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Not worth the risk: apex predators suppress herbivory on coral reefs

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Apex predators are known to exert strong ecological effects, either through direct or indirect predator–prey interactions. Indirect interactions have the potential to influence ecological communities more than direct interactions as the effects are propagated throughout the population as opposed to only one individual. Indirect effects of apex predators are well documented in terrestrial environments, however there is a paucity of information for marine environments. Furthermore, manipulative studies, as opposed to correlative observations, isolating apex predator effects are lacking. Coral reefs are one of the most diverse ecosystems, providing a useful model system for investigating the ecological role of apex predators and their influence on lower trophic levels. Using predator models and transplanted macroalgae we examined the indirect effects of predators on herbivore foraging behaviour. We show that the presence of a model reef shark or large coral-grouper led to a substantial reduction in bite rate and species richness of herbivorous fishes and an almost absolute localized cessation of macroagal removal, due to the perceived risk of predation. A smaller-sized coral-grouper also reduced herbivore diversity and activity but to a lesser degree than the larger model predators. These indirect effects of apex predators on the foraging behaviour of herbivores may have flow-on effects on the biomass and distribution of macroalgae, and the functioning of coral reef ecosystems. This highlights that the ecological interactions and processes that contribute to ecosystem resilience may be more complex than previously assumed.

Predation is arguably one of the most influential selection pressures acting on living organisms and can play a vital role in not only regulating prey populations, but also shaping entire communities (Paine 1966, Hixon et al. 2002). In particular, changes in the density and distribution of large-bodied or apex predators can exert strong ecological effects that cascade through an entire ecosystem (Estes et al. 1998, 2011, Ripple et al. 2001, 2014, Frank 2008, Sandin et al. 2008). Apex predators are typically characterized by conservative life history traits, such as slow growth rates, late sexual maturity, and low fecundity, and are often preferentially targeted by humans for food or game (Pauly et al. 1998, Myers and Worm 2003). Consequently, apex predators are often the first to be become extinct or locally extirpated. Understanding the roles that apex, and other large-bodied predators play in shaping ecological communities is becoming increasingly important as natural communities become progressively more disturbed.

The effects of predators on ecological communities may manifest through either direct (i.e. consumptive) or indirect (i.e. non-consumptive) interactions (reviewed by Schmitz et al. 2004). Although studies reporting direct effects of predators on ecosystems are common (Estes et al. 1998, Ripple et al. 2014), there is a growing body of evidence that the indirect effects of predators can have an equally dramatic effect on the structure and functioning of entire ecosystems (Preisser et al. 2005, Creel and Christianson 2008, Madin et al. 2010a). Given the severe consequences that a predation event poses, prey are under considerable pressure to successfully detect and avoid predators. Prey species often alter their behaviour and/or foraging patterns in response to changes in predation risk, and this in turn may influence the distribution and/or abundance of the prey's resources (Ripple et al. 2001, 2014). In particular, increased predation risk indirectly influences the foraging patterns of herbivores, which can lead to changes in plant diversity, productivity, nutrient cycling, trophic transfer efficiency and energy flux (Schmitz et al. 2008). For example, African herbivores change their habitat preference to more open habitats when in the presence of predatory lions, presumably as a response to the increased ability to detect predators in these areas (Valeix et al. 2009). Similarly, increased populations of wolves and other large carnivores in Yellowstone National Park reduced and redistributed herbivorous elk populations, subsequently decreasing herbivory and increasing tree height in high predation risk areas (Fortin et al. 2005, Ripple et al. 2014). Although these indirect predator–prey interactions are ubiquitous in ecological communities (e.g. terrestrial: Rypstra and Buddle 2012; aquatic: Peacor and Werner 2001; marine: Frid et al. 2012), there is a paucity of information on the effects of large-bodied or apex predators in tropical marine ecosystems (but see Madin et al. 2010a).

Coral reefs are one of the world's most taxonomically diverse ecosystems, harboring approximately 5000 species of fishes that perform numerous functions and create a complex network of species interactions (Sheppard et al. 2009). Worldwide, overfishing and habitat degradation has greatly contributed to the decline of reef fish populations (Jackson et al. 2001), particularly apex predators such as reef sharks (family Carcharhinidae), groupers (family Serranidae) and trevally (family Carangidae) (Friedlander and DeMartini 2002, Robbins et al. 2006, Nadon et al. 2012). The contribution of apex predators to the well being of coral reef ecosystems is unclear, but is potentially important (Heithaus et al. 2008, Ruppert et al. 2013). For instance, differences in population parameters (e.g. size, longevity, reproduction and body condition) of prey fishes (Ruttenberg et al. 2011, Walsh et al. 2012), and rates of coral recruitment and disease (Sandin et al. 2008) have been correlated to variation in apex predator density, however little experimental evidence exists (see Madin et al. 2010a for exception). Thus, a better understanding of apex predators and their ecological role is imperative for guiding management actions that aim to preserve or enhance ecosystem resilience.

Herbivorous fishes perform a critical ecosystem function on coral reefs, mediating the competition for space between corals and algae. Reductions in the densities of herbivorous fishes underpin the expansion of macroalgae in many reef systems (Hughes et al. 2007, Rasher et al. 2013). While such reductions in herbivory have been linked to overfishing of the herbivores themselves (Williams and Polunin 2001, Mumby et al. 2007), similar responses may manifest through changes in predator communities (Ruppert et al. 2013). Outputs of theoretical models suggest that changes in apex predator density could indirectly influence macroalgal biomass via mesopredator release and/or changes in prey behaviour (Bascompte et al. 2005). Two previous studies examining the effects of predators on herbivores revealed that differences in foraging behaviour (i.e. distance from shelter) were related to predator densities (Madin et al. 2010a, 2012), however no study has demonstrated a causal relationship between predators, herbivore foraging activity and algae consumption. Therefore, the present study aimed to investigate the effects of apex predators on the foraging behaviour of herbivorous reef fishes. Specifically, we examined the effect of predator presence on the consumption of macroalgae by herbivorous fishes. We selected the blacktip reef shark *Carcharhinus melanopterus* and the coral-grouper *Plectropomus leopardus* as model apex predator species because they occupy high trophic positions (Speed et al. 2012, Frisch et al. 2014), are numerically common, geographically widespread, have a broad diet that includes herbivorous fishes (Stevens 1984, St. John 1999) and are harvested across their geographic range by fishers (Frisch et al. 2012).

Material and methods

Study site and species

The study was conducted during November and December 2012 on reefs adjacent to Lizard Island (14°40′S, 145°28′E) in the northern Great Barrier Reef (GBR), Australia (Supplementary material Appendix 1 Fig. A1). To quantify the effect of predators on the consumption of macroalgae, bioassays of *Sargassum* were transplanted to two sites both in the presence and absence of model predators. *Sargassum* was selected as it is locally abundant on inshore reefs of the GBR, has been used extensively in previous studies (McCook 1996, Hoey and Bellwood 2010), and is the dominant taxon following coral–algal phase-shifts on Indo-Pacific reefs (Hughes et al. 2007, Rasher et al. 2013). Model predator species included the coral-grouper and the blacktip reef shark. Coral-grouper hover over reefs near schools of prey for long periods, while blacktip reef sharks are more mobile. Both species are known to have small to moderate home ranges and exhibit high levels of site fidelity (Zeller 1997, Papastamatiou et al. 2011).

Experimental design

Sargassum swartzii (Ochrophyta: Phaeophyceae) was collected from the windward reef flat of inshore reefs in the Turtle Island Group (14°43′S, 145°212′E), approximately 25 km west of Lizard Island (Supplementary material Appendix 1 Fig. A1). Individual *Sargassum* thalli of similar height (ca 50 cm) were removed by cutting the holdfast as close to the point of attachment as possible. All *Sargassum* were returned to Lizard Island and placed in a large aquarium with flow-through seawater within 90 min of collection. Individual *Sargassum* thalli were spun in a mesh bag for 30 s to remove excess water, weighed (mean = 79.2 g ± 2.9 standard error, SE) and randomly allocated to one of six treatments: three predator treatments, a predator-absent treatment, an object control, and a herbivore exclusion control. To test the effect of predator presence on herbivory, we used realistic models constructed of fiberglass taxidermic casings (Fig. 1). Three predator-present treatments consisted of a blacktip reef shark (170 cm total length, TL), a large coral-grouper (76 cm TL) or a small coral-grouper (48 cm TL). Three different sized predators were used to simulate a gradient in predation risk (i.e. high for the reef shark, medium for the large coral-grouper and low for the small coral-grouper). During a pilot study, the small coral-grouper was attacked by a giant trevally *Caranx ignobolis* and investigated by a whitetip reef shark *Triaenodon obesus* suggesting that replicate models were perceived as life-like representations (Supplementary material Appendix 1 Video A1). The predator-absent treatment consisted of a *Sargassum* thallus in the absence of a predator model in order to obtain 'natural' rates of herbivory. The object control was a 78 cm length of PVC pipe (12 cm diameter), which was intended to control for the effect of any object on herbivore foraging behaviour. An exclusion cage was used to control for the effects of handling and/or translocation on the reduction in *Sargassum* biomass. Each treatment was replicated ten times within each of two sites; a lagoon and a back reef site (Supplementary material Appendix 1 Fig. A1). Replicate treatments were conducted over a 30-day period and the location of each treatment, within each site, was randomized from day to day.

Individual *Sargassum* thalli were attached to the reef at a depth of 2–4 m (following the methods of Hoey and Bellwood 2009), and positioned approximately 0.5–1 m in front of model predators (and object control). All *Sargassum* thalli

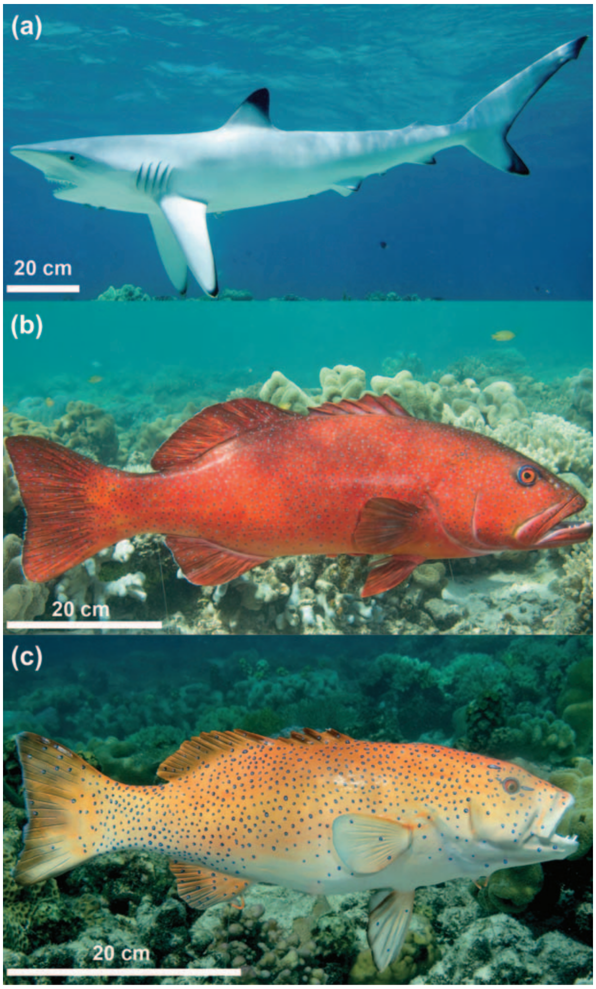

Figure 1. Photographs of the three predator models. (a) blacktip reef shark, *Carcaharinus melanopterus* (170 cm total length), (b) large coral-grouper, *Plectropomus leopardus* (76 cm total length), and (c) small coral-grouper, *P. leopardus* (48 cm total length).

were deployed between 09:00–11:00 and collected after 4.5 h. A minimum distance of 50 m separated adjacent treatments within each site. Underwater video cameras were placed approximately 3 m from the *Sargassum* to record any feeding activity by herbivorous fishes. Filming was continuous for the 4.5-h experimental period with a small scale bar being placed on the focal plane of the *Sargassum* for approximately 10 s allowing calibration of fish sizes from the video footage. After 4.5 h, all thalli were collected, spun and weighed as described previously. Filming was conducted at four of the six treatments (i.e. reef shark, large coral-grouper, small coral-grouper and predator-absent treatment); the exclusion cage and object control were not filmed as these treatments were established solely to examine the effects of handling and experimental artifacts, respectively. All video footage was viewed and the number of bites taken from the *Sargassum* by each species and size of fishes was recorded.

Statistical analyses

To determine if the relative removal rates of *Sargassum* biomass varied among sites and treatments, a two-factor analysis of variance (ANOVA) was used. The analysis was based on the proportion of initial (or transplanted) biomass that was removed during 4.5 h on the reef. Similarly, the total number of bites taken from the *Sargassum* (for all species combined) was compared amongst sites and treatments using a two-factor ANOVA. The proportion of biomass removed and total bites were arcsine-square root and $\log_{10}(x+1)$ transformed, respectively, to improve normality and homoscedasticity. ANOVAs were followed by Tukey HSD post hoc tests to resolve differences between means. Variation in bite rate of different herbivorous fish species among sites and treatments was analysed using a two-factor multivariate analysis of variance (MANOVA). Data was $\log_{10}(x+1)$ transformed to improve multivariate normality. Significant MANOVA effects were further examined using Bonferroni-corrected two-factor ANOVAs (adjusted alpha value of 0.0125) and Tukey HSD post hoc tests. A two-sample Kolmogorov-Smirnov test was used to examine the size-frequency distributions of herbivorous fishes observed feeding on *Sargassum* between treatments at both sites. In all cases assumptions of normality and homogeneity of variances were examined a priori via residual analysis and Bartlett's test, respectively. All data in the text and figures are the untransformed arithmetic mean (± standard error; SE) unless otherwise stated.

Results

The relative removal rates of *Sargassum* differed among sites ($F_{1,108} = 11.05$, $p = 0.001$) and predator treatments ($F_{5,108} = 50.05$, $p < 0.001$), with the effect of predator treatment being consistent among sites (site × predator treatment: $F_{5,108} = 2.03$, $p = 0.08$). In the absence of a model predator, or in the presence of the object control, the majority of *Sargassum* biomass was consumed (57–60%) in the 4.5 h period (Fig. 2). There was, however, a ten-fold reduction in the *Sargassum* biomass consumed in the presence of the two larger predator models at both sites (5–6% 4.5 h^{-1}; Fig. 2). Removal rates of *Sargassum* in the presence of a small coral-grouper model were intermediate, with 51 and 24% 4.5 h^{-1} removed from the lagoon and back reef respectively. Reductions in *Sargassum* biomass due to handling were low (5% 4.5 h^{-1}) and indistinguishable from the large coral-grouper and reef shark treatments (Fig. 2).

Analysis of the video footage revealed that feeding activity on the *Sargassum* was dominated by three species: the bluespine unicornfish *Naso unicornis*, the barred rabbitfish *Siganus doliatus* and the long-finned drummer *Kyphosus vaigiensis* (Fig. 3). In total, 21 853 bites from nine fish species were recorded on the transplanted *Sargassum* across all treatments and sites, with *N. unicornis*, *S. doliatus* and *K. vaigiensis* accounting for 93.2% of the bites. The remaining six species (*Calotomus carolinus*, *N. brevirostris*, *N. lituratus*, *S. canaliculatus*, *S. corallinus* and *S. puellus*) accounted for 6.8% of bites and were therefore grouped into 'other' species for subsequent analysis. The overall bite rate (i.e. for all species combined) varied significantly among predator treatments ($F_{3,72} = 101.79$, $p < 0.001$), but not sites ($F_{1,72} = 2.29$, $p = 0.13$) or the interaction of site and predator treatment ($F_{3,72} = 0.78$, $p = 0.51$). The number of bites taken from the *Sargassum* was markedly lower in the presence of the reef shark (3.6 ± 1.7 bites 4.5 h^{-1}) and

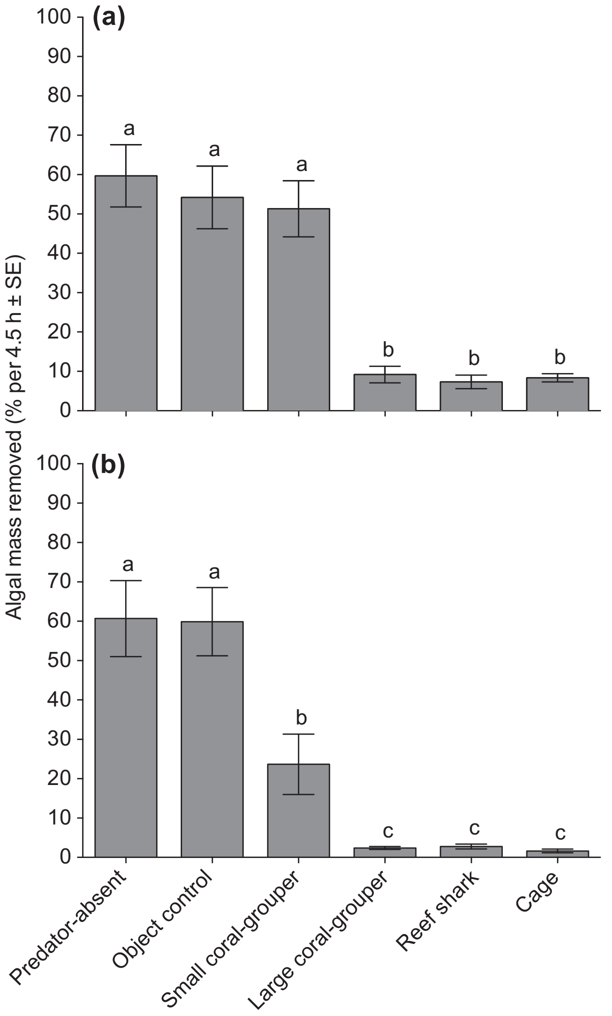

Figure 2. Relative removal rates of *Sargassum* among treatments at (a) lagoon and (b) back reef sites ($n = 10$). The letters above each bar indicate homogeneous subsets (Tukey's tests).

large coral-grouper (3.2 ± 2.7 bites 4.5 h^{-1}) models than in the presence of the small coral-grouper (181 ± 25.4 bites 4.5 h^{-1}) or in the absence of a predator (905 ± 185.4 bites 4.5 h^{-1}; Fig. 3). Given that feeding was negligible on the *Sargassum* in the presence of the large coral-grouper and reef shark models (Fig. 3), these treatments were not included in any subsequent analyses.

Comparisons of the feeding rates of the four fish taxa (i.e. *N. unicornis*, *S. doliatus*, *K. vaigiensis* and 'other' species) between the predator absent and small coral-grouper treatments revealed that feeding generally decreased in the presence of the small coral-grouper model, however the differences were not consistent among sites or fish taxa (predator treatment × site: Pillai's trace = 0.34, $F_{4,33} = 4.18$, $p = 0.008$; Fig. 4). The feeding rate of *N. unicornis* decreased markedly in the presence of the small coral-grouper at the back reef site (from 494.7 ± 154.1 to 6.6 ± 6.4 bites 4.5 h^{-1}), but displayed no change at the lagoon site (Fig. 4a; Supplementary material Appendix 1 Table A1). The feeding rates of *S. doliatus* and 'other' fishes showed significant and consistent declines in the presence of the small coral-grouper (Fig. 4b, d; Supplementary material Appendix 1 Table A1).

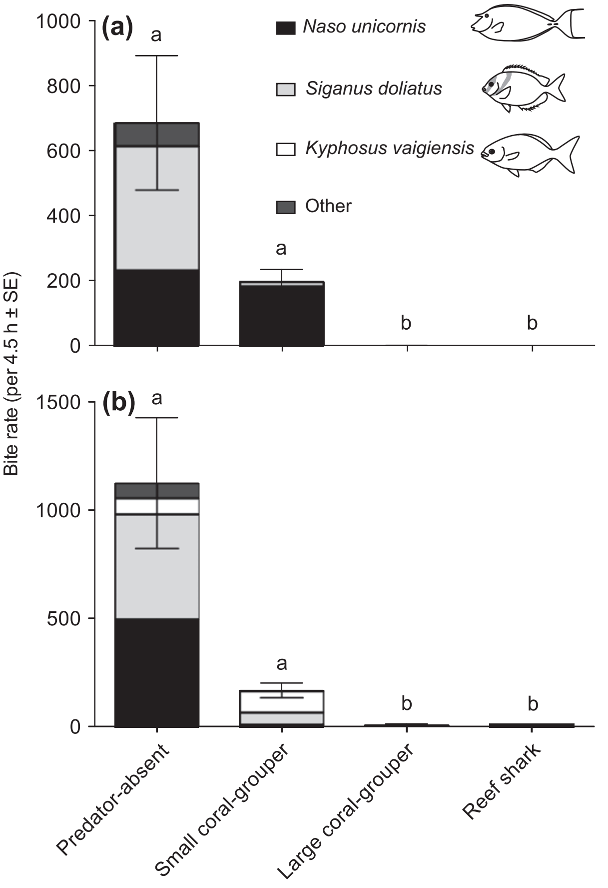

Figure 3. Mean bite rate per 4.5 h treatment time at (a) lagoon and (b) back reef sites. The relative contributions of the three dominant species and other species are shown. Other species include *Calotomus carolinus, Naso brevirostris, N. lituratus, Siganus canaliculatus, S. corallinus* and *S. puellus*. Letters above each bar indicate homogeneous subsets (Tukey's tests). Note differences in scale on y-axis.

In contrast, the feeding rate of *K. vaigiensis* differed between sites, but showed no response to the presence of the small coral-grouper (Fig. 4c; Supplementary material Appendix 1 Table A1).

The species richness of herbivorous fishes recorded feeding on the *Sargassum* was greatest in the absence of a predator, and decreased with the presence and size of the predator models (Supplementary material Appendix 1 Table A2). This pattern was consistent across both sites (Fisher's exact test, $p > 0.75$). There were also differences in the size frequency distribution of herbivorous fishes observed feeding in the presence of the small coral-grouper and the predator-absent treatment (Kolmogorov–Smirnov lagoon: $D = 0.16$, $p < 0.001$; back reef: $D = 0.59$, $p < 0.001$) with marked reductions in the number of smaller fishes (≤ 25 cm TL) observed feeding in the presence of the small coral-grouper at both sites (Fig. 5).

Discussion

Apex predators are suggested to play a strong role in indirectly influencing populations of trophic levels that are directly linked to ecosystem functions (Terborgh and Estes

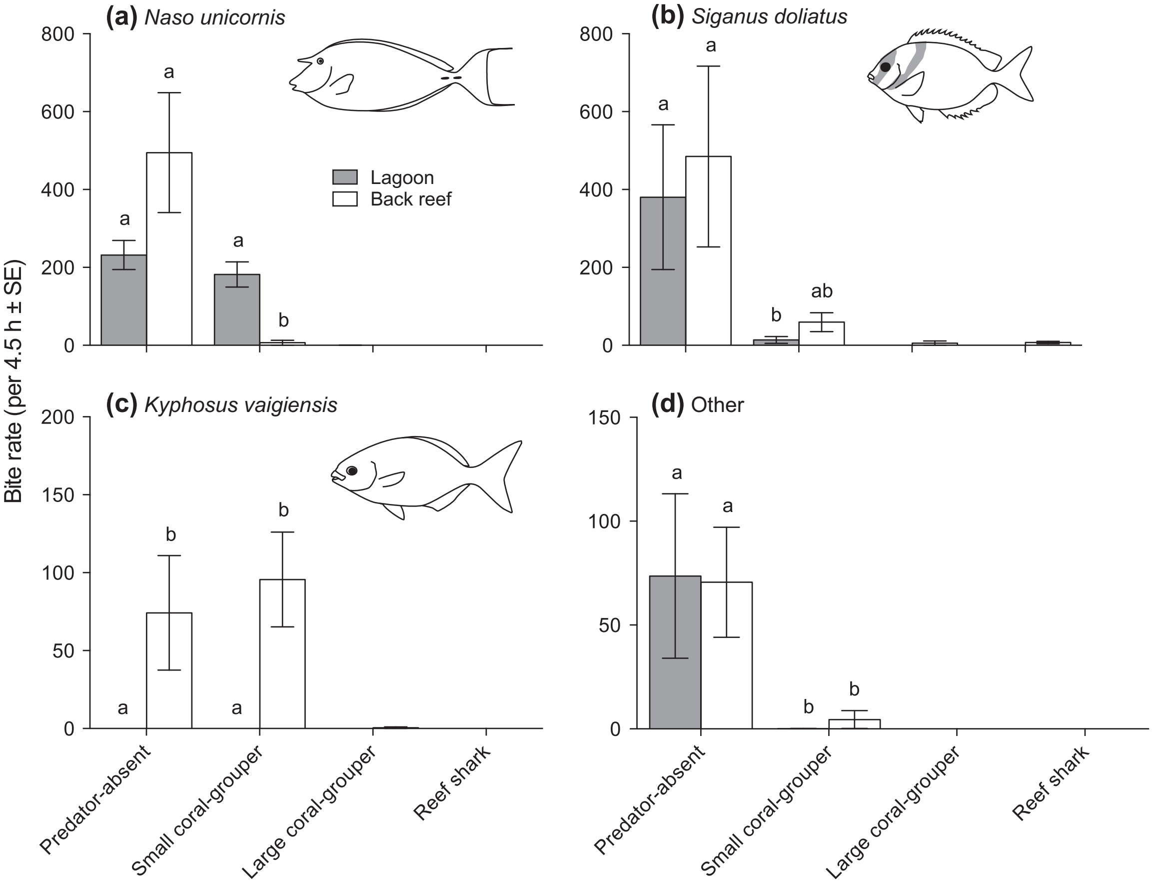

Figure 4. Mean bite rate of (a) *Naso unicornis*, (b) *Siganus doliatus*, (c) *Kyphosus vaigiensis*, and (d) other species, which includes *Calotomus carolinus, N. brevirostris, N. lituratus, S. canaliculatus, S. corallinus* and *S. puellus*. Letters above each bar indicate homogeneous subsets (Tukey's tests). Large coral-grouper and reef shark treatments were not included in analyses (MANOVA) because group means were close to zero. Note differences in scale on y-axis.

2010), yet there have been few attempts to explicitly demonstrate this in tropical marine systems (see Madin et al. 2010a for exception). Using model predators to simulate predation risk, we found that large predators can have a profound influence on the key ecological process of herbivory on coral reefs, supporting the view that apex predators can influence organisms that are linked to ecosystem functions. In the absence of predators the consumption of macroalgae by herbivores was high (ca 60%), but decreased with increasing predation risk. The consumption of macroalgae was reduced by approximately 20% in the presence of the smallest predator (48 cm coral-grouper), and was almost completely suppressed in the presence of the two larger model predators (170 cm blacktip reef shark and 78 cm coral-grouper), presumably due to the perceived risk of predation. Video footage revealed that the overall feeding rate and the number of herbivorous fish species observed feeding on the macroalgae all decreased with increased predation risk. This response to increasing predation risk was most pronounced in smaller (< 25 cm TL) herbivores, with feeding by these fishes declining markedly in response to even the smallest predator. Given the crucial importance of herbivore foraging activity in the functioning of coral reef ecosystems, these results have important implications for our understanding of ecosystem processes and the effects of apex predators on coral reefs.

The observed herbivore foraging behaviour and decreased rates of macroalgal consumption near predator models indicate that herbivorous reef fishes display a threat-sensitive response to the presence (or absence) of a potential predator (Helfman 1989). Organisms often make tradeoffs between predator avoidance and other fitness-related behaviours (e.g. foraging or reproduction; Lima and Dill 1990), and these tradeoffs can vary depending on the risk level posed by the predator. In the present study the consumption of macroalgae and the feeding rate of herbivores both significantly decreased as predation risk increased. While feeding by herbivores was almost completely suppressed in the proximity of the two larger predators, the presence of the smallest predator had a disproportionate effect on the smaller (< 25 cm TL) herbivores. As shallower bodied individuals will be more vulnerable to predation than deeper bodied individuals, this may explain their reluctance to feed near model predators. Together, these results support the supposition that herbivores exhibit threat-sensitive predator avoidance behaviour. Macroalgal removal and bite rate patterns were consistent among all taxa, with the exception of the drummer, *K. vaigiensis*, near the small coral-grouper model; probably because the small coral-grouper does not represent a threat to this robust and deep-bodied species (i.e.

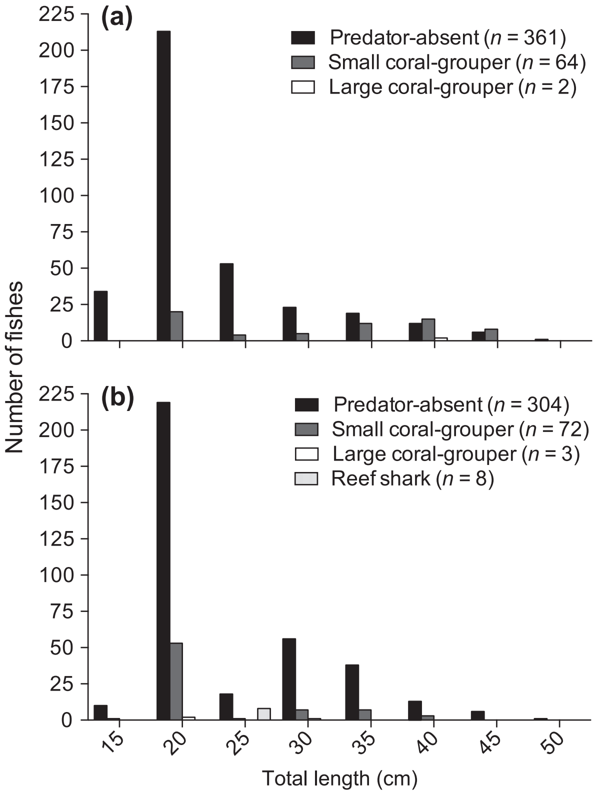

Figure 5. Size frequency distribution of herbivorous reef fishes observed feeding at (a) lagoon and (b) back reef sites. The x-axis labels represent size-class midpoints. Values of n are the total number of fishes observed feeding. No values are present for the reef shark treatment at the lagoon site because no individuals were observed feeding. Large coral-grouper and reef shark treatments were not included in analyses (Kolmogorov–Smirnov tests) because group means were close to zero.

the gape limitation of the small coral-grouper meant that it did not represent a predator for all but the smallest *K. vaigiensis*). Notwithstanding, all herbivorous taxa and size classes exhibited the greatest response in the presence of the large coral-grouper and reef shark models. While the presence of static predator models in the present study are likely to have resulted in a redistribution of foraging effort to areas of lower predation risk, as opposed to an overall reduction in foraging rates by herbivores, this behavioural response has potentially important implications for the distribution and biomass of algae on coral reefs. Changes in the densities of predators over larger spatial scales may influence the spatial distribution of herbivore foraging, and/or the overall rates of algal consumption. Further investigations are therefore warranted to assess whether the reaction of herbivores to different densities of mobile apex predators, as opposed to stationary models, integrates up to broad-scale community-level effects.

High algal cover is typically viewed as a sign of degradation on coral reefs, with algae negatively affecting the fecundity, recruitment, and growth of corals (Hughes et al. 2007, Mumby and Steneck 2008). Given that herbivorous fishes play a key role in preventing the proliferation and expansion of algae (Hughes et al. 2007, Mumby and Steneck 2008), any changes to their behaviour may influence this critical ecosystem process. For example, if predation risk to herbivores alters their activity levels or spatial habitat use this could change the rate at which their impact permeates reef ecosystems. In addition to the changes in foraging of macroalgal consuming (i.e. browsing) fishes in the present study, predator biomass and/or presence has been shown to negatively influence excursion distances of small grazing fishes (i.e. fishes that feed predominately on algal turfs and associated materials) on reefs in the central and western Pacific (Madin et al. 2010a, 2012). Further, several studies have suggested that the 'grazing halos' surrounding structurally complex patch reefs or coral bommies are a result of increased predation risk and hence reduced herbivore feeding with increasing distance from the reef edges (Madin et al. 2011, Downie et al. 2013). Therefore, it appears that behavioural responses to predation risk may be widespread among herbivorous fishes on coral reefs.

Whilst previous studies have highlighted the indirect effects of predators on herbivore behaviour and have linked this to variation in the distribution of algae (Madin et al. 2010a, b, 2011, 2012), the present study is the first to directly quantify the effects of predation risk on algal consumption. Together, these findings demonstrate that changes in foraging behaviour, as a result of the perceived risk of predation, does suppress localized herbivory. These results, however, must be interpreted with prudence. The predator models in this study were stationary, concentrating the risk of predation spatially and thus potentially exaggerating predator effects on herbivore foraging behaviour at the site of the *Sargassum* assay. Indirect effects of mobile predators, such as live reef sharks, are likely to be subtler due to their constant movement. Furthermore, the presence of the predator models in this study represent an acute (short-term) predation risk, and while herbivory was reduced in the presence of the predator models, this localized suppression of herbivory may not necessarily lead to long-term increases in algal biomass within the ecosystem. The perceived risk posed by the predator models may have only led to a redistribution of foraging effort of the herbivorous fishes to areas of lower perceived risk, resulting in heterogenous foraging patterns and patchily distributed macroalgae (Madin et al. 2010b). However if predator densities and the associated predation risk increases over greater spatial and temporal scales, our results may suggest that herbivore foraging effort, and subsequent algal consumption, has the potential to substantially decrease on a community-wide scale. While this prediction is supported by studies in terrestrial systems that have shown significant decreases in foraging effort as a consequence of increased predation risk (see review by Verdolin 2006), it appears to be in contrast to the findings of a study of Caribbean reefs (Mumby et al. 2006). Focused on the direct effects of predation, Mumby and others (2006) demonstrated that a Caribbean marine reserve supported both higher predator biomass (and presumably increased predation risk), higher densities of large-bodied parrotfishes and lower abundance of macroalgae than adjacent fished reefs. It should be noted that parrotfishes are heavily targeted by fishers throughout much of the Caribbean (Rakitin and Kramer 1996), and as such it is difficult to differentiate the positive effects of reduced fishing mortality on parrotfishes from the negative effects of enhanced predation. Further investigation is warranted in order to determine whether these patterns are consistent across ecosystems.

Reefs protected from fishing are typically associated with higher densities of apex predators (Robbins et al. 2006, Nadon et al. 2012, Ruppert et al. 2013) and lower macroalgal cover (Mumby et al. 2006, Sandin et al. 2008, Babcock et al. 2010). As mentioned previously, protected reefs can support higher abundances of both predators and herbivores, because the negative effects of fishing outweigh the negative effects of increased predation, since herbivores become less vulnerable to predation with increasing size (Mumby et al. 2006). The size dependent behavioural effects observed in the present study may therefore provide a mechanism by which herbivores and apex predators can co-exist in relatively high abundances. While low macroalgae cover is typically viewed as a direct result of the higher herbivore biomass on protected reefs, the potential role of predators in influencing algal assemblages through behaviourally-mediated cascades should not be discounted. For example, a recent study on the GBR found that the presence and foraging of both grazing and browsing fishes was negatively related to macroalgal biomass and suggested this was a response to increased predation risk (Hoey and Bellwood 2011). Another study in the central Pacific highlighted that reefs with large predator populations limited the foraging distances of grazing fishes and led to a mosaic of patches of high macroalgal biomass interspersed with closely cropped substrata (Madin et al. 2012). The suppressed rates of macroalgal consumption near predator models provide confidence in our findings that predator presence suppresses localized herbivory, and invariably favours the accumulation of macroalgae biomass on a local scale, however it is unclear whether predation risk will influence algal biomass over larger, reefal scales. Therefore, it is likely that the mechanisms regulating macroalgal growth on coral reefs are more complex than previously understood.

The indirect effects of carnivores on plants mediated by herbivores have been defined as behaviourally-mediated trophic cascades (Dill et al. 2003) and have been documented in numerous ecosystems (Shurin et al. 2002, Preisser et al. 2005). Here we reveal that apex predators influence herbivore foraging behaviour, which has the potential to drastically influence the amount of macroalgal cover on coral reefs. While our results are consistent with trophic cascade theory, the relatively small spatial scale and the potential reallocation of foraging effort by herbivores calls for caution when interpreting these results. In order to accurately demonstrate a trophic cascade a reduction in herbivory across the entire ecosystem (or reef) would have to be observed. Therefore, while our study provides evidence for a 'trophic interference' by apex predators, further studies examining these effects on a larger scale (with contrasting densities of predators) are needed. Trophic cascades involve the influence of both direct and indirect effects of predators, for which there is little data for the tropical marine environment, particularly for large predators. Our study provides the first information on the effects of these large predators and forms a useful basis for future studies.

Evidence from terrestrial systems indicates that apex predators exert a strong influence on other ecosystem components (Estes et al. 2011). However, evidence for behaviourally-mediated or indirect effects of apex predators is rare in the marine realm, particularly on coral reefs. Our findings clearly demonstrate that apex predators can have a strong local influence on a key ecological process on coral reefs; herbivory. Given that apex predators are heavily exploited throughout the world, it is imperative that we better understand both the direct and indirect consequences of their exploitation. Gradients in apex predator density (e.g. inside or outside protected areas) may provide a useful tool in resolving the complexity in the linkages between apex predators, herbivores and algal assemblages.

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Supplementary material (available online as Appendix oik-01318 at <www.oikosjournal.org/readers/appendix>). Appendix 1