



# Compensating in the wild: is flexible growth the key to early juvenile survival?

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We explore the mechanisms underlying the survival of a cohort of a coral reef fish (*Pomacentrus amboinensis*) in the first month following settlement. To investigate the extent to which growth history immediately following settlement is linked to early survival, we tagged 900 fish the morning after settlement and recaptured the survivors ( $n = 34$ ) 30 days later. Otolith analysis showed that individuals that were larger at settlement preferentially survived the first month in benthic habitats. We also compared these survivors with conspecifics from the same cohort that were collected at settlement and then outgrown in two experimental feeding conditions to produce fast- and slow-growing fish. Comparison of the growth histories exhibited by the survivors to those of experimental conspecifics revealed that survivors exhibited relatively slow initial growth during their first few days on the reef, followed by a period of accelerated growth. We suggest that the flexibility in growth potential of young fish allows for the occurrence of periods of rapid (and compensatory) growth that might enhance post-settlement survival by attenuating the high risk of size-selective mortality.

Most organisms have complex life cycles consisting of two or more temporally and spatially discrete stages (Wilbur 1980, Hellriegel 2000). Ontogenetic shifts between stages are typically accompanied by pronounced changes in body size (Werner and Gilliam 1984). Since body size has a profound influence on key fitness attributes in many species (Stearns 1992), understanding variations in body size and in the time required to attain a size (hence growth rate), has become of central focus in life history theory (Abrams et al. 1996, Arendt 1997).

In species where size at an early age has immediate consequences for survival, differences in resource availability can strongly affect individual growth rates and thus stage-specific performance through size-dependent behavioural interactions and physiological processes (Niva and Jokela 2000). The tradeoff between eating (i.e. growth) and getting eaten (i.e. mortality) is particularly marked during the larval and juvenile stages of these species (Martel 1996). In marine fishes, this tradeoff is often examined within the theoretical framework of the growth–mortality hypothesis (Anderson 1988). It suggests that the large and well documented

variations in year class success of fish populations are generated by the interaction of the processes of growth and mortality during early life history. Rapid growth at this time is expected to enhance survival through the covariation of size with attributes that influence the vulnerability of young fish as prey (the ‘bigger-is-better’ hypothesis, Miller et al. 1988), their physiological tolerances (Sogard 1997) and by reducing the time spent in this vulnerable life history phase (the ‘stage duration’ hypothesis, Houde 1987). Consequently, growth histories may have utility in predicting survival potential of fishes if individual trajectories can be examined throughout early life (Meekan and Fortier 1996, Bergenius et al. 2002).

Recent studies of reef fishes have found that growth advantages manifested in the larval phase are maintained upon settlement from the plankton, influencing which individuals survive in benthic habitats (Searcy and Sponaugle 2001, Shima and Findlay 2002, Vigliola and Meekan 2002, Hoey and McCormick 2004, Raventos and Macpherson 2005, Jenkins and King 2006). However, in some cases newly settled fish appear to be capable of modifying individual growth

trajectories established during larval life by compensation upon settlement (Bertram et al. 1993, McCormick and Hoey 2004, Gagliano et al., unpubl.). Variation in growth during early life history is largely a reflection of parental contributions and environmental factors, such as temperature (Green and McCormick 2005) and food availability. Any compensatory mechanism allowing individuals to vary their growth rates with some level of independence from environmental fluctuations would be advantageous, particularly immediately after settlement when juveniles suffer heavy losses (Doherty et al. 2004, Almany and Webster 2006). Although compensatory responses have been widely documented in terrestrial plants and animals (reviewed by Arendt 1997), demonstration that compensatory growth in fish occurs under natural conditions is extremely limited (Carlson et al. 2004, Gagliano et al., unpubl.) and comes solely from manipulative experiments (Letcher and Terrick 2001, McCormick and Hoey 2004, Johnsson and Bohlin 2005).

Otolith analysis has become a common tool for the description of growth and mortality patterns during the early life history of reef fishes. Increment patterns within otoliths reveal daily patterns in size at a given age and growth (Stevenson and Campana 1992). Differences in the shape of otolith pairs can also provide information on the condition of individuals growing under varying environmental conditions (Cardinale et al. 2004, Gagliano and McCormick 2004). Here, we use otolith analysis to determine if the survival of a common coral reef fish, *Pomacentrus amboinensis*, was linked to growth history during the early juvenile period. We compare size at a given age and growth rates of wild recruits with conspecifics from the same cohort, for which growing conditions were known, in order to explore the mechanisms underlying survival patterns observed in the natural population in the first month after settlement. Our aims were to establish if fish surviving the first month after settlement from the plankton to the reef had undergone selective mortality based on size and growth rate and secondly, to explore if young fish were capable of compensating for earlier sub-optimal growth by increasing growth trajectories and thereby reducing their chances of size and/or growth-selective mortality.

## Methods

### Study site and species

The study was conducted at Lizard Island (14°38'S, 145°28'E) on the northern Great Barrier Reef. The target species, the Ambon damsel *Pomacentrus amboinensis*, is abundant and settles in high numbers on the fringing reef around the island during October to

February after a pelagic larval life of 15–23 d (Kerrigan 1996). At settlement *P. amboinensis* rapidly metamorphoses into the juvenile form (McCormick et al. 2002) and remains strongly site-attached throughout its life (McCormick and Makey 1997, Booth 2002), providing an ideal model for tracking the growth history and survival of individual fish. Information on the growth history of this species can be readily extracted from otoliths. Growth rings in these structures are deposited daily and provide a good proxy for somatic growth of individual fish (Pitcher 1988) and the shape of otolith in this species records information on the juvenile feeding history (Gagliano and McCormick 2004).

### Growth and survival on reef

Settlement of *Pomacentrus amboinensis* is episodic and peaks around the time of the new moon (Meekan et al. 1993). Immediately following a settlement pulse in November 2003, we searched a 500 m section of reef for newly settled individuals and tagged 900 in situ. Fish could be identified as newly settled from their size and coloration (McCormick and Makey 1997). Tagging was done underwater by transferring individuals into a small clip-seal plastic bag and injecting a fluorescent elastomer tattoo (Northwest Marine Industries Inc.) beneath the epidermis using a 29G hypodermic needle. Fish recovered within one minute of tagging and were released at the site of capture. Elastomer tags have a 100% retention rate and are known to have no effect on either mortality rates or growth (Hoey and McCormick 2006). After 30 days post-settlement all surviving tagged individuals ( $n = 34$ ) were collected from the reef. The percentage of tagged fish recaptured after 30 days on the reef reflected the extremely high levels of juvenile mortality and was consistent with previously documented estimates for this species at this same location (McCormick and Hoey 2004, Almany and Webster 2006). All recaptured individuals were killed by cold shock and photographed against a scale bar. Standard length (SL, mm) was measured on these images using image analysis software (Optimas 6.5). Sagittal otoliths were then removed, cleaned and stored dry for growth analysis. To avoid biases in back-calculating somatic growth from otoliths (Hare and Cowen 1997, Thorrold and Hare 2002), all comparison of relative size and growth were based on otolith measurements only, unless specified otherwise.

To determine if mortality during the first month after settlement was size-selective we compared the radii of transverse sections of sagittal otoliths (Fig. 1 in Wilson and McCormick 1999) from the nucleus to the settlement mark of the survivors of the November settlement pulse 30 d after tagging ( $n = 34$ ), with those of a random sample of newly metamorphosed fish

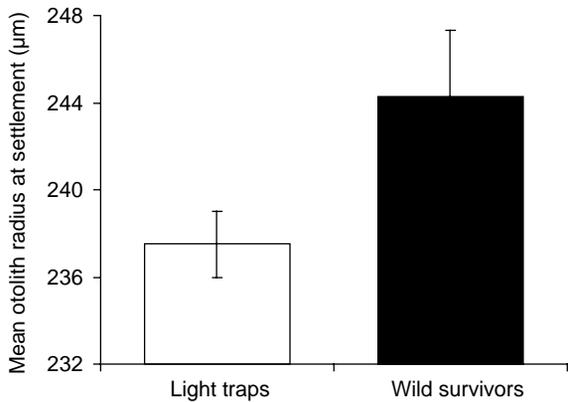


Fig. 1. *Pomacentrus amboinensis*. Comparisons of mean otolith radius at settlement ( $\mu\text{m} \pm \text{SE}$ ) of *P. amboinensis* collected by light traps (white bar) and individuals surviving the first month after settlement on the reef (black bar). Otolith radius was used as a proxy for size at settlement. Note: y-axis begins at 232  $\mu\text{m}$ .

caught in light traps (trap design in Meekan et al. 2001) 30 days earlier ( $n=52$ ). Individuals obtained from traps were used to characterize the size range fish of the recruitment pulse immediately prior to settlement and mortality on the reef as previous studies have shown that there is a strong correlation between light trap catches and settlement patterns of *P. amboinensis* (Milicich et al. 1992, Meekan et al. 1993). These fish were collected by three traps moored over sandy bottom, approximately 100 m apart and 30 to 50 m from the reef edge in late November 2003. Traps were deployed 1 m below the surface prior to dusk and then cleared of fish just after dawn the following morning.

### Growth trajectories under differing feeding regimes

A random sample of 52 newly metamorphosed *P. amboinensis* collected by light traps on the same day as the tagging study began were removed from the traps and placed in blue plastic 1 l aquaria ( $n=1$  fish aquaria<sup>-1</sup>) supplied with a constant flow of seawater. Aquaria were held outdoors, ensuring that temperature ( $29 \pm 0.3^\circ\text{C}$ ), salinity ( $34 \pm 0.1$  ppt) and light regimes remained as similar as possible to the natural environment. Fish were randomly assigned to two feeding regimes for 30 d. In the first, fish were fed 24–36 h-old *Artemia* sp. nauplii ad libitum, and in the second they were fed nauplii every third day. Fish fed ad libitum were fed three times throughout the day to ensure that they always had food in their tank during daylight hours. Fish fed every third day received food once only in the morning of every third day. Aquaria were inspected daily and cleaned of algal growth. After

30 d fish were sacrificed, body dimensions were measured and otoliths removed for analysis.

### Otolith shape and growth

To quantify the two-dimensional shapes of both left and right sagittal otoliths, we used Fast Fourier analysis as described in Gagliano and McCormick (2004). Briefly, a grey-scale image of each sagitta was captured using an image analysis system and camera linked to a microscope. The distal edge of the otolith rostrum was chosen as a common landmark point to start each of the automated tracings. The silhouette of each otolith was represented by a series of successive cosine waves, having amplitude and phase angle components. The amplitude of each cosine wave was the Fast Fourier shape descriptor (also termed “harmonic”) and all harmonics were standardised by the 0th and 1st harmonics, to exclude any confounding effect of otolith size and its position on the screen. The first six harmonics determine the gross shape of the otolith, such as its elongation, triangularity and squareness, whereas successive harmonics measure increasingly finer details in the otolith silhouette. The number of harmonics to be used as shape descriptors for the left and right sagittae of each fish was set to the first 20 (excluding the 0th and 1st harmonics) because the contribution of higher order harmonics (i.e. 21 and above) to the definition of the shape was negligible.

Otolith growth trajectories were measured from thin transverse sections through the nucleus of left sagittae, after the otoliths were mounted in thermoplastic cement (Crystal Bond<sup>TM</sup>), ground and polished using 12 to 0.3  $\mu\text{m}$  lapping films (Wilson and McCormick 1997). Increment widths were examined at  $400\times$  magnification and measured along the longest axis of the otolith using a video image-analysis system linked to a compound microscope.

### Analyses

We used otolith analysis to compare the age and size of fish in the initial cohort (i.e. light trapped fish) with those of individuals that survived 30 d after settlement. We estimated age at settlement by counting the number of days individuals spent in the pelagic environment before settlement (i.e. PLD). Otolith radius at settlement was used as a proxy for fish size at settlement, based on the assumption that there was a strong relationship between somatic and otolith size. Evidence for this assumption is shown by studies that have recorded significant correlations between standard length (SL) and otolith radius (OR) of newly settled *P. amboinensis* (Pitcher 1988, McCormick and Hoey 2004) and it was verified by calculating a regression

relationship between fish SL and otolith radius for fish ranging from 10.5 to 31.3 mm SL ( $SL = 2.82 + 39.04 \times OR$ ,  $r^2 = 0.77$ ,  $p < 0.001$ ,  $n = 508$ ). Furthermore, the assumption of homogeneity of slopes in the relationship between fish SL and otolith radius among the 3 fish groups was tested (ANCOVA model,  $p = 0.34$ ) prior to comparisons of otolith growth profiles.

To examine whether mortality was size-selective, we used a one-way ANOVA to compare age and otolith radius at settlement between fish collected by light traps (i.e. the presumed initial population) and survivors 1 month after settlement. We also examined growth patterns at the end of the experiment (30 d) by comparing body size (SL, mm) of survivors to fish fed ad libitum and fish fed every third day using one-way ANOVAs.

We compared the shape of each otolith pair of fish fed ad libitum, fish fed every third and survivors using the first 20 standardised harmonics and a set of multivariate statistical tools. The hypothesis of no difference in otolith shape among the three groups was tested using multivariate analysis of variance (MANOVA), followed by a canonical discriminant analysis (CDA) to examine and display the patterns of difference identified by MANOVA (Tabachnick and Fidell 2001). Vectors of the original harmonics were plotted to aid interpretation of differences among groups. The length of the vectors described the relative importance of each harmonic in discriminating among groups. Each group was represented by 95% confidence cloud around group centroids (Seber 1984).

The 30 d experimental period was divided into 10 d intervals beginning from the settlement mark. We compared the otolith growth profiles of fish fed ad libitum, fish fed every third day and survivors collected from the reef over each of these growth periods using repeated measures MANOVA and ANOVA (Chambers and Miller 1994). The otolith growth profiles were based on the mean otolith radius ( $\mu\text{m}$ ) at age and mean otolith growth rate ( $\mu\text{m d}^{-1}$ ). The former measured the distance of each increment from the settlement mark, to provide information on the cumulative growth (size at a given age); the latter measured the width of adjacent increments after the settlement mark for an estimate of the daily otolith growth.

## Results

### Size selectivity of natural mortality

We found that juveniles recaptured from the reef one month after settlement had settled at similar ages to the fish caught in the light traps ( $F_{1,66} = 0.027$ ,  $p = 0.87$ ). However, fish that survived the first month after settlement in benthic habitats had significantly larger

otolith radii at settlement than fish obtained from light traps ( $F_{1,79} = 5.44$ ,  $p < 0.05$ ), suggesting that the members of the cohort that were smaller at settlement were selectively removed within the first 30 d of benthic life (Fig. 1).

### Fish size

Despite belonging to the same cohort, survivors collected from the reef and fish in the two feeding treatments all differed significantly in SL one month after settlement ( $F_{2,82} = 357.37$ ,  $p < 0.001$ ) with survivors being the largest (wild > fed ad libitum > fed every third d, Fig. 2).

### Otolith shape comparison

A MANOVA comparing the shape described by the first 20 harmonics from both left and right sagittae suggested that there were differences in the shape of otoliths of survivors and those fish in the experimental feeding treatments (Pillai's trace,  $F_{80,82} = 3.912$ ,  $p < 0.001$ ). Most of the variation among these groups (95%) was due to differences between laboratory fish (feeding treatments) and the survivors (canonical variate 1, Fig. 3). Although wild fish were located well away from both laboratory groups along canonical variate 1, they occupied a similar position to fish fed every third d along the second variate. The arrangement of the three groups along this second axis suggests that wild fish may have experienced intermittent feeding conditions sometime during the 30 d following settlement. The overall discrimination among the three groups by the analysis was mostly driven by differences in the shape of the otoliths, represented by low-order harmonics (Fig. 3).

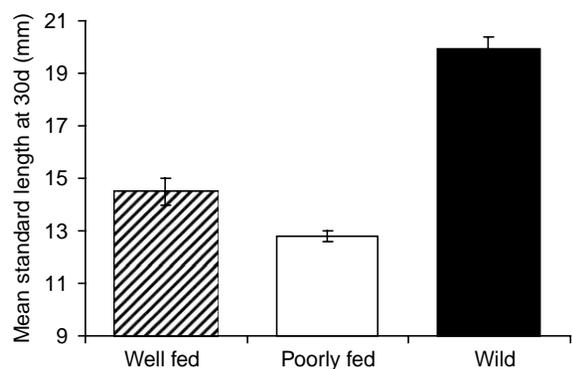


Fig. 2. *Pomacentrus amboinensis*. Comparison of mean standard length (mm  $\pm$  SE) of fish from the three treatments 30 d after settlement: wild survivors (black bar) and well fed (fed ad libitum, hatched bar) and poorly fed (fed every third day, white bar). Note: the y-axis begins at 9 mm.

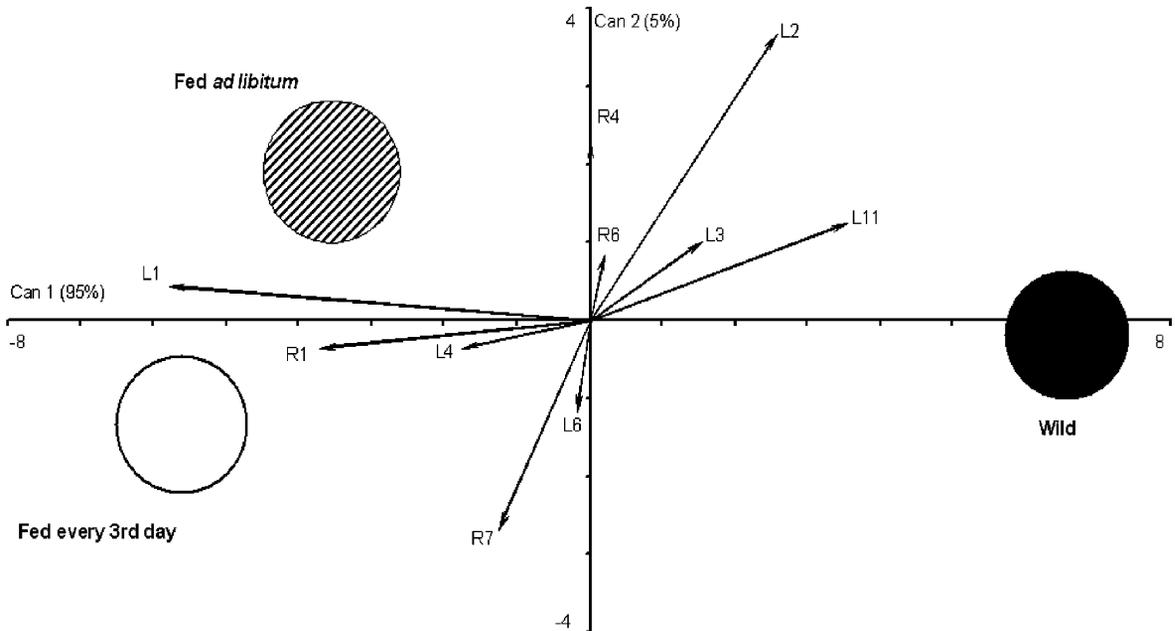


Fig. 3. *Pomacentrus amboinensis*. Comparison of the otolith shape of *P. amboinensis* surviving the initial 30 d following settlement on the reef and individuals from the same cohort kept in known growing condition (fed ad libitum and fed every third day) over the same period. Displayed are the results of a canonical discriminant analysis using Fast Fourier descriptors (or harmonics) of both the left (L) and the right (R) sagittal otolith. The first 10 harmonics are represented as vectors. Ninety-five percent confidence clouds around group centroids (treatments).

Results of the jackknifed cross-validation tests indicated high rates (79%) of classification success among groups.

highest rate in mean otolith growth (survivors > fed ad libitum > fed every third d, Fig. 5c).

### Otolith growth profiles

Otolith growth profiles differed significantly among survivors and experimental fish (Table 1). The mean otolith radius of survivors over the first 10 d after settlement closely resembled the profile of fish fed every third d in the laboratory (Fig. 4) and then changed trajectory during from 11–21 d after settlement, ultimately resulting in the largest otolith radius at 30 d in comparison with fish from the feeding treatments. This result suggests that survivors experienced similar growth conditions to fish fed every third d during the first 10 d of benthic life.

Mean otolith growth rates ( $\mu\text{m d}^{-1}$ ) just prior to settlement were similar among survivors and the feeding treatments (Pillai's trace,  $F_{8,50} = 0.875$ ,  $p = 0.544$ ). During the first 10 d immediately following settlement, growth rates altered significantly among groups (Table 1ai, bi). Fish fed ad libitum initially grew faster than the survivors or intermittent feeding treatment (Fig. 5a). Differences in growth among the groups declined from 11–20 d, with survivors having the highest growth rates at this time (Fig. 5b; Table 1aii, bii). By 30 d, all groups had different growth rates with survivors having the

### Discussion

Mortality of *Pomacentrus amboinensis* during the first month after settlement was found to be negatively correlated with size at settlement. The present study supports recent findings by McCormick and Hoey (2004) showing higher survival of *P. amboinensis* that were bigger at settlement. Similar findings indicating that larger initial size increased the survival probabilities of newly settled fish have also been previously reported for other reef fish species (e.g. *Chromis cyanea*, Carr and Hixon 1995, Hawn et al. 2005; *Dascyllus albisella*, Booth 1995; *Pomacentrus moluccensis*, Brunton and Booth 2003). Other studies, however, have found no obvious advantages to being larger at settlement (McCormick and Kerrigan 1996, Searcy and Sponaugle 2001, Hoey and McCormick 2004). Holmes and McCormick (2006) recently showed that the extent to which mortality was size selective immediately after settlement can differ among locations separated only by 100's of metres. These conflicting results suggest that mortality at settlement is not always selective for small body size, and that whether it is or not may depend on the relationship between size and other morphological

Table 1. *Pomacentrus amboinensis*. Results of repeated-measures MANOVA (a, within-subject effects) and ANOVA (b, between subject effects) that compared otolith radius (mm) at age and daily otolith growth rate ( $\text{mm d}^{-1}$ ) of the three fish groups (fed ad libitum, fed every third d and wild) for the growth period (i) 0 to 10 d; (ii) 11 to 20 d and (iii) 21 to 30 d post-settlement. Pillai's trace statistics was used as the multivariate test statistic. Significant results are in bold.

a. Source		DF <sub>effect</sub>	DF <sub>Error</sub>	Pillai's	F	p	b.		DF	MS	F	p
i	Radius at age	9	19	0.980	131.064	<b>≤0.0001</b>	i	Groups	2	0.001	3.859	<b>0.034</b>
	Radius at age × groups	18	40	0.973	2.107	<b>0.025</b>		Error	27	0.001		
	Daily growth	9	19	0.287	0.8510	0.581		Groups	2	0.001	3.798	0.035
	Daily growth × groups	18	40	0.690	1.1711	0.328		Error	27	0.001		
ii	Radius at age	9	19	0.983	120.680	<b>≤0.0001</b>	ii	Groups	2	0.004	3.680	<b>0.037</b>
	Radius at age × groups	18	40	1.060	2.507	<b>0.008</b>		Error	27	0.001		
	Daily growth	9	19	0.595	3.104	<b>0.018</b>		Groups	2	0.001	7.284	<b>0.003</b>
	Daily growth × groups	18	40	0.678	1.139	0.354		Error	27	0.001		
iii	Radius at age	9	16	0.985	117.419	<b>≤0.0001</b>	iii	Groups	2	0.013	5.701	<b>0.009</b>
	Radius at age × groups	18	34	1.061	2.1353	<b>0.028</b>		Error	24	0.002		
	Daily growth	9	16	0.462	1.524	0.221		Groups	2	0.001	25.363	<b>≤0.0001</b>
	Daily growth × groups	18	34	0.788	1.229	0.294		Error	24	0.001		

and physiological traits (e.g. body condition or growth, Hoey and McCormick 2004). For example, a recent study by Sponaugle et al. (2006) showed that warmer water temperature enabled smaller settlers *Thalassoma bifasciatum* to reach or exceed size-at-age of larger, cooler water settlers. Smaller settlers were frequently in better condition at settlement and swam faster than larger conspecifics (Grorud-Colvert and Sponaugle, pers. comm.). These results suggest that smaller recruits may be able to reduce risk-taking behaviour by sheltering more and consuming less food, and have greater probability of success in escaping a predator. Ultimately, the nature and magnitude of mortality around settlement may depend on the conditions into which individuals settle (Rice et al. 1997).

In the current study, the otolith record of size at settlement provided evidence that individuals that were larger at settlement preferentially survived the first month on the reef. This may either be the result of the summation of size-selective processes throughout the 30 d period, or alternatively, intense size selection occurring immediately after settlement, followed by the maintenance of this pattern through either the random loss of individuals or less intense selection in the same direction as the initial losses. By preferentially removing smaller fish from a cohort, size-selective mortality reduces the size variation in the cohort over time, decreasing the likelihood of further selection (Sogard 1997). If so, size-selective mortality may operate over a relatively narrow temporal window (Sogard 1997, Searcy and Sponaugle 2001). McCormick and Hoey (2004) have recently shown that mortality of *P. amboinensis* could be directed toward smaller individuals within the first 9 d of settled life. This finding alongside results from the present study support the hypothesis that size-selective mortality operates only during a short initial period and its intensity declines rapidly after the first week post-settlement. However, more intensive sampling of the wild population is

required to conclusively differentiate between the two alternatives.

Comparison of wild survivors to alternative laboratory-derived growth profiles suggests that survivors of this selective mortality initially had relatively slow growth during the first few days on the reef, after which their growth gradually accelerated. In the absence of the wild fish that did not survive to day 30, the laboratory growth profiles gave us an indication of possible growth profiles at the extremes of the food availability range. The marked difference in trajectories between experimental and wild caught fish suggests that fish who survived in the wild were able to 'catch-up' or compensate for an initial period of reduced growth. The initial depression of growth immediately after settlement suggests that optimal growth may be constrained by the eco-physiological abilities of new recruits to perform effectively vital activities, such as feeding (through trophic specialization). Although settlement per se can be an overnight event for many species (McCormick et al. 2002), examples from both tropical and temperate species show that fishes can take a number of days to weeks to fully adopt a benthic feeding mode after settlement (Randall 1961, Labelle and Nursall 1985, Clements and Choat 1993, McCormick and Makey 1997). As small fishes have limited capacity to store energy (Schultz and Conover 1999), this may result in an initial period of slow growth.

Given that susceptibility to predators is generally higher for the smaller individuals (growth-mortality hypothesis; Anderson 1988), any mechanism allowing individuals to increase rates of growth to attain a larger body size is expected to be beneficial. By reaching a size threshold that substantially enhances post-settlement survival, juveniles may attenuate the effect of size-specific (i.e. 'bigger-is-better' hypothesis; Miller et al. 1988) as well as stage-specific mortality ('stage-duration' hypothesis; Houde 1987). In our study, individuals that adapt to the local predation climate

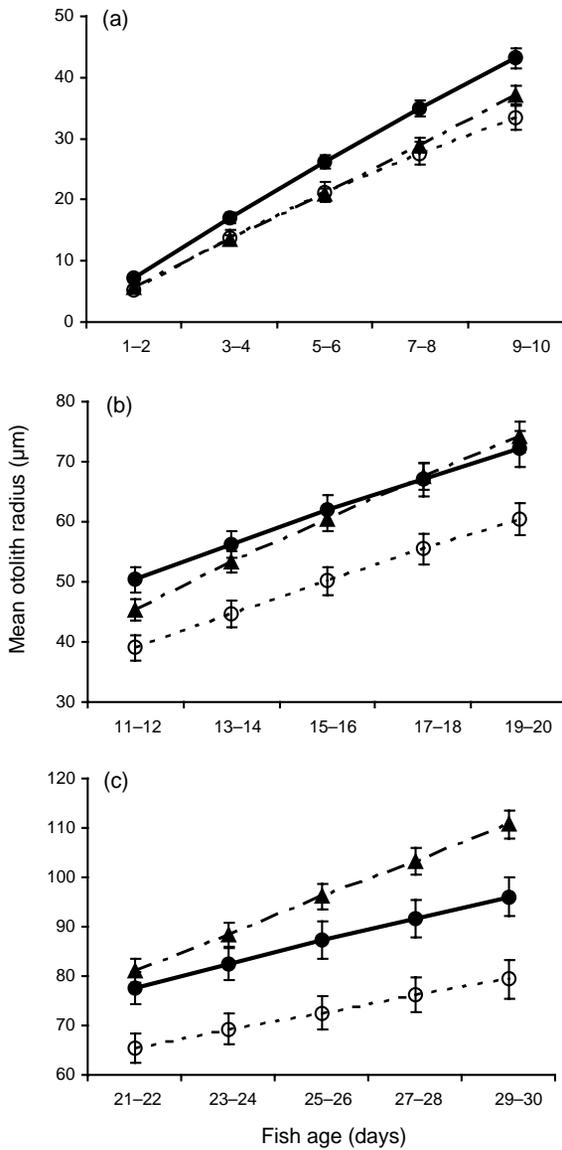


Fig. 4. *Pomacentrus amboinensis*. Comparison of mean otolith radius ( $\mu\text{m} \pm \text{SE}$ ) at age of wild survivors ( $\blacktriangle$ ) and conspecifics fed ad libitum ( $\bullet$ ) and fed every third day ( $\circ$ ) from settlement to 10 d after settlement (a), 11 to 20 d after settlement (b), and 21 to 30 d after settlement (c).

after an initial critical period of transition were rewarded with survivorship, and possibly with a higher probability of gaining access to food. An increase in foraging success following a period of low feeding may be associated to greater energy assimilation-conversion efficiency (Skalski et al. 2005) that is quickly manifested in the growth trajectory of surviving recruits. As a result, survivors at 30 d were able to mitigate the effect of a poor start to some extent through a compensatory mechanism and ultimately achieve a larger body size relative to the experimental treatments.

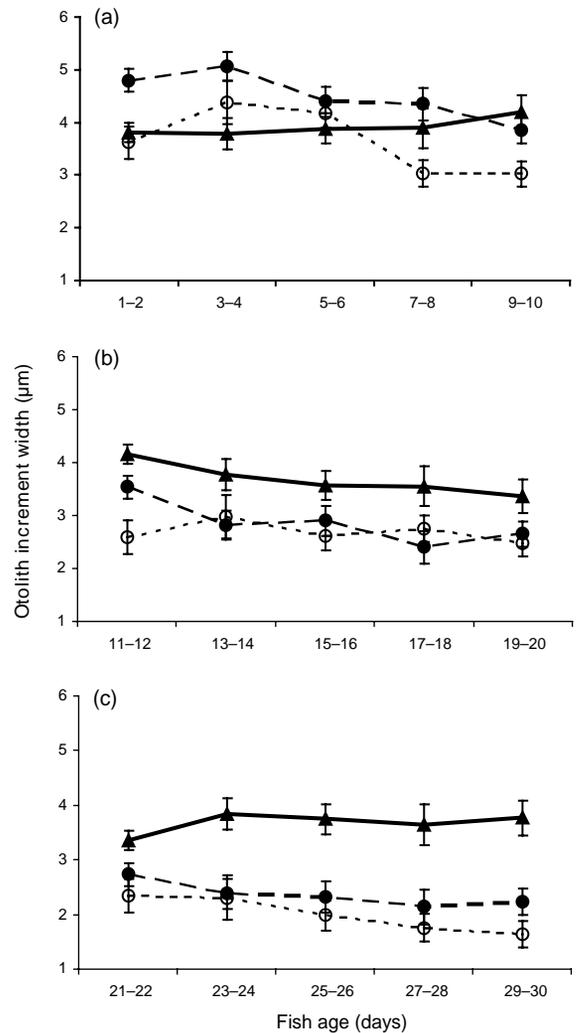


Fig. 5. *Pomacentrus amboinensis*. Average otolith growth rate ( $\mu\text{m d}^{-1} \pm \text{SE}$ ) of wild survivors ( $\blacktriangle$ ) and conspecifics fed ad libitum ( $\bullet$ ) and fed every third day ( $\circ$ ) from settlement to 10 d after settlement (a), 11 to 20 d after settlement (b), and 21 to 30 d after settlement (c).

In this study, we observed extremely high mortality of young fish over a relatively short period (i.e. 30 d) and found that survivors had a slow start and steep growth trajectory. This finding indicates that growth rates can be under very strong phenotypic selection immediately after settlement (Gagliano et al., unpubl.) and suggests that survivors of this cohort had a growth strategy that enhanced survival probabilities under that specific selective environment. This points to the possibility that selective processes act on particular growth trajectories which include periods of faster (and compensatory) growth (i.e. genetic response, Carlson et al. 2004). Alternatively, growth compensation may be triggered by behavioural and morphological changes

occurring at a particular time shortly after settlement. This implies a plastic growth response that effectively ameliorates the risk of mortality directly associated with size-selective predation and ultimately nutritional stress. At this stage, this study cannot provide conclusive evidence for either of these two possible responses and their evolutionary consequences. Nonetheless, it underscores a clear need for better understanding of the mechanisms giving rise to and maintaining variation in growth in natural populations.

In conclusion, we have shown that recruits surviving on the reef were growing differently than conspecifics maintained in the laboratory, indicative of flexibility in growth potential associated to environmental and ecological conditions. This study has provided a comparative description of the growth trajectories of survivors, showing that successful individuals may have initial slow growth rates, possibly due to physiological limitations and behavioral naivety. Nevertheless, they are capable of very fast growth once they have worked out how to exploit the appropriate resources. We have demonstrated the occurrence and ecological relevance of size-selective and developmental processes that contribute to the observed patterns of growth and survivorship. We have also shown that accelerated growth, as observed in wild fish during the compensatory period has immediate benefits in terms of increased size and improved survival. While the ecological benefits of rapid growth may be easily observed, the costs of compensatory growth may be more difficult to detect, particularly if individuals accelerate growth only when doing so is least costly (Carlson et al. 2004). Our findings suggest that the immediate benefits of an accelerated growth strategy during a specific period of extremely high mortality risk may outweigh the potential long-term costs (but see Gotthard 2001, Morgan and Metcalfe 2001, Metcalfe and Monaghan 2001, Royle et al. 2005). Identifying the ecological and evolutionary implications of rapid growth and uncovering the trade-offs between short-term gains and long-term drawbacks in natural populations remains an open challenge to evolutionary ecologists.

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