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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Predator identity and time of day interact to shape the risk–reward trade-off for herbivorous coral reef fishes

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Abstract Non-consumptive effects (NCEs) of predators occur as prey alters their habitat use and foraging decisions to avoid predation. Although NCEs are recognized as being important across disparate ecosystems, the factors influencing their strength and importance remain poorly understood. Ecological context, such as time of day, predator identity, and prey condition, may modify how prey species perceive and respond to risk, thereby altering NCEs. To investigate how predator identity affects foraging of herbivorous coral reef fishes, we simulated predation risk using fiberglass models of two predator species (grouper *Mycteroperca bonaci* and barracuda *Sphyraena barracuda*) with different hunting modes. We quantified how predation risk alters herbivory rates across space (distance from predator) and time (dawn, mid-day, and dusk) to examine how prey reconciles the conflicting demands of avoiding predation vs. foraging. When we averaged the effect of both predators across space and time, they suppressed herbivory similarly. Yet, they altered feeding differently depending on time of day and distance from the model. Although feeding increased strongly with increasing distance from the predators particularly during dawn, we found that the barracuda model suppressed herbivory more strongly than the grouper model during mid-day. We suggest that prey hunger level and differences in predator hunting modes could influence these patterns. Understanding how context mediates NCEs provides insight into the emergent effects of predator–prey interactions on food webs. These insights have broad implications for understanding how anthropogenic alterations to predator abundances can affect the spatial and temporal dynamics of important ecosystem processes.

Keywords Florida Keys coral reefs · Landscape of fear · Behaviorally mediated indirect interaction · Predator–prey interactions · Predator hunting mode · Predation risk · Trophic cascade

Communicated by Joel Trexler.

This study deserves to be a Highlighted Student Paper, because it is an important of broad ecological relevance. There is now substantial literature demonstrating the importance of non-consumptive effects of predators in multiple disparate ecosystems. However, this study is one of the first to address the multiple contingencies that affect the strength and importance of these effects, and their consequences for altering spatial and temporal dynamics of critical ecosystem processes in a coral reef ecosystem. This research advances our understanding of non-consumptive effects and is relevant to the conservation and management of ecosystems particularly in light of human-mediated predator removal and recovery.

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Introduction

Foragers must often balance conflicting needs, such as obtaining food and avoiding predation. The resolution of these decisions comes in the form of trade-offs, where foragers forgo highly profitable feeding opportunities to stay safe (Lima and Dill 1990; Werner and Anholt 1993). Predators can strongly influence ecological communities via these sub-lethal or non-consumptive effects (NCEs) (Schmitz et al. 1997; Preisser et al. 2005; Ripple and Beschta 2007; Heithaus et al. 2008). Yet, the risk that a prey species will tolerate often depends on ecological context, such as the physical environment (e.g., light availability, habitat complexity), predator attributes (e.g., hunting mode), and prey condition (e.g., hunger state) (Heithaus et al. 2007; Preisser et al. 2007; Schmitz 2008; Martin et al. 2010), potentially altering the outcome of NCEs. Thus, to gain a more complete understanding of the strength and importance of NCEs, it is important to identify sources of contingency (i.e., the ecological contexts that influence the strength and nature of risk effects) in predator–prey interactions.

Prey must evaluate multiple factors to assess potential threats and make anti-predator decisions (Liley and Creel 2007; Creel 2011). Predator identity is likely an important factor with riskier predators and situations eliciting greater anti-predator responses (Helfman 1989). For example, prey is more likely to engage in energetically expensive avoidance behaviors for large predators that pose a greater threat (Hill and Weissburg 2013), multiple predators (Reynolds and Bruno 2013), or those that are more predictably encountered, such as sit-and-wait or ambush hunters (Thaker et al. 2011). Prey also anticipates and responds with adaptive behaviors to diel changes in risk (Kronfeld-Schor and Dayan 2003). Many predators possess adaptations for detecting prey in low-light conditions and primarily hunt during twilight periods when their diurnal prey, which may be well adapted for finding resources in daylight, is at a disadvantage (Munz and McFarland 1973). Therefore, prey often decreases their predation vulnerability during diminished light conditions of dawn and dusk by seeking cover or altering their habitat use (Einfalt et al. 2012).

On coral reefs, recent work has shown the importance of predation risk for determining foraging behavior of fishes (Madin et al. 2010a; Catano et al. 2014, 2015b; Rizzari et al. 2014). However, few studies have investigated how anti-predator responses in prey vary with predator identity and time of day (but see Rizzari et al. 2014). Coral reefs house high-diversity fish communities with multiple types of large predatory fishes where both predator and prey species exhibit diel changes in activity (Hobson 1972). Smaller prey fishes often encounter predators with different hunting strategies, including sit-and-wait (e.g., grouper),

sit-and-pursue (e.g., barracuda), and active, coursing predators (e.g., sharks and jacks), which likely necessitate different anti-predator strategies and states of vigilance. In addition, predator avoidance strategies often follow diel patterns with prey becoming more wary at dawn and dusk when predators are more active and more successful (Danilowicz and Sale 1999; Holbrook and Schmitt 2002). Thus, incorporating contextual variation in anti-predator responses will be important for understanding the role of NCEs on coral reefs. This knowledge will be especially important for feeding behavior of herbivorous fishes that are critical for removing algae and facilitating corals on reefs (Adam et al. 2015).

Here, we investigated how predator identity affects foraging behavior of herbivorous fishes and how responses of these fishes may vary with time of day. In a controlled experiment on a coral reef in the Florida Keys (USA), we used fiberglass predator models of a similarly sized black grouper (*Mycteroperca bonaci*, a sit-and-wait predator) and great barracuda (*Sphyraena barracuda*, a sit-and-pursue predator) to simulate predation risk during three times of day: dawn, mid-day, and dusk. We measured how herbivory by parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) changed with increasing distance from the models to examine how herbivorous fishes reconcile the conflicting demands of avoiding predation vs. foraging. We hypothesized that herbivory would decrease as predation risk increased (i.e., near predator models) and that herbivorous fishes would perceive low-light conditions at dawn and dusk as riskier, resulting in even further suppression of herbivory at points even farther from the models. In addition, we expected both predator models to reduce foraging activities; however, we expected the barracuda to have a greater effect at farther distances from the model because of its greater propensity to chase prey over longer distances.

Methods

Site description

Conch Reef (24°57′N/80°27′W) lies in the Florida Keys reef tract which is a large bank reef system located ~8 km offshore of the Florida Keys, USA. Experiments were conducted in Nov 2013 during a 7-day saturation diving mission to the Aquarius Reef Base (ARB), a 13 × 6 × 4-m undersea laboratory anchored at 19 m to the sea floor at Conch Reef. ARB is located within a "Research Only Area" of the Florida Keys National Marine Sanctuary (FKNMS), where all recreational uses, including fishing, boating, and diving, are prohibited. The location is similar in benthic structure to other reefs of the Florida Keys and characterized by high relief spur and groove reef habitat.

Experimental sites were located at least 50 m from the ARB habitat at depths of 15–18 m.

Experimental design

We used fiberglass models of two predators (ca. 90 cm fork length), black grouper (*Mycteroperca bonaci*; Fig. 1a) and great barracuda (*Sphyraena barracuda*; Fig. 1b), to simulate risk beginning at three different times of day: dawn (0700 h), mid-day (1200 h), and dusk (1630 h). During these trials, local sunrise occurred at 0645 h and local sunset at 1730 h. Experimental sites (*n* = 6) were separated by a minimum of 20 m to facilitate independence. It is unlikely that most reef herbivores, particularly territorial species with high site fidelity, would move among trial locations over such distances (Catano et al. 2015a). The models were anchored to the seafloor using nails and monofilament line, and feeding responses of herbivorous fishes were evaluated using standardized assays of a palatable seagrass (*Thalassia testudinum*). Each assay consisted of five seagrass blades that were each cut to 10 cm, scraped free of epiphytes, and clipped to wooden clothespins (Fig. 1b). Assays were then secured to the seafloor at 0.5, 1, 2, 3, and 4 m from either predator models or control areas of reef with no models. Assays and models were collected after 2 h of deployment, and we determined the percentage of seagrass removed over the course of the trial by measuring the length of each remaining blade. At each time period (i.e., dawn, mid-day, and dusk), fish feeding responses to a control, barracuda model, and grouper model were tested over the course of 6 days resulting in *n* = 6 replicates of each treatment at each time period. We rotated the control and models randomly among the six experimental sites, so that the same predator treatment was used only once at a single site for each day to minimize any potential effect of treatment order and habituation to the models.

In prior experiments, a model control (a large plastic carboy of similar dimensions to the predator model) did not affect fish foraging behavior, while the grouper model significantly suppressed foraging behavior as compared to a control (i.e., no model or model control) (Catano et al. 2015b). Thus, fishes responded to the predator models because of the threat of predation, not simply because they were a novel object in the water column. We did not include model controls in this study, because our previous work clearly showed that the responses of prey fishes to the predator model were due to the model looking like a predatory fish (Catano et al. 2015b).

Many parrotfish species (mostly *Sparisoma* spp.) readily consume *T. testudinum*; however, it is rarely eaten by surgeonfishes or juvenile parrotfish. Therefore, to understand how predator treatments could affect different herbivore species, we used cameras to record feeding on the assays
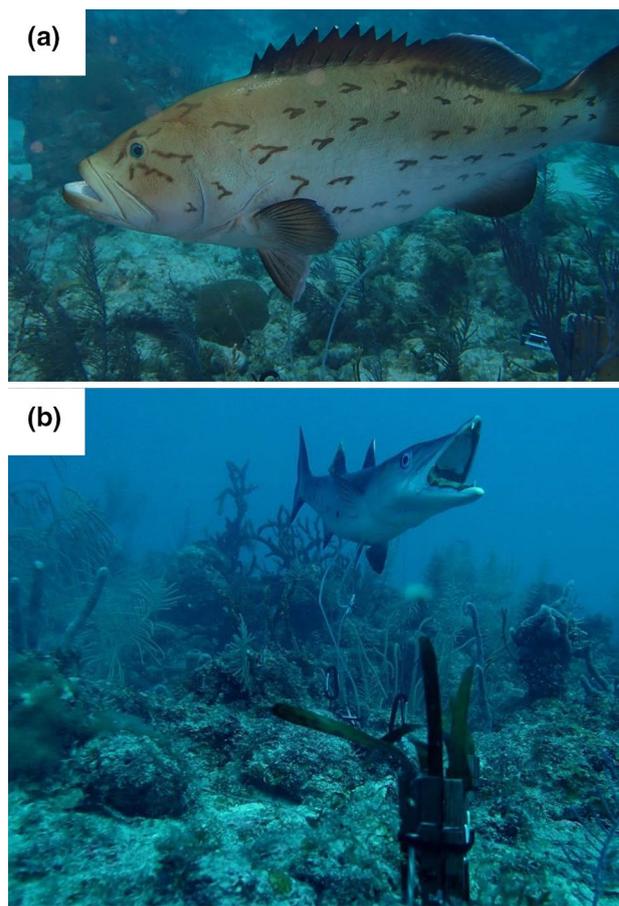

Fig. 1 Predator models (ca. 90-cm fork length) of **a** black grouper (*Mycteroperca bonaci*) and **b** great barracuda (*Sphyraena barracuda*) anchored to the seafloor with a standardized assay of *Thalassia testudinum* in the foreground

and on the benthos on half of all trials (three/time period/predator treatment). To capture the responses of the suite of herbivorous fishes, we counted bites from all herbivorous fishes on the benthos that were within a 25-cm radius of the seagrass assay in addition to counting the bites taken on seagrass. We estimated fish size to the nearest 5 cm using markers of known length in the camera's field of view.

Changes in ambient predator abundance across time periods could also alter levels of background predation risk (i.e., chronic risk integrated over time or space), which could also impact herbivore feeding behavior. These diurnal changes in natural risk could have influenced the impact of our predator models. Therefore, we estimated background predation risk by counting adult piscivorous fishes of the families Carangidae, Lutjanidae, Serranidae, and Sphyraenidae that are known to consume adult parrotfishes and surgeonfishes (based on Randall 1967) that passed through the video frame. We then calculated the number of predators observed per hour of observation. We were unable to

calculate predator biomass, because we could not reliably estimate the size of these fishes as they moved through the video frame.

Statistical methods

All statistical analyses were conducted using R version 3.0.1 (R Core Team 2013). Parametric assumptions of normality and homoscedasticity were verified using plots of the residuals. First, to understand how uncontrolled factors, such as background levels of predation risk, could have influenced foraging, we used the analysis of variance (ANOVA) to test differences in predators observed per hour among time periods (i.e., dawn, mid-day, and dusk). We also tested if natural predator abundance varied among the treatments using ANOVA. Finally, we examined if herbivores became habituated to the predator models over the period of the study by testing the effect of day on consumption during predator trials using simple linear regression.

We examined the effect of predator treatment (i.e., grouper model, barracuda model, or control), time period (i.e., dawn, mid-day, or dusk), and their interaction using ANOVA on the following two feeding metrics: (1) percent seagrass consumed per hour and (2) bites per hour on seagrass or benthos (within the 25 cm radius). These metrics reveal different aspects of herbivory. Seagrass consumed measures the impact of herbivory (i.e., the amount of primary production removed), which could have been attributed to many fishes taking small bites, or several taking larger bites. Bites per hour more directly address herbivore feeding behavior by measuring how many bites were actually taken (not how much seagrass mass was removed). Thus, by utilizing both metrics, we are measuring both the behavioral change (change in bite rates) and the outcome of that change (amount of food removed). For bites per hour, we included the effect of natural predators, because we had video samples and predator data for each trial where this metric was calculated. We only had data on natural predator abundance for half of the seagrass consumption trials, and therefore, we ran a separate ANOVA for this subset of trials ($n = 3$). For all of the above analyses, we pooled all distances to understand the overall effect of the models vs. the control. We did not find significant time period × treatment interactions (see "Results"); therefore, we used specified pairwise t tests with false discovery rate correction (Benjamini and Hochberg 1995) to evaluate significance in contrasts among levels of predator treatments and/or time periods.

Next, to understand how foraging changed with distance from the predator models, we used analysis of covariance (ANCOVA) to examine the effect of distance (the covariate), time period, and their interaction on the two foraging metrics for each predator model separately. For the barracuda model, we found a significant interaction
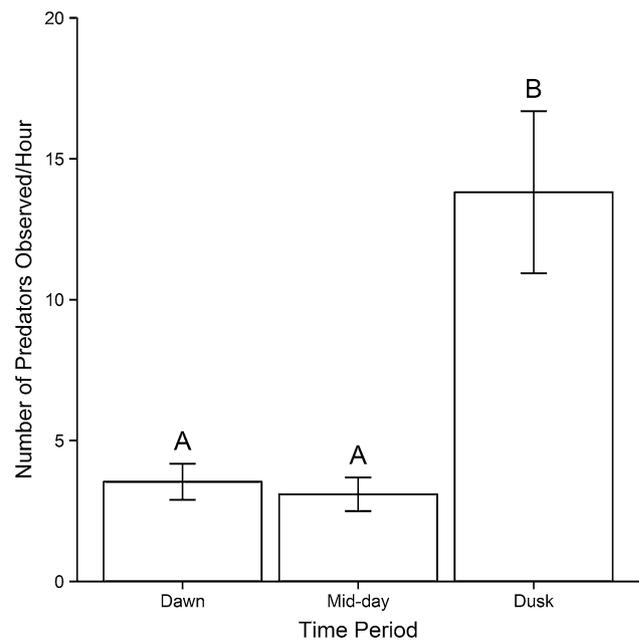

Fig. 2 Number of predators observed (h^{-1}; mean ± SE) during dawn ($n = 30$), mid-day ($n = 27$), and dusk ($n = 23$) periods. *Letters above bars* indicate significance based on a Tukey HSD post hoc test

between distance and time period for seagrass consumption (see "Results"). Thus, we ran separate regressions between distance and seagrass consumption for each time period to determine the source of the interaction. When there was not a significant interaction between distance and time period but a main effect of time (see "Results"), we examined the effect of time period on adjusted mean bite rates using Tukey's post hoc comparisons. Adjusted means were calculated by calculating mean bite rate while holding the continuous covariate (distance) at a constant value (at its mean).

Results

Natural predators were observed more frequently on video during dusk relative to either dawn or mid-day, which were statistically indistinguishable from one another (Fig. 2, $F_{2,77} = 14.48$, $p < 0.001$). There was no difference in natural predator observations among the treatments, although there was a trend towards more visitations to the barracuda and grouper models over the controls ($F_{2,77} = 2.70$, $p = 0.07$). Predators that visited the barracuda and grouper models appeared to investigate the models before swimming off. However, the number of natural predators observed did not influence either the number of bites herbivorous fishes took on seagrass and the surrounding benthos (Table 1) or the amount of seagrass consumed (Table S1).

The amount of seagrass consumed ($\beta = 1.44 \pm 0.86$, $R^2 = 0.01$, $p = 0.10$) and the number of bites taken ($\beta = 5.6 \pm 3.7$, $R^2 = 0.02$, $p = 0.14$) did not change over the duration of the study, suggesting that fishes did not become habituated to the presence of the predator models. All of the bites on the seagrass were taken by *Sparisoma aurofrenatum*. The majority of bites on the benthos were taken by *S. aurofrenatum* (56%), followed by *Acanthurus coeruleus* (14%), *Scarus taeniopterus* (12%), *Acanthurus bahianus* (8%), and *Scarus iserti* (6%). Fishes varied in size from 5–40 cm (mean 15 ± 0.13), and the majority of parrotfishes observed were the initial phase (86%).

When averaged across all distances and time periods, seagrass consumption declined by 37% in the presence of the barracuda (*t* test, $p = 0.02$) and by 30% in the presence of the grouper model (*t* test, $p = 0.05$) relative to the control. The amount of seagrass consumed between the barracuda and grouper treatments was statistically indistinguishable (*t* test, $p = 0.59$; Table 1; Fig. 3a) when averaged across all distances and time periods. Overall, the greatest amount of seagrass consumption occurred during dawn, declining significantly at mid-day and again at dusk (Fig. 3a). When we examined the number of bites herbivorous fishes took on seagrass and the surrounding benthos, bite rates declined by ca. 50% in the presence of the barracuda vs. the control (*t* test, $p = 0.03$), whereas the grouper model did not suppress bite rates as compared to the control (*t* test, $p = 0.30$; Table 1; Fig. 3b). Overall, the number of bites was similar for dawn, mid-day, and dusk.

When we examined the spatial effect of the predators on seagrass consumed, we found differences between the two models in how they impacted seagrass consumption across time (Fig. 4a, b). For the grouper model, the magnitude of this effect (i.e., the slope of this relationship) was similar for all three time periods. However, there was a trend for a distance $\times$ time period interaction ($p = 0.09$) with potentially stronger suppression of feeding with increasing distance at dusk (i.e., there may have been a shallower slope at dusk relative to other time periods; Fig. 4a; Table 2). After accounting for the effect of distance, overall, more seagrass was consumed at dawn than at dusk for the grouper model (Tukey HSD test; $p = 0.01$). Mid-day had intermediate rates that were not significantly different from either dawn ($p = 0.09$) or dusk ($p = 0.63$). For the barracuda model, the effect of distance varied depending on time of day as indicated by the significant distance $\times$ time period interaction (Table 2). Seagrass consumption increased with increasing distance from the barracuda model more rapidly at dawn relative to dusk (dawn: $\beta = 6.51 \pm 1.71$, $R^2 = 0.32$, $p < 0.001$ and dusk: $\beta = 2.19 \pm 1.11$, $R^2 = 0.09$, $p = 0.06$; Fig. 4b). However, at mid-day, the barracuda model suppressed seagrass consumption similarly across the different distances ($\beta = 2.37 \pm 1.67$, $R^2 = 0.03$, $p = 0.17$). Thus,

Table 1 Summary of ANOVAs testing for effects of natural predators, predator treatment (i.e., barracuda decoy, grouper decoy, or control), time period (i.e., dawn, mid-day, or dusk), and their interaction on the percentage of seagrass consumed, and the total bites on seagrass or benthos

	% Seagrass consumed		Total bites	
	F	*p*	*F*	*p*
Natural predators	N/A		0.53	0.47
Predator	4.29	0.01	3.86	0.04
Time period	16.15	<0.001	1.89	0.14
Predator $\times$ time period	1.32	0.26	0.66	0.68

even though when pooled across distance, there was no difference in seagrass consumption between the predator models, at mid-day, there was less consumption at further distances from the barracuda relative to the grouper model.

Although the barracuda model suppressed overall bite rates more than did the grouper model (Fig. 3), the spatial effect of both predators on bite rates was similar for the three time periods with bites increasing similarly with increasing distance from the models (Table 2; Fig. 4c, d). On average, four times more bites were observed at 4 m relative to 0.5 m from the predators. Time period did not influence the effect of the grouper model on bite rates (Table 2). However, time period did influence bite rates for the barracuda model with over twice as many bites taken at dawn (46 bites/h) relative to either mid-day (22 bites/h; Tukey HSD, $p = 0.05$) or dusk (20 bites/h; Tukey HSD, $p = 0.05$).

Discussion

Anti-predator decisions often vary depending on attributes of predator, prey, and their physical environment (Liley and Creel 2007; Heithaus et al. 2009; Creel 2011). Yet on coral reefs, these important contingencies remain poorly explored despite the recent emphasis on predators as major drivers of foraging behavior of their prey, especially herbivorous fishes (Madin et al. 2010a, b; Catano et al. 2014; Rizzari et al. 2014). Our work shows that herbivorous fishes exhibited a threat-sensitive response by decreasing foraging near models of large predatory fish, but that the effect of different predators depended on time of day. When compared to normal foraging activity, barracuda models suppressed overall rates of herbivory by parrotfishes and surgeonfishes nearly twice as much relative to the grouper models. Furthermore, the barracuda model suppressed herbivory by 50% at mid-day and dusk as compared to dawn, while the herbivory rates were similar across all three time periods for the grouper model. Although both predator
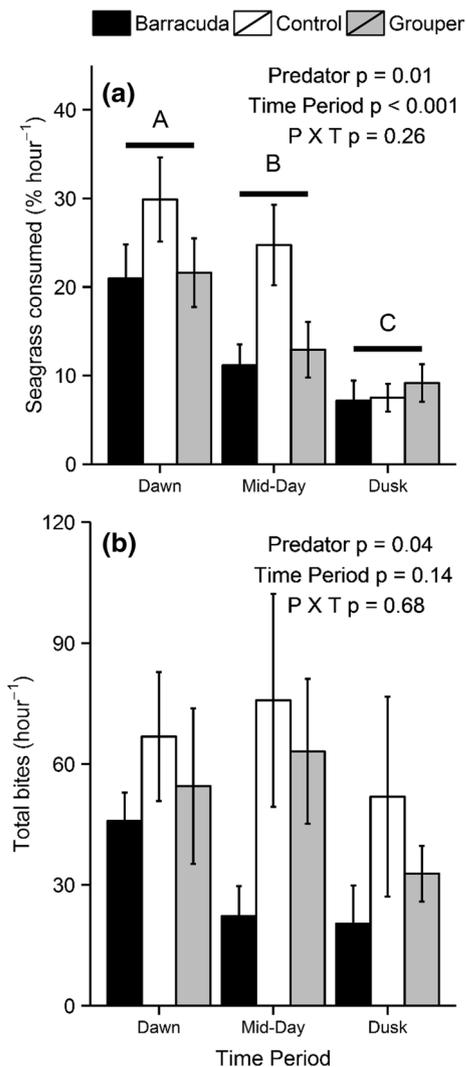
Fig. 3 a Seagrass consumed (% h^{-1}, $n = 30$/treatment) and **b** total bites (h^{-1}, $n = 10$/treatment) for the barracuda model (*black bars*), control (*white bars*), and grouper model (*gray bars*) during dawn, mid-day, and dusk (mean ± SE). *Different letters above bars* in panel (**a**) indicate significant differences among time periods based on pairwise contrasts with false discovery rate correction. Results of two-way ANOVAs testing for the effects of predator and time period and their interaction (P × T) on each feeding metric are indicated on each panel

models similarly decreased the amount of seagrass consumed by the parrotfish *Sparisoma aurofrenatum*, barracuda models generated larger 'zones of fear' by suppressing foraging at greater distances from the model than did the grouper. Yet, this difference was strongly apparent only during mid-day. In fact, overall, time of day had a strong influence on the food for safety trade-off, with fishes consuming the greatest amount of seagrass at dawn, as compared to mid-day and dusk, and foraging closer to the models, even the seemingly riskier barracuda models. Thus, herbivorous fishes on coral reefs show complex responses

to acute predation risk that are shaped by the magnitude of threat (i.e., distance from predator models), predator identity, and time of day.

Evidence from multiple ecosystems shows that top predators have an important functional role by consuming their prey and by influencing prey behavior (Estes et al. 2011). Both these consumptive and non-consumptive effects of predators could drive changes in herbivore feeding (Preisser et al. 2005). However, it is unlikely that consumptive effects of predators on herbivorous fishes strongly influenced herbivory rates in our experiment. Herbivorous fishes are locally abundant on reefs in the Florida Keys (Burkepile et al. 2013), often the numerically abundant trophic group, making their depletion at the scale of our feeding assays unlikely. Furthermore, given the relatively large home ranges of most reef-associated piscivorous fishes (e.g., Farmer and Ault 2011; O'Toole et al. 2011), it is unlikely that predation would have selectively impacted some of our experimental sites and not others to a degree that would have confounded our experiment. Thus, the overwhelming signal on herbivore feeding in our study should be from the non-consumptive effects of predation risk.

Our work shows that the threat of predation alters prey behavior by decreasing bite rates and decreasing removal of primary producers (i.e., amounts of seagrass consumed). However, the effect of risk was even stronger on prey behavior than resource consumption. For instance, overall, at mid-day, we found bite rates to be substantially less in the barracuda treatment relative to the grouper, while seagrass consumption remained similar (Fig. 3). The apparent mismatch between these two metrics could be due to the fact that our bite rate metric included bites on both seagrass and the benthic algae surrounding assays by both parrotfishes and surgeonfishes, whereas resource consumption was only measured from seagrass where bites were only from one species of parrotfish. Thus, measuring overall herbivore bite rates may be a better representation of the overall effect of risk from these two different predator decoys.

Similar to other recent studies (Madin et al. 2010a; Catano et al. 2014, 2015b; Rizzari et al. 2014), we demonstrate that herbivorous reef fish, like many other taxa (Teplitsky et al. 2005; Kesavaraju et al. 2007; Monclús et al. 2009), perceives and responds to both the presence and magnitude of risk. However, our work also shows that these fishes respond differently depending on predator identity, although these responses did depend on time of day for each predator type. Barracuda models more strongly suppressed feeding rates at mid-day and dusk, and generated a larger zone of fear during mid-day as compared to grouper models. The various strategies that predators use to find and attack prey can elicit different types of anti-predatory responses in prey. Predators that use a "sit-and-wait" or "sit-and-pursue" strategies, which involve remaining in a

Fig. 4 **a**, **b** Seagrass consumed (%h⁻¹, *n* = 6/treatment) and **c**, **d** total bites (h⁻¹, *n* = 2/treatment) for grouper and barracuda treatments (mean ± SE) with increasing distance from models. *Solid lines* represent fitted linear regressions for three time periods: dawn (*circles with solid lines*), mid-day (*triangles with short dashed lines*), and dusk (*squares with long dashed lines*; Table 2)
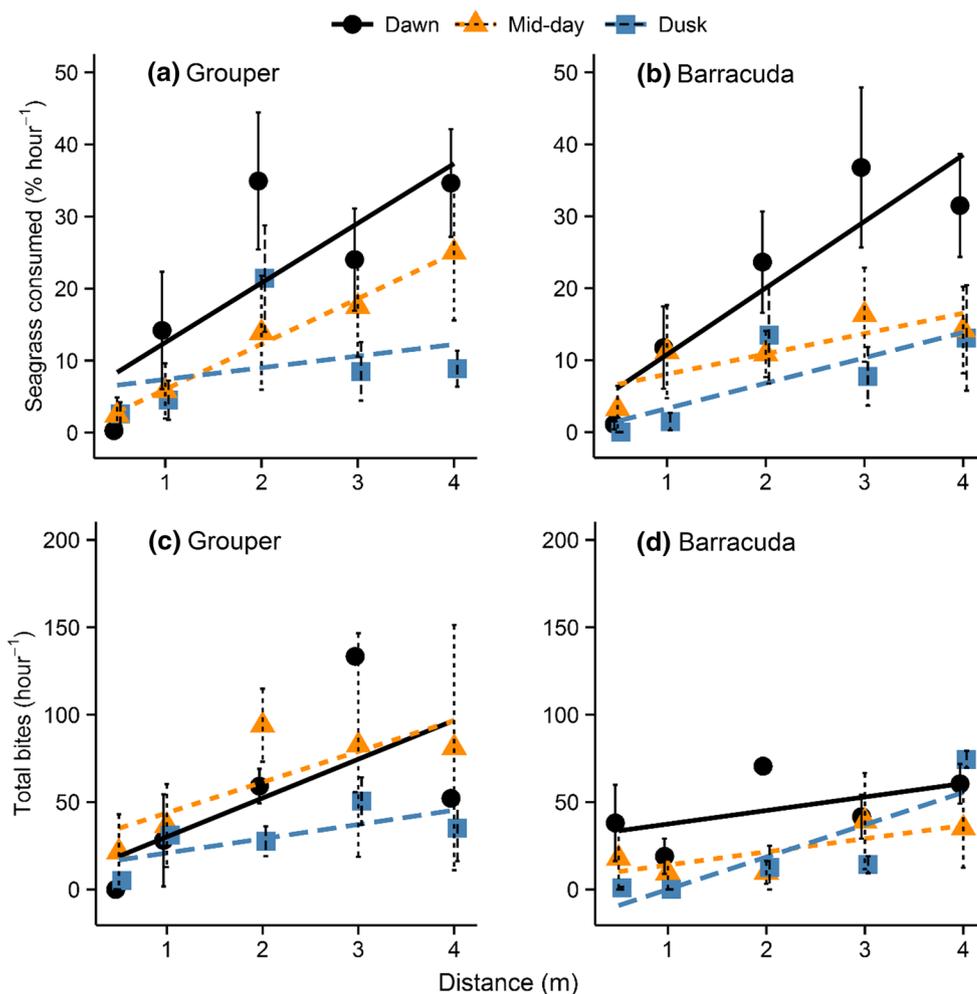

Table 2 Summary of ANCOVAs testing for effects of distance among three time periods (i.e., dawn, mid-day, or dusk), and their interaction for the (a) grouper and (b) barracuda decoys on the percentage of seagrass consumed, and the total bites on seagrass or benthos

	% Seagrass consumed		Total bites	
	F	*p*	*F*	*p*
(a) Grouper				
Distance	17.95	<0.001	4.51	0.05
Time period	5.10	0.008	1.29	0.30
Distance × time period	2.40	0.09	0.32	0.73
(b) Barracuda				
Distance	19.85	<0.001	12.65	0.001
Time period	7.51	<0.001	4.96	0.01
Distance × time period	3.04	0.05	1.31	0.29

fixed location until a prey is within striking or pursuit distance, respectively, provide predictable point source cues that are likely to evoke behavioral responses in their prey (Schmitz 2007; Preisser et al. 2007). While both strategies often cause prey to reduce their activity, preys are more likely to also reduce their habitat domain (i.e., the spatial range of activity) when predators adopt pursuit strategies (Schmitz 2007). For example, in a grassland ecosystem, sit-and-wait spiders decreased grasshopper activity but did not change their foraging range, whereas sit-and-pursue spiders both reduced grasshopper activity and constricted their foraging range (Miller et al. 2014). Thus, predators that engaged in pursuit had a greater impact on the spatial scale of their prey's movement.

Although both black grouper and barracuda are important reef predators, they have different hunting tactics and modes of attack. Groupers are opportunistic feeders (Randall 1967) that tend to forage during dawn and dusk to take advantage of low-light conditions and decreased detectability by their prey (Koch 2011). They typically adopt a "sit-and-wait" strategy, lying in wait for prey until it is near enough to swallow using their large mouths and operculum as a vacuum (Thompson and Munro 1978). Barracuda typically forage diurnally, feeding in shallow habitats during

the early morning and early evening, and will either stalk or "sit-and-pursue" their prey, remaining at a fixed location and rushing to attack prey when they are within striking vicinity (de Sylva 1963). Barracuda have long striking distances, approximately equivalent to their body length (Porter and Motta 2004), and pursue prey at high velocities (≈ 12.2 m/s) once an attack ensues (O'Toole et al. 2010).

These differences in hunting tactics may have influenced the responses of herbivorous fishes, because the barracuda suppressed feeding activity (i.e., total bites; h^{-1}) nearly twice as much as the grouper relative to the control, regardless of time of day. Although both predators had similar overall effects on the amount of seagrass consumed, they had differential effects on seagrass consumption depending on distance from the model. At dusk, seagrass consumption increased with distance from the model similarly for both the grouper and barracuda. However, at mid-day, there was approximately twice as much seagrass consumed 4 m from the grouper model relative to the barracuda model. High-light intensity during mid-day may have allowed fishes to easily perceive differences between the predator models. Fishes may have been more hesitant to forage as closely to the barracuda model, because they tend to be more active diurnally and because of their tendency to quickly pursue prey over longer distances. Barracuda likely represented a greater potential threat during mid-day and resulted in stronger anti-predator responses, generating a wider 'zone of fear'. However, the barracuda and grouper generated similar 'zones of fear' at dawn, when feeding was the highest overall, and dusk, when feeding was slowest. In a similar study, Rizzari et al. (2014) found no differences in herbivore feeding rates between an actively hunting predator model (a blacktip reef shark) and a sit-and-wait predator model (a large coral grouper). However, herbivory was examined only at very close distances from the models (0.5–1 m). At these proximities, we also observed similarly low feeding rates for both the barracuda and grouper models. In our study, the impact of predator identity only became apparent at further distances, primarily during mid-day.

Although the impact of predator identity in our study was context-dependent, predator-specific risk effects could be an important yet unexplored area of research in marine ecosystems. These effects could be particularly important in areas of selective fishing practices that target economically important species and larger individuals and alter the composition of predatory species on reefs. For instance, in the Florida Keys, large predatory fishes, including snapper and grouper, are heavily fished and often abundant only in marine reserves, while barracuda are generally not targeted and are abundant in both fished and unfished areas (Bohnsack et al. 1994). Thus, selective fishing practices and reserve implementation could alter the landscape of

predation risk in complex ways. Assessments of marine reserves that measure reserve success in terms of increases in density, biomass, and body size of targeted fishes (e.g., Halpern and Warner 2002; Halpern 2003) often overlook the importance of changes in predator functional diversity (Jennings et al. 1996). Understanding the variable effects of multiple predators with different hunting modes may provide a more nuanced and realistic view of predator–prey interactions and greater insight into their likely emergent effects on food webs.

In addition to the differential effects of predators, prey often must cope with diel variability in predation risk. Crepuscular periods are often more risky for diurnal species due to increased predator activity and lower light levels that make detection of predators more difficult (Hobson 1972; Danilowicz and Sale 1999; Holbrook and Schmitt 2002). In addition, prey experience diel periodicity in physical state (e.g., hunger) that can affect their tolerance of risk. Hunger may drive prey to forage in potentially riskier situations, thereby decreasing the strength of NCEs (Heithaus et al. 2007). As a consequence, prey may exhibit seemingly maladaptive behaviors during periods of high risk. For example, dark-eyed juncos (*Junco hyemalis*) with reduced energy reserves often fed in very dim light during dawn when predation risk was highest, while their counterparts that had normal reserves avoided feeding during these risky times (Lima 1988).

We found that herbivorous reef fish exhibited diel changes in risk taking behavior that may have been influenced by changes in light availability, their hunger level, and predator identity. Our video footage showed that predator activity increased roughly 300% at dusk relative to mid-day and dawn. Although we did not find a statistical relationship between predator activity at the feeding assay sites and declines in seagrass consumption or bite rates, herbivore foraging was at its lowest level at dusk, with fishes consuming only about a third of the amount of seagrass at dusk relative to dawn. This decline in feeding at dusk may have also been influenced by hunger levels of herbivorous fishes as they were likely more satiated near dusk after a day's worth of feeding. This increasing satiation throughout the day likely decreased fishes' willingness to approach the predator models to feed. At dawn, herbivores were significantly more willing to approach the predator models (i.e., there was a greater effect of distance on feeding at dawn), although feeding at the closest proximity to the models was quite low. High hunger levels at dawn may have influenced these patterns as these fishes are generally inactive at night (Dubin and Baker 1982; Helfman 1986; Hay et al. 1988), and their guts are nearly completely empty by morning (Polunin et al. 1995). Thus, the need to rapidly fill their empty guts early in the day may make herbivorous fishes more willing to risk foraging near predators

relative to other times of day when they likely would have been much less hungry.

This pattern was much more evident for the barracuda model than the grouper model, further supporting the importance of predator identity in shaping NCEs. While feeding at the farthest distances from the barracuda was high at dawn, herbivores appeared to avoid these same distances at both mid-day and dusk. However, herbivores were more willing to feed at these same distances at mid-day and dusk when the grouper was present, further suggesting that herbivores may have perceived the barracuda as risker. Although we did not manipulate hunger level directly, our data support the idea that herbivores are more willing to trade food for safety when more satiated and that this trade-off is stronger for predators with a wider 'zone of fear'. The abundance of natural predators may have influenced the decline in feeding at dusk relative to dawn, but it would not explain the decline in feeding at mid-day when natural predators were at similar abundance to dawn. Although we could not disentangle the potential impact of hunger and natural predator abundance, our data suggest that they both likely impact herbivore foraging. It is important to note that dawn and dusk, although similar in their absolute levels of light availability, differ in their patterns of light availability, with levels increasing at dawn and decreasing at dusk. Although we are unable to test this with our data, the differences in light patterns could have also attributed to differences in feeding between dawn and dusk.

In both terrestrial (Schmitz 2008; Valeix et al. 2009; Thaker et al. 2011) and marine ecosystems (Heithaus et al. 2007; Wirsing et al. 2010; Burkholder et al. 2013), considerable evidence supports the importance of context-dependent factors (e.g., predator identity and prey defense traits) in influencing the magnitude of risk effects. Understanding contingencies that influence NCEs in coral reef systems will yield a broader framework for predicting the dynamic effects of predation risk on prey behavior, which is both vital and timely in an era of top predator declines (Heithaus et al. 2008). By altering patterns of herbivory, predators could alter the functioning of coral reef ecosystems via behaviorally mediated trophic cascades (Dill et al. 2003). We demonstrate that predation risk alters both behavior of prey (i.e., bite rates) and ultimately the consumption of primary producers (i.e., seagrass consumed). On reefs, the fear of predation may concentrate herbivory in areas of low risk. Spatially constrained grazing is more likely to lead to increases in coral recruitment and coral cover relative to areas where the same amount of grazing is more diffuse (Sandin and McNamara 2012), suggesting that fear-driven changes in herbivory could ultimately impact coral dynamics on reefs.

Furthermore, predator identity could alter the outcome of behaviorally mediated trophic cascades (Schmitz 2008), with more threatening predators having a greater impact on benthic communities. For coral reefs, theoretical modeling suggests that differences in predator biomass across reefs can dramatically alter the distribution of herbivore foraging intensity, thereby altering the spatial heterogeneity of macroalgae, and their potential negative effects on corals, through risk-avoidance behaviors in herbivores (Madin et al. 2010a). However, this model and most other studies that have investigated the role of NCEs in reef communities (Madin et al. 2010b; Catano et al. 2014) have quantified risk by aggregating all species of predators into a single metric of overall predator biomass. Yet, predators not only vary in the types of fishes they consume (Randall 1967), but our work also shows that different species of predators may also differentially intimidate prey depending on the context of the interaction. Thus, metrics that integrate biomass of all predators are potentially unrealistic for estimating the cascading impacts of predator–prey interactions. Therefore, to understand the consequences of predators on the benthos, we argue for an increased emphasis on individual predator effects, particularly in systems with high predator functional diversity. Incorporating the impact and context-dependent nature of NCEs will be imperative for understanding how coral reefs will respond to predator losses from overfishing and to predator recovery through the establishment of marine reserves.

Author contribution statement LBC, DEB, KMB, and MBB designed the study; LBC and MBB performed the research; LBC conducted statistical analyses; LBC, DEB, and KMB wrote the manuscript; all authors contributed to editing.

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