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Positive and Negative Effects of a Threatened Parrotfish on Reef Ecosystems

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Abstract: *Species that are strong interactors play disproportionately important roles in the dynamics of natural ecosystems. It has been proposed that their presence is necessary for positively shaping the structure and functioning of ecosystems. We evaluated this hypothesis using the case of the world's largest parrotfish (*Bolbometopon muricatum*), a globally imperiled species. We used direct observation, animal tracking, and computer simulations to examine the diverse routes through which* B. muricatum *affects the diversity, dispersal, relative abundance, and survival of the corals that comprise the foundation of reef ecosystems. Our results suggest that this species can influence reef building corals in both positive and negative ways. Field observation and simulation outputs indicated that* B. muricatum *reduced the abundance of macroalgae that can outcompete corals, but they also feed directly on corals, decreasing coral abundance, diversity, and colony size.* B. muricatum *appeared to facilitate coral advancement by mechanically dispersing coral fragments and opening up bare space for coral settlement, but they also damaged adult corals and remobilized a large volume of potentially stressful carbonate sediment. The impacts this species has on reefs appears to be regulated in part by its abundance—the effects of* B. muricatum *were more intense in simulation scenarios populated with high densities of these fish. Observations conducted in regions with high and low predator (e.g., sharks) abundance generated results that are consistent with the hypothesis that these predators of* B. muricatum *may play a role in governing their abundance; thus, predation may modulate the intensity of the effects they have on reef dynamics. Overall our results illustrate that functionally unique and threatened species may not have universally positive impacts on ecosystems and that it may be necessary for environmental managers to consider the diverse effects of such species and the forces that mediate the strength of their influence.*

Keywords: benthic, *Bolbometopon*, coral, function, diversity, management, simulation, threatened species

Efectos Positivos y Negativos de un Pez Loro Amenazado Sobre Ecosistemas Arrecifales

Resumen: *Las especies que son interactuantes intensos juegan papeles desproporcionadamente importantes en la dinámica de los ecosistemas naturales. Se ha propuesto que su presencia es necesaria para moldear positivamente la estructura y función de los ecosistemas. Evaluamos esta hipótesis utilizando el caso del pez loro más grande del mundo (*Bolmometopon muricatum*), una especie en peligro globalmente. Usamos observación directa, seguimiento de individuos y simulaciones con computadora para examinar las diversas formas en que* B. muricatum *afecta la diversidad, dispersión, abundancia relativa y supervivencia de los corales que son la base de los ecosistemas arrecifales. Nuestros resultados sugieren que esta especie puede influir en la construcción de arrecifes de manera tanto positiva como negativa. La observación de campo y*

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las simulaciones indicaron que B. muricatum *redujo la abundancia de macroalgas que pueden competir con corales, pero también se alimenta directamente de corales, lo cual disminuye la abundancia, diversidad y tamaño de la colonia de corales.* B. muricatum *pareció facilitar el avance de coral al dispersar mecánicamente fragmentos de coral y abrir espacio para su establecimiento pero también dañó corales adultos y reactivó un gran volumen de sedimento de carbonato potencialmente estresante. El impacto de esta especie sobre los arrecifes parece ser regulado en parte por su abundancia – los efectos de* B. muricatum *fueron más intensos en escenarios poblados con altas densidades de este pez. Las observaciones realizadas en regiones con abundancia alta y baja de depredadores (e. g., tiburones) generaron resultados que son consistentes con la hipótesis de que estos depredadores de* B. muricatum *pueden jugar un papel en la regulación de su abundancia; por lo tanto, la depredación puede modular la intensidad de los efectos que tienen sobre la dinámica de los arrecifes. En general, nuestros resultados ilustran que especies funcionalmente únicas y amenazadas pueden no tener impactos universalmente positivos sobre los ecosistemas y que puede ser necesario que los manejadores ambientales consideren los efectos diversos de tales especies, así como las fuerzas que median la intensidad de su influencia.*

Palabras Clave: Béntico, *Bolbometopon*, coral, diversidad, especie amenazada, función, manejo, simulación

Introduction

Certain key species can have a powerful influence on ecosystem diversity and functioning. The removal of such species can precipitate pronounced ecological change (e.g., keystone species; Paine 1992; Wootton 1997; Terborgh & Estes 2010) and can directly shape the physical architecture of their environment (e.g., ecosystem engineers; Wright et al. 2002). Most reports in the literature on these key species consider instances where, from the point of view of managers, they exert strong positive effects on ecosystems. For example, sea otters (*Enhydra lutris*) protect the integrity of kelp forests and promote carbon storage (Terborgh & Estes 2010; Wilmers et al. 2012); wolves (*Canis lupus*) promote biodiversity in riparian communities (Ripple & Beschta 2004), and beavers (*Castor canadensis*) engineer increases in landscape-level species richness (Wright et al. 2002). There are, however, examples of instances where the effects of functionally dominant species appear less positive. For instance, African elephants (*Loxodonta africana*) are agents of deforestation and reduce biodiversity (Cumming et al. 1997) and Snow Geese (*Chen caerulescens*) contribute to wetland destruction (Kerbes et al. 1990).

Given the substantial influence of this class of functionally important species, many argue that protecting species with unique functional roles is synonymous with the protection of ecosystems themselves (Bellwood et al. 2003; Soulé et al. 2005). The ubiquity of this connection, however, remains unclear. To evaluate the putative linkages between the functional importance of a species and its effects on ecosystem structure and dynamics, we examined the influence of the bumphead parrotfish (*Bolbometopon muricatum*) on coral reef ecosystems. There has been relatively little research on the ecology of this large (world's largest parrotfish) and threatened (Vulnerable; IUCN 2013) fish (Dulvy & Polunin 2004). First evidence collected in a study that focused on the feeding ecology of *B. muricatum* suggests that it may occupy a functionally unique role in coral reef communities and may be vitally important to ecosystem stability and resilience (Bellwood et al. 2003). As such *B. muricatum* provide a superb model for examining how strongly interacting species influence key elements of ecosystem structure and function.

We investigated a range of aspects of the ecology of *B. muricatum* and examined the impacts these different functions have on the diversity and dynamics of coral reefs. Because the effects of any species are also controlled in part by their abundance and behavior and these parameters are in turn often regulated by top-down processes such as predation, we examined how predators may modulate the effects that *B. muricatum* has on its environment. While this approach omits important bottom-up processes and interactions between top-down and bottom-up forces, it helps clarify the particular influence of *B. muricatum* on reefs. To determine the long-term effects this species may have on coral reef ecosystems, we constructed a basic computer simulation that models some of its potential multiyear summary effects on reef interactions. Our results contribute to the understanding of the ecology of this understudied and imperiled species and knowledge of the larger role that strong interactors play in shaping ecosystems.

Methods

Study Site and Focal Follows

This research was conducted at two biogeographically similar central Pacific atolls in the Northern Line Islands Archipelago: largely unpopulated Palmyra (5°52'N, 162°04'W; perimeter 40.8 km; population approximately 20) and populated Tabuaeran (3°51'N, 159°19'W; perimeter 52.3 km; population approximately 3000) (McCauley et al. 2013). Palmyra is protected as a US National

Wildlife Refuge and hosts high densities of large coral reef fish (McCauley et al. 2012*a*, 2012*b*). Densities of large fish, particularly sharks and other top predators, have been much reduced at Tabuaeran by fishing (McCauley et al. 2012*c*). *B. muricatum* are a preferred target of fishers on Tabuaeran and are harvested with nets and spears in forereef, backreef, and lagoons. From 2006 to 2010, we spent approximately 130 d in the water at Palmyra and Tabuaeran searching for or making observations of *B. muricatum.* We collected data from June to November.

The majority of our *B. muricatum* feeding ecology data was collected during focal follows of individual fish at Palmyra Atoll. Timed follows were conducted at backreef sites (landward side of reef crest; depth 1–5 m) at the east end of Palmyra. Densities of *B. muricatum* in this area were the highest we had thus far encountered at Palmyra, although we did not comprehensively survey the entire atoll. During focal follows 1–2 observers with snorkels shadowed a single *B. muricatum* until it was lost or until nightfall. *B. muricatum* at Palmyra can be followed at close range (1–3 m) without a perceptible change in fish behavior. To ensure that all information included in our analyses came from unperturbed animals, we only used data from focal follows lasting >60 min. Mean follow duration was 3.2 h, and the longest follow lasted 5.3 h. Unique scale and forehead patterning of *B. muricatum* permitted us to identify individuals involved in follows and allowed us to make coarse minimum estimations of the size of the *B. muricatum* population resident in the region of reef where our research was concentrated (Supporting Information). We report only focal follow data collected from adult animals (>50 cm total length [TL]). We tracked the movements of approximately 75% of the fish that were followed with a GPS logger (attached to the observer) and estimated the foraging area used by individual tracked fish and the area used collectively by all tracked fish (Supporting Information).

Feeding Ecology

We recorded the bite rates and identity of materials consumed by *B. muricatum* during all follows. We identified 3 major categories of substrate upon which *B. muricatum* fed: live scleractinian corals, dead coral substrate, and macroalgae. Live scleractinian corals included all macroscopic living stony corals. The dead coral category included all coral bench rock with no visible (>25 mm) adult living corals or coral rubble. These "dead" coral substrates are biologically active and often host superficially and interstitially living biota (e.g., turf and crustose coralline algae, boring reef invertebrates, newly settled microscopic coral recruits). We defined macroalgae as algae >10 mm in height.

We estimated *B. muricatum* bite size and bite volume and coupled this information with bite rate data to approximate the quantities of different reef materials removed by these fish. Three functionally different kinds of bites were recognized: branching coral bites (i.e., bites taken from the erect live corals in the genera *Pocillopora* and *Acropora*); divot bites (bites delivered to all other non-branching substrate surfaces; e.g., dead corals, live encrusting and massive corals); and bites to macroalgae (Supporting Information). The mass of material removed with these 3 bite types was estimated using field measurements and published conversion values (branching bites $n = 205$; divot bites $n = 64$; macroalgae bites $n = 400$; Supporting Information). We estimated the quantity of material annually removed by individual *B. muricatum* as

$$m_{\text{total}} = \left[\left(\overline{x}_{\text{branch}}\, m_{\text{branch}}\right) + \left(\overline{x}_{\text{divot}}\, m_{\text{divot}}\right) + \left(\overline{x}_{\text{algae}}\, m_{\text{algae}}\right) \right] t, \qquad (1)$$

where $\overline{x}_{\text{branch}}$, $\overline{x}_{\text{divot}}$, and $\overline{x}_{\text{algae}}$ are the mean number of branching coral bites, divot bites, and macroalgae bites respectively taken by individual *B. muricatum* per hour;m_{branch}, m_{divot}, and m are the mean masses of each respective bite type; and t is the total number of daylight hours per year. These estimations were subsequently standardized by foraging area to calculate the quantity of reef material that individual *B. muricatum* consumed in their core use area and by the minimum size of the local population of *B. muricatum* observed in the reef space where GPS tracking was undertaken (Supporting Information).

To examine the feeding preferences of *B. muricatum*, we surveyed the abundance of different substrate types in our backreef study site (Supporting Information). This benthic survey data was coupled with information on *B. muricatum* consumption to estimate resource selection ratios (Hoey & Bellwood 2008). Reef substrate composition was surveyed using a point-intercept method at 10 cm increments along 25 m transects ($n = 8$ replicates). For these analyses, we aggregated benthic substrates into 5 groups: pocilloporid corals (e.g., *Pocillopora* spp.); encrusting acroporid corals (e.g., *Montipora* spp.); other corals (i.e., all remaining coral species); dead coral (as above); and erect macroalgae (as above). While other sessile benthic organisms were present (e.g., sponges, cyanobacteria) in Palmyra's backreefs, they were much less common than these 5 benthic groups.

Defecation Rates and Material Redistribution

We recorded the rate of defecations produced by adult *B. muricatum* during all focal follows (Supporting Information). Using *B. muricatum* forage intake rates (calculation described above), we estimated the quantity of material that *B. muricatum* annually redistributed across reefs. We assumed *B. muricatum* has an absorption efficiency comparable to other parrotfish (approximately 3%; Targett & Targett 1990) and that all material they do not absorb is defecated back onto the reef. We used the same methods employed to calculate area specific consumption rates to estimate the total annual mass of fecal material deposited per unit reef by our entire study population of *B. muricatum* (Supporting Information). Because the size of the particles in *B. muricatum* fecal cast may determine the ecological impact this material has on the corals upon which it settles, we directly measured the size (by mass) of *B. muricatum* fecal particles ($n = 22$).

Coral Dispersal

To determine if *B. muricatum* contributes to the dispersal of corals by fragmenting them during feeding, we measured the number of live coral fragments produced per hour (and not subsequently consumed) in a subset of *B. muricatum* focal follows ($n = 711$ min; 6 focal follows; Supporting Information).

Predator Modulation

To generate preliminary insight into how predators may control the behavior and abundance of *B. muricatum*, we compared observations of *B. muricatum* and their human and nonhuman (i.e., sharks) predators on the fished reefs of Tabuaeran with the unfished reefs of Palmyra. We used 2 strategies to explore these effects. First, we collected bite rate data during focal follows of *B. muricatum* at Tabuaeran (same methods as described above; $n = 4$) and compared these results with *B. muricatum* bite rate data from Palmyra. Second, to determine if the anthropogenic removal of *B. muricatum*'s predators changes how they use high-risk habitats, we compared abundances of *B. muricatum* in habitats (forereefs) of Palmyra and Tabuaeran that predators usually prefer. Large-bodied reef sharks (maximum biomass > 20 kg) prey on parrotfishes (Wetherbee et al. 1997). This suggests they have the capacity to prey on *B. muricatum* juveniles and perhaps also adults, although large parrotfish species, like *B. muricatum*, are believed to attain size-escape thresholds from some of their piscine predators (Mumby et al. 2006). In our system, the numerically dominant large shark is *Carcharhinus amblyrhynchos* (grey reef shark), although at least 3 other large shark species are also present (e.g., *Galeocerdo cuvier*, *Sphyrna lewini*, *Carcharhinus galapagensis*) and a host of smaller species. *C. amblyrhynchos* can be common on the deep forereefs but are much less frequently observed in shallower reefs (e.g., the backreef areas where all Palmyra focal follows were conducted) (Friedlander et al. 2010; Supporting Information). The abundance of *B. muricatum*, *C. amblyrhynchos* (recorded as presence or absence), and all reef sharks (all species pooled, including species <20 kg) was recorded in these high-risk forereef areas by divers using a series of belt transects laid along a 10–12 m depth isobath (McCauley et al. 2012*b*). Nine forereef sites were surveyed 7 times each at Palmyra and 5 forereef sites were surveyed 4 times each at Tabuaeran. All surveys at Tabuaeran were conducted on the west side of the atoll, near high-density human settlements where fishers were active. Differences measured at these 2 atolls were compared with Welch's t tests and chi-square tests in Program R (R Development Core Team 2011). To elucidate how the residents of Tabuaeran may have contributed to differences observed in these comparisons, we used ethnographic surveys to examine harvest patterns of *B. muricatum* and sharks (Supporting Information).

Simulation

To examine some of the possible long-term impacts of *B. muricatum* on coral reef ecosystems, we constructed a simulation, implemented in Program R, that modeled basic reef dynamics and *B. muricatum* foraging. The simulation was populated with 5 benthic classes: branching pocilloporid corals; encrusting acroporid corals; massive poritid corals; erect macroalgae; and uncolonized substrate. Parameters describing the growth, recruitment, size distribution, and abundance of these benthic classes were incorporated in the simulation, and values were drawn from field data collected at Palmyra or from the literature. We used our empirical data on *B. muricatum* density, feeding rates, and food preferences to model its foraging in the simulation. We ran the simulation with 3 different scenarios of *B. muricatum* density: high density, after densities reported by Bellwood et al. (2003) on the Great Barrier Reef (GBR) (50 *B. muricatum*/ha); medium density, after densities observed at Palmyra (0.3 *B. muricatum*/ha); and none (no *B. muricatum* present; Supporting Information). Simulation scenarios were run for 75 iterations (1 iteration = 1 year time step), and 50 overall replicate runs were completed. By contrasting results between these different scenarios, we were able to examine some of the possible effects that *B. muricatum* had on coral and algae abundance (percent change in cover $[T75 - T0)/T0]$), coral colony size, and overall coral community diversity (measured using the Shannon diversity index for corals only). Additional details of the simulation are outlined in Supporting Information.

Results

Feeding Ecology

We gathered 1745 min of focal follow data from 5 *B. muricatum* individuals and recorded 5910 bites. These animals took an average of 3.3 bites/min (SE 0.20) (Table 1). The most bites were taken from dead coral substrate (59.3%) and living scleratinian corals (40.1%) (Fig. 1). Very few bites were taken from macroalgae (0.6%).

Table 1. Comparisons of key parameters of *Bolbometopon muricatum* ecology between survey sites at unfished (Palmyra) and fished (Tabuaeran) atolls.

Parameter	*Palmyra (unfished)*	*Tabuaeran (fished)*	*p*	t, χ^2	*df*
B. muricatum bites/min (SE)	3.3 (0.2)	3.1 (0.6)	0.83	0.23	3.7
B. muricatum (% present)	0	35	<0.0001	24.4	1
C. amblyrhynchos (% present)	73	0	<0.0001	29.2	1
All reef sharks (% present)	97	18	<0.0001	52.5	1

Table 2. Mean (SE) *Bolbometopon muricatum* rates of consumption of live coral, dead coral, and macroalgae gathered during focal follows at Palmyra Atoll.

Parameter	*Live coral*	*Dead coral*	*Macroalgae*	*Total*
bites $\mathrm{min^{-1} \cdot indv^{-1}}$	1.4 (0.2)	1.9 (0.1)	0.02 (0.007)	3.3 (0.2)
$\mathrm{kg\ yr^{-1}\ indv^{-1}}$	2140 (350)	2330 (150)	10 (4)	4480 (340)
$\mathrm{g \cdot d^{-1}\ m^{-2}\ indv^{-1}}$ [a]	1.5 (0.5)	2.2 (0.9)	0.009 (0.003)	3.7 (1.2)
$\mathrm{g \cdot yr^{-1}\ m^{-2}\ pop^{-1}}$ [b]	68.6 (11.2)	74.6 (4.8)	0.3 (0.1)	143.5 (10.9)

Note: Mass-based consumption rates were standardized by data on space use from GPS tracked fish to generate spatially explicit estimates of consumption.

[a] *Consumption by individual* B. muricatum.

[b] *Consumption estimated for the local population of* B. muricatum *present in the focal study site at Palmyra (see Supporting Information).*

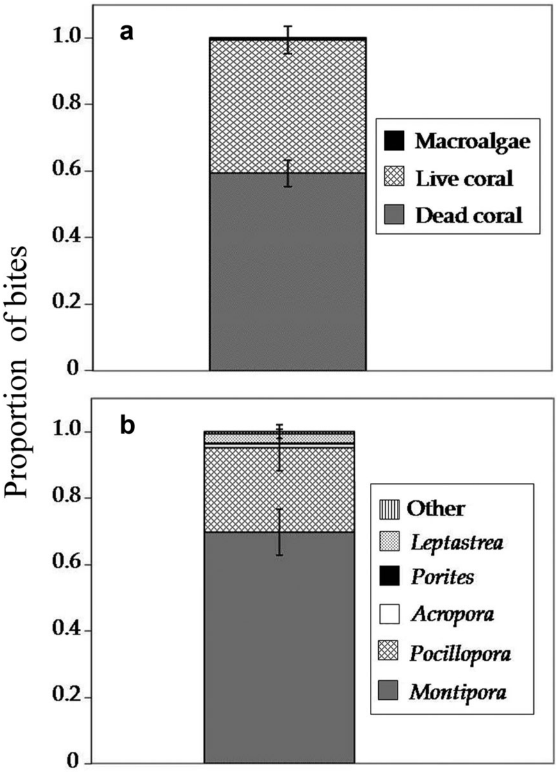

Figure 1. Proportion (SE) of (a) total bites taken by Bolbometopon muricatum *on different general substrate types and (b) bites of live coral taken from different coral genera.*

Bites of branching coral removed pieces of live coral with a mean weight of 8.4 g, divot-style bites removed 4.4 g, and macroalgal bites took in 1.9 g of material. Using these values, we estimated that a single adult *B. muricatum* consumed on average 4480 kg of material from the reef every year. The majority of this intake by mass was also split between living and dead coral (Table 2). The average individual *B. muricatum* consumed approximately 3.7 g (SE 1.2) of material from every square meter of reef that it traversed in a day (Table 2). This rate of consumption scales up to approximately 143.5 g (SE 10.9) of material removed from every square meter of reef in our study area each year by the entire local population of *B. muricatum* in this region ($n = 6$; Supporting Information). Such approximations, however, need to be interpreted cautiously because consumption by *B. muricatum* is almost certainly not uniformly distributed across a reef.

Of the food types consumed by *B. muricatum* (Fig. 1), they exhibited a strong preference for pocilloporid corals (mass-based selectivity index [SI] = 4.9) and pronounced aversion for other corals (SI = 0.3) and macroalgae (SI = 0.05). Dead coral (SI = 1.0) was eaten approximately in proportion to its ambient abundance, and encrusting acroporid coral was slightly less preferred (SI = 0.8).

Defecation Rate, Material Redistribution, and Coral Dispersal

Adult *B. muricatum* defecated, on average, 21.8 times/h (SE 1.0). We estimated that 1 *B. muricatum* adult defecates approximately 4345 kg of material back onto the reef each year. This equates to approximately 140 g (SE 10) of fecal material deposited annually on each square meter of reef by the entire studied population in the reef region. Analysis of the particle size distributions of fecal castes that settled onto reefs revealed that particles between 75 and 212 μm were the most common (30.2%, SE 2.9), although there was also a substantial fraction of larger particles (Supporting Information).

While feeding, adult *B. muricatum* generated an average of 14.4 fragments of living coral per hour (SE 3.5). The majority of these unconsumed fragments (>80%) were from colonies of *Pocillopora* and measured 1.0 cm in basal diameter (SE 0.03) and 3.6 cm in height (SE 0.13); 90% of these fragments were >2 cm in height (Supporting Information).

Predator Modulation

The putative *B. muricatum* predator *C. amblyrhynchos* was commonly sighted during surveys of the forereef at Palmyra, but these sharks were completely absent in surveys of the forereef at Tabuaeran (Table 1). Abundances of all reef sharks pooled (including *C. amblyrhynchos*, *C. melanopterus*, and *Triaenodon obesus*) reflected the same pattern. Data from surveys of residents of Tabuaeran indicated sharks are a top harvest target, suggesting that fishing is likely to be responsible for reductions in shark abundance (Supporting Information). Our comparisons of *B. muricatum* use of the forereef at these 2 atolls indicated that populations of *B. muricatum* were common at Tabuaeran but completely undetectable on the forereefs of Palmyra (Table 1). Comparisons of the feeding behavior of *B. muricatum* indicated that despite these observed differences in habitat use at these 2 atolls (all *B. muricatum* data from Tabuaeran derived from the forereef; all *B. muricatum* data from Palmyra derived from the backreef), there was no significant difference between bite rates of this species at these sites (Table 1).

Simulation

In our simulation, *B. muricatum* caused declines in overall coral community diversity (Fig. 2a); scenarios with the highest densities of *B. muricatum* exhibited the sharpest reductions in diversity. These diversity declines were associated with reductions in the evenness of coral taxa. *B. muricatum* also effectively reduced the relative abundance of all 3 coral types (Fig. 2b). Pocilloporid corals, those that were highly preferred feeding targets by *B. muricatum*, showed the largest relative reductions in abundance. While macroalgae increased in all versions of the simulation, its growth was suppressed by *B. muricatum*, most substantially so in the high-density *B. muricatum* scenario. *B. muricatum* also exerted a negative impact on the size structure of benthic constituents in the simulation. Here again reductions in size were greatest in high-density *B. muricatum* scenarios and were most pronounced for branching pocilloporid corals (Figs. 3 & 4). Outputs from the simulation were not overly sensitive to variability in parameter values (Supporting Information).

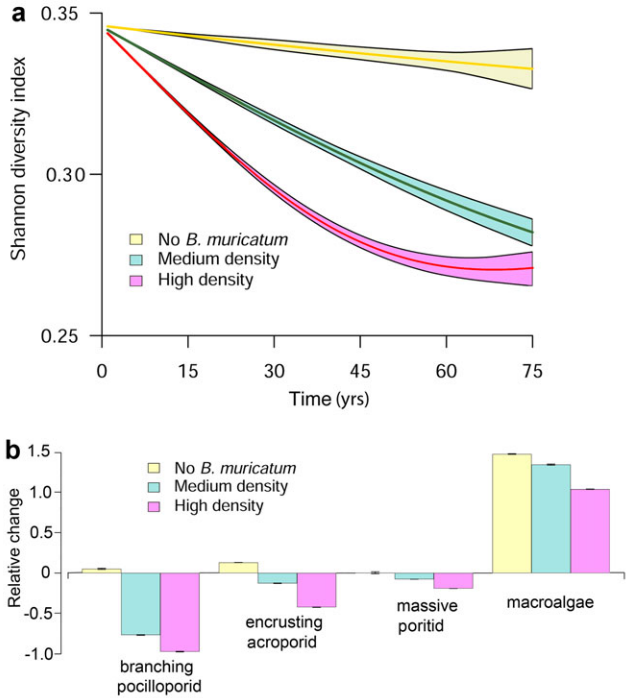

Figure 2. Outputs from computer simulation designed to predict the effects of Bolbometopon muricatum *foraging on benthic community dynamics: (a) changes in the diversity (Shannon index) of corals over time with high densities of* B. muricatum*, medium densities of* B. muricatum*, and no* B. muricatum *and (b) relative proportional change in abundance of corals and macroalgae when exposed to the 3 densities of* B. muricatum*. Error buffers depict 95% confidence intervals of returns from 50 replicate simulations, each run for 75 years.*

Discussion

Our results demonstrate that *B. muricatum*, through a diverse set of mechanisms, assumes a functionally unique and dominant role in coral reef ecosystems. The most conspicuous and perhaps most powerful effect *B. muricatum* has on reef ecology is delivered via individuals' intense direct consumption of reef substrate (Fig. 1). Consumption at our field site was split almost evenly between living coral and dead coral substrates; only a very small amount of macroalgae was eaten. The constant removal of dead coral, or once living coral turned reef base rock, likely has important effects on the dynamics of the diverse communities colonizing this substrate. For new corals attempting to recruit and establish on this substrate, such effects may be both beneficial (i.e., opening of competition-free space) and deleterious (e.g., physical removal of new recruits) (McCauley et al. 2010; Arnold & Steneck 2012). The high volume of feeding by *B. muricatum* directly on adult live corals (2.1 t · yr^{-1} · $individual^{-1}$) very likely has pronounced

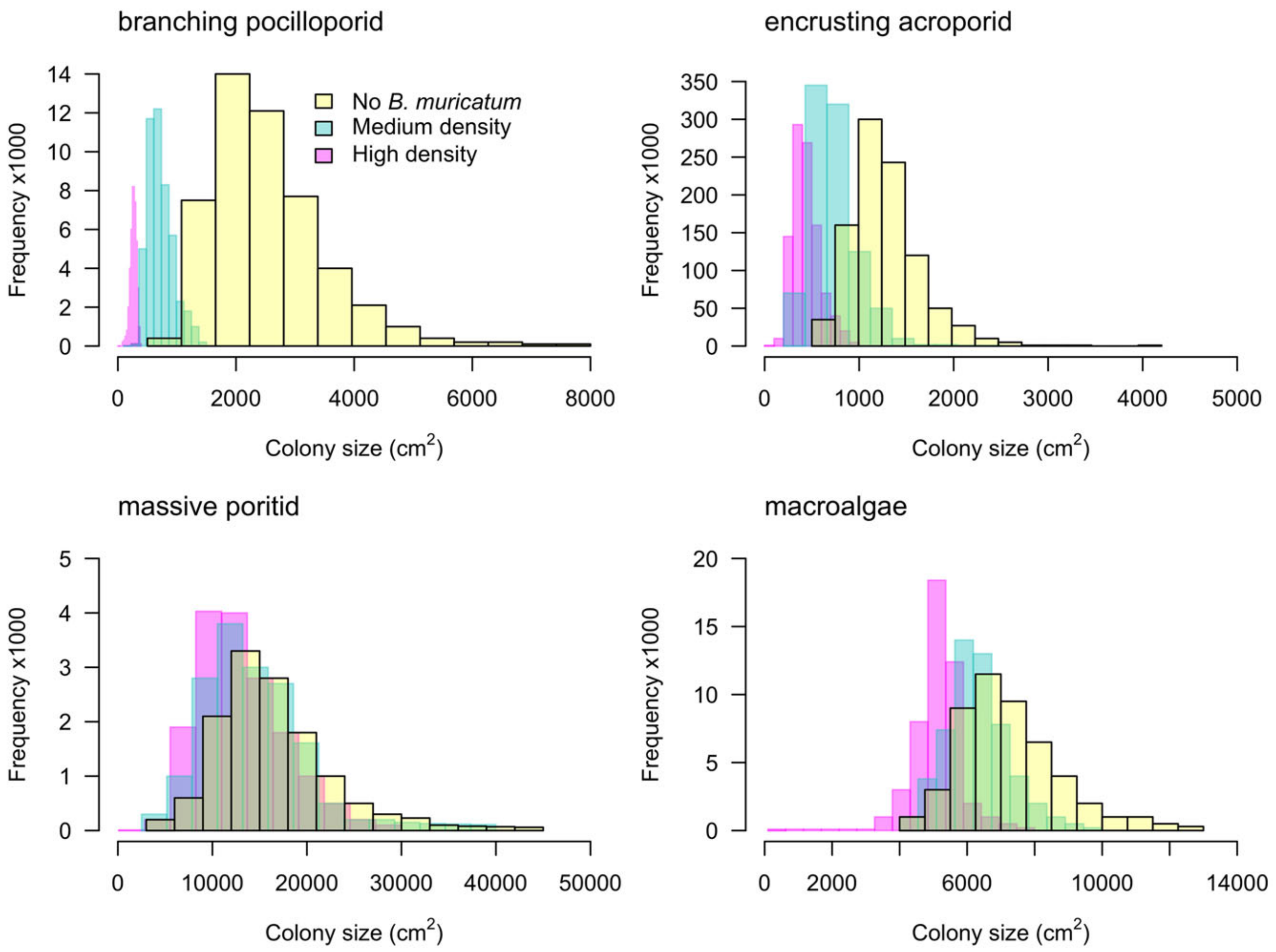

Figure 3. Size distribution of 3 corals and macroalgae used in the simulation that modeled the effects of B. muricatum *on reef benthic communities. Results presented for simulations stocked with high densities of* B. muricatum*, medium densities of* B. muricatum*, and no* B. muricatum*. Plots represent idealized composites of 50 replicate simulations, each run for 75 years. Colony size is represented as colony diameter.*

effects on the health and ecology of these corals. Corallivory by much smaller-bodied consumers can negatively impact corals (Miller & Hay 1998), and *B. muricatum* presumably has even more intense effects given the larger bites and larger coral intake rates of this species (Lokrantz et al. 2008).

The high volume of indigestible material in the diet of *B. muricatum* necessitates that it excrete the vast majority of what it consumes. We estimated that an individual at Palmyra defecates approximately 4.3 t of material annually atop its reefs. When standardized by area, this rate of biosedimentation is less than rates of abiotic and anthropogenic sedimentation, which are typically considered deleterious to coral health (Rogers 1990). Nevertheless, the discrete fashion by which *B. muricatum* fecal casts fall out on reefs and the considerable proportion of hard-to-reject, large-sized particles that this feces contains suggest that this source of deposition may still be stressful to corals (Supporting Information).

The extremely high rates by which live coral fragments are produced during *B. muricatum* feeding (approximately 14 fragments/h) suggest this action of fragmentation may influence the dynamics of coral colony expansion. Asexual reproduction via fragmentation is a common means of reproduction in many stony corals, although in most instances this is driven by physical disturbance. *B. muricatum* feeding provides an alternative biotic pathway for the advancement of this mode of coral reproduction. *Pocillopora* spp. were most frequently fragmented by *B. muricatum*, presumably because of their more fragile branching architecture. This is the same coral *B. muricatum* most prefers to feed on and was predicted by the simulation to be highly reduced in abundance and size by *B. muricatum*—introducing the possibility that the negative direct effects of *B. muricatum* consumption on this coral may be partly offset by the positive effects of increased dispersal. Animal-aided propagule dispersal has been

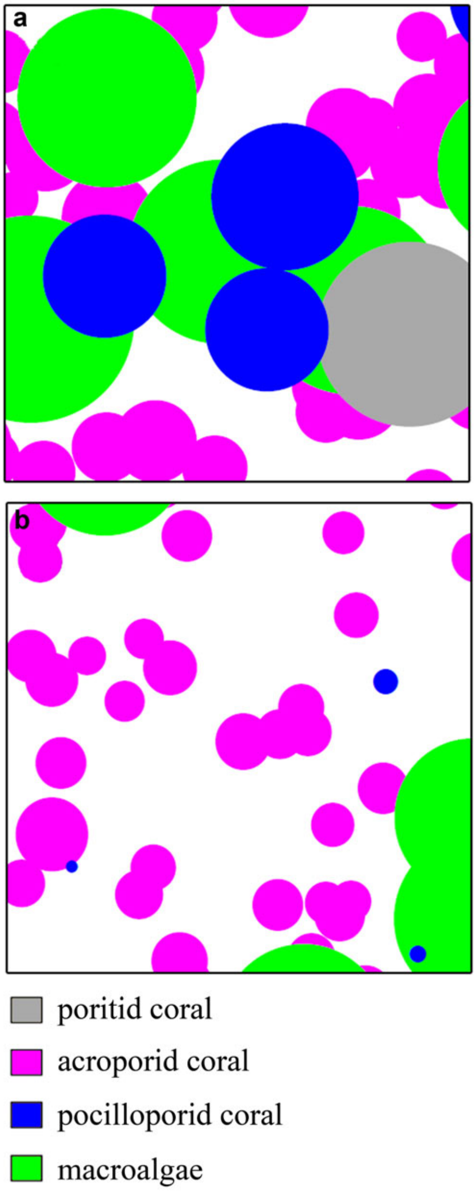

Figure 4. Illustration of sections of reef from simulations that modeled the influence of B. muricatum *on benthic dynamics. Panels depict a randomly selected subsection of the reef from scenarios containing (a) no* B. muricatum *and (b) those with high densities of* B. muricatum *after 75 years (an integrative visualization after 50 replicate model runs) (circles represent coral colonies and algal patches).*

extensively studied in terrestrial settings; however, this is one of very few examples of analogous behaviors in marine ecosystems (Guzmán & Cortés 1989; Vermeij et al. 2013).

The direction and strength of the impact of the aforementioned components of *B. muricatum*'s functional role on reef ecosystems are likely to be strongly determined by their abundance and behavior. We provide preliminary evidence that these factors may in turn be controlled by exposure to both human and marine predators. At protected Palmyra, there was no fishing for *B. muricatum*, but there was also no fishing for *B. muricatum*'s predators (e.g., sharks). Large sharks are extremely abundant on Palmyra's deep forereefs. *B. muricatum* appears to largely avoid these high-risk, shark-rich forereef zones, but it is relatively common in certain of the shallower backreef areas of Palmyra, where these large sharks are rare. Tabuaeran is much the opposite. The inhabitants of Tabuaeran fish for both *B. muricatum* and large sharks, but the sale of sharks is the easiest way to generate cash income and they are particularly effective at catching sharks (Supporting Information). Large sharks were not detectable on Tabuaeran's forereefs, and *B. muricatum* actively used the forereef here, possibly as a result of the relaxation of local predation risk. Sites on the GBR where *B. muricatum* reach extremely high densities (e.g., Yonge and Hicks Reefs; Bellwood et al. 2003) are also areas where large reef sharks have been severely depleted (Robbins et al. 2006). Links between these observed fishing-induced declines in shark abundance and apparent shifts in habitat use by *B. muricatum*, however, remain only speculative at this point. Alternate hypotheses for these patterns are that fishing for *B. muricatum* at Tabuaeran, while it is conducted in all reef types, may be forcing *B. muricatum* onto the forereef and that the quality of the forereef at Palmyra and Tabuaeran for *B. muricatum* is not comparable (e.g., differences exist in forage quality or abundance of *B. muricatum* physical refugia). Observations about relationships between large sharks and *B. muricatum* need to be collected from a broader geographic area, and more must be learned about the influence of predators on *B. muricatum* ecology before these provocative first observations can be properly substantiated.

Using our computer simulation, we were able to synthesize some of the short-term empirical observations made of the foraging ecology of *B. muricatum* and to develop preliminary projections about the longer term effects it may have on reefs. Four main predictions emerged from this effort (Fig. 4): *B. muricatum* may reduce the diversity of prominent coral species groups; reduce the abundance of corals; slow the expansion of fast-growing macroalgae, despite its relatively small intake rates of this food type; and reduce the size of coral colonies and algae patches. The decreases in coral community diversity, abundance, and size in the simulation scenarios populated with *B. muricatum* occurred despite the fact that *B. muricatum* also tempered the expansion of macroalgae—a major competitor of corals (Ferrari et al. 2012). It seems that, in the case of *B. muricatum* and in the context of the coral taxa we modeled, the positive effects that arose from their consumption of algae are likely outweighed by the negative effects of their intense consumption of the corals themselves. The simplicity of this simulation provides a valuable first view of some of the potential impacts *B. muricatum* may have on reefs. Conclusions we derived from this simulation should, however, be interpreted with a good deal of caution. The simulation lacked important information on interactions of myriad other reef species that shape coral communities; bottom-up processes that regulate coral ecology and fish abundance and behavior; and other dynamic processes in reefs.

Interpretations of the ecology of strong interactors, such as *B. muricatum*, whose numbers have been reduced substantially must necessarily be made on the basis of undesirably low volumes of data drawn from a constrained number of study sites. Nevertheless, the same declines that are problematic for the study of these unique and rare species also increase the imperative to characterize their effects on ecosystems. Results generated from our empirical and simulation exercises provide initial support for the same conclusion: *B. muricatum* plays a key functional role in coral reef ecosystems. However, for corals, literally the foundation of this ecosystem, these functions appear to have both positive and negative impacts that are often manifest simultaneously. *B. muricatum* reduced the abundance of fast growing macroalgae that compete with corals, but the species also reduces coral abundance and diversity of corals. Its feeding facilitates coral reproduction by opening up bare space on reefs where coral recruits can establish and by dispersing coral fragments—but it may also negatively affect corals by directly damaging adult corals and potentially stressing corals as a result of fecal biosedimentation.

The mixed tenor of these observations calls forth the question: do functionally dominant species such as *B. muricatum* promote or compromise the structural and operational integrity of ecosystems? Our simulation models suggest that the answer to this question may be determined by the abundance of these strong interactors. Increasing the density *B. muricatum* caused more severe drops in both coral diversity and abundance. These results are in line with predictions generated in the GBR which suggest that when *B. muricatum* occur in extremely high densities their consumption may approach or even outpace rates of coral calcification (Bellwood et al. 2003).

Key interactors in other ecosystems can have destabilizing impacts on ecosystem functioning. Perhaps the best parallel is provided by the African elephant. The intense consumption and physical damage elephants levy on tree communities has a strong impact on the structural architecture and biological diversity of their environment (Asner et al. 2009). Where elephants are particularly dense, these effects can become alarming to managers (Cumming et al. 1997). The similarities between the case of *B. muricatum* and African elephants draw attention to the potential that these functionally unique and dominant species may have to cause rapid and pronounced changes in their respective ecosystems. Our observations of interactions between *B. muricatum* and large shark predators, while preliminary in nature, are consistent with the hypothesis that managing multispecies populations through ecosystem-based management may be an important means for mediating some of these strong effects. Areas where *B. muricatum* populations reach densities that are high enough to exert these intense effects on reef ecosystems are, however, likely to be extremely rare. Overfishing has severely reduced *B. muricatum* in all but a few locales (Dulvy & Polunin 2004; Bellwood et al. 2012). Furthermore, the growth potential of remaining populations, even in the absence of fishing, appears to be restrained substantially by natural demographic bottlenecks and recruitment limitation inherent to this species (Bellwood & Choat 2011).

Our results support the notion that increases in the abundance of strong interactors like *B. muricatum* may not always go hand in hand with the maintenance of sought after ecosystem functions and properties. While it has been anathema in conservation biology to consider the potentially deleterious impacts of ecologically unique or imperiled species, frank characterizations of the diversity of impacts that they have on ecosystems will increase the accuracy of the descriptions made of their ecology and will empower managers to make more informed decisions about the conservation of their populations and the ecosystems in which they are embedded.

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Supporting Information

A discussion of the identification of individual *B. muricatum* (Appendix S1), details of *B. muricatum* GPS tracking, population size, and general information on the reef study sites (Appendix S2), a description of *B. muricatum* bite types (Appendices S3 and S4), information on our calculations of the mass of material removed by *B. muricatum* (Appendix S4), discussion on *B. muricatum* fecal casts (Appendix S5), additional details on coral fragmentation and dispersal (Appendix S6), additional details on predator surveys (Appendix S7), a discussion of ethnographic surveys of fishing preferences at Tabuaeran

(Appendix S8), additional details on the computer simulation (Appendix S9), and a plot of fecal particle size distribution (Appendix S10) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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