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Selective predation for low body condition at the larval-juvenile transition of a coral reef fish

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Abstract Mortality is known to be high during the transition from larval to juvenile life stages in organisms that have complex life histories. We are only just beginning to understand the processes that influence which individuals survive this period of high mortality, and which traits may be beneficial. Here we document a field experiment that examines the selectivity of predation immediately following settlement to the juvenile population in a common tropical fish, *Pomacentrus amboinensis* (Pomacentridae). Newly metamorphosed fish were tagged and randomly placed onto replicated patches of natural habitat cleared of resident fishes. After exposure to transient predators for 3 days, fish were recaptured and the attributes of survivors from patch reefs that sustained high mortality were compared to individuals from patch reefs that experienced low mortality. Seven characteristics of individuals, which were indicative of previous and present body condition, were compared between groups. Predation was found to be selective for fish that grew slowly in the latter third of their larval phase, were low in total lipids, and had a high standardized weight (Fulton's *K*). Traits developed in the larval phase can strongly influence the survival of individuals over this critical transition period for organisms with complex life cycles.

Keywords Metamorphosis · Condition at settlement · Selective mortality · Larval growth history · Growth-mortality hypothesis

Introduction

The selective loss of individuals from a population is the foundation of the theory of natural selection (Roff 1992).

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As an organism grows, its habits change, as do the mortality agents that influence selection and, consequently, the species' patterns of abundance. Understanding the selective loss of individuals throughout their life cycle is fundamental to our understanding of population regulation.

Processes influencing which individuals survive to reproduce are complicated by a major transitional stage in organisms that have complex life histories (e.g. many plants, insects, marine invertebrates and fish, and amphibians; Werner 1988; Pechenik et al. 1998). This transition between developmental stages is often rapid and is typically accompanied by morphological, physiological and behavioural changes as the organism adapts to its new environment (Wilbur 1980; McCormick and Makey 1997; McCormick et al. 2002). These changes are energetically costly and bring a new set of challenges for developing organisms, which may influence their probabilities of survival. Typically, only a very small fraction of the total offspring produced actually survives the larval or propagule stage to metamorphose into juveniles (Jansen 1971; Bailey and Houde 1989; Morgan 1995). Hence, small changes in the way mortality agents act can greatly influence the number of individuals reaching the juvenile phase (Houde 1987; Pepin and Myers 1991), and the phenotypes of those individuals. Despite this, few studies have examined the strength and direction of selective loss of individuals at this crucial transition between larval and juvenile developmental stages.

Most marine reef fishes have complex life cycles, where a relatively sedentary reef-associated adult produces larvae that spend a number of weeks in the plankton, prior to settling onto the reef to join the juvenile population. Although mortality is almost absolute in the larval phase (Leis 1991), those that do survive suffer high losses immediately following settlement (Webster 2002). Upwards of 57% of juvenile coral reef fishes may die within the first 2 days after settlement (Webster and Almany, submitted). Of those that survive this initially high mortality, few survive through to maturity (e.g. Jones 1990). Selective forces are therefore strongest in the larval

stage and immediately after settlement to the reef, suggesting that the transition between stages is a critical period (McCormick 1998; Searcy and Sponaugle 2001; McCormick and Hoey 2004).

Clearly all fish larvae do not have an equal chance of survival, instead varying in traits that may influence their susceptibility to mortality (Ferron and Leggett 1994). This variation is initially driven by parental contributions, which may be modified by environmental conditions experienced throughout the life cycle. If this initial variation is maintained, then fast-growing larvae will be larger and thus potentially less vulnerable to predators than slower-growing larvae of the same age (the “bigger-is-better” hypothesis; Miller et al. 1988; Bailey and Houde 1989). Consequently, they will be the first to achieve juvenile form and settle, reducing the period they are exposed to planktonic predators (the “stage-duration” hypothesis; sensu Leggett and Deblois 1994). Advantages obtained in the larval phase are believed to extend into the juvenile phase to influence an individual’s probability of survival (Sogard 1997). Recent studies of tropical reef fishes have suggested that advantages gained prior to hatching are positively correlated to larval growth and dictate survival in later life stages (Vigliola and Meekan 2002). Variations in larval growth rates have also been demonstrated to influence the number of larvae surviving up to settlement (Bergenius et al. 2002; Wilson and Meekan 2002). However, few studies have examined selection at the larval-juvenile transition for reef fishes (but see Searcy and Sponaugle 2001; Shima and Findlay 2002). We explore this issue for a common coral reef fish.

Characteristics that may be influential in determining survival during and immediately after the settlement transition include size (Booth 1995; McCormick and Hoey 2004), prior growth history (Shima and Findlay 2002), lipid content (Booth and Hixon 1999; Booth and Alquezar 2002), sensory development (McCormick 1993) and burst swimming speed (McCormick and Molony 1993). All of these traits have been found to display high levels of variability within a species on a range of spatial and temporal scales (Wellington and Victor 1989; McCormick and Molony 1993; McCormick 1994; Sponaugle and Cowen 1994, 1997; Kerrigan 1996; Searcy and Sponaugle 2000). It is upon this phenotypic variation amongst individuals that selective processes act. If mortality at settlement is selective with respect to some aspects of individual quality, then settlers in better condition should contribute proportionately more to the juvenile population than those in poor condition (Suthers 1998).

The present study examines the selectivity of mortality immediately following settlement in a common tropical damselfish, *Pomacentrus amboinensis* (Pomacentridae). Here we use a short-term experiment to examine whether mortality is selective with respect to seven measures of fish quality. Results indicate that prior growth history, manifested as growth rate and lipid levels, strongly affects the survival of fishes in a patch reef habitat.

Materials and methods

Study site and species

The study was conducted at Lizard Island (14°38’S, 145°28’E) on the northern Great Barrier Reef, Australia during November 1998. The model species was *Pomacentrus amboinensis*, a ubiquitous pomacentrid that typically settles in high numbers to a variety of habitats, from sheltered lagoons to exposed windward reefs, on the northern Great Barrier Reef (Kerrigan 1994). *P. amboinensis* has a pelagic larval duration of 15–23 days and settles at 10.3–15.1 mm standard length (Wellington and Victor 1989; Kerrigan 1996) with its juvenile body plan largely complete, and undergoes a rapid (less than 12 h) change in body pigmentation (McCormick and Makey 1997; McCormick et al. 2002). *P. amboinensis* is found at highest densities when associated with small patch reefs at the base of shallow reefs and, once settled, these omnivorous pomacentrids are relatively site-attached, making them ideal for field experiments.

Field experiment design

To determine the selectivity of mortality immediately following settlement, a field experiment was conducted on 15 patch reefs (approximately 0.7×0.7×0.7 m) on the leeward side of Lizard Island. A random sample of newly metamorphosed fish was placed on patch reefs surrounded by sand and exposed to natural predation. After 3 days, the period of highest mortality for this species (McCormick and Hoey 2004), fish were recaptured and the body condition of individuals from patch reefs that sustained high mortality was compared to those that sustained low mortality.

Newly metamorphosed *P. amboinensis* were caught using light traps as they came into the vicinity of the reef to settle (for design see Stobutzki and Bellwood 1997). Traps were anchored on the leeward side of Lizard Island in approximately 16 m of water, positioned so that the collection slots were 1 m below the surface. Fish were removed from the traps at 0730 hours, returned to the laboratory and maintained in 40 l aquaria with running seawater for 4 h. Three hundred individuals captured in a single night were each transferred to a small clip-seal plastic bag to avoid scale damage and tagged through the bag with a fluorescent subcutaneous elastomer tattoo (Northwest Marine Technologies Inc.) using a 29-gauge hypodermic needle. A detailed study of this tagging technique showed that tagging had no significant effects on mortality or growth over a 2-week period, and that tags had a 100% retention rate (Hoey 1999).

The patch reefs used in the experiment were of similar size and structural complexity, and composed of a combination of live and dead *Pocillopora damicornis*, known to be a preferred habitat for the species (Öhman et al. 1998). These were positioned on a sand flat in 3 m of water, 15 m from the edge of the nearest reef. Reefs were arranged in a five by three matrix with adjacent reefs being separated by 8 m. Immediately prior to releasing the tagged fish, the patch reefs were cleared of all fishes and potential invertebrate predators using a fence net, small hand nets and clove oil.

Twenty randomly selected, tagged fish were released onto each of the 15 patch reefs. This density is representative of the natural levels observed during settlement pulses at Lizard Island, where densities on similar-sized patches may reach up to 65 recruits (McCormick, unpublished data). Newly settled fish on adjacent reefs were tagged with a different colour so that migration between reefs, or settlement of new individuals, could be detected. A visual census shortly after releasing the fish revealed that all individuals were associated with their experimental patch reef. Only two individuals were found to have migrated to an adjacent patch reef during the 3-day experiment. No tagged individuals were observed during a census of the adjacent contiguous reef at the conclusion of the experiment.

After 3 days, reefs were re-censused and were categorized according to the survival of tagged fish: high (>75% survival; range 80–95%, $n=4$); intermediate (50–75% survival; $n=7$); or low (<50% survival; range 25–45%, $n=4$). There was no spatial gradient in

survivorship among the patch reefs with respect to distance from the contiguous reef or position within the patch reef matrix. Due to the lack of resident predators, mortality among reefs was a consequence of action by transient piscivores. These predators include lizardfish (*Synodus* spp.) and juvenile lutjanids (primarily *Lutjanus gibbus*), which are known to prey on recently settled reef fishes (Sweatman 1984, 1993) and were observed in the vicinity of patch reefs during censuses. Fish from four reefs classified as having high survivorship (>75% survival) and four reefs classified as having low survivorship (<50% survival) were collected using a fence net, small hand nets and clove oil, before being killed by cold shock and subsequently frozen prior to processing. Fish from the high survivorship patch reefs were used as a 'control' group, representing a random sample of the fish released onto the reefs, followed by 3 days of growth. Fish from the low survivorship reefs represent a subset of the initial sample, which had been exposed to high levels of predation.

Condition measures

The selectivity of mortality was assessed with respect to seven measures of morphology and body condition: standard length (SL, mm); wet weight (mg); Fulton's condition index [$K=(\text{wet weight, kg})/(\text{SL, m})^3$]; sagittal otolith radius at settlement (a proxy for relative size at settlement; μm); pre-settlement growth (mean width of the last seven increments prior to the settlement mark; $\mu\text{m day}^{-1}$); post-settlement growth (mean width of the three increments after the settlement mark; $\mu\text{m day}^{-1}$); and total lipid content (mg g^{-1} dry body weight). Otolith increment width was used as a proxy for fish growth, which is based on the assumption that there is a strong relationship between somatic and otolith growth. This is a generally held assumption that is supported by a number of studies (e.g. Suthers 1998; Campana 1999), and a positive linear relationship between otolith radius and standard length has been demonstrated for *Pomacentrus amboinensis* (11.3–18.4 mm SL, $n=292$, $r=0.86$; Hoey 1999). Cross-sections of the sagittal otoliths were produced following the protocol of Wilson and McCormick (1997). Increment measurements were made along the longest axis of the otolith, from the nucleus to the outer-most complete ring, using a high power compound microscope with polarized transmitted light, linked to a computer image analysis system (Sigma Scan). Furthermore, the formation of daily otolith increments has been validated in recently settled *P. amboinensis* (Pitcher 1988) and it is assumed that pre-settlement increments are also deposited on a daily basis. A conspicuous settlement mark, which is formed in this species (Wilson and McCormick 1997), was used as a reference point for the division between larval and post-settlement increments.

The total lipid content of each fish was determined gravimetrically using chloroform-methanol extraction. Fish were freeze-dried and weighed to the nearest 0.1 mg then homogenized in 2 ml of distilled water. Lipid was extracted from duplicate 500 μl aliquots of each sample of homogenate using the methods of Bligh and Dyer (1959) and Mann and Gallagher (1985). Aliquots of 1 ml solvent extract were dried to a constant weight at 60°C and weighed to the nearest 0.01 mg. The mean of the duplicates was expressed as total lipid in mg g^{-1} dry weight. The coefficient of variation between duplicates was less than 14% for all samples.

Analyses

The frequency distributions of condition measures from fish within low survival patch reefs were compared to those from the high survival patch reefs using Kolmogorov-Smirnov two-sample tests (K-S test). Frequency distributions were compared, rather than mean values, as selective processes operate on trait distributions and are not always reflected in changes in the mean value of the trait (Miller 1997). Correlations and partial correlations (controlling for standard length) among the seven condition measures were also examined.

Results

Variability in condition

The total lipid content of *Pomacentrus amboinensis* collected from control reefs was the most variable of the seven condition measures (Table 1). Wet weight, post-settlement otolith growth rate and Fulton's K displayed moderate levels of variation. In contrast, both measures of fish length (standard length and otolith radius at settlement) were the least variable among fish (Table 1).

Selectivity of early post-settlement mortality

A comparison of the frequency distributions of individual traits between high (control) and low survivorship reefs suggested that mortality had been selective toward three attributes: total lipid content, pre-settlement otolith growth rate and Fulton's K (Table 2). The frequency distributions for standard length, wet weight, relative size at settlement (i.e. otolith size at settlement) and post-settlement growth rates did not differ between treatments, suggesting that predators were not selective for these traits in this habitat (Table 2).

A comparison of the distributions of total lipid content between treatments suggested that individuals that had low lipid levels were selectively preyed upon (Table 2; Fig. 1a). The proportion of fish with total lipid content less than 150 mg g^{-1} dry weight was substantially greater for high survival (52.2%) than low survival (13.3%) reefs. Similarly, predation appeared to be selective towards fish with low pre-settlement otolith growth rates (Table 2; Fig. 1b). High survivorship reefs had a greater proportion of individuals with pre-settlement otolith growth rates below 19 $\mu\text{m day}^{-1}$ than low survivorship reefs (41.8% and 23.3% respectively).

Table 1 Summary of the variability in seven measures of body condition for *Pomacentrus amboinensis* that have been settled on patch reefs for 3 days and sustained low levels of mortality ($n=67$)

Condition measure	Mean	Range	CV
Standard length (mm)	12.4	11.3–13.7	4.0
Wet weight (mg)	63.5	36.4–110.5	25.4
Fulton's K	32.7	21.6–43.1	16.5
Otolith radius at settlement (μm)	247.7	201.7–282.0	6.3
Pre-settlement otolith growth rate ($\mu\text{m day}^{-1}$)	19.6	16.7–25.0	9.1
Post-settlement otolith growth rate ($\mu\text{m day}^{-1}$)	6.0	3.7–8.9	17.8
Total lipid (mg g^{-1})	155.9	45.1–373.3	43.5

Table 2 Comparison of the frequency distributions of seven measures of body condition for *P. amboinensis* between two groups of fish from the same settlement cohort: one that sustained high

mortality ($n=30$), the other that sustained low mortality ($n=67$). The results of Kolmogorov-Smirnov two-sample tests are summarized

Condition measure	<i>D</i> statistic	Kolmogorov-Smirnov <i>Z</i>	Significance level
Standard length (mm)	0.121	0.553	0.920
Wet weight (mg)	0.290	1.320	0.061
Fulton's <i>K</i>	0.326	1.483	0.025*
Otolith size at settlement (μm)	0.178	0.809	0.530
Pre-settlement otolith growth rate ($\mu\text{m day}^{-1}$)	0.306	1.395	0.041*
Post-settlement otolith growth rate ($\mu\text{m day}^{-1}$)	0.193	0.876	0.426
Total lipid (mg g^{-1})	0.498	2.267	$6.9 \times 10^{-5}***$

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

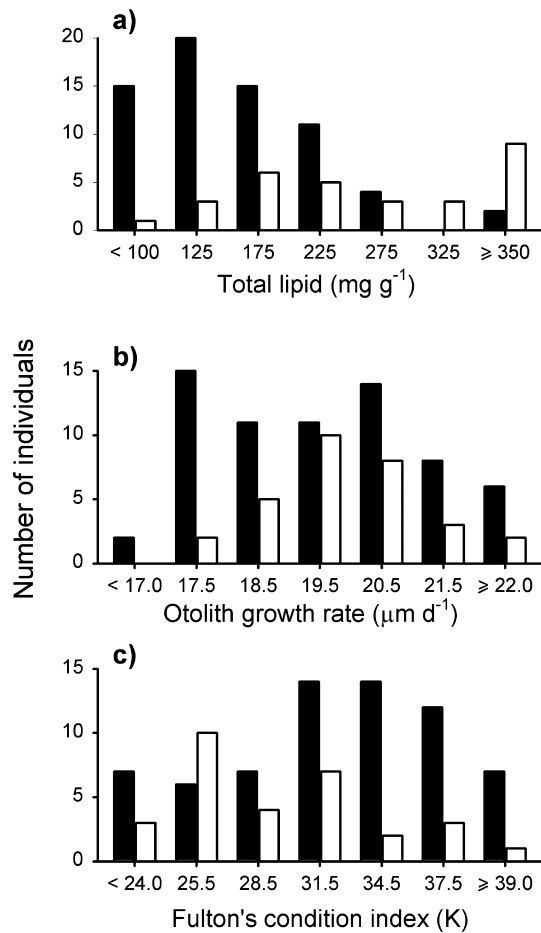


Fig. 1a-c Comparison of the frequency distributions of three measures of body condition between newly settled *Pomacentrus amboinensis* exposed to high levels of predation (open bars, $n=30$) and those exposed to low levels of predation (solid bars, $n=67$). **a** Total lipid content (mg g^{-1} dry body weight); **b** otolith growth rates ($\mu\text{m day}^{-1}$) for the 7 days prior to settlement; **c** Fulton's condition index (weight/length³)

In contrast, fish from the low survivorship reefs had lower values of Fulton's *K* than those from high survivorship reefs (Fig. 1c). The proportion of fish with Fulton's *K* greater than 33.0 was substantially greater for high survival (49.3%) than low survival (20.0%) reefs.

This suggests that the *P. amboinensis* that survived high predation pressure were those of lower bulk.

Comparison of measures of condition

Correlations among the seven measures of condition were generally weak, with the exception of relationships between morphological measures and their derivative, Fulton's *K* (Table 3). Total lipid content of *P. amboinensis* was negatively related to standard length (Table 3), suggesting that smaller recruits had a tendency to have a higher proportion of lipid than larger recruits. Not surprisingly, there was a strong relationship between pre-settlement growth and relative size at settlement (i.e. otolith size at settlement). Interestingly, there was no relationship between pre- and post-settlement otolith growth. However, there was a negative relationship between relative size at settlement and post-settlement otolith growth, suggesting that there may be some compensatory growth occurring. The relationships among condition measures remained relatively unchanged after removing the effects of standard length (Table 3).

Discussion

Mortality of *Pomacentrus amboinensis* was found to be selective at settlement. In this patch reef habitat, it appears that transient predators selectively removed individuals with lower lipid levels, slower pre-settlement growth and higher Fulton's *K*. Thus, processes that affect the condition of individuals during the pelagic larval phase not only influence the strength of cohorts (e.g. Bergenius et al. 2002; Wilson and Meekan 2002) but also the survival probabilities of settling individuals within a cohort.

The absence of different post-settlement growth rates between reefs, together with the short duration of the experiment, suggests that the observed differences in condition between high and low survival populations were present at settlement and were not simply the result of a density-dependent reduction in competition in the low survival populations. The growth of juvenile coral reef

Table 3 Correlations among seven measures of condition of *P. amboinensis* recruits from low mortality patch reefs 3 days after settlement. Pearson correlation coefficients are given. Partial correlations controlling for standard length are given in parentheses. $n=67$

	Wet weight	Fulton's <i>K</i>	Size at settlement	Pre-settlement growth	Post-settlement growth	Total lipid
Standard length	0.831***	0.519***	0.337***	0.092	-0.007	-0.355**
Wet weight		0.898***(0.982***)	0.164(-0.222)	-0.012(-0.161)	0.092(0.156)	-0.221(0.143)
Fulton's <i>K</i>			0.026(-0.185)	-0.100(-0.174)	0.135(0.162)	-0.064(0.150)
Size at settlement				0.544***(0.547***)	-0.276*(-0.291*)	-0.153(-0.038)
Pre-settlement growth					0.052(0.052)	-0.153(-0.129)
Post-settlement growth						-0.110(-0.120)

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

fishes has been shown to be density dependent within naturally occurring densities, but these effects are only evident weeks to months after settlement (e.g. Doherty 1982; Victor 1986; Jones 1987; Forrester 1990). Furthermore, food deprivation experiments have shown that there is a considerable lag in the response of various condition measures, including total lipid content and Fulton's *K*, in both juvenile (Weber et al. 2003) and adult fishes (Molony and Sheaves 1998). The generality of this time lag in the response of lipid content and Fulton's *K* to feeding levels suggests that the present results are likely to be the consequence of selective mortality.

Few previous studies have examined the selectivity of mortality immediately after settlement, particularly with respect to body condition. Searcy and Sponaugle (2001) used the width of the metamorphic band in the otolith of two Caribbean wrasse species (*Halichoeres bivittatus* and *Thalassoma bifasciatum*) as a measure of body condition at settlement. The width of this band is thought to represent growth during a 3- to 5-day period of non-feeding whilst individuals are buried in the sand metamorphosing, a common phenomenon amongst wrasses (Sponaugle and Cowen 1997). By comparing newly settled fish with fish 6 or more days after settlement, they suggested that mortality was selective for body condition. Similarly, higher total lipid content increased the survival of a Caribbean damselfish, *Stegastes partitus* for the period 7–17 days after settlement (Booth and Hixon 1999). The lipid levels of recently settled individuals were manipulated in aquaria by feeding them either a high or low ration diet for a period of 7 days. Fish fed a high-ration diet exhibited higher survivorship than individuals from the low-ration diet when exposed to a piscivorous fish in an aquarium or released onto a reef for 10 days (Booth and Hixon 1999). These findings suggest that if the differences in condition of individuals at settlement are maintained, the advantages gained in the larval phase may extend several weeks after settlement. In contrast, experimental trials have shown predation by lizardfish, *Synodus variegatus*, on newly settled goatfish, *Upeneus tragula*, to be non-selective with respect to total lipid content (McCormick and Kerrigan 1996). This lack of selectivity was attributed to the ambush capture strategy employed by the predator (Sweetman 1984). In general it

appears that body condition, in the form of available or excess energy, is important for reef fish at settlement and may determine which individuals survive this period of high selection.

Our findings support recent studies from a range of reef systems that have found that larval growth is important for survival immediately after settlement. Higher larval growth rates have been shown to increase the survival probability of a temperate serranid *Paralabrax clathratus* during the first 5 days after settlement (Shima and Findlay 2002). High pre-settlement growth rates have also been found to enhance survival of one Caribbean wrasse (*H. bivittatus*) but not another (*T. bifasciatum*) during their first 2 weeks on the reef (Searcy and Sponaugle 2001). Furthermore, the results of a caging experiment that manipulated access by different size classes of predators to newly settled *P. amboinensis* suggested that, in almost all cases, predation was selective for individuals with low pre-settlement growth (McCormick and Hoey 2004). Pre-settlement growth appears to play an important role in post-settlement survival in most species studied to date.

Interestingly, *P. amboinensis* with higher Fulton's *K* suffered greater mortality than those that had lower weight to length ratios. This result is surprising as Fulton's *K* is a starvation-dependent index, with higher *K* values thought to represent fish in better condition (Suthers 1998). In contrast to the present study, Booth and Hixon (1999) reported a positive relationship between Fulton's *K* and survivorship for recently settled *S. partitus*. This inconsistency may be related to a difference in growth form between the two species, exposure to predators who exhibit different prey preferences, or simply by the actions of selective predation targeted toward one or more traits that have negative associations with Fulton's *K*. Irrespective of the process, the effectiveness of Fulton's *K* as a measure of condition at developmental boundaries is questionable.

Our study found no obvious advantage to being large at settlement. Evidence to date suggests that size does not always influence the survival probabilities of newly settled fishes. Larger initial size was found to increase survival of recently settled domino damselfish, *Dascyllus albisella* in one year of a 2-year study (Booth 1995). McCormick and Hoey (2004) monitored the fate of naturally settled *P.*

amboinensis on a contiguous reef and showed that individuals who were slightly larger at settlement (<1 mm SL difference) had improved survival probabilities. In contrast, Searcy and Sponaugle (2001) found that otolith length at settlement (a proxy for size at settlement) did not influence survival of two wrasses, *H. bivittatus* and *T. bifasciatum*. Predation by lizardfish, *S. variegatus*, on newly settled goatfish, *U. tragula*, has also been found to be non-selective for size (McCormick and Kerrigan 1996). These contrasting results suggest that predation is not always directed toward size, and that the relationships among the various morphological and biochemical aspects of condition that influence survival may determine whether size is found to be important or not.

Generally, studies have found poor relationships between measures of condition, suggesting that selection with respect to one trait has little influence on the patterns of variability in other traits (McCormick and Molony 1993; Kerrigan 1996). Morphological measures of condition, including Fulton's *K*, have been found to be both positively (Booth 1995; Booth and Hixon 1999) and negatively (McCormick and Molony 1993, present study) related to total lipid content in coral reef fishes at settlement. In addition, Kerrigan (1996) found that the relationships among morphological variables and total lipid levels changed among three recruitment seasons and between species for two congeneric damselfish, *P. amboinensis* and *P. nagasakiensis*. These relationships are not surprising, given the different ecological functions of growth, tissue energy and morphological indices. However, these studies do suggest that caution is required in inferring the significance of selection toward a trait (e.g. size) in relation to other measures of condition, particularly when the relationships among body condition measures are unknown.

Our present inability to assess biochemical and physiological measures of condition non-destructively or in retrospect has restricted our focus to using readily measurable morphological traits as indicators of condition (but see Booth and Hixon 1999; Booth and Alquezar 2002). The importance of size at a particular developmental stage has been emphasized in the literature, with the extension of the 'bigger-is-better' hypothesis, developed from larval research (Leggett and Deblois 1994), to the juvenile phase (Sogard 1997). This importance of size pervades the literature of many other organisms that exhibit complex life cycles (e.g. tadpoles: Tejedo 1993; marine snails: Moran and Emler 2001). Part of this emphasis on size is that many performance characteristics have been related to size (Bailey and Houde 1989; Fuiman and Higgs 1997). However, these relationships can break down once developmental stage is accounted for (e.g. Neilson et al. 1986; McCormick and Molony 1993). In the present study, size and the proxy for size at settlement (otolith radius at settlement) were the least variable of the traits measured, with measures of body condition (i.e. lipid levels, pre- and post-settlement growth and Fulton's *K*) showing 2–10 times as much variability. A re-examination of a similar dataset for newly metamorphosed goatfish, *U.*

tragula (McCormick and Molony 1993), shows the same trend in variability, with the lowest variability in standard length (5.5% CV), and 3–6 times as much variability in measures of body condition and performance (total lipid content 31.4% CV, Fulton's *K* 17.6% CV, burst speed 24.4% CV). It may be that selectivity directed toward other aspects of body condition and performance may be more important than size, but size is the only variable measured under the usually untested and possibly unfounded assumption that other measures of quality will be positively correlated with size.

This study indicates that the condition of coral reef fish at settlement has important ramifications for their subsequent survival and recruitment to the adult population. Although total lipid content and pre-settlement growth rates influenced the survival of newly settled *P. amboinensis*, the poor correlation between condition measures suggests that no single measure comprehensively describes the quality of an individual at settlement (Ferron and Leggett 1994). Predator–prey and competitive interactions tend to be species-specific and may respond differently to particular components of condition. Therefore, when assessing condition it is necessary to consider a variety of measures to adequately describe the relative fitness of an individual.

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