

Carry-over effects - the importance of a good start

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Abstract. Every organism has a history and its past experiences shape its present capabilities and may greatly influence the outcome of future events. For marine organisms with complex life cycles, seemingly discrete life stages separated by periods of rapid change (metamorphosis) have led researchers to focus on processes that occur within stages. Recent research highlights the interconnections among life stages and underscore that phases within a life cycle are functionally coupled. Success in one stage biases the probability of outcomes in subsequent stages. The present study reviews research on model species of tropical reef damselfish, *Pomacentrus amboinensis*, to highlight the fundamental importance of effects that ‘carry-over’ from previous life stages and potentially generations. Research strongly suggests that the physiological state of parents (particularly mothers) during gametogenesis pro-rate offspring success and may even influence their fitness.

Key words: parental effects, metamorphosis, coral reef fish, history, phenotypic selection

Introduction

The life cycles of marine organisms are comprised of a series of discrete life stages. Transitions between stages differ in their nature and the magnitude of change and are species specific. Each life stage will have a different primary role (development, growth, recruitment, reproduction), and will be responsive to, and affected by, prevailing conditions differently. Because of the dramatic changes in function, physiology and environment that characterize sequential life stages it cannot be expected that advantages gained in one life stage (e.g. the ability to capture planktonic particles) will necessarily result in an advantage in the next stage. However, recent evidence suggests that the way individuals respond to conditions in one life stage can influence their characteristics in subsequent life stages. Individual characteristics of one particular life stage have been found to positively influence the next life stage, but they can also influence multiple life-stages and even may extend between generations (Green and McCormick 2005; Giménez 2006).

Because the intensity of selection on phenotype, life history or behavioural traits will change with ontogeny it is important to know the extent to which an individual’s characteristics are influenced by its history and the extent to which its success is independent of past events.

How an individual’s history influences present and future outcomes, now known as ‘carry-over effects’, has recently become a focus of interest for marine researchers. Researchers on invertebrates in particular have recently focused attention on the links between life stages (Podolsky and Morany 2006 and references in same issue), possibly because of the greater ease of laboratory rearing and relatively short longevities of invertebrates. Researchers on fishes have typically underplayed the importance of life history interconnections, despite a large body of research from a diverse range of fields that underscores their importance.

Our objective is to highlight the importance of carry-over effects to coral reef fishes by briefly reviewing research on one Indo-Pacific damselfish (*Pomacentrus amboinensis*) that has been used as a model for many different types of biological, ecological and evolutionary studies. Using these studies we emphasise the interconnection among life stages and the ramifications of these for population dynamics. The link between the quality and performance traits of fish and their numerical population consequences has been explored elsewhere (Jones and McCormick 2002).

Parental influences on larval traits

Recent research suggests that parental attributes of coral reef fishes greatly influence developmental and performance trajectories of larvae through the provisioning of the gametes during gametogenesis, as shown in other organisms (Mousseau and Fox 1998). Studies of *P. amboinensis* have emphasized the importance of maternal body condition and physiological state in influencing embryo and larval phenotype, with female

effects being stronger than male effects (Table 1). A study that monitored the reproductive output of 40 breeding pairs on 2x2m patch reefs found that females of smaller size that were in better than average body condition produced larvae that had larger nutritional stores (Table 1), while female age had little influence on larval attributes at hatching. When females were placed into three size categories it was evident that small females produced larvae that were both longer and had larger yolk-sacs at hatching (Table 1).

Table 1: The influence of female and male *P. amboinensis* attributes on larval morphology at hatching, from breeding pairs on 40 patch reefs in the Lizard Island lagoon, Great Barrier Reef (GRR). Significant partial correlations are given; ns indicates no significant relationship between the two variables at $\alpha=0.05$. Condition of females (cond) was quantified as the residuals of a length/wet weight regression. Females ranged between 40.8 to 66.4mm standard length, and were 2 to 6 years old. n = 25 per comparison. Larvae were preserved and measured as per McCormick (2006) and aged following Maddams (2007). Larval attributes are for the second clutch produced. Source: Maddams and McCormick unpublished data.

Larval traits	Breeder attributes			
	♀ size	♀ age	♀ cond	♂ size
Larval length	ns	ns	ns	ns
Yolk sac area	-0.65	ns	0.60	ns
Oil globule area	-0.60	ns	0.47	ns
Eye diameter	ns	ns	ns	ns
Head depth	ns	ns	-0.46	ns

Experiments that supplementary fed breeding pairs in the field have shown that maternal body condition influences the yolk-sac size of larvae at hatching, but has little influence on larval length (Kerrigan 1997; McCormick 2003; Fig. 1).

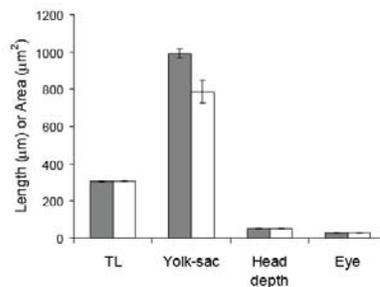


Figure 1: Comparison of morphologies of larvae at hatching from *P. amboinensis* breeding females that have (grey) or have not been supplementary fed (white bar) in the field for 5 min per day (from McCormick 2003). Errors are standard errors.

In contrast, parental interactions that alter maternal stress levels, such as density-dependent interactions with con- or hetero-specifics, directly influence larval length at hatching through a mechanism involving the stress hormone, cortisol (McCormick 1998, 1999, 2006, 2009; McCormick and Nechaev 2002). Experimental manipulations of maternal cortisol within naturally occurring limits were able to produce larvae that spanned the complete size range that naturally occurred in the wild, emphasizing the importance of this mechanism (McCormick 1999, 2006). Interestingly, laboratory manipulations of maternal testosterone were found to influence yolk-sac utilization rates.

Maternal stress has also been shown to influence the inter-relationships among early life-history traits in *P. amboinensis*. By manipulating the cortisol environment of individual embryos, Gagliano and McCormick (unpublished data) have been able to show that the fundamental relationship between early life history traits changes, emphasizing the potent role of the maternal state at gametogenesis for subsequent larval performance and survival (Fig. 2). Laboratory manipulations of cortisol and testosterone have previously been shown to influence the relationship between larval standard length at hatching and yolk sac area (McCormick 1999).

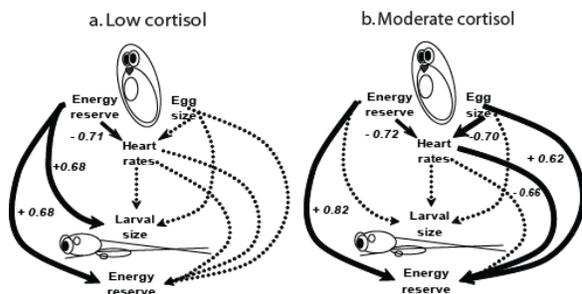


Figure 2: Summary of the correlations among early life history attributes of *P. amboinensis* embryos at 36 h post-fertilization (pf) with heart rate at 84 h pf and attributes of newly hatched larvae. Correlations for embryos incubated with no additional cortisol added to seawater (a) are compared to embryos incubated in seawater supplemented with a cortisol solution (10² ng/ml) to mimic moderate levels of maternal interactions (b). Protocols followed McCormick (1999) and Gagliano et al. (2007b). n=72. Bold lines represent significant relationships.

Similar laboratory manipulations have indicated that aspects of the sensory system are also influenced by maternal stress. Recent experiments found that maternal stress directly influenced the fluctuating asymmetry (FA) of the sagittal otoliths (Gagliano and McCormick submitted). A field experiment showing the relationship between otolith asymmetry and attraction to specific sounds suggests that FA may be important in navigation (Gagliano et al. 2008). There is also the indication from field data on *P. amboinensis* (Gagliano and McCormick submitted) and on a tropical lizardfish (*Saurida suspicio*) (Lemberget and McCormick 2009) that larval survival is directly and strongly related to the degree of otolith FA. These studies directly link larval survival and cohort strength to maternal influences.

Initial characteristics influence larval and juvenile survival

The ubiquitous problem of collecting identifiable larva at anything other than the start or end of their larval stage has made studying the processes that influence survival difficult for tropical marine organisms. This has meant that much of the research conducted on fish larvae to date has examined the Olympians that survived the larval phase. From these we attempt to make inferences on the processes that facilitated their survival, and what influenced those that died.

In the most comprehensive study to date, Gagliano et al. (2007a) serially sampled a pulse of *P. amboinensis* from production through to 2 months post-settlement (ps) and examined phenotypic selection using the history of growth stored in otoliths. They found strong links between early life history traits and persistence, with even the earliest traits, such as size of the sagittal otolith at hatching, still being selected for well into the juvenile phase (Table 2). Of the diverse traits measured, growth during the larval phase was the trait with the longest duration of influence, with selection still being detectable 6 weeks into the juvenile phase (Table 2).

Table 2: Carry-over effects of (a) phenotypic traits, as represented by otolith size, and (b) otolith growth on subsequent survival from serial samples of a reproductive pulse of *P. amboinensis* from Lizard Island, GBR. Summary indicates the duration that selection on various attributes is detectable and the direction of that selection. ns, no significant selection. (after Gagliano et al. 2007a).

Attribute selected	Detectable	Direction
to:		
<i>a. Phenotype</i>		
Hatch	2 wks ps	-
Settlement	4 wks ps	-
2-wks ps	ns	
3 wks ps	4 wks ps	-
4 wks ps	ns	
<i>b. Growth period</i>		
Larval phase	6 wks ps	-
First 2 wks ps	3 wks ps	+
Third wk ps	4 wks ps	-
Forth wk ps	ns	

Field and laboratory experiments have shown that settlement represents a critical phase for *P. amboinensis* with mortality showing a Type III trajectory and being highly selective for a variety of traits (McCormick and Hoey 2004). Overall, fish that were larger at settlement, that had larger lipid stores and who had higher larval growth, had a survival advantage (Table 3). The attributes that influence *P. amboinensis* survival at settlement are, however, dependent upon the location they settle into and the resident community at that location (Holmes and McCormick 2006).

A field experiment by McCormick and Meekan (2007) showed the characteristics that influence prey survival were dependent upon the patch-work of predator selection-fields into which the naïve juveniles settled. Juveniles that settled into nesting

Table 3: Summary of the selectivity of mortality on various phenotypic attributes for newly settled *P. amboinensis* that were naïve to predators. A positive selection direction means that individuals that had a larger value on that trait had a higher probability of mortality. In the laboratory trials the dottyback, *Pseudochromis fuscus*, was used. Laboratory and field trials with weight and burst speed were size standardized. ns, non-significant effect. FA: fluctuating asymmetry. References: 1, Gagliano et al. 2007a; 2, Gagliano and McCormick 2007; 3, Hoey and McCormick 2004; 4, McCormick and Hoey 2004; 5, Holmes and McCormick 2009; 6, Gagliano et al. 2008.

Phenotypic trait	Field (F) or Lab(L)	Selection direction	Reference
Otolith size at hatching	F	-	1

Otolith size at settlement	F	-	1,
Size at settlement	F	-	2, 3, 4
	L	-	5
Weight at settlement	FandL	+/ns	5
Lipid levels at settlement	F	-	3
Burst speed at settlement	FandL	ns/ns	5
Fulton's condition factor	F	+	3
Larval growth	F	-	1, 3
Otolith FA at settlement	F	+	6

territories of male *P. amboinensis* were exposed to positive selection by the dotyback *Pseudochromis fuscus*, which prefers large recruits and who were not evicted by aggressive male territory holders. Outside the territories, where the juveniles were exposed to a broader range of predators, larger individuals had higher survival.

Initial larval characteristics influence individual fitness

Recently, studies of marine organisms have found a link between early life history traits and adult success. Many tropical fishes exhibit complex ontogenies involving sex change. The most common form is protogyny, where juveniles first mature as females and then undergo sex change in the event of the appropriate social trigger (monandric protogynous hermaphroditism; Munday et al. 2006). In these species, individuals that attain the status of male get to monopolise matings and have the highest fitness. *P. amboinensis* is a damselfish that exhibits protogynous hermaphroditism. Male and dominant female *P. amboinensis* were collected from around Lizard Island and growth histories were reconstructed using otolith increment widths from cross sections of the sagitta as a proxy for growth. For a portion of these fish (up to 7 years old) it was possible to obtain measurements from the larval otolith. Those females that had undergone sex change and became males were found to have significantly smaller increment widths compared to those that were still female ($t = 2.32$, $df 11$, $p = 0.04$; Fig. 3). Of the six other species from 2 families that we have examined, 3 have shown similar relationships, with significant differences in larval growth starting with the hatch mark, between females and those fish that become males later in life (1 out of 2 sandperches, 2 out of 4 wrasse; Walker et al. 2007; McCormick and Ryen unpublished data).

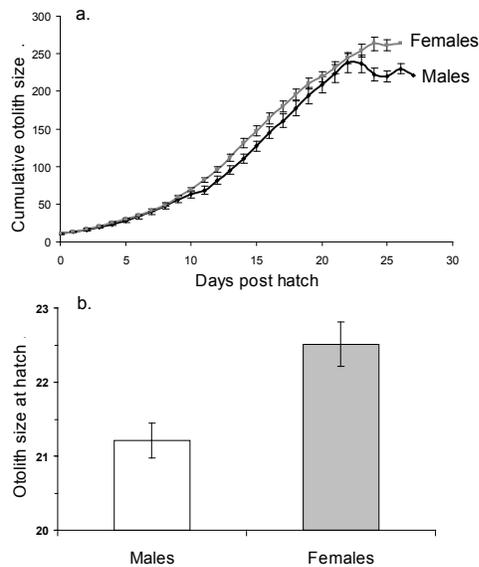


Figure 3: Early otolith growth of females and females that have changed sex to become males showing cumulative otolith growth through the larval phase (a), and differences in increment widths between sexes at hatching (b). Errors are standard errors ($n = 8$ females and 5 males).

Transgenerational effects

The pelagic larval phase of almost all coral reef fishes makes it difficult to track the fate of individuals from when first produced from parents of known history through to becoming an old member of a reproductive group (i.e. one with measurable fitness). While transgenerational studies are presently being conducted on a brooding

species (*Acanthochromis polyacanthus*; e.g. Donelson et al. 2008), the rarity of the strategy to have non-dispersive larvae means that results, whilst useful, will have limited applicability to the population dynamics of most marine fishes. We must therefore make the best of inferences we can make on the connections between generations.

Otoliths are a valuable record of relative growth and may prove a useful tool in linking parental influences to the growth dynamics of their offspring. Unfortunately, while we know that the relationship between somatic growth and otolith growth can be individualistic (Campana and Jones 1992), we have little understanding of the plasticity of the relationship, the factors that will influence it and the potential lag effects for most life stages of fish (see Molony and Choat 1990 for juveniles). A recent study that has simulated the effects of maternal stress on the embryogenesis of individual *P. amboinensis* found that maternal cortisol levels not only influenced the strength of the relationship between early life history traits, but influenced the fundamental relationships between phenotypic traits and otolith size at hatching (Table 4). Under a low stress scenario, otolith size at

Table 4: Relationship of otolith (sagitta) size at hatching with early life history attributes for *P. amboinensis* embryos individually reared from fertilized eggs under three simulated maternal stress levels. Low stress (no addition of cortisol, equivalent to parents being on a patch reef alone); Moderate stress (addition of low cortisol dose, equivalent to the mother interacting with 2 conspecifics on a patch reef); High stress (high cortisol dose, equivalent to the mother interacting with 4 to 6 other conspecifics on a patch reef). For detailed methods see Gagliano and McCormick (submitted).

Treatment	Otolith size at hatch versus			
	Yolk size of egg	Heart rate	Yolk size at hatch	Length at hatch
Low cortisol	-0.71	-0.78	-0.69	ns
Mod cortisol	ns	ns	ns	+0.63
High cortisol	-0.88	ns	ns	ns

hatching was negatively related to initial and hatching yolk size and to heart rate (at 84h post-fertilization; a proxy for metabolism). This is opposite to the relationship found for 7 juvenile freshwater pike, where metabolism was positively associated with the width of increments deposited (Armstrong et al. 2004). Interestingly, when simulated maternal stress increased, the relationships between early life history attributes changed. It was only under moderate levels of stress that a positive relationship was found between otolith size at hatching and larval length (Table 4). It is this positive relationship between otolith size and larval size that is often assumed to be present in previous studies (Vigliola and Meekan 2002). Clearly further work is required to determine the drivers of increment width.

While the exact meaning of the otolith size at hatching is presently unclear, evidence suggests that maternal effects are likely to have a major influence on the relationship between early life history traits and otolith characteristics. The relationship between initial otolith size and fitness, together with the influence of maternal stress on larval size and otolith FA (McCormick 2006; Gagliano and McCormick submitted), suggest that maternal characteristics may play an important role in predetermining the subsequent fitness of individuals; the ultimate carry-over effect.

Carry-over effects have been documented in many marine phyla. There are many studies of fish that have shown that previous history influence future success (Berkely et al. 2004; Sponaugle and Grorud-Colvert 2006). These links occur between adjacent life-stages, across multiple stages and across generations. To date, few marine studies have managed to demonstrate transgeneration effects because of the logistical difficulties in linking all the stages in organisms with complex life cycles. Available data, such as that compiled here for one model fish species, suggests that transgenerational effects may be very important in influencing population dynamics. The key is to focus attention on how an individual's history influences present and future outcomes. The recent findings of high levels of self replenishment on small spatial scales for reef fishes with substantial larval durations (Almany et al. 2007) opens up additional possibilities for rapid local scale adaptation to changing conditions through maternal effects. The strong physiological, developmental, behavioural and performance links between stages and potentially between generations, mean that carry-over effects are fundamental forces that have been important in the shaping of existing populations and communities. The challenge is to define the extent to which carry-over effects influence present day dynamics and their importance in ecological and evolutionary time scales.

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