The role of early life history traits on the survival of a coral reef fish

Thesis submitted by
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Statement on the contribution of others

This thesis includes some collaborative work with my supervisors Assoc. Prof. Mark McCormick and Dr Mark Meekan (Australian Institute of Marine Sciences). While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation and final synthesis of results into a format suitable for publication. My co-authors provided intellectual guidance, financial support, technical instruction and editorial assistance.

Acknowledgements

General Abstract

Selective mortality within a population, based on the phenotype of individuals, is the foundation of the theory of natural selection. Even small phenotypic differences among individuals early in ontogeny can strongly affect survival and performance later in life. Consequently, variation in early life history traits can have important repercussions on population structure and dynamics. Yet, the role of phenotypic variation throughout the ontogeny of tropical marine fishes remains largely unexplored. This study examined the extent to which environmental and parental effects generate variation in the early life history of a tropical marine fish (*Pomacentrus amboinensis*) and the consequences of such variation for survival in the wild.

Variation in early life history traits and survivorship during embryonic and larval development of the coral reef damselfish, *P. amboinensis* was examined in relation to water temperature. High rearing temperature (31ºC) strongly defined the relative number of embryos that successfully hatched and their post-hatching longevity. Embryonic mortality was significantly higher in hotter rearing environments (31ºC) than in cooler ones (25 and 29ºC) and accounted for over 54% of mortality prior to hatching across all three rearing temperatures. Under high temperature conditions, the probability of embryonic survival was largely determined by the initial size of the yolk-sac with larger energy stores reflecting enhanced rates of survival. Following hatching however, the survival advantages afforded by yolk-sac size switched to egg size, a commonly cited indicator of fitness. Yet, the benefits associated with egg size were heavily dependent on temperature. Overall, early environmental conditions and intrinsic developmental schedules had a significant influence on the outcome of selective mortality by producing substantial shifts in selective pressure through the early ontogeny of this species.

The extent to which maternal condition at the time of gametogenesis affected the relationships among early life history traits and survivorship during early development of

P. amboinensis was examined in a field study. Maternal condition was manipulated by altering food availability, a key factor influencing maternal energy allocation to offspring. Surprisingly, maternal condition had no effect on the *number* of offspring that successfully completed the embryonic phase, nor did it influence the relative number of individuals that survived to a given time after hatching. Nonetheless, maternal nutritional state did significantly affect offspring *quality* by causing substantial changes in individual egg composition (i.e. yolk-sac and oil globule size) and thus, the energetic value of embryos and hatchlings. By acquiring additional nutritional resources, supplemented mothers gained a fitness advantage over fish feeding on natural levels of plankton. Most importantly, however, they passed this advantage on to their offspring by provisioning their eggs with greater energy reserves (yolk-sac and oil globule size) than non-supplemented fish. Among offspring originating from supplemented mothers, those with larger yolk-sacs were more likely to hatch successfully and survive for longer periods on these reserves after hatching. Among offspring from non-supplemented mothers, yolk-sac size was either inconsequential to offspring survival or, peculiarly, individuals with smaller yolk-sac sizes were favoured. Mothers appear to influence the physiological capacity of their progeny and in turn, the efficiency of individual offspring to utilise endogenous reserves. Interestingly and contrary to theoretical predictions, there were no significant differences in egg size in relation to maternal nutritional state, suggesting that provision of energy reserves, rather than egg size, more closely reflected the maternal condition. Overall, the maternal environment greatly influenced the relationship between offspring life history characteristics and survival through energy-driven selective mechanisms.

To determine the relevance of these findings to patterns of future survival on the reef, the early life history traits of *P. amboinensis* surviving on the reef were compared with those of individuals from that same cohort at earlier times. Growth information stored in the otoliths of individual fish revealed that both maternally-determined condition at

hatching and environmental conditions encountered early in the larval life had strong carry-over effects. Consistent with the findings presented above, wild individuals with larger energy stores were found to survive through to settlement and beyond in the new reef environment. Interestingly, results revealed that not all selective advantages established during embryonic and larval phases were maintained later in life. The direction of selective pressures acting on growth rates changed significantly and repeatedly during the first few weeks of post-settlement life. These changes in phenotypic selection may mediate growth-mortality trade-offs between the risk of predation and that of starvation during early juvenile life.

To explore the mechanisms underlying early juvenile survival, growth histories exhibited by individuals that survived the first 4 weeks on the reef were compared with conspecifics outgrown experimentally to produce fast- and slow-growing fish. Nutritional conditions experienced by new recruits during the first few weeks contributed noticeably to observed patterns of juvenile survival. Results revealed considerable flexibility in the growth rates of young fish. Specifically, the occurrence of periods of rapid (presumably compensatory) growth may enhance post-settlement survival by attenuating the high risk of size-selective mortality.

By exploring the causes and consequences of phenotypic variation in the life of a tropical reef fish, this study unveiled the significant contribution past and present events make in sculpting patterns of survival in the wild. In addition, it suggests that changes in selective pressures that shape an individual's life are a critically important mechanism maintaining phenotypic (and hence genetic) variation within a population and, ultimately regulating the dynamics of natural populations.

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General Introduction

The existence of individual variation in phenotype and the selective mortality of individuals based on this variation are the fundamental principles of the Darwinian theory of natural selection (Mayr 1997). Since the genotype is the *cause* of the phenotype, the action and expression of discrete genes are clearly an important source of the observed phenotypic variation. However, alongside an individual's genetic makeup, a suite of non-genomic factors and environmental regimes experienced during an individual's lifetime interact to affect its phenotype and ultimately, lead to a high degree of phenotypic variation at the population level (Sultan and Sterns 2005). Specifically, the physical environment and ecological conditions experienced by an individual (environmental effects) and those experienced by its parents (environmentally-induced parental effects) can substantially influence the range of phenotypes expressed by a single genotype and exposed to selection (*phenotypic plasticity*, West-Eberhard 1989).

The ubiquity of phenotypic plasticity has been increasingly recognised (Gilbert and Bolker 2003) and there is now extensive evidence that plants and animals are capable of developing in a number of distinctly different ways tailoring their morphological, physiological and behavioural response to environmental cues (Schlichting and Pigliucci 1998). *Ranunculus* plants that produce distinct leaf morphs depending on whether they are submerged or exposed to air are a classic example (Cook and Johnson 1968). Similarly, *Pheidole* ants that become winged queens or develop into wingless soldiers or workers depending on temperature shifts experienced during embryogenesis are another example (Abouheif and Wray 2002). Further, the development of long spiny "helmets" in young *Daphnia* waterfleas and the increased production of toxic defensive compounds in the leaves of *Raphanus* seedlings recently described by Agrawal et al. (1999) are two remarkably revealing examples of predator-activated phenotypic plasticity, where the defensive phenotype is induced across generations via maternal effects.

Linking phenotypic variation and ontogeny with survival

Although environmentally-induced effects shape virtually all aspects of an individual's life history, phenotypic plasticity is not evenly expressed throughout the lifetime of the individual but is often induced during sensitive periods in the early development of both animals (Bateson et al. 2004) and plants (Wright and McConnaughay 2002). Moreover, even under the same developmental circumstances, genetically identical individuals are unlikely to respond in the same way to the same environmental inputs (Sholtis and Weiss 2005). It follows that the phenotypic variation observed among individuals arises from unique differences in individual developmental pathways established in well-defined and critical early life periods and to which individuals are committed for the rest of their life (Bateson 2001, Metcalfe and Monaghan 2001). This is particularly important for organisms with complex life cycles, where each age or stage experiences its own distinct set of ecological, biological and environmental interactions (*ontogenetic niche shifts*, Wilbur 1980) and even small variation in the sequence of early developmental events can greatly influence which individuals survive to reproduce (Ziehe and Demetrius 2005, Benton et al. 2006).

Many organisms including plants, amphibians, insects, marine invertebrate and fishes have complex life cycles consisting of two or more temporally and spatially discrete phases tailored for dispersal, growth or reproduction (Hellriegel 2000). Ontogenetic shifts between subsequent phases are typically accompanied by pronounced changes in body size (*size-structured populations*, Werner and Gilliam 1984). Since body size has a predominant influence on physiological and fitness attributes in many species (Roff 1992, Stearns 1992), variation in this trait and its consequences for key life history components, including fecundity and survivorship, have been examined and documented extensively. For example, size mediates the outcome of light competition in plant species (e.g. Schmitt et al. 1986) and foraging capacity (including cannibalism) and predation risk in animal species

(e.g. amphibians, Ziemba and Collins 1999; insects, Hopper et al. 1996; fishes, Sogard 1997). In each case, body size determines to a large extent the type and strength of ecological interactions experienced by an individual throughout its lifetime and translates into size-specific patterns of survival at the population level. Because initial body size is often positively related to growth, fecundity and survival at later stages, it seems logically intuitive to use egg, larval or juvenile size as a template to predict which and how many individuals will survive to the adult population (e.g. fishes, Sogard 1997; reptiles, O'Brien et al. 2005; amphibians, Gray and Smith 2005). There are, however, many instances where individuals of identical size have different fates (e.g. references in Sogard 1997). This suggests that size as a descriptor is not sufficient to explain the demography of individuals (Pfister and Stevens 2003, Pfister and Wang 2005), when differences among individuals may be expressed in terms of other traits that are independent of size (Blanckenhorn 2000, Pfister and Stevens 2002).

So how do we know that phenotypic selection is acting on the measured trait? Studies that have incorporated information on multiple phenotypic traits into analyses of phenotypic selection and population dynamics have been particularly informative. For example, sprint performance rather than body size has been found to be a good predictor of survivorship of juvenile lizards (Miles 2004), and variation in metabolic rates has been linked to social status in juvenile salmonids regardless of their size (Metcalfe et al. 1995). Similarly, competitive success of gregarious parasitoid offspring is not affected by variation in size, but depends on their ability to cooperate with siblings (Lalonde 2005). By examining patterns of phenotypic variation among individuals in a suite of traits, whether integrating performance capabilities, physiological and developmental conditions or behavioural components of fitness, we can provide crucial insights into the pattern and processes shaping the dynamics of natural populations. The present study employs a

multivariate approach to quantify the role of phenotypic variation throughout ontogeny on the survival of reef fish.

Variation in early life history traits and survival in fishes

Most organisms experience high mortality rates during the early phases of their lives (Roff 1992). These early mortality rates are exceptionally high and variable in fishes, leaving very few individuals to survive to the adult population (Bailey and Houde 1989, Jones 1990, Heath 1992). It is increasingly recognized that those individuals surviving the intense mortalities that take place during the embryonic, larval and early juvenile phases are a not a random subset of the population. Rather, individuals with certain attributes have better chances of survival than their conspecifics from the same cohort (Ferron and Leggett 1994). Given the environmental heterogeneity in physical and biological conditions that characterize the early life of fishes, it is not surprising that early life history attributes of fishes can be extremely variable and thus, the opportunity for selective loss of individuals from the population based on such phenotypic variation can be substantial (Cushing 1995). Determining the sources and consequences of variation in the early life history of fishes is one of the main challenges to understanding the role of selective processes that lead to differential survival and ultimately regulate wild fish populations.

The ramifications of early life phenotypic variation for the persistence of fish populations have been examined in the context of a wide range of environmental conditions. The effects of temperature (e.g. Pepin 1991, McCormick et al. 1999, Smyder and Martin 2002), salinity (e.g. Swanson 1996, Hurst and Conover 2002), oxygen (e.g. Collins and Nelson 1993, Breitburg et al. 1999), turbidity (e.g. Grecay and Targett 1996, Fiksen et al. 2002) as well as food availability (e.g. Limburg et al. 1999, Pepin 2004) and the presence of predators (e.g. DeBlois and Leggett 1991, Paradis et al. 1999) and competitors (e.g. Marschall and Crowder 1995, Fromentin et al. 2001) have been the

traditional focus of almost 100 years of research on fishes (Hjort 1914). Conversely and in spite of being one of the two sources of phenotypic variation, environmentally-induced parental effects in fishes are a relatively modern topic in fish research (Blaxter 1969, Solemdal 1970 and recently reviewed by Heath and Blouw 1998). The present study aims to quantify the phenotypic variation that arises as early as the egg stage through parental (maternal) effects and its influence in determining survival, as this initial level of variation is modified through ontogeny by the environment.

As discussed earlier, the quality of an individual is expressed in a number of phenotypic attributes, which may be predictive of survival. In fishes, the importance of a variety of ecological, physiological and behavioural early-life history traits, and the intrinsic correlations among them, has been widely recognized (see Govoni 2005, and references therein). Size has been by far the most intensely studied early life history (ELH) trait, and variation in this trait and its consequences for survival have been documented extensively, particularly in temperate systems (e.g. Chambers et al. 1989, Pepin 1991, Bernardo 1996a, Johnston and Leggett 2002). Size-based differences in vulnerability of fish eggs, larvae and juveniles to predators and their susceptibility to starvation or other sources of mortality have constituted the theoretical foundations for our understanding of early life dynamics in fish populations (Anderson 1988). It is generally accepted that larger individuals are more likely to survive than smaller conspecifics (e.g. McGurk 1986, Miller et al. 1988, Cowan and Houde 1992, Sogard 1997), although the validity of size-selective theory has been repeatedly questioned (e.g. Pepin et al. 1992, Leggett and DeBlois 1994, Cowan et al. 1996, Einum and Fleming 2000).

To date, evidence of the selective nature of mortality (whether size-dependent or not) has largely originated from research in cold temperate localities and interpretations of the significance of ELH traits to the survival of tropical marine fishes have greatly relied on the theoretical framework developed for temperate species. The extensive research and

excellent techniques developed in temperate regions have provided a valuable starting point for studies of tropical fishes. However, temperate and tropical fishes differ significantly in critical biological and ecological early life attributes (see Leis and McCormick 2002, p. 173) and thus, caution against direct application of predictions from studies of temperate species on tropical ones has been increasingly invoked (e.g. Kerrigan 1995, Leis and McCormick 2002, Green 2004). Recently, researchers have started to examine the effects of selective mortality on the abundance and composition of cohorts of marine fishes in tropical regions (Searcy and Sponaugle 2001, Bergenius et al. 2002, Vigliola and Meekan 2002, Wilson and Meekan 2002, Brunton and Booth 2003, McCormick and Hoey 2004, Hoey and McCormick 2004, Sponaugle and Pinkard 2004, Sponaugle et al. 2006, McCormick and Holmes 2006). Most of these studies have examined the selective nature of mortality during the larval and early juvenile phase, and have emphasized the importance of events that take place in the pelagic environment to influence larval growth history and survival. The extent to which variation in maternal condition, and traits prior to or at hatching, determine survival through to settlement and later stages is yet to be explored. It is also unknown whether initial selective advantages established early in life are maintained throughout the lifetime of a fish.

The study system

The present study examines the role of variation in early life history traits on the survival of coral reef fishes, using the damselfish *Pomacentrus amboinensis* as a model species. This is an extremely abundant and common member of coral reef communities on the Great Barrier Reef (GBR). Because it can be readily manipulated (injected, tagged, transplanted etc.) in field and laboratory experiments, it has been the focus of many ecological studies and continues to offer a unique opportunity to address complex process-oriented questions, which would otherwise be intractable with larger fishes. Nonetheless,

given that commercially important species have the same basic life history features as ornamental species, the outcomes of this study will aid in the understanding of ecological processes regulating exploited fish populations.

P. amboinensis is a site-attached and demersal spawner with a predictable breeding season (October-January). Spawning pairs can be isolated on patch reefs and their conditions manipulated in the field without difficulty (Plate 1A). Such patch reefs are a natural part of the habitat they exploit. Pairs readily lay clutches on artificial benthic nests (e.g. terracotta pots or half plastic pipes), where eggs are tended by the male parent throughout the embryonic developmental period for 4 d (Plate 1B). Offspring from specific adults can be easily monitored and collected (Plate 1C-F). Following hatching, *P. amboinensis* offspring undergo a 15-23d dispersive planktonic phase before returning to the reef (Kerrigan 1996), where they predictably settle in high numbers and can be easily identified and collected from coral reef habitats (Plate 1G).

P. amboinensis is a good model organism for the study of phenotypic selection because the species displays considerable variation in a number of early life history traits (McCormick, 1999). In addition, information on the life history of this species can be readily extracted from ear-bone structures (otoliths), where distinct marks are formed on the day of hatching (Wellington and Victor 1989) and settlement (Wilson and McCormick 1999) and the formation of increments following settlement has been validated to occur on a daily basis (Pitcher 1988). Otolith traits are permanent records of individual life histories and therefore ideal for studies exploring phenotypic variation and selective processes across varying life stages.
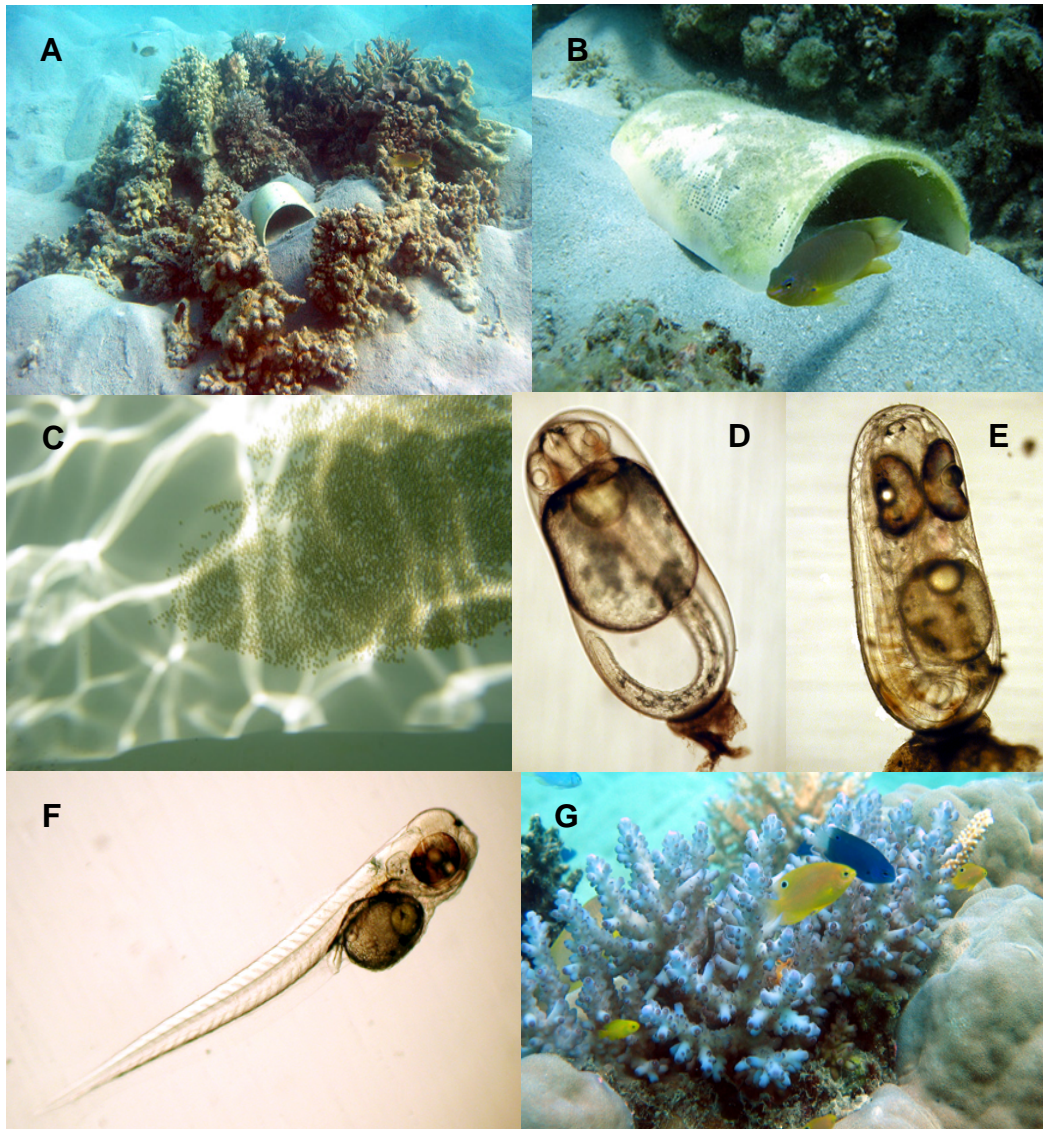
Panel 1. (A) Experimental patch reef, (B) *Pomacentrus amboinensis* male parent defending a benthic nest made of a half plastic pipe, (C) a clutch of 1-day old eggs laid on the ceiling of the half plastic pipe nest, (D-E) developing embryo at 36 (left) and 84 (right) hours post-fertilisation, (F) newly hatched *P. amboinensis* and (G) recruits settled on reef habitats after the dispersive pelagic phase.

Aims and thesis outline

The present study tests the generalities of prevailing theories on the role of variation in early life history characteristics on the survival of coral reef fishes in order to achieve a better understanding of the selective nature of processes influencing natural populations. By combining field manipulations and controlled laboratory experiments, this study aims to: *(1)* quantify the role of embryonic environment and maternal condition in

influencing offspring phenotypic characteristics from fertilization to the exhaustion of endogenous nutritional reserves, *(2)* identify which of these early characteristics determine survival of selected individuals over the larval phase, and *(3)* establish whether such characteristics remain advantageous throughout the life span of the fish, thereby determining patterns of survival in the field.

These aims are addressed in a series of 4 discrete studies according to the chapters outlined below. ***Chapter 1*** explores the extent to which the most pervasive environmental factor, namely temperature, induces variation in the relationships among ELH traits and survivorship during embryonic development and larval life. ***Chapter 2*** examines how maternal condition at the time of gametogenesis affects the relationships among ELH traits and offspring survivorship during early development. ***Chapter 3*** combines information from the previous two chapters to provide a direct estimate of the nature and intensity of selective mortality acting on phenotypic variation from the embryonic stage, through the planktonic larval phase, to weeks and months after settlement. By exploring the role of phenotypic selection throughout ontogeny, this chapter aims to identify which individual attributes are the most influential in determining natural patterns of juvenile survival. The role of selective processes in shaping patterns of early survival on coral reefs is further examined in ***Chapter 4***, where the mechanisms mediating growth-mortality trade-offs during early benthic life are explored.

Although individual chapters are written as stand-alone publications (see Appendix C for a complete list), they are clearly bound together by a common theme. By determining the importance of phenotypic variation through the progression of life history stages to patterns of survival in coral reef fishes, this study represents a novel contribution to our understanding of processes regulating marine fish populations, and more generally addresses a central issue in modern evolutionary ecology.

Chapter 1

Temperature-induced shifts in selective pressure at a critical

developmental transition

1.1 Introduction

Variation in life history traits leads to variation in survival among individuals (Stearns 1992). Life history traits are affected by physiological, ecological and behavioural regimes that differentially influence early survival and which individuals ultimately enter adult populations. Because individuals at birth are generally poorly developed, relatively small and limited in their ability to avoid predation, starvation and transport to detrimental habitats, most organisms experience high mortality rates during the early phases of their lives (Roff 1992). These early mortality rates are particularly high in marine teleost fishes, where mortality has been estimated to be near 100% (Bradford and Cabana 1997). Although the embryonic and larval periods account for only a small proportion of the total life span of fishes, very small changes in selective mortality during these crucial ontogenetic periods can have far greater repercussions on population fluctuations than changes occurring in later life stages (Houde 1987, Pepin and Myers 1991, Cushing and Horwood 1994).

A wide range of extrinsic variables, both abiotic (e.g. salinity, oxygen, light, pH) and biotic (e.g. food availability, social organization), interact with the developmental program of an individual to influence the expression of its early life history traits. Of these, temperature is undoubtedly among the most important variables for ectotherm ontogeny because of its pervasive effects on biological rate processes, altering nearly all physiological functions (Johnston and Bennett 1996). In across-taxa analyses, temperature alone has been reported to account for over 50 % of the variability in early survival (Houde 1989). In teleosts there is abundant evidence that temperature has a profound effect on life

history traits through its influence on development and growth, and consequently physiological and behavioural capabilities (Koumoundouros et al. 2001). Since the most substantial morphological, physiological and behavioural changes occur almost exclusively over the relatively short period of embryonic and larval life (Fuiman and Higgs 1997), temperature can be considered a major agent driving the large variation in traits during the early life history of fish.

Because fish ontogeny is a multiplicative process that proceeds continuously with temporary accelerations (Kamler 2002), selective processes in the larval phase are expected to act on the collection of changes derived from the embryonic phase and influence the phenotypic characteristics of those surviving. Egg size is certainly one of the most intensely studied early life history traits, and variation in this trait and its consequences for survival has been documented extensively, particularly in temperate systems (e.g. Chambers et al. 1989, Bernardo 1996a, Johnston and Leggett 2002). Larger eggs appear to confer higher survival to propagules than smaller ones, because they commonly generate larger larvae at hatching (e.g. McGurk 1986). Ultimately, larger larvae can be expected to be better equipped to capture food, more resistant to starvation, and less susceptible to predators (the 'bigger-is-better' hypothesis, Miller et al. 1988).

Despite the widespread acceptance of the 'bigger-is-better' paradigm, there is contrasting evidence about the ubiquity of this hypothesis (e.g. Litvak and Leggett 1992, Leggett and DeBlois 1994, Lankford et al. 2001, Green and Fisher 2004). Indeed, fitness consequences of egg size variability can change dramatically among environments such that selection may favour different size eggs under different environmental conditions (e.g. Einum and Fleming 1999), or its influence may not be revealed when the object of selection is a correlated trait (Einum and Fleming 2000). Yet, little is known about the influence of environmental conditions on embryonic trait interrelationships and how ontogenetic changes in the relationship among early life history traits affect survival during

and immediately after the embryonic stage. This study therefore set out to experimentally test the generality of the "bigger-is-better" hypothesis by investigating the interrelationship of life history traits at the individual level for a tropical damselfish (*Pomacentrus amboinensis*), from fertilization to the exhaustion of endogenous nutritional reserves. This study examined the extent to which variation in offspring survival may be influenced by individual phenotypic characteristics, and investigated temperature-induced shifts in trait association and survival. *P. amboinensis* is a good model organism for the study of the factors influencing trait interrelationships because the species displays considerable variation in a number of early life history traits (McCormick 1999).

1.2 Materials and methods

Experimental animals

Egg clutches used in this experiment were collected in late December 2003 at one location on the fringing reef at Lizard Island, Great Barrier Reef (14º 40′ S, 145º 28′ E). Three clutches of newly fertilized eggs spawned on artificial nesting substrata (McCormick 1999) were obtained in the morning following a pre-dawn spawning (Fig 1.1a) and transferred into well-aerated flow-through system aquaria in the laboratory. Eggs were removed from each clutch using a scalpel and individual embryos were transferred with a fine brush to 16 ml wells of 6-well tissue culture plates (Fig 1.1b).
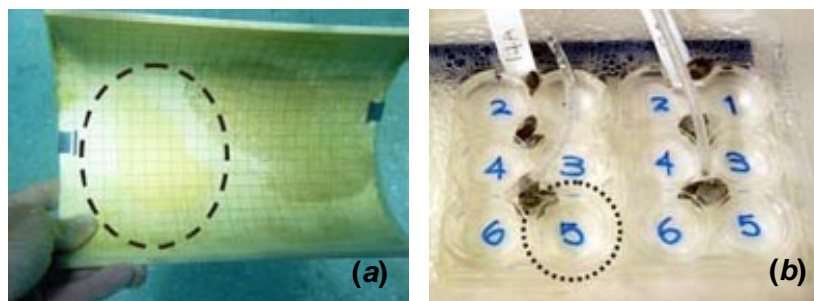
Fig 1.1. (*a*) Clutch of newly fertilised eggs spawned on artificial benthic nest indicated by the dotted circle and (*b*) 6-well tissue culture plates, where individual embryos (one in each well as indicated by the dotted circle) were allowed to developed in isolation.

Plates were placed in perforated seawater baths and submerged ($\sim$ 4 cm deep) with a surface flow of aerated seawater (3 ± 0.4 l h^{-1}) to maintain high oxygen levels around the negatively buoyant eggs and minimize potential bacterial infections. Embryos were taken from two positions in the clutch: periphery (within 1 cm of the edge) and centre to account for the potential variability associated with the position of the egg within a clutch. In total, 216 embryos from all clutches were randomly apportioned among all 3 temperature treatments (25, 29 and 31ºC) to account for the potential effect of variability among clutches. Embryos were allowed to develop in isolation at the 3 different temperatures in two replicate plates. The 29ºC temperature group was referred to as the control treatment, being held at the same seawater temperature recorded on the reef where the clutches were collected. The 25 and 31ºC temperature groups were referred to as the cold and hot treatment respectively. The cold and hot treatments were obtained by using header tanks with chillers and heating units respectively. These temperatures were chosen to represent the realistic temperature range on the northern Great Barrier Reef during the entire breeding season.

Measurements

To define the extent to which temperature may influence the expression of early life history traits prior to hatching and subsequent survival of offspring, embryos from the 3 temperature treatments were monitored during their development at 36 and 84 h post-fertilization (hpf). Key criteria to measure the developmental stage of *P. amboinensis* embryos were the presence of a rudimentary heart at 36 hpf and the complete development of the a*rteria caudalis* to the end of the notochord at 84 hpf (McCormick and Nechaev 2002). Based on these criteria, all embryos that survived to the fixed observation times (i.e. 36 and 84 hpf) were assessed to be at a comparable developmental stage among the 3 incubation temperatures.

The dorsal side of individual embryos was photographed under a compound microscope (10x magnification) at 36 and 84 hpf and egg size (maximum egg length, mm), yolk-sac size (yolk-sac area, mm^2) and oil globule size (oil globule area, mm^2) measured from these calibrated digital images using the image analysis programme, OPTIMAS 6.5 (OPTIMAS Corporation ^{TM}). Heart rates (heart beats/min) were measured by 3 replicated 1-minute counts of heart beats at 84 hpf. Pre-hatching mortality and time of hatching were recorded. Following hatching, unfed larvae were inspected every 12 hours until death as a measure of post-hatching longevity.

Statistical analyses

Prior to analysis, longevity measures were square root-transformed to meet the assumptions of normality and homogeneity of variance, allowing parametric tests of significance. The effect of temperature, clutch identity and position of origin within the clutch on pre- and post-hatching longevity were analysed using repeated-measures analysis of variance, with time (number of hours at death) as the within-subjects factor and temperature treatments (25, 29 and 31ºC), clutch identity and position of origin (centre and periphery) as between-subjects factors. Differences among temperature treatments, between clutches and between positions were identified using a post-hoc Tukey honestly significant difference (HSD) test at a significance level of 0.05/k, where k was the number of sampling times (k=2). The effect of time to hatch on post-hatching longevity among temperature groups and within a temperature group was tested by one-way ANOVA and t-test respectively.

To measure the effect of selective mortality on a phenotypic characteristic of embryos prior to and after hatching, partial regression coefficients of longevity on the phenotypic traits were calculated as described in Lande and Arnold (1983). Phenotypic selection gradients (β) representing the change in mean value of a phenotypic trait due to

selective mortality were standardized (β') by the standard deviation units of each trait, except survival. Prior to the multiple regression analysis, the assumption of no collinearity of the independent variables was met by examining the levels of correlation among traits.

1.3 Results

Mortality occurred prior to and after hatching. Clutch identity and position within the clutch had no influence on survival prior to or after hatching (clutch identity: $F_{2,155}=2.679$, p=0.072; position within the clutch: $F_{1,155}=0.466$, p=0.496). However, pre- and post-hatching mortality were strongly dependent on temperature treatment ($F_{2,155}=26.773$, p<0.001). Survival prior to hatching was significantly compromised at high temperatures (31ºC), where mortality was 3.6 times higher than in the cold temperature treatment (Tukey HSD, p<0.001) and accounted for over 54% of all mortality occurring prior to hatching across temperature treatments. After hatching, larval longevity without food in the high temperature treatment was also significantly reduced with hatchlings surviving no longer than 36 hours. Embryos developing at 25 and 29ºC had similar survival rates prior to and following hatching (Tukey HSD, p=0.699).

Eighty percent of all eggs hatched at about 85 h post-fertilization, regardless of the temperature at which they were incubated. The remainder hatched a day later (i.e. 108 hpf) and had all been incubated at 25ºC. Despite these differences in hatching time, time to hatch (85 *vs* 108 hpf) had no significant effect on post-hatching longevity overall ($F_{1,97}=0.6364$, p=0.427), or within the 25ºC group ($t_{41}=-0.38$, p=0.709).

Initial yolk-sac area was the only trait that covaried with pre-hatching survival. In the highest temperature treatment, rate of survival was higher amongst embryos with larger initial yolk-sac area than those with smaller yolk-sacs ($F_{1,50}=26.12$, p<0.001, Fig 1.2). No selective mortality based on yolk-sac area was detected for embryos reared at 25 and 29ºC.
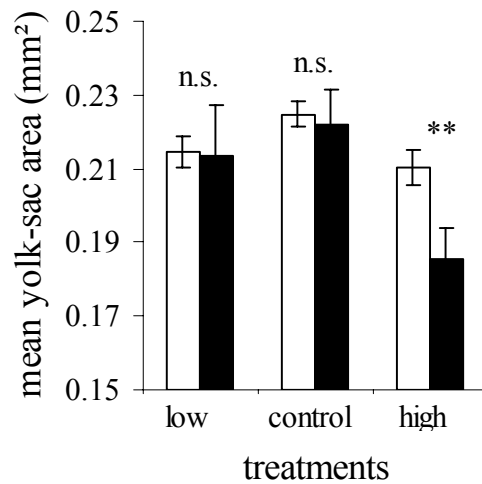
Fig 1.2. Mean yolk-sac area (mm2) of *P. amboinensis* embryos that died before hatching (black bars) and embryos that survived to hatch (white bars) at low (25ºC), control (29ºC) and high (31ºC) incubation temperature. Error bars are 95% confidence intervals. n.s., no significant difference; ** significant difference at $\alpha = 0.025$.

The effect of yolk-sac size on survivorship disappeared after hatching. Initial egg size and heart rate combined with the effect of temperature to affect post-hatching longevity (egg size: $F_{2,114}=3.375$, p<0.001; heart rate: $F_{2,114}=2.230$, p<0.05). An examination of phenotypic selection gradients, using longevity as a measure of fitness, found a clear trend for the survival of individuals that displayed larger initial egg size and higher heart rates at 84 hpf (Fig 1.3).
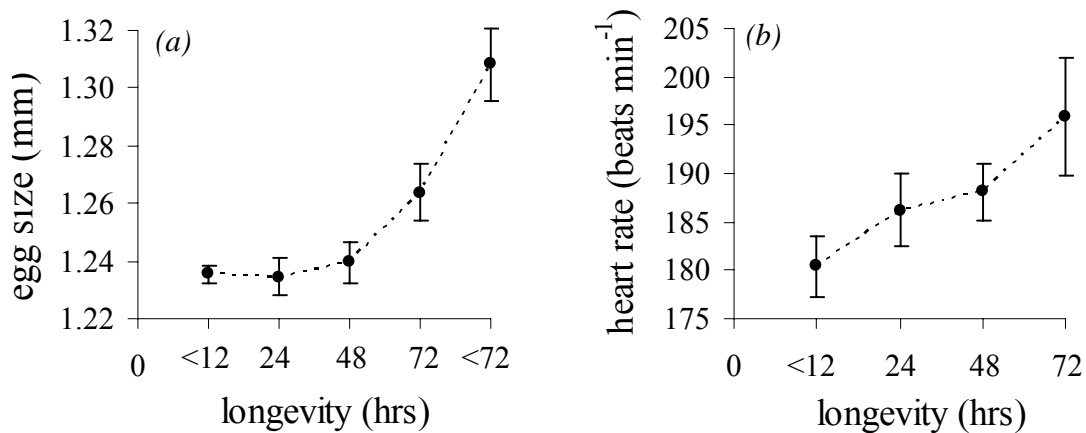
Fig 1.3. Longevity of larval *P. amboinensis* in relation to (a) initial egg size (mm) at 29ºC and (b) heart rate (beats min-1) at 31ºC recorded at approximately 84 hours post-fertilization. Error bars are 95% confidence intervals.

However, no significant correlation was observed between the two traits (r=0.092) and phenotypic selection gradients indicated that selective mortality operating on initial egg size was intense on individuals in the 29ºC group exclusively, while selective pressure against individuals that had low heart rate at 84 hpf was only experienced by larvae in the 31ºC group. No selective mortality was observed in individuals kept at 25ºC (Table 1.1).

Table 1.1. Phenotypic selection gradients (β ± SE) for initial egg size (maximum egg length, mm) and metabolic rate (heart beats per min), using post-hatching longevity of *P. amboinensis* larvae from 3 temperature groups as a measure of fitness. Temperature groups (25, 29 and 31ºC) corresponded to the natural temperature range recorded on the northern Great Barrier Reef during breeding seasons. Standardized selection gradients (β') are in standard deviation units. r^2-values are for the multiple regression; $p < 0.05$ in bold.

	Post-hatching longevity			
	β ± SE	β' ± SE	r^2	p
Low temperature (25ºC)				
initial egg size	12.77 ± 11.88	0.19 ± 0.18	0.05	0.291
heart beat rate	0.02 ± 0.03	0.11 ± 0.17		0.521
Control temperature (29ºC)				
initial egg size	18.01 ± 6.90	0.33 ± 0.09	0.11	**0.030**
heart beat rate	0.01 ± 0.01	0.01 ± 0.12		0.348
High temperature (31ºC)				
initial egg size	20.23 ± 16.50	0.23 ± 0.19	0.37	0.235
heart beat rate	0.04 ± 0.01	0.49 ± 0.18		**0.017**

1.4 Discussion

By examining temperature-induced shifts in selective mortality in *P. amboinensis*, the present study highlights the profound effects of temperature on an individual's viability of the early life stages of tropical fishes. Although the generality of the present study is limited by the restricted number of clutches from which eggs were collected, the study does have some broad reaching implications. To our knowledge, this is the first study to explore the interrelationships among early life history traits at the level of the individual for a tropical reef fish and relate these to early survival. Here, we demonstrate changes in intensity of phenotypic selection on these traits in response to temperature variations and between ontogenetic stages.

Initial yolk-sac size was important for embryo survival to hatching at the high temperature but was inconsequential to initial survival for embryos reared at control or lower temperatures. This suggests that whether phenotypic selection alters the distribution of this trait or not depends on the environmental conditions to which individuals are exposed (Lynch and Gabriel 1987). Given that yolk-sac contains the only nutritional reserves available to the embryo for its development, embryos with larger yolk-sac have higher probabilities of growth and survival, at least, up until hatching. Temperature is known to directly influence the rate and efficiency with which yolk is converted into tissue (Blaxter 1988), and yolk is depleted more rapidly as temperature rises throughout the range of thermal tolerance (Collins and Nelson 1993). Temperature extremes have been found to limit the range for normal embryonic development by affecting protein and fat metabolism at upper and lower extremes respectively (Ehrlich and Muszynski 1982). Thus, elevated temperature may operate directly on the rate and efficiency of yolk absorption by altering processes associated with yolk protein metabolism.

Interestingly, no ramifications of yolk-sac size on embryonic success to hatching were observed at ambient and low temperatures. This may be because low temperatures

principally affect lipid metabolism (Ehrlich and Muszynski 1982), which is relatively unimportant until after hatching, when activity and energy requirements increase (Heming and Buddington 1988). Overall, evidence suggests that *P. amboinensis* embryos are provisioned with sufficient yolk to survive the range of temperatures they would naturally encounter at the study location, but they have reduced ability to compensate metabolically for the effects of temperatures at the high end of their range.

Yolk-sac size was not related to post-hatching longevity, indicating a shift in the importance of this trait with ontogeny. The lack of relationship between initial yolk-sac size and post-hatching longevity agrees with previous findings in temperate fish (Chambers et al. 1989). However, it diverges from conventional generalizations (Blaxter 1988) by suggesting that an initially larger amount of yolk reserves does not directly lead to hatchlings that survive longer before irreversible starvation. Yolk-sac during the embryonic phase serves as a primary nutrient reserve and the delivery rate of such nutrients through the circulatory system is determined by variable developmental rhythms and irregular accelerations in tissue growth (McCormick and Nechaev 2002). As yolk utilization is influenced by variable metabolic rates throughout the egg stage, yolk reserves at hatching rather than at the beginning of embryonic development are more likely to affect post-hatching longevity. Unfortunately, yolk-sac size at hatching was not measured in the present study.

Post-hatching longevity was affected by initial egg size and pre-hatch embryonic heart rate. In the high temperature treatment in particular, post-hatching longevity was positively affected by heart rate just prior to hatching. Heart rate is closely dependent on incubation temperature and the ontogenetic stage of the embryo. Shortly before hatching, the chorion is softened and dissolved by a hatching-enzyme and increased embryonic activity assists in breaking through the egg envelope (Yamagami 1988). In *P. amboinensis*, the enhanced activity of the embryo at the start of the chorion dissolution and consequently

the raised energetic demands are associated with an increase in heart rate (McCormick and Nechaev 2002). At higher temperature, the dissolution of the egg envelop by enzymatic action occurs faster (Yamagami 1988), heart rate further increases and embryonic movements become more rapid (Klinkhardt et al. 1987). The present finding suggests that slow heart rate may be a symptom of physiological problems and consequently reduced viability. In contrast, individuals with higher metabolism may have a greater efficiency in utilizing yolk reserves and mobilizing additional nutrients from the dissolution of the chorion. Individuals with higher metabolism have been shown to have a greater capacity for energetically expensive activities in salmonids (Metcalfe et al. 1995). Consequently, despite a cost associated with elevated energy demand, higher metabolic rate may be advantageous when translated into higher metabolic scope and consequently greater potential for fast growth (Priede 1985).

Despite the assumption that selection favors larger egg size in a wide range of taxa (reviewed by Roff 1992), in the present experiment initial egg size positively influenced larval survival only at ambient temperatures. This study found no effect of initial egg size on post-hatching longevity at high and low temperatures, suggesting that benefits associated with initially larger egg size can shift or even disappear in response to the thermal environment. While sharing the view that larger eggs confer higher survival to offspring than smaller eggs (Miller et al. 1988, Houde 1989, Pepin and Miller 1993), the present study also showed that the magnitude of size-related effects on longevity depend strongly on the thermal environment. Some characteristics of the offspring environment can directly influence what will be the optimal egg size in fish (Hutchings 1991, Einum and Fleming 1999, Einum et al. 2002), suggesting that temperature-induced shifts in trait optimum may not be rare (Norry and Loeschcke 2002). Thus, because egg size does not appear to be advantageous at all points in development and under all circumstances (e.g. discrete stages model, Hendry et al. 2001), the heterogeneity of developmental

opportunities imposed by temperature conditions might be one reason why we do not see a continual evolution towards an increasingly larger egg size.

Conclusions

This study has demonstrated that environmental conditions under which *P. amboinensis* embryos develop and hatch have a great influence on their post-hatching life. Although the current experiment cannot distinguish between behavioural choices of parents to maximize maternal fitness from those that may maximize offspring fitness, several lines of reasoning suggest some form of adaptation to local environmental conditions that maximize embryonic survival rates. Nonetheless, when and under which conditions embryonic development occurs is ultimately dependent on a parental choice, and their ability to alter their environment (Green and McCormick 2005). The present study emphases the complexity of combined parental and environmental effects that ultimately shape the variability and magnitude of larval supply to reef environments.

Chapter 2

Maternal condition influences phenotypic selection on offspring

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2.1 Introduction

Understanding the factors affecting variation in phenotypic patterns among individuals is of fundamental interest to evolutionary ecologists because this variation influences the dynamics and evolution of populations across a wide range of taxa (Sinervo 1990, Chambers and Leggett 1996, Mousseau and Fox 1998). Any phenotypic variation that arises in offspring as a consequence of the phenotype or environment of the parents, independent of their chromosomal contribution, has been increasingly recognized as the outcome of environmentally induced parental effects (Lacey 1998). In particular, maternal effects have been shown to strongly influence offspring development and survival and have effects that last into subsequent generations, thereby determining patterns of selection response (Kirkpatrick and Lande 1989) and shaping the rate at which traits evolve (Riska 1989).

In both plants and animals, parents and particularly mothers can influence progeny phenotype in a variety of ways including: variable provision of nutrients (LaMontagne and McCauley 2001, McCormick 2003); transmission of antibodies (Gasparini et al. 2002), symbionts (Stouthamer et al. 1993), and hormones (Adkins-Regan et al. 1995, McCormick 1999), as well as toxins and pathogens (Taubeneck et al. 1994); and through cultural conditioning as a result of parental behaviour (Bernardo 1996b, Mazer and Wolfe 1998). Regardless of the way these resources are transmitted, maternal contribution is ultimately limited by the level of resources that are available to the mother for her own needs. As a result, maternal provisioning among offspring is not always equal (e.g. Mappes et al. 1997) or maximised (e.g. Boersma 1997), causing a conflict between parents (mothers) and their offspring over resource allocation (parent-offspring conflict, Trivers 1974).

Mothers have many options in how they partition resources to their offspring. For mothers living in variable environments, past and present environmental conditions may provide an indication of the optimal investment to reproduction. When conditions vary predictably, mothers may be expected to evolve phenotypic plasticity, whereby mothers respond to the environmental cues they experience and adjust offspring phenotype in a way that enhances offspring fitness (Mousseau and Dingle 1991). For those organisms where the maternal environment is a good predictor of the offspring environment, maternal effects may be considered adaptive (Bernardo 1996b, Mousseau and Fox 1998, Donohue and Schmitt 1998) and variability in maternal allocation to their offspring may significantly influence progeny success. This is likely to be a successful strategy for organisms whose progeny does not move far from the mother, or are liberated as juveniles into the maternal environment (e.g. Bull and Baghurst 1998, Beekey et al. 2000, Dane 2002, Russell et al. 2004). In contrast, in organisms that have a dispersive early life phase, such as wind dispersed seeds or current dispersed larvae, offspring may experience a vastly different environment from the mother, and we may not expect such a strong coupling between the maternal response and offspring environment.

When mothers face an unpredictably heterogenous environment and cannot foresee the environment in which their progeny will develop, the adaptive value of offspring traits also become variable and unpredictable (Kaplan 1992). Under these circumstances, a trait's response to selection may evolve with a time lag or even in a direction opposite to that favoured by selection (Kirkpatrick and Lande 1989, Cowley and Atchley 1992). Accordingly, mothers may employ a 'bet-hedging' strategy, where an increase in phenotypic variance among offspring will also increase the probability that at least some individuals will survive, regardless of the changing environmental conditions (Philippi and Seger 1989). The phenotypic diversification produced by this strategy may ultimately

favour long-term maternal fitness at the expenses of the quality and survival of most offspring.

The quality of individual offspring is expressed in complex interrelationships among a suite of correlated traits. Although quality is defined by a variety of traits, studies of maternal effects on progeny quality have commonly explored the relationship between a single offspring trait, typically propagule size, and a specific aspect of the maternal environment, often food availability (Rossiter 1996). Yet maternal effects are more likely to result from the composite contribution of interacting abiotic, nutritional and other ecological characteristics of the maternal environment, and are most likely to be reflected in a number of offspring traits other than propagule size alone. While there is little doubt that propagule size is correlated with offspring fitness, potentially significant sources of maternal effects may remain undetected or misinterpreted if we assume that offspring fitness increases monotonically with egg size (the optimality propagule size theory, Smith and Fretwell 1974). In fact, maternal influence on propagule size is not able to explain variation in offspring phenotypic patterns and performance as expected from theoretical models, particularly when maternal effects are expressed in correlated traits not considered (cf. Lande and Arnold 1983).

This study investigated the role of maternal effects in influencing progeny characteristics from fertilization to the exhaustion of endogenous nutritional reserves in a coral reef damselfish (*Pomacentrus amboinensis*). *P. amboinensis* provides a good model organism for the study of maternal investment because differences in energy allocation are often manifested in variation in a number of early life history traits (McCormick 1999). Given that food availability is a major limiting factor influencing the growth and reproduction of individuals (Jones 1986, Kerrigan 1997, McCormick 2003), manipulation of food gave us the opportunity to alter this key resource influencing maternal energy allocation to offspring. Hence, using a combination of field manipulations and laboratory

experiments, the present study examined shifts in associations among early life history traits and survival of offspring that is induced by nutritionally and non-nutritionally mediated maternal effects.

2.2 Materials and methods

Experimental procedure

To determine the effect of maternal condition on the quality of offspring and their survival from the egg to the larval stage, a field experiment was conducted on 10 isolated patch reefs in the lagoon of Lizard Island (14º 40' S, 145º 28' E) on the Great Barrier Reef, Australia during November 2004. Experimental patch reefs were constructed on sand, 20 to 40 m off the edge of the main reef in 3 to 6 m of water. Reefs (~ 0.5 high x 1 × 2 m) were composed of a mixture of rubble and live coral, resembling patch reefs this species uses as a natural part of its habitat, and positioned 15 to 20 m apart. Ten breeding pairs of *Pomacentrus amboinensis* were captured from the main reef and measured (standard length, [SL]) to the nearest millimetre with callipers. Each pair was then transferred onto an experimental patch reef and randomly assigned to either a "supplemented" or a "non-supplemented" feeding treatment. The diet of 5 pairs was supplemented with ground pilchards and barramundi pellets (Formula 87510V7 with 50% crude protein, 12% crude fat and 2.5% crude fibres) for 10 min each day (supplemented treatment), while the remaining 5 pairs fed on naturally available plankton (non-supplemented treatment). Female body size (SL) for the two patch reef treatments did not differ statistically at the start of the experiment (t-test for independent samples, P = 0.57). Body size of females from the two patch reef treatments was re-measured at the end of the experiment (45 d later) to quantify the extent to which the manipulation of food altered female condition and potentially influenced maternal energy allocation to her offspring.

The spawning activity was monitored daily both on the patch reefs (supplemented and non-supplemented) and the main adjacent reef (reef). An initial 30-d period of treatment acclimation was allowed before collecting clutches of newly fertilized eggs laid on artificial nests (plastic half-pipes). One clutch per breeding pair was collected from each of the 3 treatments (supplemented, non-supplemented and reef). A total of 15 clutches were photographed with an underwater digital camera to enable the later determination of clutch size (measured as total area, mm^2), and then transferred to well-aerated aquaria with flowing seawater (28.3 ± 0.03ºC). Eggs were removed from each clutch using a fresh scalpel and transferred individually to 2 replicate 6-well tissue culture plates (n=12 eggs per clutch) using a fine brush. Plates were housed in perforated plastic containers and submerged in seawater as described Chapter 1. In total, 60 embryos from each of the 3 maternal conditions (supplemented, non-supplemented and reef) were allowed to develop in isolation.

Embryonic traits and survival

To define the extent to which maternal condition influenced early life history traits prior to and at hatching and the survival of offspring, embryos from the 3 treatments were individually monitored throughout their development. Embryos were photographed under a compound microscope (at 10× magnification) at 36 hours post-fertilization (hpf) just prior to the formation of main organs and systems (McCormick and Nechaev 2002) and at 84 hpf at completion of embryonic development (2-4 hours prior to hatching). Egg size (maximum egg length, mm), yolk-sac size (yolk-sac area, mm^2) and oil globule size (oil globule area, mm^2) were measured from the calibrated digital images using Optimas 6.5. Treatments were randomized to minimize the effect of unavoidable delays (max 45 min) caused by the time required to photograph each individual embryo. Any pre-hatching mortality and the date at hatching were recorded for each embryo. Following hatching,

unfed larvae were inspected every 6 hours until death as a measure of post-hatching longevity.

Statistical analyses

To quantify the extent to which the manipulation of food altered maternal condition (measured as female body size, SL), this study used a repeated-measures ANOVA with the beginning and end of experimental manipulation as the within-subject factor and treatment (supplemented and non-supplemented) as the between-subjects factor. Differences between the supplemented and non-supplemented feeding treatment were identified using a post-hoc Tukey's honestly significant difference (HSD) test at a significance level of $p < 0.05/k$, where k was the number of observation times (k = 2).

Least squares regression coefficients between clutch size and the coefficient of variation (CV) of egg size for each maternal treatment were calculated to determine whether there was evidence of bet-hedging. If bet-hedging occurred, the coefficient of variation of egg size was expected to be higher in non-supplemented females and in larger clutches. Prior to analysis, offspring longevity measures were square root-transformed to meet the assumptions of normality and homogeneity of variance. Initial offspring traits (egg size, yolk-sac and oil globule area measured at 36hpf), hatching success and post-hatching longevity were analysed with mixed model ANOVAs, where clutch identity (nested within maternal treatments, i.e. supplemented, non-supplemented, reef) was defined as a random effect and maternal treatment as a fixed effect. The effect of maternal treatments on embryonic traits throughout development was analysed using a repeated-measures ANOVA with developmental time (36 and 84 hpf) as the within-subjects factor and treatments (supplemented, non-supplemented, reef) as the between-subjects factor. Differences among treatments were identified using a post-hoc Tukey's HSD test at a corrected level of significance ($p < 0.025$).

A logistic regression model was used to determine the phenotypic traits affected by maternal condition that predicted whether embryos would successfully hatch or die before hatching. Given the high variability in the attributes of offspring within individual clutches (44-69% of the total variation), data were analysed without considering which clutch individuals were from allowing to examine how individual phenotypes affected survival. To identify the minimum number of variables that predicted hatching success within each treatment, the best subsets model was used. This involves a likelihood score criterion and the Wald test (z) to evaluate the statistical significance of each of the regression coefficients. A multiple regression analysis was then used to identify the phenotypic traits of *P. amboinensis* embryos that best predicted post-hatching longevity. Prior to the multiple regression analysis, the assumption of no colinearity of the independent variables was checked by examining the correlation among traits. By calculating partial regression coefficients of post-hatching longevity on the phenotypic traits of individual embryos, the effect of selection pressure on a trait when other traits were held constant was described. To measure the occurrence and intensity of directional phenotypic selection, directional selection gradients (β) were estimated as described in Lande and Arnold (1983). Standardised directional selection gradients (β') allowed a direct comparison of strength of selective mortality on phenotypic traits. All statistical analyses were performed using STATISTICA 6.1.

2.3 Results

Effect of supplementary food on mothers

Manipulation of food altered the condition of females from the supplemented patch reefs (treatment × experimental time interaction, $F_{2,8} = 6.00$, $P < 0.05$). Females from supplemented patch reefs increased by 8% in body size (SL) from the start of food supplementation and were significantly larger than their non-supplemented counterparts at

the termination of the experiment (Tukey's HSD, P < 0.01, Fig 2.1). In contrast, body size (SL) of non-supplemented females did not change during the course of the experiment (Tukey's HSD, P = 0.17).
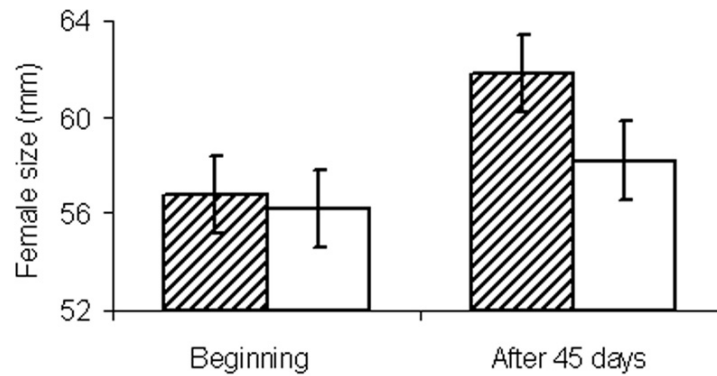
Fig 2.1. Body size (SL, mm) of females from supplemented (hatched) and non-supplemented (white) patch reefs at the beginning of the feeding experiment and after 45 days of food manipulation. Error bars represent SE.

Effect of maternal condition on offspring traits

Maternal condition affected clutch size ($F_{2,12}$ = 4.57, P < 0.05), resulting in significantly larger clutches produced by females living on the main reef compared to those produced by supplemented females (Tukey's HSD, P < 0.05). There was no detectable effect on egg size ($F_{2,155}$ = 2.44, P = 0.13) and no significant relationship was found between clutch and egg size for any of the treatments (all r^2 < 0.20). Egg size differed substantially among clutches within maternal treatments ($F_{12,155}$ = 12.61, P < 0.001) and size variation (measured as CV) was 1.4 to 1.7 times greater in clutches from non-supplemented fish on isolated experimental reefs and those living on the main reef compared with clutches produced by supplemented mothers. However, there was no significant relationship between clutch size and CV of egg size for any of the treatments.

Maternal condition had a clear effect on the yolk-sac or oil globule size of the egg ($F_{2,155}$ = 8.63, P <0.001 for yolk-sac size; $F_{2,155}$ = 6.04, P <0.05 for oil globule size). Supplemented mothers produced eggs with 10% more yolk reserve than non-supplemented

mothers on either the patch reefs or the main reef (Tukey's HSD, P < 0.001 in both cases). Yolk-sac size also differed among clutches within maternal treatments ($F_{12,155}$ = 1.947, P < 0.05) and supplemented mothers spawned clutches with 0.8 and 1.9 times greater range of yolk sizes compared to non-supplemented and main reef mothers respectively. This study also found significant differences in oil globule size among all three treatments, where eggs spawned by supplemented mothers had the largest oil globules and eggs from mothers on the main reef had the smallest (Tukey's HSD, P < 0.05; supplemented > non-supplemented > reef).

Offspring quality and survival variation

Mortality occurred both before and after hatching. Different maternal feeding treatments did not affect the number of embryos that successfully hatched ($F_{2,155}$ = 0.60, P = 0.56) or their post-hatching longevity ($F_{2,155}$ = 0.12, P = 0.89). Despite the differences in yolk allocation among treatments, the initial amount of yolk reserve (at 36 hpf) had no direct influence on the hatching success of embryos (z = 3.12, P = 0.08, Table 2.1). However, initial yolk-sac size was negatively related to post-hatching longevity for embryos from the non-supplemented treatment (Table 2.2), where embryos with smaller yolk-sacs survived longer after hatching. As development advanced, embryos originating from the supplemented treatment still had comparatively larger yolk reserves (treatment × developmental time interaction, $F_{2,147}$ = 2.14, P = 0.12), even after consuming 6% more yolk than embryos compared to the other two treatments in the intervening 48 hours (Fig 2.2A). Embryos from the supplemented treatment with large yolk-sacs just prior to hatching (at 84 hpf) had higher hatching success (Table 2.1) and survived longer after hatching (Table 2.2). However in the non-supplemented treatments, the amount of yolk reserve available to embryos just prior to hatching (at 84hpf) had no relationship with

hatching success (Table 2.1) and did not significantly influence post-hatching longevity (Table 2.2).

Table 2.1. Hatching success of embryos based on their phenotype and maternal condition. Results are based on logistic regression model for yolk-sac and oil globule size at 36 and 84 hpf as predictor variables of hatching success ("survived to hatch" or "died before hatching") of *P. amboinensis* larvae originating from 3 different maternal environments. Regression coefficients (B), their standard errors (SE) and the Wald test (z) are given with statistical significance ($p < 0.05$ in bold).

| | **Hatching success** | | | |
	B	SE	*z*	p
Natural main reef				
yolk-sac size at 36 hpf	-5.43	15.63	0.120	0.729
oil globule size at 36 hpf	-11.80	122.99	0.009	0.924
yolk-sac size at 84 hpf	0.72	14.23	0.003	0.960
oil globule size at 84 hpf	-287.56	128.36	5.018	**0.025**
Non-supplemented patch reef				
yolk-sac size at 36 hpf	-26.04	14.74	3.122	0.077
oil globule size at 36 hpf	143.99	96.27	2.237	0.135
yolk-sac size at 84 hpf	2.16	16.36	0.017	0.895
oil globule size at 84 hpf	-45.99	94.48	0.237	0.626
Supplemented patch reef				
yolk-sac size at 36 hpf	12.69	11.30	1.263	0.261
oil globule size at 36 hpf	-16.36	12.35	1.753	0.185
yolk-sac size at 84 hpf	286.65	136.62	4.402	**0.036**
oil globule size at 84 hpf	108.99	98.00	1.237	0.266

Table 2.2. Post-hatching longevity of unfed larvae based on their phenotype and maternal condition. Results are based on multiple regression analysis with directional selection gradients ($\beta \pm SE$) for yolk-sac and oil globule size at 36 and 84 hpf, using post-hatching longevity of *P. amboinensis* larvae originating from 3 different maternal environments as a measure of survivorship. Standardized selection gradients (β') are in standard deviation units. R^2-values are for the multiple regression; $p < 0.05$ in **bold**.

	Post-hatching longevity			
	$\beta \pm SE$	$\beta' \pm SE$	R^2	p
Natural main reef				
yolk-sac size at 36 hpf	-37.34 ± 85.67	-0.08 ± 0.18	0.12	0.665
oil globule size at 36 hpf	120.75 ± 670.13	0.03 ± 0.17		0.858
yolk-sac size at 84 hpf	24.29 ± 80.25	0.05 ± 0.18		0.764
oil globule size at 84 hpf	-1367.53 ± 643.10	-0.39 ± 0.18		**0.039**
Non-supplemented patch reef				
yolk-sac size at 36 hpf	-155.58 ± 71.63	-0.30 ± 0.14	0.20	**0.035**
oil globule size at 36 hpf	-50.19 ± 474.38	-0.02 ± 0.15		0.916
yolk-sac size at 84 hpf	-87.13 ± 83.05	-0.15 ± 0.14		0.300
oil globule size at 84 hpf	-719.14 ± 453.50	-0.24 ± 0.15		0.120
Supplemented patch reef				
yolk-sac size at 36 hpf	89.70 ± 66.02	0.19 ± 0.15	0.19	0.118
oil globule size at 36 hpf	-79.13 ± 71.77	-0.18 ± 0.17		0.276
yolk-sac size at 84 hpf	1687.48 ± 735.54	0.09 ± 0.15		**0.027**
oil globule size at 84 hpf	409.20 ± 569.23	0.13 ± 0.18		0.475
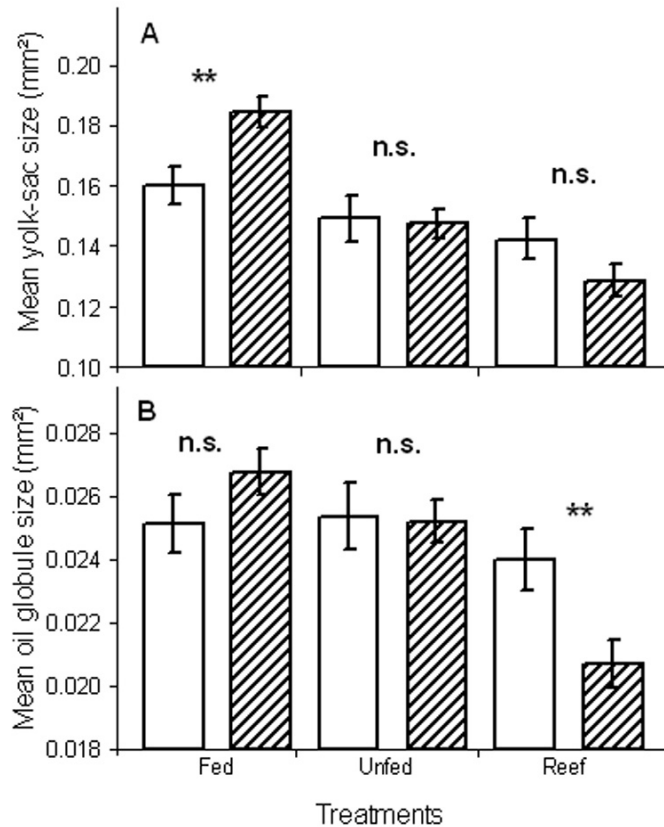
Fig 2.2. Mean yolk-sac (A) and oil globule area (B) measured just prior to hatching (84 hpf) for *Pomacentrus amboinensis* embryos originating from supplemented and non-supplemented mothers on experimental patch reefs and mothers living on a natural adjacent reef. Individuals that did not survive to hatch are represented by the white bars and those that survived to hatch are represented by the hatched bars. Error bars are SE. *n.s.*, no significant difference; ** significant difference at $\alpha = 0.025$.

In embryos from the main reef, oil globule size rather than yolk-sac size just prior to hatching was related to hatching success (Table 2.1). Main reef embryos initially had smaller oil globules than those originating from the patch reefs. Although these differences among treatments were maintained as development advanced (treatment × developmental time interaction, $F_{2,147} = 1.41$, $P = 0.25$), main reef embryos reduced the size of their oil globule by 8% more than embryos from the other two treatments over the 48h period between measurements (Fig 2.2B). The size of the oil globule just prior to hatching (at 84hpf) was important for both hatching success and post-hatching longevity for embryos originating from the main reef (Table 2.1 and 2.2, Fig 2.3). Oil globule size at both 36 and

84 hpf did not, however, show any direct relationship with embryonic success to hatch and larval longevity in the two patch reef treatments (Table 2.1 and 2.2).
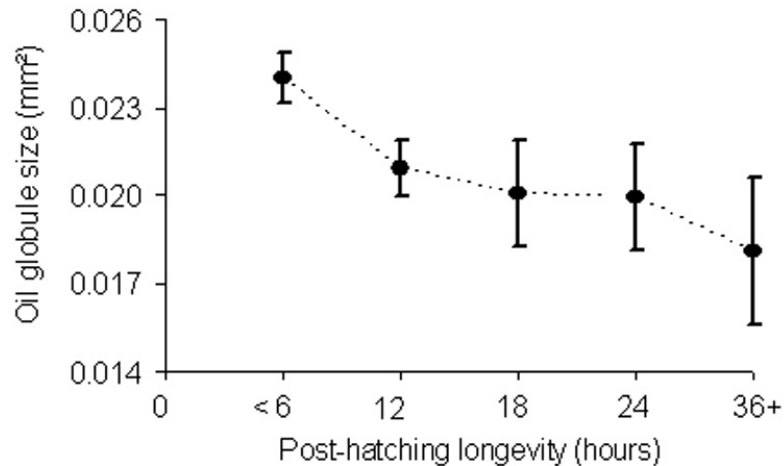
Fig 2.3. Relationship between longevity of larval *P. amboinensis* originating from the natural reef and oil globule size (mm) just prior to hatching (at 84hpf). Error bars represent SE.

2.4 Discussion

By manipulating the maternal environment of *P. amboinensis*, this study was able to demonstrate that maternal condition at the time of gametogenesis influences traits that predict larval survival. Maternal energy allocation to offspring measured as yolk-sac and oil globule size, induced shifts in the intensity of selective mortality throughout the early development of this species.

Smith and Fretwell's optimal offspring size theory suggests that maternal reproductive investment is traded-off between egg size and egg number with an increase in one requiring a corresponding decrease in the other. Although there was evidence that the nutritional condition of mothers did significantly affect clutch size, no evidence for a linear trade-off between egg size and clutch size was found. Regardless of their physiological condition, *P. amboinensis* mothers produced a wide-variety of egg sizes. What this study did find was that supplemented females enhanced the quality of their eggs by provisioning

them with significantly larger energy reserves. Both yolk-sac and oil globule sizes were larger in eggs from nutritionally supplemented mothers suggesting that the trade-off may be more accurately reflected by the relationship between egg quality and clutch size rather than egg size and clutch size. This finding underscores two important observations that have traditionally been assumed for many different taxa. Firstly, egg size may not always be a good proxy for egg quality, and secondly, egg size may not accurately reflect maternal investment in reproduction.

Provision of energy reserves in the yolk-sac and oil globule more closely reflected the differences in the maternal environment and influenced larval survival. Supplementary feeding enhanced body condition of females which led to the production of offspring with the largest yolk-sacs, a finding consistent with previous studies (e.g. Kerrigan 1997; McCormick 2003). To my knowledge, the present study is the first to demonstrate that increased yolk provisioning is translated into a survival advantage during the embryonic period and after hatching in a tropical species. Given that the yolk reservoir of free and protein bound amino acids is the substrate for energy production and synthesis for tissue growth during the egg stage (Finn et al. 1996), it is not surprising that a larger amount of yolk during embryogenesis is associated with higher hatching success. At hatching and thereafter, the main metabolic fuel for species with discrete oil droplets in the yolk (e.g. *P. amboinensis*) is derived from neutral lipids enclosed in the oil globule (Rønnestad et al. 1998). However, yolk constituents are essential for sustaining maintenance and tissue growth when the developing fish have just hatched and are learning to feed effectively (Heming and Buddington 1988). Larger amount of yolk reserves may, therefore, lead to hatchlings that survive longer before irreversible starvation, as suggested by numerous studies on temperate fish (e.g. Blaxter and Hempel 1966; Chambers et al. 1989).

Depending on the offspring environment, benefits associated with a larger yolk-sac may not always be detectable (Chapter 1). By examining the relationship between yolk-sac

size and survival of *P. amboinensis* eggs developing at 3 different temperatures, I showed that yolk-sac size was only important for embryonic success to hatching at the highest temperature and had no ramification on post-hatching longevity of larvae. The link between yolk-sac size and selective larval survival may also only be detectable when maternal investment in individual offspring within a clutch is highly variable. This study found that there was high variability in the attributes of larvae within individual clutches, regardless of the food resources available to *P. amboinensis* mothers. However, this differential maternal investment to eggs within a clutch was particularly marked in the supplemented treatment, where strong phenotypic selection on yolk-sac size was detected. The present finding suggests that supplemented mothers may have sufficient resources to be able to allocate the same amount of energy in each egg (which would be in the best interest of individual offspring, thereby reducing within-clutch yolk-size variability), but instead they hedge their bets by provisioning some offspring with more yolk reserves while investing less energy in others, which maximizes maternal investment under unpredictable environmental conditions.

In low food conditions, represented by both the non-supplemented treatment and the main reef, mothers may be limited in the amount of energy available to fuel gametogenesis (Jones and McCormick 2002) and this may result in a reduction of maternal investment in offspring quality (e.g. yolk-sac). Although under these circumstances selection for a larger yolk-sac size is expected (Kerrigan 1997), this study found that yolk-sac size had no effect on embryonic survival. For post-hatching longevity, yolk-sac size was also either inconsequential (main reef) or offspring with smaller yolk-sac sizes were actually found to be favoured (non-supplemented treatment). The reasons why a larger yolk-sac may be an undesirable trait in offspring originating from the non-supplemented treatment are unclear. One possible explanation for differences in the selective value of yolk-sac size may be differences in the conversion efficiency of yolk reserves. Von

Westernhagen (1988) provides examples in marine fish of how metabolic or osmotic disturbance in embryos can prevent the proper use of the energy stored in the yolk. Important embryonic physiological functions such as metabolic activity, development and osmoregulation are governed by maternally-derived hormones (Lam 1994). Because offspring rely entirely on maternally-derived hormones until the development of their own endocrine system after hatching (Lam 1994; Sampath-Kumar et al. 1997), the present findings suggest that the initial level of hormones such as testosterone that non-supplemented females transferred into the egg yolk may have affected the efficiency of yolk use (McCormick 1999). Given that testosterone levels in breeding females are closely associated with, and triggered by, behavioural interactions with conspecifics (McCormick 1998), the social isolation of non-supplemented females on patch reefs may cause a reduction in the natural levels of this hormone (McCormick 1998). Low hormonal levels have been previously reported to inhibit embryonic physiological functions in fish (e.g. sturgeon larvae, Blaxter 1969) and other vertebrates (e.g. birds, Jacobs and Wingfield 2000 and humans, Parker et al. 1989). The present findings suggest that eggs from the non-supplemented treatment may be less efficient than those with a different hormonal balance in transforming yolk into body tissue, thereby retarding growth and reducing survivorship.

Survival benefits associated to the size of the oil globule were observed in offspring from the main reef exclusively, and the direction of the relationship between this trait and offspring hatching success and post-hatching longevity was opposite to that typically predicted. This study found that a smaller oil globule just prior to hatching confers higher hatching success (i.e. number of eggs successfully hatched) and greater post-hatching longevity (Table 2.2; Fig 2.2). These results are unexpected, given that the oil globule provides the main substrate in the aerobic energy from hatching and thereafter (Norton et al. 2001), and consequently a positive relationship between oil globule size and post-hatching longevity rather that hatching success would intuitively be predicted. Size of

the oil globule was positively correlated with larval survival in capelin, *Mallotus villosus* (Chambers et al. 1989) and in walleye, *Stizostedion vitreum* (Moodie et al. 1989). Larvae from walleye eggs with the smallest oil globule were both smaller and slower-growing compared to those larvae hatched from eggs with larger oil globules. Recently, Berkeley et al. (2004) also showed that oil globule size strongly affects larval growth and survival in black rockfish (*Sebastes melanops*), suggesting that enhanced growth rates of larvae with larger oil globules at hatching provide clear benefits in allowing larvae to quickly grow through a window of vulnerability from predation and other environmental challenges. Although it is generally accepted that fast growth can provide many survival advantages (Stearns 1992), these benefits vary and are not always detectable (cf. Meekan and Fortier 1996; Metcalfe and Monaghan 2003) because fast growth clearly comes at an energetic (metabolic) cost (Rombough 1994). Given that energy expenditure associated with physiological rates, such as growth, is closely tied to metabolism (Savage et al. 2004), the present findings suggest that slow-growing larvae with low metabolic rates may be favoured by energy-driven selective mechanisms in stressed (e.g. food limited) environments. The rate at which energy stored in the oil globule are used up could explain how embryos with smaller oil globules, and presumably slower growth rates (Moodie et al. 1989; Berkeley et al. 2004) survived for a significantly longer time after hatching. Obviously further work is required to clarify this interesting result, but the result does highlight that a large oil globule is not always purvey a survival advantage.

The present study showed that offspring viability arising from maternal investment in progeny quality is not always reflected in offspring size. Instead, it may be directly affected by the quantity, and probably the quality, of endogenous reserves available to individual propagules. This study did not examine the susceptibility of individual offspring to other directional selection agents such as predation. Consequently, it cannot establish how the relationship between early life history traits such as egg and larval size, and

behavioural processes such as predator avoidance may interact to influence differential survival among offspring (but see Fuiman et al. 2005), and subsequently how maternal investment may be related to performance of their offspring (but see Mappes et al. 1997). This study emphasises the complexity of selective processes during the embryonic and larval phase and highlights the limitations in our current understanding of larval development and energetics.

Conclusions

The present findings suggest that maternal condition influences offspring physiological capacity and in turn their efficiency to utilise endogenous reserves. This suggests that energy-driven mechanisms may operate to determine offspring viability, particularly in stressful maternal environments (i.e. low food levels and high breeding density). Although there is little doubt that an offspring's phenotype integrates information derived from the maternal environment, offspring themselves are directly affected by local environmental conditions, which can shift the optimal value of a trait or a combination of traits (Chapter 1). The ramifications maternal effects on offspring performance in relation to the offspring environment clearly merit further investigation.

Chapter 3

Survival against the odds: ontogenetic changes in selective pressure

mediate growth-mortality tradeoffs

3.1 Introduction

The population dynamics of many animals including insects, amphibians, aquatic

invertebrates and fish involve multiple life stages, in which individuals change their habitat

use or diet with ontogeny (i.e. ontogenetic niche shifts; Wilbur 1980). As individuals shift

between niches, their scope for growth and survival vary in relation to the physical and

biological environment they encounter (Altwegg and Reyer 2003). Niche-specific

morphological, physiological and behavioural characteristics determine which individuals

will have better chances of avoiding predators and obtaining resources to grow and survive

to the next life stage. Understanding the mechanisms generating such phenotypic variation

across ontogenetic stages is critical for animals with complex life cycles, where the effect

of events occurring at one life stage can propagate through time (carry-over effects) and

has profound demographic and life-history consequences on population dynamics

(Pechenik et al. 1998, Hellriegel 2000, Beckerman et al. 2002, De Roos et al. 2003).

The extensive phenotypic variation existing among individuals in a population is

largely the result of variable growth (Jones and German 2005). Historically, studies of

animal populations have examined growth central parameters such as rates, durations, time

of onset and offset as major factors influencing the survival of individuals across

ontogenetic niches. Although growth and its associated parameters are based on the

individual, the variation in those values is important to population dynamics (e.g.

DeAngelis and Gross 1992). In fish populations, the focal role of growth is best

encapsulated in the growth-mortality hypothesis (Anderson 1988), which provides a

theoretical framework to examine carry-over effects of larval condition on post-

metamorphic survival. The theory suggests that faster growing larvae ("growth-rate" mechanism, Anderson 1988) may be able to gain survival advantages by shortening the pelagic stage ("stage-duration" mechanism, Houde 1987) and potentially reducing predation and/or starvation risks by attaining a larger size at a given age ("bigger-is-better" mechanism, Miller et al. 1988). Advantages gained during the larval phase are then believed to extend to the post-settlement phase and influence individual chances of survival (Sogard 1997).

An increasing number of studies have used otolith analyses to describe growth and mortality patterns during the early life history of fishes and shown that larval growth history strongly influences juvenile survivorship in benthic habitats (e.g. Searcy and Sponaugle 2001, Vigliola and Meekan 2002, Raventos and Macpherson 2005, Jenkins and King 2006). Events prior to hatching (via maternal effects) also have the potential to affect post-settlement survivorship (Vigliola and Meekan 2002, Raventos and Macpherson 2005), but research has not yet quantitatively linked these processes. Similarly, despite some evidence that post-settlement processes have the capacity to breakdown patterns established at settlement (Schmitt and Holbrook 1999, Webster 2002) and potentially obscure the effects of larval experience on juvenile success (Bertram et al. 1993, McCormick and Hoey 2004), few studies have linked larval and early post-settlement growth histories to persistence of juveniles in benthic habitats (but see Searcy and Sponaugle 2001, Vigliola and Meekan 2002, McCormick and Hoey 2004).

In the present study, growth histories recorded in the otoliths of a common coral reef fish, *Pomacentrus amboinensis*, were used to determine the extent to which variation in life history characteristics among individuals within a cohort influences survival through ontogenetic niche shifts. Specifically, this study aims to quantify the shape and magnitude of selective mortality acting on phenotypic variability from the end of the embryonic stage, through the planktonic larval phase, to weeks and months after settlement. By doing so, it

identifies which individual attributes are the most influential in determining patterns of juvenile survival in the field.

3.2 Materials and methods

Study species

This study focused on the Ambon damselfish (*Pomacentrus amboinensis*), a common and abundant coral reef fish on the Great Barrier Reef. The complex life cycle of this species begins during full moon in benthic nest sites where females lay eggs that are tended by a male until the completion of embryonic development and hatching. Following hatching, *P. amboinensis* offspring undergo a 15-23 d dispersive planktonic phase (Kerrigan 1996) before returning to the reef during the subsequent new moon period, at which time they rapidly (less than 12 h) metamorphose into the juvenile form (McCormick et al. 2002) and settle directly into adult coral reef habitats. Once settled, *P. amboinensis* remain strongly site-attached throughout benthic life (McCormick and Makey 1997, Booth 2002).

Field Sampling

In late October 2004, the daily spawning activity of *P. amboinensis* was monitored at 6 sites (about 1.5-2 km apart) on the fringing reef around Lizard Island (14º 40′ S, 145º 28′ E) on the northern Great Barrier Reef, Australia. These sites were distributed across all the habitats and depths where *P. amboinensis* occur at the study location so as to obtain as representative a sample as possible of the traits in the population reproductive output for that pulse. A total of 42 egg clutches spawned on plastic half-pipes that had been adopted by males as nesting substrata (McCormick 1999) were collected. Prior to dusk on the night of hatching, clutches were brought into the laboratory and placed in well-aerated aquaria of flowing seawater at 28 ºC (ambient). All wild clutches successfully hatched in the

laboratory and all individuals from each clutch hatched within a 20-30 min period. Immediately after this hatching period, subsamples of approximately 100 newly hatched larvae were collected from each clutch using a small hand net and a fine brush, and immediately preserved in 30% ethanol freshwater solution stored at –19 ºC. This preservation method for newly hatched larvae allowed accurate measurement of morphology and otolith dimensions with a negligible error due to shrinkage (Gagliano et al. 2006).

During the new moon in November, large numbers of newly metamorphosed *P. amboinensis* were captured using light-traps (Fig 3.1, see Meekan et al.. 2001 for trap design) as they approached the reefs surrounding Lizard Island. Traps were moored over sand approximately 100 m apart and 30 to 50 m from the reef edge. They were suspended from a buoy 1 m below the surface prior to dusk and then cleared of fish just after dawn the following morning for 12 d centred around the time of the new moon. This period was likely to encompass the majority of the settlement pulse for the month (Kerrigan 1996).
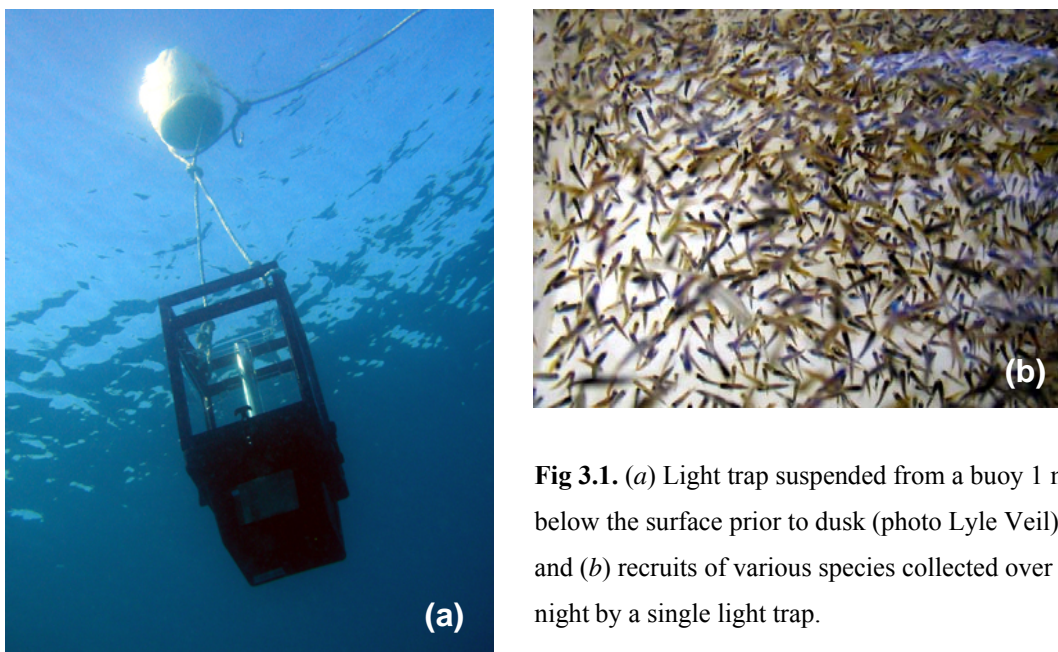
Fig 3.1. (*a*) Light trap suspended from a buoy 1 m below the surface prior to dusk (photo Lyle Veil) and (*b*) recruits of various species collected over night by a single light trap.

Light trap caught fish were sacrificed immediately following capture and preserved in 70% ethanol. Individuals from this same lunar cohort (i.e. those who originally settled on

the reef during the new moon in November) were sampled on SCUBA 2, 3, 4, 6 and 8 weeks after settlement from reef habitats using hand nets and an anaesthetic (5:1 ethanol:clove oil mixture). A total of 635 juveniles was collected from the reef. Effort was spread over different habitats and locations of a large fringing reef to ensure sampling would not bias subsequent collections and account for potential spatial variability of traits (Vigliola and Meekan 2002). After each collection, juvenile fish were immediately preserved in 70% ethanol.

Data collection

Twenty newly hatched larvae were randomly selected from each clutch and photographed individually against a scale bar under a dissecting microscope. Larval body dimensions, including standard length (SL), yolk-sac area (YK) and oil globule area (OG) were measured on these images using image analysis software (Optimas 6.5). Sagittal otoliths, or ear bones of individual hatchlings were located under a compound microscope at 40x magnification using a polarised light source (Fig 3.2) and otolith size (maximum diameter, μm) was recorded as a measure of size-at-hatching.
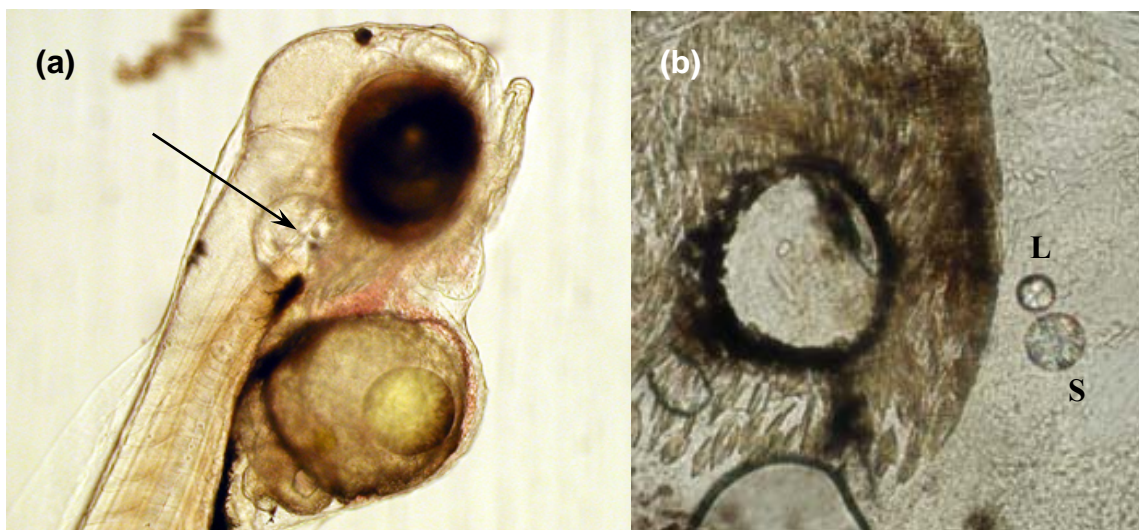
Fig 3.2. (*a*) Head of a newly hatched *P. amboinensis* with otoliths visibly located behind the eye as indicated by the arrow. (*b*) The sagittal otolith (denoted by the letter S) and the smaller lapillar otolith (denoted by the letter L) are both present at this developmental stage.

Over 7,000 *P. amboinensis* settlers caught by light traps in November were used to generate a complete size frequency distribution. All individuals were measured to the nearest 0.1 mm standard length and then size-corrected to account for shrinkage effects due to 70% ethanol preservation (estimated at 11% for standard length during the first month of preservation, after which shrinkage of this attribute becomes negligible). A total of 410 individuals were then randomly sub-sampled in proportion to the numbers occurring in 1mm size classes of standard length within the size range represented in the entire light trap collection.

To compare the early life history of *P. amboinensis* surviving on the reef with that of the population at earlier times, the information stored in the otoliths of individual fish from each of the 7 collections (i.e. newly hatched through to 8 weeks post-settlement) were examined. Like in many other tropical and temperate fishes, *P. amboinensis* form a mark on the day of hatching that is represented by the increment closest to the spherical nucleus of the otolith (Wellington and Victor 1989). Furthermore, the settlement mark of this species appears as a single dark ring followed by a marked decrease in increment width (Wilson and McCormick 1997) and the formation of increments after settlement has been validated to occur on a daily basis (Pitcher 1988). Pelagic larval duration (PLD), size-at-age (distance from the nucleus to selected increments) and growth rates during specific periods (distance between selected increments) were measured from thin transverse sections through the nucleus of left sagittae. To obtain otolith cross sections, sagitta were mounted in thermoplastic cement (Crystal Bond [TM]), ground and polished using 12 to 0.3 μm lapping films as described in detail by Wilson and McCormick (1997). Each otolith was examined under 40x magnification and measured along the longest axis using a video image-analysis system linked to a compound microscope. To ensure the analyses only included fishes that were part of the same November cohort, the number of increments from the settlement mark to the edge of the otolith of all benthic juveniles in our collections

were counted and fish that were older or younger (<15%) than expected at the date of capture from the reef were excluded.

Data analyses

This study tested for the presence of size- and growth-selective mortality in the cohort of newly settled *P. amboinensis* by comparing the distribution of otolith characteristics at a given age among successive collections from the time at hatching to 8 weeks after settlement. For example, distributions of size-at-settlement of all benthic juveniles (i.e. post-settlement survivors) were compared with those of all newly metamorphosed settlers caught by light traps (i.e. our samples of the population from which these originated) to test for size-selective mortality acting on this trait at the time of settlement. A shift (i.e. change in skewness) in the survivors' distribution to the left and a decline in mean size-at-settlement would suggest that smaller individuals had higher survival rates than larger conspecifics at settlement (i.e. negative directional selection). Similarly, a shift to the right and an increase in mean size would indicate that phenotypic selection favoured larger individuals. Size and growth rate distributions (survivors vs. original population) for each pair of samples (i.e. ages) were compared using the non-parametric Kolmogorov-Smirnov two-sample test because of its sensitivity to changes in location, dispersion and skewness of the distributions, while making no assumptions on the distribution of data (Sokal and Rohlf 2001). The significance of all comparisons was based on a α-level of 0.05. The frequency distribution of pelagic larval duration (PLD), size-at-hatching, size-at settlement, size-at-age (2, 3 and 4 weeks post-settlement) as well as growth rates during the pelagic larval phase, the first 2 weeks on the reef and the 3rd and the 4th week post-settlement were examined. In our comparison of hatchling characteristics to later life stages, that hatchlings collected from benthic nests around Lizard Island were assumed to be a representative sample of the attributes of the fishes that settled on the fringing reefs around the island.

Although this is an untestable assumption, I believe it is justifiable given that recent evidence has suggested a high degree of self-recruitment at this location (e.g. Wilson and McCormick 1997, Jones et al.. 1999, James et al.. 2002) and the extensive range of habitats and environmental conditions sampled around the entirety of Lizard Island during the present study.

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 within the targeted cohort were based on and refer to otolith measurements only, unless specified otherwise. The advantage of using otolith traits for studies of phenotypic selection is that these measurements are permanent individual records unmodified by age and growth, thus providing a convenient means for quantifying phenotypic selection (*cf* Swain 1992). We estimated the intensity of linear (S_i) and non-linear selection (C_i) as:

$$S_i = \frac{\bar{z}_{after} - \bar{z}_{before}}{SD_{before}} \quad \text{and} \quad C_i = Var_{after} - Var_{before} + S_i^2$$

where $\bar{z}_{before}$ and $\bar{z}_{after}$ are the mean and Var_{before} and Var_{after} are the variance of size (or growth) z before- and after-selection respectively (Brodie et al. 1995).

Because phenotypic selection can have different forms (i.e. linear and non-linear), the form of phenotypic selection acting on size and growth rate of larval and juvenile *P. amboinensis* was also examined using the non-parametric approach pioneered by Schluter (1988) and modified by Anderson (1995) and Sinclair et al.. (2002), for cross-sectional data. This spline-based regression method describes relative survival as a smoothly changing function of size or growth, making no assumptions of the underlying fitness function, and allows calculation of 95% confidence bands about the curve. Briefly, I first estimated the conditional probability $h(z)$ that a fish of size (or growth) z at a given age was caught in the sample of survivors (i.e. after-selection sample), given that it was caught in one of the two samples. To do this, fish caught before-selection were coded as 0 and those

caught after-selection as 1, and *h(z)* was estimated using a generalized additive model assuming a binomial error distribution and a logit link as *per* Sinclair et al.. (2002) and given by:

$$h(z) = e^u / (1 - e^u)$$

where *u* is a cubic B-spline smooth function of z, with a smoothing parameter λ chosen by generalized cross validation. The relative survival function *f(z)* was then given by:

$$f(z) = \frac{n_{before}}{n_{after}} \left[\frac{h(z)}{1 - h(z)} \right]$$

where n_{before} and n_{after} are the numbers in the before- and after-selection group.

Finally, the probability (π) of a newly hatched fish surviving the pelagic phase and reaching benthic habitats as a function of its larval characteristics (standard length, SL; yolk-sac area, YK; oil globule area, OG) was estimated using logistic regression analysis. These larval characteristics are important because they are directly influenced by maternal provisioning to offspring (McCormick 2006, Chapter 2) and thus enable the quantification of potential carry-over effects of maternally-induced variation on offspring survival. Although individual survivorship was not directly recorded, I used these larval characteristics associated with change in the distributions of otolith size-at-hatching as a proxy for survival. To do this, both the size-frequency distributions at settlement (i.e. comparing newly hatched larvae with settled fish) and the form of phenotypic selection acting on otolith size-at-hatching during the planktonic phase were examined and then the range of otolith sizes representing individuals unlikely to survive to settlement was identified (i.e. low probability of survival representing less than 1% of the surviving size-frequency distribution; Fig 3.4). All hatchlings likely to survive were then dummy-coded as '1' and all those unlikely to survive the pelagic phase based on their otolith size-at-hatching coded as '0'. To identify the minimum number of variables that predicted survival to settlement, we used the best subsets model. This involves a likelihood score criterion and

the Wald test (z) to evaluate the statistical significance of each of the regression coefficients. All traits included in the analysis met the assumption of no colinearity.

3.3 Results

Individuals surviving the intense size-selective mortality that occurred during the dispersive pelagic phase had significantly smaller otoliths at hatching ($\bar{z}_{before}$ = 0.029 mm, $\bar{z}_{after}$ = 0.023 mm; K-S test, p<0.001; Fig. 3.3A and 3.4A). Selective mortality of individuals with larger otoliths at hatching was also pronounced during the first 2 weeks following settlement on reef habitats ($\bar{z}_{before}$ = 0.023 mm, $\bar{z}_{after}$ = 0.022 mm; K-S test, p<0.001), indicating that selection for this trait operated between life history stages (Fig. 3.3A). Logistic regression analysis based on dummy-coded individuals showed that the probability (π) of a newly hatched fish surviving the planktonic phase and reaching reef habitats depended on both body size, SL (Wald test Z = 22.40, p < 0.001) and amount of yolk-sac reserves, YK (Wald test Z = 8.81, p < 0.003) at hatching (logit (π) = 5.60 - 2.14SL + 8.25YK). Specifically, smaller body size and larger yolk-sac reserves at the time of hatching were associated with smaller otolith size and higher survival probability.

The significant selective loss of individuals with faster larval growth during the planktonic phase continued to occur weeks to months after settlement, influencing survivorship of subsequent life stages on benthic habitats (Fig 3.3B and 3.4B). Growth during the planktonic phase was a stronger determinant of survivorship than growth at older ages (Fig 3.3B). Importantly, I found that selective mortality based on larval growth was generally non-linear and changed form across ontogenetic stages (Fig 3.3B and 3.5).

A

	settlement	2 wks	3 wks	4 wks	6 wks	8 wks
hatching	**-3.14 (9.89)**	**-1.12 (1.45)**	0.23 (0.05)	0.00 (0.92)	-0.22 (0.05)	0.42 (0.18)
settlement		**-3.25 (10.55)**	**-1.44 (2.06)**	**-0.58 (0.33)**	-0.44 (0.20)	-0.35 (0.13)
2wks ps			-1.73 (2.98)	-0.27 (0.07)	-0.11 (0.01)	-0.25 (0.06)
3 wks ps				**-2.98 (8.88)**	-2.22 (4.93)	-2.56 (6.54)
4 wks ps					-0.30 (0.09)	-0.50 (0.25)

B

	settlement	2 wks	3 wks	4 wks	6 wks	8 wks
pelagic phase		**-1.34 (1.81)**	**-1.29 (1.67)**	**-0.61 (0.38)**	**-0.33 (0.11)**	-0.43 (0.18)
first 2 wks ps			***0.91 (0.82)***	0.27 (0.07)	0.22 (0.05)	-0.46 (0.21)
3rd wk ps				**-0.89 (0.79)**	-0.17 (0.03)	-0.77 (0.59)
4th wk ps					-0.53 (0.28)	-0.35 (0.12)

Fig 3.3. Quantitative estimates of selective mortality based on (A) size and (B) growth of *P. amboinensis* from hatching to 8 weeks post-settlement (ps). The significant effect of each trait at a given time is described by the grey ($p<0.001$) and white boxes ($p>0.001$) based on Kolmogorov-Smirnov two-sample tests. Values on each box describe change in units of phenotypic standard deviations and represent the intensities of linear and non-linear (in brackets) phenotypic selection acting on individual traits at a given time.
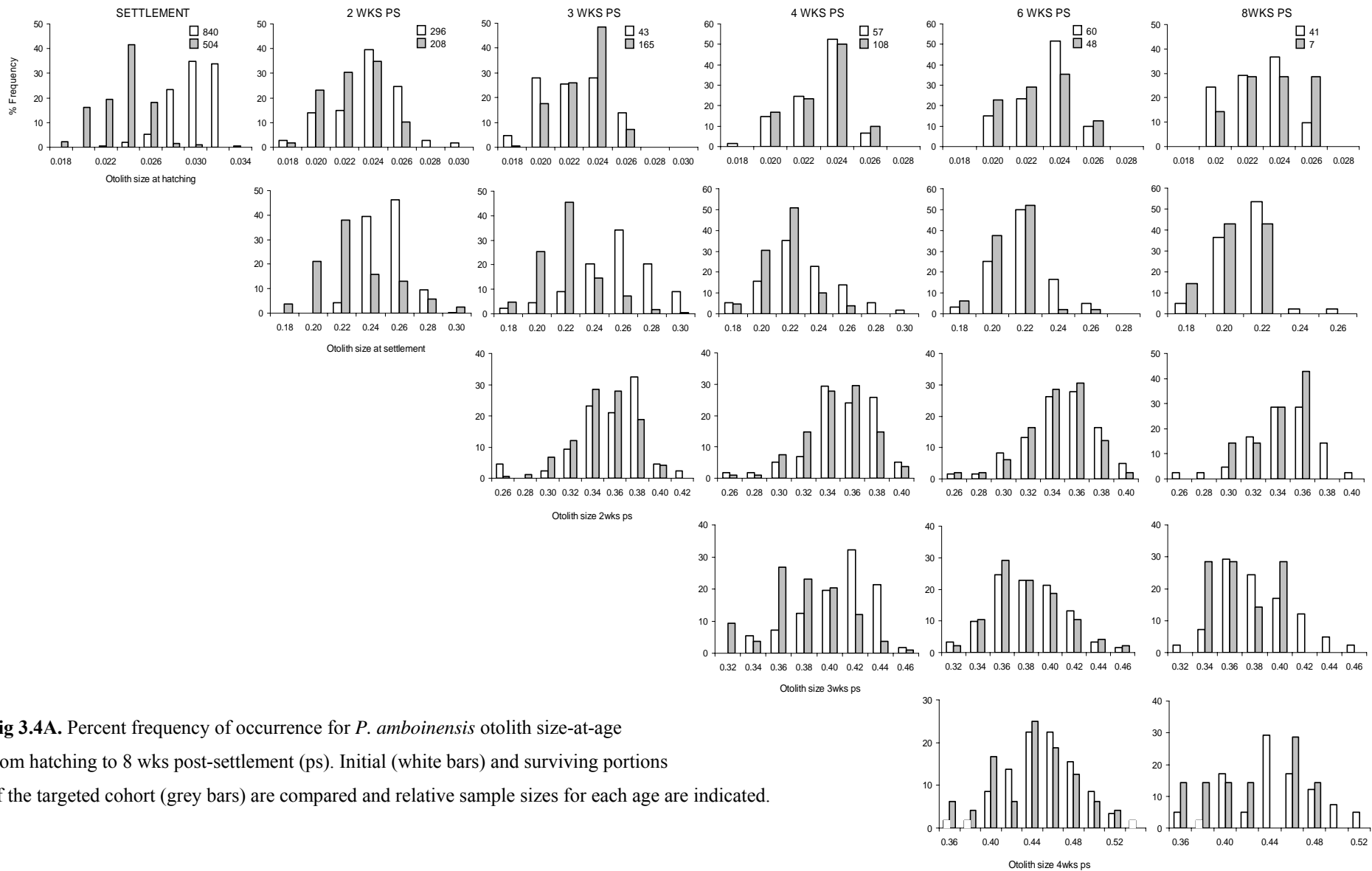
Fig 3.4A. Percent frequency of occurrence for *P. amboinensis* otolith size-at-age from hatching to 8 wks post-settlement (ps). Initial (white bars) and surviving portions of the targeted cohort (grey bars) are compared and relative sample sizes for each age are indicated.
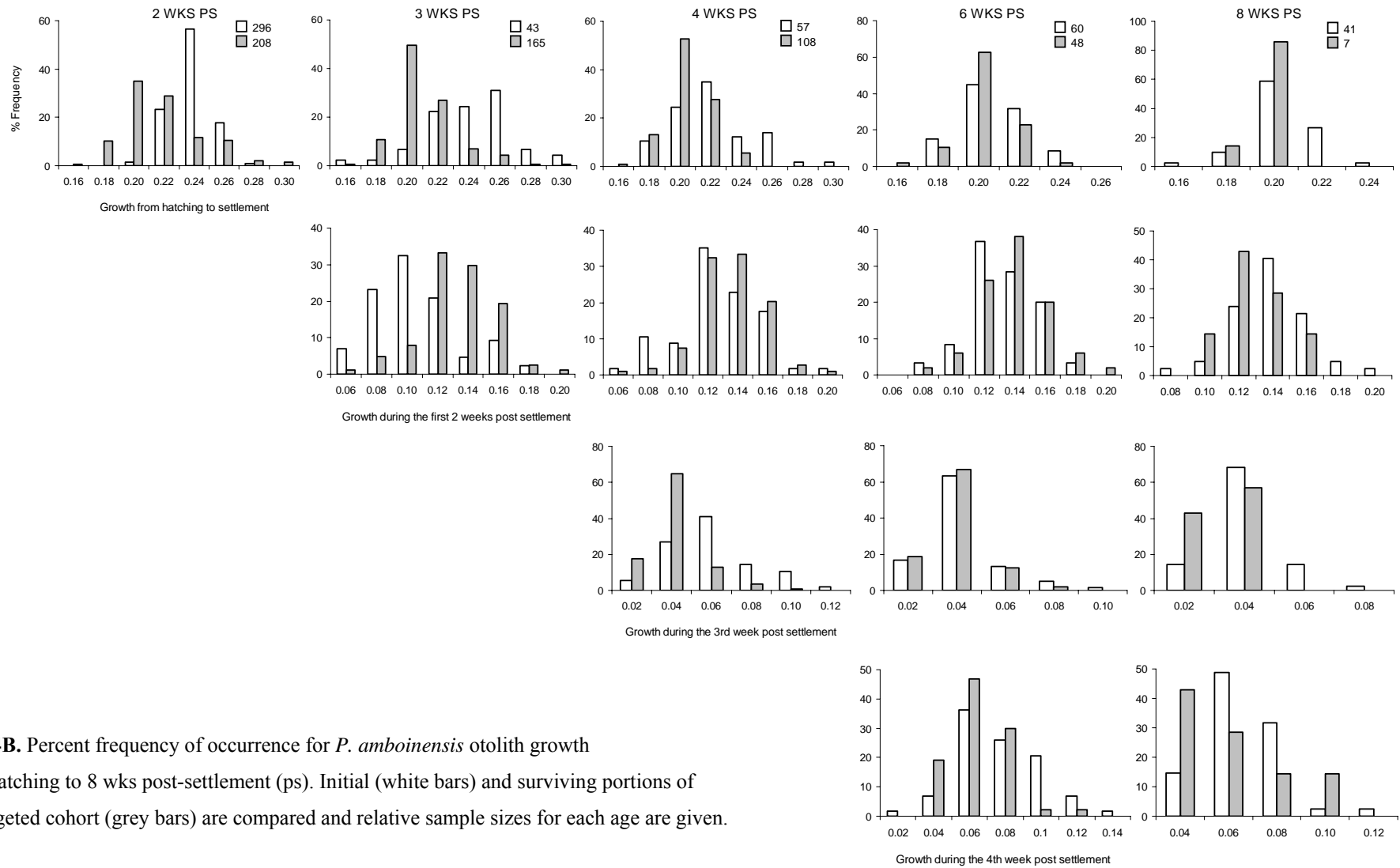
Fig 3.4B. Percent frequency of occurrence for *P. amboinensis* otolith growth from hatching to 8 wks post-settlement (ps). Initial (white bars) and surviving portions of the targeted cohort (grey bars) are compared and relative sample sizes for each age are given.

This study detected no selective mortality based on pelagic larval duration, PLD (K-S test, $p > 0.10$). Juveniles collected from the reef settled at similar ages to recruits collected at settlement by light traps (mean PLD was 17.80 d and 17.66 respectively) and variation in PLD among individuals was low (recruits PLD range: 15-22 d; juvenile PLD range: 15-22 d; CV < 9%).

Although selective mortality of this cohort after settlement was strongly associated with larval characteristics, we also detected significant selection based on juvenile traits including otolith size-at-settlement and growth over the first 2-3 weeks following settlement on the reef (Fig 3.3 and 3.4). Smaller initial size conferred higher survival probability to newly settled *P. amboinensis*. However, despite of being slower-growing as larvae and the smaller members of the cohort at settlement, survivors of the early juvenile period were those individuals who grew faster during the first 2 weeks on the reef (Fig. 3.3B, 3.6A and B). This study found that the growth rates in the larval and early juvenile period (first 2 weeks) were inversely related ($r = -0.46$, $p < 0.001$). Interestingly, those individuals who continued to grow at a faster rate throughout the 3rd week post-settlement were preferentially lost from the cohort (Fig. 1), as shown by a significant switch over in the direction of the phenotypic selection curve (Fig. 3.6B and C).

Fig 3.5. Changes in intensity and shape of selective pressure acting on the pelagic growth of *P. amboinensis* from settlement to 6 weeks later. Thin lines are 95% confidence bands.
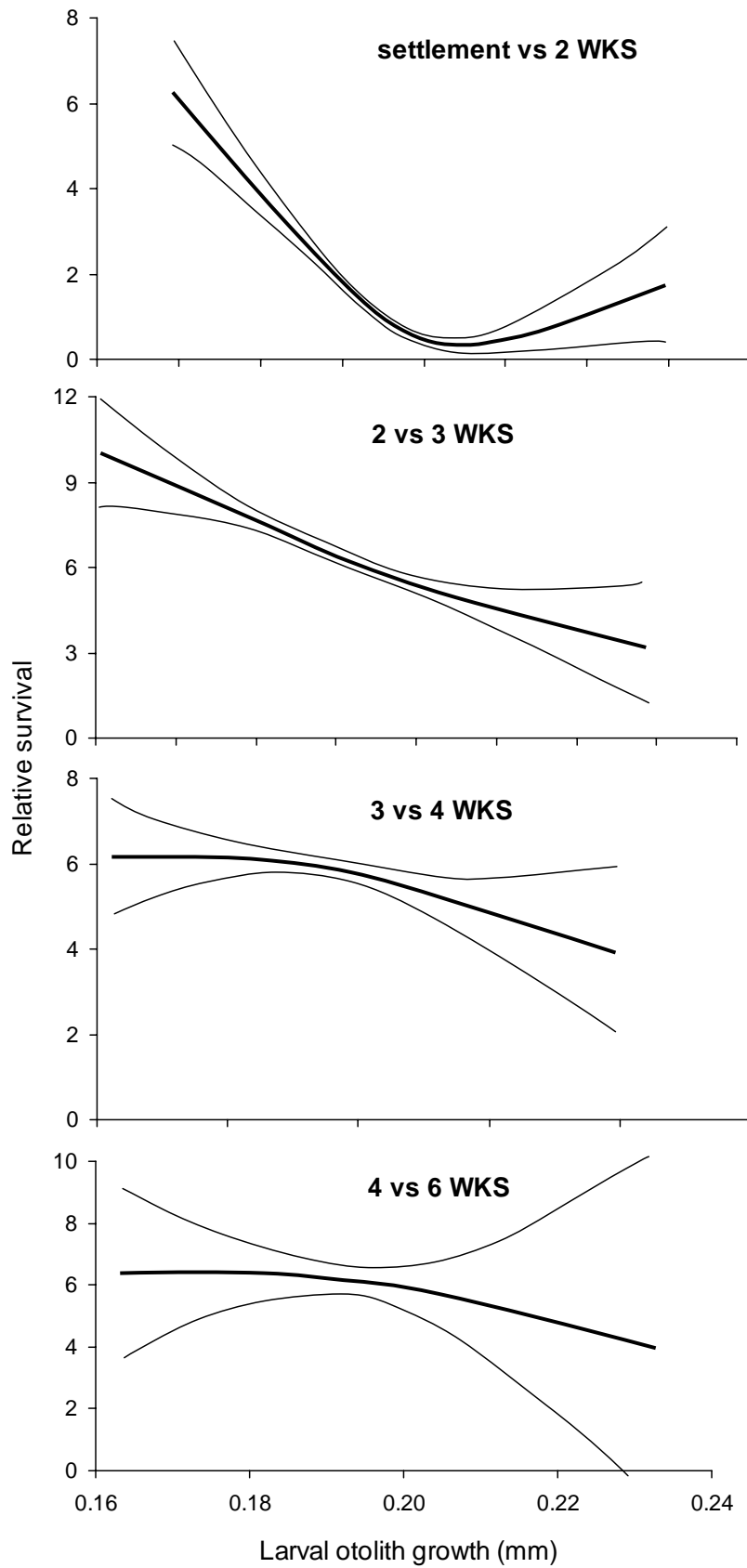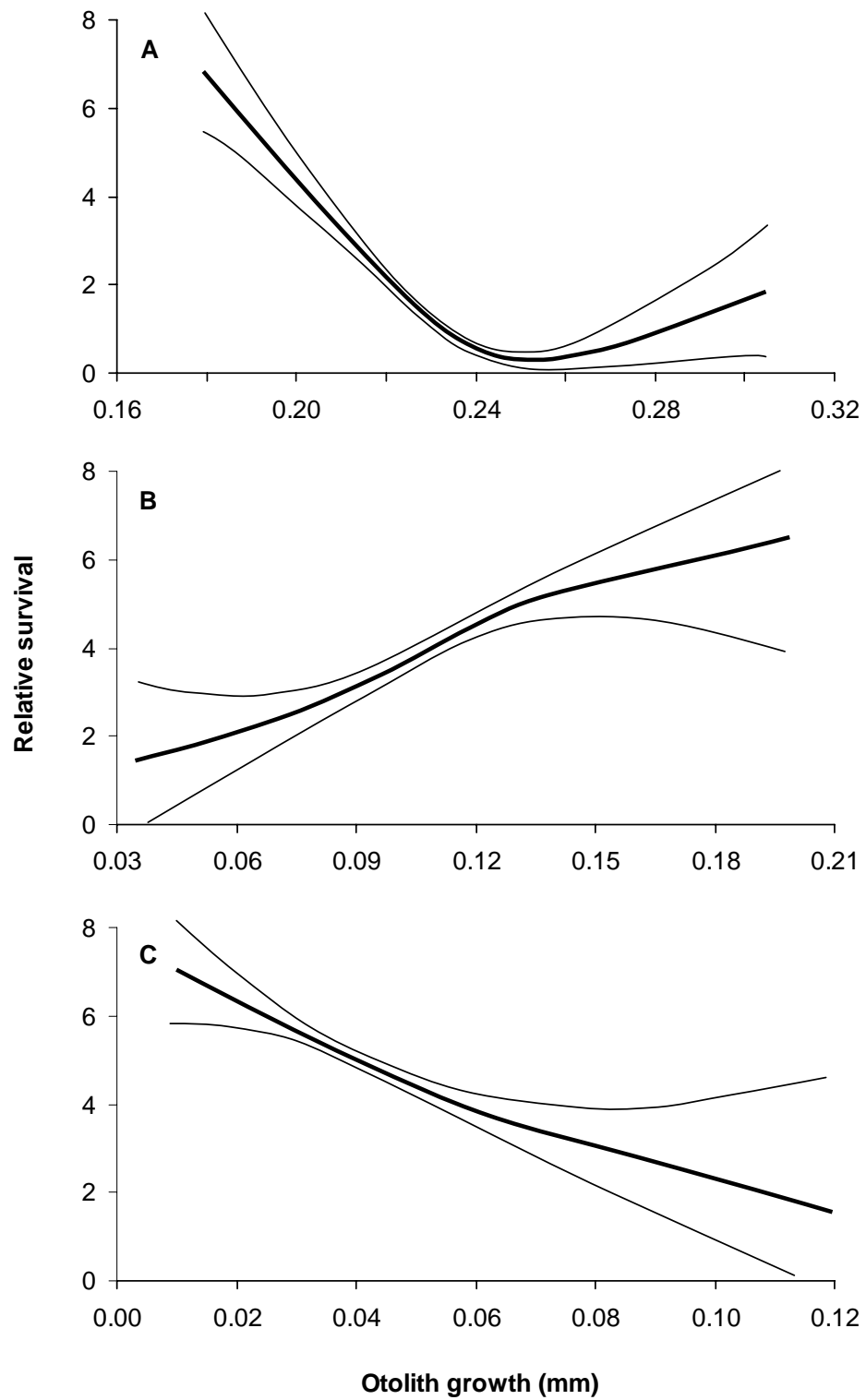
Fig 3.6. Growth-dependent relative survival of *P. amboinensis* (A) from hatching to settlement, (B) during the first 2 weeks and (C) the 3rd week post-settlement. Thin lines are 95% confidence bands.

DISCUSSION

By exploring the links between life stages of a coral reef fish, this study demonstrated how juvenile survivorship is significantly influenced by processes taking place in the pelagic environment, or even before hatching of larvae via parental effects. Specifically in this study of *P. amboinensis*, individuals surviving the intense size-selective mortality that occurred during the dispersive pelagic phase had significantly smaller otoliths at hatching. The present study found that otolith size-at-hatching closely reflected a combination of early larval characteristics (i.e. larval body size and amount of yolk reserves) and contrary to theoretical expectations (bigger-is-better hypothesis, Miller et al. 1988), there was no apparent survival disadvantages of being small at hatching, when small body size was coupled with large energy reserves. Given that both larval size and yolk-sac size are known to be directly linked to maternal condition in this species (Chapter 2; but see also Kerrigan 1997, McCormick 2003, 2006), the relationship between otolith size, larval characteristics and condition of parental stock clearly deserves further investigation. Furthermore, selective mortality of individuals with larger otoliths at hatching was also pronounced during the first 2 weeks following settlement on reef habitats, indicating that selection for this trait operated across life history stages (i.e. carry-over effect).

Pelagic larval growth was by far the most influential and long-lasting trait associated with juvenile persistence on the reef. Selective mortality based on larval growth was generally non-linear and changed form across ontogenetic stages. Given the heterogeneity of physical and biological processes inherently experienced by organisms with complex life cycles, changes in the shape and magnitude of selective mortality over time may help maintain phenotypic variation in larval growth and ultimately preserve (genetic) variation in fish populations (Swain 1992, Meekan and Fortier 1996, Hare and Cowen 1997). This could also explain why we do not see a progressive evolution towards faster larval growth

rates as one might predict based on the idea that faster-growing individuals within a cohort enjoy higher probability of survival (the growth-rate mechanism, Anderson 1988).

In contrast to the results based on pelagic larval growth, no patterns of selective mortality based on pelagic larval duration (PLD) was detected. The low variation in PLD among individuals suggests that selective mortality with respect to this trait had limited potential to occur within this cohort (*cf* Sogard 1997). There appears to be low intra-cohort variability in larval duration in this family of reef fishes (Robertson et al.. 1990) and the results from the present study combined with previous findings on other pomacentrid species (e.g. Macpherson and Raventos 2005, Hawn et al.. 2005) suggest that theoretical predictions of the stage-duration mechanism (Houde 1987) are unlikely to be applicable to this group of fishes.

Although the present study showed that larval traits strongly influenced patterns of selective mortality within this cohort weeks after settlement, juvenile characteristics also significantly shaped early survivorship of individuals on reef habitats. Specifically, smaller rather than larger initial size conferred higher survival probability to newly settled *P. amboinensis*. This result contrasts with predictions of the growth-mortality hypothesis (Anderson 1988), which proposes that faster growth at this time enhances survival through the covariation of size with behavioural, physiological and other morphological attributes that reduce potential predation and/or starvation risks. However, the present finding supports recent evidence indicating that the extent of size-selective mortality of newly settled reef fish can differ among locations separated by only 100's of metres (Holmes and McCormick 2006). This suggests that the characteristics of the predator assemblage and prevailing environmental conditions can lessen or even negate any advantage to being large at settlement.

Interestingly, survivors of the early juvenile period were those individuals who were slower-growing as larvae and smaller at settlement but grew faster during the first 2 weeks

on the reef. The present finding of an inverse relationship between growth rates in the larval and early juvenile period (first 2 weeks) is consistent with earlier laboratory studies (Bertram et al.. 1993, 1997) and recent field experiments (McCormick and Hoey 2004) in that it demonstrates that growth rates throughout the planktonic life are not necessarily maintained during the early post-settlement period. This also suggests that changes in the direction of phenotypic selection can promote the occurrence of compensatory responses during early juvenile life (see review by Ali et al.. 2003)

Faster growth during the first few days on the reef is expected to be advantageous by enabling initially smaller settlers to quickly outgrow high vulnerability to gape-limited predators (bigger-is-better hypothesis, Anderson 1988). However, we found that individuals who maintained a faster growth trajectory throughout the 3rd week post-settlement were preferentially lost from the cohort. It may be that young fish faced with intense selective pressure to grow at a faster rate during the earlier periods of benthic life had high foraging motivation (Nicieza and Metcalfe 1999) and may be willing to take potentially greater predation risk for possible gains in food resources (e.g. Biro et al.. 2004, 2005). If so, significant changes in behaviourally mediated mortality could be expected to occur over narrow time frames (Chapter 4).

Conclusion

Overall, the present analyses revealed that strong size- and growth-selective mortality generally removed the larger and faster growing members of the cohort. Larval growth during planktonic life was by far the most enduring trait influencing survivorship of young fish settled on reef habitats. The selective loss of individuals with faster larval growth observed in the present study is counter to the prediction of the growth-rate mechanism (Anderson 1988). While the theory is supported by a large number of both field and laboratory studies, there are a number of examples of studies that have found that faster

larval growth does not always confer greater survival benefits (e.g. Cowan et al.. 1996, Fuiman et al.. 2005) or detected no selective mortality based on larval growth (e.g. Searcy and Sponaugle 2001). The lack of consistency in trends of selective mortality based on larval growth may be the result of masked ontogenetic changes in the form and intensity of selectivity. While this is clearly a complicating factor to our understanding of selective processes influencing early survival of young fish, unveiling changes in selective curves over different portions of the life history may ultimately enable us to better appreciate the dynamics governing the complex life cycles of many species.

Chapter 4

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

4.1 Introduction

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 (e.g. 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 trade-off 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 trade-off 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 (e.g. 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 (Chapter 3, but see also Bertram et al. 1993, McCormick and Hoey 2004). Variation in growth during early life history is largely a reflection of parental contributions and environmental factors, such as temperature (Green and McCormick 2005b) 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 (Chapter 3, but see also Carlson et al. 2004) 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 age and growth (Campana and Stevenson 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). This study uses 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. It compares size at 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. The aims of this study 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.

4.2 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. 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, a 500 m section of reef was searched for newly settled individuals and 900 recruits were tagged *in situ*. Fish could be identified as newly settled from their size and coloration (Fig 4.1a, see also 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 (Fig 4.1b). 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 in press). After 30 days post-settlement all surviving tagged individuals (n=34) were collected from the reef.

Fig 4.1. (*a*) Newly settled *P. amboinensis*, (*b*) underwater tagging of newly settled individuals with an elastomer tattoo and (*c*) retention of the fluorescent subcutaneous tag in an individual recaptured a month later.

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 (e.g. 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 the radii of transverse sections of sagittal otoliths from the nucleus to the settlement mark of the survivors of the November settlement pulse 30d after tagging (n = 34) were compared with those of a random sample of newly metamorphosed fish caught in light traps (see Meekan et al. 2001 for trap design) 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 60 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) supplied with a constant flow of seawater. Aquaria were held outdoors, ensuring that temperature (29 ± 0.3 ºC), salinity (34 ± 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 3rd d. 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 3rd d 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.
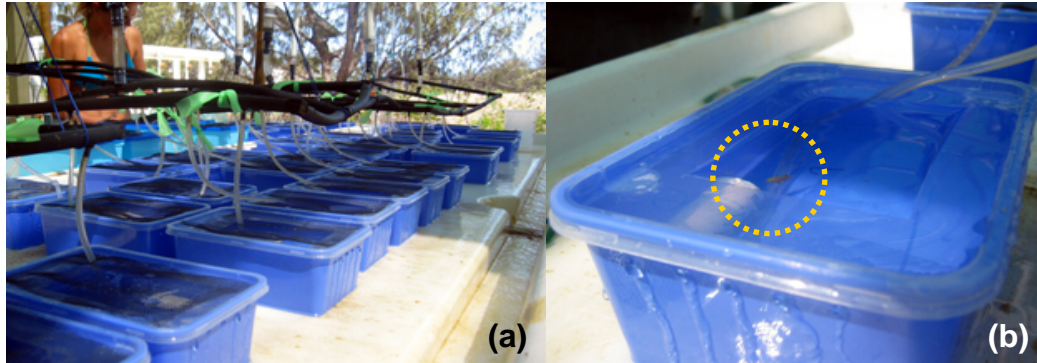
Fig 4.2. (*a*) Outdoor aquaria set up for the experimental feeding groups. (*b*) Each blue aquarium hosted an individual fish (in the yellow circle).

Otolith shape and growth

To quantify the 2-dimensional shapes of both left and right sagittal otoliths, this study 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 6 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 ™), ground and polished using 12 to 0.3 µm lapping films (see Wilson and McCormick 1997). Increment widths were examined at 400x magnification and measured along the longest axis of the otolith using a video image-analysis system linked to a compound microscope.

Analyses

Otolith analysis was used to compare the age and size of fish in the initial cohort with those of individuals that survived 30 d after settlement. Age at settlement was estimated 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*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, a one-way ANOVA was used 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. This study also examined growth patterns at the end of the experiment (30d) by comparing body size (SL, mm) of survivors to fish fed *ad libitum* and fish fed every 3rd day using one-way ANOVAs.

The shape of each otolith pair of fish fed *ad libitum*, fish fed every 3rd and survivors were compared using the first 20 standardised harmonics in a multivariate environment. 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 30d experimental period was divided into 10 d intervals beginning from the settlement mark. The otolith growth profiles of fish fed *ad libitum*, fish fed every 3rd day and survivors collected from the reef over each of these growth periods were compared using repeated measures MANOVA and ANOVA (Chambers and Miller 1994). The otolith growth profiles were based on the mean otolith radius (µm) at age and mean otolith growth rate (µm d^{-1}). The former measured the distance of each increment from the settlement mark, to provide information on the cumulative growth (size at age); the latter measured the width of adjacent increments after the settlement mark for an estimate of the daily otolith growth.

4.3 Results

Size selectivity of natural mortality

This study found that 1-month old juveniles recaptured from the reef had settled at similar ages to recruits 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 4.3).
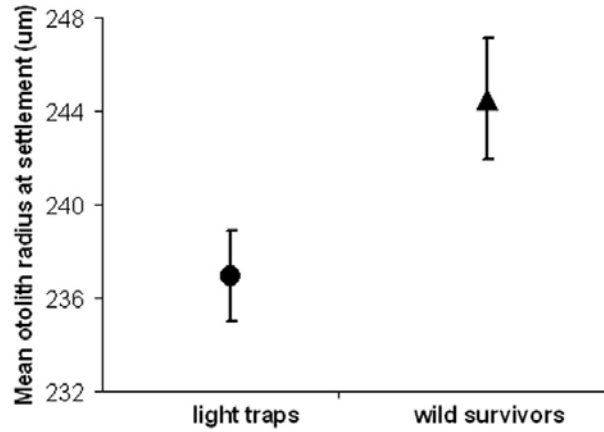
Fig 4.3. Comparisons of mean otolith radius at settlement (μm ± SE) of *P. amboinensis* collected by light traps (●) and individuals surviving the first month after settlement on the reef (▲). Otolith radius was used as a proxy for size at settlement.

Morphology

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 the largest (wild > fed *ad libitum* > fed every 3rd d, Fig 4.4).
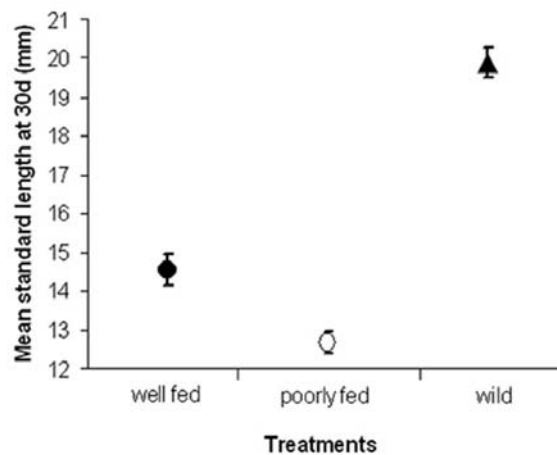
Fig 4.4. Comparison of mean standard length (mm ± SE) of fish from the three treatments 30 d after settlement: wild survivors (▲) and well fed (fed *ad libitum*, ●) and poorly fed (fed every 3rd day, ○).

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 4.5).

Fig 4.5. 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 3rd 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).

Although wild fish were located well away from both laboratory groups along canonical variate 1, they occupied a similar position to fish fed every 3rd d along the second variate. The arrangement of the 3 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 3 groups by the analysis was

mostly driven by differences in the shape of the otoliths, represented by low-order harmonics (Fig 4.5 and 4.6). Results of the jack-knifed cross-validation tests indicated high rates (79%) of classification success among groups.

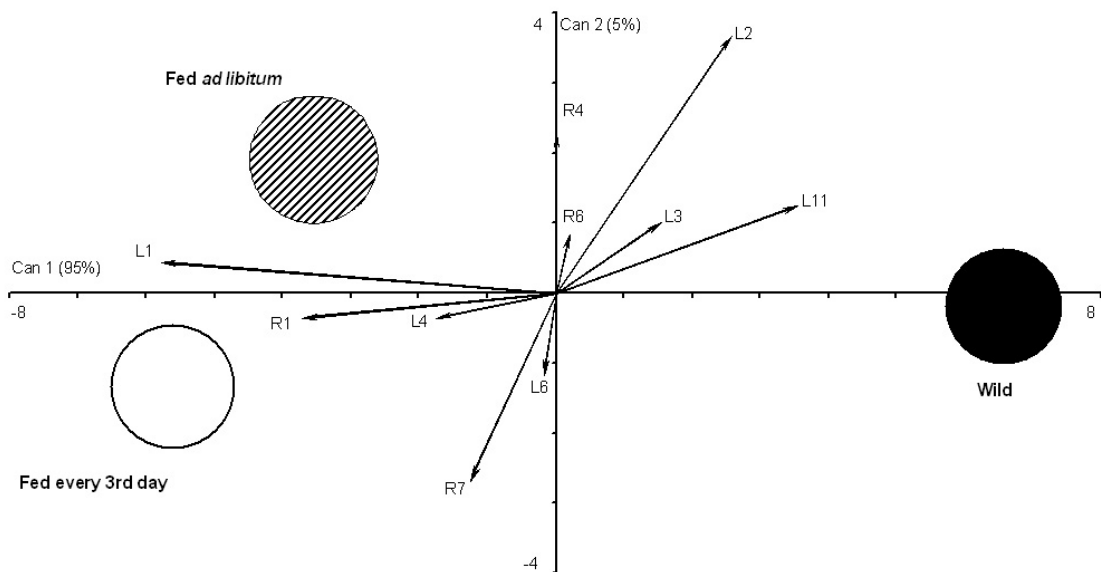**Fig 4.6.** Otolith shape of *P. amboinensis* (*a*) surviving the initial 30 d following settlement on the reef and individuals from the same cohort (*b*) fed every 3rd day and (*c*) fed *ad libitum* over the same 30 d period.

Otolith growth profiles

Otolith growth profiles differed significantly among survivors and experimental fish (Table 4.1). The mean otolith radius of survivors over the first 10 d after settlement closely resembled the profile of fish fed every 3rd d in the laboratory (Fig 4.7) and then changed trajectory during from11-21 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 3rd d during the first 10 d of benthic life.

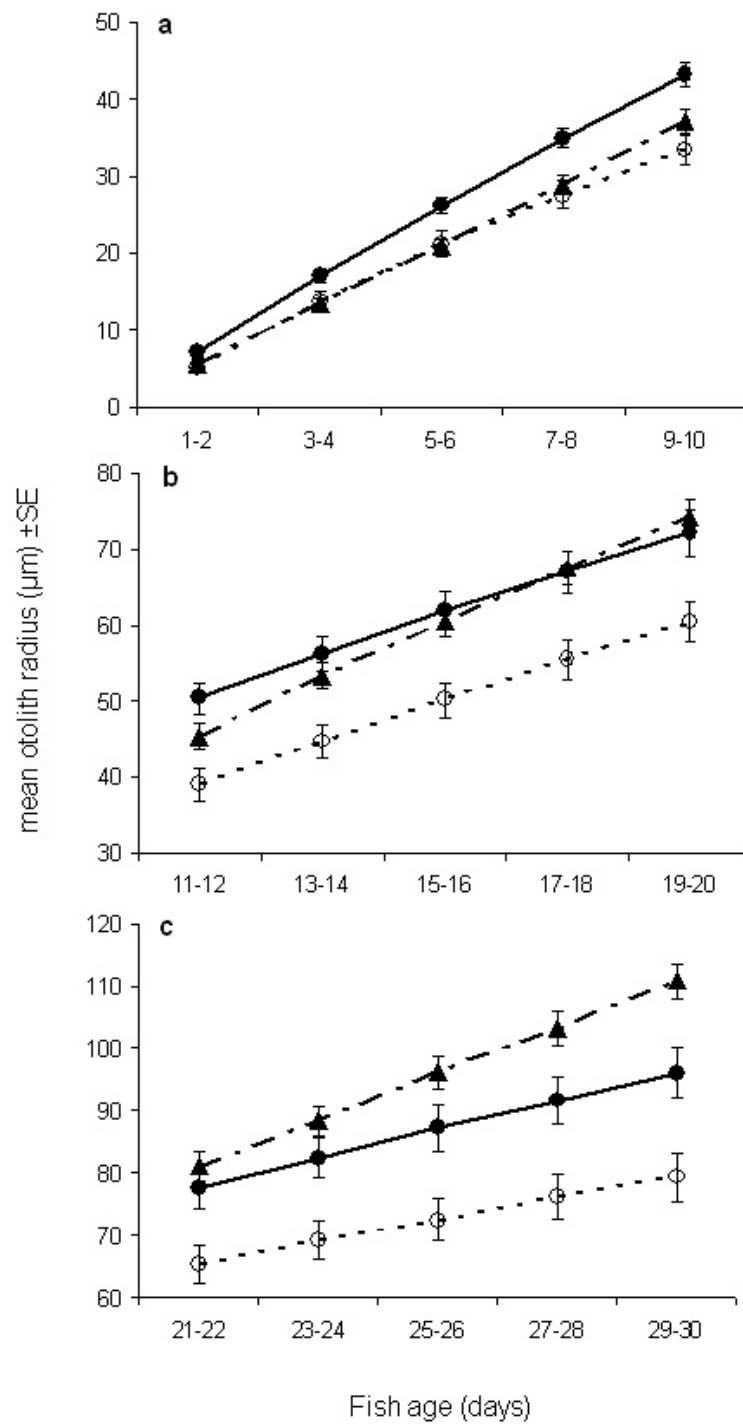**Fig 4.7.** Comparison of mean otolith radius (µm ± SE) at age of wild survivors (▲) and conspecifics fed *ad libitum* (●) and fed every 3rd day (O) from settlement to 10 d after settlement (a), 11 to 20 d after settlement (b), and 21 to 30 d after settlement (c).

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Table 4.1. 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 (mm d^{-1}) of the 3 fish groups (fed *ad libitum*, fed every 3rd 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.		df_{effect}	df_{error}	Pillai's	F	p	**b.**		df	MS	F	p
i	Radius at age	9	19	0.980	131.064	**≤0.0001**	i	Groups	2	0.001	3.859	**0.034**
	Radius at age*Groups	18	40	0.973	2.107	**0.025**		Error	27	0.001		
	Daily growth	9	19	0.287	0.850	0.581		Groups	2	0.001	3.798	**0.035**
	Daily growth*Groups	18	40	0.690	1.171	0.328		Error	27	0.001		
ii	Radius at age	9	19	0.983	120.680	**≤0.0001**	ii	Groups	2	0.004	3.680	**0.037**
	Radius at age*Groups	18	40	1.060	2.507	**0.008**		Error	27	0.001		
	Daily growth	9	19	0.595	3.104	**0.018**		Groups	2	0.001	7.284	**0.003**
	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	**≤0.0001**	iii	Groups	2	0.013	5.701	**0.009**
	Radius at age*Groups	18	34	1.061	2.135	**0.028**		Error	24	0.002		
	Daily growth	9	16	0.462	1.524	0.221		Groups	2	0.001	25.363	**≤0.0001**
	Daily growth*groups	18	34	0.788	1.229	0.294		Error	24	0.001		

Mean otolith growth rates (μm 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 4.1ai, bi). Fish fed *ad libitum* initially grew faster than the survivors or intermittent feeding treatment (Fig 4.8a). Differences growth among the groups declined from 11-20 d, with survivors having the highest growth rates at this time (Fig 4.8b; Table 4.1aii, bii). By 30 d, all groups had different growth rates with survivors having the highest rate in mean otolith growth (survivors > fed *ad libitum* > fed every 3rd d, Fig 4.8c).
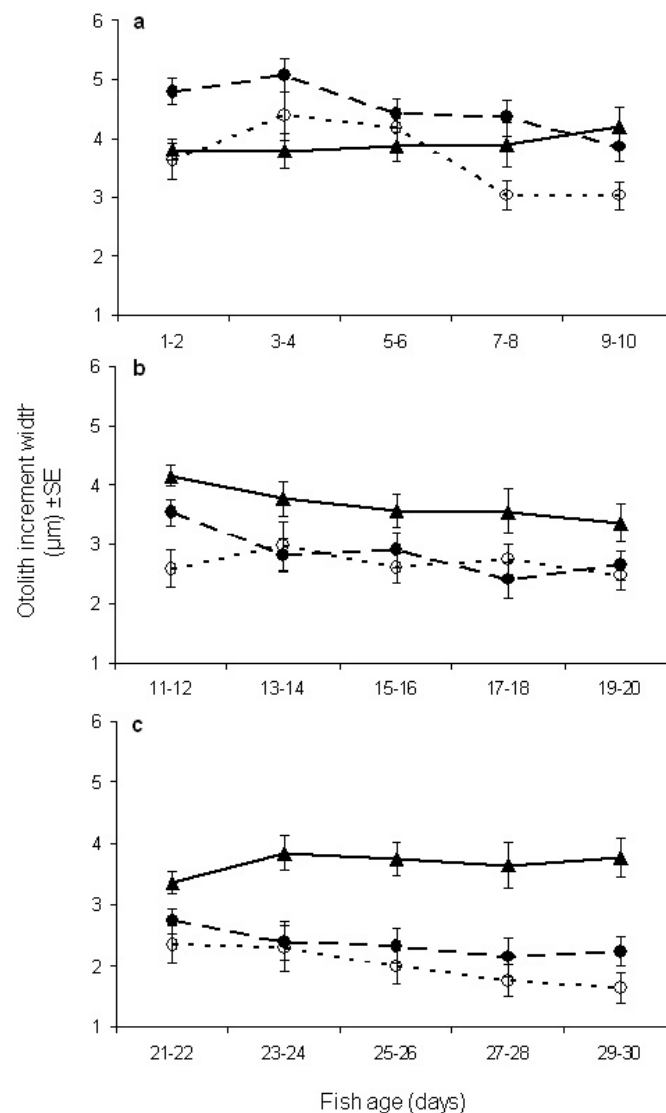

Fig 4.8. Average otolith growth rate (μm d^{-1} ± SE) of wild survivors (▲) and conspecifics fed *ad libitum* (●) and fed every 3rd day (O) from settlement to 10 d after settlement (a), 11 to 20 d after settlement (b), and 21 to 30 d after settlement (c).

4.4 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 (in press) 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 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, personal 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 30d 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 Spounagle 2001). McCormick and Hoey (2004) have recently shown that mortality of *P. amboinensis* could be directed toward smaller individuals within the first 9d 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 (Wilson and

McCormick 1999), 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 (e.g. 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 the present study, individuals that adapt to the local predation climate 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 30d 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.

In this study, extremely high mortality of young fish was observed over a relatively short period (i.e. 30d) and survivors were found to have a slow start and steep growth trajectory. This finding indicates that growth rates can be under very strong phenotypic selection immediately after settlement (Chapter 3) 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.

Conclusions

This study has 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 behavioural naivety. Nevertheless, they are capable of very fast growth once they have worked out how to exploit the appropriate resources. This study has demonstrated the occurrence and ecological relevance of size-selective and developmental processes that contribute to the observed patterns of growth and survivorship. It has 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). The present 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.

The idea that events during early development can have a marked effect on survival and reproductive success later in life, although intuitively difficult to accept at first has rapidly become a central concept to our understanding of life history evolution and population dynamics (e.g. Sedinger et al. 1995, Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002, Cam et al. 2003, Bateson 2005, van de Pol et al. 2006). By exploring the role of early condition in the life of a coral reef fish, the present study found that environmental differences experienced early in life, whether arising from differences in parental or environmental quality, can not only have immediate consequences for survival, but also profoundly influence life-history trajectories later in life.

Environment conditions and parental quality

Environmental conditions, in particular rearing temperature, were found to have a strong effect on the relative number of *Pomacentrus amboinensis* embryos that successfully hatch and their survival duration (Chapter 1). Besides generating a marked reduction in the variability of phenotypic characteristics of individuals, water temperature during early growth and development of *P. amboinensis* embryos caused significant changes in metabolic processes. Elevated temperature was found to directly alter processes associated with yolk protein metabolism during the embryonic phase and also affect individual larval performance and viability through higher heart rates. Similar patterns of plasticity in the expression of metabolic activity and the profound effects of temperature on an individual's developmental physiology are common (see *metabolic theory*, Brown et al. 2004). While temperature is undoubtedly a major agent driving the large variation in traits during the early life history of fish, its significance in shaping developmental plasticity has

only recently been rediscovered in the context of ecological developmental biology or 'eco-devo' (*sensu* Gilbert and Bolker 2003, Sultan 2003).

The renewed interest in the developmental and ecological mechanisms that regulate the dynamics of natural populations has re-emerged partly due to the current global environmental deterioration, particularly climate change. For example, failure to take into account the temperature-dependent developmental processes influencing phenotypic variation during early ontogeny can have considerable implications for our conservation efforts (e.g. sea turtles, Morreale et al. 1982). While the importance of the vulnerability and quality of early life stages to the success and survival of later life phases has long been recognized in marine fish populations (Hjort 1914), research efforts have largely focused on cold-water fish taxa. In tropical systems, species experience much smaller ranges of seasonal change and interannual fluctuations in climate, and thus may be less tolerant to environmental variability than their temperate counterparts (Ebeling and Hixon 1991). Findings from the present study emphasize the importance of understanding the processes regulating variability in recruitment success of marine fishes in tropical systems.

By examining temperature-induced shifts in selective mortality in *P. amboinensis*, the results of this study highlighted the potentially devastating effects of climatic change on the developmental quality and viability of the early life stages of tropical fishes. Unfortunately, patterns of temperature-mediated plasticity are complex and their importance in shaping adaptive responses at the population level remains difficult to predict (Stillwell and Fox 2005). To quantify the long-term consequences of different thermal environments on the developmental physiology of individuals and their offspring, there is need for studies that explore the role of temperature-induced phenotypic variation in marine fish populations. Ultimately, this information may assist us in predicting the consequences of environmental change for these populations.

Rearing conditions under which offspring develop are to some extent under parental control. In both plants and animals, parents often alter the rearing environment of their offspring in a way that alleviates the negative effects of unfavourable environmental conditions, thereby increasing offspring survival and fitness later in life (i.e. *parental care behaviours*, Clutton-Brock 1991). Examples in which parental care has been examined in plants include: *Plantago* plants that thermoregulate reproduction and embryonic development of their offspring (seeds) by altering the amount of reflected light (Lacey and Herr 2005), and *Ranunculus* flowers that promote pollen quality and performance by closely tracking the sun's rays (i.e. *heliotropism*, Galen and Stanton 2003). In several fish species, parental activities such as nest building, cleaning, fanning, brooding, guarding and even cannibalising their own eggs have been shown to at least partly mitigate the negative repercussions of unusually stressful physical environments (e.g. Payne et al. 2002, Green and McCormick 2005a, Kolm and Ahnesjö 2005). Since offspring are often unable to leave unfavourable environments (e.g. adverse thermal conditions), parental care behaviours are pivotal to enhancing embryonic survival and hatchling phenotype (reviewed in Mousseau and Fox 1998).

Patterns of parental care depend on the balance between the benefits to one generation and the costs paid by the other (i.e. *Williams's principle*, see Gross 2005). While parenting can increase offspring growth and survival, care behaviours entail high energy expenditure and can result in substantial fitness costs to care-giving parents (Clutton-Brock 1991). The optimal solution to this cost-benefit relationship, which underlies the conflict between parents and their offspring (Trivers 1974) ultimately, depends on the past and current state of the parents themselves (e.g. Ridgway and Shuter 1994, Ng and Wilbur 1995, McNamara and Houston 1996, Qvarnström 1999). Indeed long before spawning, a variety of parental phenotypic traits, such as maternal physiological condition, interact to *directly* mould offspring phenotype and *indirectly* (through the intercorrelated effects of

parental environmental and physiological state on care behaviours) influence offspring survival.

In this study, maternal condition prior to oviposition was manipulated by altering food availability, a key factor influencing maternal energy allocation to offspring (e.g. Bateson et al. 2004, Mousseau and Fox 1998 and references therein). Maternal condition at the time of gametogenesis was found to have no effect on the relative number of *P. amboinensis* that successfully completed the embryonic phase and survived to a given time after hatching (Chapter 2). However, maternal nutritional state was found to affect offspring quality by causing significant changes in individual egg composition (i.e. yolk-sac and oil globule size) and thus, the energetic value of embryos and hatchlings. By acquiring additional nutritional resources, thereby increasing the amount of energy available for reproduction, supplemented mothers gained a fitness advantage over fish feeding on natural levels of plankton. Most importantly, however, they passed this advantage on to their offspring by producing eggs that were 10% richer in yolk reserves and had larger oil globules than non-supplemented fish (see also Kerrigan 1997, McCormick 2003). Furthermore, differences in egg quality influenced which individual offspring had a better chance of surviving the transition from embryonic to larval stages and success thereafter (i.e. *silver spoon effect*, Grafen 1988; Chapter 3).

Interestingly while egg size is generally used as a proxy for offspring quality and thus maternal investment (see examples in Chambers and Trippel 1997), this study was unable to detect effects of maternal condition on egg size or any inherent effect of this trait on offspring survival. Regardless of their physiological condition, *P. amboinensis* females were found to produce a broad range of egg sizes, presumably using size variation to spread the mortality risk of offspring in case unfavourable environments were encountered throughout development (i.e. *bet-hedging*, Philippi and Seger 1989). The high variability in egg size observed within and among maternal conditions in this study was by no means an

exceptional case for fish (see Koops et al. 2003). However by examining the fitness (survival) value of egg size at the individual level rather than at the population (mean) level, what this study shows is that egg size *per se* does not necessarily reflect maternal quality (Chapter 2) and is not an appropriate measure of offspring fitness under many circumstances (Chapter 1).

The condition of parents prior to gametogenesis and the quality of their provisioning to offspring may be a defining feature enhancing offspring fitness and survivorship. However, the present finding does not exclude that offspring fitness may be size-dependent and that an initial size advantage (e.g. larger eggs) is likely to account for an increase in growth and survival later in life (Miller et al. 1988, Houde 1989, Pepin and Miller 1993). For example, parents may be able to differentiate the developmental status of their eggs and promote offspring fitness by affecting their size before they hatch via nest-tending activities (as recently shown in salamanders, Crespi and Lessing 2004, Forester et al. 2005). Moreover, size differences at the egg stage may influence survival through competitive interactions among siblings and non-siblings from nearby clutches belonging to the same cohort. These are two exciting venues where size-related advantages could be tested. From this point of view, there is clearly huge scope for future research on the fitness value of egg size and the importance of initial size variation to individual survival later in life in wild populations.

Carry-over effects in wild populations

The importance of the long-lasting demographic consequences of phenotypic variation induced early in life has received growing recognition both at the individual and the population level of many organisms (e.g. Pechenik et al. 1998, Lindström 1999, Madsen and Shine 2000, Lummaa and Clutton-Brock 2002, Beckerman et al. 2002, De Roos et al. 2003, Reid et al. 2003, van de Pol et al. 2006, Taborsky 2006). Unfortunately in

tropical marine fishes, we have a relatively limited understanding of the extent to which parental and environmental factors generate much of the variation in life history traits and the consequences of such variation in the wild. By exploring the links between life stages of *P. amboinensis*, this study showed for one cohort that the survival of this coral reef fish weeks after settlement in reef habitats was strongly influenced by conditions experienced during early development (i.e. *carry-over effects*, Chapter 3). Individual variation in both condition at hatching induced through maternal effects and larval growth resulting from environmental conditions encountered during the planktonic phase played a significant role in determining which individuals survived through to settlement and persisted on the reef. While several authors have previously pointed out that parental effects in general, or maternal inputs in particular, are likely to have a considerable influence on larval and juvenile survivorship of coral reef fishes (e.g. Vigliola and Meekan 2002, McCormick 2003); the exciting findings arising from the present study substantiate the relevance of this relationship to survival in the wild.

While environmental conditions the individual itself (Chapter 1), or its parents (Chapter 2) experienced in the past, strongly moulded the characteristics of *P. amboinensis* surviving through settlement and thereafter (Chapter 3), present conditions experienced by new recruits on the reef environment were also found to considerably shape the observed patterns of juvenile survival (Chapter 3 and 4). For example, size at settlement and rates of early juvenile growth were found to have immediate consequences for survival. Size-dependent behavioural interactions and physiological processes can rapidly define the partitioning of available resources (e.g. food), thereby influencing individual growth rates and ultimately juvenile performance (Chapter 4). If so, to what extent are growth trajectories established in the past really relevant to the present? It depends. This study, together with earlier laboratory (Bertram et al. 1993, 1997) and recent field findings (McCormick and Hoey 2004), suggested that trajectories established throughout the larval

phase may not always be maintained during the juvenile phase. The direction of selective pressures on a trait such as growth rate was found to change rapidly over relatively short times, particularly during the initial few weeks after settlement (Chapter 3). However, data also suggested that the direction of phenotypic selection acting on a trait such as size was conserved from hatching through to weeks post-settlement. By illustrating how different selective pressures operate simultaneously on different aspects of the phenotype (and presumably preserving phenotypic variation), the present finding emphasizes the importance of a multivariate approach to studies of phenotypic selection and its role in regulating natural populations.

Concluding remarks

The study of the early life history of reef fishes (historically considered as a 'black box') and the links operating between individuals of different generations continues to be logistically challenging. By combining field manipulations and controlled laboratory experiments, this study has examined the nature of phenotypic selection occurring during the early life of *P. amboinensis* and highlighted strong links between offspring survival, current environmental conditions and variation in the parental environment. Energy-driven selective mechanisms appear to be important in influencing offspring viability and success later in life. Offspring provisioning rather than size alone may be a functional variable upon which phenotypic selection operates to shape survival patterns of this coral reef fish. While it is well established that a privileged upbringing can significantly define an individual's success in life, the causes and consequences of variation remain largely unappreciated by researchers, particularly in marine organisms. Moreover, the possibility that the impact of events occurring early in life may be transmitted across multiple generations, leading to long-term effects on population dynamics (e.g. Hercus and Hoffman 2000, Beckerman et al. 2002, Benton et al. 2005) is extremely attractive, but nevertheless

remains unexplored in marine populations. In fish, otoliths have already proven to be excellent age and growth data-loggers. Together with the functional and physiological information held within these structures, we have an unprecedented opportunity to explore the links between events and really tell the whole story of a fish life. Our ability to keep track of events shaping the life history of individuals appears to be pivotal to our success in understanding the processes regulating natural populations and predicting their responses to a rapidly changing environment. It seems that the devil may really to be in the details of individual life histories

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Appendix A. Publications arising from thesis

Gagliano, M., McCormick M.I. and M.G. Meekan. In press. Temperature-induced shifts in selective pressure at a critical developmental transition. Oecologia

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