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Disentangling trophic interactions inside a Caribbean marine reserve

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Abstract. Recent empirical studies have demonstrated that human activities such as fishing can strongly affect the natural capital and services provided by tropical seascapes. However, policies to mitigate anthropogenic impacts can also alter food web structure and interactions, regardless of whether the regulations are aimed at single or multiple species, with possible unexpected consequences for the ecosystems and their associated services. Complex community response to management interventions have been highlighted in the Caribbean, where, contrary to predictions from linear food chain models, a reduction in fishing intensity through the establishment of a marine reserve has led to greater biomass of herbivorous fish inside the reserve, despite an increased abundance of large predatory piscivores. This positive multi-trophic response, where both predators and prey benefit from protection, highlights the need to take an integrated approach that considers how numerous factors control species coexistence in both fished and unfished systems. In order to understand these complex relationships, we developed a general model to examine the trade-offs between fishing pressure and trophic control on reef fish communities, including an exploration of top-down and bottom-up effects. We then validated the general model predictions by parameterizing the model for a reef system in the Bahamas in order to tease apart the wide range of species responses to reserves in the Caribbean. Combining the development of general theory and site-specific models parameterized with field data reveals the underlying driving forces in these communities and enables us to make better predictions about possible population and community responses to different management schemes.

Key words: bottom-up; coral reef; ecosystem-based management; Exuma Cays Land and Sea Park, Bahamas; fishing pressure; generalist predator; marine protected areas; Nassau grouper (Epinephelus striatus)*; stoplight parrotfish* (Sparisoma viride)*; top-down; trophic cascades; yellowtail snapper* (Ocyurus chrysurus).

INTRODUCTION

Worldwide, there is increasing emphasis on marine ecosystem-based management (EBM) and away from policies focused on single species. Critical components of marine EBM are a consideration of linkages among species and the implementation of place-based management approaches, including marine protected areas (MPAs, also referred to as marine reserves) (Rosenberg and McLeod 2005). Thus, it is now more critical than ever to unravel the complex mechanisms driving multiple species responses to fisheries regulations and the establishment of MPAs. Despite the growing numbers of MPAs established around the world (UNEP-WCMC 2008), an understanding of their efficacy in protecting multispecies assemblages (Sale et al. 2005) and how their establishment interacts with existing fishing pressure and regulations is still limited (Hilborn et al. 2006). These significant remaining uncertainties are partly due to a persistent separation between empirical and theoretical studies of MPAs. Robust predictions about the responses of species and assemblages to reserve establishment and varying fishing pressure require an understanding of what processes and interactions are most critical for determining outcomes of protection in MPAs. Achieving this increased understanding and predictive ability in turn requires developing new theory and integrating theoretical models with empirical data.

Empirical studies of multispecies responses have shown that a large majority of species increase in density and biomass inside no-take marine reserves (Mosquera et al. 2000, Halpern 2003, Lester and Halpern 2008). However, as more marine reserves are established it is clear that the benefits of protection are not universal but vary among species, trophic levels, life histories, and duration of protection of reserves (Micheli et al. 2004*b*, Guidetti and Sala 2007, Claudet et al. 2008, Guidetti et al. 2008). Data from multiple reserves show that the magnitude of positive responses varies greatly both within and across reserves (Micheli et al. 2004*b*, Tetreault and Ambrose 2007): many species, particularly

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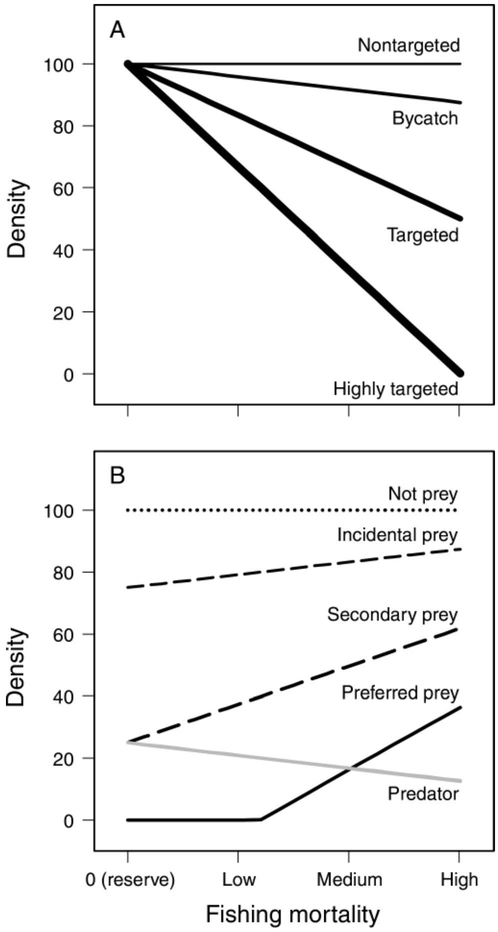

FIG. 1. Expected density trends of lower trophic level species if response to marine reserve establishment is exclusively determined by either (A) fishing mortality or (B) predation pressure. (A) Fish density as a function of fishing mortality. (B) Density of a targeted generalist predator (gray line) and its nontargeted prey (black lines) as a function of the predator's fishing mortality and attack rate. Trophic cascade effects (i.e., a negative predator–prey relationship) exist especially when predator preference for the prey is high and the prey may not be able to persist unless the predator is fished (as evidenced by the discontinuity for the preferred prey).

those targeted by fisheries, show positive responses to reserve implementation but several have little or no benefit from localized protection and some even exhibit negative responses.

Such counterintuitive declines documented within reserves can be caused by cascading trophic interactions in which densities and sizes of top predators increase inside reserves, leading to increased predation mortality and declines in prey species (Pinnegar et al. 2000). While these direct and indirect effects of protection have been documented in some cases (reviewed by Pinnegar et al. 2000), modeling and empirical studies have shown or hypothesized that complexities such as size-structured interactions and refuges for prey (Baskett 2006, Mumby et al. 2006), linkages among multiple species within food webs (Bascompte et al. 2005), and varying fishing pressure on species at different trophic levels (Mumby et al. 2006, Baskett et al. 2007, Stevenson et al. 2007) can lead to responses that are highly variable among species and settings and therefore difficult to predict based on linear food chain models. For example, contrary to trophic cascade predictions, an increase on average of 2.55 times (with a maximum of seven times) in the biomass of Nassau grouper (*Epinephelus striatus*) inside a large fully protected marine reserve (400 km^2) in the Bahamas did not coincide with declines of herbivorous parrotfishes (Mumby et al. 2006) that are prey to grouper (Claro et al. 2001). A combination of a size refuge from predation and protection from incidental mortality in fish traps for large-bodied parrotfish species inside the reserve were the hypothesized mechanisms underlying the observed benefits for both predator and prey in this large Caribbean reserve (Baskett 2006, Mumby et al. 2006). Similarly, artisanal fisheries targeting species at all trophic levels might explain significantly greater abundances of both herbivorous fishes and top predators in an unfished Pacific coral reef compared to fished reefs nearby (Stevenson et al. 2007). Thus, reserve effects may be controlled by changes in both fishing and predation mortality. Expected responses at different trophic levels could easily be predicted if either fishing or predation controlled outcomes (Fig. 1). However, because community dynamics are influenced by both fishing and predation simultaneously, it is difficult or impossible to tease apart the influences and relative importance of these different sources of mortality based solely on observed abundances and temporal trends in reserves. An integration of empirical data with trophic models including variable predation and fishing intensity as mortality terms is needed to test the role of different mechanisms in producing observed responses to reserves.

Another biological realism that has not been included in models of multispecies responses to reserves is the broad lack of feeding specialization among marine consumers. Marine predators are most commonly generalists consuming a broad range of potential prey (e.g., Bascompte et al. 2005), but existing models have assumed that trophic dynamics are very tightly coupled, representing predators as extreme specialists consuming a single prey species (e.g., Micheli et al. 2004*a*, Baskett 2006, Baskett et al. 2007). Thus, current theoretical studies may overestimate the impact of predation on protected prey populations and potentially underestimate reserve benefits for lower trophic levels. By the same token, top predators may in turn be influenced by the availability of their potential prey species. Lack of incorporation of both bottom-up and top-down controls of community dynamics, known to be important for species strongly tied to habitat including reefs, further impedes our understanding of potential reserve effects. For example, predator control of herbivorous fish has been reported in some coral reef systems, such as the

Great Barrier Reef (Graham et al. 2003) but not in the Central Pacific (Jennings and Polunin 1997, Sandin et al. 2008). Similarly, predation has been shown to interact strongly with habitat structure to influence prey dynamics of small-bodied reef fish (Hixon and Beets 1993). Bottom-up effects on reef fish include numerical increases in parrotfish abundance as food availability increases (Mumby et al. 2005) and reductions in fish density as habitat is lost through coral bleaching (Jones et al. 2004, Graham et al. 2006).

Here, we build upon existing marine reserve theory in order to reconcile the possible trade-offs of protection for prey species when their primary predators are generalists and both predator and prey may suffer mortality from fishing outside reserves. We begin our analysis by developing a general theoretical framework that allows for a simultaneous examination of the influences of trophic relationships and fishing patterns on predator–prey systems. We then implement the general model for a coral reef reserve system in the Caribbean where we have conducted extensive field studies (e.g., Mumby et al. 2006, 2007*a*, Harborne et al. 2008). Results from the general and specific models highlight how observed reserve responses relate to trophic control, breadth of predator diet, and the relative magnitudes of predation and fishing mortality and provide a mechanistic understanding of observed patterns from this and other reserves. Importantly, this work identifies processes that may drive the responses of marine multispecies assemblages due to marine reserve and fisheries regulation implementation, providing a framework and guidance for assessments of the efficacy and potential trade-offs between conservation and fisheries goals of MPAs and other EBM approaches.

A General Multi-trophic Fisheries Model

The general model developed here is designed to capture important properties of a multispecies fishery consisting of a predator with multiple prey. We use a general, tractable model to describe the key population dynamics and species interactions in harvested and protected systems in order to examine trade-offs between predation and fishing mortality. Model features are evaluated by the feasibility of matching realistic conditions, with some foresight into the patterns observed in the Caribbean.

Marine resource management and fishing typically target a few focal species that are embedded in a larger trophic web. As such, the food chain described here incorporates some key dynamics of the larger community (Fig. 2) and can be represented by three equations:

focal prey,

$$\frac{dX_i}{dt} = F(X_i) - A(X_i, N) - H(X_i) \tag{1A}$$

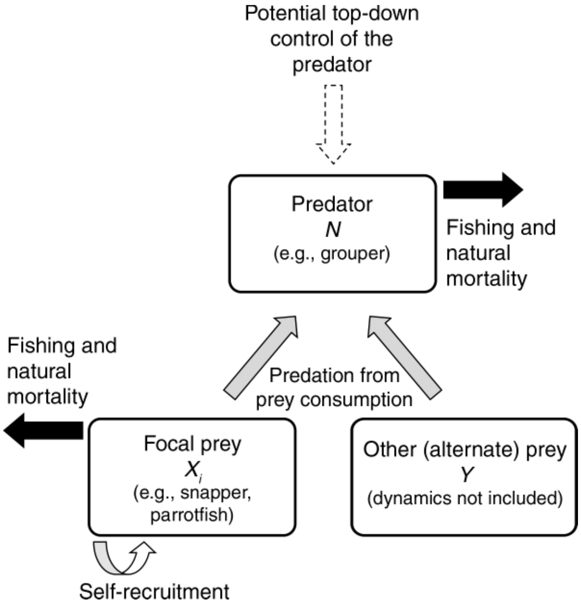

FIG. 2. Multi-trophic fisheries model schematic used to examine the trade-offs between fishing pressure and trophic control of reef fish communities, including an exploration of top-down and bottom-up effects. Arrows indicate factors considered in the model and are not indicative of flows.

other prey,

$$Y = \theta \quad \text{where } \theta \geq 0 \tag{1B}$$

and generalist predator,

$$\frac{dN}{dt} = F_N(X_i, Y, N) - H(N). \tag{1C}$$

$F(X_i)$ is the density-dependent growth rate for i number of focal prey X, which are consumed by predator N at a rate of $A(X_i, N)$ and caught by harvesters at a species-specific rate of $H(X_i)$.

The predator's population dynamics are a function of its growth rate, $F_N(X_i, Y, N)$, as it relates to prey consumption, and any losses to fishing, $H(N)$. In order to capture the importance of truly broad diets that often characterize top predators but have commonly been ignored in previous models of fished and reserve communities, we incorporate a constant pool of other prey Y that serves as a surrogate to describe the predator's breadth of diet. This pool is assumed to be constant because predation and fishing are unlikely to deplete substantially the pool of alternative prey and therefore there are no dynamic changes in Y in response to predators' foraging. The availability of focal prey and other prey determine whether the predator can persist, such that there is a minimum density of the lower trophic level that collectively sustains the predator.

We can further specify these trophic dynamics by applying a logistic growth function for the focal prey (as in Gordon-Schaefer fishery models), a linear predation mortality function, and a linear catch function for both

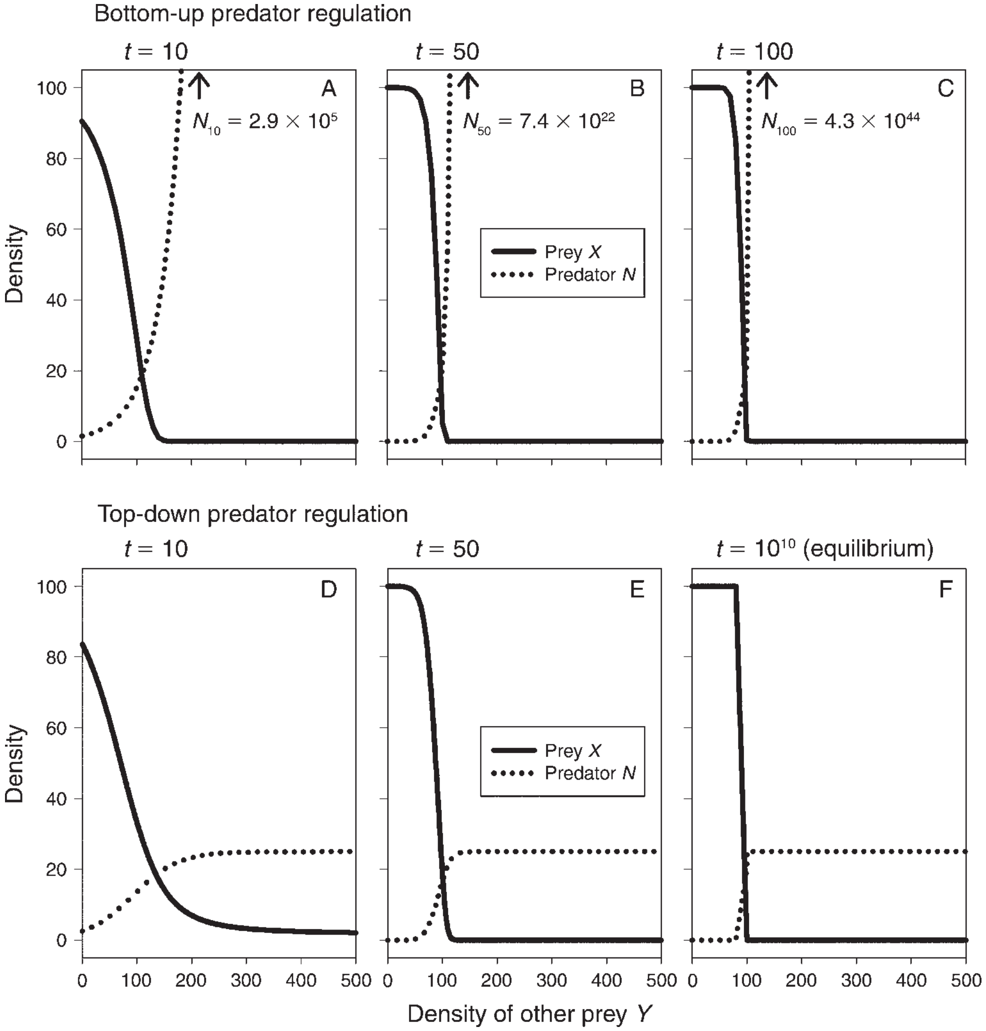

FIG. 3. Trophic response in an unfished system over time, t, relative to availability of other prey, Y. (A–C) Bottom-up regulation leads to unrealistically high densities of the predator over time if the other prey is abundantly available (see *A general multi-trophic fisheries model*; Eq. 2C.BU). (D–F) The addition of top-down regulation leads to an asymptotic increase in predator density as other prey availability increases (Eq. 2C.TD). Parameter values were chosen to illustrate the largest possible range of behaviors within the constraints of ecological reality. Unless otherwise specified, parameter values are as follows for Figs. 3–5: $i = 1$, $r_X = 1$, $K_X = 100$, $a_X = 0.05$, $h_X = 0$, $Y = 0–500$, $a_Y = 0.05$, $c = 0.01$, $d_N = 0.25$, $K_N = 25$, $h_N = 0$, where r_X is the focal prey's per capita growth rate, K is the carrying capacity, a is the attack rate of the predator, h is the fishing mortality term, Y is the density of other prey, c is the conversion efficiency, d_N is the predator's per capita mortality rate. Initial densities are set to $X_0 = 50$ and $N_0 = 12.5$. For a straightforward presentation, we show results for one focal prey species (i.e., $i = 1$), but possible scenarios of coexistence are provided in Table 1.

focal prey and the predator. However, based on ideas from apparent competition (Holt 1977) that do not depend on specific functional forms we conclude that the qualitative predictions of our general model likely apply to a broader set of predator–prey models that include different forms of negative density dependence in the focal prey growth terms.

The importance of bottom-up and top-down trophic effects was assessed by applying linear and nonlinear per capita rates of increase for the predator. A linear predator growth function generates only bottom-up trophic control in the community because predators have no implicit density-dependent regulation (Eq. 2C.BU). If the predator's diet is primarily composed of focal prey (i.e., the predator is a specialist feeder or the abundance of other prey is very low), then the density-dependent growth of the focal prey can limit the maximum abundance of predators. However, if the predator is a generalist feeder and other prey are widely available, the predator population will grow without bound over time (Fig. 3A–C). For this reason, we primarily examine a more biologically realistic form of the model with top-down predator regulation by incorporating a carrying capacity function analogous

Table 1. Possible scenarios of coexistence for the general model with two focal prey species, X_1 and X_2, where X_1 is the better apparent competitor (i.e., $r_1/a_1 > r_2/a_2$).

Possible scenarios	Focal prey		Other prey	Predator	Explanation
	X_1	X_2	Y	N	
1	✓	✓	n/a		specialist; not enough turnover of X_1 and X_2 to sustain the predator
2	✓	✓	n/a	✓	specialist; enough turnover of X_1 and X_2 to sustain the predator
3	✓		n/a	✓	specialist; high-enough turnover of X_1 to sustain the predator, predator exhausts prey species X_2 with the lower per capita growth rate and/or higher attack rate
4	✓	✓	✓		generalist; not enough availability of X_1 and X_2 and Y to sustain the predator
5			✓	✓	generalist; Y is abundant and the predator exhausts X_1 and X_2
6	✓		✓	✓	generalist; Y is abundant and the predator exhausts species X_2 with the lower per capita growth rate and/or higher attack rate; this scenario can only occur if Y is not highly abundant
7	✓	✓	✓	✓	generalist; enough availability of X_1 and X_2 and Y to sustain the predator; this scenario can only occur if Y is not highly abundant

Notes: Specialist scenarios occur when the predator, N, eats only the focal prey, whereas generalist scenarios occur when the predator eats the focal prey and the other prey Y (refer to Eq. set 2). Explanations are given for an unfished system, but the same set of possible scenarios holds for a fished system, where persistence is a function of population turnover minus fishing mortality. The scenarios described here are determined by examining the dynamics of Eq. set 2 for all biologically relevant parameter values.

to the prey logistic growth function in which the maximum growth rate of the predator population at low density is still controlled by the amount of prey it consumes, but the predator's population growth rate slows as its own density increases (Eq. 2C.TD; Fig. 3D–F). This addition is one way to explicitly include top-down regulation in the community and is appropriate for predator populations that may be limited by habitat availability, but other forms of limitation, such as handling time or saturation, can also be used to incorporate a nonlinear growth function.

The set of equations is now written as follows:

focal prey,

$$\frac{dX_i}{dt} = r_i(1 - X_i/K_i)X_i - a_iNX_i - h_iX_i \qquad (2A)$$

other prey,

$$Y = \theta \quad \text{where } \theta \geq 0 \qquad (2B)$$

and generalist predator,

$$\frac{dN}{dt} = f(X_i, Y, N)N - h_NN \qquad (2C)$$

where

$$f(X_i, Y, N) = \begin{cases} f_{\text{bottom-up}} = \left[c\left(a_YY + \sum a_iX_i\right) - d_N\right] & (2C.BU) \\ f_{\text{top-down}} = \left[c\left(a_YY + \sum a_iX_i\right) - d_N\right](1 - N/K_N) & (2C.TD) \end{cases}$$

and where r is the prey's per capita growth rate (i.e., $b - d$), K is the prey carrying capacity, a is the attack rate of the predator, c is the conversion efficiency of consumed prey into additional predators, and d_N is the predator's per capita natural mortality rate. For brevity and generalization, we use a collapsed fishing mortality term, h, to represent a range of species-specific fishing intensities and catchabilities. This linear response to fishing is often represented as $h = qe$, where q is the catchability coefficient and e is the fishing intensity (e.g., fishing effort measured as hours trawled per day or number of boats). As indicated in the equations above, r, K, a, and h can be species-specific but we assume that the conversion efficiency, c, is equal across all species.

The set of coexistence scenarios for this multiple-prey, single-predator system are presented in Table 1 and are generally a manifestation of predator-mediated apparent competition, which is extensively described in work by Holt and colleagues (e.g., Holt 1977). Fig. 3 shows that in both the bottom-up and top-down versions of the model, there is a limited region of coexistence of the predator and the focal prey that exists when other prey are not widely available and the predator population is determined by the dynamics of its prey. As the predator's breadth of diet increases or other prey become more available, the predator's population can increase and, at large numbers, can exhaust some or all of the focal prey species (Holt 1977). Clearly, fishing only the predator would cause a relaxation in apparent competition and increase the persistence and standing-stock densities of focal prey species (Holt 1977), whereas establishing a marine reserve could increase the likelihood of apparent competition and trophic cascades unless there is also some benefit of protection for the prey species.

For the remaining analysis of the general model, we focus on examining the sensitivity of these trophic relationships and the region of coexistence to three key parameters that might influence prey response to MPAs: (1) predator breadth of diet, (2) fishing mortality of both the focal prey and predator, and (3) attack rate on the prey. These parameters can capture the degree to which blanket protection of a reserve is likely to affect both predator and prey species and help explain the intertwined effects of fishing on one or more trophic levels. By examining the interaction between potential increases in predation pressure and decreases in fishing mortality, we can gain insight into the complex trade-offs driving mixed prey responses to reserve protection.

Focal prey persistence and density is sensitive to fishing effort on both the predator and the focal prey (Fig. 4, left column), whereas predator persistence and density are primarily affected by the fishing effort on its own population (Fig. 4, middle column). Accordingly, the region of coexistence of predator and focal prey decreases as fishing selectivity and intensity on the focal prey increase (Fig. 4, right column). Therefore, establishing an MPA will likely result in greater increases in density for heavily fished than for lightly fished prey species despite an increase in predation, but the region of coexistence becomes more sensitive to the abundance of other prey as fishing pressure is decreased. As such, trophic cascade effects are more likely to dominate for non-fished prey species, whereas targeted prey species can increase despite increased predator densities inside reserves.

The region of coexistence of the predator and focal prey also decreases as the predator's attack rate on the focal species increases (Fig. 5). The higher the preference of the predator for the focal prey, the more sensitive the focal prey density is to changes in the abundance of other prey (Fig. 5, left column). However, the predator's density is relatively insensitive to changes in the attack rate on the focal prey (Fig. 5, middle column). Therefore, if the predator and focal prey are strongly coupled through higher values of the attack rate, we expect to see more trophic cascade effects inside marine reserves even if the reserve offsets some fishing mortality on the focal prey. This trend of decreasing density of the focal prey inside reserves will also be more likely as the abundance of other prey increases and/or the predator's breadth of diet increases.

As we have demonstrated, the magnitude of any marine reserve benefits for focal prey species will depend upon the coupling strength of the predator and prey (e.g., predator diet preferences), but a doubling of densities inside a reserve could be realistic for targeted prey species despite increased predation pressure (Figs. 4 and 5). This prediction matches empirical observations of an average doubling of abundances in reserves for species showing positive responses to reserve protection (Halpern 2003, Lester and Halpern 2008). We also conducted a similar analysis to determine the sensitivity of the coexistence region and focal prey density to changes in population growth rates (r_i) and density-dependent processes (i.e., the carrying capacities of the focal prey and predator, K_i and K_N; see Appendix A). While both of these factors affect the magnitude and rate of response by all species to reserve protection, prey species recovery is more sensitive to changes in predation pressure and fishing mortality.

This diverse range of prey responses appropriately reflects the variability of reserve effects observed in the field (e.g., Micheli et al. 2004*b*, Guidetti and Sala 2007, Tetreault and Ambrose 2007, Harborne et al. 2008). Thus, this general model provides a theoretical foundation for elucidating the mechanisms underlying observed departures from classic trophic cascade effects (as in Mumby et al. 2006).

Application to Caribbean Trophic Relationships across a Marine Reserve

Here we refine the general model to represent a multispecies Caribbean reef community for which extensive data on species interactions and response to reserve establishment are available (e.g., Mumby et al. 2006, 2007*a*, Harborne et al. 2008). This merging of theory and empirical data on the effects of marine reserves provides some key insights into the mechanisms for observed responses in the system and provides predictions about expected responses to future reserve establishment or fisheries regulations in this region.

Specifically, we use a species-specific form of the general trophic model (Fig. 2) to examine how the implementation of a marine reserve will impact the interactions between the piscivorous Nassau grouper (*Epinephelus striatus*) and two of its prey species, stoplight parrotfish (*Sparisoma viride*) and yellowtail snapper (*Ocyurus chrysurus*). Our refined and parameterized model is based on field studies in the no-take Exuma Cays Land and Sea Park (ECLSP) in the Bahamas (Mumby et al. 2006, Harborne et al. 2008), but the results may be applicable to the larger Caribbean as these species are also found throughout most of the region.

Nassau grouper is the most valuable and thus heavily fished coral reef fish in the Caribbean (Sadovy and Eklund 1999). Intense fishing pressure and population decline have led to the implementation of new management measures, including seasonal closures and the establishment of marine reserves (Sadovy 2005). In the continued absence of the herbivorous sea urchin *Diadema antillarum* on many Caribbean reefs, large-bodied parrotfish represent the dominant herbivore and their grazing on algae provides a critical ecosystem function that enhances recruitment and survival of corals (Mumby et al. 2007*a*). In many regions of the Caribbean parrotfish are targeted by local fisheries (Hawkins and Roberts 2004). However, in the Bahamas parrotfish are generally not directly targeted but rather caught as bycatch, often within the traps set for grouper to which they are highly vulnerable (Rakitin and Kramer 1996). Therefore, fishing on parrotfish is only managed implicitly in reserves that instead aim to protect groupers and other species directly targeted by local fisheries.

A significant increase (an average of 2.55 times up to sevenfold) in the biomass of grouper in the largest and

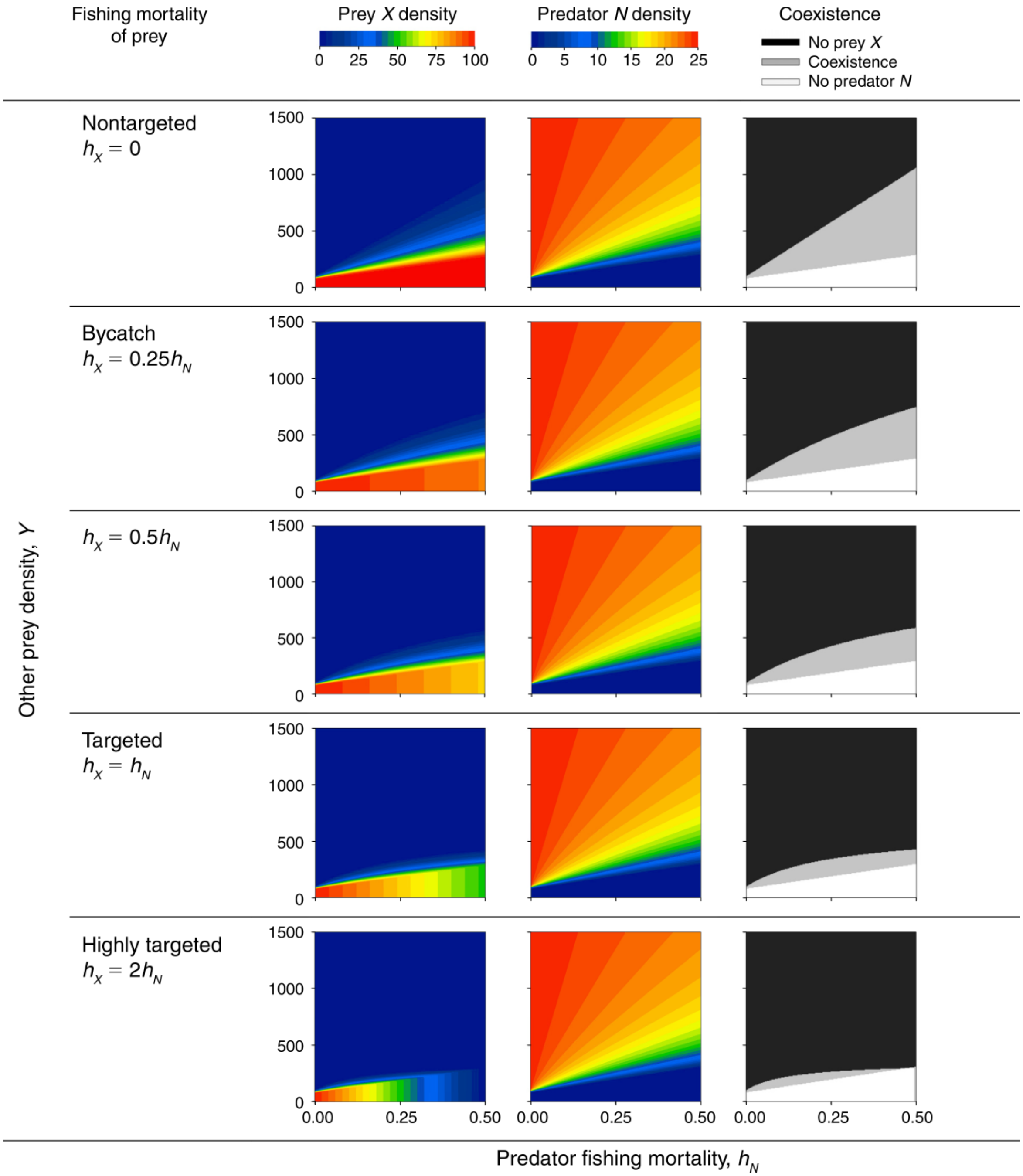

FIG. 4. Analysis of the general model with top-down control (see *A general multi-trophic fisheries model*; Eq. 2C.TD) for increasing levels of fishing effort on the focal prey (h_X). In each panel, changes in density or the region of coexistence of the predator and focal prey are shown with respect to predator fishing mortality ($h_N = 0$–0.5) and other prey availability ($Y = 0$–1500). The minimum threshold for persistence and coexistence was set to 1, and the model was run until $t = 1000$, at which time the entire system reached equilibrium. Parameter values are identical to those used in Fig. 3 unless otherwise specified.

oldest marine reserve within the greater Caribbean (i.e., Tropical Northwest Atlantic province, Spalding et al. 2007), the ECLSP (400 km^2, established in 1986), is considered a measure of the reserve's success (Chiappone and Sealey 2000, Mumby et al. 2006). However, Caribbean marine reserves exemplify the numerous possible trade-offs faced in ecosystem-based management. Successful achievement of one goal, the recovery of large-bodied predators, may conflict with another goal, maintaining overall diversity and function of coral reef ecosystems, as the increase in predators may lead to the decline of herbivorous fishes which, through the removal of algal competitors by grazing, provide a key function in maintaining corals (Mumby et al. 2007*b*). The complexity of relative responses of individual species to marine reserve protection is also confounded by incidental catch of parrotfishes as bycatch in fish traps and fishing on other species preyed upon by grouper, such as snapper, which are major targets of spearfishing (K. Broad, *unpublished data*). A theoretical understanding of these contrasting effects on multiple trophic levels that could result from marine reserve establishment will inform management and conservation of these ecosystems.

Empirical data show that the ECLSP has achieved multiple management objectives, with documented higher grouper biomass, higher herbivore biomass and grazing rates, and greater coral recruitment than adjacent fished reefs (Mumby et al. 2006, 2007*a*). However, the presence of a single continuously enforced reserve and the difficulty of teasing apart mechanisms underlying these patterns with field studies prevents elucidation of general principles for when win–win outcomes, such as those documented in ECLSP, or conversely, trade-offs between fisheries and biodiversity conservation goals are expected. Baskett (2006) examined the role that increasing sizes of parrotfish inside this reserve creates a prey size refuge and may weaken the trophic cascade between grouper and parrotfish. Here we focus on the simultaneous release of fishing mortality for both the prey and predator inside marine reserves, which is a second mechanism proposed by Mumby et al. (2006) that may be important for the breakdown of trophic effects inside ECLSP.

This Caribbean food web with grouper as the generalist predator and parrotfish and snapper as our focal prey can be modeled as follows:

parrotfish (focal prey),

$$\frac{dP}{dt} = F_P(P) - A(P,G) - H(P)$$

$$= \left(\frac{m_P}{m_{P,h} + P}\right)P - d_P P - a_P G P - q_P e_P P \qquad \text{(3A.I)}$$

snapper (focal prey),

$$\frac{dS}{dt} = F_S(S) - A(S,G) - H(S)$$

$$= (b_S - d_S S)S - a_S G S - q_S e_S S \qquad \text{(3A.II)}$$

other prey,

$$Y = \theta \quad \text{where } \theta \geq 0 \qquad \text{(3B)}$$

and grouper (predator),

$$\frac{dG}{dt} = F_G(S,P,Y,G) - H(G)$$

$$= c(a_P P + a_S S + a_Y Y)(1 - G/K_G)G - d_G G - q_G e_G G. \qquad \text{(3C)}$$

The snapper and parrotfish equations both include a density-dependent functional response (Murdoch et al. 2003). Because of key biological differences between these two species, we used different forms of density dependence. The parrotfish equation uses a density-dependent saturating function to represent a limit on available territories. Harem association for females and male territoriality are important factors determining successful mating of parrotfish (vanRooij et al. 1996). In contrast, territoriality is not an important factor in yellowtail snapper spawning (Muller et al. 2003), and we therefore use a more general form for the snapper functional response that includes a density-dependent mortality term that incorporates early juvenile mortality (Watson et al. 2002).

As in the general model, we include both top-down and bottom-up control in the grouper functional response. In this application of the model, the density-dependent term appears only in the fecundity term because grouper form spawning aggregations (Sala et al. 2001) and therefore reproductive success is directly a function of adult densities. A more detailed model could explicitly include spatial aspects of density dependence related to the life history of grouper, but our focus here is on the more general issue of trophic interactions. For other predator species it might be appropriate to include density dependence in the mortality term too as we did in the general model. This choice is important numerically, but does not change the qualitative predictions of the general model.

Detailed parameter descriptions are presented in Appendix B, and their values were gathered from the scientific and fisheries literature. Population density estimates for each species were obtained by visual fish censuses conducted at four sites within the reserve and six sites outside the reserve (see Harborne et al. 2008 for details). On average, grouper density per 200 m^2 was greater by a magnitude of 2.55 inside the marine reserve. The inside-to-outside density ratio for parrotfish and snapper was 1.38 and 2.33, respectively. The observed reserve effect from field surveys and matching model predictions are shown in Fig. 6.

Estimates of fishing effort are often difficult to obtain empirically. By first setting fishing mortality to zero and ensuring that parameter estimates successfully predict observed reserve densities, we were able to then rerun the model to estimate fishing pressure outside the reserve. This model run used to estimate fishing pressure confirms our expectations based on observations of fishing activities and interviews with fishermen in this region (Broad and Sanchirico 2008) that fishing mortality of grouper and snapper is high outside the marine reserve, but much lower for parrotfish, with fishing mortality ($h = qe$) of parrotfish 70% lower and snapper 50% greater than grouper. While the fishing mortality estimate on snapper is higher than grouper, the actual catch in units of biomass fished is predicted to be higher for grouper

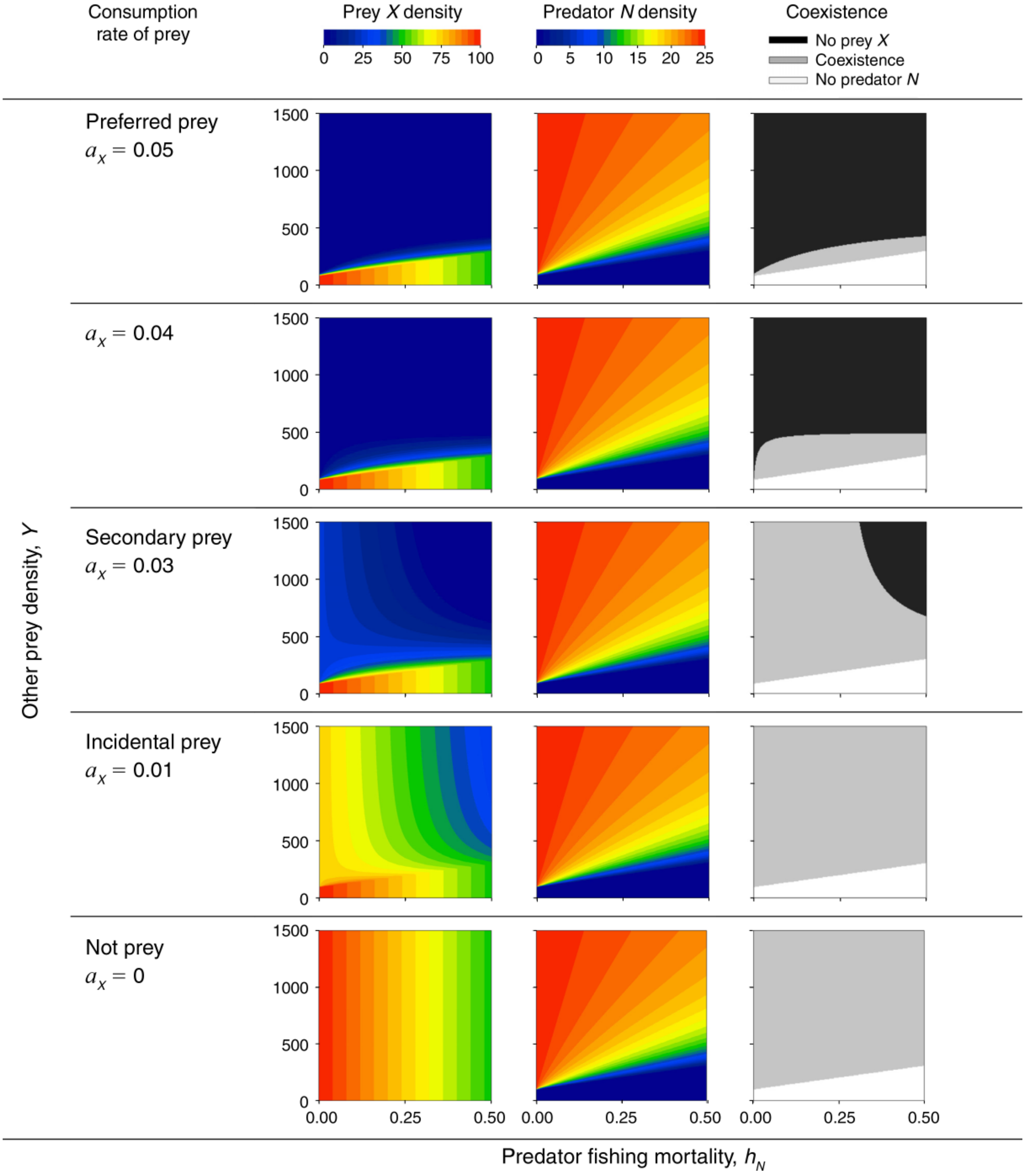

FIG. 5. Analysis of the general model with top-down control (see *A general multi-trophic fisheries model*; Eq. 2C.TD) for decreasing predator preference for the focal prey when both the predator and prey are targeted ($h_X = h_N$). In each panel, changes in density or the region of coexistence of the predator and prey are shown with respect to predator fishing mortality and other prey availability. Parameter values are identical to those used in Figs. 3 and 4 unless otherwise specified.

because of the larger size at capture for grouper. These estimates provide insight into the potential magnitude of trade-offs between fishing and predation that can occur when a protected area is established. For all three species, release from fishing pressure is likely the dominant factor driving their increase inside the marine reserve, and release from bycatch mortality for the parrotfish can outweigh additional increases in predation by grouper. By rerunning the model without predation on the focal prey species, we were able to estimate that release from fishing mortality was likely double that of predation mortality for parrotfish inside the reserve (Fig. 6). As such, fishing mortality of prey species, even when predicted to be small, is an

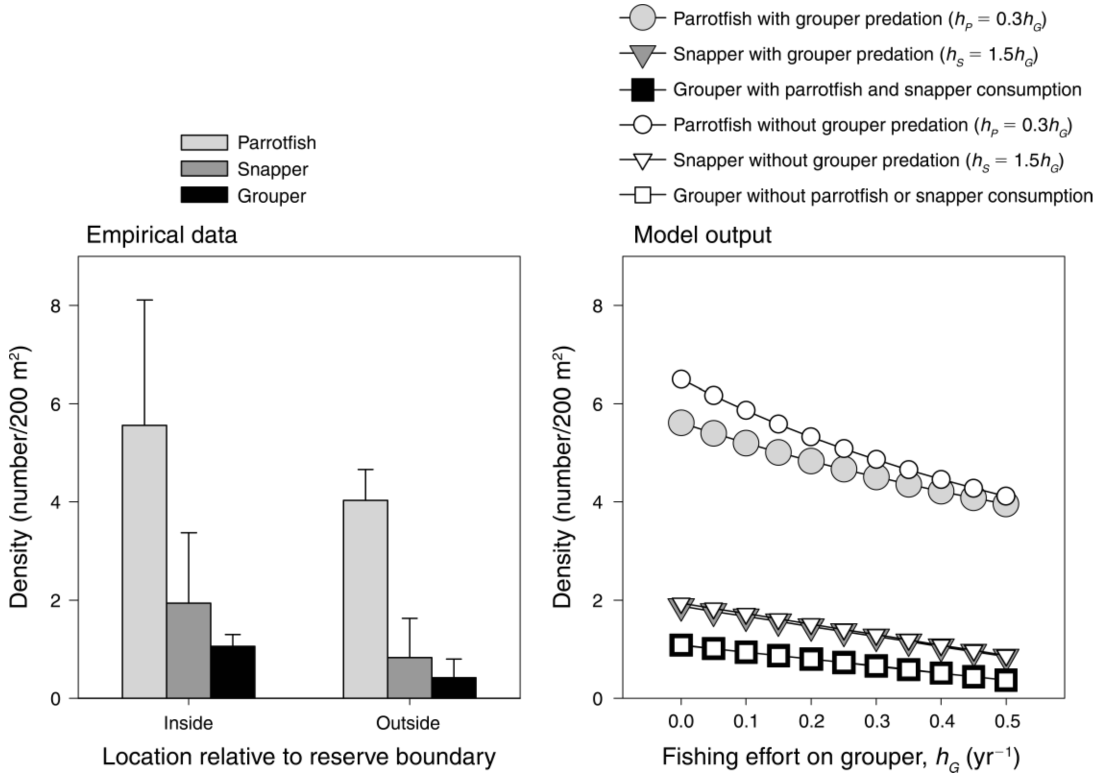

FIG. 6. Caribbean trophic model results compared to survey data from the Exuma Cays Land and Sea Park (ECLSP) in the Bahamas (mean + SD). Solid symbols show model output with Nassau grouper (*Epinephelus striatus*) predation on yellowtail snapper (*Ocyurus chrysurus*) and stoplight parrotfish (*Sparisoma viride*) (i.e., $a_P > 0$, $a_S > 0$); open symbols show model output without grouper predation on snapper and parrotfish (i.e., $a_P = a_S = 0$). Note that fishing effort on parrotfish and snapper (h_P and h_S) is scaled relative to fishing effort on grouper (h_G).

important process to factor into considerations of ecosystem-based management.

We also tested the model with and without top-down effects on the grouper population by removing or incorporating the nonlinear term, $1 - G/K_G$, in Eq. 3C similar to the general model analysis. As indicated in the previous section's model, top-down effects are needed to match real-world observed densities in this Caribbean model where the predator is a generalist feeder. These results are an important indication that future modeling efforts should take care in identifying larger system dynamics that may be crucial in marine reserve systems. Furthermore, these results suggest that simple coupled models of a predator and a single prey may be too abstract to accurately assess trophic responses for food webs that include generalist top predators.

DISCUSSION

This work identifies significant processes that may drive responses of marine multispecies assemblages due to marine reserves and fisheries regulations, providing a framework and guidance for assessments of the efficacy and potential trade-offs between conservation and fisheries goals of marine reserves and other marine ecosystem-based management approaches. Understanding and predicting the responses of multispecies assemblages to management interventions, including fisheries regulations and the establishment of marine reserves, is challenged by the complexity of interactions and factors modulating individual species responses. Models predict that individual species responses to marine reserves are influenced by the life history characteristics of species; their dispersal potential in the larval, juvenile, and adult phases; the configuration of the reserve network; and the intensity and patterns of fishing outside reserves (Hastings and Botsford 1999, Apostolaki et al. 2002, Gaylord et al. 2005, Stefansson and Rosenberg 2005, Hilborn et al. 2006, Sanchirico et al. 2006, Kellner et al. 2007, 2008). Predator–prey and competition models show that species responses are also determined by species interactions, in which the outcome can be mediated by size refuges and fishing pressures on the predator and the prey or on competitors (Micheli et al. 2004*a*, Baskett 2006, Baskett et al. 2007, Kellner and Hastings 2009). However, no model to date has accounted simultaneously for these multiple, realistic features of marine communities and none correctly predicts the wide range of possible responses to reserve establishment documented in empirical studies (e.g., Micheli et al. 2004*b*, Mumby et al. 2006, Guidetti and Sala 2007, Tetreault and Ambrose 2007, DeMartini et al. 2008, Harborne et al. 2008). This is a major impediment for designing and implementing ecosystem-based management of multispecies assemblages, as management interventions aimed at sustaining multiple species and their linkages may be ineffective in the lack of a deeper understanding of how such linkages determine responses to management. In particular, an understanding of when trade-offs in maintaining populations of predators and prey may be expected or when, conversely, reserves or fisheries regulations might benefit all trophic levels is crucial to effective management and conservation of nearshore marine communities. As a contribution toward this improved understanding, here we have developed a novel modeling framework for simultaneously addressing multiple biological features influencing multispecies responses to reserves and have combined it with empirical data.

The diverse range of prey responses we observed appropriately reflects the variability of reserve effects observed in the field. We identify some of the mechanisms underlying variable responses and determine what responses might be expected under different conditions. Specifically, density-dependent control of predator growth, availability of alternative prey for generalist predators, a reduction in predator attack rates that might arise from increasing habitat heterogeneity or prey size refuges, and release from fishing pressure within marine reserves contribute and combine to determine species responses to reserve establishment and changes in fishing pressure. We show that, under realistic assumptions about trophic control and predator diet breadth, reserve establishment can result in persistence of multispecies assemblages and simultaneous increase in both predators and prey (e.g., Micheli et al. 2004*b*, Mumby et al. 2006, Stevenson et al. 2007). Thus, this model provides a theoretical foundation for elucidating the mechanisms underlying field observations that depart from classic trophic cascade effects (as in Mumby et al. 2006).

Parameterization of our general model to a Caribbean reef ecosystem supports the hypothesis put forth by Mumby et al. (2006) and Baskett (2006) that size refuges for prey combined with its fishing mortality through bycatch outside reserves contribute to the observed increase of herbivore (i.e., parrotfish) biomass and grazing rates within a large marine reserve in the Bahamas. Our work shows that availability of alternative prey to generalist predators is an additional crucially important mechanism underlying these observed patterns and confirms that fishing intensity on the predators is much higher than for parrotfishes outside reserves. Inferring mechanisms based solely on observed snapshots of species abundances and size structure may thus fail to identify the full suite of driving factors and their interactions. Although this model was validated for a specific Caribbean system, these results may apply more broadly to other tropical and temperate reef ecosystems. Increased abundance and biomass of both top predators and species at low trophic levels was, in fact, documented broadly across a suite of locations (Micheli et al. 2004*b*), including coral reefs of the Line Islands, in the central Pacific Ocean (Stevenson et al. 2007, Sandin et al. 2008) that are characterized by significantly greater species diversity and thus food web complexity compared to the Caribbean reefs investigated here.

These results highlight the need to take a multifaceted approach to examining the consequences of marine management interventions, accounting for both fishing pressures and species interactions. Ecosystem-based management should account for linkages but applications of full food web models have proved problematic because of high uncertainty about a large fraction of needed parameters and steady-state assumptions (e.g., Pauly et al. 2000, Bascompte et al. 2005), while simple models may lack important biological realism. Here we developed a tractable model that includes some of the key complexities driving these systems and that may be applied to predict and understand the effects of EBM on multispecies assemblages. In particular, previous models have highlighted that it is critical to combine marine reserve establishment with fisheries regulations, as fishing pressure and patterns are predicted to be important determinants of conservation and fisheries benefits of reserve networks (Micheli et al. 2004*a*, Hilborn et al. 2006, Baskett et al. 2007). The work presented here provides a framework for addressing these complexities simultaneously while balancing biological realism with tractability.

Our results produce specific expectations about the impacts of fishing and marine reserves on reef assemblages within the Caribbean and possibly other regions. Grouper populations are primarily affected by direct fishing mortality. Thus, changes in fishing intensity, or, equivalently, establishment of marine reserves (Hastings and Botsford 1999), are expected to have direct effects on grouper abundance, not mediated through effects on their prey. Cascading effects of such predator increases on lower trophic levels are expected if prey are unfished and for high predator attack rates and feeding selectivity. This result suggests that trophic cascades from predator increases following reserve establishment or fishing bans are highly unlikely in Caribbean reefs and more generally coral reef ecosystems, which are characterized by generalist predators (Randall and Bishop 1967), multispecies fisheries targeting species at different trophic levels, and use of nonselective gear (traps and nets) with high bycatch levels. If some directed or incidental fishing mortality is present for prey species, increased prey abundance in reserves is expected over a broad range of predator abundance and attack rates. Finally, our results highlight the importance of considering multispecies assemblages, not only single species, in management and monitoring. Different responses to reserves for the focal species are expected, depending on the productivity and mortality of alternative prey. We found that as the abundance of alternative prey increases, the region of coexistence for both predator and focal prey expands. With further increase in alternative prey, however, predation pressure on the focal prey also increases until the region of coexistence no longer persists. Thus changes in the abundance and species composition of whole prey assemblages may affect the persistence of focal species as well. Fisheries regulations targeting multiple species simultaneously (e.g., by setting total allowable catch for species groups instead of one species at a time) and monitoring of multispecies assemblages, including nontarget species or species caught as bycatch, will be critical for sustaining coral reef assemblages and evaluating the efficacy of EBM approaches, including marine reserves.

We have focused on changes that arise due to fishing pressure in the context of a simple food web. Our approach incorporates important features, including consideration of top predator diet breadth and both incidental and direct fishing mortality across multiple trophic levels, but there are other potentially important interactions that could be explored in future research. We focus on what we consider to be the most important interactions, but our model does not include all possible competitive and predator–prey relationships that may influence the dynamics of coral reef food webs (McClanahan and Branch 2008, Sheppard et al. 2009). For example, analyses of Caribbean food webs have highlighted other strong interactions (e.g., sharks; Bascompte et al. 2005, Rezende et al. 2009), and field studies have shown trait-mediated cascading effects of the removal of Nassau grouper, with small-bodied grouper species increasing their activity in the absence of the larger Nassau grouper, resulting in decreased recruitment of coral-reef fishes, including stoplight parrotfish (Stallings 2008, 2009). Habitat complexity and heterogeneity (McClanahan and Branch 2008, Sheppard et al. 2009) may also play significant roles and are worthy of future study. Future expansion of the modeling framework used here could address these additional dynamics.

Among other factors we have not emphasized, temporal and spatial issues are likely to be most important. The empirical systems we focus on in this study include responses on decadal timescales, and some of the effects predicted from an equilibrium analysis could potentially take longer to play out. However, the agreement between our analysis and empirical patterns and our observation of the time course of our simulations suggest that this effect is likely to be less important than the dramatic changes in equilibrium levels. Nonetheless, responses are expected to vary through time; the response of predators to reserves is likely to take longer than prey, so some prey may increase initially due to release from fishing pressure, but decrease later because of increased predation (e.g., Barrett et al. 2009). Thus, the reserve effect on prey may level off or even dampen once predator densities recover. When observed patterns and our predictions differ, temporal issues should be considered as one possible explanation.

Similarly, we have not emphasized the role of spatial dynamics, which are likely to be complex. Certainly, there is exchange of individuals between reserve areas and fished areas, the rate of which will vary depending on the mobility of different species (Kramer and Chapman 1999), and the response of fishing to the establishment of reserves is likely to be spatially complex (Kellner et al. 2007), with consequent effects on ecosystem response. In general the movement of different marine species can be widely different (Shanks et al. 2003), and movement is likely to be particularly complex in our study area (Cowen et al. 2006) and have implications for the recruitment of predatory reef fish and the nature of density-dependent mortality of their prey (White 2007). Yet, again, it is likely that the simpler equilibrium effects we focus on here tell the major part of the story, with the role of spillover, exchange, and spatial correlation of predator and prey requiring further study, especially when our predictions are not matched by observation.

The challenge of managing or even understanding the response of complex food webs in light of changes in anthropogenic pressures is a daunting task. Historically, however, insights into the responses and dynamics of food webs have come from studying small food web modules consisting of a few tightly interacting species (McCann et al. 1998). This approach provides insights far beyond those obtained from looking at single species and is much more useful for predicting and understanding dynamics of food webs. We are able to draw general conclusions that relate the relative impacts of release from fishing pressure inside reserves to the effects of increased predation, identifying the mechanisms and conditions that will lead to prey depletion from increased predation in reserves or else will result in benefits of reserves to both predators and prey. We argue that the general approach developed here is an essential first step in providing scientific guidance for the implementation of ecosystem-based management. We also suggest that further insights will come from studying more carefully the temporal and spatial issues and dynamic aspects and using the ideas developed here in the context of bioeconomic analyses.

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APPENDIX A

Extended sensitivity analysis of the general multi-trophic fisheries model (*Ecological Archives* A020-072-A1).

APPENDIX B

Caribbean trophic model parameter estimates (*Ecological Archives* A020-072-A2).