

Predator density and the functional responses of coral reef fish

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Abstract Predation is a key process driving coral reef fish population dynamics, with higher per capita prey mortality rates on reefs with more predators. Reef predators often forage together, and at high densities, they may either cooperate or antagonize one another, thereby causing prey mortality rates to be substantially higher or lower than one would expect if predators did not interact. However, we have a limited mechanistic understanding of how prey mortality rates change with predator densities. We re-analyzed a previously published observational dataset to investigate how the foraging response of the coney grouper (*Cephalopholis fulva*) feeding on the bluehead wrasse (*Thalassoma bifasciatum*) changed with shifts in predator and prey densities. Using a model-selection approach, we found that per-predator feeding rates were most consistent with a functional response that declines as predator density increases, suggesting either antagonistic interactions among predators or a shared antipredator behavioral response by the prey. Our findings suggest that variation in predator density (natural or anthropogenic) may have

substantial consequences for coral reef fish population dynamics.

Keywords *Cephalopholis fulva* · Predation · Predator–prey interactions · Functional response · *Thalassoma bifasciatum*

Introduction

Predators are a key source of density-dependent mortality in coral reef fish (reviewed by Hixon and Webster 2002; White et al. 2010), and several studies have shown that per capita prey mortality increases more rapidly with prey density on reefs with higher predator densities (Schmitt and Holbrook 2007; White 2007). Missing, however, is a deeper quantitative understanding of how predator foraging behavior (i.e., attack rate and handling time) can change with changes in predator density to produce these patterns (e.g., see Harborne 2012 for one of the few studies actually quantifying a coral reef predator's functional response). In general, we expect more predators to produce higher predation rates, but high predator density can also shift predator foraging behavior, either increasing (cooperative hunting) or decreasing (interference competition) per-predator feeding rates (Sih et al. 1998; Skalski and Gilliam 2001).

Previous studies in reef fish have found both cooperative and antagonistic interactions among predators of the same and different predator species (Hixon and Carr 1997; Lukoschek and McCormick 2000; Bshary et al. 2006; Stallings 2008; Stallings and Dingeldein 2012). Changes in predator density or identity can also alter predator foraging behavior if prey exhibits common or conflicting behavioral responses in response to multiple predators (Sih et al. 1998;

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Vance-Chalcraft et al. 2007). For example, when a single grouper (Serranidae) stalks a damselfish (Pomacentridae) prey, the damselfish may avoid predation by shoaling above the reef with other damselfish. The presence of additional groupers may intensify this prey shoaling behavior, thus reducing foraging success for all groupers. In contrast, when groupers and larger transient predators such as jacks (Carangidae) are both foraging, damselfish cannot avoid grouper predation by shoaling without exposing themselves to greater predation by jacks in the water column and vice versa (the antipredator response to jacks is to dive closer to the reef, where groupers are hunting) (Hixon and Carr 1997). Thus, if prey exhibit a conflicting antipredator response, predator foraging rates can increase relative to predators foraging independently or at lower densities. Theoretical ecologists have appreciated the importance of predator dependence in modifying predator foraging behavior for some time (Skalski and Gilliam 2001; Arditi and Ginzburg 2012); however, studies on coral reefs have largely overlooked the importance of predator–predator interactions and prey antipredator behavior in modifying the abundance and distribution of prey (e.g., White 2008; White and Samhouri 2011, but see Stier et al. (2013)).

A number of factors can produce variation in predator and prey densities on reefs. The highest reported predator density on a coral reef is 24 predators m^{-2} following an exceptional grouper (*Epinephelus merra*) settlement event to Réunion Island in 1994 (Letourneur et al. 1998). Episodic settlement events such as these—as well as less extreme spatiotemporal variation in settlement rates—can produce substantial variation in both predator and prey density on coral reefs (Doherty 2002). Variable predator densities can also emerge from variable habitat quality (e.g., Hixon and Beets 1993), the location of sites relative to predator nursery habitats (e.g., Eggleston 1995; Nagelkerken et al. 2012), and from fishing pressure (e.g., Mumby et al. 2012). However, we have a limited understanding of how variable densities of both predators and prey can affect predator foraging behavior and the dynamics of predator–prey interactions (White et al. 2010; Arditi and Ginzburg 2012; Stier et al. 2013).

A mechanistic description of predator foraging behavior is particularly key to this understanding, because predator-dependent shifts in foraging behavior can modify food chain length (Schmitz 1992), the strength of species interaction in diverse food webs (Novak and Wootton 2008), the spatial distribution of predators (van der Meer et al. 1995), and destabilize predator–prey population cycles (DeLong and Vasseur 2013). Furthermore, reefs are currently experiencing heavy fishing pressure, which disproportionately reduces the abundance of top predators and increases the density of smaller-bodied mesopredators

(Sandin et al. 2008; Stallings 2009; Mumby et al. 2012). The consequences of these substantial shifts in the predator assemblage for the dynamics of reef fish populations are poorly understood.

In this study, we mechanistically evaluate the functional response of the coney grouper (*Cephalopholis fulva*) feeding on the bluehead wrasse (*Thalassoma bifasciatum*) on the Caribbean island of St. Croix, US Virgin Islands. St. Croix is an ideal study system for evaluating the effects of predator density on predator foraging behavior, because predator and prey recruitment rates of both groupers and wrasses are spatially variable but temporally consistent, a pattern often attributed to variable oceanographic currents that produce high recruitment on western reefs and lower recruitment on eastern reefs (Hamilton et al. 2006; White 2007). An earlier study documented spatial coupling of predator and prey recruitment rates and evaluated the consequences of variable predator and prey density on the mortality rates of wrasses. Specifically, prey exhibit inversely density-dependent mortality at low predator density sites and direct (positive) density-dependent mortality at high predator density sites (White 2007). Behavioral aggregation of predators to areas of high prey density is a documented phenomenon in reef fish (Anderson 2001) and a mechanism for direct density-dependent mortality (Murdoch 1994; Anderson 2001). White (2007, 2008) attributed the spatial variation in prey density dependence to the spatial gradient in predator density, essentially assuming there was a linear relationship between predator density and the strength of prey density dependence (cf. Schmitt and Holbrook 2007). In light of the potential for predator-dependent feeding behavior, we re-analyzed the original dataset by fitting mechanistic functional response models to test for potential synergism or antagonism among predators in attack rates or handling times. Either phenomenon could alter the predicted relationship between spatial variation in predator density, prey mortality, and thus prey population dynamics (White 2007; White and Samhouri 2011).

Methods

Study system and data collection

The bluehead wrasse, *Thalassoma bifasciatum*, is a small zooplanktivorous fish common on Caribbean reefs. Larval bluehead wrasse settle from the plankton onto the reef in monthly pulses, and after metamorphosing while buried in sediment for several days, emerge and spend the first week of their life sheltering near the reef substrate. Mortality is high during this time, and on the low-relief pavement reefs surrounding St. Croix, US Virgin Islands (17°45'N,

64°45'W), one of the primary predators on juvenile bluehead wrasse is the coney grouper, *Cephalopholis fulva* (White 2007).

White (2007) observed bluehead wrasse emergence and subsequent mortality on three permanent 30 × 2 m transects established at each of five study reefs surrounding St. Croix (see White and Warner (2007b) for a map of study sites). He also censused the densities of wrasse predators (primarily coney grouper) at each reef. Full details of the data collection are given in White (2007) and White and Warner (2007b), but in short the dataset consists of the number of bluehead wrasse emerging on and disappearing from each transect each day during a 6-d window following two separate monthly settlement pulses (as well as the density of coney grouper at each site during that month). Mortality data were collected at four of the sites in both months and at the fifth site in the second month only. Mortality rates on each transect were assumed to be independent from one another, so we had 3 transects × (4 sites × 2 months + 1 site-month) = 27 independent observations of prey density and mortality. The five sites differed substantially in the density of coneys (White 2007), and coney densities were relatively consistent within sites over the course of the summer (see Electronic Supplementary Material, Table S1).

For the present study, we only examined mortality during the first 24 h of observations in a month (for transects that had no newly emerged settlers on the first day, we used the first day in which any settlers were observed). In this way, all of the prey within a transect begin the trial at the same age, and because emergence occurs at dawn, we can ignore the possibility of new prey arriving during the trial period (although there was necessarily some lag between actual emergence and our initial census of new prey fish on the first day). Examining mortality in the first 24 h also removes possible bias associated with prey movement, which is very limited in the first few days post-settlement (Overholtzer-McLeod 2005; White and Warner 2007b). For simplicity and consistency with other reef fish studies, we refer to newly emerged fish as “settlers” even though they had actually settled a few days prior and had just emerged from burial in the sediment when we first observed them.

Analysis

To test for predator dependence in the functional response, we fit five distinct functional response models (Table 1) to our dataset. We used the Holling type II functional response (H2; Holling 1959) as a null model in our analysis because the H2 model assumes that feeding rates are independent of predator density. We then evaluated four additional models that describe distinct types of predator

Table 1 Five functional response models describing how the number of prey consumed per predator can shift with predator density including modifications

Model	Formula	ΔAIC	w
Holling type II (H2)	$f_{H2}(N, P) = \frac{aNP}{1+bN}$	4.3740	0.0758
Beddington–DeAngelis (BD)	$f_{BD}(N, P) = \frac{aNP}{1+bN+cP}$	4.0277	0.0902
Crowley–Martin (CM)	$f_{CM}(N, P) = \frac{aNP}{1+bN+cP+bcNP}$	5.2836	0.0481
Hassell–Varley (HV)	$f_{HV}(N, P) = \frac{aNP^m}{bN+P^m}$	0	0.6755
Ratio-dependent (RD)	$f_{RD}(N, P) = \frac{a(N/P)}{1+b(N/P)}$	3.6235	0.1104

All models include attack rate (a , $1/(\text{time} \times \text{pred}/\text{reef})$) and handling time (b/a , $\text{prey}/\text{reef}/(\text{pred}/\text{reef} \times \text{days})$) for a given predator density (P , pred/reef) and prey density (N , prey/reef). Also included are parameters c and m , which describe the magnitude of predator interference. The Beddington–DeAngelis, Crowley–Martin, and Hassell–Varley models each model the dependence of predator density in different ways, but all reduce to the Holling type II equation if their respective predator-dependent parameters are estimated as zero (i.e., BD and CM: $c = 0$, HV: $m = 0$) or one (RD: $P = 1$)

dependence (Skalski and Gilliam 2001): (1) the Beddington–DeAngelis model (BD; Beddington 1975; DeAngelis et al. 1975), in which predator density affects the predator attack rate but not handling time; (2) the Crowley–Martin model (CM; Crowley and Martin 1989), in which changes in predator density affect both attack rate and handling time; (3) the Hassell–Varley model (HV; Hassell and Varley 1969), which was created without a stated mechanistic basis but is similar in form to BD and effectively allows a nonlinear effect of predator density on attack rate; and ratio-dependent predation [RD, where attack rate depends on the ratio of predators: prey, reviewed in Arditi and Ginzburg (2012)], which is equivalent to the HV model with the parameter $m = 1$.

The five functional response models assume a constant prey density, but because bluehead wrasse settle onto the reef at night, prey would be depleted over the course of the 24-h period during our trial. Therefore, we integrated the five models over time (see Electronic Supplemental Material, ESM for details) and calculated the integrated daily feeding rate rather than the instantaneous feeding rate for each model.

The functional response models we examined are intended to describe interactions between a single predator species and a single prey species. Many reefs, including those surrounding St. Croix, have a diverse assemblage of predator and prey species. However, we argue that our approach is an effective approximation, because coney groupers and bluehead wrasse are the two most common predator and prey species on these reefs. Coney groupers comprised a large portion of the assemblage of potential bluehead wrasse predators on the study reefs (ranging from 77 to 20 % [mean 49 %] of all potential wrasse predators

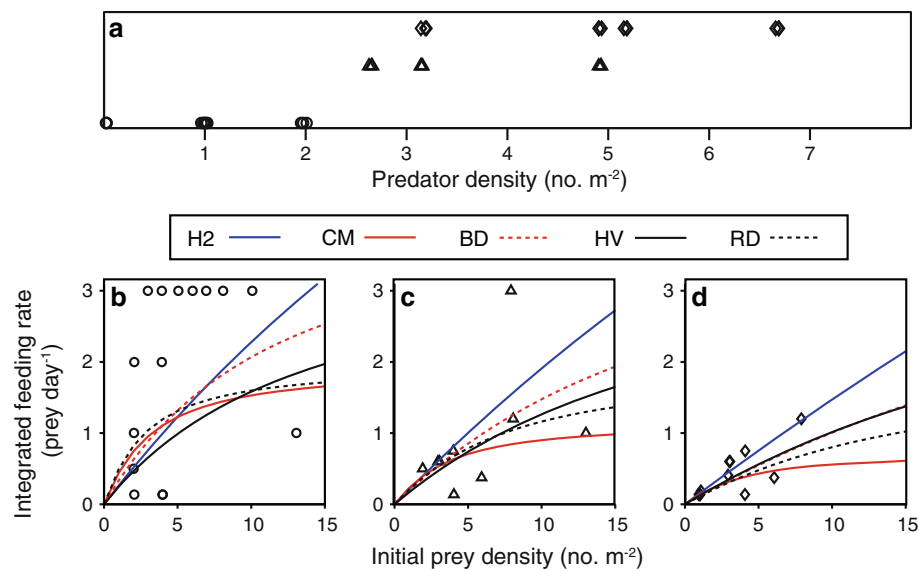


Fig. 1 Coplot of relationship between initial bluehead wrasse (*Thalassoma bifasciatum*) density and integrated feeding rate conditional on the density of coney (*Cephalopholis fulva*). **b–d** show integrated feeding rate based on the predator densities displayed in **a**: low (**b**; circle), medium (**c**; triangle), and high (**d**; diamond). The data ranges in **b–d** overlap, as indicated by **a**: the observations

corresponding to the three lowest and three highest predator densities in **c** also appear in **b** and **d**, respectively. Points in **a** are jittered slightly to show overlapping points, and symbol shapes in **a** correspond to predator densities in **b–d**. Lines in panels **b–d** represent model fits for each of the five candidate models described in Table 1. See legend for colors corresponding to each model

in 2005; White 2007) and were one of the few potential predator species that has been confirmed by gut analysis to feed on post-emergence bluehead wrasse (White and Warner 2007a; J. W. White, pers. obs.). At two sites on the southern shore of St. Croix where coney groupers constituted only ~ 20 % of predators, the transient jack *Caranx ruber* was the more abundant predator. However, re-analyzing our data excluding those two sites did not alter the conclusions of the analysis; therefore, we report the analysis including all sites. Likewise, during settlement pulses, post-emergence bluehead wrasse make up the majority of small prey fish on these reefs, with conservatively twice as many bluehead wrasse settlers than settlers of all other fish species combined (Caselle and Warner 1996; J. W. White, pers. obs.).

We fit each model to our data using the *fmincon* function in the Matlab 7.11 optimization toolbox, assuming a log-normal error structure for the data (as in Skalski and Gilliam 2001) (see ESM for details). We compared the parsimony of each model's fit using the small-sample-size-corrected AIC_c metric (Burnham and Anderson 2002).

Results and discussion

We found that the four predator-dependent functional responses afforded a much more parsimonious fit (combined AIC_c weight > 0.90) to the relationship between bluehead wrasse abundance and mortality than the

predator-independent H2 model (Fig. 1; Table 1). Of the predator-dependent models, AIC_c weights suggested greatest evidence for the Hassell–Varley (HV) model (Table 1), although the four predator-dependent models had similar fits to the data (Fig. 1). Details of the model fits, including confidence bounds on the parameters, are found in Tables S2–S11 (ESM).

A comparison of the fitted models reveals that H2 consistently overpredicted the feeding rate, particularly at higher predator densities, while the predator-dependent models fit the data better across the range of predator densities (Fig. 1). These models thus provide evidence for a negative effect of predator density on the effective predator attack rate, but they do not reveal how this effect emerges. This reduction could be attributed to antagonistic interactions among predators (e.g., exploitative or interference competition for optimal foraging microhabitats on a reef), although we are not aware of evidence for that type of antagonism among reef predators. Rather, there are multiple examples of reef predators hunting cooperatively (Lukoschek and McCormick 2000; Hixon and Carr 1997; Bshary et al. 2006; Stallings 2008; Stallings and Dingeldien 2012). A more likely explanation is that prey alter their behavior to reduce predation risk at higher predator densities (Lima and Dill 1990). Small reef fishes can detect predators via visual and olfactory cues (McCormick and Manassa 2008), and exhibit reduced foraging behavior and spend more time near shelter in areas of higher predator density (Stallings 2008; Madin et al. 2010). Juvenile

bluehead wrasse on St. Croix were observed spending less time in the water column and more time near shelters in high predator sites, but predator density was correlated with zooplankton prey abundance, so that behavioral pattern may be due to satiation rather than fear (White and Warner 2007a). Nonetheless, given the many antipredator behavioral tactics employed by reef fishes (reviewed by White et al. 2010), it is plausible that these may reduce per-predator predation rates at high predator densities.

Ecologists increasingly appreciate the importance of spatial variation in the abundance of reef fish predators, especially with the growing use of marine protected areas (e.g., Russ et al. 2008) and the discovery of relatively pristine, high predator density reefs (Sandin et al. 2008; Madin et al. 2010). Predation rates—and indirect predator effects—are expected to be greater in these high predator locations (alternatively, smaller mesopredators may be less abundant; Stallings 2009). However, the per-predator predation rate may be predator-dependent, as we have shown, and future attempts to model the direct effects of spatial variation in predator density (e.g., White and Samhouri 2011) should account for this. Here, we have provided an initial description of this phenomenon in reef fish and provided the numerical approach for future investigators to apply our technique.

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Predator density and the functional responses of coral reef fish

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Electronic Supplementary Material

Variability in predator densities on St. Croix

Predator densities were surveyed at each of the five study sites 6-7 times between 30 June and 9 September 2005. For the functional response model-fitting we used the predator density estimate from the survey closest in time to each estimate of prey mortality. However, the full suite of survey data illustrates the relative stability in predator densities over time within each site (Table S1). We fit a generalized linear mixed model with Poisson error distribution, log link, and random effects for site and for survey data nested within site (model fit using glmer in the lme4 library [Bates et al. 2013] in R 3.0.1 [R Core Team 2013]). The variance components of this model revealed that temporal variance (date within site; 0.071) was only 6.7% of among-site variance (1.048).

Details of model-fitting procedures

To estimate parameters for the functional response models while accounting for prey depletion, we integrated the change in prey density $dN/dt = -f(N,P)N$ with respect to time to obtain $N(t)$, then divided $N(0) - N(t)$ (the total number of dead prey) by P to obtain the per-predator integrated feeding rates F (Table S2). We then fit F to the observed 1-day loss of bluehead wrasse settlers (assuming all settlers that disappeared were consumed by predators) using function fmincon in Matlab 7.11. We assumed the difference between observed F_{obs} and predicted F followed a log-normal error function, so fmincon minimized the negative log-likelihood \mathcal{L} :

$$\mathcal{L} = - \sum_i \log \left[\frac{1}{\sigma \sqrt{2\pi}} e^{-\frac{[\log(F) - \log(F_{obs})]^2}{2\sigma^2}} \right] \quad (S1)$$

The variance parameter σ was also estimated from the data. We used the sqp (sequential quadratic programming) algorithm in fmincon, and restricted parameter values to biologically sensible ranges (i.e., $a > 0$, $b > 0$, $\sigma > 0$). We estimated confidence intervals for each model parameter by bootstrapping the original dataset 10,000 times and redoing the estimation, producing a multivariate distribution of values from which we calculated a correlation matrix (Tables S3-S7) and univariate confidence intervals (Tables S8-S12). Across all models, the estimates of attack rate a and handling time b were highly correlated (as one would expect given the form of the equation) and all parameters had very long-tailed distributions that had a central tendency near biologically reasonable values.

One difficulty in estimation was that Eq. S1 cannot be evaluated if F_{obs} is equal to zero (no observed deaths) or to (which results when predator density = 0). Rather than exclude those observations, we assumed that both mortality and predator density were observed with some error, so it was unlikely that either value was exactly zero. Therefore for those cases we set F_{obs} to be equal to the minimum non-zero or maximum finite values observed in the dataset. The ordering of results (i.e., which model was most parsimonious) was robust to alternative corrections we applied, such as making the minimum value 10% or 1% of the minimum observed non-zero value, so we are confident that applying this correction did not produce arbitrary conclusions.

Table S1. Summary of predator survey data on St. Croix reefs in 2005.

Site	<i>n</i> (number of surveys)	Mean coney grouper density (number per 150 m ²)	Standard error
BB	7	3.4286	0.3770
CB	7	2.8674	0.3527
NS	7	6.1198	0.3527
JB	6	0.5000	0.4072
WC	7	0.4858	0.3683

Table S2. Time-integrated solution for each functional response model

Model	Formula
H2	$N(t) = e^{\left[\log(N(0)) - \omega(\log(N(0)) + \log(b) + bN(0) - atP) + bN(0) - atP \right]}$
BD	$N(t) = e^{\left[\log(N(0)) - \omega\left(\log(N(0)) + \log(b) + bN(0) - atP + cP \log(N(0)) + \log\left(\frac{b}{cP+1} \right) \right) + bN(0) - atP + \frac{cP \log(N(0))}{cP+1} \right]}$
CM	$N(t) = e^{\left[\log(N(0)) - \omega\left(\log(N(0)) + \log(b) + bN(0) - \frac{atP}{cP+1} \right) + bN(0) - \frac{atP}{cP+1} \right]}$
HV	$N(t) = e^{\left[\omega\left(\log\left(\frac{b}{p^m} \right) + \frac{\log(N(0))P^m + bN(0) - atP}{p^m} \right) + bN(0) - atP \right]}$
RD	$N(t) = e^{\left[\omega\left(\log\left(\frac{b}{p} \right) + \frac{\log(N(0))P + bN(0) - atP}{p} \right) + bN(0) - atP \right]}$

Note: ω denotes the Wright omega function

Table S3. Correlation matrix for H2 model parameters

	<i>a</i>	<i>b</i>	σ
<i>a</i>	1	0.9256	2×10^{-16}
<i>b</i>		1	-2×10^{-14}
σ			1

Table S4. Correlation matrix for BD model parameters

	<i>a</i>	<i>b</i>	<i>c</i>	σ
<i>a</i>	1	0.9904	0.9620	-0.0308
<i>b</i>		1	0.9232	-0.0144
<i>c</i>			1	-0.0367
σ				1

Table S5. Correlation matrix for CM model parameters

	<i>a</i>	<i>b</i>	<i>c</i>	σ
<i>a</i>	1	0.9896	0.1756	-0.0153

b		1	0.1800	-0.0130
c			1	-0.0426
σ				1

Table S6. Correlation matrix for HV model parameters

	a	b	m	σ
a	1	0.8059	0.6678	0.1051
b		1	0.4226	0.1519
m			1	0.2501
σ				1

Table S7. Correlation matrix for RD model parameters

	a	b	σ
a	1	0.9953	-0.0053
b		1	-0.0023
σ			1

Table S8. Confidence intervals (95%) for H2 model parameters

Parameter	lower	median	upper
a	0.1816	0.3391	17.1913
b	1.0×10^{-10}	0.0242	14.7720
σ	1.6871	1.6871	1.6871

Table S9. Confidence intervals (95%) for BD model parameters

Parameter	lower	median	upper
a	0.1908	0.7411	434.1583
b	1.0×10^{-10}	0.1880	197.2059
c	1.0×10^{-10}	0.5587	0.8424
σ	0.5140	0.8424	1.0588

Table S10. Confidence intervals (95%) for CM model parameters

Parameter	lower	median	upper
a	0.1780	1.4853	648.6314
b	1.0×10^{-10}	0.4090	261.8480
c	-0.0921	0.6584	2.7845
σ	0.5166	0.8194	1.0665

Table S11. Confidence intervals (95%) for HV model parameters

Parameter	lower	median	upper
a	0.1654	1.4601	11.9923
b	0.0102	0.9092	8.7194
m	0.1417	0.8899	2.1249
σ	0.5389	0.8258	1.2121

Table S12. Confidence intervals (95%) for RD model parameters

Parameter	lower	median	upper
a	0.4508	1.1501	9.6793
b	0.1858	0.5478	10.5260
σ	0.5318	0.8724	1.1095