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Larval growth history determines juvenile growth and survival in a tropical marine fish

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Processes that occur around the transition between larval and juvenile life-stages can have a major effect on the population dynamics of organisms with complex life cycles. We explore the roles of larval history and selective post-settlement mortality in determining the growth and survival of newly-settled individuals of the damselfish, *Pomacentrus amboinensis* (Pomacentridae). Specifically, we determine whether the direction and intensity of selection on the recruits differs among various size-classes of predators. A mark-recapture study showed that individuals who survived 9 or more days were significantly larger at settlement than those that died within the first day (12.3 vs 11.9 mm SL), when mortality was highest (25% d^{-1}). Censuses revealed that the species and size composition of piscivores differed markedly between two reef habitats where *P. amboinensis* was common. A cage experiment, conducted in both habitats, manipulated the sizes of predators that could access newly settled *P. amboinensis* to determine whether the resulting mortality of the recently settled fish was influenced by larval growth history or size at settlement. Ten days after the start of the experiment individuals that grew slowly in the second half of their larval life had been lost from most of the experimental treatments. Small fish were also selectively lost from the coarse-mesh cage on the reef base. Significant positive relationships between pre- and post-settlement growth rates were found in both habitats for the fine mesh cages, cage controls and open patch reefs. This relationship was reversed in the coarse mesh cages in both habitats. This growth compensation was facilitated through the action of a particular size range of predators, whose impact was disrupted or masked in the open treatments by the action of a diverse predator pool. The present study underscores the complexity of the processes that influence the early post-transition growth and survival in organisms with complex life-histories.

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A fundamental goal in population ecology is to understand the processes that influence which individuals survive through to reproduction. Mortality schedules are closely linked to the life-history characteristics of the organism and its mode of reproduction (Stearns 1992). Organisms with complex life cycles, such as insects, marine invertebrates and fishes, have mortality schedules that often approximate exponential decay functions (Wilbur 1980, Booth and Brosnan 1995, Hunt and Scheibling 1997). For many of these terrestrial and marine organisms, over 99% of individuals die prior to metamorphosing to the juvenile state (Booth and Brosnan 1995, Gosselin and Qian 1997). Terrestrial plants that include dispersive propagules in their life cycle show a similar pattern of mortality (Crawley 2000). A key factor influencing dynamics of these populations is the variation in abundance of juveniles entering the population (Stearns and Koella 1986). However, the processes that govern success during this transition are complex and not fully understood.

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From the moment of conception, individuals vary in development and growth rates that will pre-dispose some individuals to a lower probability of surviving later developmental stages. These initial differences in life-history characteristics are parentally driven, being either genetically programmed, or maternal non-genetic contributions to nutrition (McCormick 2003), immunology (Lung et al. 1996) or metabolism (McCormick 1998a, Agrawal 2001). These initial effects interact with environmental conditions to result in high variability in growth and performance characteristics of the organism (Chambers and Leggett 1996, Heath and Blouw 1998, Relyea and Hoverman 2003). High larval growth may lead to size advantages in gaining access to limited resources and/or evading and escaping predators (Pechenik and Cerulli 1991, Leggett and Deblois 1994). Recent studies of tropical marine fishes have shown that the advantages associated with a high larval growth rate lead to enhanced survival through to metamorphosis and settlement to the juvenile population (Searcy and Sponaugle 2001, Bergenius et al. 2002, Shima and Findlay 2002, Wilson and Meekan 2002). However, few studies to date have examined the effects of larval history on survival after settlement.

At metamorphosis, organisms vary widely in phenotypic traits that may influence survival (McCormick and Molony 1993, Kerrigan 1996, Moran and Emlet 2001). These characteristics may include size (Berven 1990, Schmitt and Holbrook 1999), growth rate (Searcy and Sponaugle 2001, Shima and Findlay 2002, Vigliola and Meekan 2002, Hoey and McCormick in press), overall body condition (Mesa et al. 1994), fat content (Basch and Pearse 1996, Booth and Hixon 1999, Hoey and McCormick in press), sensory development (McCormick 1993) and burst speed (McCormick and Molony 1993). This suggests that during the high mortality that occurs at the transition between developmental stages, survival may be strongly influenced by larval history and the initial parental inputs.

Once juveniles have entered the population, another suite of processes may influence survival through to reproduction (Gosselin and Qian 1997, Sogard 1997). Post-settlement mortality has the capacity to distort the patterns established at settlement (Schmitt and Holbrook 1999, Steele and Forrester 2002). For juvenile marine fishes, it is the habitats they initially settle into that determine the community they interact with and the environment they experience. Habitat differences may affect competitive interactions (Jones 1988), food availability (Levin 1994) and the ability to procure food (Anderson 2001). All of these interactions can be affected by the presence and action of predators (Godin 1997). The topographic complexity of the settlement site influences not only the vulnerability of prey to predators (Connell and Jones 1991, Beukers and Jones 1998), but also the efficiency, effectiveness and selectivity of predators (Sih et al. 1985, Anderson 2001). The predator regime experienced by juveniles at this critical transition period is likely to exert a strong selective pressure that will govern those that survive to join the later life stages.

However, an individual's survival chances are not wholly pre-determined by its larval history. The larval environment is markedly different, both physically and biologically, from that experienced by juveniles. Intuitively, this would suggest that those individuals that have been disadvantaged due to their performance characteristics in the larval environment, may be able to compensate once settled (McCormick and Molony 1993, McCormick 1998b). Some individuals may have attributes suited to the new environment, which allow them to outperform individuals with high larval performance. While crucial to our understanding of the processes that influence the growth of juveniles, few studies have examined the relationship between larval and juvenile growth. To date, evidence for compensatory growth occurring around metamorphosis is limited to laboratory studies (Bertram et al. 1993). Most laboratory examples involve growth compensation following periods of limited food supply after a change to higher food availability (Soether and Jobling 1999, Morgan and Metcalfe 2001, Zhu et al. 2001). Surprisingly, evidence for compensatory growth is rare in natural biological systems. One of the goals of the present study is to explore whether predation risk influences the relative advantages of superior larval growth.

Research on tropical marine fishes has emphasised the importance of the supply of juveniles from larval sources to population dynamics (Victor 1991, Caley et al. 1996, Cowen and Sponaugle 1997). Despite this, few studies have assessed the selective nature of mortality during this important life-history transition (Searcy and Sponaugle 2001). To date no studies have explored how selective loss of individuals relates to the size characteristics of predators. A variety of freshwater and temperate marine studies have stressed the importance of the relative sizes of predator and prey in determining the dynamics of predation (reviewed by Rice et al. 1997). These findings suggest that the impact of predators on the distribution of traits in a prey population will depend upon the identity and prey-size specificity of the predators to which prey are exposed. Recent studies have found that most juvenile mortality in coral reef fish can be attributed to the action of small-bodied piscivores, rather than larger transient predators (Martin 1994, Holbrook and Schmitt 2002). Understanding how these size-related processes influence the survival of juveniles provides insight into the mechanisms that determine the abundance patterns of populations and the structure of tropical fish communities.

The broad objective of the present study was to explore the roles of larval history and selective post-settlement mortality in determining the growth and survival of newly–settled damselfish. Coral reef fishes are ideal subjects for studying the effect of history on present day ecology since a historical record of key attributes of their past phenotype, such as growth and size at settlement, are preserved in their otoliths (Campana and Neilson 1985). Using a multivariate approach we examined the factors which influence early post-settlement survival in naturally settled fish. The fate of individually tagged fish were tracked through time and their survival was examined in relation to aspects of the physical structure and biological community within their settlement site. Visual surveys examined the abundance patterns of potential piscivores and indicated a diverse size range of potential predators, which differ markedly among habitats. We then used a field manipulation in two reef habitats to examine how suites of different sized predators influenced the abundance patterns of recently settled fishes, and whether survival in the first two weeks after settlement, when mortality was greatest, was related to larval growth history. Specifically, our experiment addressed 3 questions: (a) does the size of the predators influence the selective loss of newly settled fish? Previous studies predict that large piscivores may be less selective than smaller, gape-limited predators (Hughes 1997); (b) is predation selective for individual characteristics or life history attributes? We predicted that fish who had a favourable larval history and who were in better condition at settlement (i.e. larger or faster growing), would have a greater probability of survival; (c) does the size of predators that newly settled fish are exposed to affect how prior history influences post-settlement performance? We predicted that there would be a positive relationship between larval and post-settlement growth where fishes are exposed to the full suite of predators due to selection reinforcing the advantages of initial large size at settlement. In contrast, compensatory growth may occur where newly settled fish are exposed to a restricted size range of predators, where specific predator–prey interactions may result in the breakdown of the advantages of a good larval growth history.

Material and methods

Study species and locality

The focal species was the tropical damselfish *Pomacentrus amboinensis*, a common member of the coral reef fish community in the Indo-Pacific, which typically settles in high numbers during the Austral summer. Tagging studies have shown that it moves little after settlement (McCormick and Makey 1997), making it ideal for a study that tracks the fate of individual fish. *P. amboinensis* settles relatively evenly over the reef and may occupy a wide range of depths if the appropriate microhabitat is available. Reproductive females can be distinguished from males by their smaller size, lack of nesting behaviour, slight differences in body shape (males are proportionally longer between the pelvic fins and anus) and the presence of a black margin on the caudal fin of males (during the breeding season).

The study was conducted at North Vicki's Reef in the lee of Lizard Island on the northern Great Barrier Reef, Australia (14°41′S, 145°27′E) during November/December 1998 (for the field experiment) and December 1999 (for the mark–recapture study). North Vicki's Reef has an extensive reef flat at a depth of approximately 3 m, which gradually slopes down to the reef base at a depth of 12–15 m. The study site was a 500 × 150 m section of reef with a mixture of live and dead *Pocillopora damicornis*, rubble and sand patches, making it ideal habitat for *P. amboinensis*.

Survival of newly settled fish

To explore whether fish size, the neighbouring fish assemblage or substratum characteristics influenced the survival of newly settled fish we monitored the fate of tagged fish where they naturally settled. A strip of reef (~ 50 × 150 m) extending from the reef flat to reef base was searched daily between 0730–0900 h for newly settled *P. amboinensis*. Identification of newly settled individuals was based on their size, colouration and behaviour (McCormick and Makey 1997). Upon finding a newly settled individual it was captured using a hand-net, transferred into a small clip-seal plastic bag, measured using callipers (±0.1 mm) and tagged with an individually identifiable fluorescent elastomer tattoo (Northwest Marine Industries Inc.) using a 29 gauge hypodermic needle. Fish were left in the plastic bag at the exact site of capture for 5 min (for full recovery) prior to release. All fish were released at the site of capture and were observed to begin feeding within 30 s. A detailed laboratory study of this tagging technique has shown that tagging had no significant effects on mortality or growth over a 2-week period and that tags have a 100% retention rate (Hoey 1999). The location of the tagged fish was marked with a numbered label, and recorded onto a detailed map of the study area drawn to scale using the triangulation of prominent reef features. A daily census of the whole area was conducted and the presence or absence of tagged fish was recorded. When fish appeared to be missing, a search was conducted in a 5 m radius of where the fish had been initially tagged. If the tagged individual was not found on 4 consecutive days it was recorded as dead.

Upon finding a newly settled *Pomacentrus amboinensis*, fishes of all species were counted in a circle of 1 m radius centred on the newly settled fish. Fishes were categorized as either recruit (settled within the last month ~25 mm standard length), juvenile or adult.

Pomacentrus amboinensis densities were broken down further to include the following categories: settled within the last week (~ 13–18 mm SL); settled after 1 week to 1 month (18–25 mm SL); juvenile (25–45 mm SL, with 45 mm SL being the minimum size of sexual maturity, McCormick, unpubl. data); females (> 45 mm SL and not male); male. Topography of the circular plot was quantified using the length ratio of a 2 m stretched tape to that of a tape contoured over the surface (McCormick 1994). The tapes were positioned to obtain the maximum topography within the plot, under the constraint that the tape passed through the centre of the plot. Percentage cover of benthic substrata was estimated using a 1 × 1 m grid-quadrat (121 intercepts) placed in each plot, centred over the tagging site. Benthic substrata under the intercepts were placed into one of 13 categories, chosen to include all the major benthic growth forms: 5 hard coral groups (*Pocillopora damicornis* live; *Pocillopora damicornis* dead but standing; branching live; massive live; encrusting live); soft coral; sponge; bushy red algae (*Amphiroa crassa*); turfing algae; sand; sand and rubble (~ 50% each); coarse rubble (average size > 10 cm); fine rubble (average size ≤ 10 cm). Water depth of the plot was also recorded.

Predator distributions

To quantify the diversity and abundance of potential predators of recently settled fish in each habitat five randomly placed 25 × 2 m visual strip transects were conducted at the reef base and flat. These transects were sampled in the area where the experimental cages (below) were deployed. Transects were all swum on the same morning between 7:30am and 11:00am. A recent study at Lizard Island of the two predators *Cephalopholis boenak* and *C. cyanostigma*, which commonly eat recruit fishes (Martin 1994), showed they were strongly site attached and unlikely to move between habitats (Stewart 1998).

Selectivity of predation

Predator exclusion experiment

A field experiment was conducted to determine whether habitat type or exposure to predators of 3 different size-classes influenced which newly settled *P. amboinensis* survived. To achieve this, newly metamorphosed fish were placed on patch reefs and exposed to 3 suites of predators. The survivors were then collected and compared among treatments, and to an initial sample of fish, to determine whether predation was selective for pre-settlement growth history or body size at settlement.

Experimental patch reefs (~ 0.5 × 0.5 × 0.5 m), composed of a combination of live and dead *Pocillopora damicornis* (a bushy coral), were constructed on the reef flat (3 m depth) and amongst the rubble on the reef base (12–15 m depth) of North Vicki's Reef, Lizard Island. In each habitat 24 experimental patch reefs were positioned along the reef/sand interface with adjacent patches being separated by 5 metres. Four experimental treatments were assigned to these patch reefs (two predator exclusion treatments and two control treatments) and the fate of 20 randomly selected newly settled *P. amboinensis* on each treatment replicate was monitored for up to 10 days. Limited availability of newly metamorphosed *P. amboinensis* and the logistics of tagging each fish meant that all replicates could not be established at the same time. The experimental patch reefs were therefore arranged into sets of 4 treatments in each of two habitats (representing 160 tagged fish), with one or two replicate sets of reefs being established per day. Six replicates of each treatment in each habitat were established and monitored.

Cages (0.75 × 0.75 × 0.9 m) were used to manipulate the access of different sized predators to patch reefs. Cages consisted of a rigid steel frame and galvanized steel mesh. Two different mesh sizes were used: fine mesh (12.5 mm square mesh) to exclude all large predators, but allow access for small predators; coarse mesh (40 mm hexagonal mesh) that permitted access by a wider suite of predators, while excluding larger predators. Cage controls, consisting of a frame with 12.5 mm square mesh covering two opposite sides and the roof, were used to control for the structure of the cage while providing access for all predators. The cages were placed over the experimental patch reefs and forced 100–150 mm into the substratum. Uncaged (open) patch reefs allowed predators of all sizes access to the experimental patch reefs.

Small *Synodus* spp. (Synodontidae), *Pseudochromis fuscus* (Pseudochromidae) and *Parapercis cylindrica* (Pinguipedidae) were observed within the fine mesh cages, while small *Cephalopholis boenak* (Serranidae), *Thalassoma lunare* (Labridae) and larger *P. fuscus* were observed within the coarse mesh cages during the experiment. These species are all known to prey upon juvenile fishes (Stroud 1982, Sweatman 1984, Martin 1994, Beukers and Jones 1998), indicating that the cages were successful in manipulating predator access to the experimental patch reefs.

Newly metamorphosed *P. amboinensis*, which had not experienced any reef-based predation, were used in the experiments. These were collected from light traps (Stobutzki and Bellwood 1997) positioned with the collection slots at one metre depth 16m above the sea floor, adjacent to North Vicki's Reef during November 1998. Six batches of 160 randomly selected *P. amboinensis* were tagged in the laboratory using a single fluorescent elastomer tattoo (Northwest Marine Technologies Inc.). Each batch of tagged fish was collected from a single night's light trapping, and tagged and deployed within 24 hours of capture, with the exception of two blocks of treatments that were stocked from the same night's light trap samples. To enable an examination of the selectivity of predation for pre-settlement growth history, a random sample of 30 *P. amboinensis* was also collected from these latter light trap samples and frozen for later age analysis.

From each batch of tagged *P. amboinensis*, 20 randomly selected fish of the same tag colour were allocated to each of the four caging treatments within each habitat. This density is within the natural range that occurs during the recruitment period at Lizard Island (where densities on similar sized patches may reach up to 65 recruits, McCormick, unpubl.). Fish on neighbouring patch reefs were marked with a different colour so that migration from adjacent reefs could be distinguished. Prior to releasing the tagged fish, the patch reefs were cleared of all resident fishes using a fence net, small hand nets and the fish anaesthetic clove oil (Munday and Wilson 1997).

Before releasing tagged fish onto the experimental patch reefs each cage was enclosed in a fine mesh bag to prevent escape or predation during the initial acclimatisation period. Fish were released onto the experimental reefs through an access door located in the top of the mesh bag. These bags were left over the patch reefs for at least six hours. This allowed the tagged *P. amboinensis* time to settle to the experimental reefs in the absence of any predators, and reduced the disturbing influence of experimental manipulation. Initial censuses after bag removal indicated that the majority of tagged *P. amboinensis* were associated with the experimental coral patch.

Experimental patch reefs were censused daily and the number of tagged *P. amboinensis* remaining on each reef, or that had migrated from the patch reefs, were recorded. An area of approximately 5 m radius surrounding each reef was also searched daily for any tagged fish that had migrated from their initial reef. The location of any tagged fish that were detected away from the experimental reefs was marked with labelled surveying tape. The distance from this location to the nearest experimental patch reef with fish tagged the same colour as the migrant fish was measured to the nearest 0.1 m. During daily censuses, predatory fishes and all other species on the patch reefs were counted.

Each block of treatments (i.e. 4 treatments at 2 habitats), established from the same day's light trap catch, was concluded when the survivorship of tagged *P. amboinensis* on one of the patch reefs fell below 50%. This was necessary to facilitate a meaningful comparison of the individual life history characteristics of survivors from each treatment. All surviving fish were collected with clove oil and a small hand net. The blotted wet weight (±0.0001 g) and standard length (±0.1 mm) were recorded.

Otolith analysis

Analyses of growth history from otolith microstructure were restricted to the survivors from the two blocks of longest duration. These two replicates were chosen as they were initiated on the same day and concluded after ten days. Therefore, the tagged fish from each replicate were from the catch of the same nights' light-trap samples and had been exposed to reef based predation for the same period of time. The otolith microstructure of a random sample of 30 *P. amboinensis* from the catch of the same night's light-trapping was also examined to provide a comparison to the characteristics of the surviving fish from each treatment. The sagittae were extracted from each fish and transverse sections through the nucleus were produced using the protocol of Wilson and McCormick (1999). Otolith increment width was used as a proxy for fish growth, which is based on the assumption that there is a strong relationship between somatic and otolith growth. This is a generally held assumption that is supported by a number of studies (Thorrold and Hare 2002) and a positive linear relationship between otolith radius and standard length has been demonstrated for *P. amboinensis* (11.3–18.4 mm SL, $n = 292$, $r = 0.86$; Hoey 1999). Furthermore, the formation of daily otolith increments has been validated in recently settled *P. amboinensis* (Pitcher 1988) and it is assumed that pre-settlement increments are also deposited on a daily basis. A conspicuous settlement mark, which is formed in this species (Wilson and McCormick 1999), was used as a reference point for the division between larval and post-settlement increments. Otolith increment widths were obtained using the image analysis package Sigma Scan™.

Analyses

The influence of individual size at settlement on survival of naturally settled and monitored recruits was examined using an analysis of variance (ANOVA), by dividing the 152 monitored fishes into 3 approximately equal sized groups: those that survived less than 1 d; those that survived between 2 and 8 days; those that survived 9 or more days. A Tukey's (HSD) means comparison was used to examine the nature of significant difference found by ANOVA. To examine whether the three categories of survivors were associated with different features of the fish or benthic communities a canonical discriminant analysis (CDA, Tabachnick and Fidell 1996) was undertaken. CDA identifies a number of trends in the data-set (canonical variates) that maximally discriminate among the identified groups (in this case, survival categories) and sequentially explain less of the variance in the data-set. Trends in the original variables (fish and benthic variables) are represented as vectors given by correlations of these variables with the canonical variates (also known as total structure coefficients). Ninety-five percent confidence clouds were plotted around the category centroids. The assumption of multivariate normality was examined prior to analysis.

To avoid biasing mortality estimates from the caging experiment, survival of *P. amboinensis* was calculated by excluding tagged fish which had moved. Survivorship trajectories of newly settled *P. amboinensis* were compared between habitats and among caging treatments using repeated measures MANOVA. Due to the assumptions of this test, the initiation of the experiment could not be included in the trajectory estimates since the variance was zero (i.e. $t_0 = 100\%$ survival). Because of the importance of survival during the first day to overall trajectories, values at $t = 0.1$ d were linearly extrapolated from the difference between t_0 and t_1, and this value was used as the start value of the trajectories.

The total number of newly settled *P. amboinensis* that were observed to have migrated from the experimental patch reefs was compared between habitats and caging treatments using ANOVA. Interaction terms are not included in the model due to the split plot design of the experiment.

The relationship between the survival of newly settled *P. amboinensis* on experimental patch reefs and the assemblage of fishes that had subsequently settled or migrated to the reefs was examined using a full stepwise least squares multiple regression. This approach allowed us to not only test the existence of an effect, but also estimate the strength of that effect, and compare the importance of one factor relative to that of another factor (Philippi 1993). Rather than use multiple regression to obtain a predictive equation, here we use it as a hypothesis-generating technique. Separate regressions were performed for the reef base and reef flat due to differences in the fish assemblages within each habitat. To standardize between experimental replicates (i.e. blocks) survival was calculated as the number of tagged individuals that remained on the patch reefs after a period of 3 days. This is because blocks of treatments took different amounts of time for one of the treatments to reach 50% mortality (3 to 10 d). The species assemblage on each patch reef was restricted to those individuals that were present on the reefs during the first three days. Residual examination was used to assess assumptions of normality, linearity and homoscedasticity. Condition number values (Philippi 1993) were used to assess the collinearity of variables.

Three measures of fish condition were calculated for the survivors from the two blocks of treatments of longest duration (these blocks happened to have been established on the same day, from the same light trap samples): relative size at settlement; growth rates for the 7 d prior to settlement; and growth for 10 d after settlement. Relative size at settlement and pre- and post-settlement growth rates were estimated from otolith microstructure. The distribution of relative size at settlement and pre-settlement growth rates for each combination of caging treatment and habitat was compared to that of a random sample of 30 *P. amboinensis* collected from the same night's light trapping using correspondence analysis (row standardised), followed by a posteriori Kolmogorov–Smirnov two-sample tests, with a Bonferonni correction factor for multiple tests. Correspondence analysis describes the similarity among frequency distributions (Greenacre 1984), where points closer together are more similar. It is a highly effective, though under-utilised, technique for the analysis and display of contingency tables. Correspondence analysis in its simplest form can be thought of as doing a principal component analysis on frequencies so that distances are represented in chi-squared space (rather than Euclidean space). Vectors are used to indicate the direction and strength of trends in each of the growth and size categories used in the analysis. The light trap sample represented the variability in attributes prior to the action of post-settlement processes. Individuals from both replicate blocks were pooled (for each treatment by habitat combination) since both were established from a random sample of *P. amboinensis* collected using light traps on the same night.

Results

Natural mortality rates and the predictors of survival

Newly settled *P. amboinensis* exhibited a type III mortality curve (Caley 1998), sustaining a 0.25 per capita mortality rate d^{-1} over the first day. Mortality then dropped to 0.078 per capita mortality rate d^{-1} for the next 5 days, after which it reached a relatively constant 0.013 until the end of the monitoring period 2 d later (Fig. 1).

Size at settlement was found to have a significant influence on survival ($F_{2,149} = 5.64$, $p = 0.004$). Individuals that survived 9 or more days were significantly larger at settlement than those that died within the first day (12.3 vs 11.9 mm SL), but were not significantly different in size than fish that survived between 2 and 8 d (12.1 mm SL).

A canonical discriminant analysis was used to examine which fish community or habitat characteristics best described the survival of these three survival categories of fish (i.e. 1 d, 2–8 d and > 9 d, Fig. 2). Individuals that survived less than one day were associated with areas of low topographic complexity, containing sand and rubble and male *P. amboinensis*. These males were largely non-nesting. Those that survived between 2 to 8 d were associated with areas of high topographic complexity, where the compact bushy coral *Pocillopora damicornis*

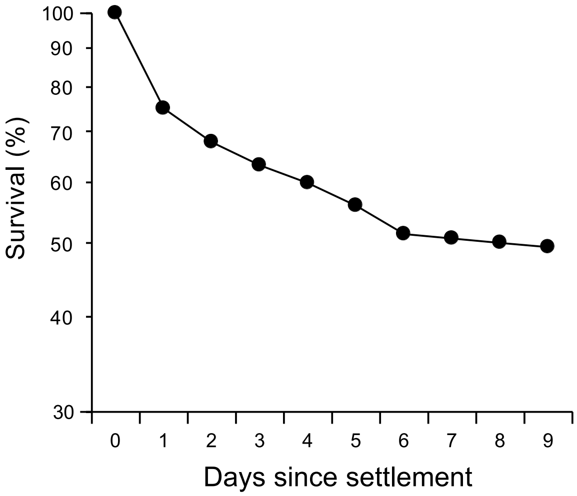

Fig. 1. Survival of naturally settled recruits of *Pomacentrus amboinensis* at Lizard Island. Data obtained from monitoring the fates of 152 tagged fish.

was common. Those that survived the longest (9 days or longer) were associated with more open, branching corals and high densities of territorial benthic pomacentrids (Fig. 2).

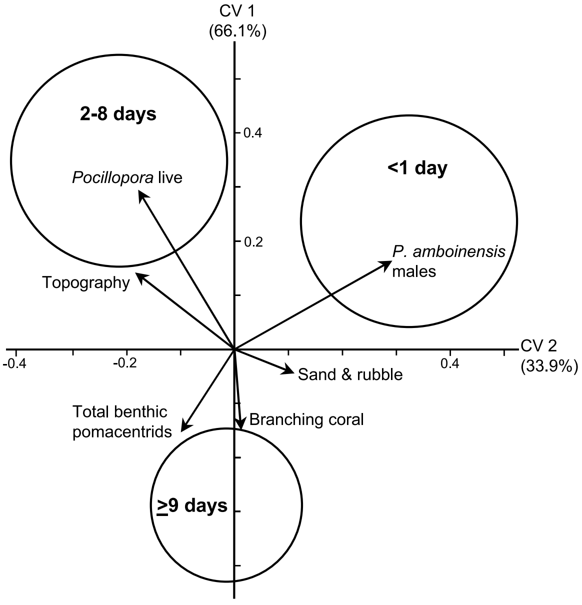

Fig. 2. Comparison of the fish and benthic assemblage characteristics that were associated with the survival of naturally settled *Pomacentrus amboinensis*, placed into 3 survival categories (< 1 d, 2–8 d, ≥ 9 d). A canonical discriminant analysis (a type of multivariate means comparison) displays the difference in benthic characteristics and the fish community among survival categories. The direction and importance (as indicated by vector length) of trends in the most influential fish and benthic variables are also displayed together with 95% confidence ellipses.

Predator assemblages between habitats

There was a greater abundance of potential predators of recruits at the reef base than the reef flat (Fig. 3). A total of 169 potential predators was identified at the reef base, while only 80 were identified on the reef flat during five 25 × 2 m visual transects. A broad size range of potential predators was present in both habitats, ranging from the small dottybacks, *Pseudochromis fuscus* (50 mm SL)) through to the much larger and transient emperors, *Lethrinus* sp. (350 mm SL). *Cephalopholis boenak* (Serranidae) and *Lethrinus* sp. (Lethrinidae) were present in relatively high numbers at the reef base, yet were totally absent on the reef flat (Fig. 3). *Pseudochromis fuscus* (Pseudochromidae) and *Parapercis cylindrica* (Pinguipedidae) were also more abundant at the reef base than on the reef flat (Fig. 3).

Migration from caged treatments

A total of 86 newly settled *P. amboinensis* out of 960 that were tagged and released were detected away from the experimental patch reef onto which they were released. There was no significant difference in the level of migration between the caging treatments ($F_{3,38} = 1.029$, $p = 0.390$) or between the reef flat and reef base ($F_{1,38} = 0.003$, $p = 0.958$). The number of individuals that had migrated from their reef ranged from 0–35% (mean 8.96%) with distances moved ranging from 0.1–6.9 m (mean 1.6 m ± 0.36). Patch reefs from the two experi-

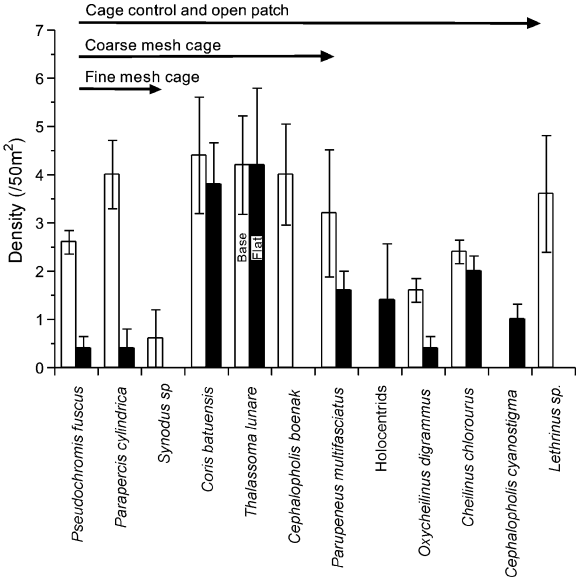

Fig. 3. Density of potential predators of newly settled fishes on the reef base (open bars) and reef flat (solid bars) habitats (±SE). Predators are ordered with respect to average size. The size of predators that can enter each of the experimental is also given.

mental blocks examined in detail below showed low levels of movement (1.50 fish/reef ±0.43 SE).

Survivorship among cage treatments

There were no differences in the survivorship of newly settled *P. amboinensis* between the four caging treatments, with high levels of variability among replicates within a habitat ($p = 0.597$, Table 1; Fig. 4a, b). Not surprisingly there was a significant difference through time, with 26 to 30% of individuals dying within the first day after the start of the experiment. Given that the cages appeared to successfully exclude different size-classes of predators, these results suggest that the different suites of predators had a similar impact on the numbers of *P. amboinensis* surviving this early post-settlement period. The mortality trajectories were found to differ between the two habitats (Table 1, significant Time × Habitat interaction). Fish on patch reefs on the reef flat sustained higher mortality than those on the reef base (Fig. 4c).

Species associations

The densities of juvenile and adult *P. amboinensis* that colonised the experimental reefs accounted for 53.3% of the variability in the survival of newly settled *P. amboinensis* in the reef base habitat (Table 2). The density of females and juveniles were both negatively associated with recruit survival, accounting for 29.3% and 15.9% of the total variability in the survival of *P. amboinensis* recruits respectively. In contrast, the density of male *P. amboinensis* was positively associated with recruit survival, accounting for 8.1% of the variability. These males were exclusively using these habitat patches as nesting sites. The fish community in the vicinity of the experimental patch reefs did not significantly account for any of the variability in the survival of experimental *P. amboinensis* on the patch reefs in the reef flat habitat.

Pre-settlement growth, size and survival

Ten days after the start of the experiment, pre-settlement growth rates of fish from most of the experimental treatments were significantly different from a random sample of the light trap caught fish that were initially placed on the patch reefs (Fig. 5). After correction for multiple tests, analysis indicated that the initial light trap sample differed in the distribution of pre-settlement growth histories from all but 3 habitat-by-treatment combinations: the fine mesh cages at the reef base, the cage controls on the reef flat, and the open coral on the reef base. Moreover, the distributions of the first two of these treatments differed considerably from the initial light trap distribution (K-S test, $p < 0.025$, $p < 0.05$ respectively), but not at the more conservative test level used to maintain an experimentwise error rate of 0.05. Generally, the initial pre-settlement growth distribution had a much greater proportion of individuals with low growth rates, than those that survived 10 d on the reef, suggesting a selective loss of individuals that grew slowly in the second half of their larval life. This is exemplified by the pre-settlement growth distributions from the coarse mesh cages at the reef base and flat (Fig. 6). There was some indication that the pre-settlement growth distribution of fish from the coarse mesh cages on the reef base differed from those of the fine mesh cages at the base (K-S test, $p < 0.025$), and the coarse mesh cages on the flat (K-S test, $p < 0.05$, Fig. 5, 6).

Similar analyses on a proxy for size at settlement, otolith radius to the settlement mark, suggest that loss was selective with respect to this trait in the coarse mesh cage at the reef base (Fig. 7, 8). Survivors after 10 d from the coarse mesh cage at the reef base had a higher proportion of large individuals and fewer small individuals compared to what was originally placed on the

Table 1. Comparison of survival of newly settled *Pomacentrus amboinensis* between two habitats (reef base and reef flat), among four treatments (coarse mesh, fine mesh, cage control, open patch reef), giving between (a) and within (b) subject effects. Results summarize a repeated measures MANOVA. P-values < 0.05 in bold.

(a) Between subject effects	df		Mean square	F	p
Habitat	1		791.626	0.6886	0.4188
Treatment	3		742.604	0.6460	0.5967
Habitat × Treatment	3		812.343	0.7067	0.5619
Error	16		1149.550		
(b) Within-subject effects	df_{effect}	df_{error}	Wilk's λ	F	p
Time	9	8	0.013726	63.87097	< **0.0001**
Time × Habitat	9	8	0.207713	3.39052	**0.0499**
Time × Treatment	27	24	0.093174	1.11480	0.3962
Time × Habitat × Treatment	27	24	0.068576	1.33656	0.2379

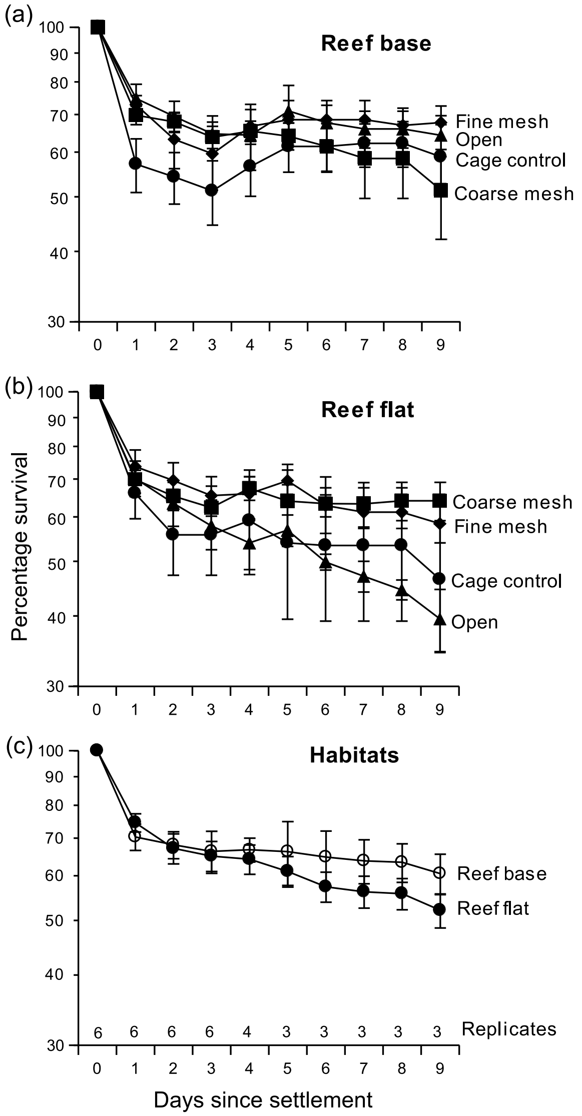

Fig. 4. Survival of newly settled *Pomacentrus amboinensis* from each of the four caging treatments on (a) the reef base, (b) the reef flat, and (c) an overall mean trend for each habitat. Standard errors are shown. The number of replicate reefs that contribute to the mean for each day since the establishment of the experiment are also given.

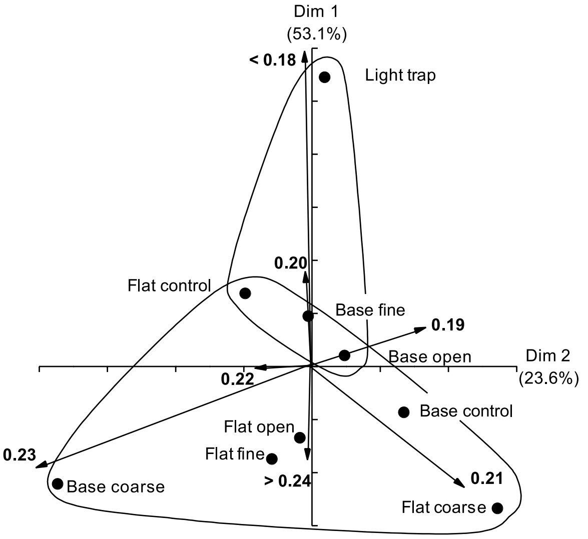

Fig. 5. Comparison of the frequency distributions of pre-settlement growth rates of *Pomacentrus amboinensis* among 4 experimental treatments in two habitats (reef flat and base) and a random sample of the light-trap-caught fish that were used to establish the treatments (representative of their initial distribution prior to loss). A correspondence analysis (row standardised) was used to compare the growth-frequency distribution patterns. Habitat-by-treatment combinations that are close to each other are similar with regard to the pattern of relative growth-frequency distributions. Vectors show the direction and magnitude of influence of various growth frequency categories (labels represent the highest value in growth-frequency categories in 0.1 μm d^{-1} intervals). Superimposed on the correspondence analysis are the results of a posteriori Kolmogorov–Smirnov two-sample tests. Treatment combinations in the same ellipse do not differ in growth-frequency distributions at an experimentwise error rate of 0.05 (Bonferroni $\alpha' = 0.01$).

experimental reefs (i.e. light trap sample), or were found on open patch reefs at the reef flat (Fig. 8).

Predator mediated relationship between pre- and post-settlement growth

The relationship between pre-settlement growth rate (mean increment width for 7 d prior to settlement) and

Table 2. The influence of cohabiting species on the survival of newly settled *Pomacentrus amboinensis* on experimental patch reefs at the reef base. Survival and fish assemblage estimates were obtained 3 d after the start of the experiment. The analysis was performed using a stepwise multiple regression. Given are the partial correlation coefficients, the regression coefficients for the cumulative model, Mallow's C(p)–a model selection diagnostic, and p-value of a test of whether the parameter significantly deviates from zero. The dependent variable was days survived, while the independent variables available for selection by the model were: *P. amboinensis* recruits, *P.amboinensis* juveniles, *P.amboinensis* females, *P.amboinensis* males (nesting), total plankton-feeding pomacentrids (excluding *P. amboinensis*), *Coris batuensis*, *Pseudochromis fuscus*, *Cephalopholis boenak*, *Parapercis* sp.

Variable	Partial r	Model r^2	C(p)	p-value
P. amboinensis females	– 0.541	0.293	8.048	0.006
P. amboinensis juveniles	– 0.399	0.452	3.738	0.022
P. amboinensis males	0.285	0.533	2.520	0.077

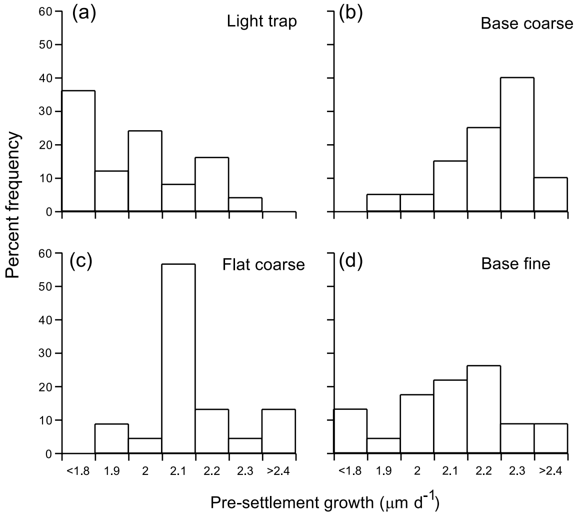

Fig. 6. Comparison of the pre-settlement growth rate frequency distributions of a random sample of fish from (a) the light trap catch used in the experiment (n = 25) with the survivors after 10 d from 3 experimental treatments that display the range of differences in frequency distributions among treatments-by-habitat combinations: (b) coarse mesh cage at the reef base (n = 20); (c) coarse mesh cage on the reef flat (n = 22); (d) fine mesh cage at the reef base (n = 23). Growth is represented as the mean increment width of the last 7 increments prior to the settlement check.

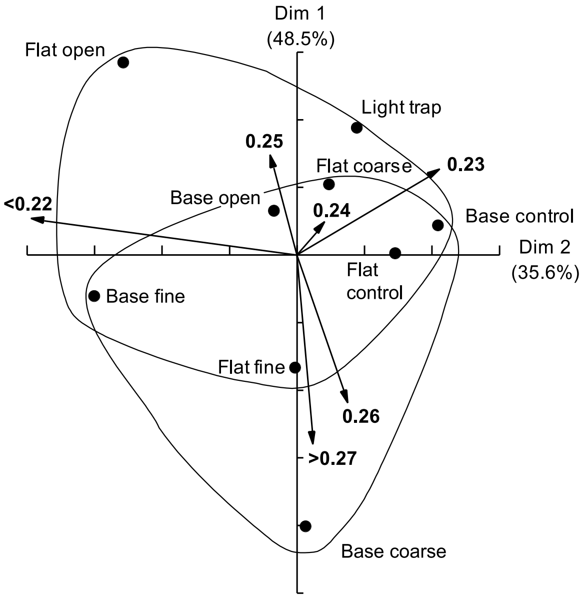

Fig. 7. Comparison of the distributions of size at settlement of *Pomacentrus amboinensis* among 4 experimental treatments in 2 habitats (reef flat and base) and a random sample of the light-trap-caught fish that were used to establish the treatments (representative of their initial distribution prior to loss). Length from the nucleus to the settlement check on a transverse section of the sagitta is used as an estimate of fish size at settlement. A correspondence analysis compares the size-frequency distribution patterns. Vectors show the direction and magnitude of influence of various size-frequency categories (labels represent the highest value in size-frequency categories that increment by 0.1 mm intervals). Superimposed on the correspondence analysis are the results of a posteriori Kolmogorov–Smirnov two-sample tests. Treatment combinations in the same ellipse do not differ in size-frequency distributions at an experimentwise error rate of 0.05.

post-settlement growth (mean increment width for the 10 d after settlement) was examined among experimental treatments. Significant positive relationships were found in both habitats for the fine mesh cages, cage controls and open patch reefs (Fig. 9), suggesting that if a fish grew fast prior to settlement, it was likely to maintain this advantage during early post-settlement life. However, this relationship was reversed in the coarse mesh cages in both habitats (Fig. 9). Fish in the coarse mesh treatment with slower pre-settlement growth rates excelled beyond fish that had the initial growth advantage at settlement.

Discussion

Juvenile mortality schedules

Accurate estimates of early post-settlement mortality are necessary to determine the relative contributions of pre- and post-settlement processes in structuring coral reef fish populations. Mortality in the first few hours to weeks following settlement has the potential to markedly influence the size and structure of the juvenile population. Unfortunately, estimates of mortality immediately after the settlement event are extremely difficult to obtain because most fish settle at night (Robertson et al. 1988, Sweatman and St John 1990, Holbrook and Schmitt 1997, 2002). Although a number of studies have described mortality schedules over the early juvenile life period, few have included the day of settlement and those immediately following. Most previous studies have used fish that have been settled for a short but often unknown period of time in experimental manipulations (Jones 1987, Booth 1995, Carr and Hixon 1995, Beukers and Jones 1998). These juveniles are no longer naïve to the action of reef predators, and may have already learnt a variety of behavioural and chemosensory survival strategies (Mathis and Smith 1992, Larson and McCormick in press) that will influence experimental results. Moreover, many studies have used artificial habitats (Caley and St John 1996, Nemeth 1998) and the dynamics in these habitats may not always mimic those of the natural environment (Connell 1997).

Mortality of newly settled *P. amboinensis* was found to be greatest in the first day after settlement (25%), with another 25% being lost in the following 5 d before slowing to minimal levels. This is best described by a

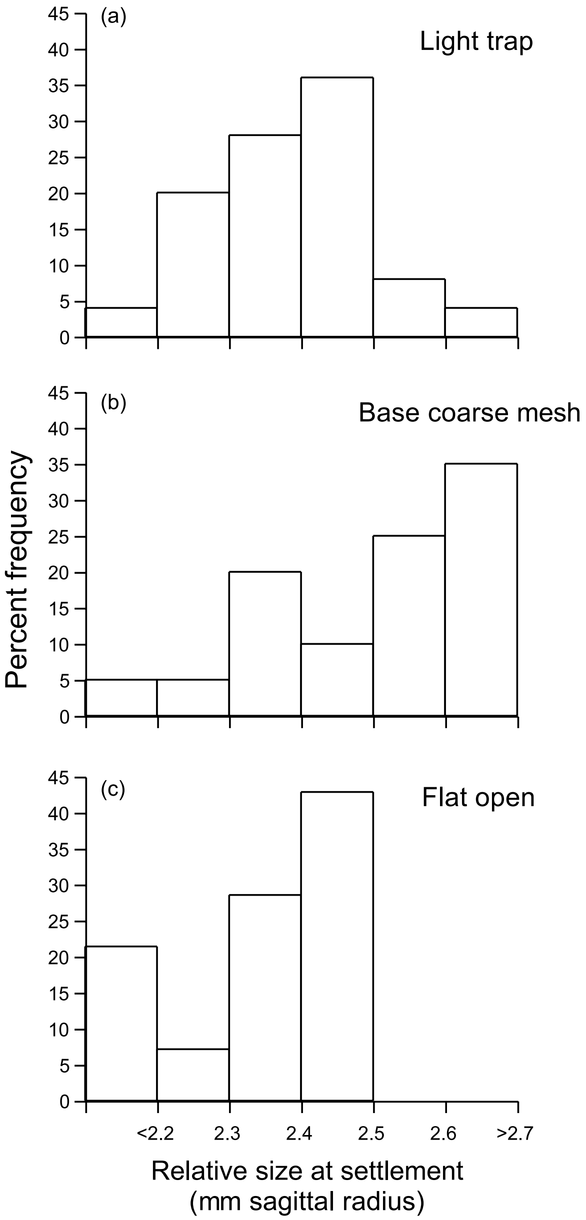

Fig. 8. Comparison of the relative size at settlement frequency distributions of a random sample of fish from (a) the light trap catch used in the experiment (n = 25) with the survivors after 10 d from 2 experimental treatments: (b) coarse mesh cage at the reef base (n = 20); (c) open coral patch on the reef flat (n = 18). Growth is represented as the mean increment width of the last 7 increments prior to the settlement check. Length from the nucleus to the settlement check on a transverse section of the sagitta is used as an estimate of fish size at settlement.

type III mortality curve, suggesting that the per capita mortality risk is higher immediately after settlement than only a few days later. Selection to reduce per capita mortality should therefore be strongest at this early stage. Caley (1998) found that only 19% of the available post-settlement survival curves for tropical fishes showed this type III trajectory, with the majority displaying type II curves. Type II curves represent a constant per capita mortality, and hence selection that is constant over the juvenile life-history period studied. However, all of the 9 studies for which mortality curves could be derived used juveniles that had been settled for an unknown period of time, or started monitoring a number of days after settlement, suggesting that they probably missed the period when per capita mortality is highest. The finding of high per capita mortality at or soon after settlement by a number of recent studies suggests that the prevalence of type III mortality curves may be underestimated. The present study may also be guilty of under-estimating early mortality, with newly settled fish being first recorded the morning following nocturnal settlement, after they had been on the reef and exposed to potential nocturnal predators for up to 10 hours and diurnal predators for 1.5 to 3 hours.

In the present study there was little difference in the mortality schedules between manipulated treatments and naturally settled fish monitored over the whole reef. This suggests that the naïve light trap caught fish, all of which had initiated metamorphosis up to 24 h prior to being placed on the experimental patches, were as susceptible to predation as naturally settled fishes, which were settling as they initiated metamorphosis. This lack of an effect of time since the start of metamorphosis may be because *Pomacentrus amboinensis* does not undergo major morphological changes at metamorphosis, or undergo an ontogenetic shift in microhabitat association (McCormick and Makey 1997, McCormick et al. 2002). However, many species undergo major changes at metamorphosis, and can naturally experience a number of relatively rapid microhabitat shifts within days of settlement (McCormick and Makey 1997). In these cases, time since the initiation of metamorphosis may need to be factored into experimental designs to allow realistic interpretation of mortality schedules.

Mortality of *P. amboinensis* was higher on the reef flat than at the reef base, in keeping with other studies that have monitored the survival of juveniles of this species (Jones 1997). This trend is somewhat surprising, given that we recorded greater abundance and diversity of potential predators at the reef base. The larger home ranges of many predators may have precluded us from obtaining an accurate estimate of predator densities in a single survey. The cryptic habits of many predators may also hamper accurate census (Stewart and Beukers 2000), though this is more likely to influence the magnitude of the abundance estimates rather than the relative difference between habitats. In the present study, habitats did not differ noticeably in topographic complexity, which may influence sampling biases (Fowler

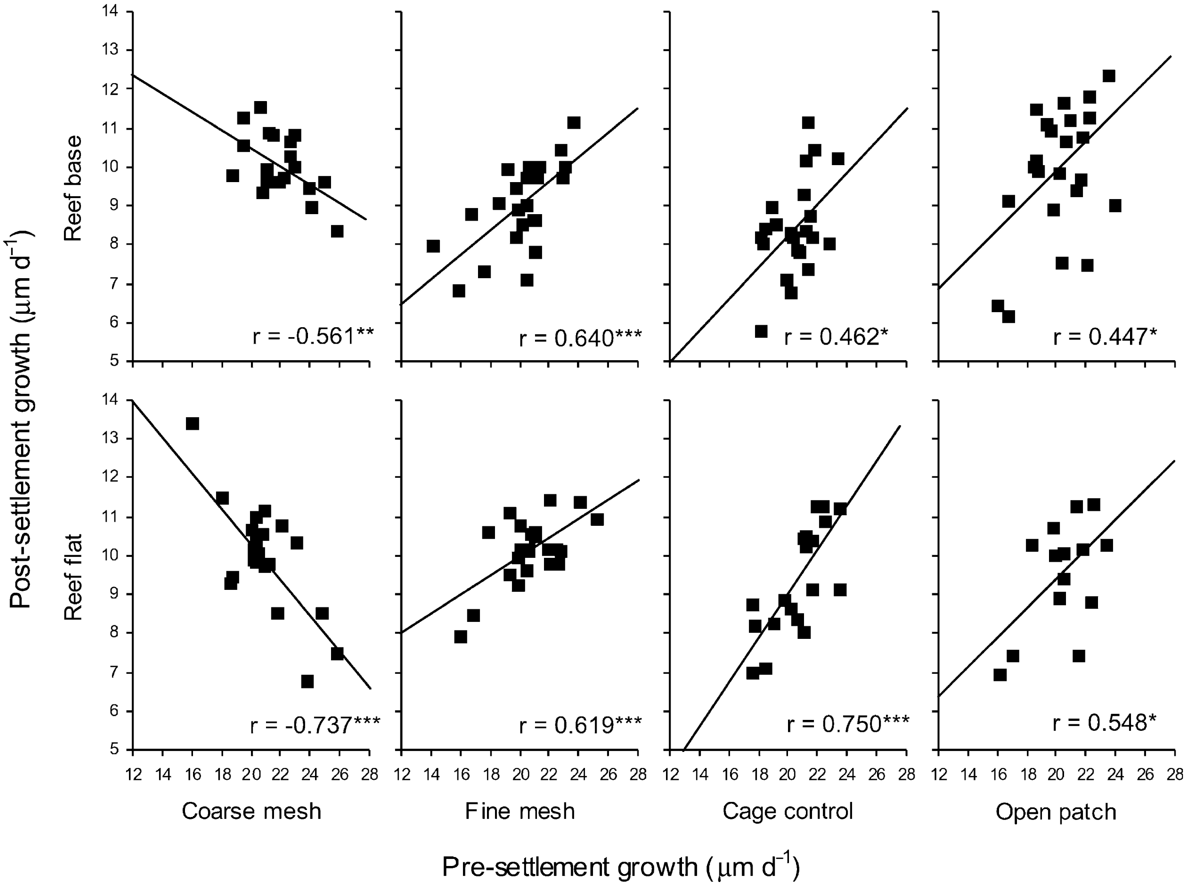

Fig. 9. Comparison of the relationships between pre-settlement growth (mean otolith increment width for 7d prior to settlement) and post-settlement growth (mean increment width for the 10d after settlement) of *Pomacentrus amboinensis* among the 4 experimental treatments in two habitats (reef base and reef flat). Correlation coefficients are given (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

1987). Whatever the reason, the lack of correspondence between enumerated predators and mortality suggests that visual counts were not an accurate indicator of the intensity of predation on newly settled fish.

Surprisingly there was no difference in the mortality schedules of newly settled *P. amboinensis* exposed to different size-classes of predators (i.e. among treatments). Although the levels of predation within each cage were not measured, observations indicated that the cages were successful in manipulating the size of the predators that could gain access to each cage. This suggests that that the small predators gaining access to the fine mesh cages may have a significant impact on the early post-settlement survival of *P. amboinensis.* This conclusion is supported by two studies which found that small or juvenile predators are more likely to prey on recently settled fish than larger adult predators (Martin 1994, Holbrook and Schmitt 1997).

Biological and physical correlates of survival

Both the topography of the microhabitat selected by the newly settled *P. amboinensis*, and the fish assemblage in the area, correlated with survival. Recruit survival was enhanced at settlement sites high in topographic complexity and cover of branching corals. Topographically complex sites may have a higher number of potential shelter sites, and the strike efficiency of predators may be reduced in complex habitats (Beukers and Jones 1997, Nemeth 1998). Studies that have manipulated habitat complexity on a scale that corresponds to potential shelter sites have found that increased reef complexity enhances survival (Caley and St John 1996, Beukers and Jones 1998, Nemeth 1998).

Interestingly, the total abundance of territorial benthic-feeding pomacentrids was positively related to the survival of *Pomacentrus amboinensis* recruits. The presence of male *P. amboinensis* who were guarding nests on the experimental reefs at the reef base also enhanced survival. The territorial nature of these fishes may reduce access by predators to the newly settled fish. Territorial damselfishes are known to influence the small scale distribution of other fish species that may prey on benthic eggs and small fish (Ceccarelli et al. 2001; such as the wrasse, *Thalassoma lunare*), particularly during the reproductive season when adults are guarding eggs. It is noteworthy however that the relationship between the abundance of territorial fishes and recruit survival was weak in the present study, suggesting that the determinants of survival are complex.

Examination of recruit persistence on the experimental patch reefs suggested that the presence of female and juvenile conspecifics reduced survival of the newly settled fish on the patch reefs at the base of the reef. The densities of these conspecifics explained 45% of the variability in the survival of *P. amboinensis* recruits. These negative relationships may be related to the presence of strong size-related dominance hierarchies on the experimental reefs. Many juvenile damselfishes, including *P. amboinensis*, form loose social groups in which strong size-related dominance hierarchies develop (Jones 1987). These size hierarchies have been shown to control the access to food by sub-ordinates (Forrester 1991) resulting in reduced growth of individuals of lower social status (Jones 1987, Forrester 1990, Booth 1995). Survival has been shown to increase (Booth 1995), decrease (Forrester 1990) or be unaffected (Jones 1987) by the presence of conspecific juveniles. Juvenile conspecifics may control sub-ordinates' access to favourable refuges making them more susceptible to predation.

Our monitoring study of newly settled individuals suggested that the factors that influenced post-settlement survival changed rapidly after settlement, thereby modifying the original patterns established at settlement (recorded the morning after settlement). Tagging individuals and tracking their fate on a daily basis enabled us to attribute changes in species and microhabitat associations to differential mortality rather than to ontogenetic shift in microhabitat usage. Fish that died within the first 24 hours after their initial census (i.e. on the morning of settlement) were associated with the density of *P. amboinensis* males (largely non-nesting) and a higher proportion of sand and rubble in their settlement site. Those that survived between 2 to 8 days were associated with areas of high topographic complexity, where the bushy coral *Pocillopora damicornis* was common. However, those that survived beyond 9 days were associated with branching corals, in areas of slightly lower topographic complexity that had high numbers of territorial herbivorous pomacentrids. Some of the trends in survival described above may be explained by individuals rapidly outgrowing the protection afforded to them by firstly the sand and rubble habitat, and then the tight bushy *Pocillopora* coral heads. A similar argument was used by Connell and Jones (1991) to explain the results of an experiment that manipulated habitat topography and examined survival of juveniles of the temperate blenny *Forsterigion varium*. These researchers found that the topographic complexity of the habitat was positively related to the survival probabilities of individuals. Most other studies have attributed the distribution of recruits to microhabitat preferences at settlement and it is likely that the contribution of differential mortality to these patterns has been extensively underestimated.

Selectivity of predation

A within-cohort comparison of fish placed under varying predation regimes found that predation was selective for size at settlement and larval growth under certain circumstances. Monitoring the fate of naturally settled fish suggested that predators removed proportionally more small individuals in the first two weeks after settlement, with small differences in size at settlement (< 1 mm) improving survival probabilities. Whether this apparent selection was due to active selection for small individuals by the predators, or was simply due to the enhanced susceptibility of smaller recruits is unknown. The manipulation of predator access to recruits by cages supported this finding, but also underscored the complexity of selectivity in a natural system. Recruits protected by coarse mesh cages at the reef base showed strong evidence for large size at settlement being advantageous for post-settlement survival up to 10 days. In contrast, fish that were large at settlement were under-represented on the open patch reefs on the reef flat, suggesting predation was selective for large individuals. These trends may simply be a function of the relatively small sample sizes that made up the distributions, which were constrained by logistics. Alternatively, the result may indicate that predators vary in their selectivity for prey. The predator assemblage differed between reef flat and base habitats so it is likely that a differing suite of predators accessed particular treatments depending upon habitat.

Few studies of marine fish have explored the importance of size to survival probabilities at settlement. Those that have obtained varied results. In an elegant study, Searcy and Sponaugle (2001) found that the relative size at settlement (i.e. sagittal otolith length) did not influence the survival probabilities of the wrasses *Thalassoma bifasciatum* and *Halichoeres bivittatus*. In a laboratory experiment, McCormick and Kerrigan (1996) also found no evidence of size-selective predation by an ambush predator (*Synodus variegatus*) on newly metamorphosed goatfish *Upeneus tragula*. Carr and Hixon (1995) found equivocal evidence for size-selective mortality for juveniles of the damselfish *Chromis cyanea*, although their results were difficult to distinguish from the consequences of density-dependent growth (Sogard 1997). Two studies on the domino damselfish *Dascyllus albisella*, found evidence for size selective predation of new recruits. In a laboratory experiment Groll (1984, cited in Booth 1995) found that small recruits (< 12 mm TL) were more likely than larger recruits to be captured by the cornet fish, *Fistularia* sp. and stomatopods. Likewise, in a tagging experiment with the same species, Booth (1995) found that smaller recruits had a higher risk of predation in one year of a two-year study. Interestingly, Booth found that survival of the smallest individuals increased with group size, showing that survival was density-dependent. Obviously, there are many factors that influence individual risk and these may vary spatially and temporally. When size relates to social status, behaviour and performance, it is likely to have survival consequences.

Mortality of *P. amboinensis* recruits was also selective toward pre-settlement growth, as measured by the widths of the last 7 increments prior to the settlement mark. Almost all treatments in both habitats displayed distributions of pre-settlement growth that suggested that individuals with the lowest pre-settlement growth had been lost from the population. This finding supports two studies that have documented the survival benefits of fast growth rates at metamorphosis and settlement. Shima and Findlay (2002) studied a temperate kelp bass *Paralabrax clathratus* and found that fast growing larvae experienced enhanced survival during the first 5 d after settlement relative to slower growing larvae. Searcy and Sponaugle (2001) found that *Halichoeres bivittatus* that exhibited high larval growth rates had the highest probability of surviving their first 14 days on the reef. By contrast, Searcy and Sponaugle (2001) also found that the survival of another wrasse, *Thalassoma bifasciatum*, over the same time period was not associated with larval growth. Similar findings were made by Vigliola and Meekan (2002), who compared the size distribution of light trap caught individuals of the damselfish, *Neopomacentrus filamentosus*, to sequential samples of the same cohort 1 to 3 months after settlement. They found no evidence of selective mortality toward pre-settlement growth or size one month after settlement. While a finer scale resolution was not the purpose of the study, the coarse monthly sampling interval makes it impossible to determine whether this sampling period may have masked ontogenetic changes in selective mortality. It is possible that mortality may have been selective early after settlement, but the direction of selectivity may have changed one or more times up to the first monthly sample, thereby masking the initial selective mortality. Interestingly, Vigliola and Meekan (2002) found that individuals that started larval life as large larvae at hatching had a better chance of surviving at least 2 months on the reef, demonstrating that events prior to hatching can have a lasting influence on juvenile survival.

Predation as a disruptor of growth advantages

To date research has suggested that fish which display high growth rates prior to settlement will maintain this growth advantage into settled life (Tupper and Boutilier 1995, Searcy and Sponaugle 2000, Vigliola and Meekan 2002). Similar examples exist for other vertebrates (Berven 1990, Meekan et al. 2003). There have been surprisingly few demonstrations of naturally occurring compensatory growth (Atchley 1984), where a larva that has performed below average during the larval phase, has performed above average after metamorphosis or vice versa. The present study is the first study conducted in the field to document growth compensation. Almost all demonstrations of growth compensation in marine fishes to date have involved fishes that have been nutritionally disadvantaged in an experimental manipulation, overcompensating upon re-feeding. This appears to be a common physiological response to reduced rations in fishes (Love 1980, Sogard and Olla 2002) and also occurs in other vertebrates (Arendt 1997, Hervant et al. 2001).

In the present field experiment feeding conditions were not manipulated, but rather the size of predators that had access to the focal species. A positive relationship between larval and post-settlement growth was found in the open and cage control treatments that are exposed to all sizes of predators. Likewise, the same relationship was found within the fine mesh cages, where only small predators could gain access. This positive relationship is not surprising and is commonly predicted given the relative advantages of a large size that comes coupled with a high growth rate at settlement. It is generally assumed and found that growth advantages gained in the larval phase are maintained and accentuated during the juvenile phase (Sogard 1997) as is consistent with the 'growth-mortality' model originally proposed for larval fishes (Leggett and Deblois 1994).

It is noteworthy, therefore, that this relationship not only breaks down in the coarse mesh cage, but is the reverse to that found in the other treatments. Moreover, it is consistent between the reef flat and reef base habitats, despite the differences in predator composition and abundance. Those *P. amboinensis* that had the highest larval growth rates were disadvantaged in some way within the coarse-mesh cage, resulting in low growth. Conversely, those fish that grew slowly as larvae were able to compensate for this poor start and displayed accelerated growth. This growth compensation will benefit individuals that had low larval growth from the coarse-mesh cages since they were exposed to growth-selective mortality. The most parsimonious explanation is that this growth compensation is facilitated by an organism that is able to gain access through the coarse mesh, but is unable to enter the fine mesh cages.

One explanation for this finding involves a change in recruits' behaviour under a perceived predation risk. A recent experimental study found that another tropical damselfish, *Pomacentrus moluccensis*, reduced the distance it foraged from shelter and the time spent foraging, which resulted in reduced growth, when exposed to piscivores (A. Abdulla, James Cook University, unpubl.). Other studies have demonstrated similar modifications to feeding patterns under the threat of predation leading to reduced foraging, or necessitating individuals to forage on lower quality resources, culminating in lower growth (Werner et al. 1983). In the present experiment it may be that common predatory species such as the moon-wrasse, *Thalassoma lunare,* and the cod *Cephalopholis boenak*, which could enter the coarse mesh cage, are effectively reducing the competitive asymmetry among recruits on patch reefs. Larger individuals are no longer willing to venture as far from the coral refuge thereby reducing their foraging efficiency. Interference competition for zooplankton food has been shown for the damselfishes *Dascyllus aruanus* and *D. albisella*, where larger individuals that are higher in social status deny smaller fish access to larger, more nutritious prey items (Coates 1980, Forrester 1991, Booth 1995). By predators disrupting the social hierarchy, smaller individuals may have a higher probability of gaining access to food of higher quality than would normally have been eaten by the larger fish. This additional food may also be assimilated more effectively by the digestive physiology of the smaller individuals that are used to more restricted rations, leading to enhanced growth. Increases in digestive efficiency have been previously attributed to restricted food consumption (Boyce et al. 2000) and can lead to an over-compensation in growth and storage once access to food is improved (Love 1980).

Why this pattern of growth compensation is not seen in the treatments open to all types of predators may be due to the disruptive or masking influences of a predator regime that includes a variety of species of assorted sizes, which utilize a range of different strategies to capture prey. No matter what the mechanism underlying the different patterns of larval and post-settlement growth among treatments, the evidence presented does show that important processes are being masked by the action of a diverse predator pool. Biological interactions can radically change the physiological response of an organism to its environment and modify the affect of prior history in influencing this response.

Conclusions

This study underscores the strong links between life history events in the larval phase and those during and after metamorphosis and settlement; and reinforces the importance of these links to cohort success. Body condition, manifest as size and larval growth history, are determined by processes prior to metamorphosis and can determine the survival of juveniles. Metamorphosis and settlement can be very expensive energetically for coral reef fishes, as it is for other taxa, since many species do not appear to feed during this period of morphological and physiological restructuring that may take hours to days to complete (McCormick et al. 2002). Some species of fish have been shown to use 50% of their lipid stores to fuel this transition (Nursall and Turner 1985, Youson 1988). This cost, together with the challenges of establishing oneself in a new habitat, mean that the risk of death through predation at or soon after settlement are exacerbated for larvae in poor body condition.

The present study highlights the complexity of the processes that influence the early post-settlement growth and survival of coral reef fishes. The outcome of who survives this initially high selective pressure is dependent upon attributes of both the prey and predators (Rice et al. 1997), and the physical and biological environment into which they settle. There may be selectivity for various life-history attributes, such as size and growth, but the outcome of these interactions will be governed by the history of the prey, and the selectivity of the predators they encounter. The prey's ability to avoid or evade a predator will be strongly influenced by the refuge space available within the habitat and access to it, which may be socially controlled. This hints at a complexity of processes that may underlie the dynamics of many species with complex life histories at this crucial life history transition.

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