Joanne S. Beukers · Geoffrey P. Jones

Habitat complexity modifies the impact of piscivores on a coral reef fish population

Abstract Patterns in juvenile mortality rates can have a profound affect on the distribution and abundance of adult individuals, and may be the result of a number of interacting factors. Field observations at Lizard Island (Great Barrier Reef, Australia) showed that for a coral reef damselfish, *Pomacentrus moluccensis*, juvenile mortality (over 1 year) varied between 20 and almost 100% among sites. Correlative data showed that juvenile mortality increased as a function of initial densities (recruitment), predator densities and the availability of preferred coral substrata. A multiple regression showed that these three variables together did not explain significantly more variation in mortality than the single factor showing the strongest relationship. This appeared to be because recruitment, predator densities and preferred coral substrata were all highly correlated, suggesting that one, two or all of these factors may be influencing juvenile mortality rates. One hypothesis was that density-dependent mortality in juveniles was the result of an interaction between predators (which appear to aggregate at high-recruitment sites) and the availability of preferred substrata (predator refuges). We tested this hypothesis by using both laboratory and field experiments to see whether fish predation could significantly alter survivorship of this damselfish, and whether this impact was dependent upon the coral substratum. The laboratory experiment was designed to test the effects of three common predators (*Pseudochromis fuscus*, *Cephalopholis boenak* and *Thalassoma lunare*) and three different coral substrata that varied in their complexity (*Pocillopora damicornis*, *Acropora nasuta* and *A. nobilis*) on the survival of juvenile *Pomacentrus moluccensis*. There was a significant interaction between predator species and microhabitat in determining survival. *Pseudochromis fuscus* and *C. boenak* were both significantly better at capturing juvenile damselfish than *T. lunare*. Juvenile survivorship was significantly better when they were given the more complex corals, *Pocillopora damicornis* and *A. nasuta*, compared with those given the open-structured species *A. nobilis*. This pattern reflects habitat selection in the field. Predators differed in their strike rates and the proportion of strikes that were successful, but all exhibited greater success at prey capture where *A. nobilis* was provided as shelter. The interaction between the effect of predator species and microhabitat structure on damselfish survival was tested in the field for a cohort of juvenile *Pomacentrus moluccensis*. We examined juvenile survival in the presence and absence of two predators that co-occur on natural patch reefs (*C. boenak* and *Pseudochromis fuscus*). The experimental patch reefs we used for this purpose were constructed from both high complexity (*Pocillopora damicornis*) and low complexity (*A. nobilis*) coral substrata. Both juveniles and predators were translocated to reefs at natural densities. The effects of predation were clearly dependent upon the microhabitat. Reefs of the high-complexity coral with predators supported the same high numbers of *Pomacentrus moluccensis* as the reefs with no resident predators. However, damselfish abundance was significantly lower on low-complexity reefs with resident predators, relative to the other treatments. Background rates of loss were high, even on preferred coral in the absence of the manipulated predator, suggesting that transient predators may be even more important than the residents. We suggest that adult abundances in this species were strongly influenced by the densities of different predators and the availability of preferred refuges.

J.S. Beukers (✉)[1] · G.P. Jones
Department of Marine Biology, James Cook University, Townsville, QLD 4811, Australia

Present address:
[1]Marine Research Labs,
Nubeana Crescent, Tasoona, Hobart, Tasmania 7053, Australia
Fax: 61-3-6227 8035;
email: Jo.Beukers-Stewart@dpif.tas.gov.au

Introduction

One of the fundamental aims of ecology is to explain whether population size is regulated, and if so, by what mechanisms (Murdoch 1994). Population size is determined by the combined effects of processes that increase and decrease counts of individuals, namely the birth and death rates. In marine systems the birth rate may be modified because the majority of larval marine organisms undergo a dispersal phase before recruiting into the adult habitat. If these populations are to be limited by recruitment then post-recruitment processes such as mortality and migration must remain relatively constant, both spatially and temporally, so that initial patterns of recruitment are not modified during the post-recruitment phase (Warner and Hughes 1988; Doherty and Fowler 1994; Caley et al. 1996). If post-recruitment mortality is variable then the possibility arises that there is some degree of regulation of these populations via density dependent processes.

Patterns of post-recruitment mortality may be influenced by various factors which make up the adult environment, such as numbers and species composition of predators, and attributes of the habitat including availability of shelter. Predation is one of the major processes influencing the size of populations and the structure of ecological communities (Paine 1966; Murdoch and Oaten 1975; Hassell 1978; Talbot et al. 1978; Taylor 1984; Sih et al. 1985). It can do so directly, by increasing mortality rates thus altering densities and age structures, and indirectly, by altering growth or fecundity. Habitat structure may mediate the effects of predation by providing individuals with refuges and hence the impact of predation may be reduced in habitats with higher numbers of refuges (Crowder and Cooper 1982; Werner et al. 1983; Menge and Sutherland 1987; Hixon and Menge 1990; Caley and St John 1996).

Prey can reduce the risk of predation in two ways: by avoiding encounters with predators or by escaping after an encounter (Sih 1987). Structurally complex habitats may reduce predation rates by providing absolute prey refuges where predators cannot physically reach prey individuals or by decreasing encounter rates between predators and their prey (Murdoch and Oaten 1975; Anderson 1984; Savino and Stein 1989; Christensen and Persson 1993). Prey have often been observed to use more complex habitats in the presence of predators (Stein and Magnuson 1976; Dill and Fraser 1984; Shulman 1984; Holbrook and Schmitt 1988a; Sih et al. 1992), and predators have been found to be less efficient foragers in more complex habitats (Savino and Stein 1982; Anderson 1984; Cook and Streams 1984; Persson and Eklov 1995). Furthermore, increasing the number of refuges or habitat complexity has been shown in some ecosystems to increase either species diversity or survivorship (Behrents 1987; Hixon and Beets 1989, 1993; Connell and Jones 1991; Diehl 1993; Caley and St John 1996). There is a growing awareness that knowledge of how demographic processes vary with structural aspects of the habitat is important for understanding the population ecology of reef fishes (Levin 1994).

Coral reef studies

The high structural complexity of coral reefs, the high species richness of coral reef communities and the open nature of coral reef fish populations have made the study of predation in this ecosystem especially difficult (Hixon and Beets 1993). Hence, relatively few coral reef fish studies have attempted to look at predation compared with other potentially important processes such as competition or recruitment. Because of this, the importance of predation in controlling populations of coral reef fish remains uncertain. In a recent review, Hixon (1991) highlighted the need to use experimental manipulation to test for a causal relationship between predators and their prey. To date none of the studies that have attempted predator manipulations have examined the effect of predators in relation to habitat structure (i.e. Bohnsack 1982; Stimson et al. 1982; Thresher 1983b; Doherty and Sale 1985). Much correlative evidence suggests that several aspects of habitat including coral cover and topographic complexity may be important in determining adult densities (Luckhurst and Luckhurst 1978; Thresher 1983a; Bell and Galzin 1984; Roberts and Ormond 1987; Sano et al. 1987). However, some studies found that habitat was not important (Risk 1972; Sale and Douglas 1984; Sale et al. 1994). Hence, without further experimental work, few generalisations are likely to emerge.

Other experimental manipulations of habitat have been performed to directly assess the importance of shelter in determining abundance (Robertson and Sheldon 1979; Fricke 1980; Robertson et al. 1981; Shulman 1984; Hixon and Beets 1989, 1993; Buchheim and Hixon 1992), but many of these used artificial structures and none have included manipulations of predators. Four of these six studies (Fricke 1980; Shulman 1984; Hixon and Beets 1989, 1993; Buchheim and Hixon 1992) showed that an increase in the number of shelter sites led to an increase in the number of study species; however, the other two studies found that habitat had little effect. In addition, Jones (1988) tested the effects of two coral species on fish survival and found that survivorship was significantly higher in the most complex coral species. Although a significant effect of habitat may be due to the effects of predation, it was not convincingly demonstrated by these experiments because habitat could be important for other reasons such as shelter from storms.

Natural history of the damselfish, *Pomacentrus moluccensis*

The lemon damselfish (*Pomacentrus moluccensis*), is one of the most abundant damselfish on the reefs around

Lizard Island. After 29 days in the plankton (Wellington and Victor 1989), and at about 10 mm standard length, larvae recruit onto the reef and are almost always associated with live coral (Sale et al. 1984; Eckert 1985; Mapstone 1988). This damselfish is planktivorous and new recruits of this species are preyed upon by several small carnivorous reef fish, including the pseudochromid, *Pseudochromis fuscus*, the small serranid, *Cephalopholis boenak*, and the abundant wrasse, *Thalassoma lunare* (Martin, 1994). The abundance of juvenile *Pomacentrus moluccensis* has been found to be positively correlated with the cover of preferred coral substrata, which were corals with corymbose or caespitose growth forms (Beukers, 1996). In addition, the abundance of predators has been shown to be positively correlated with juvenile densities (Beukers, 1996). Here we examine the consequences of these patterns for juvenile mortality, and ultimately the distribution and abundance of adult fishes.

The aim of this study was, therefore, to examine whether predators affect the survival of juvenile *P. moluccensis*, and determine whether the magnitude of any effect is modified by the microhabitat or coral substratum used as shelter. The study proceeded in three phases. Firstly, spatial patterns in juvenile mortality were examined to determine the relative strengths of correlations with initial juvenile density (recruitment), predator densities and the availability of preferred coral substrata. Secondly, an experiment was performed in aquaria to look at success rates of three predator species in capturing *P. moluccensis* when they were given the shelter of three different coral species that varied in complexity. Lastly, a field experiment was performed to test the hypothesis that predators and microhabitat interact to determine the survival of juvenile *P. moluccensis*.

Methods

This study was carried out at Lizard Island which is located in the northern section of the Great Barrier Reef Marine Park, Australia (14°42′S, 145°28′E). Lizard Island is surrounded by shallow fringing reefs, the primary habitat of *P. moluccensis*. The main island is connected to two smaller granite islands by reefs which form a protected lagoonal area. Individual study sites were located on the upper reef slope areas of reef on the exposed (eastern) and sheltered (western) sides of the island, and also in the lagoon. The study was carried out between December 1994 and January 1996.

1. Spatial variation in the mortality of juvenile *P. moluccensis*

Spatial variation in juvenile mortality was examined at eight locations distributed around the exposed and sheltered sides of the island, and in the lagoon. We examined the relative strengths of correlations between juvenile mortality and (1) initial juvenile densities, (2) cover of preferred coral substrata, and (3) predator densities. Relationships among these variables were also examined to determine their degree of independence, and a multiple regression was used to provide the best predictor of mortality rates.

Patterns of juvenile density (recruitment) were assessed along twelve haphazard transects (10 m × 1 m), at eight random sites

(hundreds of meters to a few kilometers apart), in January 1995 and 1996. All fish between 10 mm and 24.9 mm SL were counted as juveniles. Any individual > 25 mm SL was counted as an adult (*sensu* Mapstone 1988). Juvenile mortality over one year was calculated according to the following equation:

$$\%M = \frac{(R - C1)}{R}$$

Where

$\%M$ = percent mortality during the first reef associated year
R = abundance of cohort $0+$ in year 1, new recruits /100 m^2
$C1$ = abundance of cohort $1+$ in year 2, /100 m^2

The percentage of adults that were 1 year old was calculated using age structures for Lizard Island in January (Beukers 1996). This figure was then used to assess the number of adults in cohort 1 ($C1$) on each transect. Mortality estimates during the first reef-associated year were calculated for new recruits settling in 1995 at eight sites.

Along the same transects, patterns in the abundance of preferred coral substrata at the eight sites were assessed by videoing each transect using a Sony hi-8 camera. The camera was held approximately 25 cm away from the reef and 2 min was taken to film each 10 m transect. The video tape was analysed by stopping it at 20 places along each transect. Five random dots were drawn on the monitor and at each of the 20 stops the substrate under each dot was noted.

Patterns in the abundance of small predators of juvenile reef fish were censused twice at every site. Two methods were used, one developed for cryptic species and the other for non cryptic species (Beukers, 1996). For cryptic species (e.g. *Pseudochromis fuscus* and *C. boenak*), a baited point census was used to increase the likelihood of observing individuals of these species. Ten points around the circumference of a 5 m circle were marked using fluorescent tape. All cryptic predatory piscivores seen within this area were counted during a 15-min period. At the start of the observation period four pilchards were placed in a mesh bag and pulverised. At the end of the census the mesh bag was placed in a sealed bag and removed from the reef. On each of two separate occasions three spatially separate circles were counted so that a total of six circles were counted for each site.

For diurnally active, non-cryptic species (e.g. *Thalassoma lunare*) the traditional visual census method was used. At each location fish were counted within 18 m by 30 m quadrats. Each quadrat was divided into six belt transects 3 m wide, 30 m long and fish were counted by swimming along each of these in turn. Abundances were converted to densities per 100 m^2.

2. Effects of predator species and coral substratum on juvenile survival: an aquarium experiment

An orthogonal experiment was set up in December 1994, to test the effects of three small predators (*P. fuscus*, *C. boenak*, and *T. lunare*) on the survival of juveniles given three different coral species as shelter (*A. nasuta*, *A. nobilis* and *Pocillopora damicornis*). Thirty-six tanks (each 100 cm by 50 cm) were set up with 5 cm of sand covering the bottom. Two coral heads, of the species to be used as shelter, were placed in the centre of each tank. Every treatment tank contained one predator and one coral species, and additional control tanks contained the same coral species without predators. Five juvenile *Pomacentrus moluccensis* (10–20 mm SL) were placed in each tank. There were three replicates of each treatment and control. Predators were placed in the aquaria for 3 days, before juvenile *P. moluccensis* were added, to become accustomed to their surroundings. During this time they were not fed. When *P. moluccensis* were released into the aquaria, care was taken to reduce their disorientation. The five new recruits were floated in a click-seal polythene bag, above one of the coral heads, for 2 min. The bag was then gently opened and held so that the fish could swim away from the bag. There were no cases of new recruits being eaten

before they reached the coral head. New recruit survivorship in all aquaria was recorded continuously for the first hour after release, and then every 24 h for 7 days. The number of successful and unsuccessful predatory strikes made by the predator, were also counted during the first hour. Final recruit density was analysed with a two-way ANOVA testing for the effects of predators and coral substratum. This test was performed on the numbers of new recruits remaining in all treatments and controls after 7 days. This was followed by a Tukey's Studentised Range test.

3. Does habitat complexity mediate the effect of predators? A field experiment

An experiment was set up to test the effect of two predator species, which are normally resident on small patch reefs, on the survival of juvenile *P. moluccensis*. For this experiment, patch reefs were constructed from two different types of coral, one of high complexity (*Pocillopora damicornis*) and one of low complexity (*A. nobilis*). Two predator species were used that are very commonly found on small patch reefs around Lizard Island, *Pseudochromis fuscus* and *C. boenak*.

3a. Assessment of the densities of *Pomacentrus moluccensis*, *Pseudochromis fuscus* and *C. boenak* on natural reefs around Lizard Island

To determine the densities of both juvenile *Pomacentrus moluccensis* and the predators to be used in the experiment, densities on natural patch reefs were surveyed. During January 1995, the numbers of juvenile *P. moluccensis* inhabiting coral heads of *Pocillopora damicornis* and *A. nobilis* were counted on natural reefs. At each of five sites around Lizard Island a random quadrat 10 m by 10 m was set up. Inside this quadrat each coral head was censussed separately. The numbers of *Pomacentrus moluccensis* of 10–24.9 mm SL within each head were counted and the volume of coral was approximated by measuring the greatest length, its perpendicular width, and the depth of the coral head. Abundances were converted to densities per 0.315 m^3 of coral, the approximate volume of coral used for each patch reef in the field experiment. Secondly, the numbers of *Pseudochromis fuscus* and *C. boenak* were counted on 28 patch reefs selected at random at each of two patch reef sites. Selected reefs were of approximately the same size as the experimental reefs and hence this gave an estimate of the natural density of these fish on reefs similar to those used in the experiment.

3b. Experimental design

The experiment was carried out on a large flat sandy area in the lagoon of Lizard Island. A fully balanced, orthogonal experiment was set up with two factors: predator density and habitat complexity. Each factor had two levels. Resident predators were either present, at an approximately natural density of one fish of each species per reef, or absent. Patch reefs were constructed from two coral substrata, ten of *Pocillopora damicornis* and ten of *A. nobilis*. The dimension of each reef was approximately 90 cm × 70 cm × 50 cm giving each a volume of 0.315 m^3 and surface area of 0.223 m^2. They were placed on sand 30 m apart at a depth of 5 m on the highest tides. Treatments were assigned to reefs using a randomised block design with five replicates. Before the experiment started, we examined the migration rates of *Pomacentrus moluccensis* new recruits, from these patch reefs, without the influence of resident predators. Twenty *P. moluccensis* new recruits (10–20 mm SL) were released onto each reef and their numbers were monitored for one week. At the start of the experiment, a density of 15 individuals per reef was required to reflect natural densities. After one week there was some initial migration. At that time numbers were adjusted downward to establish densities of 15 per reef, and there predators were released onto the reefs. Reefs were checked daily for 1 week to monitor any emigration of predators, but none was observed. Pelagic predators were able to access all reefs equally and therefore did not influence treatment effects. Censuses of all fish on the reefs were carried out after 2 months. The numbers of *P. moluccensis* remaining in each treatment after 2 months were log transformed to normalise the data, and then a two-way ANOVA was performed to assess the effects of predator density and coral substratum. This was followed by a Tukey's Studentised Range test.

Results

Spatial variation in the mortality of juvenile *P. moluccensis*

The mortality of juvenile *P. moluccensis* varied between 20% and almost 100% among the eight sites examined. This variation was potentially explained by initial juvenile densities, predator densities and/or the availability of preferred coral substrata (Fig. 1a–c). Mortality increased as a function of recruitment levels, but the rate of increase in mortality decelerated with increasing recruitment. Fifty-three percent of the variation was explained by this relationship). There was a significant linear relationship between mortality and predator densities that explained 56% of the variation (Fig. 1b) and an almost significant linear relationship between mortality and the cover of preferred coral substrata (Fig. 1c) that explained 32% of the variation. A multiple regression using all three variables to predict mortality


Fig. 1 Relationships between the mortality (% mortality over one year) of juvenile *Pomacentrus moluccensis*, and **a** initial juvenile densities, **b** predator densities, and **c** the cover of preferred coral substrata, from a comparison of 8 sites at Lizard Island
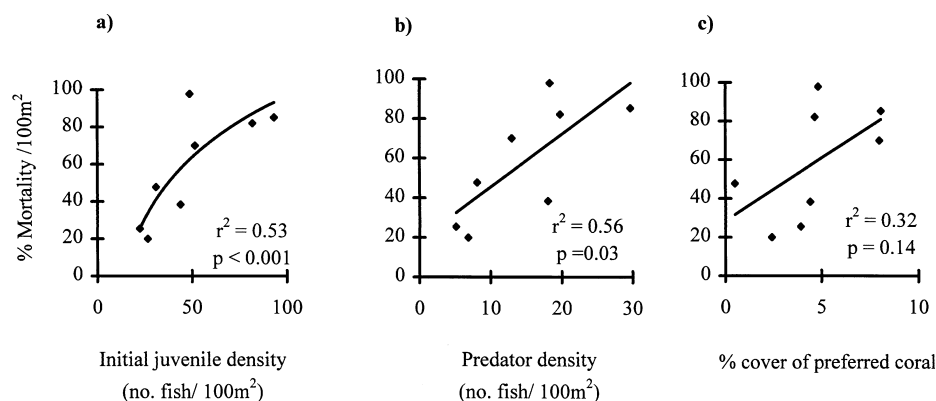
rates was not significant ($F_{[3,4]} = 1.98$, $P = 0.26$), and explained marginally more variation than recruitment or predators alone (multiple $r^2 = 0.60$). A more detailed analysis of the relationships between recruitment, predators and percentage cover of preferred corals indicated that these were unlikely to be independent variables. Pairwise comparisons showed significant positive correlations between recruitment (ln) and predators ($r = 0.93$), recruitment and cover of preferred corals ($r = 0.68$), and between predators and coral cover ($r = 0.66$), thus obscuring any potential cause-effect relationships.

Effects of predator species and coral substratum on juvenile survival: an aquarium experiment

Both predators and coral substratum had a significant effect on the survivorship of juvenile *P. moluccensis* (Figs. 2 and 3, Table 1a). The magnitude of the effects of different predators was dependent upon the coral substratum. Overall, the mean survivorship was significantly
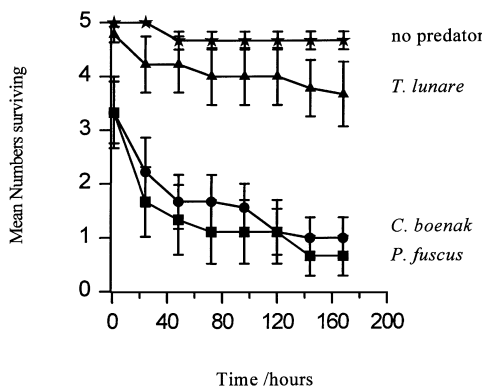
Fig. 2 Survivorship curves for *P. moluccensis* ($\bar{x} \pm$ SE) in aquaria under different predator regimes and pooled across three habitat treatments. For each data point, $n = 15$
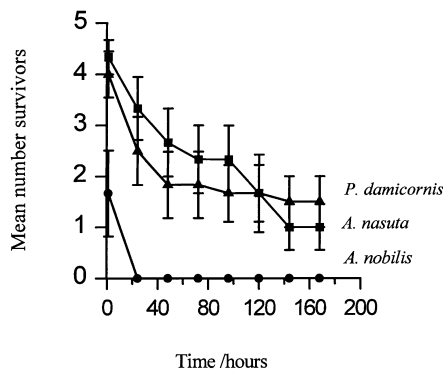

Fig. 3 Survivorship curves for *P. moluccensis* ($\bar{x} \pm$ SE) in aquaria under different habitat regimes (corals: *Pocillopora damicornis*, *Acropora nasuta*, *A. nobilis*) and pooled across two predator treatments where predation occurred (i.e. treatments with *Pseudochromis fuscus* or *Cephalopholis boenak*)

cantly lower in treatments with the predators, *C. boenak* and *Pseudochromis fuscus*, compared to the controls with no predator present (Table 1b). Survivorship was approximately 20% in the presence of these two predators and almost 100% in controls. The effect of predation by *T. lunare* was much lower, with almost 80% survival in this treatment (Fig. 2). However, the survival of *Pomacentrus moluccensis* in treatments with predators differed significantly among the three coral types (Fig. 3, Table 1a). For the two most important predators, *Pseudochromis fuscus* and *C. boenak*, survivorship was significantly better in aquaria with *Pocillopora damicornis* or *A. nasuta*, compared to those with *A. nobilis* where 100% mortality occurred. The effects of these two predators were slightly different, with *Pseudochromis fuscus* being more successful than *C. boenak* at capturing prey in *Pocillopora damicornis* (Table 1b). Survivorship ($\bar{x} \pm$ SE) was the same for all coral types when no predator was present (4.5 $\pm$ 0.41).

The two most successful predators, *Pseudochromis fuscus* and *C. boenak* both made their highest percentage of successful predatory strikes in *A. nobilis* (Figs. 4 and 5). The frequency of predatory strikes differed between the two predator species, and the frequency of strikes made by individual predators of the same species, varied with the coral species provided as shelter. *P. fuscus* made large numbers of predatory strikes with a very low success rate in the most complex coral *A. nasuta* (Fig. 4), while *C. boenak* made relatively few strikes regardless of the coral species (Fig. 5). Qualitative aspects of the behaviour of *C. boenak* also varied according to microhabitat type. In the most open coral they would continuously chase prey until a successful capture was made, which in most cases took no more than a few

Table 1 a Analysis of variance table for number of new recruits of *Pomacentrus moluccensis* present in aquaria after 7 days. Variances homogeneous. **b** Tukey's studentised range test on number of new recruits of *P. moluccensis* remaining in aquaria after 7 days. Treatments which were assigned the same category do not have significantly different means, whereas those which were assigned different categories did have significantly different means. The categories assigned were low, medium and high (*Low* low numbers remaining, *med* medium numbers remaining, *high* high numbers remaining)

a

Source	df	SS	MS	F	P
PRED	3	2.557	0.852	30.14	0.0001
CORAL	2	0.282	0.141	4.98	0.0155
PRED × CORAL	6	0.427	0.071	2.51	0.0496

b

Predator/habitat	*Acropora nasuta*	*Pocillopora damicornis*	*A. nobilis*
Pseudochromis fuscus	Low, Med, High	Low	Low
Cephalopholis boenak	Low, Med	Med, High	Low
Thalassoma lunare	Med, High	High	Med, High
No predator	High	High	High

Pseudochromis fuscus

Cephalopholis boenak
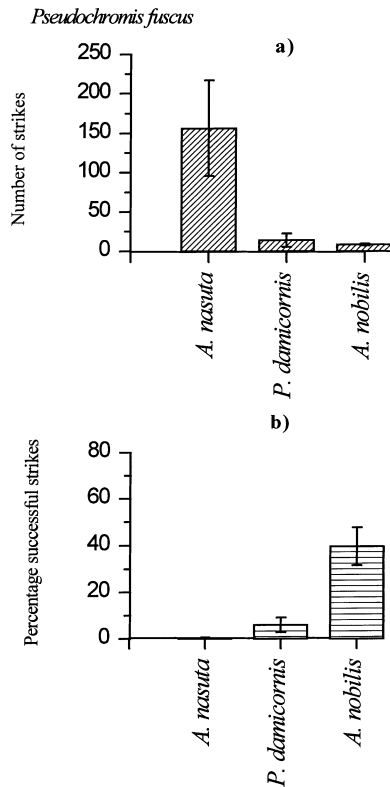
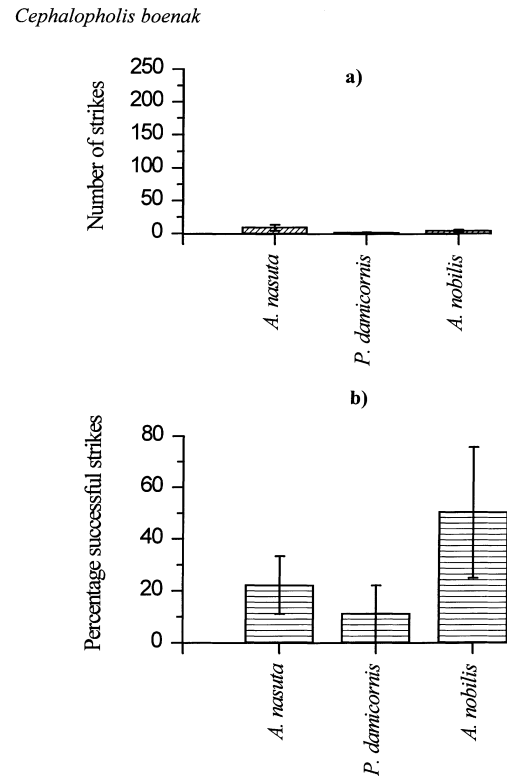

Fig. 4 Predatory strike rates for *Pseudochromis fuscus* ($\bar{x}$ ± SE) from three microhabitat types. **a** Number of predatory strikes made during the first hour and **b** the percentage of those strikes that resulted in successful capture of a *Pomacentrus moluccensis* juvenile

Fig. 5 Predatory strike rates for *Cephalopholis boenak* ($\bar{x}$ ± SE) from three microhabitat types. **a** Number of predatory strikes made during the first hour and **b** the percentage of those strikes that resulted in successful capture of a *P. moluccensis* juvenile

seconds. In the higher-complexity habitats, *C. boenak* stalked their prey, moving gradually closer and closer, and sitting motionless for long periods. The final strike was extremely quick and was more likely to be successful in all three coral species when compared to *P. fuscus* (Figs. 4 and 5).
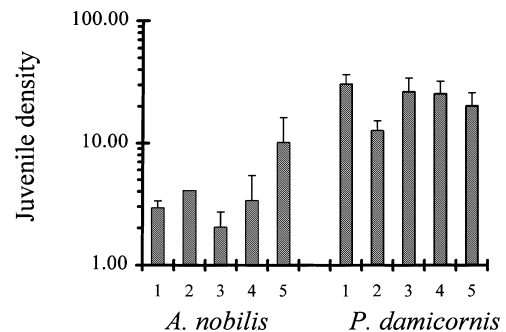
Does habitat complexity mediate the effect of predators? A field experiment

For the two coral types to be used in the field experiment, the densities of juvenile *P. moluccensis* were consistently higher in the more complex coral species (Fig. 6). These juveniles may have spent up to 3 months on the reef and this was therefore a measure of numbers recruiting plus any post-settlement modification that may have occurred. Mean densities per 0.315 m³ for *A. nobilis* were in the range 3–10 individuals and in *Pocillopora damicornis* they were 13–30 individuals. An overall average of 15 was used for the experiment.

The mean densities of *Pseudochromis fuscus* and *C. boenak* on natural patch reefs were in all cases less than one (Fig. 7). The densities of *C. boenak* varied from 0 to 3 individuals per reef, and of *P. fuscus* varied between 0 and 2 individuals per reef. In each case, the two most common situations were densities of 0 or 1 per reef,


Fig. 6 Densities (per 0.315 m³ of coral) of *P. moluccensis* ($\bar{x}$ ± SE) within coral heads of the species *Acropora nobilis* and *Pocillopora damicornis*, at 5 sites around Lizard Island. At each site all coral heads of these species within a quadrat 10 m by 10 m were censussed. There were always at least five coral heads per quadrat

so these were chosen as the two levels in the experiment. The two predators frequently co-occurred on the same reefs.

There was a significant interaction between predator density (presence, absence) and microhabitat type (Fig. 8, Table 2a). On the low complexity reefs with predators *Pomacentrus moluccensis* recruits showed significantly lower final abundance than on all of the other reefs (Fig. 8, Table 2b). The high complexity *Pocillopora*
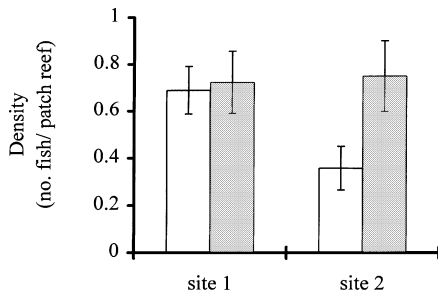
Fig. 7 Densities (per patch reef) of the two predator species ($\bar{x} \pm$ SE) used for the experiments, *Pseudochromis fuscus* and *Cephalopholis boenak*
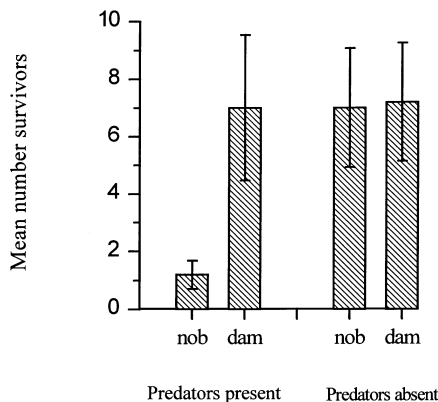
Fig. 8 Number of *P. moluccensis* ($\bar{x} \pm$ SE) that survived for 2 months, when placed on patch reefs. There were two patch reef types, *Acropora nobilis* and *Pocillopora damicornis*, and predators were either present (2 individuals) or absent. For each bar, $n = 75$

Table 2 a Analysis of variance table for number of new recruits of *P. moluccensis* present on patch reefs after 2 months. Variances homogeneous. **b** Tukey's studentised range test on number of new recruits of *P. moluccensis* remaining on patch reefs after 2 months. Treatments which were assigned the same category do not have significantly different means, whereas those which were assigned different categories did have significantly different means. The categories assigned were low and high (*Low* low numbers remaining, *high* high numbers remaining)

a

Source	df	SS	MS	F	P
CORAL	1	0.305	0.305	4.25	0.0559
PRED	1	0.409	0.409	5.69	0.0298
CORAL × PRED	1	0.364	0.364	5.06	0.0388

b

Predators/habitat	*P. damicornis*	*A. nobilis*
Predators present	High	Low
Predators absent	High	High

damicornis reefs with predators supported the same high numbers of *Pomacentrus moluccensis* as the reefs with no predators. Loss rates were high, even on reefs without resident predators. There was no significant difference in

Table 3 Analysis of variance table for number of new recruits of *Pomacentrus moluccensis* present on 20 patch reefs, 10 constructed of *Acropora nobilis* and 10 of *Pocillopora damicornis*, after 1 week without predators present. Variances are homogeneous

Source	df	SS	MS	F	P
Coral species	1	0.259	0.259	2.18	0.1570
Error	18	2.138	0.119		
Corrected total	19	2.397			

loss rates from the two reef types in the week prior to predators being added ($P = 0.1570$, Table 3), and the experiment was started with juveniles which had been resident for 1 week.

Discussion

Correlative data implicated the importance of recruitment levels, predators, and the availability of preferred coral substrata in determining patterns in the mortality of juvenile *P. moluccensis*. However, since all these factors appeared to be interrelated, the potential cause-effect relationships were obscured. The strong correlation between recruitment levels and predator densities suggested that predators may be involved in determining the apparently density-dependent mortality. If predators aggregated at high-recruitment sites this could lead to increased mortality rates as a function of the density of new recruits. However, the patterns suggested that the relative increase in their effects declined with increasing density. This may have been due to an interaction between the effects of predators and the availability of preferred shelter for the prey species. Juveniles exhibit a strong association with particular coral substrata (Beukers 1996), and recruitment and mortality increased with the availability of preferred coral cover. We tested two hypotheses, using both aquaria and field experiments: that predators do affect the survivorship of new recruits, and that their effect is modified by the availability of preferred substrata. Both hypotheses were supported by the results.

Coral substrata clearly differ in the degree of shelter they provide to species such as *P. moluccensis*. The degree of protection afforded appears to depend not only on attributes of the microhabitat itself, but also on the attributes of particular predators. In aquaria, there was a significant interaction between the effects of both predator species and microhabitat on the survivorship of *P. moluccensis*. Predator success in each microhabitat varied according to species. Both *Pseudochromis fuscus* and *C. boenak* were most successful in the structurally least complex coral species, *A. nobilis*. However, there were differences among predators. *P. fuscus* had a higher percentage of successful strikes in *Pocillopora damicornis* than in *A. nasuta*, while *C. boenak* exhibited the opposite pattern. It seems likely that this was due to the differences in their predatory behaviour. Unfortunately, it

was not possible from this experiment to show which attributes of microhabitat were important for increased damselfish survival. It would seem that more complex coral head structures provided better refuges from predation as has previously been shown in freshwater communities (Werner et al. 1983; Holbrook and Schmitt 1988b; Persson and Eklov 1995). It must be borne in mind that under conditions with several predators using different search modes and predatory behaviour, the ability of prey to avoid predation may differ substantially (Kingsford 1992).

Survivorship of *Pomacentrus moluccensis* in aquaria with the predator *Thalassoma lunare* was not significantly different from that of the controls. *T. lunare* is a mobile predator and individuals often forage in a group. In aquaria *T. lunare* individuals spent most of their time swimming up and down the glass. It is most likely that the aquaria significantly altered their behaviour, but it could also be that *T. lunare* is not a particularly important predator of *P. moluccensis*.

In the field, microhabitat modified the effects of resident predators on *P. moluccensis*. The reefs constructed from the higher complexity coral, *Pocillopora damicornis*, with predators present, supported the same high numbers of the damselfish as those with no resident predators. This is consistent with the study by Jones (1988), which found that damselfish survivorship at One Tree Reef was higher in *P. damicornis* than in a less complex coral. However, the question remains as to whether this difference was due to mortality or migration. One of the main problems that most mortality studies have is that they cannot avoid the potentially confounding effects of immigration and emigration. Our field experiment was no exception to this; however, there is some evidence against, and no evidence for, differential migration. Firstly, there was no significant difference in losses from reefs prior to adding the resident predators. The result is therefore definitely a direct effect of the addition of resident predators. Although there was some initial emigration, the experiment was started with juveniles that had remained resident for a week. Evidence for migration occurring would come from reefs that showed a net increase in numbers of *Pomacentrus moluccensis* but all reefs showed net losses. In addition, previous work has shown that *P. moluccensis* is extremely site attached (Beukers 1996; Mapstone 1988). Mapstone (1988), marked 99 *P. moluccensis* and found that only one moved further than 2 m over a period of 3 years.

Patterns of predator and microhabitat abundance could explain the distribution of adult *P. moluccensis*. While patterns in the distribution of juveniles may be explained by variation in larval supply (Doherty 1987; Milicich and Doherty 1994), patterns of the relative abundance of juveniles and adults were consistently different over the three years of this study (Beukers 1996). Both site-specific and density dependent patterns in mortality may be due to predators, but the absolute magnitude of the effect may be dependent on the magnitude of recruitment relative to the local availability of preferred coral. These experiments show that resident predators could alter patterns of distribution of *P. moluccensis* between microhabitats. Resident predators have been shown to significantly alter population abundance and size structure on natural patch reefs in the Caribbean (Carr and Hixon 1995). These effects were prey species specific so lead to changes in the relative abundance of species in the community. However, high background mortality on reefs in the absence of resident predators also implicates the role of transient predators in this and other studies.

Spatial variation in mortality rates have been observed in other studies on *P. moluccensis* (Doherty and Fowler 1994) and many other coral reef fish species (DeMartini and Anderson 1980; Jones 1984, 1986; Aldenhoven 1986; Eckert 1987; Sale and Ferrell 1988; Connell and Kingsford 1992; Booth and Beretta 1994). Doherty and Fowler (1994) observed lower abundances of adults and reduced life expectancies at a reef with relatively high recruitment when compared to One Tree Island, and suggested that this was due to differential predation. Unfortunately they only had one high recruitment reef and several low to intermediate reefs, so this result remains tentative. Spatial variation in the availability of microhabitats (Done 1982; Nelson 1994) and predator community structures (Caley, 1995) have been documented at Lizard Island. These factors could account for the observed spatial variation in mortality rates of *P. moluccensis*.

Spatial variation in mortality would modify recruitment patterns and alter numbers subsequently reaching maturity. Doherty and Fowler (1994) and Mapstone (1988) concluded that the most important factor determining *P. moluccensis* in the Southern Great Barrier Reef was recruitment. Thus it could be that while at some sites, for example where habitat is complex, recruitment rates may be the most important factor determining abundance, at others it could be a complex interaction of settlement patterns and the degree of protection provided by habitat components against the suite of predators present. The variability in the results of previous habitat studies on coral reefs would also support a pluralistic theory whereby several processes were important in structuring populations of reef fish and whose importance varied temporally and/or spatially (e.g. Jones 1991; Hixon 1991).

In this predator-prey system, variation in microhabitat and predators had significant effects on mortality rates, and could potentially account for much of the observed spatial and temporal variation in adult numbers. Given that mortality appears to be density dependent, there is some evidence that this prey population was being regulated by predator community structure and abundance, and by the availability of shelter. Where shelter is limiting the predation and competition hypotheses overlap (Hixon 1991) and thus further work is needed to evaluate the roles of both predation and competition. Several studies have shown that increasing

the number of available refuges can lead to an increase in either survivorship or species diversity (Werner et al. 1983; Behrents 1987; Holbrook and Schmitt 1988a, b; Diehl 1993; Persson and Eklov 1995), but evidence within coral reef fish communities, to date, has been sparse (but see Shulman 1984; Hixon and Beets 1993; Buchheim and Hixon 1992).

As pointed out by Hixon (1991), unproductive debates have been escalated by overgeneralising from the study of one species, at one place, at one scale, over one period. What is needed is to consider several species over a range of scales, times and places. *P. moluccensis* is the first species of coral reef fish for which different locations, spatial scales and temporal scales can be compared. This study has enabled comparisons to be made with another location on the Great Barrier Reef (Doherty and Fowler 1994) and has revealed a high degree of plasticity in mechanisms of population regulation. When considered together, these studies demonstrate empirically the dangers of both single process theories and making generalisations from small scale studies. At the same time they provide a template for the development of a model that can be tested on other species. Intra- and inter-species comparisons will allow the construction of models with predictive power and hence, generalisations will be possible.

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