NOTE

Relative swimming speeds in reef fish larvae

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ABSTRACT: In most organisms relative locomotor speed (body lengths per second [bls^{-1}]) is inversely proportional to body size. The ability of late stage reef fish larvae to achieve swimming speeds of over 40 bls^{-1} is consistent with this general scaling relationship. However, this relationship does not extend to smaller larvae which are not fully developed. Maximum critical swimming speeds appear to be limited by both developmental stage and size. At 7 mm total length when settling, the unusually small larvae of anemonefishes are able to sustain speeds of 49 bls^{-1}. This probably approaches the maximum limit for sustained aquatic vertebrate locomotion.

KEY WORDS: Swimming · Coral reef fish · Larvae · Development · Settlement

Although smaller animals move more slowly than larger animals (Alexander 1982), their relative speed in body lengths per second (bls^{-1}) is almost invariably higher. In terrestrial systems, vertebrate offspring are relatively large at the onset of independent locomotion. Only in aquatic vertebrates can we see diminutive individuals capable of independent locomotion. While reef fish larvae have been assumed to be poorly developed and capable of only limited movement (Williams et al. 1984, Roberts 1997), recent works have highlighted the potential impact of active movement in shaping dispersal patterns and settlement success (Armsworth 2000, Cowen et al. 2000, Armsworth et al. in press). These latter studies incorporate information on the remarkable swimming performance of late stage larvae of coral reef fishes, with long-term sustained swimming bouts covering the equivalent of up to 140 km, and short-term sustained swimming speeds of up to 65 cm s^{-1} (Stobutzki & Bellwood 1994, 1997, Leis & Carson-Ewart 1997). These swimming speeds appear to be quite extraordinary; however, they have not yet been compared to other fishes in terms of their relative swimming speeds.

Studies investigating the swimming abilities of tropical reef fish larvae have concentrated almost entirely on the oldest larval stages. This reflects the limitations of the light traps which are commonly used to catch larvae for behavioural experiments (Choat et al. 1993). These larvae are at a relatively advanced state of development. We set out to determine: (1) whether the swimming ability exhibited by late pelagic stage individuals is exceptional or simply a reflection of the small size of reef fish larvae, and (2) how the relative swimming speeds of larvae are influenced by developmental stage. We selected 3 study species that varied in size at settlement and rate of development, and used captive breeding techniques to conduct swimming trials throughout the developmental period of each species (following Fisher et al. 2000).

Materials and methods. Three species of reef fish were examined: *Pomacentrus amboinensis* (Pomacentridae, Pomacentrinae), *Amphiprion melanopus* (Pomacentridae, Amphiprioninae) and *Sphaeramia nematoptera* (Apogonidae). These species differ considerably in their age and size at settlement. *P. amboinensis* and *S. nematoptera* have long larval durations of ~20 and 24 d and settle at approximately 15 and 13 mm total length (TL), respectively. In contrast *A. melanopus* has a very short larval duration of approximately 9 d and settles at ~7 to 8 mm TL. Rearing methods follow Job & Bellwood (2000). Swimming experiments were carried out throughout the larval period of each species using swimming flumes following Stobutzki & Bellwood (1997) and Fisher et al. (2000). Three batches of young from each species were used in the swimming trials. At each experimental age, 8 to 12 fish were taken from each batch (without replacement) and the fastest individual swimming speed recorded (as U_{crit}; see below). Maxima rather than means were used to provide estimates of maximum swimming speeds. If larvae are exceptional swimmers, for their size, then these values will reveal the full extent of their unusual

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abilities. Fish were stimulated to swim based on positive rheotaxis and phototaxis.

Burst, cruising and critical swimming speeds have all been used to measure the swimming abilities of fish larvae (Miller et al. 1988, Stobutzki & Bellwood 1994). However, comparisons between studies are difficult because the values obtained may vary widely depending on the methods employed. Short duration observations give higher estimates of relative swimming speeds. To facilitate comparisons between published records using different taxa and developmental ages, swimming speeds were compared based solely on estimates of critical swimming speeds (U_{crit}). U_{crit} is an intermediate measure of speed, slower than burst speed, but faster than cruising speeds, and it provides a maximum performance measure of short-term sustained swimming. The flow rate against which the fish is swimming is increased incrementally at set time intervals. In the present study, larvae were subjected to incremental increases in flow rates equivalent to approximately 3 body lengths (BL) every 2 min until they could no longer maintain position for the full 2 min. The equation used to calculate U_{crit} followed Brett (1964): $U_{crit} = U + (t/t_i \times U_i)$, where U is the penultimate speed, U_i is the velocity increment, t is the time swum in the final velocity increment and t_i is time interval for each increment.

Fish larvae that were swum, or siblings of the same age, were anaesthetised in chilled water, then fixed in 10% buffered formalin. After 12 to 48 h, larvae were transferred to 70% alcohol and stored. Measurements were taken of TL (from the tip of the caudal fin to the tip of the upper jaw) and body depth (at the deepest point). Shrinkage of larvae due to fixation and preservation varies with age, from approximately 12% at 5 mm TL to 6% at 8 mm (Job & Bellwood 1996). To facilitate comparisons between studies, shrinkage has not been incorporated into the estimates; however, it must be noted that this may result in a slight overestimation of relative swimming speeds, especially in small larvae. Reynolds numbers (Re) were calculated for each species at each age using the formula: Re = $U_{crit} \times D/v$ (after Webb & Weihs 1986), where U_{crit} is the critical swimming speed in m s^{-1}, D is the body depth of the larvae expressed in m and v is the kinematic viscosity of seawater (1.03×10^{-6} m^2 s^{-1}).

The maximum U_{crit} of late stage larvae (i.e. specimens immediately before they leave the plankton to assume a benthic lifestyle) of the 3 study species were compared in a scatter plot with published values for other fish species at a range of sizes. These species included freshwater, marine, tropical and temperate fishes. U_{crit} values were obtained from Brett (1967), Larimore & Duever (1968), Jones et al. (1974), Batty (1984), Duthie (1987), Hatwell (1991), Stobutzki & Bellwood (1994), Drucker & Jensen (1996), Hawkins & Quin (1996) and Peake et al. (1997). Scatter plots were also used to describe the development of critical swimming ability and changes in Re versus TL for each of the 3 species investigated.

RESULTS

In late-stage larvae, juvenile and adult fishes, relative swimming ability (bls^{-1}) increases exponentially with decreasing BL. Smaller individuals swim at much higher relative speeds than larger individuals (Fig. 1). The late-stage larvae examined in the present study followed the general relationship between relative swimming speed and size (Fig. 1). The high relative speeds achieved by these late-stage larvae appear to be largely a consequence of their small sizes. This size-based relationship, however, did not extend to younger, smaller larvae.

At hatching all 3 species exhibited similar swimming speeds relative to their BL, ranging from 9.5 bls^{-1} for *Sphaeramia nematoptera* to 17.0 bls^{-1} for *Pomacentrus amboinensis* (Table 1). *Amphiprion melanopus* exhibited medium relative swimming speed (12.4 bls^{-1}), even though it hatches at a considerably larger size when compared to the other 2 species (Table 1). In contrast to the general negative relationship between relative swimming speed and size in fully developed fishes, the relative swimming ability of all 3 species gradually increased with length during development. The maximum relative speed was achieved only at the
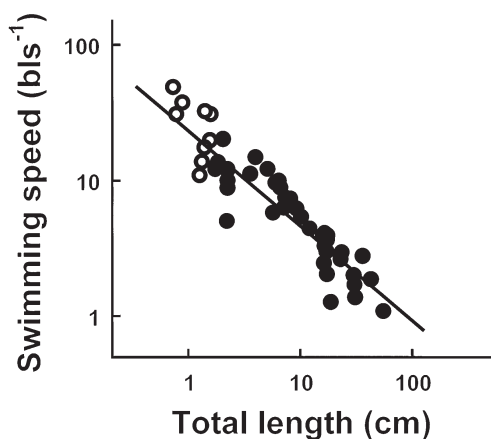

Fig. 1. Relative swimming speed versus fish body length (Log$_{10}$ scale). Literature values (●) and values from larvae in the present study (○). Larval values are for the fastest speeds achieved by late-stage larvae (3 batches per species). The regression line is fitted to the published values only. All swimming speeds are based on U_{crit} estimates. bls^{-1}: body length per second
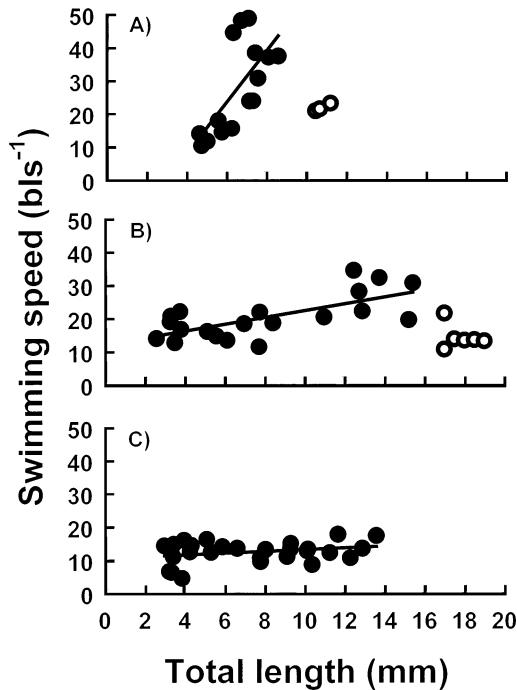
Fig. 2. Relative swimming speed of larvae versus total length for (A) *Amphiprion melanopus*, (B) *Pomacentrus amboinensis*, and (C) *Sphaeramia nematoptera*. (O) Post-settlement individuals (in *S. nematoptera* there is no marked metamorphosis at settlement; *P. amboinensis* values from Stobutzki & Bellwood 1994). The regression lines are fitted to pre-settlement larvae only
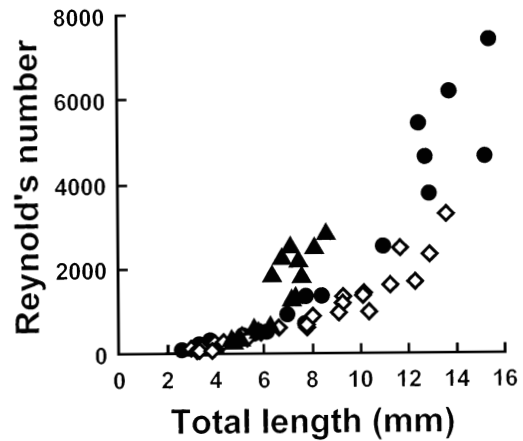

Fig. 3. Changes in Reynold's number with total length for *Amphiprion melanopus* (▲), *Pomacentrus amboinensis* (●) and *Sphaeramia nematoptera* (◇)

end of the larval phase. This occurred at different sizes in each species (Fig. 2). *A. melanopus* exhibited the fastest development of relative swimming speed, attaining a maximum relative swimming speed of 49 bls^{-1} at the end of the larval phase (cf. 34 bls^{-1} in *P. amboinensis* and 19 bls^{-1} in *S. nematoptera*) (Fig. 2). In both *A. melanopus* and *P. amboinensis*, relative speeds appear to decrease rapidly after settlement.

The Re also increased steadily throughout the larval period for each species, with changes reflecting the increase in absolute swimming speeds (Fig. 3). Only the smallest larvae, exhibiting slow relative swimming speeds, were swimming in a low Re regime (<300). As the larvae get larger, and swim faster, they rapidly

leave this 'viscous' regime. The size at which larvae leave the viscous Re regime was similar in all 3 species (approximately 4 to 5 mm TL). The maximum relative swimming speeds of the larvae, just before settlement, are achieved in markedly different Re regimes in the 3 species. *Amphiprion melanopus* attained the highest relative U_{crit} in a lower Re regime than the other 2 species (Figs. 2 & 3), reflecting the high speeds achieved by *Amphiprion* at a small size.

Discussion. The maximum relative swimming speeds of late-stage larvae are not exceptional when compared with published values for other fish species over a range of sizes. The high relative swimming speed of late-stage larvae of coral reef fishes is largely a reflection of their small size. However, they do mark the upper limit of this size-based relationship. Smaller larvae did not display even higher swimming speeds. In all species examined, the larval period was marked by a steady increase in swimming ability with the maximum relative speed being achieved at the end of the larval phase. This occurred at different sizes in each species, suggesting that speed is dependent upon both size and developmental stage.

It has been suggested that the relative swimming speeds of smaller larvae are reduced because of the effects of viscosity when swimming at low Re values (<300) (Fuiman & Batty 1997). Although this may constrain the abilities of small larvae, there is still a positive relationship between relative swimming speed and length, even after larvae leave the 'viscous' regime. This relationship is seen in all 3 species, even though it is exhibited in markedly different Re regimes. Indeed, the greatest relative swimming speeds were seen in *Amphiprion melanopus*, which achieved

Table 1. Mean length, U_{crit} and relative swimming speed at hatching for the 3 study species. Values in parentheses represent standard errors (n = 3). bls^{-1}: body lengths per second

	Total length (mm)	U_{crit} (mm s^{-1})	Relative speed (bls^{-1})
Amphiprion melanopus	3.2 (0.1)	30 (7)	9.5 (2.6)
Pomacentrus amboinensis	2.9 (0.5)	51 (3)	17.0 (2.5)
Sphaeramia nematoptera	4.8 (0.1)	60 (5)	12.4 (1.1)

these speeds at relatively low Re values. This suggests that Re values are not critical, at least for older larvae. The observed changes in the relative swimming speeds of larvae are likely to be related to developmental constraints, with swimming performance being dependent upon the developmental schedules of the neural and musculoskeletal systems. Small larvae are capable of very high tail beat frequencies when compared to adult fish (Blaxter 1986). This may reflect key changes in the physiological basis of locomotion during development, including changes in muscle types (cf. Batty 1984, El-Fiky et al. 1987).

The achievement of maximum relative swimming speeds in late-stage larvae is consistent with the ecology of reef fishes. It is these late-stage larvae (also termed presettlement stages or late pelagic stage larvae/juveniles) that undergo the transition from the pelagic to the demersal phase of their lives. During this period there is the potential for high mortality rates and exposure to strong currents. At this stage there is likely to be strong selective pressure for well developed locomotor capabilities as the fish avoid reef-based predators whilst locating suitable settlement sites (Sancho et al. 1997). It may also be noteworthy that the highest relative swimming speeds were observed in *Amphiprion malanopus*, a species with a relatively short pelagic larval duration. Given this short larval duration, it is unlikely that this species would disperse far from reefs. The well developed sensory systems of larval anemonefishes (Job & Bellwood 2000) and precocious development of swimming abilities may reflect this abbreviated period away from the reef.

Recent studies have emphasised the potential for reef fishes to maintain high rates of retention around reefs (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000). In all cases, larval behaviour was identified as a significant contributing factor. Although several studies have highlighted the extent of intraspecific variation in swimming abilities (e.g. Leis & Carson-Ewart 1997, Stobutzki 1998) these data have provided insight into the potential performance limits of reef fish larvae. Models are now appearing that specifically incorporate key aspects of larval behaviour and swimming abilities (e.g. Armsworth 2000, Armsworth et al. in press). Our findings highlight the role of fish size with these considerations: irregardless of final abilities, relative swimming ability appears to increase up to the end of the pelagic phase and decreases thereafter following a relatively predictable pattern. Furthermore, the peak abilities approximate those values expected based simply on the size of the larvae.

Overall, maximum relative swimming speeds are strongly correlated with body size, but only in individuals with fully developed locomotor systems. In reef fishes this is probably achieved only at the end of the pelagic phase. For the majority of marine fish larvae, size is not the sole constraint on swimming speed and relative swimming speed does not increase simply as a result of decreasing size. However, the high relative maximum swimming speeds of late-stage reef fish larvae are consistent with expectations for fishes of their size. This is highlighted by the precocious development seen in anemonefishes, which results in exceptionally small late-stage larvae. Settling at 7 to 8 mm TL, compared to 10 to 36 mm in other taxa, they are among the smallest larvae to settle on coral reefs (Leis & Carson-Ewart 1997), and they probably represent one of the smallest fishes with fully developed locomotor capabilities. By virtue of their small size when fully developed, at 7 to 8 mm TL and a swimming speed of 49 bls^{-1}, late pelagic stage anemonefish larvae may mark the upper limit for sustained aquatic vertebrate locomotion.

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