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## Behavioural mediation of the costs and benefits of fast growth in a marine fish

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Trade-offs between the costs and benefits of growth are thought to be mediated by behaviour, whereby rapid growth is associated with greater predation mortality because of increased foraging effort. We tested this hypothesis by collecting young *Pomacentrus amboinensis* using light traps and settling them onto patch reefs where their behaviour and survivorship were monitored for 24 h. One month later, individuals of the same cohort were collected from shallow reefs and released onto patch reefs where their behaviour and survivorship were monitored for 6 days. At settlement young fish suffered high (60% in 24 h) mortality that preferentially removed larger, faster-growing individuals. However, we could find no evidence that foraging behaviour contributed to this selective mortality. In contrast, 1 month later the same cohort underwent negative size-selective mortality where the smallest, slower-growing fish were preferentially removed by predators. Larger fish spent more time foraging, were more aggressive, swam greater distances and chased more fish than smaller individuals. Thus, consistent individual differences in behaviour contributed to patterns of mortality, but in a way that involved no apparent trade-off with growth. For *P. amboinensis*, consistent variation in growth may be maintained by spatial and temporal differences in the selective regime within the reef environment.

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Body size is a central determinant of many of the vital life history parameters of animals such as competitive ability, fecundity and survival. Life history models show that fast growth, resulting in large body size, can be beneficial so that we might expect that individuals that are capable of maximizing food intake and growth to attain the greatest body size will be favoured by selection (Stearns 1992). However, outside the laboratory, maximal growth is found only rarely, with growth rates tending to vary both within and between species (reviewed in Arendt 1997), or even with respect to status within a social hierarchy (Wong et al. 2007). These observations and some theoretical considerations suggest that there are also some costs to rapid growth and that these may limit the rate at which animals may grow (Werner & Anholt 1993; Lima 1998; Lankford et al. 2001; Munch & Conover 2003).

It has been suggested that trade-offs between the costs and benefits of growth are mediated by behaviour, whereby rapid growth is associated with greater predation mortality because of increased foraging effort (Werner & Anholt 1993; Lima 1998; Sih et al. 2004; Stamps 2007;

Biro & Stamps 2008). As all animals are prey, at least during their early life history stages, greater foraging effort can increase the visibility of prey to predators with a concomitant increase in the probability of mortality. Evidence for the role of behaviour comes from a variety of sources (reviewed in Stamps 2007; Biro & Stamps 2008), including recent studies in lake systems that have shown that fast-growing rainbow trout, *Oncorhynchus mykiss*, that had high foraging rates were preferentially removed by predators (Biro et al. 2004, 2006). This occurred because fast-growing fish were more likely to use habitats that were more productive in terms of food resources, but placed the fast-growing fish at greater risk of predation than the habitats used by slow-growing individuals (Biro et al. 2006). Such trade-offs are thought to explain the evolution of submaximal growth rates in wild populations of fishes (Biro et al. 2004, 2006) and other animals (Stoks et al. 2005).

These studies have shown that individuals exhibiting fast growth are not intrinsically more successful; however, the extent to which behavioural trade-offs are commonplace is unknown. Coral reef fishes provide an ideal model system to examine the role of behavioural mediation in influencing the benefits and costs of fast growth. Upon arrival in reef habitats from the plankton, young fishes face a very uncertain future. Naïve settlers are faced with a new suite of predators that consume the majority of arrivals, creating mortality bottlenecks (Doherty et al. 2004; Almany & Webster 2006). Survival during juvenile life may not be a matter of

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chance, but can depend on the size and growth rate of individuals (Searcy & Sponaugle 2001; Vigliola & Meekan 2002; Hoey & McCormick 2004; Vigliola et al. 2007; Gagliano et al. 2007; McCormick & Meekan 2007). The prevalence of selective mortality in this environment provides a unique opportunity to examine the role of behaviour as a determinant of growth and survivorship.

We examined the behaviour, growth and survivorship of a common reef damselfish, *Pomacentrus amboinensis*, at Lizard Island on the Great Barrier Reef (GBR), Australia, during the first month after settlement from the plankton. We collected young fish upon arrival near the reef using light traps (Doherty 1987). These fish were settled onto small patch reefs and their behaviour and survivorship monitored for 24 h, a time of intense predation mortality (Almany & Webster 2006). This experiment was repeated 1 month after settlement when individuals of the same cohort were collected from shallow reefs and distributed on the same patch reefs. Their behaviour and survivorship were monitored for 6 days. The results emphasize the dynamic nature of events in the early juvenile phase and their importance in shaping not only population density, but also the distribution of life history characteristics in reef fish populations.

## METHODS

### Study Area and Species

This study was conducted at Lizard Island, on the northern part of the GBR (14°40'S, 145°28'E) during November and December 2006 and was approved by the Animal Ethics Committee of James Cook University Australia. Our study species, *P. amboinensis*, is a common coral reef fish in the Indo-Pacific. Juveniles settle predominantly at night in a wide variety of habitats on the northern GBR (Pitcher 1988). The highest densities are found in association with small reef patches at the base of shallow (<10 m depth) reefs. Settlement from the plankton to adult reef habitats of these omnivorous pomacentrids (and many other reef fishes) occurs between October and January around new moon at this locality.

*Pomacentrus amboinensis* has a pelagic larval duration of 15–23 days and settles from 10.3 to 15.1 mm standard length (SL; Kerrigan 1996). At settlement the juvenile body plan is largely complete and the fish undergo a rapid change in body pigmentation (in less than 12 h). Tagging studies have shown that *P. amboinensis* is relatively site attached (McCormick & Makey 1997) and moves only small distances (<1 m) for some months after settlement. Owing to its abundance, size, development and relatively sedentary nature, it is an ideal species for both field observations and experimental manipulations.

### Experimental Design

#### Experiment 1

We collected late-stage pelagic larvae of *P. amboinensis* using moored light traps (see Figure 1 in Meekan et al. 2001 for design). The traps were anchored approximately 100 m from the nearest reef in 16 m of water at dusk and left in place overnight. Catches were emptied from the traps the following morning at 0700–0730 h. Fish collected from the traps were immediately transported to the laboratory where *P. amboinensis* was separated from other species and maintained in 15-litre aquaria of aerated sea water.

A random sample of *P. amboinensis* (about 100 individuals) was anaesthetized (using a clove oil and sea water solution) then killed by cold shock in a slurry of ice and sea water and immediately preserved in alcohol. The remaining fish of this species were then sorted into three size classes (large: 12.0–12.9 mm SL; medium: 11.0–11.9 mm standard length SL; small: 10.0–10.9 mm SL).

Individuals were placed into small, clip-seal polyethylene bags, and then tagged through the bag with a subcutaneous fluorescent elastomer tag (Northwest Marine Technologies, Shaw Island, WA, U.S.A.) using a 27 G hypodermic needle, so that fish could be individually identified during the experiment. Tagging has no significant effects on mortality or growth of *P. amboinensis* over a 2-week period and tags have a 100% retention rate (Hoey & McCormick 2006). After tagging, each fish was photographed against a scale bar and SL measured from this image using the computer program Image Tool 3.0 (<http://dssdx.uthscsa.edu/dig/jitdesc.html>).

Once tagged, one each of the small, medium and large *P. amboinensis* were placed into labelled 9-litre plastic bags with aerated sea water for a 1–3 h recovery period. They were then transported to the field where a bag of fish was released onto each one of 10 small patch reefs of coral rubble (30 × 30 × 30 cm) that were constructed on a sand flat just offshore of the research station. Reefs were deployed in rows in 4–5 m water depth around 50 m from the nearest area of natural reef. Prior to release of the individually tagged fish, the patch reefs were cleared of all resident fish using an anaesthetic (a clove oil and sea water solution) and hand nets. When recovered, these fish were placed on nearby natural reefs.

Fish were released on coral patches in the morning and a small wire cage (about 40 × 40 × 40 cm, 12 mm mesh size) was placed over the patch to allow the tagged fish to acclimate to their new surroundings while being protected from predators. Cages were removed 1–3 h after release of the fish between 1400 and 1700 hours (dusk at about 1845 hours). We recorded their behaviour in the afternoon of the same day approximately half an hour after the cage had been removed and again in the morning of the following day. At each of these times, each fish was observed for 3 min and the number of bites, chases of and by other fish (including identity of conspecifics), distance moved, area on reef where resident and distance the individual ventured from the reef were recorded. Observation of behaviour was aided by the use of a magnifying glass (4×) by the diver. Approximately 24 h after release on the reefs surviving fish were collected using anaesthetic (clove oil), returned to the laboratory, killed by cold shock, as above, and individually preserved and measured using callipers. This experimental protocol involving 30 fish was repeated four times during the November study period. On each occasion, fish were haphazardly selected for the trial from light trap collections that were made the previous night, so that fish included in the four trials spanned most of the new moon settlement pulse. Of the 120 fish that were tagged, 13 were not included in deployments owing to poor condition following transport from the laboratory to the field. This gave a total number of 107 fish that were used in this experiment.

#### Experiment 2

During 9 days in December 2006, we collected newly recruited *P. amboinensis* from small reefs in shallow (4–5 m) water near the research station. Our collections targeted those individuals of a size range likely to have settled during the previous new moon in November (i.e. fish from the settlement pulse used in experiment 1). These fish were brought back to the laboratory and were placed in aquaria and sorted into size classes (small: 11.0–14.4 mm SL; medium: 14.5–17.9 mm SL; large: 18.0–21.4 mm SL). Fish were individually tagged using elastomer tattoos as described above and then one individual of each of the size classes was placed into each of 10 numbered plastic bags with aerated sea water for a 1–3 h recovery period. Fish were then transferred back to the field where the three individuals (small, medium and large) in each bag were released on each of the same small patch reefs of coral rubble that had been used in the November experiment.

As in the previous experiment, fish were released in the morning and given 3–4 h to acclimate to their new environment within a mesh cage placed over the reef. Their behaviour was recorded in the afternoon of the same day (after the cage had been removed) and in the afternoon for the next 6 days. The variables recorded during these observations were the same as those recorded for the November experiment. Additionally, an estimate of the amount of time spent in aggressive (chasing), passive (hiding, chased) and feeding behaviours was recorded. After 6 days at liberty on reefs, surviving fish were collected using anaesthetic, returned to the laboratory, killed by cold shock, as above, and individually preserved and measured using callipers. This experimental protocol was repeated three times during the December study period. Of the 90 fish that were tagged, three were not included in deployments because of predation by fishes during release on reefs. This gave a total of 87 fish that were used in this experiment.

#### Otolith Analysis

Sagittal otoliths were analysed to derive age and growth data for fish collected in experiment 1. Briefly, sagittae were removed, mounted on glass slides using a thermoplastic cement (Crystalbond, [www.crystalbond.com](http://www.crystalbond.com)), ground on lapping film to produce thin transverse sections containing the nucleus, and viewed under transmitted light with immersion oil at 1000× magnification. Daily increments within each otolith were measured to the nearest 1 µm along the longest axis of each section using an image analysis system.

Daily deposition of increments in this species has been validated by a tag–recapture study (Pitcher 1988). We assumed that the increment closest to the core of each otolith was formed on the day of hatching (Campana & Neilson 1985; Wellington & Victor 1989).

The SL of each fish on every day between hatching and capture was back calculated from its otolith using the biological-intercept method (Campana 1990), which assumes that otoliths grow in linear proportion to body length (Vigliola et al. 2000). Evidence for this assumption was provided by the strong linear relationship between otolith radius and fish length for this species (unpublished data). The biological intercept was set at hatching where mean otolith radius and fish size were estimated at 3.6 µm and 3.1 mm SL, respectively (Kerrigan 1996).

#### Data Analysis

In both experiments 1 and 2, size and age frequency distributions of surviving and dead fish were compared using Kolmogorov–Smirnov (K–S) tests. Where sample sizes of dead fish were very low (experiment 2) we constructed a randomization test where we randomly assigned a probability of survival based on observed frequencies to each size class, then recalculated the median size for surviving and dead fish. This was repeated 10 000 times. We then tested the hypothesis that the observed median size of dead fish was greater than or equal to that derived from the random assignment.

Where the results of these tests were nonsignificant (experiment 1, see below) we did additional analyses of trajectories of size-at-age and growth rate back calculated from otoliths to confirm the result. These data records were compared for fish that survived experiment 1 and fish from collections made by light traps using repeated measures MANOVAs (Chambers & Miller 1995). To aid interpretation, all data sets of daily size-at-age and growth were pooled to 3-day intervals prior to analysis.

At settlement (experiment 1) and 1 month after settlement (experiment 2) behaviours of the different size classes of fish

(small, medium and large) and fish that survived and those that died were analysed using canonical redundancy analysis (Legendre & Legendre 1998). This is an analysis technique for investigating the relationship between multiple predictor (size class) and response behaviours (number of bites taken, chases made, chases by other fishes, distance swum, distance ventured from shelter, percentage time spent in aggressive, feeding or passive behaviours). Helliger's transformation (Legendre & Gallagher 2001) was applied to data to make them scale independent. Permutation ANOVA (1000 permutations) was then used to test for significance in the canonical factors (i.e. behaviour versus size and survivorship). The analysis used the statistics package Cran R version 2.9.1 (<http://cran.r-project.org/>) and the library 'vegan' version 1.15-3 (<http://cran.r-project.org/web/packages/vegan/index.html>).

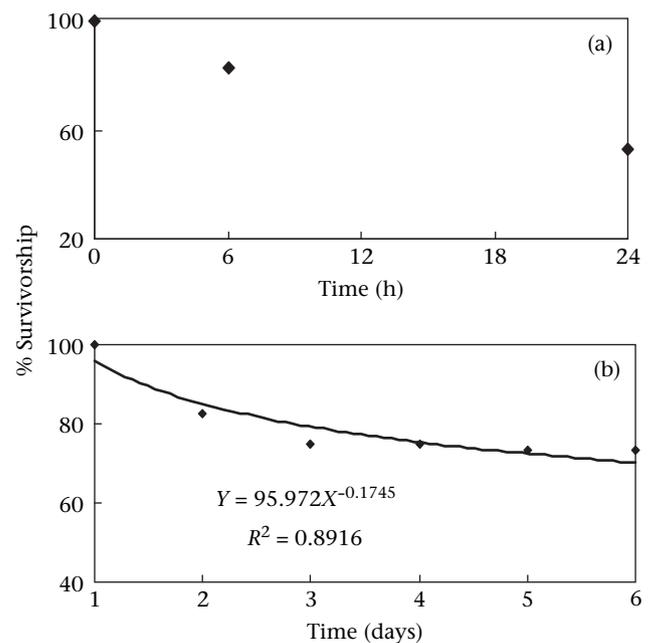
## RESULTS

### Experiment 1

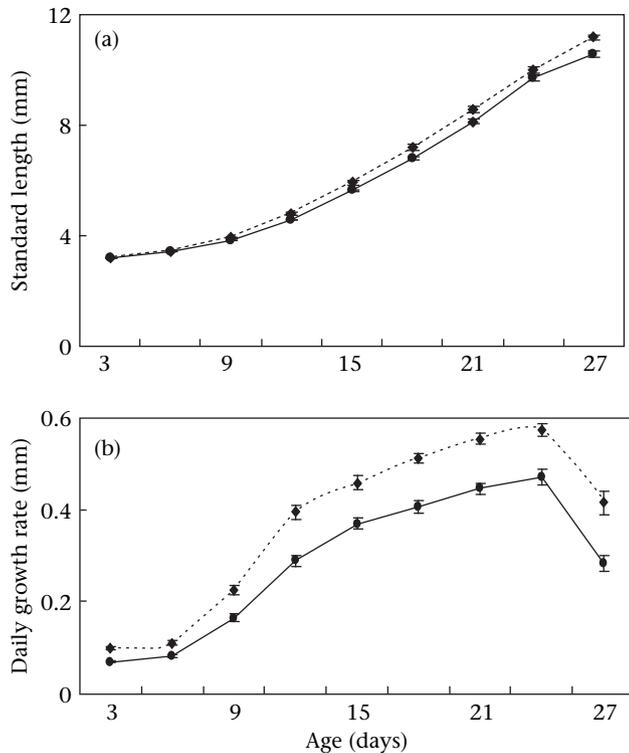
#### Mortality, size and growth

*Pomacentrus amboinensis* collected by light traps ranged in size from 10.0 to 12.9 mm SL and from 21 to 31 days of age at capture. The size distribution of fish retained from the light traps and immediately preserved did not differ from that of the fish used in the experiment (K–S test:  $P > 0.10$ ), despite the deliberate selection of fish in three size categories (small, medium and large) for the experiment.

The mortality rate of *P. amboinensis* in the 24 h following release was very high, with only 53% of the fish surviving until collection (Fig. 1a). Although frequency distributions of the size of fish that survived and died during the experiment did not suggest that size selection had occurred (K–S test:  $P > 0.10$ ), otolith analysis showed that surviving fish were significantly smaller at age (repeated measures MANOVA: Wilk's  $\lambda = 0.465$ ,  $df = 6,99$ ,  $P < 0.0001$ ; Fig. 2a), and grew slower at all ages (repeated measures MANOVA: Wilk's  $\lambda = 0.7246$ ,  $df = 6,99$ ,  $P < 0.0001$ ; Fig. 2b) than fish



**Figure 1.** Mortality trajectories of *Pomacentrus amboinensis*: (a) during the first 24 h after settlement on patch reefs of individual fish caught with light traps ( $N = 107$ ) and (b) during 6 days after relocation to patch reefs for juveniles collected from natural habitats approximately 1 month after initial settlement from the plankton ( $N = 87$ ).



**Figure 2.** (a) Mean back-calculated size-at-age and (b) daily growth of *Pomacentrus amboinensis* collected from light traps (diamonds and dashed line) and fish that survived 24 h at liberty on small patch reefs (circles and solid line). Error bars are SEs.

immediately preserved upon capture. Thus, mortality in the first 24 h after settlement preferentially removed the larger, faster-growing fish from the patch reefs.

#### Behaviour

Canonical redundancy analysis and permutation ANOVA could not identify any significant differences in behaviours between size classes of fish (small, medium and large) during the first 24 h after settlement (Table 1).

#### Experiment 2

##### Mortality, size and growth

Juvenile *P. amboinensis* collected from the reef ranged in size from 10.5 to 21.4 mm SL and in age from 34 to 63 days. Over the 6 days at liberty on patch reefs 25% of recruited *P. amboinensis* were removed by predators (Fig. 1b). Most of these were lost in the first 2 days after release of fish on the reefs. This mortality was size selective, with smaller members of the cohort being preferentially removed by predators (randomization test, probability that the randomized median size of dead fish was less than or equal to the observed median size of dead fish = 0.0396, based on 10 000 iterations, see Methods for details; Fig. 3).

#### Behaviour

There was a clear effect of size on the behaviour of fish 1 month after settlement on the reef (Table 1). Large fish took significantly more bites than medium-sized or small fish in the 3 min of observation and initiated significantly more chases than the other size classes of fish (Table 2, Fig. 4). Conversely, they were the recipients of significantly fewer chases than medium-sized or small fish (Fig. 4). Large fish swam a greater distance away from the reef

**Table 1**

Results of permutation ANOVA (1000 iterations) that tested significance of results from canonical redundancy analysis of data from experiment 1 in November and experiment 2 in December

	df	Variance	F	P(>F)
<b>November</b>				
Bites	1	0.03	0.7392	0.493
Chases.made	1	0.03	0.8372	0.433
Chased.by	1	0.05	1.3886	0.248
Swimming.range	1	0.08	2.2233	0.100
Distance	1	0.1	2.9123	0.070
Residual	80	2.71		
<b>December</b>				
Bites	1	0.12	3.5355	<b>0.02</b>
Chases.made	1	0.19	5.4266	<b>0.008</b>
Chased.by	1	0.27	7.651	<b>0.001</b>
Swimming	1	0.34	8.5407	<b>0.001</b>
Distance	1	0.08	1.5704	0.189
Aggressive	1	0.3	7.4054	<b>0.001</b>
Feeding	1	0.17	3.9821	<b>0.015</b>
Passive.hiding	1	0.14	4.0765	<b>0.009</b>
Residual	54	1.89		

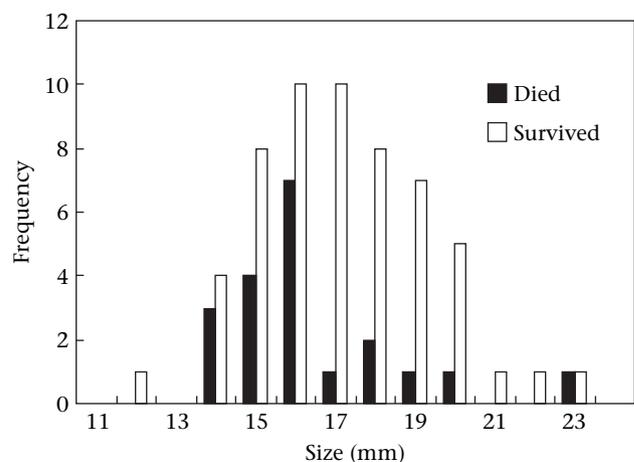
We recorded the number of bites taken, chases made, chases by other fishes, distance swum (swimming), distance ventured from shelter (distance), percentage time spent in aggressive, feeding or passive behaviours by individual fish in three size categories (small, medium and large, see text for details) during repeated 3 min observation periods of fish that survived or died during 24 h (November) or 6 days at liberty (December) on small patch reefs at Lizard Island, Great Barrier Reef. Bold results show significant factors at  $P < 0.05$ .

and a greater total distance than medium-sized or small fish (Fig. 4, Table 2).

Large fish spent significantly more time being aggressive (11%) than their smaller conspecifics (medium-sized: 8.11%; small: 0.48%; Fig. 4, Table 2). Large fish also spent significantly more time feeding (74.95%), than medium-sized (61.83%) and small (55.09%) fish (Fig. 4, Table 2). Small and medium-sized fish spent more time in passive (hiding) behaviours than large fish (Table 2, Fig. 4).

#### DISCUSSION

If behavioural or 'personality' traits (Sih et al. 2004; Reale et al. 2007) of animals mediate or contribute to growth–mortality trade-offs it is predicted that increased foraging effort will be negatively correlated with survivorship (Stamps 2007; Biro & Stamps 2008). In the 24 h after fish were settled on small patch reefs they suffered the high rates of mortality (approximately 50%) typical of many



**Figure 3.** Size–frequency distributions of *Pomacentrus amboinensis* that died and survived after 6 days at liberty on small patch reefs.

**Table 2**

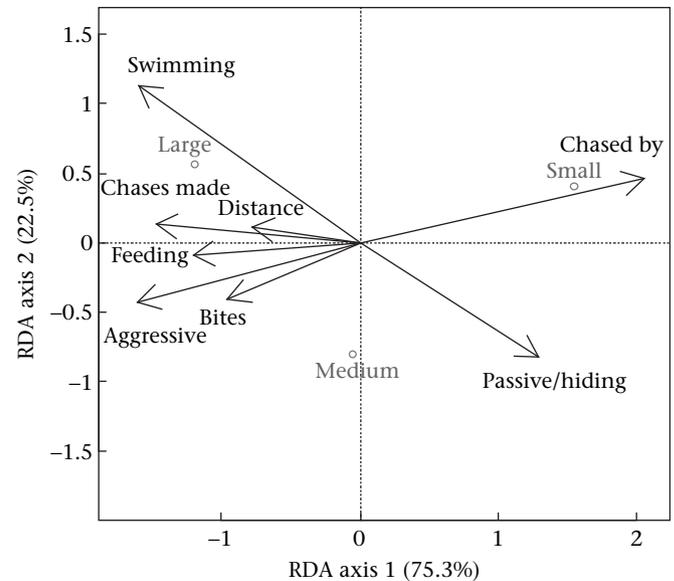
Results of permutation ANOVAs (1000 iterations) comparing behaviours of different size classes of fish

	df	Variance	F	P(>F)
<b>Small vs medium</b>				
Bites	1	1.3	29.2642	<b>0.001</b>
Chases made	1	1.13	25.3708	<b>0.001</b>
Chased by	1	0.29	6.5487	<b>0.001</b>
Swimming	1	0.37	8.2551	<b>0.001</b>
Distance	1	0.14	3.1178	<b>0.014</b>
Aggressive	1	0.3	8.6934	<b>0.001</b>
Feeding	1	0.13	3.0053	<b>0.027</b>
Passive/hiding	1	0.18	4.1212	<b>0.005</b>
Residual	54	2.41		
<b>Small vs large</b>				
Bites	1	1.3	29.2642	<b>0.001</b>
Chases made	1	1.13	25.3708	<b>0.001</b>
Chased by	1	0.29	6.5487	<b>0.001</b>
Swimming	1	0.37	8.2551	<b>0.001</b>
Distance	1	0.14	3.1178	<b>0.02</b>
Aggressive	1	0.23	6.6703	<b>0.001</b>
Feeding	1	0.13	3.0053	<b>0.035</b>
Passive/hiding	1	0.18	4.1212	<b>0.002</b>
Residual	54	2.41		
<b>Medium vs large</b>				
Bites	1	1.3	29.2642	<b>0.001</b>
Chases made	1	1.13	25.3708	<b>0.001</b>
Chased by	1	0.29	6.5487	<b>0.001</b>
Swimming	1	0.37	8.2551	<b>0.001</b>
Distance	1	0.14	3.1178	<b>0.017</b>
Aggressive	1	0.25	7.0116	<b>0.002</b>
Feeding	1	0.13	3.0053	<b>0.029</b>
Passive/hiding	1	0.18	4.1212	<b>0.006</b>
Residual	54	2.41		

The ANOVAs compared behaviours, the number of bites taken, chases made, chases by other fishes, distance swum (swimming), distance ventured from shelter (distance), percentage time spent in aggressive, feeding or passive behaviours by individual fish in three size categories (small, medium and large, see text for details) during repeated 3 min observation periods of fish during 6 days at liberty on small patch reefs (experiment 2) in December at Lizard Island, Great Barrier Reef. Bold results show significant factors at  $P < 0.05$ .

species of fish and invertebrates immediately after settlement (Gosselin & Qian 1997; Doherty et al. 2004; Almany & Webster 2006). This mortality was selective, preferentially removing the largest individuals, but did not appear to be linked to behaviour, as there were no significant differences between survivors and fish that died in risk taking or foraging behaviour, as measured by the average number of bites, swimming distance, the distance moved away from the coral and the mean number of chases. These behaviours also did not differ between size classes of surviving fish. In contrast, the mortality of fish 1 month after settlement was correlated with behaviour, when larger fish displayed greater rates of feeding behaviour, were more aggressive and moved greater distances and had a higher probability of survival than smaller fish.

These results conflict with the predictions of growth–mortality trade-offs, since, at settlement, survivorship was not negatively correlated with foraging or aggressive behaviour, while 1 month later these behaviours were positively correlated with survivorship. However, if behaviour does not mediate trade-offs, why are behavioural traits correlated within individuals? Such correlations between aggressiveness and other behaviours would be expected when these were positively related to both growth and mortality risk (Stamps 2007). For *P. amboinensis*, correlations may occur because multiple behavioural traits are negatively, rather than positively, related to mortality. The better survivorship of larger, more aggressive fish 1 month after settlement is likely to result from their access to, and exclusion of smaller fish from, safe predator refuges on patch reefs (T. H. Holmes & M. I. McCormick, unpublished data). Where outcomes of such aggressive interactions



**Figure 4.** Results of canonical redundancy analysis (RDA) of data from experiment 2. Factors in the analysis included the number of bites taken, chases made, chases by other fishes, distance swum (swimming), distance ventured from shelter (distance), percentage time spent in aggressive, feeding or passive behaviours by individual fish in three size categories (small, medium and large, see text for details) during repeated 3 min observation periods over 6 days at liberty on small patch reefs at Lizard Island, Great Barrier Reef. The percentage of variance in the data explained by each axis is shown in the axes labels.

are dependent on size, as was the case in our study, there will be selection for those fish that have greater feeding activity and thus growth rates that result in larger size. Residency in predator-safe microhabitats may also explain why larger fish were able to have greater activity rates (swimming distances) than smaller fish without incurring an increased risk of predation.

Much of the current evidence for the role of behavioural traits in growth–mortality trade-offs is correlative (Stamps 2007; Biro & Stamps 2008). Importantly, correlations among behavioural traits (e.g. boldness, feeding rate, activity) in animals that positively influence growth rate have been seen as support for predictions of the growth–mortality trade-off hypothesis (reviewed in Stamps 2007). Our study shows that this may not be the case. One month after settlement, larger *P. amboinensis* had greater rates of activity, foraging and aggression and grew faster than smaller fish; however, these traits served to increase rather than decrease their survivorship. Conversely, selective mortality of larger, faster-growing individuals may not necessarily indicate the action of behavioural traits in mediating growth–mortality trade-offs. We found no detectable differences in the behaviour of small or large fish while they were undergoing positive size selection. Why this mortality was positively selective is not known; it may simply reflect predator choice. Holmes & McCormick (2009) have shown that when simultaneously offered large and small prey items, *Pseudochromis fuscus*, one of the major predators of newly settled *P. amboinensis*, preferentially selects large recruiting fishes, presumably as an optimally evolved foraging tactic (Holmes & McCormick 2009). These predators are abundant on the shallow inshore reefs of Lizard Island (McCormick & Meekan 2007) adjacent to our patch reefs.

Our results were not an artefact of the experimental set-up and patch reefs. In terms of mortality rates and selection, our results are consistent with many other studies (Hoey & McCormick 2004; Almany & Webster 2006) and so are not likely to be caused by our interruption of the settlement process or disturbance of the animals by our experimental treatments. *Pomacentrus amboinensis*

undergoes selective mortality throughout its early life history and switching between positive and negative size selection has been shown by other studies for this species (McCormick & Meekan 2007; Gagliano et al. 2007). For damselfishes, negative size-selective mortality of older juveniles (1 month or more after settlement) appears to be a common pattern, as was the case in our study (Vigliola & Meekan 2002). However, relatively few studies have examined the pattern of selective mortality at the time of settlement (but see McCormick & Meekan 2007; Gagliano et al. 2007).

Growth–mortality trade-offs may explain why animals do not always grow at maximal rates and are also thought to be an important mechanism maintaining individual differences in growth rates for species with indeterminate growth, such as fishes (Mangel & Stamps 2001; Stamps 2007; Biro & Stamps 2008). Coral reef species have very high larval and juvenile growth rates relative to other fishes, which may have evolved to counter the high rates of mortality these stages experience in tropical habitats (Fonseca & Cabral 2007). They also commonly display variation in growth rates between individuals that are consistent through time (Searcy & Sponaugle 2001; Vigliola & Meekan 2002; Wilson & Meekan 2002; Meekan et al. 2006; Gagliano et al. 2007). In our study, differences in growth rate between small and large individuals were evident immediately after hatching and were maintained throughout larval and juvenile life (see Fig. 2), a pattern similar to that of many other damselfishes (Searcy & Sponaugle 2001; Vigliola & Meekan 2002; Gagliano et al. 2007). If growth–mortality trade-offs do not occur in *P. amboinensis*, what process maintains such consistent differences in growth between individuals? And why do relatively slow-growing individuals persist in populations? Although variation in growth rates can occur in animals held without competitors and predators in the presence of unlimited food (Ragland & Carter 2004; Martins et al. 2005), processes that might contribute to this phenomenon include frequency-dependent selection (Roff 1998), temporal and spatial variation in optimal growth rates (Mangel 1991) and a balance between mutation and selection (Santiago 1998). In addition to growth–mortality trade-offs, these same processes are also thought to maintain consistent differences in behavioural or personality traits between individuals of the same species (Stamps 2007).

The selective environment into which juvenile *P. amboinensis* settle is patchy in both spatial and temporal dimensions. McCormick & Meekan (2007) found that young fish settling within the territories of adult male conspecifics along the reef edge were subject to positive size selection, while outside territories size selection was negatively biased, so that smaller individuals were removed by predators. The juxtaposition of adult territories and unoccupied space on reefs means that newly settling fish could experience very different selective regimes for growth at very small (m) spatial scales. Differences in the action of selective mortality have also been recorded for this species at the larger (km) scale of habitats (lagoon, back-reef, windward) within an entire coral reef (Holmes & McCormick 2006). In addition to spatial patchiness, there is also considerable potential for temporal variation in selective mortality within the reef environment. At settlement, mortality acted to remove the larger, faster-growing individuals, whereas 1 month later, mortality preferentially removed the smaller, slower-growing fish. As noted above, similar changes in the direction of selective mortality during the larval and juvenile phase of this species have been recorded by Gagliano et al. (2007). Together, this spatial and temporal variation in selective pressures may be enough to maintain variation in optimal growth rates among individuals of this species.

Fishes provide the majority of examples of the interaction between growth–mortality trade-offs and personality or behavioural traits in animals (Stamps 2007). Stamps (2007) and Biro & Stamps (2008) acknowledged the importance of not only documenting correlations between behavioural traits and growth rate,

but also following the subsequent fate of individuals to show that these behaviours have the outcomes predicted by growth–mortality trade-offs. This is often difficult in behavioural studies, which may account for the relative paucity of data. Although there are few studies, evidence for growth–mortality trade-offs has been documented in a wide variety of taxa including damselflies (Stoks et al. 2005), rainbow trout (Biro et al. 2004, 2006) and house mice, *Mus musculus* (Biro & Stamps 2008). However, our study shows that correlations among behavioural and growth traits do not necessarily provide evidence of growth–mortality trade-offs and that spatial and temporal variation in the direction of growth-selective processes might be sufficient to produce both consistent variability in growth patterns among individuals and submaximal growth rates of populations.

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