

Predators target rare prey in coral reef fish assemblages

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Abstract Predation can result in differing patterns of local prey diversity depending on whether predators are selective and, if so, how they select prey. A recent study comparing the diversity of juvenile fish assemblages among coral reefs with and without predators concluded that decreased prey diversity in the presence of predators was most likely caused by predators actively selecting rare prey species. We used several related laboratory experiments to explore this hypothesis by testing: (1) whether predators prefer particular prey species, (2) whether individual predators consistently select the same prey species, (3) whether predators target rare prey, and (4) whether rare prey are more vulnerable to predation because they differ in appearance/colouration from common prey. Rare prey suffered greater predation than expected and were not more vulnerable to predators because their appearance/colouration differed from common prey. Individual predators did not consistently select the same prey species through time, suggesting that prey selection behaviour was flexible and context dependent rather than fixed. Thus, selection of rare prey was unlikely to be explained by simple preferences for particular prey species. We hypothesize that when faced with multiple prey species predators may initially focus on

rare, conspicuous species to overcome the sensory confusion experienced when attacking aggregated prey, thereby minimizing the time required to capture prey. This hypothesis represents a community-level manifestation of two well-documented and related phenomena, the “confusion effect” and the “oddity effect”, and may be an important, and often overlooked, mechanism by which predators influence local species diversity.

Keywords Confusion effect · Oddity effect · Prey selection · Predation · Species diversity

Introduction

Predation can influence species diversity (Connell 1975; Menge and Sutherland 1976; Hixon 1986; Almany and Webster 2004), and removing predators can alter top-down ecological interactions, thereby affecting diversity at lower trophic levels (Tegner and Dayton 2000; Steneck and Carlton 2001). However, the role predators play in ecological communities depends on whether they are selective in their consumption of prey. If predators are selective, their influence on diversity depends on whether they select dominant or inferior competitors (Paine 1966; Lubchenco and Gaines 1981), or abundant or rare species (Spiller and Schoener 1998; Almany and Webster 2004). Thus, understanding how predation influences species diversity depends on understanding how predators choose from among multiple prey species.

As predation intensity increases via increased feeding rates of individual predators and/or increased predator abundance, local diversity typically exhibits one of three responses: (1) no change, (2) monotonic decrease, or (3) a unimodal relationship (i.e. highest diversity at intermediate

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levels of predation intensity) (Hixon 1986). In the unimodal response, predators focus on competitively dominant (and often numerically dominant) prey species resulting in increasing prey diversity as predation intensity increases from low to intermediate levels (e.g. Connell 1978). However, the extent of predator choice may itself vary depending on the diversity of the system, the degree of variation in prey quality, and the relative costs of consuming different prey species. Most previous studies of prey selection have involved predators and prey from relatively simple, low-diversity systems (review by Hughes 1997). In high-diversity systems with multiple prey species, predators may be less selective because differences in prey quality may be small and/or difficult to assess (Landenberger 1968; Valiela 1995). In such cases, increases in predation pressure may result in no change or a monotonic decrease in prey diversity.

Many predators tend to focus on any acceptable prey species that is abundant (i.e. frequency-dependent selection) (review by Hughes 1997). The most common explanation for this pattern is that predators develop a “search image” (sensu Tinbergen 1960) for abundant species through repeated experience, although there is limited evidence for the existence of search images (Guilford and Dawkins 1987; Hughes and Croy 1993). Whatever the mechanism, frequency-dependent selection typically results in density-dependent prey mortality, and thus the widespread occurrence of density-dependent mortality suggests that predators often focus on abundant prey species (Hixon and Webster 2002). In contrast, when predators attack aggregated prey, per capita mortality often decreases as prey aggregation size increases. The explanation for this pattern, termed the “confusion effect”, is that predators experience greater difficulty singling out individual prey as aggregation size increases (Radakov 1973; Curio 1976; review by Godin 1986; Landeau and Terborgh 1986). For example, Sandin and Pacala (2005) showed that per capita mortality rates in aggregations of a coral reef fish (*Chromis cyanea*) decreased as aggregation size increased. Similarly, per capita mortality from predation by sparrowhawks (*Accipiter nisus*) is inversely related to the size of breeding aggregations of their prey, the great tit (*Parus major*) (Gotmark and Andersson 2005).

Reduction of per capita mortality via the confusion effect should be greatest when group members are identical (Theodorakis 1989). If some individuals differ from the majority (e.g. in size, colour, or behaviour), they are more conspicuous to visually oriented predators and may suffer greater mortality (Mathis and Chivers 2003). Examples include goshawks (*Accipiter gentilis*) singling out uncommon white pigeons in flocks of black pigeons (*Columba livia*) (Pielowski 1959), American kestrels (*Falco sparverius*) preferentially selecting odd-coloured mice (*Mus musculus*) (Mueller 1975), and three-spined stickleback (*Gasterosteus*

aculeatus) targeting odd-coloured water fleas (*Daphnia magna*) (Ohguchi 1981). This phenomenon, called the “oddity effect”, may be one mechanism by which predators counteract the confusion effect. Furthermore, a strategy of initially focusing on rare or odd individuals in a prey aggregation may be predicted from a cost–benefit analysis of foraging; because foraging can be viewed as an attempt to maximize the intake of energy per unit time or, conversely, to minimize the time required to obtain energy (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; review by Perry and Pianka 1997), if predators attacking aggregated prey focus on rare/odd individuals, they may reduce the time required to obtain energy by minimizing the influence of sensory confusion. However, the nature of prey selection and its influence on prey diversity in species-rich systems is largely unknown.

Fishes on tropical coral reefs are the most diverse assemblage of vertebrates on Earth (Hixon 1997). As a result of this high diversity over small spatial scales, generalist predators are faced with a wide range of potential prey species. Most coral reef fishes have a planktonic larval stage that settles to the reef to begin the benthic juvenile/adult stage of the life cycle. Newly settled fishes often occur at high density in mixed-species aggregations (e.g. Almany 2004; Almany and Webster 2004), experience intense pressure from a variety of predators, and typically suffer high mortality rates (Almany and Webster 2006). In a recent study, Almany and Webster (2004) compared patterns of juvenile species richness within 24–48 h of settlement on reefs with and without predators in both Australia and the Bahamas. At both locations reefs with predators had significantly fewer prey species than reefs without predators and, using a null model approach, the authors concluded that this was most likely caused by predators selectively consuming rare species. In this study we explicitly tested the hypothesis that predators target rare prey species and distinguish this from alternative models of prey selection. We began by examining the characteristics of natural aggregations of newly settled fishes to determine both the range and relative abundance of prey species that predators normally encounter and to validate our experimental design. Under experimental conditions, we addressed the following questions: (1) do predators prefer particular prey species, (2) do individual predators consistently select the same prey species, (3) do predators target rare prey, and (4) are rare prey are more vulnerable to predation because they differ in appearance/colouration from common prey?

Materials and methods

This study was conducted at Lizard Island, Australia (14°40'S, 145°28'E) in the northern section of the Great

Barrier Reef during November and December 2004. Reefs around Lizard Island primarily consist of shallow fringing (i.e. continuous) and patch reefs.

Study species

Our model predator was the brown dottedback, *Pseudochromis fuscus* (Pseudochromidae), which is common on shallow reefs throughout the Indo-Pacific, is known to consume newly settled and juvenile fishes in both the laboratory and field (Beukers and Jones 1997; Almany 2004), and acclimates well to aquarium conditions (Beukers and Jones 1997). Prey consisted of four congeneric damselfishes (Pomacentridae): *Pomacentrus amboinensis* (Ambon damsel), *Pomacentrus chrysurus* (whitetail), *Pomacentrus moluccensis* (lemon) and *Pomacentrus nagasakiensis* (Nagasaki damsel). As newly settled juveniles each species is distinctively coloured; at Lizard Island *P. amboinensis* are dusky yellow with a prominent black ocellus on the posterior dorsal fin, *P. chrysurus* are brown with orange on the head and a black ocellus on the posterior dorsal fin, *P. moluccensis* are a uniform bright yellow, and *P. nagasakiensis* are bright blue with a small black ocellus on the posterior dorsal fin. All four species are omnivores (Allen 1991), recruit in substantial numbers at Lizard Island around the new moon during the austral summer (October–January), and are readily collected with light traps (Milicich and Doherty 1994). We conducted experiments with damselfish collected before they settled to the reef for two reasons: (1) evidence from Almany and Webster (2004) indicates that predators selected rare prey species during the 24–48 h following settlement but not after; and (2) before settling to the reef, fish have no prior experience of reef-based predators, and thus results were not confounded by different levels of prior experience among individual prey (e.g. Griffin et al. 2001; Larson and McCormick 2005).

Field observations of relative prey abundance

To determine the natural range and relative abundance of prey that *P. fuscus* encounter, and to both validate the methodology for experiment 2 (see below) and ensure its relevance to natural conditions, we conducted field observations at the end of the November recruitment pulse. Because surveys were conducted while larvae were settling, newly settled fishes could be reliably differentiated from those which had settled in previous months by their small size and incomplete colouration. Within two distinct habitats occupied by *P. fuscus* (continuous reef and patch reef) at the south-western corner of Lizard Island, we surveyed aggregations of newly settled damselfishes that had a minimum of ten individuals, regardless of species, within a

1 × 1-m quadrat. Within each quadrat we recorded the abundance of each species, and 30 quadrats were surveyed in each habitat.

Experimental system

Eighteen identical, flow-through aquaria were constructed. Each aquarium had an internal volume of 57.4 l and the following dimensions: length = 60.0 cm, width = 25.5 cm and height = 37.5 cm. Each aquarium could be divided in half with an opaque partition. Predator shelter consisted of a 14.5-cm length of 10.5-cm-diameter PVC pipe cut in half lengthwise and placed into one half of the aquarium. Prey shelter consisted of a single, artificial (white moulded resin) branching coral (item no. 21505; Wardleys/TFH, Sydney; dimensions: 14 × 11.5 × 5 cm) placed in the other half of the aquarium. Filtered seawater and aeration were supplied to each aquarium via a central manifold. Aquaria were arranged side-by-side on two raised benches and visually isolated from each other and human observers with opaque plastic sheets.

Experiment 1: do predators prefer particular prey species, and do individual predators consistently select the same prey species?

To aid the interpretation of experiment 2 (see below), we tested whether *P. fuscus* had pre-existing, repeatable preferences for any of the four prey species when species were equally abundant. We exposed groups of two or three settlement-stage damselfish to predation in four sets of trials. As the strength of preference may depend on the range of prey available, we tested whether preferences existed given a choice between two, or among three, prey species. In the first and second set of trials, individual *P. fuscus* were given a choice of three species (first set—*P. amboinensis*, *P. moluccensis* and *P. nagasakiensis*; second set—*P. amboinensis*, *P. chrysurus* and *P. nagasakiensis*), with 12 replicates in both sets of trials. In the third and fourth set of trials prey consisted of two species (third set—*P. amboinensis* and *P. moluccensis*; fourth set—*P. amboinensis* and *P. chrysurus*), with ten and 11 replicates, respectively. We were unable to test all possible two- and three-species prey combinations or further replicate each set of trials due to limitations of larval supply and constraints on time, laboratory space and aquarium availability.

To determine whether selection of particular prey species is “hard-wired” or, alternatively, more flexible, we tested whether individual predators consistently chose prey species in the same order among sequential presentations of the same combination of prey species. We exposed three-species prey combinations (as in the first and second set of trials above) to the same predator 4 times, with 24 h

between repeated sequences, and tested ten predators on the first prey combination and 11 predators on the second. We exposed two-species prey combinations (as in the third and fourth set of trials) to the same predator twice, again with 24 h separating repeated sequences, and tested ten predators on the third prey combination and 11 predators on the fourth. We were unable to expose two-species prey combinations to the same predator 4 times due to limitations in larval supply and time constraints.

The experimental protocol for all trials was identical. Predators were collected from reefs using hand nets and clove oil as an anaesthetic (Munday and Wilson 1997), measured (standard length; SL), transferred to experimental aquaria, and acclimated for 48 h without food. Settlement-stage damselfish were collected with two light traps (see Stobutzki and Bellwood 1997 for design) deployed 0.5 km offshore of the research station. Traps were emptied the following morning, contents were sorted by species, each species was transferred to a holding tank for 24 h and fed ad libitum twice with newly hatched brine shrimp (*Artemia* sp.), and a random sample of 30 individuals of each prey species was measured (SL). To conduct a set of trials, aquaria were divided in half with an opaque partition. Prey were placed in the predator-free half of each aquarium and acclimated for 30 min. Partitions were removed and prey abundance was continuously monitored for the first 15 min, and thereafter at 15-min intervals until each trial was terminated when a single prey remained. Average (SE) SL of the four prey species used in this experiment was: *P. amboinensis* = 13.28 (0.07) mm, *P. chrysurus* = 13.31 (0.08) mm, *P. moluccensis* = 11.97 (0.05) mm, and *P. nagasakiensis* = 14.43 (0.09) mm. Average (SE) SL of predators was 57.77 (0.67) mm.

Results were analysed in two ways. First, we tested whether *P. fuscus* preferred particular species by scoring each trial based on the identity of the first species consumed. In trials with three prey species the outcome was a multinomial response with three equally probable outcomes (i.e. each species could be eaten first) assuming random predation. A likelihood ratio of this null model versus the observed result was calculated and statistical significance evaluated by testing $-2\log_e(\text{likelihood})$ against the χ^2 distribution with 1 *df* (Hilborn and Mangel 1997). An identical approach was used to analyse trials involving two prey species, except here we used a binomial outcome for each trial. Second, we tested whether individual predators exhibited the same preference for the first species consumed over four sequential trials of the same three-species prey combination. Our measure of selection was the number of species consumed first across the four sequential trials. We derived the null proportions using a randomization approach in which the experiment was simulated 100,000 times. The differences between the observed and expected proportions

were evaluated using the $-2\log_e(\text{likelihood})$ approach as described above. We did not conduct a formal analysis of the two sequences of the two-prey species combinations, but simply report the quantitative outcome of these trials.

Experiment 2: do predators select rare prey?

To test whether predators selectively target rare prey, we conducted trials in which groups of 11 settlement-stage damselfish (ten of one species and a single individual of a second species) were exposed to predation from a single predator. A total of 72 trials were completed, 36 in November and 36 in December. In November trials prey consisted of three species: *P. amboinensis*, *P. moluccensis* and *P. nagasakiensis*, whereas in December trials prey consisted of *P. amboinensis*, *P. chrysurus* and *P. nagasakiensis*. Prey species differed among months because we were limited to those species that were sufficiently abundant in light traps. We factorially manipulated species and status (common or rare) among trials during each month such that there were six replicates of each species-status combination. A random sample of 30 individuals of each prey species was measured (SL) from both November and December trials. In November trials average (SE) SLs of predators and prey were: *P. fuscus* = 56.11 (0.80) mm, *P. amboinensis* = 12.55 (0.11) mm, *P. moluccensis* = 11.10 (0.06) mm, and *P. nagasakiensis* = 14.28 (0.08) mm. In December trials average size of predators and prey were: *P. fuscus* = 55.20 (0.98) mm, *P. amboinensis* = 13.28 (0.07) mm, *P. chrysurus* = 13.31 (0.08) mm, and *P. nagasakiensis* = 14.43 (0.09) mm.

Experimental protocol was as in experiment 1, except that trials were terminated when either: (1) the rare prey was consumed, or (2) six individuals of the common species were consumed. We used the rank of consumption of the rare individual as our response variable. In trials that ended with six common individuals consumed, we assumed the rare individual would have been consumed next and assigned the trial a rank of 7. Although this procedure was liberal in measuring a positive preference for the rare individual, it had no influence on our conclusions. However, it did prevent us from detecting whether predators avoided rare prey.

To provide a statistical test for the response we constructed a null distribution of the experiment using a Monte Carlo simulation in which predators fed randomly (Fishman 1996). The simulation was repeated 1,000 times to generate a null distribution of median ranks. The observed median rank of consumption of the rare individual for each group of six replicates was compared to null distribution quantiles to evaluate statistical significance. We used the median rank of consumption rather than the mean due to slight skew in the distribution of ranks.

Experiment 3: are rare prey more vulnerable to predation because their appearance/colouration differs from common prey?

To control for differences in behaviour and size among prey species, we tested whether predators targeted rare prey based on differences in appearance by exposing a group of 11 individuals of a single species to predation after altering the appearance of one individual. Settlement-stage damselfish were collected with light traps and approximately 300 *P. amboinensis* were transferred to a large flow-through aquarium and held for 4 days, during which they were fed ad libitum twice per day with newly hatched brine shrimp. We altered the appearance of one randomly selected individual in each group of 11 with a subcutaneous injection of black elastomer (Northwest Marine Technology, USA) using a 29 G hypodermic needle (Buckley et al. 1994; Frederick 1997). Elastomer marks had approximate dimensions of 2.5 × 0.5 mm, were placed in the dorsal musculature below the dorsal fin, and were equally visible from both sides of the individual. We used black elastomer rather than other colours in this experiment because it strongly contrasted with the yellow colouration of *P. amboinensis*. To minimize confounding effects of handling and elastomer injections: (1) the ten unmarked individuals in each group were handled identically, including subcutaneous needle insertion; and (2) order of procedure (actual marking vs. pseudo-marking) in each group was random. Experimental protocol was as in experiment 2 and 25 replicates were completed. Analysis was as in experiment 2 except that the Monte Carlo simulation consisted of a group of 25 trials. Average (SE) SL of the 25 *P. fuscus* used in these trials was 55.69 (0.97) mm.

Results

Field observations of relative prey abundance

In the 30 patch reef quadrats we observed a total of 590 new settlers from 13 species of damselfish (Fig. 1a). On average (SE), there were 19.9 (1.8) fish and 3.5 (0.2) species per quadrat. Three species—*P. amboinensis*, *P. moluccensis* and *P. nagasakiensis*—accounted for >83% of all individuals and each species occurred in ≥21 quadrats. The remaining ten species were relatively rare, occurring in eight or less quadrats. The identity of the most common and least common species in each quadrat differed among quadrats (Fig. 1b). For example, *P. amboinensis* was most common in 15 quadrats but least common in six quadrats. Similarly, both *P. moluccensis* and *P. nagasakiensis* were most common in some quadrats and least common in others. The average (SE) ratio of the

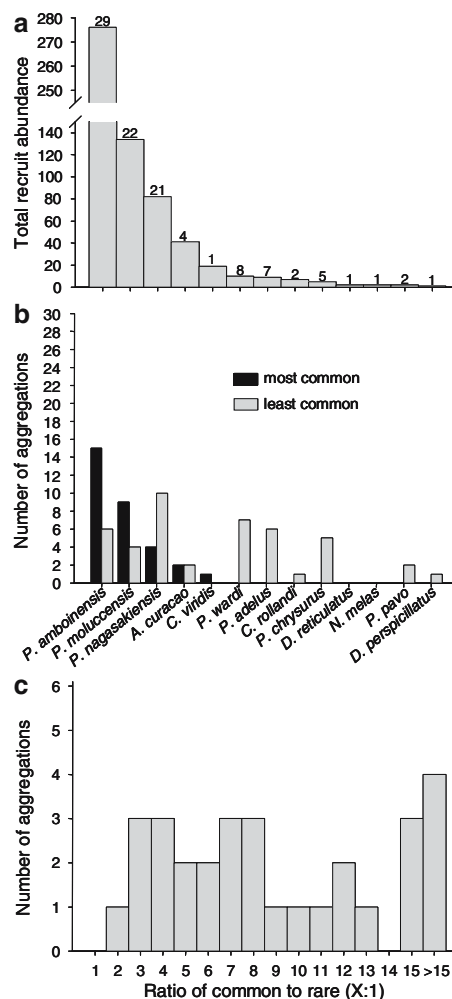


Fig. 1a–c Characteristics of 30 natural aggregations of newly settled damselfishes in patch reef habitat. **a** Distribution of the 590 new settlers among the 13 species observed pooled across all 30 aggregations. The number above each bar indicates the number of aggregations in which that species was present. **b** Number of aggregations in which each of the 13 species was most and least common. Note that more than one species could be most or least common in an aggregation. **c** Distribution of the ratio between the abundance of most common and least common species in the 30 aggregations

most common species to the least common species in the 30 quadrats was 9:1 (1.0) and ranged from 2:1 to 24:1 (Fig. 1c).

In the 30 continuous reef quadrats there were a total of 421 new settlers from 16 damselfish species (Fig. 2a). On average (SE), there were 14.1 (0.7) fish and 3.7 (0.2) species per quadrat. *P. moluccensis* was the most abundant and most common species, accounting for >63% of all individuals and occurring in all 30 quadrats. In addition, *P. moluccensis* was the most common species in 29 quadrats (Fig. 2b). The average (SE) ratio of the most common to least common species in the 30 quadrats was 9:1 (0.6) and ranged from 2:1 to 14:1 (Fig. 2c).

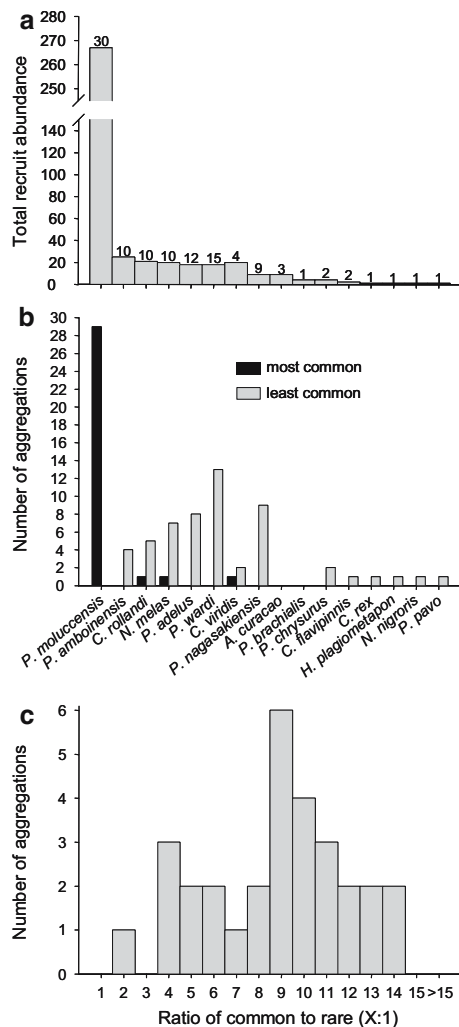


Fig. 2a–c Characteristics of 30 natural aggregations of newly settled damselfishes in continuous reef habitat. **a** Distribution of the 421 new settlers among the 16 species observed pooled across all 30 aggregations. The number above each bar indicates the number of aggregations in which that species was present. **b** Number of aggregations in which each of the 16 species was most and least common. Note that more than one species could be most or least common in an aggregation. **c** Distribution of the ratio between the abundance of most common and least common species in the 30 aggregations

Experiment 1: do predators prefer particular prey species, and do individual predators consistently select the same prey species?

In trials with three equally abundant prey species we found no evidence for predator preferences. In the first set of 12 trials *P. amboinensis* was taken first in five trials, *P. moluccensis* was taken first in five trials and *P. nagasakiensis* was taken first in two trials [likelihood ratio = 0.430, $-2\log_e(\text{likelihood}) = 1.690$, $P = 0.194$]. In the second set of 12 trials *P. amboinensis* was taken first in five trials, *P. chrysurus* was taken first in five trials and *P. nagasakiensis* was taken first in two trials [likelihood ratio = 0.430,

$-2\log_e(\text{likelihood}) = 1.690$, $P = 0.194$]. In contrast, predators exhibited strong preferences in trials with two prey species. In the third set of ten trials involving *P. amboinensis* and *P. moluccensis*, *P. amboinensis* was consumed first in eight trials [likelihood ratio = 0.146, $-2\log_e(\text{likelihood}) = 3.855$, $P = 0.050$], and in the fourth set of 11 trials involving *P. amboinensis* and *P. chrysurus*, *P. amboinensis* was consumed first in nine trials [likelihood ratio = 0.090, $-2\log_e(\text{likelihood}) = 4.818$, $P = 0.028$].

Over four sequential presentations of the same three-species prey combination there was no evidence that individual predators consistently chose the same prey species. From our null model assuming random predation, the expected proportion of trials (trial = a sequence of four repeated presentations) resulting in one, two and three prey species being consumed first was 0.04, 0.53 and 0.44, respectively. In the ten trials where *P. amboinensis*, *P. moluccensis* and *P. nagasakiensis* were prey, observed proportions were 0.00, 0.40 and 0.60 [likelihood ratio = 0.444, $-2\log_e(\text{likelihood}) = 1.623$, $P = 0.203$]. Similarly, in the 11 trials where *P. amboinensis*, *P. chrysurus* and *P. nagasakiensis* were prey, observed proportions were 0.18, 0.45 and 0.36 [likelihood ratio = 0.203, $-2\log_e(\text{likelihood}) = 3.186$, $P = 0.074$]. Over two sequential presentations of the same two-species prey combination, there was again little evidence that individual predators consistently chose the same prey species: in ten trials with *P. amboinensis* and *P. moluccensis* as prey, predators made consistent choices between repeated sequences in four trials whereas in six trials they did not, and in the 11 trials with *P. amboinensis* and *P. chrysurus* as prey, predators made consistent choices in six trials but choices differed in the other five trials.

Experiment 2: do predators select rare prey?

Across all 72 trials, predators selected rare prey more often than expected from random predation (median rank of null distribution = 6.0; median rank of consumption of rare prey = 3.0, $P = 0.05$). The rare individual was one of the first three prey consumed in 37 trials, and 27 trials ended after six common individuals had been consumed. Rare prey was targeted in some species-status combinations, but not others (Table 1). There was no evidence that predators selected prey with regard to average prey size—predators did not consistently choose either the smallest or largest species (Table 1).

Experiment 3: are rare prey more vulnerable to predation because their appearance/colouration differs from common prey?

There was no evidence that predators targeted marked individuals more often than expected from random predation across the 25 trials (median rank of consumption of marked

Table 1 Results from experiment 2 testing whether numerically rare prey are disproportionately targeted by predators. Prey in each trial consisted of 11 newly settled damselfish, ten of one species (*common*) and one individual of a second species (*rare*). A *Pomacentrus amboinensis*, C *Pomacentrus chrysurus*, M *Pomacentrus moluccensis*, N *Pomacentrus nagasakiensis*

Month	Common species ^a	Rare species ^a	Trials	Median observed rank of rare ^b	P-value
November	N ^c	A	6	2.0	0.01*
November	M	A ^c	6	2.0	0.01*
November	A ^c	M	6	4.5	0.10–0.25
November	N ^c	M	6	1.5	<0.01*
November	A	N ^c	6	7.0	0.75
November	M	N ^c	6	5.5	0.25–0.50
December	C	A	6	7.0	0.75
December	N ^c	A	6	4.0	0.10–0.25
December	A	C	6	2.0	0.01*
December	N ^c	C	6	2.5	0.01–0.05*
December	A	N ^c	6	5.5	0.25–0.50
December	C	N ^c	6	7.0	0.75

* $P \leq 0.05$

^a Ratio of common species to rare species in each trial was 10:1

^b The median rank of consumption of the rare prey in this group of trials. See [Materials and methods](#) for a complete description

^c The larger of the two species in the species pair. In December, the average size of *P. amboinensis* and *P. chrysurus* was similar (see [Materials and methods](#))

individual = 6.0, $P = 0.50$). The marked individual was among the first three individuals consumed in six trials whereas nine trials were terminated after six unmarked individuals had been consumed.

Discussion

Predation is one of the key processes influencing the structure of ecological communities. In many communities species-abundance relationships follow the general pattern of a few highly abundant species and many species that are relatively rare (Morin 1999). The influence of predators on local diversity depends, in large part, on the manner in which they select prey species (Hixon 1986). When predators select common species they may have no effect on diversity or, if common species are also competitively dominant, a positive effect on diversity through the mitigation of competitive exclusion (e.g. Paine 1966). If predators select prey randomly, a few rare species may be eliminated from the community due to chance alone, the likelihood of which increases as predation intensity increases (Hixon 1986). Less well understood or documented are cases in which predators selectively target rare prey species, which

results in a rapid decline in local diversity (Almany and Webster 2004).

The mechanisms influencing prey selection are likely to be particularly important in species-rich systems. Previous studies have highlighted obvious differences among prey species (e.g. size, shape, etc.) as important factors influencing predator choice (Hughes 1997; Sogard 1997). However, in high-diversity systems such as coral reefs, differences among many related prey species, such as damselfishes, may be minimal and/or difficult for predators to detect (Valiela 1995). We therefore hypothesized that if generalist predators from high-diversity systems are selective, the criteria used when making choices are likely to be more subtle, such as the relative abundance of prey species in an aggregation.

We first tested whether predators exhibited a preference for particular prey species when species were equally abundant. In experiment 1 we found no evidence for a preference when predators chose from among three species, but in trials with two prey species there was strong evidence that predators preferred *P. amboinensis* over both *P. chrysurus* and *P. moluccensis*. However, there was no evidence that individual predators consistently chose the same prey species in sequential presentations of the same prey combination, both in three-species and two-species trials. This suggests that prey selection is not hard-wired or based on strong preferences for particular species, but is rather more flexible and likely to depend on other factors.

Based on the results of experiment 1, and on the many previous studies demonstrating frequency-dependent prey selection, we expected to find that when faced with a group of 11 prey—ten individuals of one species and a single individual of a second species—predators would focus on the most abundant species. However, in experiment 2 we found that rare prey were selected by predators more often than expected. Comparing the results of two-prey-species trials of experiment 1 with experiment 2 trials involving the same two prey species suggests that rarity can override preferences expressed when prey are equally abundant. For example, when faced with two prey in experiment 1, one *P. amboinensis* and one *P. chrysurus*, predators strongly preferred *P. amboinensis*. In contrast, when choosing from a group of ten *P. amboinensis* and a single *P. chrysurus* in experiment 2, predators targeted rare *P. chrysurus*.

Taken together, our results suggest that rare prey are at greater risk of predation in some mixed-species prey assemblages on coral reefs, which could lead to the rapid exclusion of many rare species from the community. Although not explicitly tested in this study, we hypothesize that the most likely mechanism underlying the selection of rare prey emerges from linking the confusion effect and oddity effect. Multi-species aggregations of newly settled

juvenile fishes are common on coral reefs. When predators attack these aggregations, they may focus on rare species (oddity effect) as a means of overcoming the sensory confusion they experience when faced with multiple moving targets (confusion effect). Almany and Webster (2004) documented patterns consistent with this hypothesis on coral reefs in Australia and the Bahamas, and similar patterns have been observed in other systems. For example, Schoener and Spiller (1996) and Spiller and Schoener (1998) found that lizard predators excluded rare spider species at two spatial scales—among islands and among plots within a single island. Parmenter and MacMahon (1988) showed that rodent predators excluded several rare beetle species, as did Joern (1986) examining the impact of avian predators on grasshoppers. However, the present study is the first to demonstrate that such patterns may arise because predators actively target rare prey, and that the property of rarity itself can lead to greater predation risk.

Previous research has identified a number of factors that influence how predators select individuals from a prey aggregation, and these studies also provide insights into the relationship between the confusion and oddity effects. For example, Allen and Anderson (1984) demonstrated that prey density influences whether predators select common or rare prey from an aggregation. Using immobile pastry baits of two different colours but of uniform size and shape, they presented birds with low-density (2 m^{-2}) and high-density ($10,577\text{ m}^{-2}$) aggregations in which the two colours occurred in a 9:1 ratio. Birds selected common-coloured baits from low-density aggregations but rare-coloured baits from high-density aggregations where the confusion and oddity effects were likely more pronounced. In addition to density, the movement rate of individuals in a prey aggregation also appears to influence the strength of selection for rare prey. Wilson et al. (1990) dyed maggots either yellow or red and presented them to birds on a metal table in a dense aggregation where the two colours occurred in a 9:1 ratio. Movement rates of maggots were controlled by changing the temperature of the table, and the strength of selection for rare, odd-coloured maggots increased as prey movement rate increased. Apart from the effects of prey density and movement rates, the selection of odd prey from an aggregation is also related to differences in size and colouration/appearance between common and rare prey (e.g. Ohguchi 1981; Theodorakis 1989). However, these studies involved prey of a single type or species where behaviour was presumably similar among group members.

In the present study we found no evidence that predators selected rare prey based on size or appearance/colouration. In experiment 2 predators did not consistently select either the smallest or largest prey species. In experiment 3 we controlled for differences in behaviour between common and rare prey by using one prey species, and predators did

not select a single oddly coloured fish from a group of 11 individuals. Furthermore, closer examination of experiment 2 results suggests that differences in colouration among species in the visible spectrum were of little importance; bright blue *P. nagasakiensis* were never selected when rare, even when one of the two highly contrasting yellow species (*P. amboinensis* and *P. moluccensis*) were common, and predators selected rare *P. amboinensis* when the similarly coloured *P. moluccensis* was common. The lack of evidence for appearance/colouration or size as explanatory factors lead us to hypothesize that rare prey appeared odd to predators because their behaviour differed from the majority.

In the few studies testing how predators select from multiple prey species, differences in behaviour among species have been identified as a key factor influencing predator choice (Freed 1980; Peckarsky and Penton 1989; Einfalt and Wahl 1997). In the present study, evidence in support of this hypothesis comes from qualitative observations of prey behaviour in experiment 2. During the period of prey acclimation (i.e. before removing the opaque partition separating predator and prey), the ten common and single rare species typically aggregated together around the artificial coral. Aggressive interactions between the two species were uncommon, and the rare species occupied a variety of positions within the aggregation (e.g. centre, middle and edge). After removing the partition, the predator would often slowly approach the prey aggregation and then quickly accelerate without attempting a strike. The typical result of this action was the break up of the aggregation into smaller groups, often with many of the common individuals moving away in one direction and either the single rare individual by itself or with a few of the common species moving away in a different direction. The predator invariably shifted its focus to, and often struck at, the single rare species or the smaller group containing the rare species. Thus, differences in the behavioural responses of common and rare species to the threat of predation appear to have directly contributed to the higher mortality of rare individuals.

How can our results be reconciled with the numerous observations of predators selecting highly abundant prey (Hughes 1997)? One possible explanation is that some predators initially select rare prey, and once many of these rare individuals are eliminated, they switch to more abundant species. Consistent with this suggestion are patterns from Almany and Webster (2004) in which predators appeared to target rare species during the first 24–48 h following prey settlement, but not after. Thus, the selection of rare prey may occur over a relatively narrow time frame, and detecting such effects may require frequent sampling. It is also important to note that in the present study we observed a range of prey selection behaviour among individual

predators—some predators targeted rare prey while others focused on common prey. However, because rare species are, by definition, uncommon, a single predator in a community targeting rare prey can have substantial consequences for local diversity (Sherratt and MacDougall 1995).

If rare species are often at greater risk of predation, how do they persist in local communities? It is first important to differentiate between species that are globally rare (i.e. everywhere and always), and those that are temporally or spatially rare (e.g. the prey species in this study)—mechanisms of persistence likely differ between these two types of rarity. For example, among coral reef fishes that are globally rare there are many examples of mimicry in which rare species resemble common or unpalatable/harmful species (Moland et al. 2005). A close resemblance to, and association with, a common species may allow rare mimics to “hide” among their models and thereby avoid appearing conspicuous to predators. For species that are temporally or spatially rare, our experiments suggest that the composition of the prey aggregation has an important influence on their predation risk. In some species-status combinations in experiment 2 rare prey were at greater risk of predation, while in other combinations rare prey were “safe”. For example, rare *P. moluccensis* were targeted by predators when *P. nagasakiensis* was common but not when *P. amboinensis* was common. Thus, one would predict that in natural aggregations where *P. amboinensis* was common, rare *P. moluccensis* could persist. This prediction is supported by our field observations; in three of the four aggregations where *P. moluccensis* was rare, *P. amboinensis* was common. Apart from the identity of common and rare prey, the relative abundance of species in the aggregation may also be important. Peuhkuri (1998) tested whether the foraging rates of large fish were influenced by the relative abundance of small and large fish in single-species prey aggregations. In aggregations where the ratio between small and large fish was 5:1, large fish reduced their foraging relative to large fish in 2:1 aggregations, presumably because large fish in 5:1 aggregations were at greater risk of being conspicuous to predators. Similarly, Wolf (1985) found that rare fish species abandoned mixed-species aggregations when threatened by predators, and that they did so sooner as the ratio between common and rare species increased. These examples suggest that the conspicuousness of rare species and their vulnerability to predation may scale with the ratio between common and rare species in mixed-species prey aggregations. Further evidence for this conclusion comes from a comparison of experiment 2 trials and field surveys. In experiment 2 we used a ratio of 10:1 for common and rare prey, and rare *P. amboinensis* were targeted when *P. moluccensis* was common.

In four of six field surveys where *P. amboinensis* was rare *P. moluccensis* was common, suggesting that rare *P. amboinensis* was at risk. However, the ratio between *P. moluccensis* and *P. amboinensis* in these four aggregations was $\leq 4:1$, and in the remaining two aggregations *P. amboinensis* was rare and *P. nagasakiensis* was common; a species-status combination in which rare *P. amboinensis* was not targeted in our experiments. Whether these natural patterns represent active selection of specific aggregations by rare prey or simply document the aftermath of selective predation is unknown. However, our results suggest that both the species composition and relative abundance of species in prey aggregations may have important consequences for the local persistence of rare species.

Conclusion

Understanding the role of predation in marine systems is an urgent goal given the intense, ongoing human exploitation of predators (Pauly et al. 1998; Myers and Worm 2003). Superficially, our results suggest that removing predators will enhance local diversity on coral reefs. However, it is important to note that the predator in this study and the predators manipulated by Almany and Webster (2004) are small, generalist predators that are sometimes the prey of larger, higher trophic-level predators (e.g. St John 1999). These higher-level predators constitute the primary targets of fisheries, and removing them could release small generalist predators from predation (or competition), and thus indirectly intensify the effects of small predators on local species diversity. Whether the removal of larger predators affects the ecology of small predators is uncertain but certainly warrants further study.

Evidence from this study suggests that prey species that are numerically rare may be at greater risk of predation and exclusion from local communities by generalist predators. We hypothesize that this phenomenon arises because: (1) rare species in a multi-species aggregation are more conspicuous to predators, perhaps due to their behaviour; and (2) predators target rare prey to overcome sensory confusion. Further investigations are necessary to explicitly test this hypothesis and to understand how the characteristics of prey aggregations influence prey selection by predators and local prey diversity.

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