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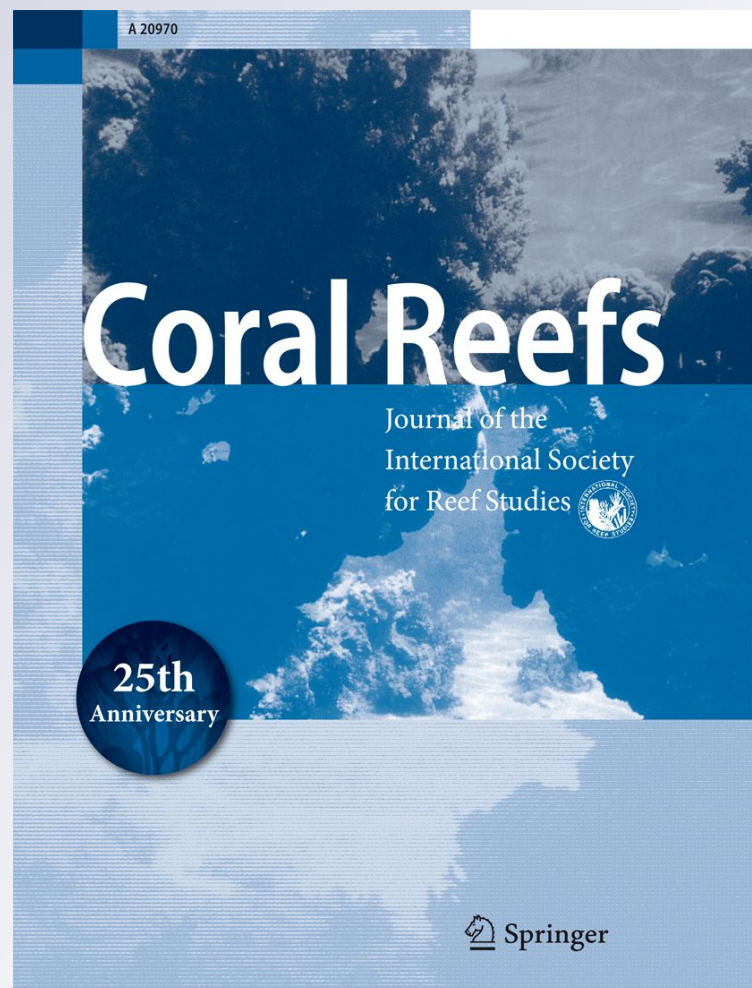
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Seasonal variation in the functional response of a coral-reef piscivore alters the inverse density-dependent mortality of its prey

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Abstract Density-dependent processes are critical for regulating species' populations, and piscivory of coral-reef fishes is frequently density dependent. However, the mechanism driving this density-dependent mortality is poorly understood, but may be caused by changes in a predator's feeding rate at different prey densities (its functional response). An aquarium experiment replicated in winter and summer examined the functional response after 22 and 47 h of *Cephalopholis cruentata* feeding on *Halichoeres pictus*. With the exception of summer data after 47 h (density-independent mortality), mortality was inversely density dependent across all prey densities and increased with higher summer temperatures. The absence of an asymptotic pattern of inverse density-dependent mortality was caused by type II (summer) or dome-shaped type IV (winter) functional responses, with the benefits of schooling likely to cause the low mortality rates at higher prey densities. Predators' functional responses may underlie the inverse density-dependent mortality reported in field studies of aggregating fishes.

Keywords Functional response · Density-dependent mortality · Predator–prey interaction · Coral-reef fishes · Piscivory · Population regulation

Introduction

Density dependence occurs when the per capita growth rate of a species' population is affected by present or past population sizes altering demographic rates and is critical for population regulation (Murdoch and Walde 1989). Juvenile coral-reef fishes experience high mortality rates (Almany and Webster 2006), and field studies have included examples of both direct (Hixon and Carr 1997) and inverse density-dependent mortality (Sandin and Pacala 2005; White and Warner 2007) because of variations in fish behaviour, predator foraging scale, habitat configuration and observational scale (White et al. 2010). However, the mechanisms causing the observed patterns of mortality are poorly understood. Density-dependent predation can be driven by at least four potentially interacting mechanisms (White et al. 2010). Firstly, there may be a numerical response with a long-term increase in predator densities where prey densities are high. Predators at sites with more prey may also exhibit a developmental response of increased growth or survival. Thirdly, density-dependent mortality can occur on shorter timescales by predators aggregating where prey densities are highest. Finally, the proportion of prey eaten by individual predators may vary depending on prey density, which is the focus of this study.

The relationship between prey abundance and the number of prey eaten within a set time period is the predator's 'functional response' (Solomon 1949, Holling 1961). Functional responses typically have one of three

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forms (Types I–III, see Juliano 2001 for descriptions). Defining functional responses are critical because they are an important influence on the stability of predator–prey interactions (Oaten and Murdoch 1975). Therefore, functional responses have been generated for a wide range of predators (Jeschke et al. 2004 review over 800 functional responses) but, to my knowledge, no functional response exists for any coral-reef piscivore.

Functional responses must be defined for individual fish and I used aquaria to expose a single Caribbean piscivore (*Cephalopholis cruentata*; graysby) to different prey densities (*Halichoeres pictus*; rainbow wrasse). Juvenile *H. pictus* are social aggregators (*sensu* White et al. 2010) that are almost invariably seen in schools (see electronic supplemental material, ESM) and appear to gain anti-predator benefits from aggregating irrespective of refuge availability. Experiments with wrasses (White and Warner 2007) and the synthetic framework for density dependence in reef fishes (White et al. 2010) suggest inverse density-dependent mortality of *H. pictus* at the scale of individual schools and a type II predator functional response.

Temperature is a key influence on functional responses in a range of taxa and ecosystems (Englund et al. 2011) and clearly has major effects on the metabolism of fishes (Clarke and Johnston 1999). In order to examine the effects of seasonal variation of both temperature and day length on functional responses of reef piscivores, the experiment was repeated in both winter and summer. Prey collection inevitably led to fish of varying sizes being used in experimental trials, providing an opportunity to assess a secondary question of whether predators fed preferentially on small or large fish within schools. Some larger, faster-growing fish recruits suffer greater mortality rates, although this pattern may be reduced among older juvenile fishes (Holmes and McCormick 2009; Meekan et al. 2010). This size-dependent mortality may be important in maintaining variation in growth among reef fishes (Meekan et al. 2010).

Materials and methods

The study was conducted at the Cape Eleuthera Institute (The Bahamas) in November 2009 and June/July 2011 (subsequently ‘winter’ and ‘summer’). *C. cruentata* individuals (hand-lining) and *H. pictus* individuals (dip nets) were collected continuously throughout the experiments on patch reefs. *C. cruentata* individuals were held unfed for at least 48 h prior to trials to ensure a constant level of starvation. Four experimental tanks (72 cm radius × 86 cm depth) under a natural light regime were used, each containing 750 l of continuously pumped and aerated sea water. Water temperatures were $25.8 \pm 0.4^\circ\text{C}$ ($n = 15$) in

winter and $28.8 \pm 0.3^\circ\text{C}$ ($n = 13$) in the summer, and day lengths were approximately 3 h shorter in the winter (~ 10.5 and ~ 13.7 h, respectively). Experimental tanks contained a shelter constructed from six 40 cm × 15 cm diameter open-ended PVC pipes fixed together to form a pyramid (see “ESM”). *H. pictus* densities from 4 to 30 fish per tank were used in the experiments (13 winter and 12 summer trials), representing naturally occurring densities on coral colonies. Each prey abundance was randomly allocated to a tank and, before introduction into the tank, *H. pictus* individuals were videoed with a scale bar in order to subsequently measure their sizes. A *C. cruentata* individual was then measured and introduced into the tank. Individual prey and predatory fishes were used in only one trial. Predatory fish were introduced at 11:00 h, which was 30–60 min after prey fishes. In the absence of previous data on reef piscivores, functional responses were generated by counting the number of remaining *H. pictus* individuals after both 22 h (09:00 h) and 47 h (10:00 h). Additional censuses were conducted after 6 h (17:00 h) and 30 h (17:00 h). Surviving prey fishes were filmed after 47 h to measure their size.

Data analysis used logistic regression (a generalised linear mixed-effect model with linear, quadratic and cubic terms, binomial error structures and the logit link function) to relate the number of prey fishes at the start of each trial against the proportion of fish eaten (Juliano 2001). The tank used for each trial was included as a random factor to account for any tank effects. Biomasses of *C. cruentata* were also included as an explanatory variable, along with mean prey size in 2011 because it varied significantly among trials (Kruskal–Wallis test $P = 0.033$; winter one-way ANOVA, $P = 0.474$). A maximal model was fitted including all factors, and then the least significant and highest order terms were removed in turn until the model contained only significant terms and further removals led to significant increases in deviance. Model simplification generally led to reductions in the information criterion (AIC_c) was used because of the high number of parameters relative to the sample size; Burnham and Anderson 2002). In one case (summer data after 47 h), the model with the lowest AIC_c had a significantly higher deviance than alternative models (ESM), but because all the terms in the model with the lowest deviance were non-significant, the more parsimonious model with the lowest AIC_c is presented here. Final models were fitted as functional response curves (relating initial prey abundances to the number eaten) by multiplying predicted per capita mortality by the starting number of prey fishes. I derived attack and maximal intake rates by fitting the integrated form of the disc equation to the functional response curve [$Ne = N(1 - e^{-a(hNe-1)})$], where Ne is the hourly rate of prey eaten, N = initial number of prey, a = attack

constant, and h = maximal intake rate (Juliano 2001; Englund et al. 2011). Differences in the size of initial versus surviving prey fishes were tested using a paired t test, with each pair of data points taken from an individual trial and representing the mean size of prey at the start and end of the experiment.

Results and discussion

Per capita mortality ranged from 3.3 to 100%, was higher in summer trials and tended to decrease with increasing prey abundance (Fig. 1a, b). Models for the winter data and summer data after 22 h contained only significant negative linear terms for initial prey abundance and intercept terms (Table 1; Fig. 1a, b; ESM). The model for the summer data after 47 h contained only an intercept term (Table 1; Fig. 1b; ESM). The biomass of *C. cruentata* individuals (15–22 cm in length, 48.9–168.8 g, mean 99.7 g) did not differ between winter and summer trials (t test, $P = 0.40$) and was not included in any model. The models suggested prey mortality was inversely density dependent for the winter data after both time periods, and this pattern was linear across the entire range of initial prey densities. Models for the summer data were inversely density dependent after 22 h and density independent after 47 h.

Inverse density-dependent mortality is typically driven by type II functional responses, and the functional responses in this study display the characteristic hyperbolic

increase in the number of prey eaten with increasing prey abundance (Fig. 1c, d). Although a type II functional response is consistent with the summer data after 22 h, type II functional responses asymptote at high prey densities leading to the inverse density-dependent mortality decreasing asymptotically. In contrast, the winter functional responses for *C. cruentata* were ‘dome-shaped’, and there was evidence that predation rates also decreased at the highest prey densities after 22 h in the summer. The shape of the functional responses were not driven by predator satiation; for example, after 47 h in the winter, *C. cruentata* individuals were capable of eating 12 fish, but only ate five when 30 prey were presented to them. The functional response after 47 h in the summer was type I shaped. Rather than suggesting a switch in functional response, this result more likely reflects that most prey were eaten within the longer time period at all stocking densities. More trials with higher prey abundances would be required to establish the true functional response for *C. cruentata* over 47 h in the summer, and the 22 h data should be considered the best assessment of its functional response during this season.

The temporal pattern of mean per capita mortality of fish eaten during each trial (Fig. 2) demonstrates that the majority (>85%) were eaten during crepuscular and nocturnal periods (17:00–09:00 h). These feeding times are typical of *C. cruentata* (Randall 1967) and indicate at least some natural behaviour within the aquaria. This crepuscular feeding also suggests that temperature, rather than

Fig. 1 Relationship between number of *H. pictus* prey and winter and summer per capita mortality and number of prey eaten by *C. cruentata* after 22 h (a, c) and 47 h (b, d). Per capita mortality regression lines (solid lines for winter data, dashed for summer data) fitted by the transformation of minimal adequate models (a, b) and multiplied by prey density to generate functional response curves (c, d)

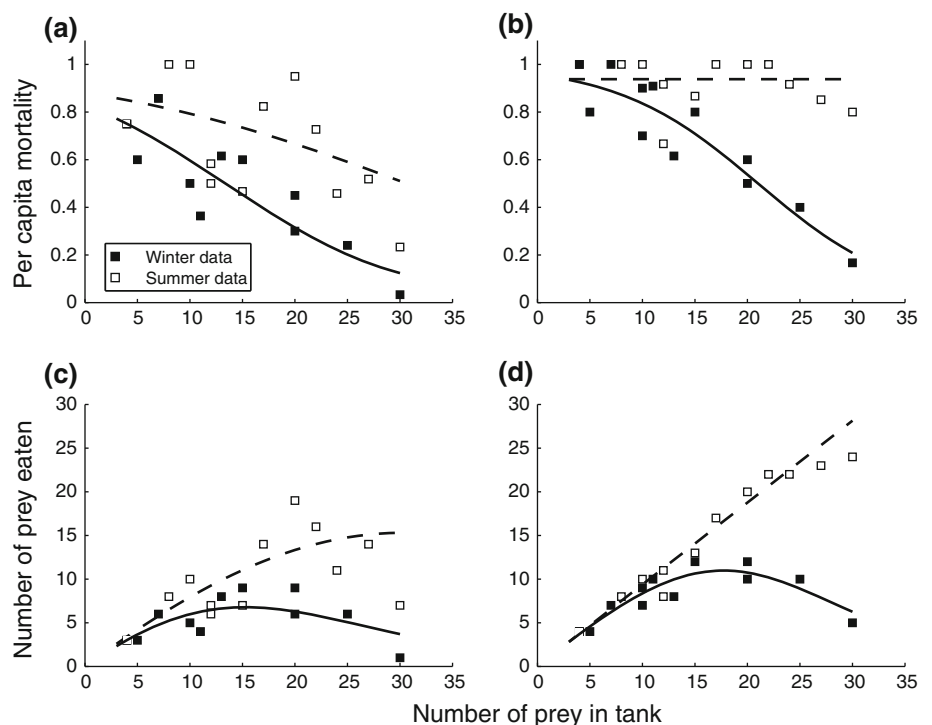


Table 1 Coefficients and significance values for each minimal adequate binomial model relating the number of prey at the start of each trial (N) to the per capita mortality rate

Model term	Winter data		Summer data	
	After 22 h	After 47 h	After 22 h	After 47 h
Intercept	1.574***	3.113***	1.995**	2.717***
N	-0.118***	-0.148***	-0.065*	ns
N^2	ns	ns	ns	ns
N^3	ns	ns	ns	ns
Predator biomass	ns	ns	ns	ns
Mean prey size	-	-	ns	ns

*** $P < 0.001$

** $P < 0.01$

$P < 0.05$

ns = $P > 0.05$

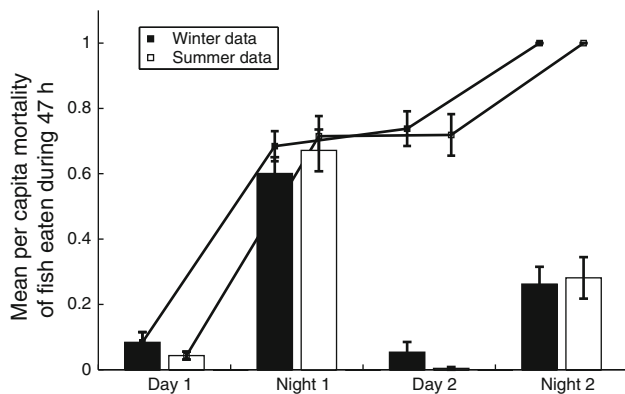


Fig. 2 Temporal and seasonal variation in mean per capita mortality rates (\pm SE) of *H. pictus* prey eaten during the 2 days (09:00–17:00 h) and two crepuscular/night periods (17:00–09:00 h) of the experiment. Individual rates given by columns, cumulative rate given by line

day length, was driving the inter-seasonal differences in *C. cruentata* piscivory. Furthermore, the increased mortality rates in the summer trials may have been driven by temperature-induced higher attack rates, rather than increased maximal intake rates, because a was only significantly different from 0 after 47 h for the summer data ($a = 0.020$, $P < 0.001$; h not significant within any model). However, a full understanding of the effects of changing season on piscivory by *C. cruentata* will require more detailed behavioural and physiological studies.

Dome-shaped curves appear to be unusual for vertebrate predators, but have been described previously as type II dome-shaped (Jeschke et al. 2004) or type IV (Taylor 1981, the term used subsequently here). Type IV functional responses were described during the original work on functional responses (Holling 1961), but have received

little attention (Taylor 1981). This lack of attention is surprising given their occurrence in a range of predator–prey systems (10% of the functional responses reviewed by Jeschke et al. 2004). Previous examples of type IV functional responses have been typified by prey interference with predation, such as aiding predator detection, causing simultaneous prey defences or confusing predators (Jeschke et al. 2004). Such benefits are well established among schooling fishes (Krause and Ruxton 2002), but more detailed experiments are required to conclusively demonstrate that schooling of *H. pictus* underlies the functional response of *C. cruentata* at high prey densities.

While schooling confers the advantage of reduced mortality rates, this benefit was not homogeneous within the school. The size of *H. pictus* individuals in trials was 13–32 mm, and the winter mean size of surviving prey was significantly smaller than prey size at the start of the trials (means of the 11 trials with surviving fish = 16.8 mm versus an initial mean of 18.2 mm; paired t test, $P = 0.047$). This increased survival of smaller fishes has been documented previously among recent settlers (Holmes and McCormick 2009; Meekan et al. 2010), possibly because of predator choice or particular behavioural traits of larger fish. In contrast, there was no change in mean size in the summer trials ($P = 0.930$), perhaps reflecting the generally larger, and therefore older, prey (Mann–Whitney U test, $P < 0.001$).

The functional response of *C. cruentata* provides new insights into the mechanisms underlying the inverse density-dependent mortality in field studies of other aggregating reef fishes (e.g. Sandin and Pacala 2005; White and Warner 2007), because both the type II and type IV functional responses demonstrated here can cause this pattern of prey mortality on reefs. For type IV functional responses, per capita prey mortality will continue to decrease linearly at high prey densities, but decrease asymptotically at high prey densities with more common type II responses. Thus, even if the low mortality rates at high prey densities are an artefact of the experimental trials, and natural functional responses are actually type II, the functional response of *C. cruentata* will still lead to inverse density-dependent mortality. However, functional responses must also be considered along with the behaviour of groups of predators, as an aggregating response of temperate serranids in the field caused density-dependent prey mortality despite a type II functional response of individuals in a laboratory experiment (Anderson 2001).

Inverse density-dependent mortality is often considered destabilising to prey populations (Taylor 1981). However, inverse density-dependent mortality at the scale of individual prey aggregations occurring simultaneously with direct density-dependent mortality at larger spatial scales will only be destabilising under extreme circumstances

(White 2011). Disentangling the range of spatio-temporal effects of piscivory within a multi-predator, multi-prey community represents a challenging research agenda, but one that is critical given the importance of predation in regulating population sizes of ecologically and economically vital fish species. A fuller understanding of the mechanistic basis of any density-dependent mortality of fishes is a critical part of this agenda.

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