# Biological and physical correlates of settlement and survival for a coral reef fish, *Pomacentrus amboinensis* (Pomacentridae)

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**Abstract** Processes that occur at and immediately after the settlement can have a major affect on the population dynamics of marine organisms with complex life cycles. We explore the factors that influence the location of settlement and the survival for a common tropical damselfish, *Pomacentrus amboinensis*. Monitoring of individuals tagged on the morning of settlement showed that 36 % of the variability in small-scale abundance of newly settled *P. amboinensis* could be explained by the presence of conspecifics that had settled within the last week, while benthic substratum characteristics only explained 14.6 %. Characteristics of the benthos and fish assemblage in the vicinity of the newly settled *P. amboinensis* accounting for only 21.5 % of the variability in survival. Cover of branching corals accounted for 6.1 % of the variability in survival among recruits, while topography and total benthic feeding damselfishes accounted for 5.1 and 4.5 % respectively. Interestingly, the only variable to positively influence both settlement and survival was topography. In general, evidence suggests that the biological and physical aspects of the microhabitat that promote settlement are not necessarily the same that promote highest survival.

**Keywords** settlement, post-settlement survival, tropical reef fish, topography, microhabitat composition

## Introduction

The transition from pelagic larvae to settled juvenile represents a key life history threshold for marine organisms with complex life cycles. For many of these organisms, it is the patterns established at settlement, modified by post-settlement processes such as predation and competition, which determine the distribution of the population overall. Despite the importance of settlement, it is unclear for most marine organisms what aspects of the biological community or physical environment influence where an individual settles.

For coral reef fishes, mortality is high immediately after settlement and trajectories typically follow a negative exponential, such that 57 % may die within the first 2 days (Steele and Forrester 2002; Webster 2002; Doherty et al. 2004). The processes that determine which juveniles survive the initially high mortality are complex and include physiognomy of the habitat (e.g. topography and shelter) and the competitor and predator assemblage in the vicinity of the settlement site. Overlying these factors is the prior history of the individual that will influence initial habitat choices, biological interactions that ensue, and whether these interactions result in an enhancement or reduction of performance characteristics and survival (Searcy and Sponaugle 2000; Shima and Findlay 2002; Hoey and McCormick 2004; McCormick and Hoey 2004). To date, few studies have tracked the fate of newly settled individuals and related this to the biological and physical characteristics of the habitat into which they settled. Such information is crucial if we are to understand the processes underlying the distribution patterns of older life stages of fishes.

The broad aim of the present study is to explore the factors that influence the location of settlement and subsequent survival of a common tropical reef fish, in relation to the environmental characteristics and the fish community that prevail. The study uses focal sampling of individually identified newly settled fish to address these objectives at a scale that is relevant to the life stage.

## Material and Methods

*Study species and locality*

The focal species of this study was the common Indo-Pacific damselfish *Pomacentrus amboinensis* (Bleeker, 1868; Pomacentridae). Tagging studies have shown that it moves little after settlement (McCormick and Makey 1997; Hoey and McCormick 2004; McCormick and Hoey 2004) which makes it ideal for a study which tracks the fate of individual fishes. The species inhabits areas of rubble, particularly where there is a mixture of live and dead tightly branching coral species such as *Pocillopora damicornis* (Linnaeus, 1758) (e.g. Öhman et al. 1998), and is consequently usually found at the interface between the reef and patches of sand (McCormick personal observation). *P. amboinensis* settles relatively evenly over the reef (Milicich et al. 1992) and may occupy a wide range of depths if the appropriate microhabitat is available. In the field, 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).

This 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 December 1998. North Vicki's Reef has an extensive reef flat at a depth of approximately 3 metres, which gradually slopes down to the reef base at a depth of 12 –15 metres. The study site was a 500m x 150m section reef extending from the reef flat to the reef base with a mixture of live and dead *Pocillopora damicornis*, rubble and sand patches making it ideal habitat for *P. amboinensis*.

*Biological and physical correlates of settlement*

We used a multivariate hypothesis-generating approach to explore the physical and biological factors that may influence where an individual settles. The assumption underlying this analysis is that the mortality that has already occurred since settlement, has not markedly biased the fish's distribution and abundance patterns. The study site was searched daily between 0730 – 0900h for newly settled *P. amboinensis* over a 2-week period. Identification of newly settled individuals was based on their size, colouration and behaviour (McCormick and Makey 1997). Upon finding a newly settled fish, fishes of all species were counted in a circle of 1m radius centred on the newly settled fish. Fishes were categorized as either recruit (settled within the last month ~ 25mm standard length), juvenile or adult. *Pomacentrus amboinensis* densities were broken down further to include the following categories: settled within the last week (~13-18mm SL); settled 1-week to 1-month (18 - 25 mmSL); juvenile (25-45 mm SL, with 45 mm SL being the minimum size of sexual maturity, McCormick unpublished data); females (>45 mm SL and not male); male. Topography of the circular plot was quantified using the length ratio of a 2m 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 the tape passed through the centre of the plot. Percentage cover of benthic substrata was estimated using a 1 x 1m grided-quadrat (121 intercepts) placed in the center of each plot. Benthic substrata under the intercepts were placed into one of 16 categories, chosen to include all the major benthic growth forms: 5 hard coral groups (*P. damicornis* live; *P. damicornis* dead but standing; branching live; massive live; encrusting live); soft coral; sponge; bushy red algae (*Amphiroa* sp.); turfing algae; sand; sand and rubble (~ 50% each); coarse rubble (average size > 10cm); fine rubble (average size $\leq$ 10cm). Water depth of the plot was also recorded.

*Survival of newly settled fish*

Survival of the newly settled fish identified daily in the monitoring study was assessed and related to the neighbouring fish assemblage, benthic characteristics and individual fish size. Upon finding a newly settled individual it was captured using a hand-net, transferred into a small clip-seal plastic bag, measured using calipers ($\pm$ 0. 1mm) and tagged with an individually identifiable fluorescent elastomer tattoo (Northwest Marine Technologies Inc.) using a 29 gauge hypodermic needle. Fish were left in the plastic bag at the exact site of capture for 5 minutes (for full recovery) prior to release. Upon release all fish returned to the site of capture and started to feed within 30s. A detailed 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 had a 100 % retention rate (Hoey and McCormick in press). The location of the tagged fish was marked with a numbered label, and recorded onto a detailed map of the study area. 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 5m radius of where the fish had been initially tagged. If the tagged individual was not found it was recorded as dead. The location was also checked on the day following the individual's disappearance.

*Analyses*

Least square multiple regression analysis was used to examine the physical or biological factors that influence where an individual settled. 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. Residual examination was used to assess assumptions of normality, linearity and homoscedasticity. Data was linearized by a log 10 transformation where necessary. Condition number values (Philippi 1993) were used to assess collinearity of variables. Because the end result is conditional on the independent variables entered, only benthic and fish assemblage variables that were likely to influence the abundance of newly settled fish were included in the analyses. Stepwise model selection was used to determine the model that accounted for greatest proportion of the variability in the number of newly settled fish. To minimise the ratio of observations-to-independent variables separate regressions were undertaken using the benthic and fish assemblages within the 1m diameter plots as independent variables (number of newly settled fish being the dependent variable). A further regression was then undertaken on the benthic and fish independent variables that had been selected as the best predictors of the density of newly settled *P. amboinensis* from the previous models.

The influence of benthic cover and the fish assemblage on the survival of natural recruits was also examined using stepwise multiple regression. Because only 55% of the monitored individuals died during the monitoring period (i.e. 45% lived for an unknown period of time beyond 9-15d), only 83 observations were used in this analysis (with survival values of 1 - 14d).

## Results

*Biological and physical correlates of settlement*

A model incorporating the fish assemblage accounted for more of the variability in the abundance of newly settled *Pomacentrus amboinensis* than a model which included benthic variables and a measure of topography (Table 1). Multiple regression indicated that 36% of the variability in newly settled *P. amboinensis* could be explained by the presence of conspecifics that had settled within the last week. Total predator density within the 2 m diameter circular plots was positively associated with the density of new recruits, explaining 5.5% of the variability, suggesting that these were attracted to the same habitat characteristics as newly settled *P. amboinensis*, or the newly settled fish themselves. The presence of adult *Dascyllus reticulatus* (Richardson, 1846; Pomacentridae), older *P. amboinensis* recruits (that settled between one week and 1 month previously) and juveniles accounted for only a minor amount of the variability in densities of newly settled *P. amboinensis* (Table 1a). Benthic variables only explained 14.6% of the variability in newly settled *P. amboinensis*. Topography accounted for 9% while the percent cover of live *Pocillopora damicornis* accounted for 2.9% of this variability (Table 1b).

*Predictors of survival*

Of the variables that appeared to influence the location of settlement in *P. amboinensis*, only 3 were significantly associated with fish survival, accounting for only 15.7% of the variability (Table 2). The cover of branching corals accounted for 6.1% of the variability in survival among recruits, while topography and total benthic pomacentrids accounted for 5.1 and 4.5% respectively. All had positive associations with recruit survival. The abundance of male *P. amboinensis* also enhanced survival, although this accounted for only a small amount of the variability (3.2%). The cover of sand and rubble was negatively related to recruit survival, and accounted for only 2.6% of the variability (Table 2). It is note-worthy that predators and potential competitors for food (total planktonic-feeding pomacentrids) did not explain a significant amount of variability in recruit survival.

Table 1. Benthic (a) and fish (b) assemblage variables that explain some of the variability in the abundance of newly settled *Pomacentrus amboinensis*. Results are from stepwise multiple regression analyses. 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. Abbreviations: WLW, settled within the last week; WLM, settled between 1week and 1 month ago.

| | Fish variables | Partial r | Model $r^2$ | C(p) | *p*-value |
|---|---|---|---|---|---|
| a. | *P. amboinensis* WLW | 0.601 | 0.361 | 18.490 | 0.0001 |
| | Predators | 0.235 | 0.416 | 6.117 | 0.0002 |
| | *Dascyllus reticulatus* adults | 0.152 | 0.439 | 2.122 | 0.0149 |
| | *P. amboinensis* WLM | 0.114 | 0.451 | 0.852 | 0.0687 |
| | Older *P. amboinensis* juveniles | 0.094 | 0.460 | 0.607 | 0.1290 |
| b. | Benthic variables | | | | |
| | Topography | 0.300 | 0.090 | 7.136 | 0.0002 |
| | *Pocillopora damicornis* live | 0.170 | 0.119 | 4.203 | 0.0285 |
| | Sand & rubble | 0.167 | 0.146 | 1.506 | 0.0304 |

## Discussion

Monitoring patterns of natural settlement indicated that *Pomacentrus amboinensis* displayed preferences for sites with specific fish-community and microhabitat characteristics. Such settlement site specificity is commonplace among tropical reef fishes and has been found for the recruits of many species that have been studied at an appropriate spatial scale (e.g. Eckert 1985; McCormick and Makey 1997; Booth and Wellington 1998; Öhman et al. 1998; Ault and Johnson 1998; Holbrook et al. 2000). Overall, the composition of the fish community where *P. amboinensis* settled explained more variability in the densities of newly settled fish than the benthic cover, at least at the small ($1m^2$) scale at which sampling was undertaken. Only 3 benthic variables accounted for a significant proportion of the variability in the abundance of newly settled *P. amboinensis.* Not surprisingly, topography, which represents a summation of the structure of the settlement site, accounted for the most variability (9 %). The cover of the bushy coral *Pocillopora damicornis*, and sand and rubble only accounted for 5.6 % of *P. amboinensis* abundance. The generally low discriminatory power of benthic cover found in the present study is in keeping with a multi-species study of microhabitat choice. Sale et al. (1984) found that benthic cover had a poor ability to classify sites chosen for settlement by the 14 most common species of reef fish examined within One Tree lagoon. They concluded that the chosen sites differed only slightly in the relative proportion of different

Table 2. A summary of the influence of benthic cover, topography and species assemblage in the vicinity of naturally settled *Pomacentrus amboinensis* on their survival. Results are from a stepwise multiple regression on a reduced dataset. 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. Mutually exclusive variables available for selection by the model were: depth, topography, total *P. amboinensis* recruits, *P. amboinensis* juveniles, *P. amboinensis* females, *P. amboinensis* males, *Dascyllus* sp. Adults, *Dascyllus* sp. recruits, total benthic-feeding pomacentrids (excluding *P. amboinensis*), total plankton-feeding pomacentrids, labrids, predators, fine rubble, coarse rubble, sand & rubble, sand, *Pocillopora* live, *Pocillopora* dead, branching live coral, encrusting live coral, massive coral, soft coral. Number of monitored replicates for this analysis was 83.

| Variable | Partial r | Model $r^2$ | C(p) | *p*-value |
|---|---|---|---|---|
| Branching coral | 0.247 | 0.061 | 0.173 | 0.025 |
| Benthic Pomacentrids | 0.213 | 0.106 | -1.647 | 0.047 |
| Topography | 0.225 | 0.157 | -3.899 | 0.033 |
| *P. amboinensis* males | 0.180 | 0.189 | -4.641 | 0.081 |
| Sand and Rubble | -0.159 | 0.215 | -4.782 | 0.119 |

benthic categories and stated that any suitable site could be occupied by individuals from a range of species. It appears that the specific location chosen at settlement may be based more on the resident fish community than the microhabitat structure of the settlement site.

In the present study, *P. amboinensis* settled where other recently settled fish and juveniles of the same species were present. Such aggregation at settlement has been found previously for social damselfish and has been attributed to the dilution effects of group living reducing per capita mortality (Sweatman 1985). Aggregative settlement could be the result of a number of processes. Fish may be individually attracted to the same unique combination of microhabitat characteristics, leading to an accumulation of juveniles over the settlement period. Given the broad range of microhabitats used by *P. amboinensis* at settlement, suggested by the low importance of all benthic attributes to settlement locality, this hypothesis is unlikely. An alternative hypothesis is that at settlement late stage larvae are attracted to cues released from the juvenile conspecifics. In a field manipulation, Sweatman (1988) found that the humbug damselfish *Dascyllus aruanus* (Linnaeus, 1758) used olfactory cues released by conspecifics to choose settlement sites. This is a likely mechanism underlying the aggregative settlement of *P. amboinensis*.

Interestingly, sites preferentially selected by *P. amboinensis* were also places where predators were most common on a local within-site scale. Two studies have found a similar relationship between the densities of coral reef fish predators and prey on patch reef and contiguous reef habitats (Beukers and Jones 1998; Stewart and Jones 2001). An aggregative response of predators to prey densities has been shown to be a mechanism underlying predator-induced density-dependent mortality (Anderson 2001).

Both topography of the microhabitat selected by the newly settled *P. amboinensis*, and the fish assemblage in the area, influenced who survived. Recruit survival was enhanced at settlement sites high in topographic complexity and cover of branching corals. Studies suggest that this relationship occurs because topographically complex sites have a higher number of potential shelter sites, and strike efficiency of predators is reduced in complex habitats (Beukers and Jones 1998, 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 *P. amboinensis* recruits, as was the density of male *P. amboinensis*. McCormick and Hoey (2004) found a similar trend for *P. amboinensis* on the experimental patches at the reef base, where piscivores were most abundant. It is likely that the territorial nature of these fishes reduces access by predators of newly settled fish (Green 1992). 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*: Linnaeus, 1758), particularly during the reproductive season when adults are guarding eggs. It is noteworthy however that these relationships were weak, suggesting that the determinants of survival are complex.

The characteristics that stimulate settlement are not necessarily the same ones that maximize survival. This is supported by further work by McCormick and Hoey (2004) who examined the species and habitat associations of *P. amboinesis* during the first two-weeks after settlement. They found that individuals that survived less than one day were associated with areas of low topographic complexity, containing sand and rubble and non-nesting male *P. amboinensis*. Those that survived between 2 to 8d were associated with areas of high topographic complexity, where the compact bushy coral *Pocillopora damicornis* 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. A number of tagging studies on newly settled individuals of this species have shown movement is limited to approximately 1m$^2$ during the first month on the reef (McCormick and Makey 1997; Hoey and McCormick 2004; McCormick and Hoey 2004). This suggests that this pattern is the result of habitat-related differential survival rather than post-settlement migration.

The factors that influence the settlement and survival of reef fishes are multivariate. The relative importance of biological and physical variables to the resulting distribution of juvenile populations is very difficult to ascertain as both settlement and predation are instantaneous events, difficult to observe in the field. By tracking the fate of newly settled individuals, and relating this to the fish community into which they settled and microhabitat characteristics of the site, the present study has been able to explore the potential relative importance of key biological and physical factors. Evidence suggests that the biological and physical aspects of the microhabitat that promote settlement are not necessarily the same as those that promote highest survival.

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