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Fishing Indirectly Structures Macroalgal Assemblages by Altering Herbivore Behavior

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ABSTRACT: Fishing has clear direct effects on harvested species, but its cascading, indirect effects are less well understood. Fishing disproportionately removes larger, predatory fishes from marine food webs. Most studies of the consequent indirect effects focus on density-mediated interactions where predator removal alternately drives increases and decreases in abundances of successively lower trophic-level species. While prey may increase in number with fewer predators, they may also alter their behavior. When such behavioral responses impact the food resources of prey species, behaviorally mediated trophic cascades can dramatically shape landscapes. It remains unclear whether this pathway of change is typically triggered by ocean fishing. By coupling a simple foraging model with empirical observations from coral reefs, we provide a mechanistic basis for understanding and predicting how predator harvest can alter the landscape of risk for herbivores and consequently drive dramatic changes in primary producer distributions. These results broaden trophic cascade predictions for fisheries to include behavioral changes. They also provide a framework for detecting the presence and magnitude of behaviorally mediated cascades. This knowledge will help to reconcile the disparity between expected and observed patterns of fishing-induced cascades in the sea.

Keywords: fishing, coral reef, food web, behavior, indirect effects, trophic cascade.

Introduction

Trophic cascades following human-induced removals or additions of predators to natural marine systems are common (McClanahan and Muthiga 1988; Sala et al. 1998; Babcock et al. 1999; Myers et al. 2007) but far from ubiquitous. Indeed, many ecologists have concluded that changes in primary producer biomass or abundance as an indirect consequence of changes in marine predator den-

sity are inconsistent (Russ and Alcala 1998; Mumby et al. 2006; Newman et al. 2006; Sandin et al. 2008; Valentine et al. 2008) because top-down effects of predator loss or recovery are not always associated with predictable changes in the densities of lower trophic levels (i.e., decreases in carnivores lead to increases in herbivores and, subsequently, decreases in primary producers). The response metrics generally used for three-trophic-level changes such as these include total primary producer percent cover (Mumby et al. 2006; Sandin et al. 2008) or biomass (Newman et al. 2006). These studies thus make the implicit assumption that top-down effects of predators manifest primarily through the pathway of direct consumptive effects on prey (e.g., herbivores), which in turn drives numerical responses in prey's food resources (e.g., benthic algae). The majority of studies of trophic cascades in the ocean involve predator alterations associated with fishing. The large variability in the occurrence of trophic cascades in these systems therefore suggests that either fishing frequently has few top-down effects or that the effects of fishing may manifest through other, unexplored pathways.

Studies in other ecosystems have demonstrated the capacity for prey behavioral changes to transmit top-down effects of changing predator abundances to lower trophic levels in diverse ways (Dill et al. 2003; Schmitz et al. 2004; Preisser et al. 2005). The "ecology of fear" (Brown et al. 1999) provides a useful lens through which to examine such changes. When prey alter their behavior in response to changes in predation risk, and this behavioral change subsequently alters the abundance and/or distribution of the prey's resources, a "behaviorally mediated" trophic cascade, or an indirect effect, can ensue (Dill et al. 2003). There is mounting evidence from both theoretical (Walters and Kitchell 2001; Frid et al. 2008; Orrock et al. 2008) and empirical (Turner and Mittelbach 1990; Heithaus and Dill 2002; Dill et al. 2003; Schmitz et al. 2004; Preisser et al. 2005; Ripple and Beschta 2006; Heithaus et al. 2007; Wirsing et al. 2007a, 2007b; Peckarsky et al. 2008; Stallings

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2008) studies that interactions through this pathway could dramatically alter entire landscapes even though they do not necessarily lead to simple changes in the abundance of lower trophic levels. For example, wolf reintroductions in Yellowstone National Park (United States) have led to decreases in ungulate foraging intensity and subsequent increases in willow tree height in wolf-rich, high-risk areas (Ripple and Beschta 2006). Heithaus et al. (2008a) propose a predictive framework that integrates density- and risk-mediated ecological effects of marine predator declines. This framework draws on empirical studies across diverse marine, freshwater, and terrestrial taxa to point out that the management of marine top-predator populations must include provisions for the maintenance of risk in addition to density effects on communities. Importantly, this framework suggests that predictions for the cascading effects of top-predator declines may be possible on the basis of basic life-history characteristics of interacting species. Building on this broad framework, Heithaus et al. (2009) provide a detailed conceptual model for predicting risk effects in natural communities that is based in part on the interaction between landscape attributes and species-specific antipredator behaviors. This model illustrates risk effects for prey inhabiting shelter-rich habitats in which they must make subsurface escapes from predators, and it suggests (counterintuitively) that prey density and subsequent rates of herbivory may actually mirror predator density. Under such conditions, this model provides expectations of how risk effects might alter primary producer distributions. Heithaus et al. (2009) provide strong evidence that this scenario may occur in habitats in which the scale of shelter versus nonshelter microhabitats is similar to that of the seagrass meadows they observed (i.e., occurring over tens of meters or more); however, it is unclear whether this prediction would hold true for coral reef ecosystems, in which the landscape heterogeneity of shelter versus nonshelter microhabitats can alternate on a scale of centimeters to meters.

Most studies of marine trophic cascades treat prey as behaviorally inert food that is consumed at rates dictated largely by the ratio of predators to prey. However, mounting evidence from diverse marine systems suggests that risk effects and resultant trait- or behaviorally mediated trophic cascades may play important roles in shaping seascape (see reviews by Dill et al. 2003 and Heithaus et al. 2008a and references therein; Trussell et al. 2002; Bruno and O'Connor 2005; Grabowski and Kimbro 2005; Byrnes et al. 2006; Stallings 2008). Many marine species exhibit highly plastic antipredator behaviors and/or morphologies (Holbrook and Schmitt 1988; Helfman 1989; Smith 1997; Motro et al. 2005; Frid et al. 2007). Behaviorally sophisticated prey, such as teleost fishes, can behave in ways that dampen their expected numerical response when faced

with large changes in predator densities. Despite the fact that behaviorally mediated trophic cascades have been widely observed in other ecosystems, they have been less often explored in the sea (Dill et al. 2003).

Empirical studies of behaviorally mediated cascades in coral reefs are rare and mostly involve a only few species in the system. However, they do provide guidance for the expectations of how behaviorally mediated cascades might alter the distribution of lower trophic levels. Stallings' (2008) manipulative study demonstrated that the behavioral responses of mesopredators to their predators were responsible for changes in the recruitment of the mesopredators' food resource (in this case, settling reef fishes). Particularly enlightening observations have come from studies of herbivorous taxa that use shelter to avoid encounters with predators. Randall (1965) provided clear evidence that grazing patterns of herbivorous fishes on Caribbean coral reefs could alter the spatial distribution of marine primary producers (algae and seagrasses) when the fish disproportionately graze areas immediately surrounding predation refuges relative to more exposed zones (known as the "halo effect"). Even relatively less sophisticated prey such as sea urchins can alter patterns of benthic spatial structure through purportedly risk-sensitive foraging in and around the halo zone (Ogden et al. 1973; Andrew 1993), although this phenomenon has not been explicitly linked to predation risk. Hay et al. (1983) provided further anecdotal evidence that the distributions of benthic macroalgae are limited to areas where herbivores are less likely to venture due to increased predation risk. Thus, while some evidence suggests that behaviorally driven cascades may occur through interactions between a few species, the broader community context of these cascades and their role in patterning the reef landscape is still poorly understood.

Changes in distribution of primary producers on coral reefs are important because algae and coral commonly compete for valuable space in which to settle and grow. The presence of abundant herbivorous fishes can lead to effectively 0% cover by fleshy macroalgae (Williams and Polunin 2001), whereas total exclusion of large herbivores can lead to the formation of massive stands of macroalgae (Bellwood et al. 2006; Hughes et al. 2007). By restricting the reef areas over which herbivores can safely forage, thereby creating areas of higher and lower effective herbivore densities, predation risk should have the capacity to indirectly influence the spatial variability of macroalgae. This spatial variability in algal success should in turn generate a mosaic of areas that are available/unavailable for colonization by corals and other sessile invertebrates. The spatial pattern of primary producer biomass may thus be a better metric of cascading predator effects than just changes in the average of primary producer biomass.

In this study, by using a simple model representing behavioral responses to predation intensity and confronting both its assumptions and predictions with empirical data, we addressed two questions. First, can removal of predatory fish by human fishers lead to cascading changes in coral reef benthic community structure via the prey behavioral-response pathway (fig. 1)? In light of empirical studies of the behavioral responses of marine herbivores to differences in predation risk (Trussell et al. 2002; Heithaus et al. 2007, 2008*b*; Wirsing et al. 2007*b*), the results from studies of other systems involving human-mediated changes in predator abundance (Ripple and Beschta 2006) and diversity (Byrnes et al. 2006) suggest that this is likely to occur. Second, what are the expected patterns of macroalgal distribution under different predation risk sce-

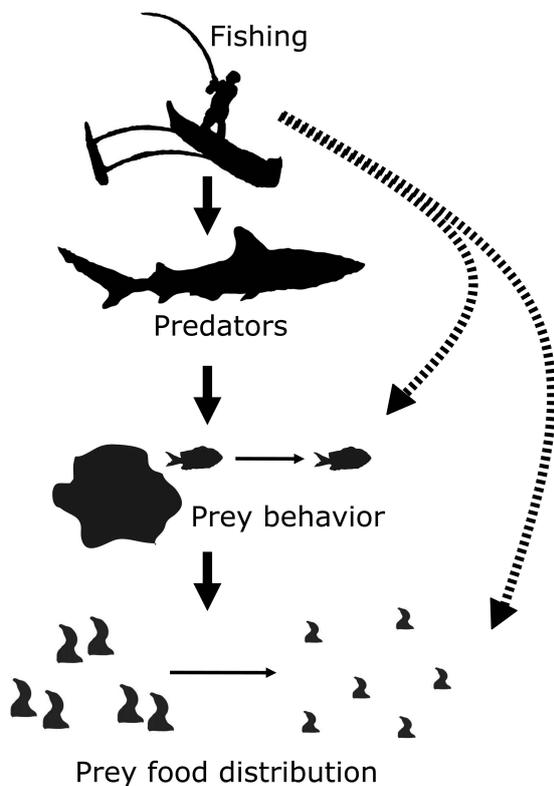


Figure 1: Schematic of indirect (cascading) effects of fishing through the pathway of prey behavior. Solid vertical arrows represent direct effects; dashed arrows indicate indirect effects. As human fishing removes predatory fishes, and hence predation risk, smaller fishes (e.g., herbivores) respond by altering their foraging and other behaviors (e.g., resulting in greater foraging excursions from the shelter). Changes in foraging patterns lead to changes in the spatial distribution and of their food source (e.g., algae). Human fishing therefore indirectly impacts both herbivore behavior and primary producer distribution.

narios? Risk effects are known to alter prey habitat and space usage; indeed, this response is one of the most common mechanisms by which behaviorally mediated indirect effects are transmitted (Trussell et al. 2006). An abbreviated cross-section of studies involving herbivores as prey in natural terrestrial (Schmitz et al. 1997; Creel et al. 2005), freshwater (Power et al. 1985), and marine (Trussell et al. 2002; Heithaus et al. 2007; Wirsing et al. 2007*b*) systems provide details of the range of possible ways in which foraging patterns can change in response to predator alterations. These and many other studies demonstrate that spatial and/or temporal areas of high risk are less likely to be grazed and areas of lower risk are at elevated risk of disproportionately high grazing intensity. In field experiments and natural communities, these risk effects have led to substantial changes in primary producer abundance (Power et al. 1985; Schmitz et al. 1997; Ripple and Beschta 2006), nutrient composition (Heithaus et al. 2007), and/or spatial/temporal heterogeneity (Gastreich 1999; Trussell et al. 2002; Ripple and Beschta 2006), providing compelling clues as to what may be expected for coral reefs under intense fishing pressure.

Our goal is to provide a framework for empirically detecting the presence/magnitude of behaviorally mediated trophic cascades in this system. We show that prey behavioral responses that alter spatial foraging patterns could drastically alter the expectations for community changes in response to food web alterations. Finally, we explore the model predictions with empirical evidence from coral reef systems. Observed spatial distributions of primary producers show strong concordance with the model predictions for the consequences of behaviorally mediated trophic cascades.

Methods

Model Construction and Assumptions

To generate predictions for the spatial distribution of macroalgae over the reef benthos as an indirect consequence of differences in fishing pressure, we developed a spatially explicit model of herbivore foraging areas and resultant macroalgal heterogeneity. We focused our analysis on site-attached, nonfarming, benthic herbivorous and omnivorous fishes that are subject to predation risk imposed by fishes such as snappers, groupers, and other predatory families that are harvested by humans. Although it is motivated by coral reef species, the model should be generally applicable to any herbivore that takes shelter from predators as it forages.

Fish are assumed to forage as a one-dimensional random walk away from a home shelter (e.g., a coral colony or reef matrix that provides refuge from predation) to

which they return when faced with a predator. The resulting diffusive spread of individual fishes from each shelter is described by the normal probability density function in the following form (Denny and Gaines 2000):

$$F(t, \delta) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(-\frac{x^2}{4Dt}\right),$$

where F represents the foraging intensity, or the cumulative probability over time of one individual fish grazing at each point along the benthos relative to its shelter; x is the distance from the shelter; t is the time that an individual fish “walks” before returning to its shelter; and D is the diffusion coefficient defined by the equation

$$D = \frac{\delta^2}{2\tau},$$

where δ is the step length, or the distance that a fish swims in one time step, and τ is the time step, or the interval over which subsequent steps occur.

Predation risk is integrated into the model at two temporal scales. Chronic risk, or the average ambient predation risk faced by prey on a given reef, is risk integrated over time (Madin et al. 2010). The diffusion coefficient D scales with the level of chronic predation risk on a reef: step length δ decreases with increasing predation risk, regardless of whether a predator is actually encountered. Fish under greater chronic risk of predation are assumed to move away from shelters at a slower, more cautious rate. More cautious foraging influences the shape of the foraging intensity distribution. Acute risk is the immediate temporal-scale risk each individual experiences while foraging (Madin et al. 2010). It is defined as the likelihood of encountering a predator while foraging away from the shelter, and it is represented in the model by t , the time parameter. In the model, the durations of individual foraging excursions are set by the frequency of predator encounters; at each pass of a predator, the fish returns to its home shelter. Fish on reefs with higher abundances of predators therefore have a lower probability of venturing far from their home shelter than fish on reefs with fewer predators, for two reasons: they proceed more cautiously from the shelter, and they return to the shelter more frequently.

In this model, each foraging excursion of a single fish is treated as an individual particle diffusing over the reef benthos. Each fish’s foraging excursion begins at a shelter and moves a fixed distance along the benthos at each time step with equal probability in either the positive or the negative direction; the direction of each step is independent of the previous step’s direction. Shelters are randomly allocated to points along the reef benthos; their abundance

is dictated by their observed abundance at the study reefs. Each shelter is assumed to provide shelter to one herbivorous fish; from this shelter, the fish radiates out in its foraging excursions. Individual probability distributions of foraging intensity thus take the form of a normal distribution about each shelter. The summed values of the overlapping foraging territories (or lack thereof) of individual fish represent the cumulative foraging intensity for each point over the reef benthos.

The probability of a given point along the benthos being covered with macroalgae is determined by the cumulative foraging intensity, or the probability that the reef is within the foraging area of one or more fish. The foraging model could be coupled to a model of algal population dynamics, but for simplicity we assume that if the cumulative foraging intensity is less than an arbitrarily determined foraging threshold, then macroalgae will successfully colonize a given point along the benthos. Otherwise, macroalgae are assumed to be absent. Although data do exist in the literature regarding the relationship between herbivorous fish biomass and macroalgal percent cover (Williams and Polunin 2001), the model’s dimensionless foraging intensity value does not correspond with a particular value of biomass of herbivorous fish. For this reason, the same arbitrary threshold value (foraging threshold = 1) is assigned to this parameter for both higher- and lower-risk reefs.

The model is based on a number of key assumptions:

1. Herbivore grazing radiates from the shelter. The level(s) of chronic and/or acute predation risk affect the distance that herbivores will venture from the shelter to forage.
2. For any given point along the reef benthos, fish foraging is directly proportional to the amount of time spent by individual herbivores at that point.
3. Risk is equal among all individual herbivores.
4. There is no relationship between feeding rate and excursion (i.e., foraging) area.
5. All substrate is suitable habitat for macroalgae.
6. Grazing by herbivorous fishes maintains primary producers in a “cropped” state, creating areas in which both turf algae and other benthic space occupiers (e.g., corals) can grow; all other areas are assumed to be colonized by macroalgae.
7. Net primary production of macroalgae is constant and equal among sites.

The model’s output is a spatially explicit characterization of the spatial heterogeneity (as defined by the size and number of macroalgal patches) over the reef benthos.

Empirical Testing of Model Predictions

To test the model’s assumptions and its predictions for how fishing for predators should indirectly alter the spatial

heterogeneity of macroalgae, we quantified predation risk, foraging excursion area, feeding rates, macroalgal distribution, and shelter distribution at atolls in the Northern Line Islands (eastern Indo-Pacific Ocean) that differ markedly in terms of human fishing pressure on predatory fishes. Predation risk and prey foraging excursion area were quantified at 11 sites within three of the archipelago's atolls (Palmyra Atoll [$N = 6$], Tabuaeran Atoll [$N = 3$], and Kiritimati Atoll [$N = 3$], except where noted below), and feeding rates, macroalgal distribution, and shelter distribution were quantified at six sites within two of the atolls (Palmyra [$N = 3$] and Kiritimati [$N = 3$]). Palmyra Atoll, an incorporated territory of the United States, has experienced virtually no harvesting of reef fishes, while Kiritimati and Tabuaeran atolls, both of the Republic of Kiribati, have increasingly dense human populations and intensities of fishing pressure. Further details on the fishing pressure exerted on these reefs and their resultant differences in predator assemblages can be found in articles by Stevenson et al. (2007), DeMartini et al. (2008), and Sandin et al. (2008). The reefs of Palmyra and Kiritimati atolls provide an ideal comparison of the cascading effects of human fishing pressure because they are biogeographically similar (i.e., they are both located in the Intertropical Convergence Zone and are under the influence of the equatorial countercurrent [Stevenson et al. 2007]), but they have experienced dramatically different levels of historical human influence, most notably, far more intense fishing pressure on predatory fishes at Kiritimati than at Palmyra (Stevenson et al. 2007; Sandin et al. 2008). This recent historical fishing pressure has dramatically affected the overall biomass and density of top predators (Sandin et al. 2008) as well as the overall fish assemblage structure (i.e., it has led to an inverted trophic biomass pyramid; DeMartini et al. 2008). Despite these changes, however, overall herbivore biomass remains essentially unchanged between the two atolls (Sandin et al. 2008). This point is key to our comparison of herbivore behavior between these two atolls, because we have therefore been able to control for potential effects of interspecific competition on foraging behaviors.

Sites within the atolls were separated by at least 1 km and ranged in depth from 2 to 10 m. All sites used for benthic video surveys (i.e., to quantify macroalgal and shelter distribution) were situated on the northwesterly sides of the atolls, in ocean-facing (i.e., nonlagoonal) habitat, although one site at Palmyra did experience reduced wave action relative to the others by virtue of its location behind the nonemergent reef crest. Tidal fluctuations and resultant delivery of sediments and nutrients from lagoon waters were not directly measured; however, the predominant outlets for the lagoons of both atolls are located on their westerly ends, suggesting that these sites should ex-

perience similar input levels. Benthic video surveys were completed during the northern hemisphere summer/fall (July–November) to avoid any confounding effects of seasonality, although such effects are unlikely at these sites given their equatorial location (roughly 1° and 5°N).

We used a range of species of common nonpredatory fishes to quantify bite rates and excursion sizes over a range of both chronic and acute predation risk. One of these species, the blackbar damselfish (*Plectroglyphidodon dickii*) is a small, site-attached benthic omnivore that feeds primarily on algae (Jones et al. 2006) and represents the functional group by which the model is broadly motivated. Additional species were used to test the generality of the observed behavioral patterns across other functional groups. Excursion sizes were also therefore quantified for the bullethead parrotfish (*Chlorurus sordidus*), a large, mobile herbivore; the whitecheek surgeonfish (*Acanthurus nigricans*), a medium-bodied, mobile herbivore; and the bicolor chromis (*Chromis margaritifer*), a small, site-attached zooplanktivore. In terms of body size, which is a proxy for vulnerability to predation, the blackbar damselfish and the bicolor chromis are similar, with maximum total lengths (TLs) of 11 and 9 cm, respectively. The whitecheek surgeonfish and the bullethead parrotfish are both substantially larger, with maximum TLs of 21 and 40 cm, respectively; however, the former is the only one of the study species to have a physical antipredator defense (i.e., sharp, razorlike “scalpels” on the caudal peduncle). This range of body sizes and physical defenses (or lack thereof) may affect the likelihood that each species will take greater or fewer risks while foraging in the presence of predators. To test the generality of the model's assumption of constrained excursions with increasing predation risk, excursions were defined as the distance or area of reef over which individuals move during 5-min observations. Bite rates were quantified for the first three of these species, as well as for the lined bristletooth (*Ctenochaetus striatus*), a medium-bodied, mobile detritivore/herbivore. Our methods followed the protocols outlined in Madin et al. (2010); further details on these methods can be found there.

As in the model, predation risk was quantified at two temporal scales. Chronic risk gives an estimate of the ambient predation risk faced by prey at a particular site, and it is analogous to risk integrated over time. Chronic risk was quantified by averaging the estimates of the biomasses of all piscivorous fishes across at least 15 replicate, haphazardly placed 60-m² belt transects within each site. Linear regressions performed on normalized data were then backtransformed and used to examine the relationship between prey excursion sizes and chronic predation risk. In this case, chronic risk was represented by average predator biomass per unit reef area, and prey excursion size was standardized by species' maximum predicted excursion

values, where units and maximum values vary by species: the blackbar damselfish was represented by a unitless ratio of prey excursion area to shelter area, with a maximum value of 15; the bullethead parrotfish and the whitecheek surgeonfish were represented by excursion area, with maximum values of 80 and 30 m², respectively; and the bicolor chromis was represented by excursion distance, with a maximum value of 35 cm. Acute risk provides an estimate of the immediate risk to which each observed individual was exposed during the observation period. It was quantified by recording all piscivorous fishes that swam within a defined area (a ~1.5- or a 3-m radius for the smaller and larger groups of focal prey species described above, respectively) surrounding each focal prey fish. Acute predation risk was calculated for the two mobile prey species (the bullethead parrotfish and the whitecheek surgeonfish) as the biomass of predators that each focal prey fish encountered during the 5-min observation period. The number of predators encountered was calculated as the number of piscivores that came within the 3-m-radius sphere surrounding the focal prey individual at any time during the 5-min observation period. For the two focal prey species for which it was feasible (the blackbar damselfish and the bicolor chromis), this metric also incorporated the amount of time that each predator spent in the immediate vicinity of the focal individual. For these species, the immediate vicinity was defined as the 3-m side-length cube of water surrounding the focal individual. In this instance, acute risk was calculated as the biomass of predators multiplied by the duration of their visits that each focal prey fish experienced over the 5-min observation period. Backtransformed best-fit upper 95% prediction intervals, which were based on a negative log-likelihood optimization function performed on normalized data, were then used to examine the relationship between prey excursion sizes and acute predation risk. Predation risk in this analysis was measured as predator biomass for mobile prey species and predator biomass multiplied by duration (in the vicinity of the prey individual) for site-attached prey species. For ease of comparison, both prey excursion size and predation risk value were standardized by species' maximum values. Units and maximum predation risk values vary by species: the blackbar damselfish and the bicolor chromis were represented by predator biomass times duration in the vicinity plus a constant, with maximum values of 1,100,000 and 150,000 g s⁻¹, respectively, and the bullethead parrotfish and the whitecheek surgeonfish were represented by predator biomass plus a constant, with maximum values of 80,000 and 17,000 g, respectively. Excursion-size units (as indicated above for chronic risk) and maximum values again varied by species: the maximum value for the blackbar damselfish was 230, for the bullethead parrotfish it was 1,400 m², for the whitecheek surgeonfish it was 700

m², and for the bicolor chromis it was 80 cm. Acute risk was measured only at Palmyra and Tabuaeran atolls.

In order to test the model's assumption that herbivore grazing radiates from the shelter and herbivores return to shelters when confronted with predators, additional focal individuals of *C. margaritifera* were observed when presented with model predators of three sizes (plastic sharks of 14, 25, and 74 cm TL). Although these models were in the form of small sharks, our objective was simply to present an object that prey individuals would perceive as a potential predation threat; objects of similar sizes but other shapes could be substituted. First, each of 15 focal prey individuals was observed for 3 min immediately before the series of model predators was presented. This period served as a control for each individual's behavior under natural conditions and was contiguous with the model predator presentations. At the end of the 3-min period, the focal individual was sequentially exposed to remotely operated small, medium, and large model predators via an underwater pulley system, with the order of model predator sizes varying haphazardly among focal individuals. Excursion values were calculated as the means over all model predator sizes of all observations of excursion distance from the shelter before the model was presented ("no predator" treatment), while the model predator approached and was between 1 and 2 m from the focal fish ("approach"), while the model predator was within 1 m on either side of the fish ("closest"), and again when it was departing and was between 1 and 2 m from the fish ("departure").

In order to test the model's predictions, macroalgal patch size and abundance over the reef benthos was quantified at Palmyra and Kiritimati atolls. Three 10-m transects were examined at each site, for a total of nine transects per atoll. Digital video was used to generate a spatially continuous record of noncryptic benthic organism distributions along 10-m × 10-cm swaths of benthos. Each 10-m transect was divided into 100 equidistant segments (located 10 cm apart) along the length of the transect. At the boundary between each segment, the 10-cm width of the transect was divided into 10 points separated by 1 cm. These points (1,000 in total per transect) served as the markers at which the adjacent benthos was categorized as one of the following: fleshy macroalgae, turf algae, crustose coralline algae (CCA), hard coral (branched), hard coral (unbranched), soft coral, sand, bare (i.e., containing no living organism), other, or indeterminate. For all subsequent analyses, the substrate was simply categorized as macroalgae or "other" (i.e., all other categories combined).

Patches of macroalgae were identified as any segment (i.e., the 10-cm lengthwise portions of the transect) of reef benthos with at least 10% cover of macroalgae along its 10-cm width, with the size of the patch determined by the number of contiguous segments (each separated by 10 cm)

meeting this criterion. Patches were then smoothed using a 50-cm moving window such that only those segments whose five-interval average was at least 20% macroalgae were subsequently counted as patches. This method eliminated isolated points of macroalgae (e.g., those represented by, e.g., only one 1-cm segment point within a 10-cm radius) from being considered as patches. An average per-transect frequency distribution of macroalgal patch sizes (to incorporate both patch size and abundance) was subsequently calculated for each of the two study atolls for comparison with each other and with model outputs. A two-sample Kolmogorov-Smirnov test was then used to determine whether the size-frequency distributions for the two atolls were significantly different from one another. Because macroalgae can prevent the settlement of other benthic reef organisms where they grow, this metric is inversely related to the size and spacing of patches of reef that are available for colonization by organisms such as reef-building corals.

In order to quantify shelter availability at the two study reefs for model parameterization, we identified the range of shelter sizes that would potentially provide shelter to the herbivorous fishes on which the model is based (i.e., small, site-attached, nonfarming benthic herbivorous and omnivorous fishes). This range was determined on the basis of the assumptions that adult small, site-attached fishes (e.g., of the family Pomacentridae) range in body size between roughly 5 and 20 cm TL and that individuals within this size range will be able to utilize shelters that are at least 2 cm larger than their body height (calculated as $\text{height} = 0.413 \times \text{TL}$; E. Madin, unpublished data). The resultant range of shelter sizes encompasses holes and crevices within the reef matrix that have diameters of 4–10 cm. Shelter density over this range was then estimated from the digital video transects described above.

Model Parameter Value Optimization

The model was run for 1,000 iterations for each of a range of parameter value combinations of the model's two risk-based parameters, δ (step length) and t (time; representing chronic and acute risk, respectively; values of δ range from 0.001 to 1 m; values of t range from 1 to 10,000 s), to generate frequency distributions of predicted macroalgal patch sizes for each combination. Parameter value ranges were chosen to range from extremely low to extremely high risk of both types. Parameter values for these two risk-based parameters were then optimized using sums-of-squares to determine the best-fit combination of values for the empirical macroalgal heterogeneity distributions from each atoll (using the "optim" function in the R software environment [R Development Core Team 2008]). Sums-of-squares values were based on the correspondence

between the model's predicted frequency distribution of macroalgal patch sizes and those observed at the two study reefs. Two-sample Kolmogorov-Smirnov tests were subsequently used to determine whether the frequency distributions resulting from the best-fit parameter value combinations for each atoll were statistically different from the empirical distributions they were optimized to represent.

As discussed above, lower values for each of the risk parameters correspond to higher predation risk. For example, a value of 0.001 for the chronic-risk parameter δ corresponds to a prey fish moving only 1 mm per time step because of a high risk of predation, whereas a value of 1 corresponds to the prey fish moving 1 m per time step as a consequence of relatively low risk of being attacked. Likewise, for the acute-risk parameter t , a value of 1 represents a high predation risk situation, where a predator passes the prey fish every second; a value of 10,000 means that a predator passes only once every 10,000 s, or ~ 3 h, thereby representing a low predation risk. We therefore expected that the optimal parameter value combinations would be for lower (i.e., riskier) values at Palmyra relative to Kiritimati. Because both parameters relate to the antipredator behavioral responses of herbivorous reef fishes to their predators, they predict the same direction of change in terms of individual foraging intensity distributions. In other words, as the values of both parameters increase, they accentuate each others' effects on the model's predictions. As a result, the hypothesized lines of figure 2 show a negative relationship between the two risk parameters. It is important to note that this does not in-

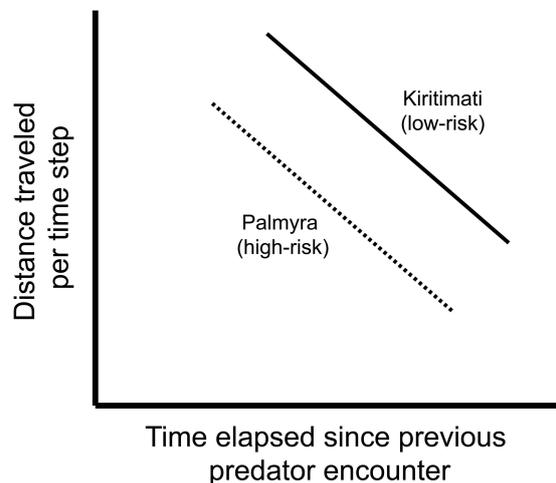


Figure 2: Schematic of expectations for optimal parameter value combinations. Lower parameter values represent higher risk for both parameter types. The X-axis is the acute-risk parameter t ; the Y-axis is the chronic-risk parameter δ .

dicating a negative relationship between the parameters themselves (i.e., low chronic risk does not correspond to high acute risk, or vice versa), but rather it reflects the expectation that they should trade off with one another to generate optimal fits to empirical data. In other words, the model output that best fits the empirical data may be generated by many different parameter value combinations, so long as an increase in either the chronic or the acute-risk parameter is offset by a decrease in the other. Figure 2 captures the resulting trade-off by using a line to represent the multiple parameter value combinations that are expected to collectively create a “ridge” of optimal fits to the empirical data. This trade-off both is biologically meaningful and has important implications for the model’s predictions.

Results

By varying two simple parameters, both of which are related to the predation risk faced by small herbivorous reef fishes, our model demonstrates that dramatically different distributions of foraging intensity and, thus, macroalgal distribution, can result (fig. 3). In agreement with our model’s predictions, the spatial heterogeneity of macroalgae, measured as the size and abundance of macroalgal patches, was greater at Palmyra than at Kiritimati (two-sample Kolmogorov-Smirnov test: $D = 0.2286$, $P = .051$). The basis for the construction and assumptions of this model rested on a number of characteristics of the study systems and the herbivorous reef fishes as well as

observed and hypothesized relationships between herbivore foraging and macroalgal abundance/distribution.

One of the key assumptions of our model is that herbivore grazing radiates from the shelter, and the level(s) of chronic and/or acute predation risk affect the distance that herbivores will venture from that shelter to forage. This assumption is supported by empirical data from a number of herbivorous and other prey fish species, including one small, site-attached herbivore (the blackbar damselfish) from the functional group by which the model is motivated. Figure 4 (based on data from Madin et al. 2010) uses observations from across the Line Islands archipelago to show that foraging excursion areas do indeed decline as both chronic (fig. 4a) and acute (fig. 4b) risk increase. Likewise, figure 5 shows that as individual model predators approach (and subsequently depart from) the individual home shelters of prey individuals, prey individuals become more wary. Specifically, prey reduce the excursion distances from their home shelter as the model predator approaches, hovering increasingly close (often retreating to within the shelter of the reef matrix) when the model predator is immediately adjacent to the shelter and then reemerging (albeit with apparently increased wariness) as the model predator departs the shelter vicinity (fig. 5).

Our model also assumes an equal abundance of shelters from predation at both atolls. Refuges from predation risk (openings/crevices in the reef matrix in which small fish can take shelter from larger, predatory fishes), while of a qualitatively different nature at the two atolls, are equally abundant for the size classes of fishes considered by the model (two-sample Kolmogorov-Smirnov test: $D =$

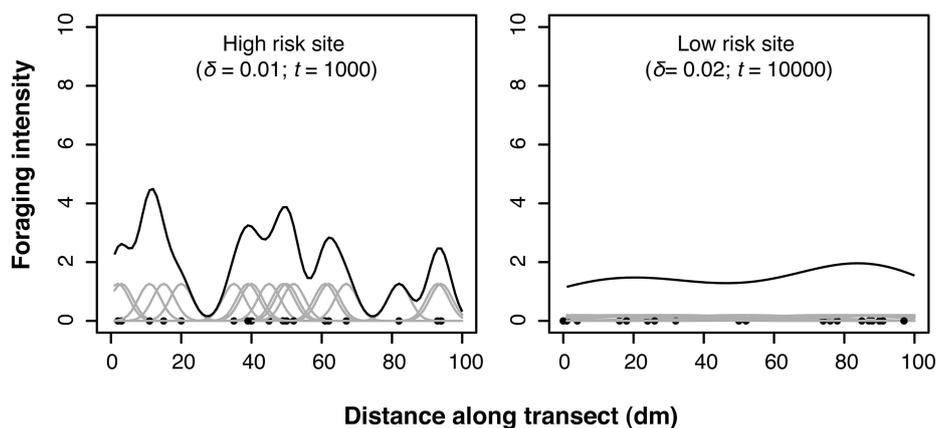


Figure 3: Example (one iteration) of the model’s predicted foraging intensities over the reef for an unfished (high-risk) site and a fished (low-risk) site. Points are randomly distributed shelters along the reef benthos. Gray lines are foraging intensity curves for individual fish occupying each of the shelters. Black lines represent predicted cumulative foraging intensity over the benthos. Parameters δ (step length) and t (time) represent chronic and acute risk, respectively.

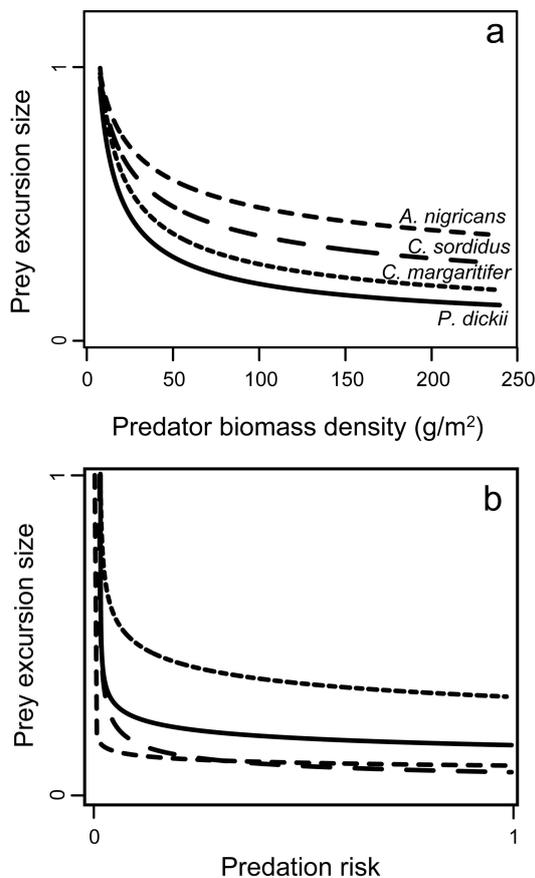


Figure 4: Standardized prey excursion size with relation to chronic (a) and standardized acute (b) predation risk for four prey fish species of different functional groups. Prey species are blackbar damselfish (*Plectroglyphidodon dickii*; solid line), bullethead parrotfish (*Chlorurus sordidus*; thick dashed line), whitecheek surgeonfish (*Acanthurus nigricans*; medium-width dashed line), and bicolor chromis (*Chromis margaritifer*; thin dashed line). In a, lines are back-transformed linear regressions performed on normalized data for chronic-risk values from 11 sites in the Northern Line Islands. The X-axis represents average predator biomass per unit reef area. The Y-axis is standardized by species' maximum predicted values (see "Methods" for details). In b, lines show best-fit upper 95% prediction bounds based on a negative log-likelihood optimization function where predation risk is measured by predator biomass for mobile prey species and by predator biomass \times duration for site-attached prey species. Both axes are standardized by species' maximum values (see "Methods" for details). Data are from work by Madin et al. (2010), which contains further details on the underlying data.

0.0486, $P = .983$). The main qualitative difference between the shelters found at the two atolls is that shelters at Palmyra are most commonly formed from either live scleractinian corals or dead coral covered in CCA, whereas shelters at Kiritimati are most commonly formed by either live scleractinian corals or dead coral covered in turf algae.

Variation in the two risk parameters in our model, chronic risk δ (step length) and acute risk t (time), led to the expected pattern of macroalgal heterogeneity (i.e., patch size and abundance). Both parameters affect the shape of the individual foraging intensity distributions. Examples of parameter value combinations at extreme values within the risk spectrum and the corresponding predicted foraging intensity distributions over the reef are shown in figure 3. As either chronic or acute risk are lowered (parameters δ and t increase, respectively), the shape of the distribution becomes more flattened and spread. As both risk types are lowered, this change is increasingly pronounced. With a random distribution of shelter locations along the reef benthos (drawn from a random uniform distribution using the function "runif" in R), on average, this translates into a more evenly distributed cumulative foraging effort (i.e., the sum of all overlapping individual foraging distributions over the reef) where risk is lower and a more patchy cumulative foraging effort where risk is higher (fig. 3). As a result, our model predicts that more and larger areas are likely to be left ungrazed when risk is high, and vice versa. These ungrazed areas are those that are located far from shelters, and thus from individual foraging areas, and hence experience a very low probability of being grazed. These patches can be thought of as "too risky" to warrant grazing by herbivorous fishes that are subject to predation risk, despite the high potential food reward.

In general, grazed substrate on reefs tends to be covered in "cropped" substrate—that is, CCA, turf algae, and/or bare substrate (Williams and Polunin 2001)—or benthic organisms whose colonization is limited to occurring on cropped substrate, such as scleractinian corals. In order to grow into a visible individual, a macroalga must be left ungrazed for a sufficient amount of time in order to grow into its fleshy form (Hixon and Brostoff 1996), after which point it may become chemically defended and less palatable (Hay 1991). On the basis of this knowledge, our model predicts that on low-risk reefs, the substrate will be more homogeneously dominated by cropped/previously cropped substrate (such as turf algae), whereas high-risk reefs will be more heterogeneous, with larger and more abundant patches of macroalgae interspersed among cropped/previously cropped substrate. Indeed, this pattern was observed at the two study atolls, with Palmyra having significantly greater heterogeneity in its macroalgal distribution than Kiritimati (as described above; fig. A1 in the online edition of the *American Naturalist*). Importantly, this difference is not due to differences in herbivore densities or net grazing rates, because, as described above, overall herbivore density is roughly comparable at the two atolls (Sandin et al. 2008) and grazing rate does not scale with foraging area (fig. A2 in the online edition of the *American Naturalist*). It is also important to

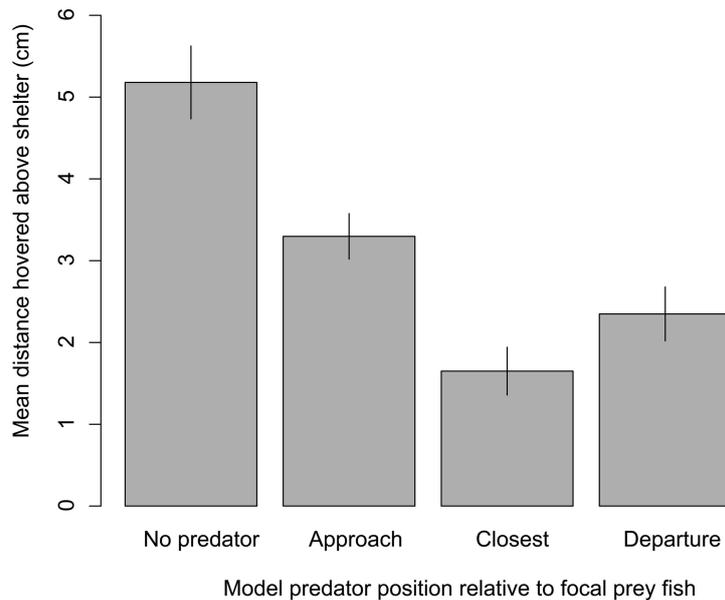


Figure 5: Prey excursion size in relation to acute perceived predation risk measured as distance between model predators and prey. Prey species is bicolor chromis (*Chromis margaritifer*). “No predator” treatment represents baseline behavior before initial model predator presentation. Bars are means (\pm SE). Prey individuals: $N = 22$.

note that while only a small portion of the benthos at the Kiritimati site is occupied by macroalgal patches, much of the remaining substrate is covered in algae in the form of cropped turf algae, resulting in far greater overall turf coverage at Kiritimati than at Palmyra (as described by Sandin et al. 2008; fig. A1).

Optimized values for the model’s two risk parameters, chronic and acute risk, demonstrated the expected trade-off with one another (fig. 2) but were consistently lower for Palmyra relative to Kiritimati (fig. 6). For any given value of one risk parameter, the corresponding optimal value(s) were consistently lower at Palmyra relative to Kiritimati (in a linear fashion), thus indicating a better fit at Palmyra with the overall higher-risk parameter set. The best-fit model parameters for each atoll ($\delta = 0.0045$ [Palmyra] and 0.1585 [Kiritimati]; $t = 5,623.41$ [Palmyra] and 112.20 [Kiritimati]) generated frequency distributions of macroalgal patch sizes that were statistically indistinguishable from the empirical data for both sites (two-sample Kolmogorov-Smirnov test: $D = 0.4286$, $P = .54$ [Palmyra] and $D = 0.2857$, $P = .94$ [Kiritimati]).

Discussion

By building on recent evidence that herbivorous and other nonpredatory coral reef fishes modify their foraging be-

havior in predictable ways in response to fishing-induced changes in predation risk (fig. 4; Madin et al. 2010), this study explores the cascading consequences of this response for the benthic reef community. We show how the simple behavioral responses observed as a function of predation risk can lead to dramatically different spatial distributions in benthic macroalgae, one of the key competitors of corals, and we provide a mechanistic basis for understanding why these patterns occur (fig. 1).

Many studies have examined the indirect effects of fishing on primary producer percent cover or biomass in coral reefs (Russ and Alcala 1998; Mumby et al. 2006; Newman et al. 2006; Sandin et al. 2008) and other marine systems (reviewed in Salomon et al. 2010), but to our knowledge, no studies have explored the effects on primary producer spatial heterogeneity as a consequence of changes in predator abundance. This gap is significant, however, both because of the ecological implications of macroalgal distribution for the broader reef community and, importantly, because it represents an alternate pathway by which top-down forces may affect change within the reef community. Our results inform the predictions for and the metrics to quantify the indirect effects of predator loss in marine systems, and as such they may pave the way for more conclusive studies of these indirect effects.

Our model sheds light on the mechanism(s) driving the

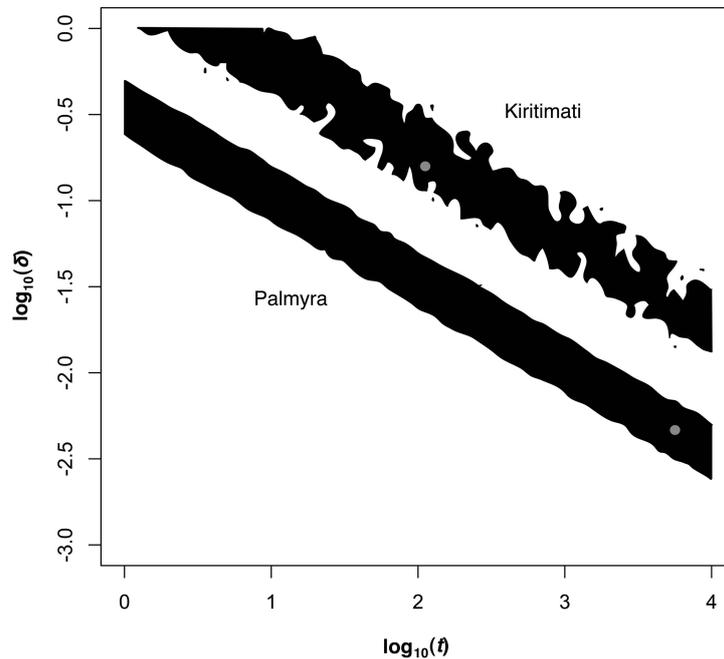


Figure 6: Parameter value space for fits to observed data from unfished (Palmyra) and fished (Kiritimati) reefs. Bands are the first decile (i.e., 10% quantile) of $\log_{10}(\text{sums-of-squares values})$ for model fits to empirical data from each atoll, where lower sums-of-squares values represent better-fitting parameter value combinations. Lower parameter values indicate higher predation risk for both parameters. The X-axis is the \log_{10} of acute-risk parameter t ; the Y-axis is the \log_{10} of chronic-risk parameter δ . Gray circles represent best-fit parameter value combinations for each atoll.

observed patterns of spatial heterogeneity of macroalgae at two atolls under different levels of human predator harvest. It has long been noted that coral reefs are often subject to high variance in both grazing and algal growth, resulting in a landscape dominated by patchiness in primary producer biomass (Randall 1965; Ogden et al. 1973; Strong 1992). Previous work in this system (Madin et al. 2010) has identified two temporal scales, chronic and acute, of predation risk faced by small reef fishes (sensu Lima and Bednekoff 1999). By explicitly considering the characteristic behavioral responses of prey to these types of risk, our model provides evidence that these responses are a mechanism that can maintain and/or generate wholesale changes in benthic macroalgal distribution. It is well known that across a variety of marine systems, predation risk can exclude herbivores from areas in which they would otherwise forage, for example, areas without adequate shelter (Hay 1981; Andrew 1993; McCook 1997). Other studies have also demonstrated a clear link between herbivore control of algae and shelter availability (Hay and Taylor 1985; Lewis and Wainwright 1985). Our model integrates these lines of knowledge by linking an underlying analytical diffusion (random-walk) model of individual foraging

intensity with simulations of shelter distribution over a reefscape. In so doing, the model describes with qualitative accuracy the net effect of changes in herbivore foraging behaviors on the heterogeneity of macroalgae observed at the study reefs.

The model's two key parameters, chronic and acute risk, trade off to generate multiple optima, but they consistently predict greater macroalgal heterogeneity under conditions of higher predation risk. These two parameters ultimately describe the shape of the foraging intensity curve for individual herbivores, but they act in fundamentally different ways. The chronic-risk parameter in the model (δ , step length) affects the distance that a fish ventures from the shelter with each time step, regardless of the presence of predators. Madin et al. (2010) have shown that, on average, prey fishes on Palmyra's relatively high-risk reefs have smaller foraging excursions than do those on relatively lower-risk reefs, such as those at Kiritimati, regardless of whether individuals were recently exposed to a predator. The acute-risk model parameter (t , time), affects the amount of time that an individual forages before encountering a predator and returning to its shelter. This parameter is therefore independent of the value of the chronic-risk parameter,

and its effect is dictated only by the density of predators in the immediate vicinity of the herbivore. Inclusion of both parameters in the model is critical, however, to discern among predictions that would be made under different predator-removal scenarios. Situations involving sudden, as opposed to gradual, changes in predator abundance represent the cases in which the values of these parameters would be most divergent. For example, for a reef that had been previously unfished (and thus is predator rich) but that was subject to a burst of intense predator harvest (e.g., shark finning), the chronic-risk parameter would have a low value (indicating high perceived risk), whereas the acute-risk parameter would be assigned a high value to represent the long intervals between current predator encounters. Alternatively, in a previously predator-poor lake system that had recently been stocked with predatory fishes for the purpose of sport fishing, the parameter values would be reversed. In this case, perceived chronic risk would be low, whereas acute risk would be high to represent the high likelihood encountering a predator. Under more gradual changes in predator abundance, values of these two parameters would converge such that perceived chronic risk would scale with acute risk, or the frequency of individual predator encounters. Depending on the response time of various herbivorous taxa to changes in predation risk, these differences in the effects of the parameters may be of greater or lesser relevance. For example, some higher-order marine taxa (e.g., fishes, marine mammals) may rapidly alter their behavior in response to changes in predator abundance. However, many other taxa (e.g., invertebrate marine herbivores) that forage in a way similar to that described by the model (i.e., in foraging bouts that radiate outward from a central shelter) may potentially respond over longer time-scales, including those of relevance to effects on primary producer communities. Because the relationship between the two risk parameters is linear, using intermediate values of both parameters results in a predicted frequency distribution of macroalgal patch sizes that is intermediate relative to the high- and low-risk extremes of Palmyra and Kiritimati, respectively. By incorporating both risk parameters, however, the model is flexible and can generate predictions under a variety of scenarios and, potentially, for a range of taxa.

Because the two parameters affect the shape of the individual foraging intensity curve in a qualitatively similar manner (see "Methods"), however, they necessarily trade off to generate optimal parameter value combinations (expected pattern, fig. 2). The bands, or "ridges," in figure 6 represent the lowest decile (10% quantile) of sums-of-squares values for fits between the model's predictions and the empirical data for each atoll. These bands thus show the parameter space for the model's two risk parameters, δ (step length) and t (time), from which the best-fitting 10%

of model predictions are generated. The inverse relationship between these two parameters is clearly seen in figure 6 where the bands of optimal parameter values occur. The key point to be made from figure 6 is that for any given value of either risk parameter, the corresponding value of the other risk parameter generating an optimal model fit to the empirical data is lower (indicating greater risk) for Palmyra than it is for Kiritimati. In other words, for a value of the acute-risk parameter $\log_{10}(t)$ of 2, the corresponding value of the chronic-risk parameter $\log_{10}(\delta)$ is lower for Palmyra (~ -1.5) than it is for Kiritimati (~ -0.5). Because parameter values are plotted on a \log_{10} scale, small differences along either axis correspond to extremely large (i.e., order-of-magnitude) differences in their values. This indicates that the model based on higher chronic and/or acute risk better describes the empirical macroalgal heterogeneity found at Palmyra, and the model based on lower risk better describes Kiritimati's macroalgal heterogeneity.

Because the model's cumulative foraging intensity over the reef is dependent on the number and distribution of shelters, it is sensitive to differences among reefs in the density of shelters. The different predictions made under an assumption of different shelter densities have not been empirically tested. Inclusion of this parameter into the model, however, allows it to be flexible enough to be used for reefs that do in fact differ in shelter abundance.

Our model rests on the key assumption that between reefs that are under different levels of predation risk, sizes of herbivore foraging areas differ but their overall aggregate feeding rates do not. Figure 4 (based on data from Madin et al. 2010) demonstrates that across a suite of four reef fish species (three predominant herbivores and one zooplanktivore), foraging areas decline with increasing predation risk. In particular, foraging excursion areas are significantly greater at the atoll experiencing higher fishing pressure and thus lower predation risk for reef fishes (Kiritimati) than at the unfished, higher-risk atoll (Palmyra; Madin et al. 2010). We also found that for a suite of four herbivorous fish species observed in this system (including the three herbivorous species from the previous study), feeding rate, measured as bites per unit time, does not scale with foraging area (fig. A2). This result is consistent with the findings of Barneche et al. (2009) for a suite of 20 herbivorous damselfish species from 18 locations globally. Importantly, Sandin et al. (2008) demonstrated that overall herbivore biomass (i.e., incorporating all herbivorous fishes in the study system) does not differ appreciably between these two study atolls. On the basis of these data, this key assumption of our model is supported.

Additionally, our model assumes that the herbivorous reef fish we modeled behave in a simplistic, randomly walking fashion. While this assumption is certainly not reflective of the complex antipredator and foraging be-

aviors that teleost fishes exhibit (Smith 1997), we think that it nonetheless effectively captures the net result of these behaviors in relation to the study's objectives. In making this assumption, we have enabled the model to be generalizable across taxa and systems whose taxa exhibit subtle (or dramatic) differences in either of these types of behaviors. Importantly, it allows the model to be applied to systems and/or taxa for which detailed behavioral data are lacking. We therefore conclude that this simplifying assumption lends strength to the model.

Our model is motivated by one functional group of reef fishes: small, site-attached grazing herbivores. Many different functional groups of herbivores ultimately control the standing stock of primary producers on coral reefs (Bellwood and Wainwright 2002), and indeed, complementary feeding by multiple herbivore taxa has been shown to play an important role in maintaining coral reef benthic structure through algal consumption (Burkepile and Hay 2008). Although they are generally one of the most numerically dominant groups of fishes, site-attached, nonfarming herbivores are only one group of many. One of the most obvious and functionally important groups of herbivorous fishes not considered by the model are the mobile grazers (parrotfishes [family Scaridae], surgeonfishes [family Acanthuridae], rabbitfishes [family Siganiidae], etc.). These taxa are particularly important because of their ability to remove large amounts of algal biomass per individual; some also contribute significantly to bioerosion of the reef matrix (Bellwood and Wainwright 2002). While no studies have, to our knowledge, quantitatively distinguished between the effects on macroalgae of site-attached, nonfarming herbivores and their larger, more mobile counterparts, all herbivorous fishes susceptible to predation must rely to some extent on shelters for protection from predators. Larger, more mobile fishes—particularly in their juvenile and subadult stages—are no exception. Their grazing areas should therefore be increasingly expected to include areas immediately surrounding shelters as the risk of predation increases. For this reason, although the model does not explicitly account for these species, its predictions should qualitatively capture the net effect of their grazing patterns. Unfortunately, without comparative data between these two groups of herbivores, it is not possible to rule out the possibility that the net effect of these larger fishes is greater than that of the smaller fishes on which the model is based. Another abundant and functionally important group of herbivorous fishes are the so-called farming damselfishes, which selectively cultivate mixed-species turf algal assemblages within their territories (Ceccarelli et al. 2005). In terms of total primary producer biomass, their foraging areas generally have higher biomasses than the adjacent areas outside of their territories (Ceccarelli et al. 2001). At first glance this

would appear to contradict the model's assumptions and predictions. However, these fishes primarily farm mixed-species algal turfs and maintain them in an early-successional state, weeding out and preventing fleshy macroalgae from growing in their territories (Ceccarelli et al. 2001). For this reason, fleshy macroalgae are more likely to be found outside of their territories than within them (Ceccarelli et al. 2001), and so this group should affect macroalgal patch size and abundance in the same qualitative way as their nonfarming counterparts. The fact that the model is based on one particular functional group therefore makes its predictions conservative, as is evidenced by the fact that it captures the patterns observed at Palmyra and Kiritimati that are shaped by the collective foraging behaviors of all functional groups of herbivorous fishes. Inclusion of multiple functional groups of herbivores into future iterations of the model would likely lend greater accuracy to its predictions.

Coral reef ecosystems are far more complex than the simple three-trophic-level food chain used for simplicity in our model. Indeed, coral reefs contain a high degree of opportunistic feeding and omnivory, blurring the lines between one trophic level and another and allowing for compensatory dynamics among taxa. Likewise, many artisanal fishers on coral reefs simultaneously harvest from multiple trophic levels (e.g., when using nets), thereby dampening the expected numerical effects of predator harvest by also harvesting their prey (e.g., herbivores). Coral reefs also contain many specialized guilds, with different primary food sources within the broad trophic groupings of predator, herbivore, and primary producer. All of these characteristics of coral reefs and their fisheries could cause attenuation of the expected top-down numerical (although not necessarily the expected behavioral) effects through a reef ecosystem. For the sake of creating a tractable, generalizable model, we have based our model on a simple three-trophic-level system (sensu Abrams 1991, 1995). However, we believe that doing so does not inordinately compromise the utility or generality of our model with regard to most circumstances. While omnivory within the predator guilds may lead to one type of predator occasionally consuming another, smaller predator, this should not remove the threat that the larger predator would pose to an herbivore as long as the herbivore remained a principal prey. Similarly, human harvest at multiple trophic levels may also remove prey species (e.g., herbivores) in addition to predators, but this should not affect the threat that the remaining predators have on the remaining herbivores. Predators of different guilds and body sizes will undoubtedly pose different levels of threat to different guilds and body sizes of prey (Stallings 2009). Interestingly, Schmitz and Suttle (2001) documented in an old-field system that three different species within the same hunting-

spider guild had qualitatively different effects on grasshopper prey, and subsequently, on primary producers, as a function of their different hunting styles. Despite these known complexities, we chose to model a simple three-trophic-level system because consideration of each pairwise interaction between such groups would not only have been impossible on the basis of existing behavioral data, it would have necessarily led to a model of inordinate complexity and limited generality for other systems. A notable exception to the relevance of our model would be a situation in which mesopredator release occurs as an indirect consequence of predator removal (review by Ritchie and Johnson 2009), thereby increasing abundance or changing behavior of midlevel predators of herbivores via the removal of a guild of top predators that do not ordinarily consume herbivores themselves. In this case, the net effect of fishing would be an increase in the predation risk for herbivores, likely leading to a reversal of the model's predictions for macroalgal heterogeneity. A related scenario in a density-mediated context, in which the reverse situation occurred—a top predator began consuming a key mesopredator, leading to the release of predation pressure on herbivores and subsequent regrowth of primary producers—has been documented in the kelp forests of western Alaska (Estes et al. 1998). This example highlights the effect that an additional trophic level beyond the three considered here can have on our model's predictions.

Finally, our model assumes an equal rate of net primary production of macroalgae at both atolls. This assumption is untested; however, the available evidence suggests that if indeed there is a difference in this rate, it is likely to be in the direction of higher primary productivity at Kiritimati relative to Palmyra due to the stronger upwelling Kiritimati receives (Sandin et al. 2008). One possible outcome of this disparity would be similar macroalgal standing stock between the two atolls but greater total herbivore consumption, and thus greater herbivore biomass, at Kiritimati relative to Palmyra. However, herbivore biomass is roughly equivalent at the two atolls (Sandin et al. 2008). Thus, our assumption of equal primary production rates at the two atolls is conservative; the alternative expected effect on macroalgal distribution would be larger and more abundant patches of macroalgae at Kiritimati relative to Palmyra, in contrast to predicted (model) and observed (empirical) patterns.

These results lend further support to the call for more integrated management approaches that include the maintenance of both density and risk effects of predators in marine communities (Dill et al. 2003; Heithaus et al. 2008a). More specifically, our findings provide theoretical and empirical justification for the assertion by Thrush and Dayton (2010) that protection of essential fish habitats, such as physical refugia from predators, must be an im-

portant consideration of future ecosystem-based management approaches in order to maintain key ecological functions that shape marine landscapes.

This study provides a mechanistic basis for revising our simple predictions of the cascading, top-down effects of fishing on coral reefs. Our model demonstrates how human removal of predators from coral reefs (i.e., fishing) can indirectly influence the spatial heterogeneity of a key group of benthic organisms, the fleshy macroalgal complex, via behavioral responses by their prey. This effect is significant within the context of the overall structure of coral reefs because macroalgae are one of the primary competitors of scleractinian corals, the engineers of the reef matrix, for valuable space on the reef benthos. Therefore, in addition to any indirect effects on individual prey fish fitness that human fishing may have via their behavioral responses (Werner et al. 1983; Diehl and Eklov 1995), fishing may dramatically alter the competitive balance among key benthic organisms and in turn influence the spatial structure of the reef benthos. These effects, however, are more complex than has generally been assumed in the context of trophic cascades. Most earlier studies exploring the indirect effects of human predator harvest on primary producers (i.e., trophic cascades) have relied on total primary producer biomass or percent cover as the response metric, while ignoring its fine-scale spatial heterogeneity. To our knowledge, macroalgal spatial heterogeneity has never before been considered as a response variable in the context of trophic cascades in a marine system. These effects could be particularly important, though, if competition between corals and macroalgae is nonlinear, for example, if larger or more numerous patches of macroalgae have a disproportionately greater competitive advantage over corals. This study demonstrates that the top-down, indirect effects of predators may take an alternate pathway through reef food webs, with outcomes that are qualitatively different from those that are often assumed to result.

The results presented here add to the emerging conceptual unification of trait-mediated effects, particularly when compared with findings originating from different study designs and ecosystem types. This study further highlights the importance of considering landscape features and, in particular, the role that they play in mediating risk effects, in future studies of this nature. This relationship is well established (see partial review by Wirsing et al. 2010), and Heithaus et al. (2009) recently proposed a conceptual model integrating landscape features and prey escape tactics described above. Our study did not aim to explicitly test the predictions arising from this model; however, our results raise the question of whether this framework will apply to systems and taxa for which the scale of refugia are similar to that of prey individuals, such as is the case in the coral reef system studied here.

In a meta-analysis of density and risk effects spanning terrestrial, aquatic, and marine systems, Preisser et al. (2005) found that cascading, density-mediated effects of predators attenuated through ecosystems, while behavioral or risk effects attenuated far less and produced a stronger signal on prey resources. While our study examined only the pathway of risk effects, Sandin et al. (2008) examined possible cascading, density-mediated effects in the same reef system and found no evidence of a density-driven trophic cascade. When considered together, the findings of Sandin et al. (2008) and this study provide evidence from natural reef communities that lend support to Preisser et al.'s (2005) result. Similarly, these collective results support the assertions by Creel and Christianson (2008), which were derived in large part from the terrestrial wildlife literature, that the numerical and behavioral effects of predators on prey do not necessarily change in parallel and indeed may be negatively or positively correlated or uncorrelated.

Our understanding of the role of humans in instigating risk-mediated trophic cascades has begun to coalesce in recent years, with documented cases emerging from a range of systems. Hebblewhite et al. (2005) described a case in which the spatial habitat usage of a top predator (wolves) changed in response to the presence of humans, ultimately leading to a trophic cascade affecting multiple trophic levels by altering their densities, demographics, and/or diversity. Unlike in this study, the observed risk effects in that system occurred between humans and top predators, as opposed to between top predators and their prey. Few other examples of behaviorally mediated trophic cascades driven by human-induced top-predator alterations exist (but see Ripple and Beschta 2006), although Byrnes et al. (2006) cleverly linked a long-term kelp forest monitoring data set with mesocosm experiments and concluded that declines in marine predator diversity led to cascading risk effects. Notably, of these examples, only Byrnes et al. (2006) examined the cascading effects of predator declines, as opposed to predator recolonization, which we examine here. This seemingly minor distinction has important implications, however, because our results lend much-needed insight into predictions for the kinds of ecosystem alterations we can expect due to continued global declines in marine top predators (Jackson et al. 2001; Myers and Worm 2003; Heithaus et al. 2008a). We hope that this insight may better equip conservation practitioners and resource managers in the move toward true ecosystem-based management, in which the full suite of potential ecological interactions and impacts guide policy decisions.

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