Response of predators to prey abundance: separating the effects of prey density and patch size

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Abstract

We tested the relative and combined effects of prey density and patch size on the functional response (number of attacks per unit time and duration of attacks) of a predatory reef fish (*Cheilodactylus nigripes* (Richardson)) to their invertebrate prey. Fish attacked prey at a greater rate and for longer time in large than small patches of prey, but large patches had naturally greater densities of prey. We isolated the effects of patch size and prey density by reducing the density of prey in larger patches to equal that of small patches; thereby controlling for prey density. We found that the intensity at which fish attacked prey (combination of attack rate and duration) was primarily a response to prey density rather than the size of patch they occupied. However, there was evidence that fish spent more time foraging in larger than smaller patches independent of prey density; presumably because of the greater total number of prey available. These experimental observations suggest that fish can distinguish between different notions of prey abundance in ways that enhance their rate of consumption. Although fish may feed in a density dependent manner, a critical issue is whether their rate of consumption outstrips the rate of increase in prey abundance to cause density dependent mortality of prey. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Density dependence; Patch size; Predation; Prey density; Prey number

1. Introduction

In behavioural ecology, almost entire books or substantial sections thereof have been devoted to the behaviour of predators in relation to patch quality and prey abundance (e.g. Krebs and Davies, 1986; Stephens and Krebs, 1986). Their basis can be traced to the early

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idea that prey abundance affects predatory responses (Lotka, 1925; Volterra, 1926) and the later ideas of optimal foraging theory (MacArthur and Pianka, 1966); emphasising the patchiness of prey and patch quality as important predictors of predatory response. Differences in abundance and availability of prey among patches affect a predator's functional response and numerical response. The functional response predicts a predator's consumption rate (number of prey taken per predator) as a function of prey density (Solomon, 1949; Holling, 1959) whereas a numerical response (number of predators attracted to prey) results in the redistribution of predators to patches with higher prey availability (Hassell, 1978). A critical measure, therefore, is the description of abundance of prey among patches.

Three different measures of prey abundance are alternately used, but each represent different spatial characteristics of abundance. Prey abundance is described as the number of individuals per unit area (prey density), or the size of patch that the prey occupy (patch size) or total number of prey within the patch (group size). Studies of predation by fish on marine benthos often focus on only one of these aspects of prey abundance: prey density (e.g. Stewart and Jones, 2001), or patch size (e.g. Whitlatch et al., 1997) group/school size (e.g. Connell, 2000). These different notions are often highly inter correlated in any ecological system (Gaston, 1994). Frequently, the size of a patch has a positive influence on the total number of individuals (group size) (review: Pickett and White, 1985) and larger patches have greater densities of prey (review: Connor et al., 2000).

Importantly, these measures frequently elicit very different effects on species interactions (see review of insect-plant foraging: Kareiva, 1983), hampering the capacity to make precise predictions about population dynamics (Kunin, 1997). In marine systems, the different notions of abundance may be hard to differentiate; particularly for mobile prey (e.g. schooling fish) that continually change in density (distances between individuals) and patch size (volume they occupy). Where possible, however, it may be useful to understand which aspects of prey abundance create the strongest predatory responses in fish. This knowledge may assist in predicting the circumstances in which predatory fish shape assemblages of their prey. There remains considerable uncertainty about the effects of predatory fish (Choat, 1982; Hall et al., 1990; Connell, 2001), despite the idea that their foraging is a key ecological process shaping the abundances of subtidal marine organisms (reviews: Hay, 1991; Hixon, 1991; Wilson et al., 1991; Bax, 1998).

We tested the relative and combined effects of prey density and patch size on the functional response (number of attacks per unit time and duration of attacks) of a predatory reef fish (*Cheilodactylus nigripes* (Richardson)) to their invertebrate prey. Initially, we tested their functional response to small and large patches of invertebrate prey, in which larger patches had naturally greater densities of prey. Then, we isolated the effects of patch size and prey density by reducing the density of prey in larger patches to equal that of small patches; thereby controlling for prey density.

2. Methods

Mensurative and manipulative experiments were done on boulder reefs (5 m in depth) in Abalone Cove, West Island, South Australia ($35°36'$ S, $138°35'$ E; Melville and Connell, 2001). At West Island, the main feeding habitat of *C. nigripes* is characterised

by different sized boulders (0.03–3 m in diameter) that are covered with thick mats of articulated coralline algae (Melville and Connell, 2001). *C. nigripes* prey upon mobile invertebrates using a powerful suctorial force produced by the rapid expansion of the buccal cavity (Cappo, 1995). This striking movement, associated with an audible crack, identifies an attack on prey. These diurnal predators have home ranges of ∼ 100 m^2 (Cappo, 1995) feed solitarily or sometimes as pairs (Connell, personal observation) and attain 400 mm in total length (Kuiter, 2000). These characteristics of *C. nigripes* combined with their slow and docile swimming behaviour and neutral response to divers make them ideal for testing hypotheses about feeding behaviour.

This study proceeded in four steps. First, it was necessary to identify which of the mobile invertebrates within articulated coralline algae were prey for *C. nigripes*. We tested for feeding selectivity by collecting benthic prey at the same time and place individual fish (18–39 cm TL) were sampled. Fifteen fish were shot by hand spear and the anterior third of the alimentary tract was removed and preserved in 20% buffered formalin within 30 min of spearing. Mobile invertebrates within articulated corallines were sampled within a 2-m^2 area from which each fish was sampled ($n = 15$). Articulated corallines and associated invertebrates were collected with four replicate cores (5.3 cm^2; volume, 70 ml) placed ∼ 1 m apart within each locality a fish was speared. Both fish and habitat samples were stored in 10% buffered formalin, sorted through a 500-μm mesh sieve and identified and counted with a magnifying lamp (× 2). Replicate core samples ($n = 4$) were combined into a single sample to enable direct comparison with the single gut sample of each fish (Mantel's permutation test: $n = 15$ comparisons). Mantel's test describes the relation between two multivariate distance matrices (i.e. the composition and abundance of taxa between core and gut samples) with Pearson's correlation coefficient, *r* (Mantel, 1967; Legendre and Fortin, 1989). Significance testing of *r* is achieved by random permutations (999) of the replicate sample units for one of the matrices. The probability is calculated as the number of values equal to, or larger than, the observed value of *r* divided by the total number of permutations (999).

Second, differences in the density of prey between small (< 40 cm^2) and large (> 160 cm^2) patches were tested. Within each patch size (small vs. large) replicate boulders ($n = 10$ boulders/patch size) were sampled with four replicate cores (5.3 cm^2; volume, 70 ml) at each of two sites separated by at least 25 m. Each boulder represented a discrete patch of articulated coralline algae; hence a patch was delineated by a boulder and patch size defined by the size of boulder. Analysis of variance was used to test whether differences in prey density occurred between patch sizes and a description of how these data were treated are provided with the analysis (Table 1).

Third, we tested the hypothesis that *C. nigripes* attack prey at a greater rate and duration in larger than smaller patches. Fish were observed for up to 3 min during which time the attack rate (attacks per minute) and the length of time it fed (attacks up to 3 min) within a patch were quantified. These observations were made on adult fish (>200 mm TL) within each of 10 small and 10 large patches ($n = 10$ fish/patch size) and repeated at each of the two sites. A pilot study established that 3 min was sufficient time to provide optimal for maximizing the precision of estimates of attack rate. The two sites were selected on the basis that the attack rate of *C. nigripes* was unaffected by a neighbouring colony of New Zealand fur seals (*Arctocephalus forsteri*: Lesson 1828 (Connell, in press)). Analysis of

Table 1

ANOVA testing for differences in prey density between small and large patches (Patch size) at two sites (Site)

Source	df	MS	F	P
Patch size (Ps)	1	11885.08	179.30	*
Site	1	1248.86	2.74	NS
Boulder (Ps × Site)	36	456.26	2.66	**
Patch × Site	1	66.30	0.15	NS
Residual	120	171.80		
Total	159			

Data were untransformed and variances were not heterogeneous according to Cochran's C-test.
"Patch size" was treated as fixed and orthogonal to "Site" which was treated as a random factor. "Boulder" was random and nested within "Patch size" and "Site".
Ten boulders (Boulder) were sampled, four replicate cores were collected within each boulder, site and patch size combination.
NS: $P > 0.05$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

variance was used to test whether attack rate and duration differed between patch sizes and a description of how these data were treated are provided with the analysis (Table 2).

Fourth, pursuing these observational data, we experimentally assessed the hypothesis that *C. nigripes* attacked prey at a greater rate and longer duration in larger than smaller patches because prey are more dense in larger patches. We predicted, therefore, that if prey density was reduced in larger patches to match that of small patches, predation intensity would not differ between these patch sizes and be less than untouched (natural) large patches (i.e. predation intensity large = small < untouched large). Alternatively, if predators primarily respond to larger patches or numbers of prey, it was predicted that predators would continue to distinguish between large and small patches of equivalent prey density.

Within one site, boulders required for these three experimental treatments (small, large, untouched large; $n = 7$ replicate boulders/treatment) were identified and then randomly allocated treatments to ensure they were interspersed. Manipulating prey density by removing or adding prey to patches was unlikely to produce treatments of different prey density that would last the duration of the experiment; particularly for mobile inverte-

Table 2

ANOVA testing for differences in (a) rate of attack and (b) duration of attacks between naturally small and large patches (Patch size) at two sites (Site); ($n = 10$ replicate fish)

Source	df	(a) Attack rate			(b) Attack duration		
		MS	F	P	MS	F	P
Patch size	1	192.28	593.46	*	36.12	100.57[a]	***
Site	1	9.45	1.30	NS	0.03	0.07	NS
Patch × Site	1	0.33	0.04	NS	0.47	1.31	NS
Residual	36	7.28			0.36		
Total	39						

[a] Post-hoc pooling of the interaction term with the residual enabled a more powerful test of the main factor "Patch size" ($P > 0.25$: Winer et al., 1991) and the resultant F-ratios are given. "Patch-size" was treated as fixed and orthogonal with the random factor "Site". Data were untransformed and variances were not heterogeneous according to Cochran's C-test.

Table 3
ANOVA testing the effects of reducing prey density in large patches on (a) the rate of attack, (b) duration of attacks and (c) the total number of attacks ($n = 7$ observations)

Source	df	(a) Attack rate			(b) Attack duration			(c) Total attacks		
		MS	F	P	MS	F	P	MS	F	P
Treatment	2	24.74	5.74	**	13.38	27.97	**	958.90	103.09	***
Residual	18	4.31			0.48			9.30		
Total	20									

Data were untransformed and variances were not heterogeneous according to Cochran's *C*-test.

brates (e.g. gammarid amphipods, the primary prey). Prey density was, therefore, reduced by thinning their habitat; articulated coralline algae. This manipulation did not fragment the mats of corallines, but did reduce the overall density of arborescent branches of algae. Articulated corallines were removed from large patches with scissors until sampling revealed that prey density in these patches was similar to naturally small patches, but less than untouched large patches (ANOVA: $F_{2,18} = 14.11$, $P < 0.001$; SNK: large = small < untouched large). This preceding analysis on prey density was done on samples from seven replicate patches of each patch type (i.e. large, small, untouched large) in which four replicate cores (area, 5.3 cm^2; volume, 70 ml) were combined so that analysis was done on a single sample per patch (area, 21.2 cm^2; volume, 280 ml). The attack rate and duration of fish predation on prey within these replicate patches were then observed within 4 days of manipulation using the same protocol described for the mensurative experiment. Analysis of variance was used to test whether attack rate and duration differed among treatments and a description of how these data were treated are provided with the analysis (Table 3).

3. Results

Mantel's permutation test detected a significant correlation in the composition and abundances of prey between gut and habitat samples ($r = 0.522$; $P < 0.001$). These data suggested that *C. nigripes* is a non-selective predator whose diet tends to reflect the relative abundances of prey available (cf. Kingsford, 1992). This analysis indicated that all taxa sampled within articulated coralline algae could be treated as prey. Gammarid amphipods (*Orchestia marmorata*, *Byblis mildura*, *Birubis* sp., *Amphitoe* sp., *Maera masteri*, *Gamarella beringar*, *Ceradocus dooliba*, *Ceradocus sillickensis*) accounted for the most substantial proportion (87%) of prey in the guts of fish.

Prey density was greater in large than small patches (Fig. 1), despite considerable variation from boulder to boulder within each patch size and site (Table 1: SNK tests). Predation intensity (attack rate and duration of attacks) was greater within larger patches at both sites (Fig. 2; Table 2). To enable a stronger test of the effects of patch size on duration of attacks, the interactions term (Patch size × Site: $P > 0.25$) was pooled with the residual (Winer et al., 1991).

The effect of reducing prey density on attack rate was striking. The attack rate in manipulated large patches did not differ from small patches, but attack rate in both these
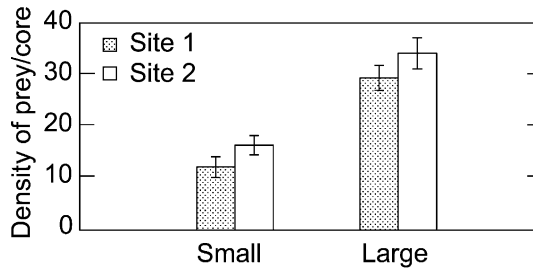
Fig. 1. Graph showing the density of prey per core (area, 5.3 cm^2; volume, 70 ml) between small and large patches. Sampling was replicated among 10 boulders for each patch-size and repeated at two sites; ± S.E: $n = 4$ replicate cores.

patch types were substantially less than in untouched large patches (Fig. 3a; Table 3a, SNK: Large = Small < untouched Large). The reduction of prey density also negatively affected attack duration, but its effect was not as strong as that detected for attack rate (Fig. 3b; Table 3b, SNK: Small < Large < untouched Large). A reduction in prey density caused a reduction in time that predators foraged in manipulated large patches, but they foraged longer in these large patches (that have a greater total number of prey) than small patches of equivalent prey density.

The total number of attacks over a three minute period varied substantially between prey densities, but not patch sizes. Large patches with greater densities of prey (untouched large patches) received five times more attacks than large patches with equivalent densities to small patches (Fig. 3c). While large untouched patches received the greatest number of
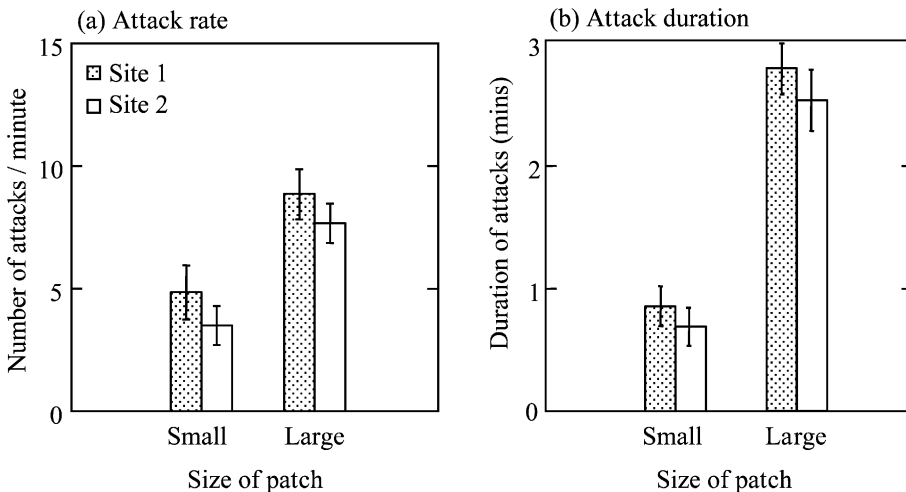

Fig. 2. Graphs showing (a) the rate of attacks per minute and (b) duration of attacks (up to 3 min) between small and large patches at each of two sites; ± S.E: $n = 10$ replicate fish.
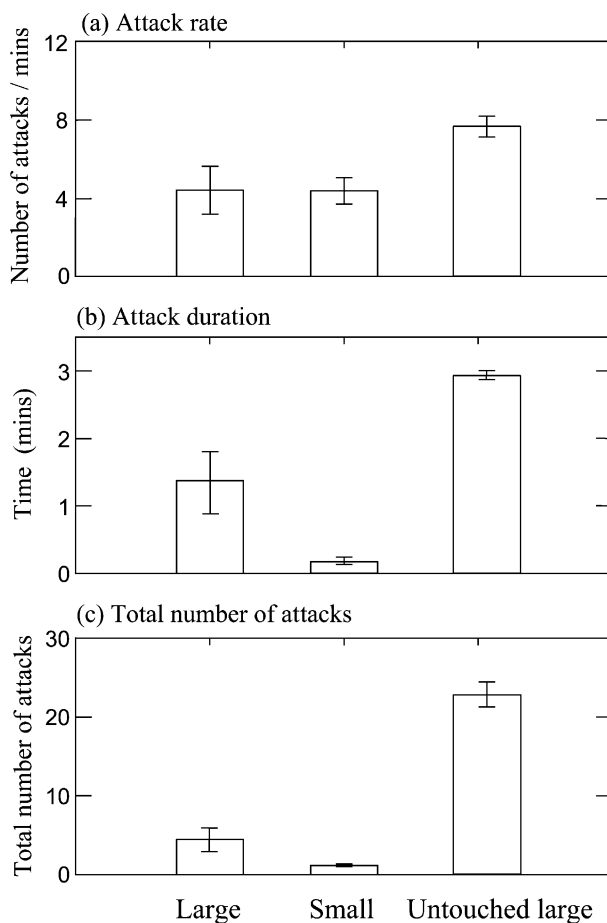
Fig. 3. Graphs showing the effect of reducing prey-density in large patches (Large) to match that of small patches (Small) compared with untouched, large patches (Untouched Large) on (a) the rate of attacks per minute, (b) duration of attacks (up to 3 min) and (c) total number of attacks over 3 min (product of (a) and (b)); $\pm$ S.E: $n=7$ replicate fish.

attacks, small patches received a similar number of attacks as large patches with equivalent densities (Table 3c; SNK Small = Large < untouched Large).

4. Discussion

Our experimental manipulations suggest that it is the density of prey (prey density) within a patch rather than their total number (group size) or size of a patch they occupy (patch size) which most strongly influences the functional response of *C. nigripes*.

Whereas predators fed more intensely (combined attack rate and duration of attacks) in larger patches of prey which naturally contained both greater prey density (number unit

area) and total prey number (number per patch), it was not possible to know which aspect of abundance predators were responding to without controlling for prey density. Various studies demonstrate greater rates and duration of attacks against prey that occur in greater densities (Micheli, 1997; Bosch and Waser, 2001) or in larger patches (Lindstroem, 1989; Cresswell, 1994; Shipley and Spalinger, 1995). Others fail to detect an effect of one aspect of prey abundance on predators (e.g. patch size; Anderson and Connell, 1999), but cannot falsify the tenet that per capita rate of predation increases with prey abundance when other aspects of abundance have not been controlled.

Our experimental reductions of prey density among large patches allowed comparison of small and large patches which differed only in the total number of prey and the size of patch they occupied. A major difficulty of manipulative field experiments which involve clearing or removing organisms is the risk of introducing artifacts through disturbance (Underwood, 1986). The contribution of such artifacts to experimental effects are assessed by procedural controls which reproduces the experimental method of removal but does not affect the abundance of the organisms. In the present study, however, we were unable to establish an adequate control which would disturb the mobile invertebrates (i.e. remove parts of their habitat) without negatively affecting their abundance. We are confident, however, that the reduction in feeding rate and duration of *C. nigripes* is a response to a reduction to prey density, particularly because the feeding activities of such benthic carnivores are well known to be positively (i.e. increase feeding rate and duration) and not negatively related to benthic disturbances (Doherty and Sale, 1985; Hall et al., 1990; Glasby and Kingsford, 1994).

The experiment provided two lines of evidence that the total number of prey (which increases as patch size increases) and patch size had little affect on predatory response. First, predation was substantially greater in patches with greater prey density, largely independent of patch size. Second, predators did not strongly differentiate between large and small patches of equivalent prey density. Despite the primacy of prey density, it was apparent that other factors such the total number of prey (prey number) within a patch caused them to remain longer in larger patches. Despite reducing the density of prey in large patches to match densities in small patches, the greater amount of habitat (and therefore total number of prey) appeared to be more attractive to predators than smaller patches of equivalent prey density. A corner stone of optimal foraging theory (Abrams, 1982) predicts that feeding rates are a response to encounter rate and handling time of prey. Hence, at constant prey density it is likely that a predator's rate of encounter with prey is greater than that in small patches of the same density of prey.

An important finding of this study is that predatory fish can respond quite differently to different aspects of prey abundance. While different measures of abundance are often correlated, they may differ widely in their power to predict the predatory responses of fish and subsequent patterns of prey mortality. This distinction may be worth of consideration when testing, interpreting or reviewing the effects of density dependent (often some form of *abundance* dependent) predation. Currently, most discussion on predatory responses to varying prey abundance and their consequences for "density" dependent mortality use a combination of different and sometimes undefined methods of measuring "density".

Importantly, information on the functional and numerical responses of predators provides a powerful context for evaluating density dependent mortality of prey. The basis

of recent observations of predator-induced, density-dependent mortality in fish (Hixon and Carr, 1997; Connell, 1998) may be traced to the functional and numerical responses of predators to prey abundance (Connell, 2000). Anderson (2001) powerfully demonstrated that both the functional and numerical responses of predatory fish to prey abundance are strongly linked to different patterns of mortality. Strong negative numerical and functional responses to smaller densities, patches and aggregations of prey can offer a refuge from predation (Keough, 1984; Connell, 2000). Alternatively, larger and denser patches of prey can act as refuges despite greater numerical loss to predators (Codella and Raffa, 1995). In spite of strong aggregative (numerical) responses of predators to larger and denser patches of prey, their greater number (group size of prey) can swamp the consumption rate of predators to reduce predation risk relative to smaller and less dense patches of prey (Turchin and Kareiva, 1989).

In conclusion, foraging by fish is thought to be a key ecological process shaping the abundances of subtidal organisms (but see: Connell, 2001). The patterns of abundances formed by fish may, in part, be tied to their functional and numerical responses to varying prey abundance. Our study shows that fish can distinguish between different notions of prey abundance. The intensity at which they attack prey (combination of attack rate and duration) was primarily a response to prey density rather than the size of patch they occupy. However, the time that a fish spends foraging in a patch may depend on the total number of prey available. These experimental observations suggest that fish can feed in a density dependent manner. The critical point is whether their consumption rate outstrips the rate of increase in prey abundance to cause density dependent mortality of prey.

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