

Temperature-induced shifts in selective pressure at a critical developmental transition

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Abstract Selective mortality within a population, based on the phenotype of individuals, is the foundation of the theory of natural selection. We examined temperature-induced shifts in the relationships among early life history traits and survivorship over the embryonic and larval stages of a tropical damselfish, *Pomacentrus amboinensis*. Our experiments show that temperature determines the intensity of selective mortality, and that this changes with ontogeny. The size of energy stores determined survival through to hatching, after which egg size became a good indicator of fitness as predicted by theoretical models. Yet, the benefits associated with egg size were not uniform among test temperatures. Initial egg size positively influenced larval survival at control temperature (29 °C). However, this embryonic trait had no effect on post-hatching longevity of individuals reared at the higher (31 °C) and lower (25 °C) end of the temperature range. Overall, our findings indicate that the outcome of selective mortality is strongly dependent on the interaction between environment conditions and intrinsic developmental schedules.

Keywords Bigger is better hypothesis · Early life history traits · Egg size · Selective mortality · Coral reef fish

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 are generally poorly developed, relatively small and limited in their ability to avoid predation at birth, and they often experience 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 a fish, 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 for ectotherm ontogeny because of its pervasive effects on

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biological rate processes, altering nearly all physiological functions (Johnston and Bennett 1996). In cross-taxonomic 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. Yet, patterns of temperature-mediated plasticity are complex and their importance in shaping adaptive responses at the population level of many organisms remains difficult to predict (Stillwell and Fox 2005).

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 of fishes, and variation in this trait and its consequences for survival have been documented extensively, particularly in temperate systems (e.g. Chambers et al. 1989; Bernardo 1996; Johnston and Leggett 2002). Larger eggs appear to confer higher survival to offspring than smaller ones, because they commonly generate larger larvae at hatching (e.g. McGurk 1986). Ultimately, larger larvae are expected to be better at food capture, 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 also evidence that does not support it (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. We therefore set out to experimentally

test the generality of the “bigger is better” hypothesis by investigating the interrelationships of life history traits at the individual level for a tropical damselfish (*Pomacentrus amboinensis*), from fertilization to the exhaustion of endogenous nutritional reserves. We 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 studying the factors influencing trait interrelationships because the species displays considerable variation in a number of early life history traits (McCormick 1999).

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 (14° 40' S, 145° 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 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 six-well tissue culture plates. Plates were placed in perforated seawater baths and submerged (~4 cm deep) with a surface flow of aerated seawater ($3 \pm 0.4 \text{ l h}^{-1}$) to maintain high oxygen levels around the negatively buoyant eggs and to 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 three temperature treatments (25, 29 and 31 °C) to account for the potential effect of variability among clutches. Embryos were maintained individually throughout the study and allowed to develop in isolation at the three different temperatures in two replicate plates. The 29 °C 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 31 °C temperature groups were referred to as the cold and hot treatments 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.

Embryonic traits and survival

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 three temperature treatments were monitored during their development at 36 and 84 h post-fertilization (hpf). Key criteria used 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 *arteria 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 three incubation temperatures.

The dorsal side of each individual embryo was photographed under a compound microscope (10× magnification) at 36 and 84 hpf, and egg size (maximum egg length, mm), yolk-sac size (yolk-sac area, mm²) and oil globule size (oil globule area, mm²) were measured from these calibrated digital images using the image analysis programme OPTIMAS 6.5 (OPTIMAS Corporation). Heart rates (heart beats/min) were measured by three replicated 1-min counts of heart beats at 84 hpf and used as a proxy for metabolism. Pre-hatching mortality and time of hatching were recorded. Following hatching, unfed larvae were inspected every 12 h until death as a measure of post-hatching longevity based only on pre-existing reserves. Individual differences in post-hatching longevity were measured as a realistic representation of relative differences in time available (and opportunity) to encounter suitable food before irreversible starvation in the wild. Limited food availability may be a realistic condition in the pelagic environment of tropical waters, as food availability is notoriously limited and patchy at both temporal and spatial scales and starvation is implicated as one of the major sources of mortality in fish larvae (Kerrihan 1997).

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 (ANOVA), with time (number of hours at death) as the within-subjects factor and temperature treatments (25, 29 and 31 °C), 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 is 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 embryonic characteristic 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 for 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.

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 (31 °C), 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 in the high temperature treatment was also significantly reduced with hatchlings surviving no longer than 36 h. Embryos developing at 25 and 29 °C 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 25 °C. 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 25 °C 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). No selective mortality based on yolk-sac area was detected for embryos reared at 25 and 29 °C. The effect of yolk-sac size on survivorship disappeared after hatching. Initial egg size and heart rate affected post-hatching longevity at specific temperatures (egg size at 29 °C: $F_{(2,114)} = 3.375$, $P < 0.001$; heart rate at 31 °C: $F_{(2,114)} = 2.230$, $P < 0.05$, Fig. 2). 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. However, no significant correlation was observed between the two traits (25 °C group: $r = -0.065$, $P = 0.714$; 29 °C group: $r = 0.005$, $P = 0.969$; 31 °C group: $r = 0.336$, $P = 0.118$), and phenotypic selection gradients indicated that selective mortality operating on initial egg size was intense on individuals in the 29 °C group exclusively, while selective pressure against individuals that had a low heart rate at 84 hpf was only experienced by larvae in the 31 °C group. No selective mortality was observed in individuals kept at 25 °C (Table 1).

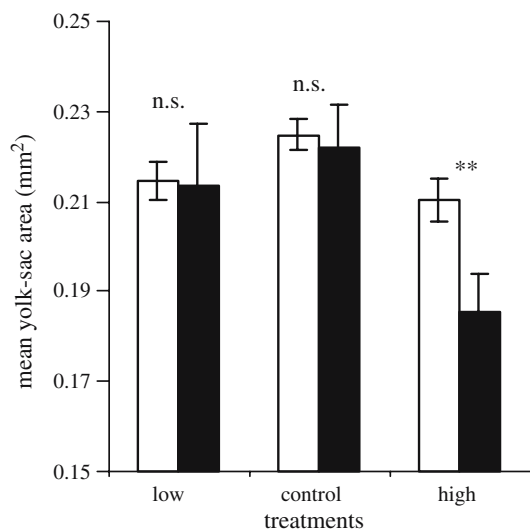


Fig. 1 Mean yolk-sac area (mm^2) of *P. amboinensis* embryos that died before hatching (black bars) and embryos that survived to hatch (white bars) at low (25 °C), control (29 °C) and high (31 °C) incubation temperature. Error bars are 95% confidence intervals. n.s. no significant difference; **significant difference at $\alpha = 0.025$

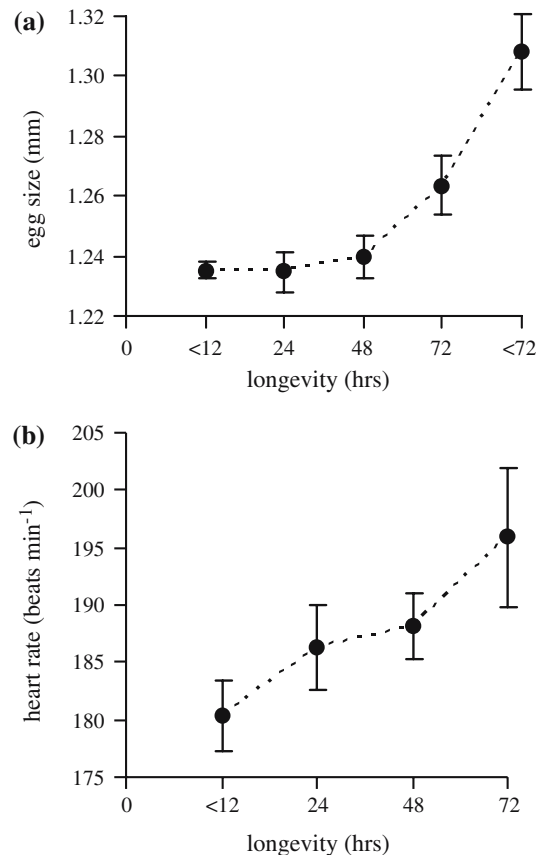


Fig. 2a–b Longevity of larval *P. amboinensis* in relation to (a) initial egg size (mm) at 29 °C and (b) heart rate (beats min^{-1}) at 31 °C recorded at approximately 84 h post-fertilization. Error bars are 95% confidence intervals

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 during 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 had no significant effect on initial survival for embryos reared at control or lower temperatures. This suggests that whether phenotypic selection alters the distribution of

Table 1 Phenotypic selection gradients ($\beta \pm \text{SE}$) for initial egg size (maximum egg length, mm) and metabolic rate (heart beats per min), using post-hatching longevity of *P. amboinensis* larvae from three temperature groups as a measure of fitness

	Post-hatching longevity			<i>P</i>
	$\beta \pm \text{SE}$	$\beta' \pm \text{SE}$	r^2	
Low temperature (25 °C)				
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 (29 °C)				
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 (31 °C)				
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

Temperature groups (25, 29 and 31 °C) 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

this trait or not depends on the environmental conditions to which individuals are exposed (Lynch and Gabriel 1987). Given that the yolk sac contains the only nutritional reserves available to the embryo for its development, embryos with larger yolk sacs 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 of 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, we observed no ramifications of yolk-sac size on embryonic success to hatching 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. During the embryonic phase the yolk sac serves as a primary nutrient reserve and the delivery rate of such nutrients through the circulatory system is determined by variable developmental rhythms and periodic 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 could not be 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 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 envelope by enzymatic action occurs more quickly (Yamagami 1988), heart rate increases further and embryonic movements become more rapid (Klinkhardt et al. 1987). The present findings suggest that slow heart rate may be an indicator of reduced physiological viability. In contrast, individuals with higher metabolism may be more efficient at 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 favours larger egg size over a wide range of taxa (reviewed by Roff 1992), the present experiment found that initial egg size positively influenced larval survival only at

ambient temperatures. In a recent study, Gagliano and McCormick (2007) showed that *P. amboinensis* females produce a broad range of egg sizes within and among clutches, and this may be a means of spreading the mortality risk of offspring in case unfavourable environmental conditions are encountered throughout development (i.e. bet-hedging, Philippi and Seger 1989). While there is little doubt that propagule size is correlated with offspring fitness, the present study showed that the magnitudes of size-related effects on longevity depend strongly on the thermal environment. We 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. Some characteristics of the offspring environment can directly influence the optimal egg size in fish (Hutchings 1991; Einum and Fleming 1999, 2002), suggesting that temperature-induced shifts in trait optima 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 large egg size.

This study has demonstrated that environmental conditions under which *P. amboinensis* embryos develop and hatch have a great influence on their post-hatching life. Besides generating a marked reduction in the variability of phenotypic characteristics of individuals, water temperature during early development of *P. amboinensis* embryos caused significant changes in metabolic processes. In particular, elevated temperature was found to directly alter processes associated with yolk protein metabolism during the embryonic phase and also to affect individual larval viability through higher heart rates. While the present results may only be applicable to this particular set of environmental parameters, similar patterns of plasticity in the expression of metabolic activity are common, and the profound effects of temperature on an individual's developmental physiology are widespread (see metabolic theory, Brown et al. 2004).

Although the current experiment cannot distinguish between behavioural choices of parents to maximize maternal fitness and those that may maximize offspring fitness, several lines of reasoning suggest some form of adaptation to local environmental conditions that maximizes embryonic survival rates. Nonetheless, the conditions under which embryonic development occurs are ultimately dependent on parental choice. The

capacity of parents to alter their environment in a way that alleviates the negative effects of unfavourable environmental conditions may also increase offspring survival and fitness later in life (Clutton-Brock 1991). In several fish species, parental activities such as nest building, cleaning, fanning, brooding, guarding, and even cannibalizing 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 2005; Kolm and Ahnesjö 2005). Since offspring within demersal eggs are unable to leave unfavourable environments (e.g. adverse thermal conditions), parental care behavior is pivotal to enhancing embryonic survival and hatchling phenotype (reviewed in Mousseau and Fox 1998). The present study emphasises the complexity of combined parental and environmental effects that ultimately shape the variability and magnitude of larval supply to reef environments.

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