about larval dispersal, another species-specific trait that is likely to influence responses to protection (i.e., Palumbi 2001), was available for only a small subset of species and was not included in these analyses.

Variation and correlates of species responses to protection

We quantified the effects of protection in no-take reserves on fish species as the natural log of the ratios

[6] ⟨http://www.fishbase.org⟩

between abundance within reserves and in reference conditions (response ratio, ln R; Gurevitch and Hedges 1993, Osenberg et al. 1997, Hedges et al. 1999). Positive response ratios indicate that the species has greater abundance within reserves than in reference conditions, whereas negative values are indicative of greater abundances in reference conditions compared to reserves. In some cases, separate comparisons had been conducted within different habitat types and depth strata within each study. Comparisons between reserves and reference conditions conducted in different habitat types or depth strata were kept separate in this meta-analysis because sampling had targeted different assemblages. Thus, separate response ratios (and similarity values, see *Community responses to protection*) were calculated for each comparison.

To assess the potential correlates of responses of species to protection, we conducted multiple regression analyses examining the relationship between the magnitudes of individual species responses (i.e., response ratios, ln R) and the species' exploitation level, trophic level, body sizes, and adult mobility. In addition, duration of protection and reserve size were included in these models as potentially important variables influencing responses of species with varying life histories and mobility. We hypothesized that species characterized by large body size and/or large home ranges may exhibit strong positive responses to protection in relation to reserve size, whereas reserve size should not influence responses for smaller, sedentary species.

Response ratios for each species in the data set were the dependent variables in these analyses, and the duration of protection, reserve size, the species trophic level, and maximum body size were the independent variables. Exploitation level and adult mobility of each species were also included in the model as categorical variables, ranging from 1 to 4 for exploitation level (i.e., 1 for nontarget species and 4 for heavily fished species) and from 1 to 3 for adult mobility (with 1 corresponding to sedentary or territorial species and 3 to highly mobile or migratory species). Backward elimination of terms was used to retain in the model only the variables that explained significant amounts of the variation in the dependent variable, using the conservative significance level of 0.10. Data on abundances in reserves and reference conditions were available for a total of 376 species. Multiple observations were available for several species, yielding a total of 920 observations.

To determine whether increasing numbers of species responded to protection through time, we examined the relationship between the proportion of species showing strongly positive responses to protection (i.e., ln $R \geq$ 0.69; see below) with duration of protection. We subdivided response ratios into strongly positive (i.e., abundances in reserves are twice or greater than that seen in reference conditions, resulting in ln $R \geq$ 0.69), strongly negative (i.e., abundances in reference con-

ditions are twice or greater than that seen in reserves, resulting in ln $R \leq -0.69$), and intermediate ($-0.69 <$ ln $R <$ 0.69). These thresholds were chosen because previous meta-analyses of studies of marine reserves found that, on average, protection in no-take reserves results in abundances that were double those in reference conditions (Halpern 2003). The proportion of species falling in each of these categories was calculated for each study in the data set. To examine whether greater proportions of species showed positive responses to protection with increasing duration of protection, we used multiple regression analyses with the proportions of species showing positive (ln $R \geq$ 0.69) or negative (ln $R \leq -0.69$) responses as the dependent variable and duration of protection and reserve size as the independent variables. Finally, to examine which characteristics of species correlated with their increased or decreased abundances within marine reserves, we calculated the proportion of species showing positive (ln $R \geq$ 0.69), negative (ln $R \leq -0.69$), and intermediate responses ($-0.69 <$ ln $R <$ 0.69) by trophic group and by exploitation and mobility categories.

Responses of species groups to protection

We determined how species groups responded to protection by examining the mean magnitudes and the temporal trends of their response ratios (ln R). Species were grouped in different categories based on their trophic level, exploitation status, or mobility. Response ratios were combined by calculating weighted averages within each category (Hedges and Olkin 1985, Gurevitch and Hedges 1993). Weights were defined as the inverse of the sampling variance for each study. Sampling variances were approximated, following Hedges and Olkin (1985), as

$$v_i = \left[\frac{(N_i^{\mathrm{R}} + N_i^{\mathrm{C}})}{(N_i^{\mathrm{R}} N_i^{\mathrm{C}})}\right] + \left[\frac{(\ln R_i)^2}{2(N_i^{\mathrm{R}} + N_i^{\mathrm{C}})}\right]$$

where N_i^{R} and N_i^{C} are the sample sizes for the ith study for the reserve and reference conditions, respectively, and ln R_i is the response ratio for the study. Weighted means of response ratios were calculated as

$$\ln R{+} = \sum (w_i \ln R_i) \bigg/ \sum (w_i)$$

where $w_i = 1/v_i$. Averages of the mean response ratio for each category (i.e., trophic groups, exploitation levels, and mobility categories) weighted by the sampling variance (Hedges and Olkin 1985, Gurevitch and Hedges 1993) were considered significantly different from 0 (i.e., there is a significant effect of protection on that particular group) when the 95% confidence limits around the mean did not overlap 0.

Temporal trends in the response ratios of different trophic, exploitation, and mobility groups were examined using multiple regression analysis as described above. Response ratios for each category were the de-

pendent variable and duration of protection, reserve size, and the numbers of species in each group were the independent variables. Species richness within each group was included because groups composed of large numbers of species may exhibit stronger positive responses due to the higher probability of including species that benefit from protection. Because multiple analyses were conducted on the same data set, the significance level for tests conducted on each group was adjusted using the Dunn-Sidék correction, as $\alpha = 1 - (1 - \alpha)^{1/k}$, with $\alpha = 0.05$ and k = the number of separate comparisons (e.g., $k = 6$ separate comparisons for each of the six trophic groups, yielding an adjusted significance level of 0.009) (Sokal and Rohlf 1995).

Community responses to protection

We quantified changes in community structure in terms of species and trophic groups using the Bray-Curtis similarity index (Bray and Curtis 1957). Bray-Curtis percentage similarity expresses the distance between pairs of samples on a scale between 0 and 100, with 0 indicating that the two samples do not share any of the species and 100 signifying that the samples have identical species composition and species have identical abundances. Intermediate values can result from samples containing the same species in different relative abundances or varying to different degrees in their species composition. The pair of samples used in each similarity calculation was the reserve and the reference from each study. Abundances of individual species and trophic groups were square-root transformed before calculating Bray-Curtis similarity to decrease the influence of the most abundant species (Clarke and Warwick 1994).

Temporal trends in community and trophic similarity were examined using multiple regression models. In addition to the duration of protection, reserve size and species richness were included as variables that may influence responses of fish assemblages to protection. Full models included the percentage similarity between reserves and reference conditions as the dependent variable and the duration of protection, reserve size, and number of species surveyed in each study (for species similarity) or the number of species within each trophic group (for trophic similarity) as the independent variables.

We compared trophic structure between reserves and reference conditions by calculating the proportions of the total fish abundance or biomass in different trophic groups for each study. Mean proportions, weighted by the sampling variance, were calculated separately for reserves and reference conditions. Because only five studies reported biomass data, temporal trajectories of trophic and community similarity could not be examined in terms of biomass, and biomass data were used only to calculate mean proportional contributions of different trophic groups to total biomass. Analyses

TABLE 1. Multiple regression analysis of response ratios for each species in the data set.

Variable	Slope	P
Model with significant variables only (overall, $r^2 = 0.03$, $F_{3,916} = 8.2$, $P = 0.0001$)		
Intercept	1.26	0.01
Duration of protection	0.04	0.002
Trophic level	−0.46	0.002
Exploitation level	0.26	0.009

Note: The independent variables in the full model were duration of protection (in years), size of reserves (in hectares), trophic level, exploitation level, maximum length, and adult mobility.

were conducted using the statistical package SAS version 6.12 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Variation and correlates of species responses to protection

Duration of protection, trophic level, and exploitation level explained a significant but extremely small (only 3%) amount of the variation in the magnitudes of individual species responses to protection, expressed as response ratios (Table 1). In contrast, reserve size, maximum length of species, and adult mobility exhibited no significant relationship with response ratios of individual species (Table 1). The magnitudes of individual species responses to protection showed a weak but significant positive relationship with duration of protection (Fig. 1a). More interestingly, response ratios of individual species to protection exhibited broad variation, ranging from strongly negative to strongly positive in all studies (Fig. 1a, b). Some fraction of species in almost all communities showed decreased abundances (i.e., abundances within reserves half or less than abundances in fished, reference conditions) within reserves regardless of duration of protection. Between 5 and 91% (mean 35.8%, SD = 18.2) of species, in separate studies, showed strong increases in abundance (ln $R \geq 0.69$) within reserves compared to reference conditions (Fig. 1b), while a substantial percentage of species, between 0 and 36% (mean 19.2%, SD = 10.5), showed strong decreases in abundance (ln $R \leq -0.69$) in reserves (Fig. 1b).

The proportions of species showing positive (i.e., ln $R \geq 0.69$; see *Methods: Variation and correlates of species responses to protection*) responses to protection did not increase significantly with increasing duration of protection (Table 2 and Fig. 1b). Similarly, species exhibiting negative (i.e., ln $R \leq -0.69$) responses to protection showed no temporal trend associated with increasing duration of protection (Table 2 and Fig. 1b). This result, combined with the positive temporal trend in the magnitudes of individual species responses, suggests that communities within no-take reserves and in reference conditions tend to diverge through time (see *Community responses to protection*) because some spe-
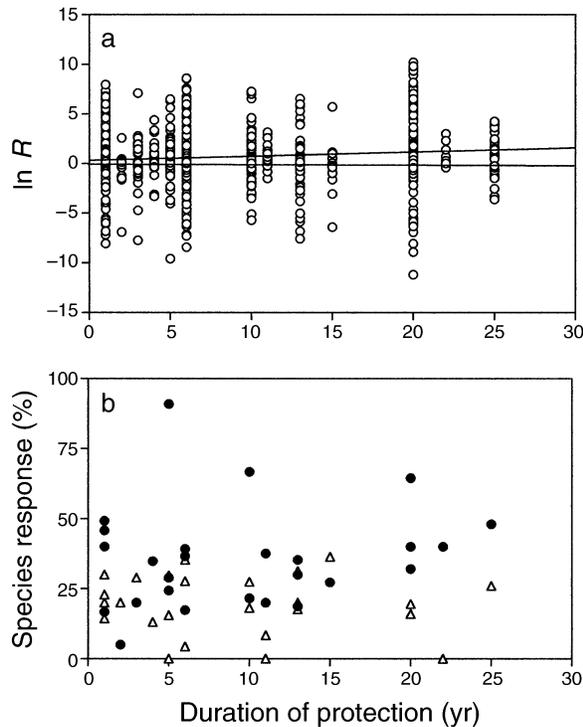
FIG. 1. (a) Response ratios (ln R, calculated as the natural log of the ratios between abundances within reserves and in reference conditions) of individual species. (b) Percentages of species within each study exhibiting positive responses (solid circles; $\ln R \geq 0.69$, see *Methods: Variation and correlates of species responses to protection*) or negative responses (open triangles; $\ln R \leq -0.69$) to protection in reserves ranging from one to 25 years of protection.

cies exhibit stronger responses to protection through time rather than because of increasing numbers of species responding through time.

No trends were apparent in the representation of different trophic groups among species exhibiting negative, positive, or intermediate responses to protection (*G* test on frequencies of negative, positive, or intermediate species responses, by trophic group categories: $G = 17.6$, df = 10, $P > 0.05$; Fig. 2a). In contrast, a greater proportion of species showing negative responses to protection (i.e., $\ln R \leq -0.69$) were not targeted by fishing or aquarium trade compared to species showing positive or intermediate responses (*G* = 81.1, df = 6, $P = 0.0001$; Fig. 2b). In addition, species showing negative responses comprised a greater proportion of species characterized by low mobility compared to species showing positive or intermediate responses (*G* = 29.9, df = 4, $P = 0.0001$; Fig. 2c). Species showing negative responses to protection tended to be more commonly in the families Blenniidae, Gobiidae, Anthinae, and Apogonidae and to a lesser extent Diodontidae, Atherinidae, Pomacentridae, and Labridae.

Responses of species groups to protection

Meta-analysis of response ratios for different trophic groups indicated that protection in reserves is associated with significantly greater abundances, relative to reference conditions, for all trophic groups except the omnivores (Fig. 3a). Because of a significant temporal trend of response ratios for piscivorous fishes (Fig. 4f and Table 3), we recalculated mean response ratios separately for reserves protected for different amounts of time. For piscivorous fishes, overall response was significantly greater than 0 both in assemblages protected for at least 10 yr and in assemblages protected for <10 yr. However, the magnitude of the response ratio was, on average, approximately six times greater in assemblages protected for at least 10 yr (mean response ratio ln $R = 0.92$, 95% CL = 0.81, 1.04) than in those protected for <10 yr (mean ln $R = 0.16$, 95% CL = 0.02, 0.30). When the extreme negative value (Fig. 4f) was deleted, overall response was still four times smaller for assemblages protected for <10 yr (mean ln $R = 0.22$, 95% CL = 0.07, 0.37) compared to assemblages protected for at least 10 yr. Meta-analyses of response ratios by exploitation categories indicated that nontarget species show no overall response to protection, whereas species targeted by fishing or aquarium trade show positive overall responses to protection (Fig. 3b). All three mobility categories exhibited significant increased abundances within reserves (low mobility, mean ln $R = 0.08$, 95% CL = 0.04, 0.11; intermediate mobility, mean ln $R = 0.27$, 95% CL = 0.25, 0.29; high mobility, mean ln $R = 0.52$, 95% CL = 0.48, 0.55).

To determine whether different trophic groups varied in their response to protection through time, we examined temporal trends in the response ratios for each trophic group. Only piscivorous fish exhibited significant temporal trends in their response to protection in no-take reserves (Table 3 and Fig. 4). To examine whether these results were driven by the extreme negative value of response ratio (Fig. 4f), we repeated the

TABLE 2. Multiple regression analysis of percentage of species showing positive responses (i.e., twice as abundant or more within no-take reserves than in reference conditions) and negative responses (i.e., twice as abundant or more in reference conditions than within no-take reserves) to protection.

Response (Y) and variable	Slope	P
Positive response (overall, $r^2 = 0.07$, $F_{2,23} = 0.8$, $P = 0.44$)		
Intercept	0.33	0.0001
Duration of protection	0.01	0.34
Reserve size	−0.00	0.33
Negative response (overall, $r^2 = 0.02$, $F_{2,23} = 0.3$, $P = 0.76$)		
Intercept	0.20	0.0001
Duration of protection	−0.002	0.53
Reserve size	0.00	0.63

Note: The independent variables in the full model are duration of protection (in years) and size of reserves (in hectares).
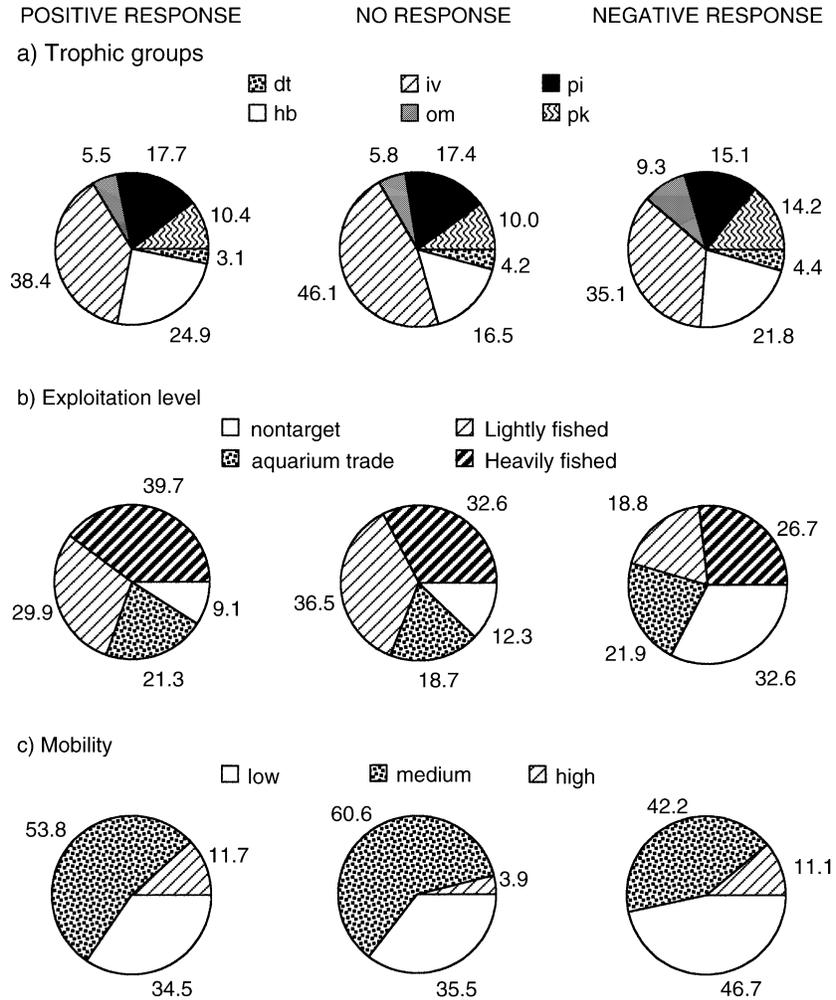
POSITIVE RESPONSE   NO RESPONSE   NEGATIVE RESPONSE

a) Trophic groups

dt   iv   pi
hb   om   pk

5.5 17.7   5.8 17.4   9.3 15.1
10.4   10.0   14.2
3.1   4.2   4.4
38.4   46.1   35.1
24.9   16.5   21.8

b) Exploitation level

nontarget   Lightly fished
aquarium trade   Heavily fished

39.7   32.6   18.8   26.7
29.9   9.1   36.5   12.3   21.9
21.3   18.7   32.6

c) Mobility

low   medium   high

53.8   60.6   42.2
11.7   3.9   11.1
34.5   35.5   46.7

FIG. 2. Percentages of species exhibiting positive (ln $R \geq 0.69$), intermediate (i.e., no response, $-0.69 < \ln R < 0.69$), and negative (ln $R \leq -0.69$) responses to protection in different (a) trophic groups (hb, herbivores; dt, detritivores; om, omnivores; iv, invertebrate feeders; pk, planktivores; pi, piscivores), (b) exploitation levels, and (c) adult mobility categories.

analysis after eliminating this value. After the lowest value was deleted, backward elimination of nonsignificant terms left the duration of protection as the only independent variable in a model explaining 17% of variation, although the probability value for duration of protection ($P = 0.01$) was only marginally significant at the adjusted significance level of 0.009 (see *Methods*). For all other trophic groups, relationships between the magnitude of the response, measured as the log ratio of abundances within reserves over reference conditions, and the duration of protection were nonsignificant (Table 3 and Fig. 4a–e). The size of reserves and the number of species composing the trophic group did not explain a significant amount of variation in response ratios for any of the trophic groups (Table 3). None of the exploitation ($P = 0.40$–0.97) or mobility ($P = 0.14$–0.82) species groups exhibited significant relationships with duration of protection.

Community responses to protection

Similarity in species composition between fish assemblages within no-take reserves and reference conditions decreased with increasing duration of protection, indicating that assemblages tended to diverge in their species composition through time (Fig. 5a). However, this trend was not statistically significant ($P = 0.07$; Table 4) when the whole data set was included in the analysis. In separate analyses conducted on temperate (i.e., rocky reefs, estuaries, and seagrass beds) and tropical (coral reefs) fish assemblages, the negative relationship between species similarity and duration of protection was significant for tropical but not for temperate systems (Table 4). Both temperate and tropical assemblages exhibited wide variation in similarity values, even for reserves of similar ages (Fig. 5). In addition to duration of protection, the number of species in each study explained a significant amount of vari-
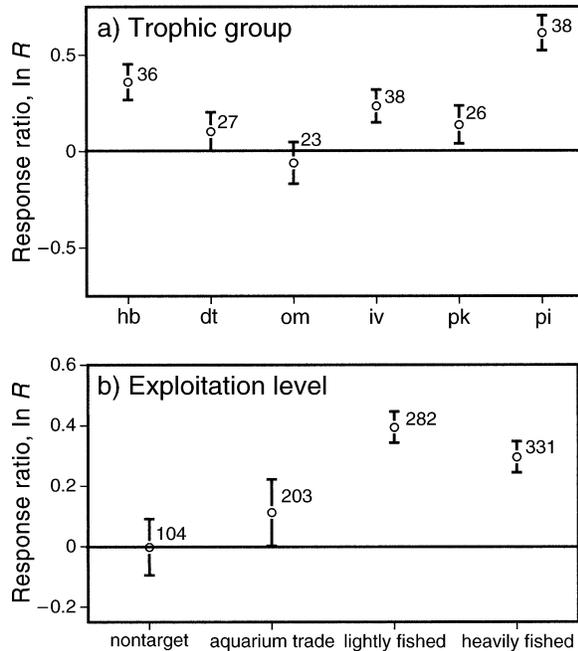
FIG. 3. Results of meta-analyses of the response ratios ($\ln R$) for (a) each of six trophic groups (hb, herbivores; dt, detritivores; om, omnivores; iv, invertebrate feeders; pk, planktivores; pi, piscivores) and (b) four exploitation levels (nontarget species, species targeted by the aquarium trade, and species lightly or heavily fished). Mean response ratios, weighted by sampling variances, are reported for each category. Bars represent 95% CI. When confidence intervals do not overlap 0, weighted averages are considered significantly different from 0. The number of comparisons within each category is reported to the right of each mean.

ation in similarity (Table 4), with species-rich assemblages showing lower similarity than those containing fewer species. There was no significant relation between similarity and reserve size (Table 4).

Similarity between the trophic structure of fish assemblages within reserves and in reference conditions also showed large variability and a weak and nonsignificant (Table 4) negative trend with increasing duration of protection (Fig. 5b). There was no significant relationship between trophic similarity and reserve size or number of species within trophic groups (Table 4).

The proportions of total fish abundance in different trophic groups were similar between reserves and reference conditions (Fig. 6a). When similar calculations were repeated using the biomass data, there were clear differences between reserves and reference conditions (Fig. 6b). The proportion of the total fish biomass that was piscivorous fishes was greater in reserves (range 10–43%, mean 24.5%, SD = 10.9) than in reference conditions (range 5–24%, mean 15.5%, SD = 5.5), whereas the opposite was true for herbivorous fishes (reserves, range 1–71%, mean 45%, SD = 28.4; reference, range 1–80%, mean 56%, SD = 27.0). Proportional piscivore biomass within reserves was signifi-

cantly greater than in reference conditions ($T = 2.6$, df = 9, $P = 0.03$). Because biomass data were available for only 10 separate comparisons between protected and fished areas from five studies (Appendix), it was not possible to examine the temporal trajectories in the community trophic structure in terms of biomass.

DISCUSSION

Meta-analyses of studies of the effects of no-take marine reserves on fish communities yielded three key results. First, species in all assemblages showed wide variation in their responses to protection. In particular, up to a third of species in different assemblages (19% on average) appeared to be negatively affected by protection and had abundances within reserves that were half or less those documented in reference, fished conditions. Second, protection appears to influence the trophic structure of fish assemblages, with abundances of top predators increasing gradually through time and top predators accounting for greater proportions of the total biomass in the protected assemblages, though this result is based on only 10 comparisons from five studies (Fig. 6b). These results indicate that no-take marine reserves are an effective tool for rebuilding top trophic levels, typically depleted through fishing (e.g., Pauly et al. 1998, Jackson et al. 2001), although recovery of long-lived top predators will likely require long time frames (e.g., Jennings 2001, Russ 2002, Russ and Alcala 2003). Thus, the similarity of contributions of predatory fishes to total fish abundances in reserves and fished areas (Fig. 6a) may result from the relatively short duration of protection (<10 yr) in many of the reserves in this data set. Third, the structure of fish assemblages protected in no-take reserves diverges through time from reference, fished conditions, though this trend is statistically significant only for coral reef ecosystems. Thus, in addition to general responses of aggregate variables (e.g., abundance or biomass of families or all whole assemblages; e.g., Mosquera et al. 2000, Halpern 2003) to protection, synthesis of results from multiple studies shows that the distribution of abundances or biomass among different species is affected by protection and that effects on resulting community structure vary depending on the duration of protection. The result that changes in fish assemblages continue over time for decades following protection has important implications for setting protection targets and monitoring reserve effectiveness.

Variation in species responses to protection was significantly correlated to the degree to which species were exploited outside the no-take reserves, in addition to the duration of protection and trophic level. Species targeted by fishing or by aquarium trade showed overall significant increases in abundance within protected areas (Fig. 3). A large proportion of species negatively affected by protection are not targeted by fishing or aquarium trade (Fig. 2), resulting in an overall lack of response to protection for nontarget species (Fig. 3).
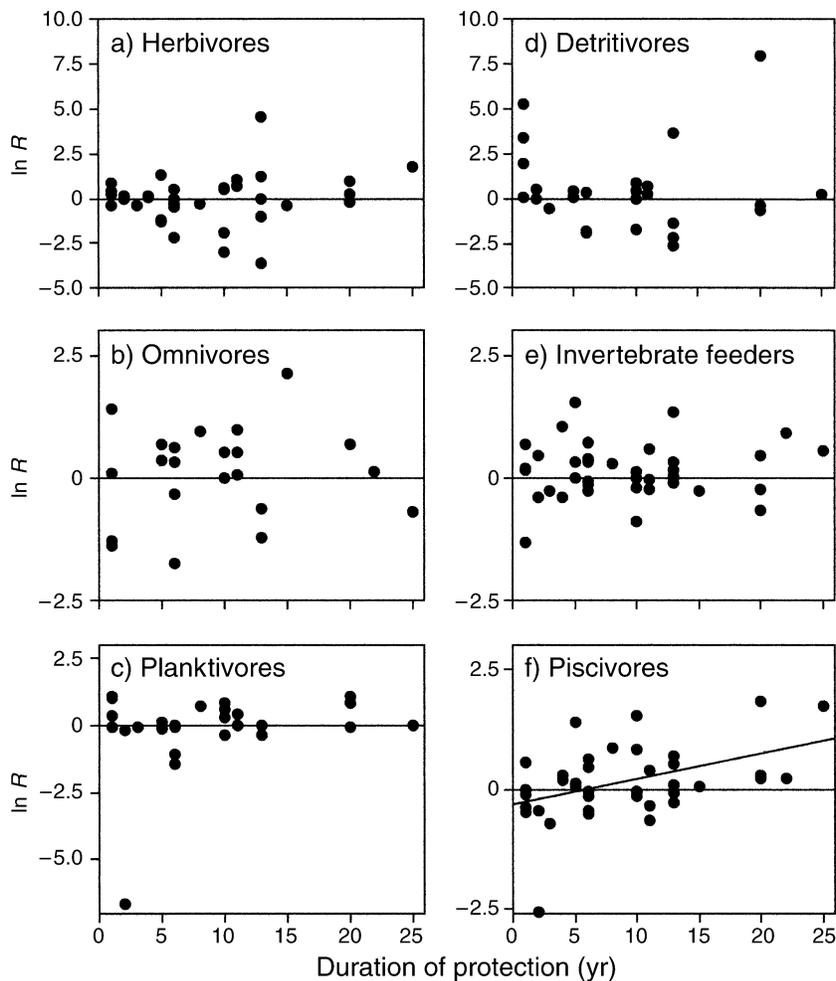
FIG. 4. Response ratios (ln R) vs. duration of protection for each of six trophic groups. A statistically significant temporal trend was found only for piscivores.

The nearly ubiquitous occurrence of strong negative effects of protection on some species in the assemblages (Fig. 1), most often nontarget species characterized by low mobility (Fig. 2), particularly in the families Blenniidae, Gobiidae, Anthinae, and Apogonidae, is evidence of indirect effects of protection. That is, some species may increase in abundance within fished areas and, conversely, decline in reserves because of the enhanced abundances of their predators or competitors that commonly occur within MPAs. Indirect effects of protection have been difficult to demonstrate and most case studies involve relatively sedentary herbivorous invertebrates, primarily sea urchins and limpets (Pinnegar et al. 2000). In contrast, our analyses suggest that indirect effects are common, but easily missed because they typically do not occur over whole trophic levels, but rather in individual species belonging to different trophic levels (e.g., Polis 1999). Stronger and more widespread indirect effects of protection may become apparent in reserves protected for sufficient durations of time to allow build-up of top

predator abundances and biomass. Build-up of top predators may result in major changes in community structure through cascading trophic interactions (Sala et al. 1998, Steneck 1998) in older reserves (e.g., sites protected for decades).

The magnitude of individual species responses to protection showed a weak but significant increase through time (Fig. 1a). In contrast, the proportions of species showing positive (i.e., ln $R \geq 0.69$; see *Methods: Variation and correlates of species responses to protection*) or negative (i.e., ln $R \leq -0.69$) responses to protection did not increase significantly with increasing duration of protection (Fig. 1b). Thus, temporal trends of community similarity (Fig. 5a) are likely due to some species showing stronger responses to protection through time rather than to increasing numbers of species responding through time. This result has important implications for monitoring of reserve effectiveness because species' long-term responses to protection may be determined (and therefore predict-

TABLE 3. Multiple regression analysis of response ratios for each trophic group.

Trophic group and variable	Slope	P
Herbivores (overall, $r^2 = 0.05$, $F_{3,32} = 0.5$, $P = 0.67$)		
Intercept	−0.52	0.27
Duration of protection	0.04	0.37
Reserve size	0.00	0.95
No. species	0.02	0.38
Detritivores (overall, $r^2 = 0.03$, $F_{3,23} = 0.2$, $P = 0.90$)		
Intercept	0.07	0.95
Duration of protection	−0.04	0.66
Reserve size	−0.01	0.94
No. species	0.35	0.48
Omnivores (overall, $r^2 = 0.31$, $F_{3,19} = 2.8$, $P = 0.07$)		
Intercept	0.77	0.22
Duration of protection	−0.01	0.64
Reserve size	0.00	0.08
No. species	−0.14	0.16
Planktivores (overall, $r^2 = 0.28$, $F_{3,22} = 2.8$ $P = 0.06$)		
Intercept	−0.81	0.25
Duration of protection	0.06	0.16
Reserve size	−0.01	0.06
No. species	0.07	0.35
Invertebrate feeders (overall, $r^2 = 0.04$, $F_{3,35} = 0.5$, $P = 0.67$)		
Intercept	0.23	0.29
Duration of protection	0.01	0.83
Reserve size	−0.00	0.24
No. species	−0.01	0.58
Piscivores (overall, $r^2 = 0.31$, $F_{3,34} = 5.2$, $P = 0.005$)		
Intercept	−0.78	0.04
Duration of protection	0.07	0.01
Reserve size	−0.00	0.11
No. species	0.04	0.31

Note: The dependent variables in the full model are duration of protection (in years), size of reserves (in hectares), and total number of species within each trophic group.

able) by their response in the first few years after protection.

The size of reserves and the mobility of species did not have significant effects on species and community responses to protection. Differential species responses associated with adult mobility and reserve size may be expected because high mobility or small reserve size may lead to high probabilities that individuals cross the reserve boundaries and are caught. Halpern's (2003) analyses also showed that reserve size did not explain significant amounts of variation in the responses of total abundance and biomass to protection. Together, these results suggest that, across different assemblages, multiple species are able to benefit from reserve protection regardless of their mobility. However, the lack of an effect of species mobility on their responses to protection may be explained by the strong positive correlation between mobility and exploitation level among the species in this data set ($r = 0.38$, $P = 0.0001$, $N = 920$). Thus, mobile species tend to be subject to intense fishing pressure and the expected dependence of effects of protection on species mobility may be

obscured by the counteracting dependence on exploitation level.

Similarity in species composition and relative abundances between protected and reference assemblages tended to decrease with increasing duration of protection, although only significantly so in tropical assemblages. This indicates that protected assemblages become increasingly different from what they were prior to the reserve establishment or from sites that are not protected from fishing and other extractive human activities (Fig. 5a). Moreover, changes in community structure associated with protection exhibited a linear trend with duration of protection (Fig. 5a), with no indication of reaching a plateau within the 25-yr time frame considered in this study. These results suggest that continuous change in the relative dominance of different species reported for a few case studies (e.g., Babcock et al. 1999, McClanahan 2000, Shears and Babcock 2002) may be a general response of marine assemblages to protection. What is even more striking, however, is the large variability in similarity values,
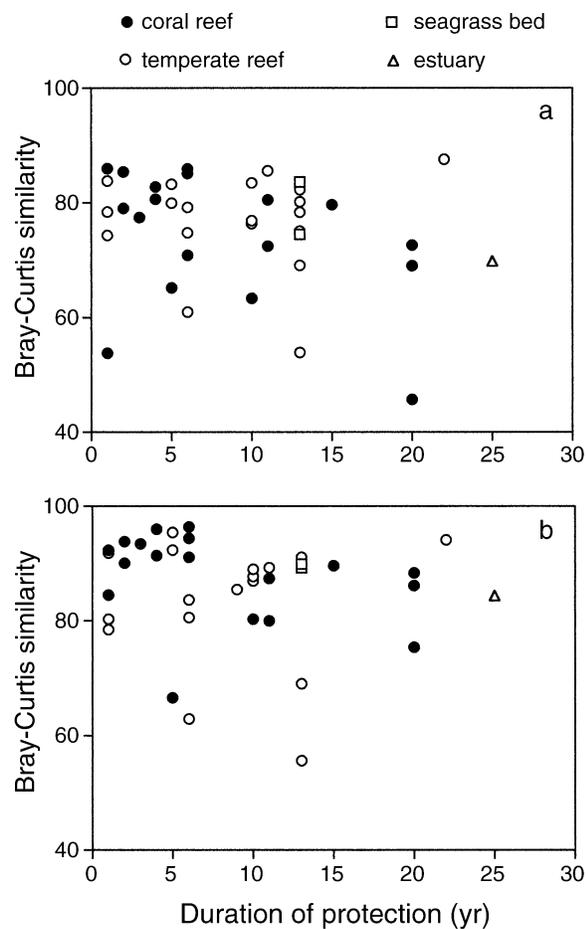

FIG. 5. Bray-Curtis percentage similarity in (a) species and (b) trophic group composition of fish assemblages between no-take reserves of varying ages (i.e., duration of protection, in years) and reference conditions.

TABLE 4. Multiple regression analysis of Bray-Curtis percentage similarity in (a) species and (b) trophic structure for all studies in the data set, temperate systems, and coral reefs.

Model and variable	Slope	P
a) Species similarity		
All studies (overall, $r^2 = 0.31$, $F_{3,36} = 5.3$, $P = 0.004$)		
Intercept	85.36	0.0001
Duration of protection	−0.40	0.07
Reserve size	−0.00003	0.84
No. species	−0.17	0.001
Temperate systems (overall, $r^2 = 0.01$, $F_{3,18} = 0.06$, $P = 0.98$)		
Intercept	78.66	0.0001
Duration of protection	−0.06	0.87
Reserve size	−0.001	0.86
No. species	−0.03	0.78
Coral reefs (overall, $r^2 = 0.59$, $F_{3,14} = 6.6$, $P = 0.005$)		
Intercept	87.30	0.0001
Duration of protection	−0.66	0.04
Reserve size	0.0001	0.97
No. species	−0.19	0.003
b) Trophic similarity		
All studies (overall, $r^2 = 0.04$, $F_{3,35} = 0.5$, $P = 0.66$)		
Intercept	85.8	0.0001
Duration of protection	−0.20	0.41
Reserve size	0.0002	0.34
No. species	0.02	0.73
Temperate systems (overall, $r^2 = 0.02$, $F_{3,17} = 0.08$, $P = 0.97$)		
Intercept	80.58	0.0001
Duration of protection	0.10	0.84
Reserve size	0.0004	0.91
No. species	0.06	0.70
Coral reefs (overall, $r^2 = 0.16$, $F_{3,14} = 0.9$, $P = 0.47$)		
Intercept	89.84	0.0001
Duration of protection	−0.44	0.15
Reserve size	0.0001	0.50
No. species	0.005	0.92

Note: The dependent variables in the full model are duration of protection (in years), size of reserves (in hectares), and (a) total number of species or (b) total number of species within each trophic group, i.e., herbivores, detritivores, omnivores, planktivores, invertebrate feeders, and piscivores.

even for reserves of similar ages. Such broad variation in effects of protection on community structure suggests that local conditions may play an important role in determining the responses of a specific assemblage. Local fishing patterns, the degree of degradation that occurred before protection, or the presence of species that are strong interactors in that system may underlie part of the observed large variation in community responses to protection.

Significant temporal trends in community similarity in tropical but not in temperate systems may be an artifact of the specific locations and design of the studies in this data set. The influence of the particular group of studies available on the results is a common problem in meta-analyses (e.g., Gurevitch and Hedges 1993). Alternatively, greater numbers of species in the coral reef fish assemblages may drive the different responses

to protection between tropical and temperate ecosystems. In particular, species richness explained a significant amount of the variation in community similarity between protected and reference assemblages from coral reefs. In assemblages containing large numbers of species, there may be a greater likelihood of some species responding to protection. In addition, the coral reef assemblages in these studies may have been generally subject to greater human impacts compared to the temperate reefs, though the data on the history and intensity of human pressure on these systems needed for a direct comparison are not available.

Trophic composition does not show a significant temporal trend (Fig. 5b), and effects of protection on the trophic structure of fish assemblages are evident only when trophic structure is examined in terms of biomass, not abundance (Fig. 6). Assemblages protected from fishing for 3–13 yr had greater relative proportions of predatory biomass than fished assemblages. These relative differences in trophic group biomass indicate a shift in the trophic structure of fish assemblages protected from fishing. When assemblage composition is quantified in terms of abundance, species-level changes in abundance in no-take reserves and the increase in the abundances of top predators through time do not result in observable changes in relative abundances of whole trophic groups. Effects of protection on the distribution of fish biomass among different trophic groups may occur because species in top trophic levels are typically characterized by large sizes and protection from fishing allows them to attain larger sizes (e.g., Halpern 2003). A combination of increased abundances and increased individual sizes of piscivorous fishes likely explains their greater proportional contribution to fish biomass in no-take reserves compared to reference conditions.

In contrast to the rapid responses of other biological variables to protection, changes in species composition and relative dominance and in trophic structure seem to occur gradually and over relatively long time frames. Halpern and Warner (2002) showed that significant increases in total abundances and biomass in marine reserves typically occurred within a few years (1–3 yr) after the reserve establishment. In contrast, our analyses of trophic group responses suggest that recovery of trophic structure likely requires decades. This conclusion is supported by the following observations. First, temporal trends in the magnitude of piscivorous fish responses were weakly positive, with no indication of having reached a plateau in reserves protected for more than a decade (Fig. 4f). Second, increased piscivores abundance did not result in overall changes in their relative contribution to total abundances even when the older reserves in this data set (protected for at least 10 yr) were included in the analyses (Fig. 6a). However, greater mean proportions of piscivores were observed in terms of biomass, probably through the combined effects of protection on size structure in ad-
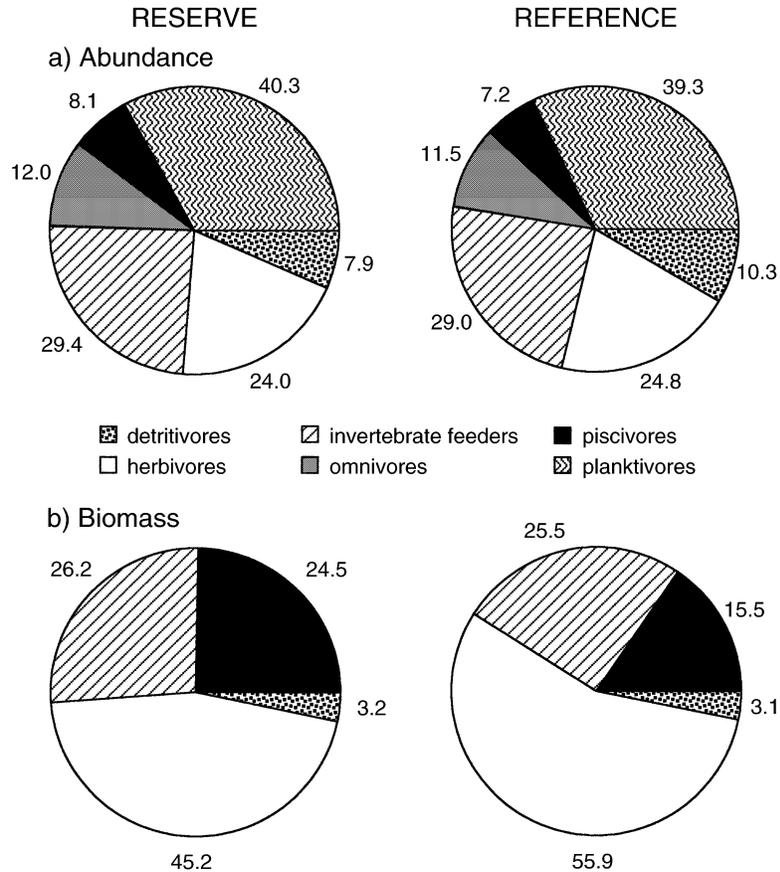
FIG. 6. Percentages of (a) total fish abundances and (b) biomass in different trophic groups. Percentages are weighted means of values from (a) 38 abundance comparisons between protected and fished areas from 20 individual studies and (b) 10 biomass comparisons from five studies.

dition to abundance. Thus, exploited communities respond quickly to protection, but subsequent temporal trends in responses vary depending on the specific community attribute considered (e.g., total community abundance or biomass vs. community species composition and relative abundances, or trophic structure). The different temporal trajectories of responses of aggregate community descriptors and community structure to protection have important implications for evaluation of MPAs because these variables are linked to different ecological functions of communities (e.g., productivity vs. maintenance of diversity and resilience in the face of natural disturbances) and their variation is likely underlain by different processes (e.g., Micheli et al. 1999).

Significant but slow changes in the community and trophic structure of fish assemblages within no-take marine reserves have important implications for the management and monitoring of reserves. In particular, while temporary closures may be effective for rebuilding populations and increasing yields of short-lived, fast-growing species (e.g., scallops in Georges Banks; Murawski et al. 2000), recovery of trophic structure and of ecological interactions structuring marine as-

semblages may require decades and may entail a series of sequential transient states. This consideration supports the notion that reserves aimed at conserving and restoring whole assemblages and ecological processes should be established as permanent no-take zones. Even though practical reasons (i.e., limited time and resources) have often constrained the evaluation of reserves efficacy to snapshot comparisons of some biological variable before and some time after the reserve establishment, or between reserves and some reference, unprotected sites (e.g., Palumbi 2001, 2002, Halpern 2003), evaluation of the effectiveness of reserves in allowing for the recovery of whole assemblages from human impacts should focus on long-term temporal trajectories of change. Long-term monitoring would explicitly account for the dynamic nature of marine assemblages, for the likely occurrence of unanticipated changes and lags in responses from indirect effects, and for the fact that the time scales over which ecological systems are influenced by natural and human disturbances are largely unknown, but likely longer than most ecological studies (e.g., Magnuson 1990).

A crucial question is how these observed changes in the abundances of top trophic levels and in their pro-

portional contribution to total biomass compare to what might be observed in truly pristine ecosystems. The long history of human exploitation of all of the sites in this data set, lack of information about actual enforcement and compliance to fishing restrictions within the reserves, and the general lack of baseline data for the sites make it impossible to address this question. Data from the northwestern Hawaiian islands, one of the marine ecosystems that has been indicated as possibly the closest to pristine (Jackson et al. 2001), indicate that approximately 50% of fish biomass is accounted for by top predators, specifically large piscivorous snappers, groupers, carangids, and sharks (Friedlander and DeMartini 2002). A direct comparison of this estimate to those from the studies synthesized here is not possible because of system-specific characteristics that are likely to influence the carrying capacities of the sites and because of the broad variability in the sampling methods and community components targeted. However, the Hawaiian value suggests that the mean proportional biomass of piscivores observed in the reserves reviewed here may be well below what the systems could potentially support. Widespread historical overfishing of virtually all marine ecosystems has dramatically altered the baselines that can be used to set desired targets (Pauly 1995, Dayton et al. 2000, Jackson et al. 2001). In the absence of meaningful baselines, modeling provides tools for making inferences about the pre-exploitation trophic structure of different marine ecosystems (e.g., Christensen 2002).

The snapshot comparisons among reserves protected for different amounts of time are clearly not a replacement for actual time series data (e.g., Jennings 2001, Russ 2002, Russ and Alcala 2003). Thus, a limitation of this study is that temporal trajectories in community change in MPAs are inferred from a time sequence populated by different systems. Another significant limitation of the data set is that in many cases the reference sites may not be true controls. This is because of two other possible effects of reserves, not addressed here: export of organisms to areas outside of reserve boundaries and fishing effort displaced to other areas. Both of these factors could affect community structure in reference areas, producing misleading response ratios. Halpern et al. (2004) investigated this possibility in the small subset of marine reserve studies that have full before–after–control–impact designs. They found that in most cases biological variables in control areas increased over time, but at a slower rate than areas under protection. This suggests that the divergence of similarity of protected areas relative to reference sites over time as shown in this paper may actually be an underestimate of the reserve effect.

Despite these limitations, studies of community changes from multiple protected systems provide an invaluable opportunity to examine the generality of species and community responses to protection, identify the most important correlates of responses, and generate hypotheses about patterns and trends of recovery from exploitation. Synthesis of data from these multiple human-exclusion "experiments" indicate that the level of exploitation, trophic level, and the duration of protection explain small but significant amounts of variation in individual species responses to protection, with species targeted by fishing showing overall enhanced abundances in protected areas and top trophic levels showing positive temporal trends in their response to protection. Using marine reserves of different ages belonging to the same ecosystem provides a way to explore ecological succession in protected areas and possibly to guide attempts to actively restore degraded ecosystems. In particular, it may be possible in some cases to accelerate recovery of top predators and of their role in shaping coastal marine communities through restocking of juveniles and/or adults or through the provision of suitable habitat. Analyses of existing data from marine reserves and further experimental work in this area may provide important insights about recovery and restoration of whole marine communities.

Evaluation and management of MPAs should acknowledge that while rapid responses of heavily fished, fast-growing species may commonly occur soon after reserves establishment, recovery of whole assemblages and ecosystem function (e.g., the top-down effects of predatory fishes) will likely require longer time frames. Realistic expectations concerning the conservation and fishery benefits of MPAs should be based on the observation that transient states in community structure, indirect effects of protection, and lags in responses are common. Scaling up these results to more meaningful spatial and temporal scales will require long-term monitoring of networks of reserves, combined with modeling and historical reconstruction of ecosystem changes (e.g., Jackson et al. 2001, Christensen 2002, Botsford et al. 2003, Gerber et al. 2003).

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APPENDIX

A summary table of studies included in the meta-analyses of the effects of protection in marine reserves on fish community structure is available in ESA's Electronic Data Archive: *Ecological Archives* A014-033-A1.