

The importance of attitude: the influence of behaviour on survival at an ontogenetic boundary

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ABSTRACT: Behavioural traits can strongly influence fitness and survival and are important mediators of life history trade-offs. This study explored the links between mortality trade-offs associated with fast growth during larval life and behaviour of individuals during an important life history transition. Longitudinal sampling of a cohort of damselfish settling on a reef at the end of their larval stage found that individuals with small otolith sizes at hatching and low otolith growth rates were selectively removed from the local population, while there was no apparent selection for size or body condition over the first 24 h after settlement. Selection against slow growth (initial larval growth and maximum growth) and small size at hatching and settlement were accentuated over the first month after settlement. Detailed behavioural assessments of naïve larvae settled onto habitat patches and monitored for 24 h found that initial boldness aided survival, but individuals that ventured larger distances from shelter suffered higher mortality. Correlations of growth with behavioural attributes were generally poor; however, there was a weak correlation between boldness and maximum growth. A measure of flexibility in the maximum distance ventured from shelter was positively related to initial otolith growth. Our results suggest that although early growth which is relatively slow leads to higher mortality later in life, and behavioural attributes influenced survival, there were only weak correlations between growth history and behaviour. This may be due to strong selective pressures on young fish to learn novel behaviours rapidly after settlement. Selection may promote behavioural flexibility at this key ecological transition.

KEY WORDS: Behaviour · Boldness · Coral reef fish · Larval growth · Mortality · Phenotypic selection · Settlement

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INTRODUCTION

Behaviour is the ultimate reaction by an organism to a stimulus and is a function of an interaction between genotype, physiology and history (Krebs & Davies 1987). The decision-making frameworks that underlie behaviour are multivariate in nature (Tinbergen 1963), and there is strong selection pressure for flexibility (Hsu et al. 2006); thus, it is often difficult to identify the relative contribution of each component at different stages of an organism's life history.

While success is measured by relative growth for many species, there is generally posited to be a trade-off between growth and mortality (Stamps 2007). High growth can covary with behavioural attributes such as

boldness, activity or even aggression that in some cases may predispose an animal to mortality due to predation (Stamps 2007, Biro & Stamps 2008). It is therefore important to understand the interrelationship between behaviour and growth and whether certain types of behaviours necessarily mediate success. Individual differences in behaviour may reflect underlying genetic differences (Dingemanse et al. 2002, 2003) and provide the raw material upon which natural selection can act (Réale & Festa-Bianchet 2003). Very few studies have assessed whether or not behavioural traits can be subject to selection, although some have shown phenotypic or genetic correlations between behaviour and fitness-related traits, such as growth and reproductive output (Nussey et al. 2006).

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Understanding the proximate factors influencing behavioural decisions in the face of predation is particularly important at ontogenetic boundaries in life histories. For organisms with complex life cycles, such as many amphibians, invertebrates and fishes, the end of the larval stage represents a critical period when newly metamorphosing organisms are exposed to very high levels of predation (sometimes >90%) as they transition into juvenile habitats (Gosselin & Qian 1997, Almany & Webster 2006). The behavioural decisions made by prey in response to a predation threat at this time determines who survives and the type and frequency of traits that will percolate to subsequent life stages. The naïve individuals that recruit into the system occupied by juveniles and adults bring with them the baggage of genetic and non-genetic influences which have affected them prior to and during the larval phase and which have influenced their growth and development through to settlement and will bias their subsequent success.

Mortality has been found to be selective for a wide variety of traits. Larval growth history typically correlates strongly with growth after metamorphosis and has been found to influence not only lifetime fitness but also who survives well into settled life for a variety of marine vertebrates and invertebrates (e.g. Vigliola & Meekan 2002, Marshall et al. 2003, McCormick & Hoey 2004). One study found that a proxy for the size at which a fish hatched had detectable levels of selection upon it for 3 wk after settlement, while size at settlement was still being directly influenced by selective mortality for at least 3 mo into the juvenile phase (Gagliano et al. 2007). A number of recent studies of harem sex-changing marine fishes have shown that growth-related attributes of larvae at hatching indicated who would change sex to become the reproductive dominant (Walker et al. 2007, McCormick & Gagliano 2009, Munday et al. 2009, McCormick et al. in press). It appears that growth correlates with other aspects of individual quality that prorate success.

Growth per se cannot be targeted for selection by a predator, but rather predators choose prey based on phenotypic characteristics that make one individual detectably different from another nearby. In fishes and many other animals, it is likely that selection by predators focuses on the behaviour of prey, as growth has been found to correlate with aspects of behaviour that will influence vulnerability, such as activity levels, distance from shelter, inquisitiveness and boldness (Stamps 2007, Biro & Stamps 2008, Meekan et al. 2010). Thus, an understanding of the interrelationships among growth, mortality and behavior requires studies that simultaneously measure these variables on the same individuals, particularly as they transition the critical periods of ontogenetic boundaries in the life cycle.

Tropical reef fishes provide an ideal model for such studies. For most species a record of daily growth and size, extending from hatching to the early juvenile age, can be obtained from the earstones (i.e. otoliths) of the acousto-labyrinth sensory system. Furthermore, these fishes undergo mortality bottlenecks (Doherty et al. 2004, Almany & Webster 2006) at settlement during which time selective predation removes the majority of young fish that arrive from the plankton (e.g. Hoey & McCormick 2004, Figueira et al. 2008, Holmes & McCormick 2009). Juvenile behaviour also shows high levels of individual variability (Meekan et al. 2010, C. Mero & M. I. McCormick unpubl. data) and consistent differences have been found among individuals (Biro et al. 2009).

The present study examined the extent to which loss is selective for aspects of growth and morphology of a juvenile tropical damselfish *Pomacentrus wardi* and explored the role of prey behaviour in mediating this mortality. We focused on the period immediately after settlement and the month following, during which time fish must acquire new skills and information necessary to survive. Theory predicts that when mortality is high there will be a trade-off against high growth because animals that exhibit high growth rates will take more risks to satisfy energy demands (Stamps 2007).

MATERIALS AND METHODS

Study species and collection. *Pomacentrus wardi* is a site-attached damselfish that is common on the shallow reefs of the Indo-Pacific. Adults and juveniles occur in shallow lagoons, where they inhabit the reef edge or reef top associated with rubble. Larval duration is 16 to 21 d and fish are 13 to 14 mm standard length (SL) at the end of the larval stage. Newly settled fish are found as solitary individuals associated with conspecific adults and subadults.

Newly settled *Pomacentrus wardi* are subject to an array of resident and transient predators. The most common predators at our study site on the shallow (2 to 3 m depth) coral reefs of Lizard Island, northern Great Barrier Reef, Australia (14° 41' S, 145° 27' E), were the moon wrasse *Thalassoma lunare*, the dottyback *Pseudochromis fuscus*, 2 species of lizardfishes, *Synodus variegatus* and *S. dermatogenys* (Beukers & Jones 1998, Holmes & McCormick 2006, 2010), and an array of flatfishes. All predators can be seen striking at and occasionally capturing recently settled and juvenile reef fishes during the summer recruitment period.

The study was conducted during December 2007. Light traps (see Meekan et al. 2001, their Fig. 1 for design) were used to collect *Pomacentrus wardi* at the end of their larval phase. Traps were moored at least

100 m away from the reef edge and fished overnight and catches were brought back to the Lizard Island Research Station just after dawn. Fish were placed into aquaria with aerated flowing seawater for 24 h (density: ~50 to 100 per 40 l) where they were fed *Artemia* once per day. Research over the last 2 decades suggests that fishes collected in light traps are intercepted as they come into the vicinity of the reef to settle, and most are in the process of metamorphosis to their juvenile form (Milicich et al. 1992, Wilson & McCormick 1997, McCormick et al. 2002). At this stage they also appear to display active and consistent choices of habitat (e.g. Öhman et al. 1998) and have little post-settlement movement over the initial juvenile phase (McCormick 2009), suggesting that they are not attempting to return to the pelagic arena. A random sample of 60 to 100 *P. wardi* from each day's catch was anaesthetized using clove oil, killed by immersion in ice slurry and then preserved in 70% ethanol as a baseline for the assessment of growth history and determination of selective mortality. SL and blotted wet weight of fish were measured immediately after death.

A random sample of approximately 20 *Pomacentrus wardi* from the light traps was used each day for 12 d in an assessment of field behaviour and survival (see 'Selectivity mortality' below). Fish from the same pulse that had been settled for 1 wk and 1 mo were collected with a handnet and clove oil from a shallow back reef 150 to 300 m from the site of light trap deployment. These anaesthetized fish were killed by immersion in ice slurry and then preserved in 70% ethanol.

Water temperature was recorded every hour using a calibrated data logger (32K StowAway Tidbit) deployed 150 m from the study site at the same depth. Water temperature at the site averaged 28.3°C (range: 27.0 to 29.9°C) over the study period.

Selective mortality. The selectivity of mortality on the main reef was quantified by comparing the body size (SL), condition and early growth histories of the sample of fish collected immediately prior to settlement by the light traps with those of the survivors of the same cohort from 3 time periods (24 h, 1 wk and 1 mo) after a large settlement event on a shallow back reef. The light trap samples were used to quantify the distribution of traits in the cohort prior to the action of any selective loss that may have occurred during or after settlement. Changes in the distributions of these traits in fish from the same cohort collected 24 h, 1 wk and 1 mo after settlement were regarded as evidence of selective mortality (Hovenkamp 1992, Meekan & Fortier 1996). Larval growth history was determined by the analysis of growth increment widths on cross-sections of the sagittal otoliths (prepared following the protocol of Wilson & McCormick 1997). The early life

history traits examined were: size of otolith at hatching (i.e. radius of the first increment); size of otolith at settlement (i.e. distance from the nucleus to the settlement check, Wilson & McCormick 1999); initial growth rate between hatching and 3 d (i.e. growth rate expressed as otolith growth [$\mu\text{m d}^{-1}$] from linear regression from Day 0 to Day 3); linear growth rate (the regression slope of days of linear growth between inflexions at the accelerating and decelerating parts of the instantaneous growth curve); and maximum growth rate (from the steepest part of the larval otolith growth trajectory). Because more fish were collected from the light traps than could be processed due to time constraints, fish were subsampled in proportion to their abundance in each 0.5 mm size class. A total of 121 fish were processed for a baseline assessment of growth history. The fish that had been settled for 24 h were the survivors of the behavioural assessment study (see below). Cohort identity of fish that were collected from reefs 1 wk and 1 mo after settlement was confirmed using daily increment counts of otolith cross-sections from the outer margin to the settlement mark. As the date of capture was known, the date of settlement could then be determined and their identity as part of the same cohort as the fish collected by light traps confirmed.

A body condition index was calculated as the residuals of a SL by weight regression plot for the pre-settlement and 24 h samples together. Selection on body condition was only examined between the pre-settlement and 24 h samples since post-settlement processes were expected to confound the comparison of samples separated by longer time periods.

Field assessment of behaviour, space use and persistence. Within 2 h of collection, randomly chosen fish were placed into individual clip-seal bags containing aerated seawater and measured for SL with calipers (± 0.1 mm). Fish were kept individually in aquaria for 24 h, where they were fed *Artemia*, and then transported in labeled clip seal bags and released onto small rubble reefs (18 × 12 × 12 cm) made from dead *Pocillopora damicornis* (a common bushy hard coral) set on a shallow sandflat 4 to 6 m from the reef edge. Patches were cleared of any fishes or invertebrates prior to release using a hand net. Captured fishes were released on natural reefs away from the study area. A small wire cage (~30 × 30 × 30 cm, 12 mm mesh size) was placed over the patch to allow fish to acclimate to their new surroundings while being protected from predators. Cages were removed 30 min to 1 h after release of the fish between 09:00 and 11:00 h. Assessments were made 2 to 3 times (i.e. after the initial acclimation period, the evening after release and the following morning). Water temperature during the census periods averaged 28.6°C (range: 27.4 to 29.7°C).

A pilot study using tagged fish examined the propensity for fish caught in light traps to move after they had been released onto patch reefs similar in size and position to those used in the present study. Light trap-caught fish ($N = 20$) were placed individually into a small clip-seal plastic bag and tagged through the bag with a 27G hypodermic needle (as per Hoey & McCormick 2006) to achieve individual identification. This left a 1.5 to 2 mm long stripe of colour, which was visible under the scales. Once individually released onto a patch reef, a small mesh cage (as above) was placed over the patch for 40 min to 1 h to prevent initial predation. Censuses were carried out at 6 to 8 h intervals, and when fish were missing from patches, the neighbouring reefs (4 to 5 m away) and reef edge were searched for migrants. No evidence of movement of tagged individuals from their allocated patches was detected. Findings of no movement in the days immediately following settlement have been found by other studies on damselfish (e.g. McCormick & Makey 1997, McCormick 2009).

The behaviour of fish was assessed immediately upon the removal of the cage, at the end of the first day in the field and on the morning of the second day prior to collection. Behaviour of the fish was assessed by a scuba diver positioned 1.5 m away from the patch. A magnifying glass (4 \times) aided the assessment of bite rates and space use over the 3 min focal animal sampling period. Six aspects of activity and behaviour were estimated: total distance moved (cm); distance ventured from the coral patch (categorized as % time spent within 0, 2, 5 or 10 cm away from the patch); maximum distance ventured (MaxDV, cm); height above substratum (categorized as % time spent within the bottom, middle or third of the patch); behaviour (% time spent foraging, lurking or other); and boldness (recorded as a continuous variable on a scale from 0 to 3 at 0.5 increments, where 0 is hiding in hole and seldom emerging; 1 is retreating to hole when scared and taking more than 5 s to re-emerge, weakly or tentatively striking at food; 2 is shying to shelter of patch when scared but quickly emerging, purposeful striking at food; and 3 is readily venturing away from coral patch, exploring with no hiding and striking aggressively at food). At the end of the 3 min observation period, the fish was approached with a finger and the fish's reaction and latency to emerge from shelter was taken into account in the assessment of boldness. Two additional variables were made from these variables to summarize information and reduce the number of variables that were required in analyses. Mean distance ventured was calculated from the sum of the proportions of time spent in each of the distance categories multiplied by the distance that each category represented. Relative height on the patch was summarized as a cumulative proportion of

the time spent at varying heights over the 3 min observation period, with the top of the patch taken as height of 1, mid a height of 0.5, and bottom a height of 0. Two additional variables were created to summarize the magnitude of changes in behaviour (plasticity) in 2 key variables (boldness and MaxDV). These new variables were the difference in the magnitude of the variables between Censuses 1 and 2.

A pilot study using 10 fish found that 3 min were sufficient to characterize the behaviour of the individual fish. Fish were observed for 3 min periods 3 times consecutively and the above behavioural variables were recorded at the end of each interval. Comparison of the individual coefficients of variation (CV) for the behaviours were generally low (ranging from 0 to 0.15), with the one exception being total distance moved, where the CV (0.25) was greatly affected by one individual that increased its total movement between 3 min intervals from 2 to 4 cm (i.e. a relatively small distance).

Statistical analyses. The frequency distributions of otolith-derived variables were compared among the 4 serial samples of the same cohort: (1) the baseline, pre-settlement sample (collected from the light traps as fish came into the vicinity of the reef to settle); (2) the experimental fish that had been seeded and left on patch reefs for 24 h prior to collection; (3) a sample collected 1 wk after settlement; and (4) a sample collected 1 mo after settlement. The distributions of traits were compared using Kolmogorov-Smirnov (K-S) 2-sample tests. The correlations of growth parameters were examined for the pre-settlement sample using Pearson correlations.

To examine whether behavioural variables contributed to survival through to the third (and last) census, logistic multiple regression was undertaken using survival as the dependent variable and the behavioural traits at the initial census as the independent variables (81 survived, 105 died). Best subset model selection was used, with Akaike Information Criterion (AIC) as the model selection criterion. Behaviours used in the analysis were from the first census: bite rate, total distance moved (\log_{10} -transformed), mean distance ventured, maximum distance ventured and boldness. In addition, since temperature is known to influence behaviour in the laboratory (Biro et al. 2009), water temperature at the first census was included as an independent variable. Behavioural characteristics displayed by the survivors at the second census did not significantly influence whether individuals subsequently survived until the third census and so are not presented. To display the difference in key variables (boldness and MaxDV) between fish that survived and died, with the effect of other variables held constant, analysis of covariance (ANCOVA) was employed (i.e. least mean square adjusted means).

Multivariate ANCOVA (MANCOVA) was used to test for differences in behaviour among the 3 censuses, while removing the effect of variable water temperature (the covariate). Total distance moved was $\log_{10}(x+1)$ -transformed to conform to assumptions of the analysis. One-factor ANCOVA (with census as the factor) indicated that 3 variables were influenced by temperature: bite rate, total distance moved and MaxDV. A canonical discriminant analysis was used to further examine differences in behaviour among censuses found by MANCOVA. The residuals of the relationships with temperature were used for the 3 variables found to be influenced by water temperature.

To explore whether behaviour may be a mechanism underlying the selection on growth attributes, separate best-subset multiple regressions were used to examine the relationships between behavioural variables (boldness, Max DV and the change in MaxDV and boldness between Censuses 1 and 2) against 6 otolith-based growth variables: otolith size at hatching, otolith size at settlement, pre-settlement otolith growth (i.e. otolith size at settlement divided by pelagic larval duration), initial growth rate, linear growth rate and maximum growth rate. These 3 behavioural variables were focused on since they had been found to influence survival to the third census. Analyses were run using boldness and MaxDV observations from the initial and second censuses.

RESULTS

Selective mortality

The correlations among growth parameters for the pre-settlement sample of fish were generally poor, suggesting each had information that was independent of the other measures of growth. Otolith size at hatching had a weak positive relationship with linear growth rate ($r = 0.26$, $p < 0.005$). Otolith size at settlement was positively associated with linear growth rate ($r = 0.38$, $p < 0.0001$) and maximum growth rate ($r = 0.36$, $p < 0.0001$). Initial growth rate was negatively associated with linear growth rate ($r = -0.36$, $p < 0.0001$) and maximum growth rate ($r = -0.34$, $p < 0.0001$). Lastly, linear growth rate was moderately correlated to maximum growth rate ($r = 0.83$, $p < 0.001$).

There were marked differences in the shapes of the otolith increment trajectories among the 4 consecutive samples from the same cohort of fish, suggesting that mortality was selective for various traits and that the importance of the traits differed through time (Fig. 1). There was a difference in the frequency distribution of otolith sizes at hatching among the 4 samples (Fig. 2A). The 24 h and 1 wk samples differed from the pre-settlement (light trap) sample, displaying a much lower representation of small otoliths, while having an

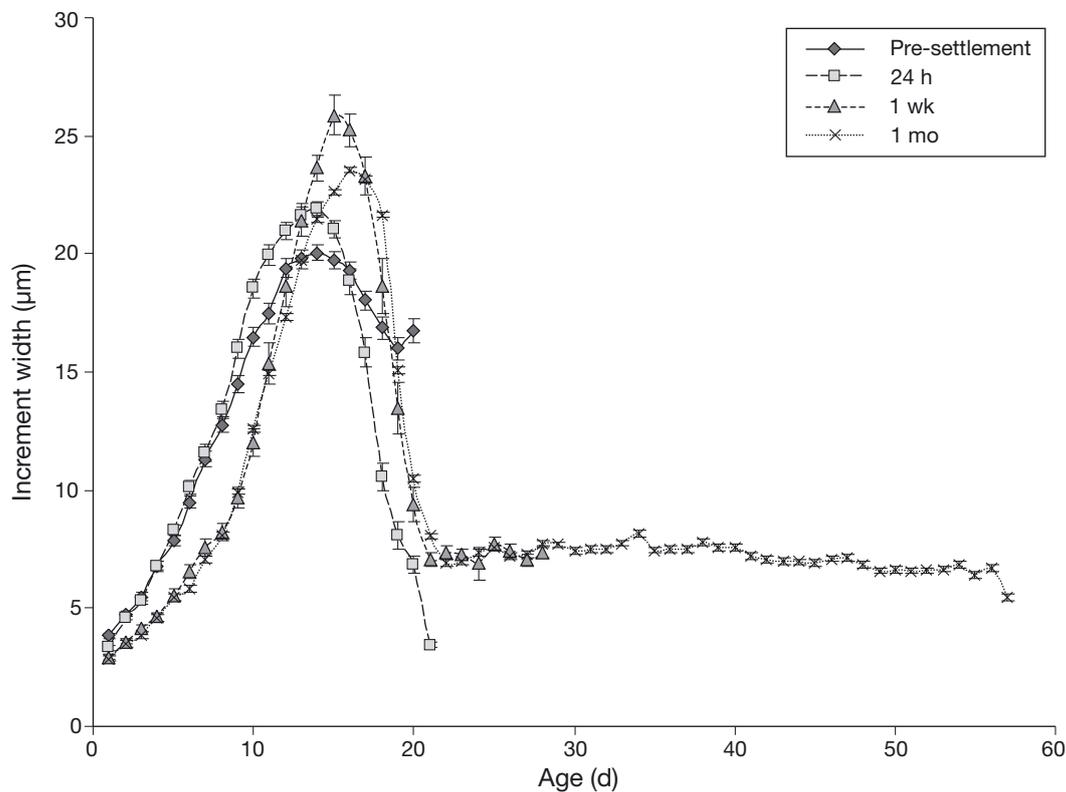


Fig. 1. *Pomacentrus wardi*. Comparison of instantaneous otolith growth trajectories of a cohort of damselfish collected prior to settlement using light traps (pre-settlement) and at 3 later times: after 24 h on reefs (fish whose performance was assessed and monitored), 1 wk after settlement and 1 mo after settlement. Error bars are SE

over-representation of large otolith sizes, suggesting a strong selection for fish with large otoliths at hatching (K-S tests: $p < 0.0001$). This positive size selection was further accentuated in the 1 mo sample ($p < 0.001$).

Loss over the first 24 h for the experimental fish was 59%. The pattern of size selection was similar for the otolith size at settlement, with an overall trend for fish with smaller otolith sizes to be removed from the population through time (Fig. 2B). In this instance, there was no significant difference between the pre-settlement and 24 h samples ($p > 0.05$), but these significantly differed from the 1 wk and 1 mo samples ($p < 0.0001$), which also differed from one another ($p < 0.001$).

There was no difference in the initial larval growth (i.e. from Days 0 to 3 after hatching) of fish collected at the pre-settlement stage and those allowed 24 h liberty on patch reefs (K-S test, $p > 0.05$; Fig. 3A). However, fish from both samples differed in initial growth rate from fish that survived 1 wk and 1 mo of benthic life (which did not differ from one another, $p > 0.05$), with a lower representation of fish with low initial otolith growth ($p < 0.0001$; Fig. 3A). This suggests the selective loss of fish with low initial otolith growth.

The linear growth phase in the first half of the larval period was also modified by selective loss through time, with a gradual loss of individuals from the cohort that displayed low initial otolith growth (all distributions differed from one another at $p < 0.001$; Fig. 3B). Maximum larval growth rate displayed the same trends as linear growth rate, with the steady loss of individuals that exhibited low growth (Fig. 3C). All distributions differed from one another at $p < 0.001$, with the exception of the distributions represented by the 1 wk and 1 mo samples, which differed from one another at $p = 0.049$.

There was no selective loss of individuals in relation to body condition index between pre-settlement and 24 h samples (K-S test: $p > 0.10$).

Behaviour, space use and persistence to 24 h

A best-subset logistic multiple regression with survival to Census 3 (~24 h post-settlement) as the binary dependent variable was significant ($df = 2$, $p = 0.0012$) and indicated that the initial assessment of boldness and MaxDV (Wald statistic = 9.492, $df = 2$, $p = 0.002$; Wald statistic = 3.980, $df = 2$, $p = 0.046$, respectively) best explained the difference between the survivors and those that did not survive (Table 1). Solutions with the next 6 lowest AIC values had 3 to 5 independent variables, and these additional variables were not consistently included in the competing models. Survival to Census 3 was not significantly related to the behav-

oural attributes recorded at the end of the first day (Census 2) (MANOVA, Pillai's trace = 0.065, $df = 6$, 156, $p = 0.101$). Temperature at either Census 1 or 2 did not have a significant influence on survival in these analyses. Multiple regressions on a more restricted data set (not including fish that died between Census 1 and 2) found that neither of the composite behavioural variables that summarized behavioural change in an individual between Census 1 and 2 (for boldness and MaxDV) accounted for significant amounts of the variability in mortality that occurred prior to the third census.

For the fish that survived through the Census 3, behaviour differed in Census 1 compared to subsequent censuses (MANCOVA, Pillai's trace_{12,452} = 0.171, $p < 0.0001$). Water temperature, the covariate, was also significant (Pillai's trace_{6,225} = 0.081, $p = 0.004$). ANOVA suggested that temperature had a minor but significant effect on bite rate, total distance moved and MaxDV ($p = 0.003$, 0.02 and 0.03, respectively), and only the variables mean distance ventured and relative height significantly changed over the 3 censuses ($p = 0.006$ and 0.0007, respectively). Boldness did not appear to change significantly among the censuses or be influenced by water temperature. A canonical discriminant analysis showed that in Census 1, fish exhibited greater boldness, moved greater distances from the patch, were closer to the substratum and had lower bite rates than in subsequent censuses (Fig. 4). Behaviour of fish did not differ between Census 2 and 3 (Fig. 4).

There was no relationship between initial boldness and any of the attributes associated with previous growth history of the survivors at the end of the experiment (multiple regression, $p > 0.05$, all terms non-significant). However, boldness in Census 2 was found to significantly correlate with maximum growth, though this relationship was weak (partial $r = 0.27$, $p = 0.023$) and the overall multiple regression of boldness at Census 2 with individual growth characteristics was non-significant ($p = 0.133$). There was a poor correlation between boldness assessments among the 3 censuses ($r = 0.05$ to 0.1, $p > 0.05$). There was also no relationship between the change in boldness between Census 1 and 2, and Census 2 and 3, with any of the growth measures (multiple regression, $p > 0.05$, all terms non-significant for both dependent variables).

There was no significant relationship between MaxDV and previous growth history of survivors (multiple regression, $p > 0.05$, all terms non-significant). There were also no significant correlations between the MaxDV of the 3 different censuses ($p > 0.05$). There were, however, significant correlations between both measures of flexibility in MaxDV (i.e. the difference

between the magnitude of MaxDV between Census 1 and 2, and Census 2 and 3). The difference in MaxDV between Census 1 and 2 was found to be significantly related to initial otolith growth ($R^2 = 0.31$, $F_{1,75} = 8.205$, $p = 0.005$). Likewise, the difference in MaxDV between Census 2 and 3 was found to be related to initial otolith

growth ($R^2 = 0.31$, $F_{1,75} = 7.823$, $p = 0.006$). None of the other growth-related variables explained a significant amount of variability in the best subset models.

The levels of consistency in behaviour across the first 24 h after settlement differed among individuals (Fig. 5). Only 12% of the fish that survived 24 h dis-

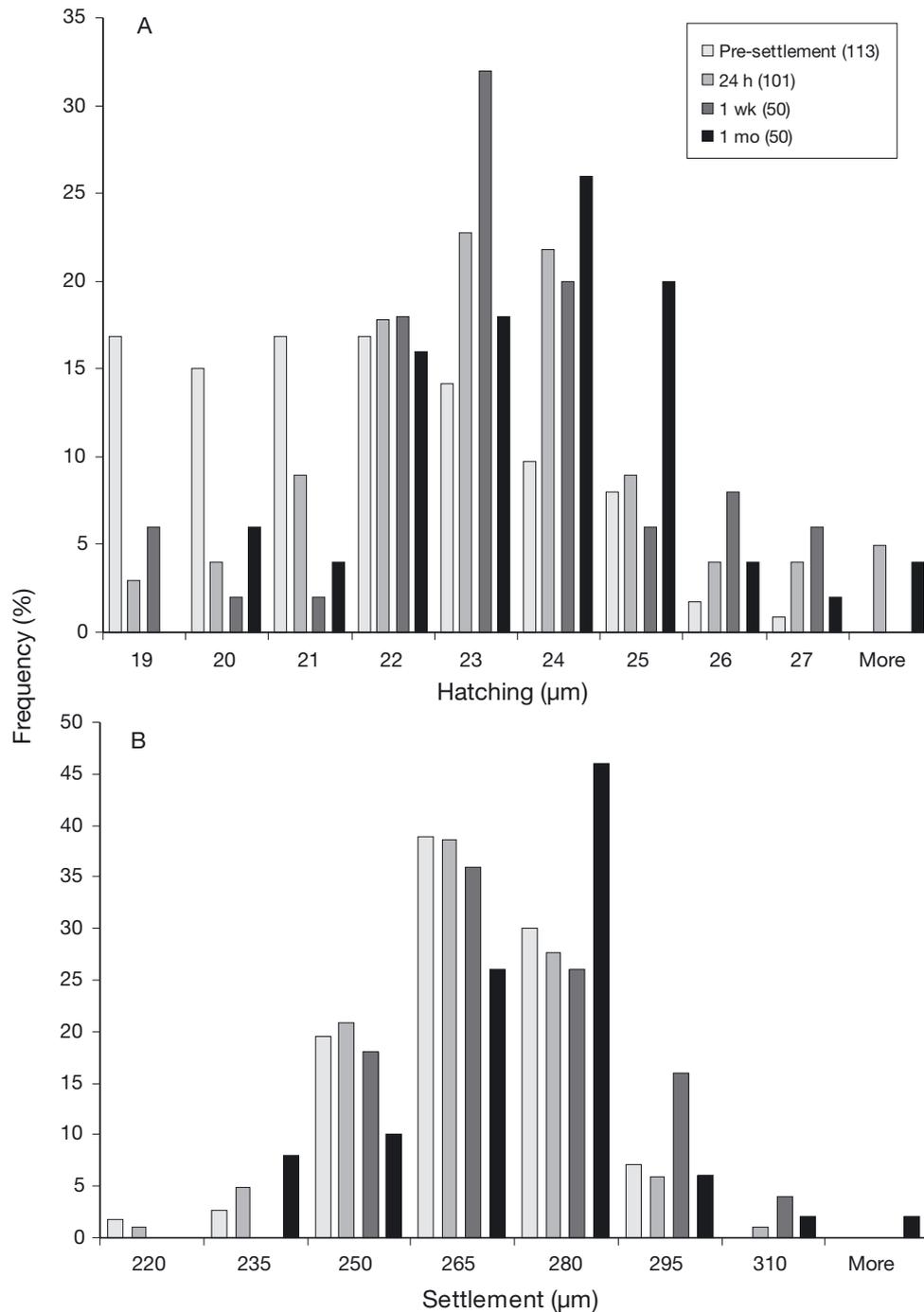


Fig. 2. *Pomacentrus wardi*. Frequency distributions of otolith size at (A) hatching and (B) settlement from a single cohort of damselfish collected prior to settlement using light traps (pre-settlement) and at 3 later times: after 24 h on reefs (fish whose performance was assessed and monitored), 1 wk after settlement, and 1 mo after settlement

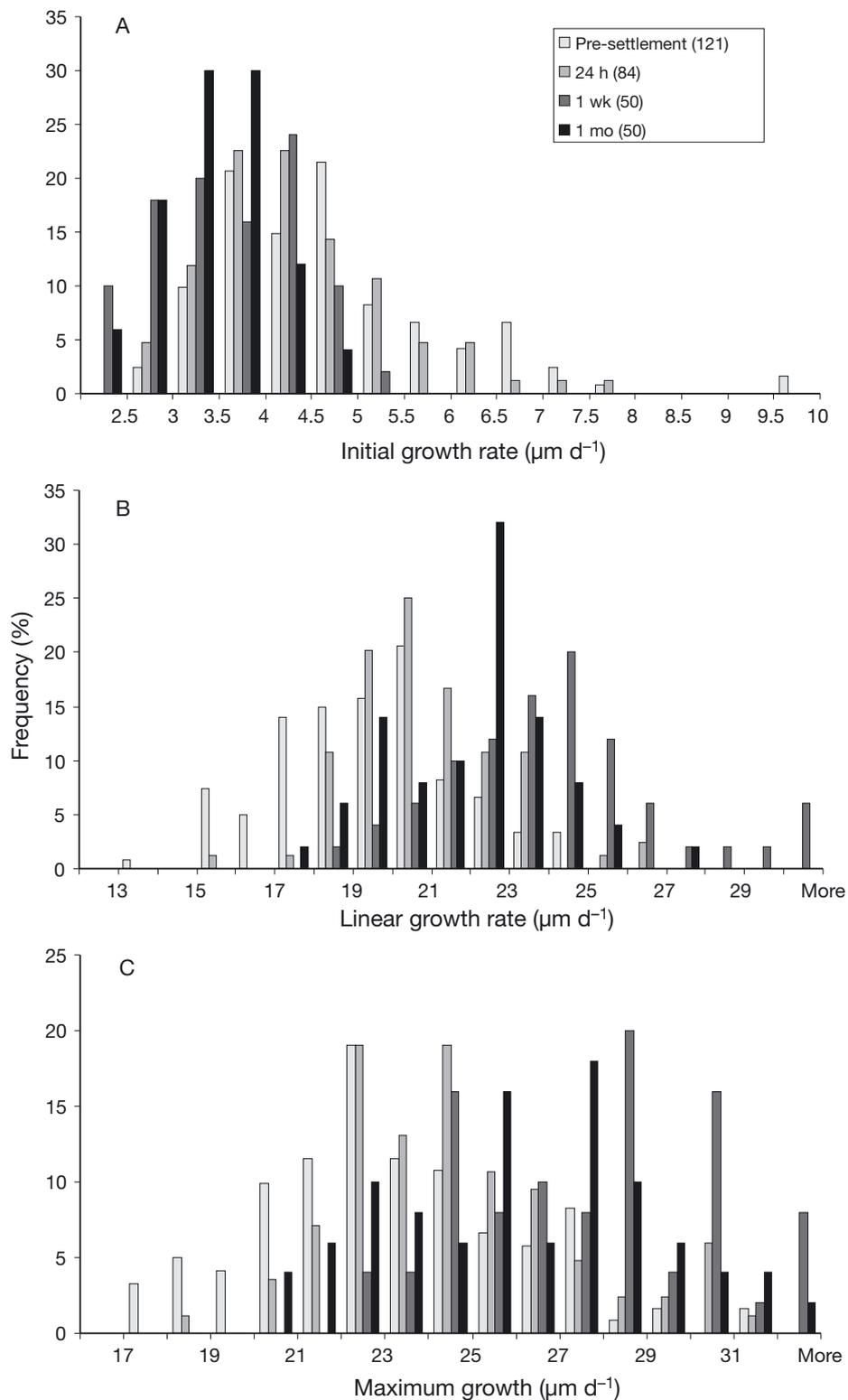


Fig. 3. *Pomacentrus wardi*. Comparison of the frequency distributions of otolith-based growth measures ($\mu\text{m d}^{-1}$) during the larval phase of a cohort of damselfish collected just prior to settlement using light traps (pre-settlement) and 24 h after settlement (fish that were behaviourally assessed), 1 wk after settlement, and 1 mo after settlement. Growth measures were: (A) initial growth rate from 0 to 3 d after hatching; (B) linear growth rate between inflexions at accelerating and decelerating parts of otolith increment width trajectory; and (C) maximum otolith growth

played no change in the boldness measure, while 13% exhibited changes in boldness of 2.5 or more points (out of a maximum possible change of 6 points, e.g. a fish that went from a boldness of 3 at Census 1, to 0 at Census 2, and back to 3 in Census 3) between the 3 censuses (Fig. 5A). For maximum distance ventured from the patch, 27% of individuals showed small changes of 1 cm or less, while 11% showed increases or decreases of ≥ 7 cm between censuses (Fig. 5B).

Table 1. *Pomacentrus wardi*. Comparison of boldness and maximum distance ventured (MaxDV; cm) for the initial census between newly settled damselfish that survived 24 h on the reef and those that died. Data are means \pm SE; effect of other behaviours has been partialled out by ANCOVA (see 'Materials and methods' for details)

	Boldness	MaxDV
Survived	1.66 \pm 0.07	1.89 \pm 0.18
Died	1.38 \pm 0.06	2.39 \pm 0.16

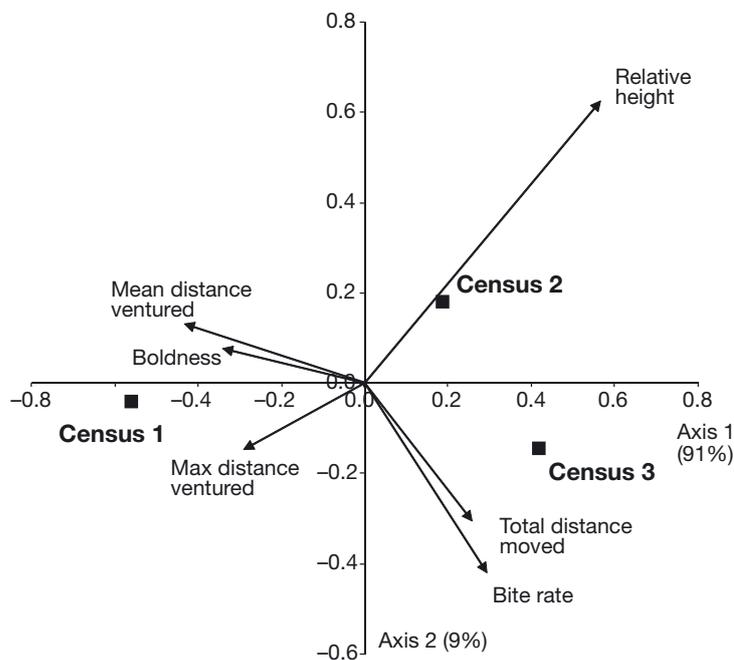


Fig. 4. *Pomacentrus wardi*. Comparison of the behaviour of damselfish immediately after a 20 to 30 min acclimation period on the reef (Census 1), after 4 h on the reef (Census 2) and the following morning (\sim 24 h after release). Displayed are the results of a canonical discriminant analysis showing the position of census centroids (multivariate means) together with the direction and importance (as indicated by vector length) of trends in behavioural attributes. Behaviours are defined in 'Materials and methods'. Data are only for the survivors after a 24 h period (i.e. after Census 3). Any effect of water temperature on behaviour has been removed by residual analysis (see 'Materials and methods')

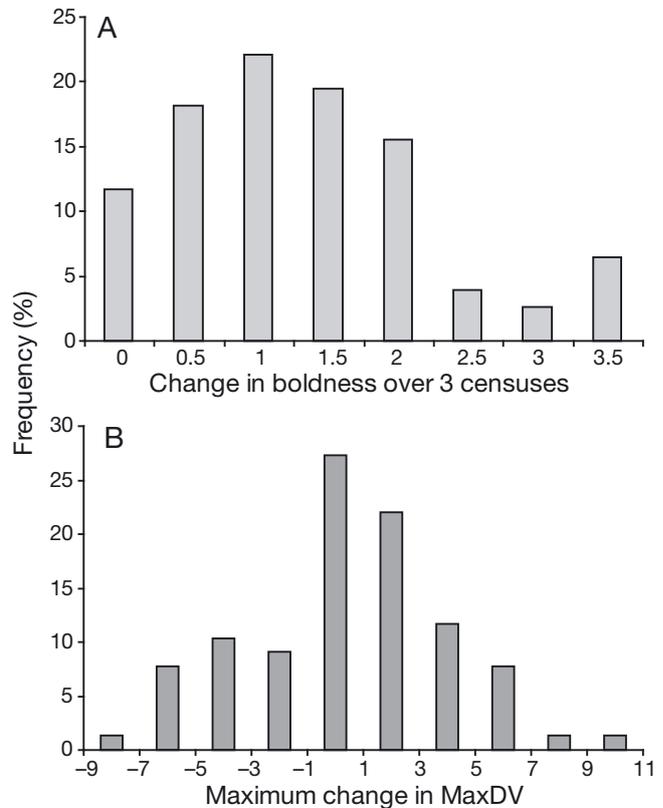


Fig. 5. *Pomacentrus wardi*. Consistency of 2 behaviours exhibited by damselfish among 3 censuses within 24 h, shown as frequency (%) of individuals exhibiting various degrees of changes in behaviour over the 3 censuses: (A) cumulative change in boldness measures (scored on a scale from 0 to 3) regardless of direction of change; (B) maximum change (cm) over the 3 censuses in the maximum distance ventured (MaxDV) from the patch. N = 77 fish

DISCUSSION

Recent studies have emphasized the selective nature of survivorship during critical periods in the life cycle of organisms with complex life histories, such as amphibians and fishes (Lagrue et al. 2007, Pechenik & Levine 2007, Vigliola et al. 2007). The present study adds to other recent work (e.g. Meekan et al. 2010) that highlights the variable nature of selection on growth at different times in the early life stages and emphasizes the potential importance of behavioural traits in influencing the direction and intensity of that selection.

Boldness was found to influence survival, with fish that were initially bold exhibiting greater survival over the first day after settlement, when mortality is typically highest (e.g. Rumrill 1990, McCormick & Hoey 2004); in the present study, 59% of experimental individuals were lost during the first day. Our results contradict the hypothesis that bold individuals are risk

prone and may be more vulnerable to predation than shy individuals in high mortality areas (Boissy 1995, Sih et al. 2004). Instead, these results are similar to those of Réale & Festa-Bianchet (2003), who found that for bighorn sheep *Ovis canadensis*, bold individuals had higher survival than shy sheep under threat from mountain cougars *Puma concolor*. Other studies have found that bold individuals tend to inspect predators, and since predator inspection deters attacks, predators are less likely to initiate attacks on bold individuals than shy individuals (e.g. Godin & Davis 1995). Bold pumpkinseed sunfish *Lepomis gibbosus* fed more and made more predator inspections than shy sunfish (Coleman & Wilson 1998). Our results do not preclude the possibility that the initial boldness exhibited by fish that survived over the first 24 h covaries with a trait that may be detrimental to their survival later in life, or when there are changes in the context in which the behavioural trait is exhibited.

Similar to other studies of tropical fishes (e.g. Shima & Findlay 2002, Vigliola & Meekan 2002, Hoey & McCormick 2004, Meekan et al. 2010), we found that mortality after settlement was selective and was correlated with larval characteristics and growth. Individuals with small otolith sizes at hatching and low otolith growth were selectively removed from the local population over the first 24 h after settlement. However, prey selection by a predator is unlikely to target growth history per se, but instead some visible manifestation of growth history, such as fish size or a behavioural attribute that correlates with growth history. Over the first 24 h on the reef, there was no significant selection for settlement size or body condition, so while selection occurred with respect to larval growth, it was not due to its potential influence of body attributes at settlement. A recent study found that otolith size at hatching correlated with heart rate, a proxy for metabolism, in a tropical damselfish ($r = -0.78$; Gagliano & McCormick 2009). If this relationship is the same for *Pomacentrus wardi*, then it suggests that mortality is selective against larvae with high metabolism. Since metabolism is often correlated with activity levels (McCormick & Nechaev 2002, Garamszegi et al. 2006, Careau et al. 2008), it may be speculated that early larval growth history and post-settlement mortality may be coupled by a behavioural or performance trait that covaries with metabolism.

Behaviours that are relevant to the context in which an animal lives will promote survival (Cote et al. 2008, Smith & Blumstein 2008). Therefore, it may be expected that the consistency with which behaviours are demonstrated will depend on the stability of the individual's behavioural regime. In the present study, although behaviours were consistent over the short term for *Pomacentrus wardi*, assessments hours apart

were poorly correlated. The behavioural variability found through time may be due to the changing environment within which individuals find themselves. The context dependency of behaviours has been shown in numerous other organisms. For instance, juvenile sunfish *Lepomis gibbosus* exposed to a novel threatening stimulus and a non-threatening stimulus displayed consistent individual differences within both contexts, but individual differences did not correlate across contexts (Coleman & Wilson 1998). In the present study, visual or olfactory detection of predators in the vicinity by fish may have led to reductions in space use and influenced the values of the behavioural traits recorded through time. Research has shown that organisms that are best able to learn the signs of danger and react in an appropriate manner have enhanced survival (Mathis et al. 1996). During periods of high mortality, such as immediately after settlement, there should be selection for the ability to rapidly learn and display behaviours that are appropriate to the situation, i.e. those which both maximize fitness-associated behaviours and minimize the probability of capture or damage. This raises the question of whether fish that have exhibited fast previous growth have done so because of their behavioural adaptability rather than exhibiting a consistently shy or bold personality. At the level of the individual, every situation that affects survival and potential fitness may require a different suite of adaptive responses (Coleman & Wilson 1998). If this is the case, then consistency in a shy–bold continuum may be adaptive in some contexts, but not others.

Little is known about the consistency of behaviours of marine fishes through time, or the extent to which they exhibit behavioural syndromes where suits of behaviours covary across contexts. A recent laboratory study of newly settled *Pomacentrus wardi* found that latency to re-emerge from shelter after they had been approached by the handle of a hand net differed among individuals (Biro et al. 2009). While there was a general trend for increased boldness with increasing temperature, approximately half of the individuals changed in their relative rank of boldness, demonstrating strong individuality in response to the new environmental conditions in the laboratory.

It may be that the plasticity in an individual's response may be subject to selection. In some situations it may be advantageous to be bold and take risks, but to avoid risk in other situations (Coleman & Wilson 1998). In the present study, plasticity in the propensity of individuals to venture away from shelter was found to be related to initial larval growth rate. Distance ventured significantly influenced an individual's survival with those fish that ventured furthest having lower survival probabilities. This relationship between growth

and behaviour may help explain how aspects of past growth that do not appear to relate strongly to subsequent growth history or phenotypic characteristics, such as size at metamorphosis, may still be selected upon much later in life. Interestingly, initial boldness and maximum distance ventured from shelter correlated poorly with behaviour in the later censuses.

It is notable that there were relationships between initial behavioural attributes and survival throughout the first 24 h on the reef, given that most of the mortality occurred between Census 2 and 3. This suggests that the behaviour exhibited initially represented an aspect of personality that related to some aspect of vulnerability later on. Some of the traits that may be associated with vulnerability were higher during Census 1, namely boldness, distance ventured from the patch and closeness to the substratum, suggesting that these traits may have simply been more overt during this exploratory phase. An alternative explanation is that initial behaviours, and aspects of previous growth history, covary with the occurrence of rare behaviours that influence vulnerability, but which were not quantified adequately using our methods.

A large body of literature on larvae of a variety of taxa suggests that once an individual has a growth advantage, these advantages are maintained (the growth–predation hypothesis; Anderson 1988). Arendt (1997) argues that because predators are gape limited there should be selection for high growth, particularly during periods of high mortality such as during the juvenile life stage. Strong size-selection has recently been demonstrated by a number of common piscivores that feed on juvenile reef fishes (McCormick & Meekan 2007, Holmes & McCormick 2010). The mechanism by which these advantages are maintained is suggested to be behavioural, facilitated by performance characteristics, such as large size and burst speed (Miller et al. 1988, Bailey & Houde 1989, Leggett & Deblois 1994). However, detailed analyses of selection on growth over larval and juvenile life phases, such as the present study, suggest that the direction and intensity of selection on growth may change with ontogeny (e.g. Gagliano et al. 2007, Meekan et al. 2010). Growth rate over the first 3 d after hatching did not appear to be selected for during the first day on the reef. However, by the end of the first week, most individuals that displayed high initial growth were lost from the population. In contrast, high growth later in the larval stage (as recorded by growth during the second third of the larval phase) and maximum growth rate appeared to promote later survival. Together, these findings suggest that survivors to 1 mo after settlement were those fish that displayed slow initial growth followed by high subsequent larval growth rather than those fish that grew consistently fast as larvae.

Our longitudinal study suggests that this growth signature, rather than being a feature common to all field-caught fish, is actually a characteristic of the survivors of post-settlement selection. Moreover, this growth-selective loss does not occur in the initial 24 h when mortality is typically highest for demersal fishes (in the present study 59%; McCormick & Hoey 2004, Almany & Webster 2006), but from Day 2 to 7 after settlement. It appears fish that had slow initial growth followed by very fast growth demonstrated attributes that lowered their risk of predation. A contrasting theory to the growth–predation hypothesis, principally developed through resource deprivation experiments, suggests that fast growth will lead to high mortality due to its covariance with risk-taking behaviour (Metcalf & Monaghan 2001, Stamps 2007). In the present study, fast growth in the early larval phase appears to have a trade-off with mortality that is not manifested until fish have survived the larval phase and become juveniles. These lag or carryover effects of previous growth history have important ramifications for determining which individuals survive periods of high mortality (Metcalf & Monaghan 2001, Gagliano et al. 2007).

Compensation for slow growth at the start of larval life may have subsequently affected survival probabilities. Fish that are forced to compensate for slow growth are found to demonstrate accelerated growth once conditions for growth improve, and these individuals are usually physiologically more efficient in processing energy. This metabolic advantage is usually relatively short-term in adult fishes, but has been shown to have lasting effects in early life history stages (Mortensen & Damsgård 1993, Ali et al. 2003, Gagliano & McCormick 2007). While survivors appear to have the signature of growth compensation early in the larval stage, this growth appears to have enhanced survival in the juvenile phase. However, there is also some evidence that fish who maintained high growth for longer were removed between 1 wk and 1 mo after settlement, suggesting that high growth may exact a cost later in life. Compensatory growth has been found to have a variety of detrimental effects later in life in other organisms, including decreased physiological capacity, increased risk of disease, reduced cognitive abilities and higher mortality rates (Mangel & Munch 2005, Fisher et al. 2006, Fraser et al. 2007, Inness & Metcalfe 2008).

The possibility that the manipulations of the monitored fish enhanced mortality cannot be discounted. However, a number of observations suggest that if there was an impact, it was minimal. Firstly, mortality over the first 4 to 5 h (between Censuses 1 and 2) was minimal. Secondly, the direction of selective mortality was consistent with the trends in selection on all otolith-associated traits through time. Thirdly, the daily rates of mortality were similar to those recorded by

other studies of newly settled damselfishes (e.g. Hoey & McCormick 2004, McCormick & Meekan 2007, Holmes & McCormick 2009, Meekan et al. 2010).

Evidence presented here suggests that the transition from pelagic to benthic environments represents a period that is dynamic with respect to the mechanisms that influence survival. Mortality was selective for growth and size attributes, but the timing and intensity changed rapidly over the first month of settled life. Behaviour may be expected to be variable at settlement as fishes are naïve to the environment and community into which they recruit and have to rapidly learn behaviours that enhance survival in their new environment. One interpretation of the poor correlations among behavioural assessments of individuals through the first 24 h is that the novel cues proffered by their new environment are variable in timing and spatial distribution, with individuals learning how best to respond to these as they are encountered. Evidence suggests that the drivers of growth can have a lasting carryover effect on survival potentially through their covariation with behaviour traits, such as boldness.

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