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Temperature influences swimming speed, growth and larval duration in coral reef fish larvae

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Abstract

The effects of temperature on growth, pelagic larval duration (PLD) and maximum swimming speed were compared in the tropical fish marine species *Amphiprion melanopus*, to determine how temperature change affects these three factors critical to survival in larvae. The effects of rearing temperature (25 and 28 °C) on the length of the larval period and growth were examined in conjunction with the effects of swimming temperature (reared at 25 °C, swum at 25 and 28 °C, reared at 28 °C, swum at 25 and 28 °C) on critical swimming speed (U-crit). Larvae reared at 25 °C had a 25% longer pelagic larval duration (PLD) than larvae reared at 28 °C, 12.3 ($\pm$0.3) days compared with 9 ($\pm$0.6) days at 25 °C. To offset this effect of reduced developmental rate, growth and U-crit were measured in larvae reared at 28 and 25 °C at the same absolute age (7 days after hatching (dah)) and same developmental age (7 dah at 28 °C cf. 11 dah at 25 °C), corresponding to the day before metamorphosis. Larvae reared at 25 °C were smaller than larvae reared at 28 °C at the same absolute age (7 dah at 25 °C cf. 7 dah at 28 °C), yet larger at similar developmental age (11 dah at 25 °C cf. 7 dah at 28 °C) when weight and standard length were compared. This stage-specific size increase did not result in better performance in larvae at the same developmental age, as there was no difference in U-crit in premetamorphic larvae reared at either temperature (7 dah at 28 °C c.f 11 dah at 25 °C). However, U-crit was considerably slower in 7-day-old larvae reared at 25 °C than larvae of the same absolute age (7 dah) reared at 28 °C. Swimming temperature controls demonstrated that a change in temperature immediately prior to swimming tests did not effect swimming performance for larvae reared at either temperature.

A decreased in rearing temperature resulted in longer larval durations, reduced growth rates and slower swimming development in larvae. However, the magnitude of the response of each of these traits varied considerably. As such, larvae reared at the lower temperature were a larger size at metamorphosis but had poorer relative swimming capabilities. This study highlights the importance of measuring a range of ecologically relevant traits in developing

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larvae to properly characterise their relative condition and performance in response to environmental change.

Keywords: Development; Fish larvae; Growth; Swimming

1. Introduction

All organisms have lethal limits to their temperature range (e.g. Hokanson, 1977) and yet within this range they also have optimal temperatures for development of structure and function (Rombough, 1997). Within an ectotherms tolerance limits, variation in temperature will influence metabolism (see Rombough, 1997) and therefore related physiological processes, affecting growth (Nicieza and Metcalfe, 1997), development (Koumoundouros et al., 2001), and performance—encompassing physiological and behavioural capabilities (Fuiman and Higgs, 1997; Koumoundouros et al., 2002). Growth is the most commonly measured response in ectothermic animals and is often measured in isolation as indicative of response to temperature (e.g. McMullen and Middaugh, 1985; Zhang and Runham, 1992). However, temperature influences a range of characters, and early development such as the larval phase is especially susceptible to temperature change (Rombough, 1997).

Ontogeny is a complex collection of steps and intervals, and is dependent on the timing of developmental processes (Kovac, 2002). The timing of these ontogenetic steps and intervals in many marine ectotherms is plastic (Koumoundouros et al., 2001) and environmental change can cause shifts in the rate of ontogenetic change. Temperature, in particular, causes variation in rates of fish development in the embryonic (Heath et al., 1993), larval (Björnsson et al., 2001; Hunt von Herbing et al., 1996) and juvenile stages (Beacham and Murray, 1990; Benoit and Pepin, 1999). A decrease in the rate of ontogeny caused by a change in temperature results in a longer larval duration and increases exposure to the high-risk pelagic larval environment (Atkinson, 1996). Moreover, through varying rates of development, temperature can influence the size of the organism at which ontogenetic transformations occur.

Performance is an expression of the physiological and behavioural capabilities of an organism (Fuiman and Higgs, 1997) and can exhibit effects of a changed environment. Swimming speed and behaviour are often used as measures of the performance capabilities of a fish as they are important to dispersal (Leis and McCormick, 2002), prey capture (Hunt von Herbing et al., 2001), predator avoidance (Rice et al., 1987; Fuiman, 1993) and avoiding advection away from suitable habitat (Armsworth, 2001). Temperate marine fish show large responses to temperature change through swimming performance at all stages of development. Incubation temperature affects swimming escape velocity (Johnston et al., 2001), thermoclines determine vertical distribution in larvae (Batty, 1994) and swimming temperature affects critical swimming speed (Koumoundouros et al., 2002) and spontaneous swimming activity (Fuiman and Ottey, 1993) in juveniles. Further, temperature induced morphological changes may have indirect effects on the development of swimming performance, as the development of

functional structures such as muscle, gills and biochemical pathways are retarded (Taylor et al., 1997).

Growth, larval development and swimming performance in temperate fish species have distinctive responses to temperature change. The relative importance of temperature change in the tropics has been alluded to (Rombough, 1997; Hunt von Herbing, 2002), but rarely tested. Tropical latitudes generally have little temperature fluctuation relative to temperate environments, due to the large ocean surfaces and absence of a cold season (McGregor and Nieuwolt, 1998). For example, the Great Barrier Reef, Australia sea surface temperature fluctuates from 4 to 6 °C seasonally, and 1 °C diurnally (McGregor and Nieuwolt, 1998). Accordingly, temperature variation of only a few degrees represents a proportionally large change for organisms that are adapted to this relatively stable thermal environment, as physiologically expensive adaptations to temperature change are not often maintained in relatively stable systems (Feder, 1978; Relyea, 2002). As a consequence, small changes in temperature could have a disproportionately greater impact on development of tropical fish larvae than larvae in temperate systems with naturally large temperature variation.

The objective of this study was to examine the combined changes in developmental rate, growth rate (size) and swimming performance (in terms of critical swimming speed) to a change in environmental temperature in a tropical marine fish *Amphiprion melanopus*. The results are compared to other studies to determine the magnitude of response in each trait for this tropical species per degree of temperate change compared to temperate fish larvae.

2. Materials and methods

2.1. Larval rearing and experimental protocol

The study species is an anemonefish, *A. melanopus*, from the family Pomacentridae and occurs from Indonesia in the north and along the 7° of latitude spanned by the Great Barrier Reef, Australia. They lay benthic eggs and have a short larval duration, which lends them to experimental manipulation. Broodstock were collected from the northern section of the Great Barrier Reef, adjacent to Cairns (16°8′S, 145°7′E), and would naturally experience temperature fluctuations from 25 to 30 °C annually. *A. melanopus* larvae were reared in an indoor laboratory at the James Cook University aquarium facility following the methods of Green and McCormick (1999). Eggs were obtained from adult broodstock maintained at 28 °C and conditioned to lay eggs onto cement blocks lined with acetate sheeting. On the night the eggs were due to hatch, they were transferred indoors where larvae were hatched into a 70-l glass aquarium held at 28 °C. Upon hatching, 10 larvae were sampled, preserved in 70% ethanol and later used for measurements of standard length and wet weight. Immediately after hatching, between 300 and 400 larvae were transferred at random into ten 70-l glass aquaria held at 28 °C. Temperature in five tanks was gradually adjusted to 25 °C overnight. Through the remainder of the larval phase, five tanks were maintained at 28 °C and five tanks at 25 °C. This was repeated for three clutches of larvae from three separate pairs of broodstock. Larvae were reared using

the 'green water' method described by Daintitch (1993), where *Nannochloropsis* sp. algal culture is added to tanks each morning. Tanks were lit by fluorescent lights simulating a 14:10-h light/dark summer light cycle, and maintained as a semi-closed system, flushed nightly with temperature controlled water (25 and 28 °C) when the lights were off. Larvae were fed rotifers (*Brachionus* sp.) at a density of approximately 5 ind. ml^{-1} for 1–3 days after hatching, and on day 3 after hatching *Artemia* nauplii were added at 1–2 ind. ml^{-1}.

2.2. Quantifying the effects of temperature

Length of larval duration was used to determine the effects of temperature on the ontogenetic rate of *A. melanopus*, and metamorphosis was used to mark the end of the larval period. The metamorphosis in marine fish from pelagic larvae to demersal juvenile can entail a shift in habitat, appearance or structure of the fish and is species specific (McCormick et al., 2002). In *A. melanopus*, the stage when the post-orbital stripe becomes pigmented coincides with a shift in habit and is a more discrete measure than full body pigmentation (Green and McCormick, 1999). In the current study, fishes within individual tanks were grouped to determine the number of days until metamorphosis, otherwise described as the pelagic larval duration (PLD), and a tank was considered metamorphosed when greater than two-thirds of all the fish in each tank had a visible post-orbital stripe. Developmental rate was calculated following Fuiman et al. (1998) as $R_{dev} = 1/age$, where R_{dev} is the developmental rate and age is the numbers of days since hatching.

Critical swimming speed (U-crit, following Brett, 1964) was used to determine the effects of rearing temperature on the functional swimming capabilities of larvae. U-crit is a measure of the maximum sustainable swimming speeds of larvae. As temperature treatment significantly affected the length of the pelagic larval duration, we measured the critical swimming speed of larvae both at a similar age in days after hatching (dah), as well as on the day before metamorphosis for both temperature treatments. Larvae were swum 7 dah for both temperature treatments and at 11 dah for fish reared at 25 °C, an a priori sampling decision to coincide with 1 day prior to the average time taken to metamorphosis for 28 and 25 °C treatments, respectively (Green, unpublished data). This allowed for a comparison of critical swimming speed between fishes of similar absolute age as well as similar developmental age (cf. Job and Bellwood, 2000). Two fish were swum from each of the five replicate tanks from each temperature treatment (25 and 28 °C), making a total of 10 larvae per clutch swum at each temperature. To control for the effects of temperature per se on critical swimming speed, within each clutch, 6 fish randomly selected from the 28 °C treatments were swum at 25 °C, and 6 fish randomly selected from the 25 °C treatments were swum at 28 °C, (Fig. 1). Fish were acclimatised to the new swimming temperatures over 4 h prior to swimming. This experimental protocol resulted in five rearing/swimming temperature and age combinations with between 6 and 10 individual larvae used for each treatment (see Fig. 1).

2.3. Swimming experiments

Swimming experiments were carried out using a three channel experimental swimming flume (cf. Stobutzki and Bellwood, 1997). This apparatus consisted of a Perspex chamber

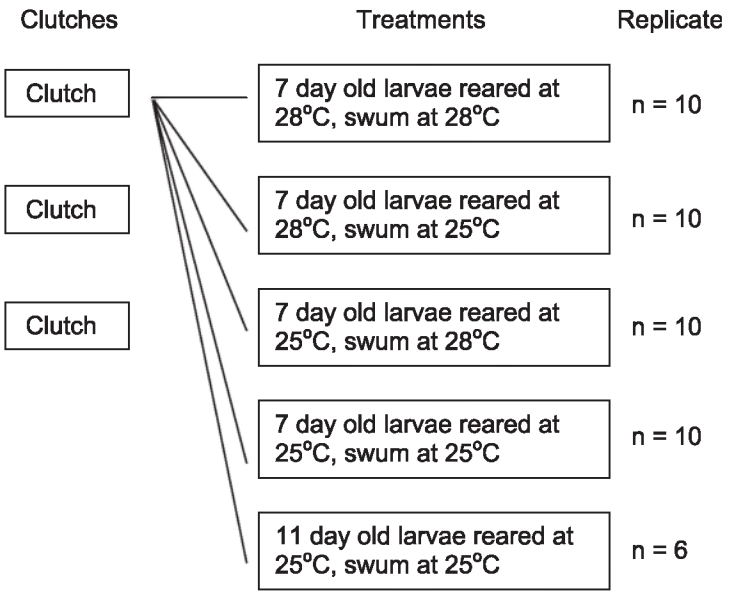

Fig. 1. Experimental design tree showing the five different treatments and levels of replication.

divided into three channels, with flow straighteners at the mouth of each channel to produce laminar flow. A 270 lpm 2.4 kW Onga™ pump circulated water through the system and a gate valve calibrated with a protractor controlled the volume (and therefore current speed). Calibration was carried out by recording the volume of water passing through the chamber over a set time period for different angles on the protractor. Recorded volumes were divided by the sum of the cross-sectional area of the each channel to determine speed.

The maximum swimming speed of larvae was determined following the methods of Bellwood and Fisher (2001). Two fish were placed in each channel and allowed to acclimatise for several minutes before the start of the experiment. The speed was then increased by three body lengths per second (2.0 cm s^{-1}) every 2 min until the fish could no longer maintain position in the swimming channel. The speed and time spent in the last interval was recorded. The critical swimming speed (U-crit) of larvae is calculated as: U-crit $= U+(t/t_i \times U_i)$, where U is the penultimate speed, U_i is the velocity increment (2 cm s^{-1}), t is the time swum in the final velocity increment and t_i is the set time interval for each velocity increment (2 min).

Fish from all swimming treatments were retained after each experiment and preserved in 70% ethanol. These samples were used to determine standard length and wet weight of larvae from each treatment for each clutch. All specimens were preserved for 2 months and treated in the same manner so any shrinkage due to ethanol storage would be proportional. As growth of *A. melanopus* is linear during the larval phase (plotted from Green and McCormick, 2001), growth rates were estimated according to the formula: $R_g=(L_s - L_h)/T_s$, where R_g is the rate of growth in mm day^{-1}, L_s is the length (mm) at sampling time, L_h is the length (mm) at hatching and T_s is the time (days) from hatching to sampling.

2.4. Comparison to other studies

To compare the Q_{10} from this study with temperate studies the changes in rates of growth (mm day^{-1}), PLD (developmental rate) and swimming performance (bl s^{-1}) from the available literature were expressed as Q_{10} values. Q_{10} is a thermodynamic expression of temperature effects and is commonly employed to standardise a rate of change in response to temperature to a common index. It describes the response of biological processes to a change in temperature of 10 °C (Schmidt-Nielsen, 1997) and can be calculated by the following equation: $Q_{10}=[R_2/R_1]^{10/(T_2-T_1)}$, where T_1 and T_2 are the temperatures over which the change was recorded, R_1 is the rate of a process at T_1, and R_2 is the rate of the process at T_2. Like many rate processes, Q_{10} varies exponentially with temperature.

Where there was a range of experimental temperature changes and related responses in the rate measured, Q_{10} was calculated between each temperature increment and the mean and standard error were calculated.

2.5. Data analysis

As there was no difference in the pelagic larval duration among the five tanks within each treatment for each clutch, a paired *t*-test (Zar, 1999) was used to test if temperature significantly increased pelagic larval duration within each clutch. A two-way factorial MANOVA (following Tabachnick and Fidell, 1996) was used to compare the size (total length and weight) of larvae from the five rearing/swimming temperature and age combinations for each clutch (Fig. 1). A second two-way factorial MANOVA was used to compare the absolute swimming speed (cm s^{-1}) and speed in body lengths per second (bl s^{-1}) of larvae from the five treatments (Fig. 1). Both MANOVAs were performed using the statistical package SPSS. The models tested in both cases were: treatment + clutch + treatment × clutch + error (as per experimental design illustrated in Fig. 1). The assumptions of homogeneity of variance and normality were tested using Levene's test and

Table 1
Two-way MANOVA comparing total length and weight across the three different clutches and among the five treatments

	F	*df*	*P*
Multivariate tests (Pillai's trace)			
Clutch	11.654	4, 166	<0.001
Treatment	13.4999	8, 166	<0.001
Treatment × clutch	1.591	16, 166	0.076
Between-subject effects (total length)			
Clutch	32.400	2, 83	<0.001
Treatment	46.993	4, 83	<0.001
Between-subject effects (weight)			
Clutch	8.773	2, 83	<0.001
Treatment	49.386	4, 83	<0.001

Between-subject effects are only shown for significant multivariate tests.

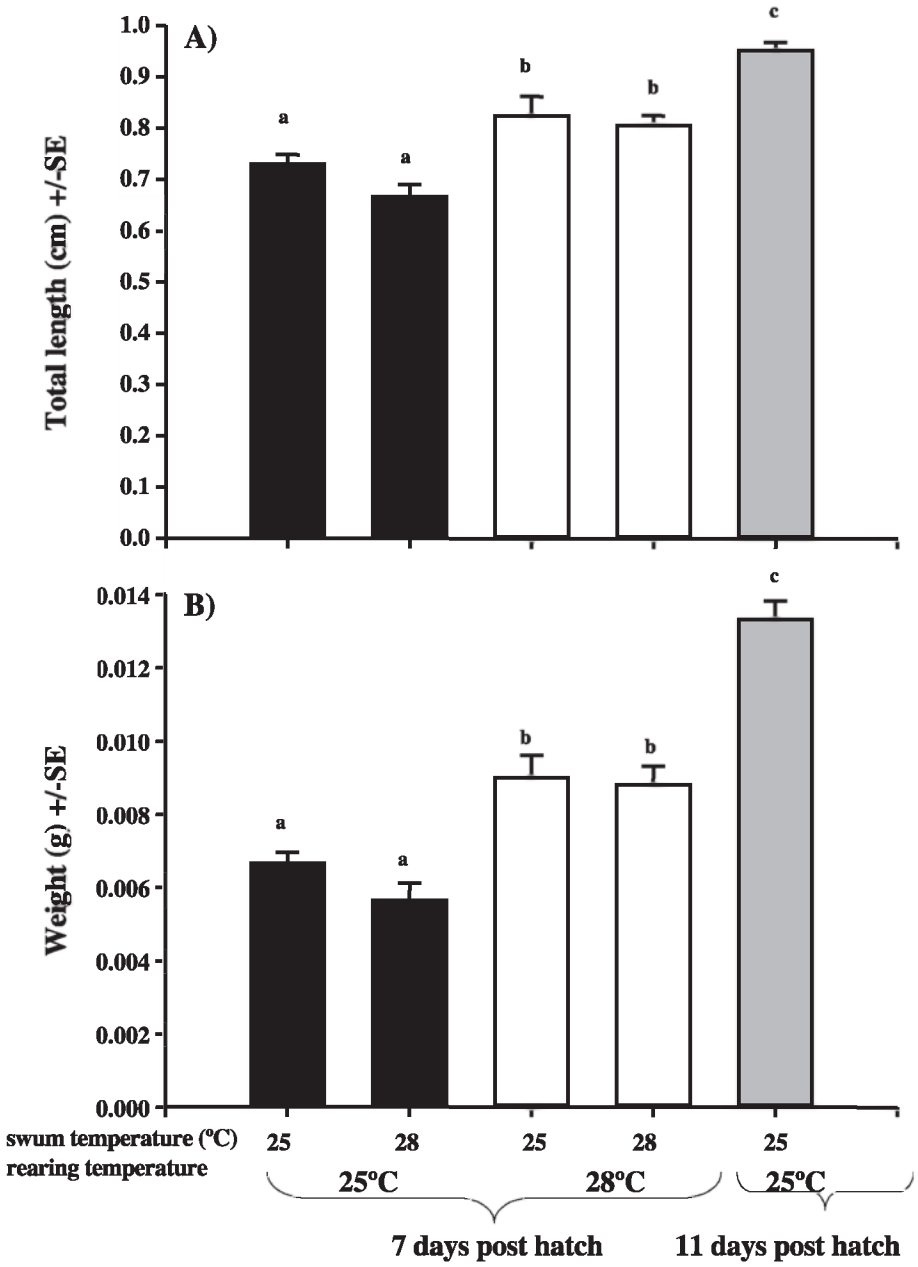

Fig. 2. Average total length (A) and weight (B) of 7-day-old fish reared at 25 °C (black bars) and 28 °C (white bars) and 11-day-old fish reared at 25 °C (grey bar). Letters above bars indicate significant subgroups. For larvae reared at 28 °C, 7-day-old fish represent 1 day prior to metamorphosis. For larvae reared at 25 °C, 11-day-old larvae represent 1 day prior to metamorphosis.

graphically using residual and qq plots and it was found that these assumptions were not violated. Pillai's trace was used as the multivariate test of significance. Significant effects were explored using univariate ANOVAs for each variable and Tukey post hoc analysis (Zar, 1999).

3. Results

3.1. Temperature effects on development rate

A lower rearing temperature significantly increased the pelagic larval duration of *A. melanopus* larvae, slowing down developmental rate such that larvae reared at 25 °C required 25% more time to reach metamorphosis. *A. melanopus* larvae reared at 28 °C metamorphosed at 9 dah (± 0.6 days) compared with 12.3 dah (± 0.3) at 25 °C ($t=9.75$, $df=2$, $p<0.05$).

3.2. Temperature effects on size

Different rearing temperatures also caused a significant difference in size of larvae between temperature treatments (Table 1). When larvae from the same clutch were reared at two temperatures, larvae cultured at the higher temperature were bigger than their siblings at the same absolute age. Seven-day-old (premetamorphic) larvae reared at 28 °C were significantly bigger than 7-day-old larvae reared at 25 °C, both in total length and weight (Fig. 2). Rearing temperature also affected size of larvae of similar developmental age, with larvae reared at a lower temperature attaining larger size for developmental age than similarly developed siblings. Premetamorphic larvae reared at 25 °C (11 dah) were significantly larger than premetamorphic reared at 28 °C (7 days after hatching; Fig. 2).

Table 2
Two-way MANOVA comparing absolute swimming speed (cm s^{-1}) and swimming speed in body lengths per second (bl s^{-1}) across the three different clutches and among the five treatments

	F	*df*	*P*
Multivariate tests (Pillai's trace)			
Clutch	67.784	4, 200	<0.001
Treatment	42.487	8, 200	<0.001
Treatment × clutch	9.661	16, 200	<0.001
Between-subject effects (cm s^{-1})			
Clutch	15.768	4, 100	<0.001
Treatment	16.906	2, 100	<0.001
Treatment × clutch	1.304	8, 100	0.250
Between-subject effects (bl s^{-1})			
Clutch	29.504	4, 100	<0.001
Treatment	12.246	2, 100	<0.001
Treatment × clutch	1.924	8, 100	0.064

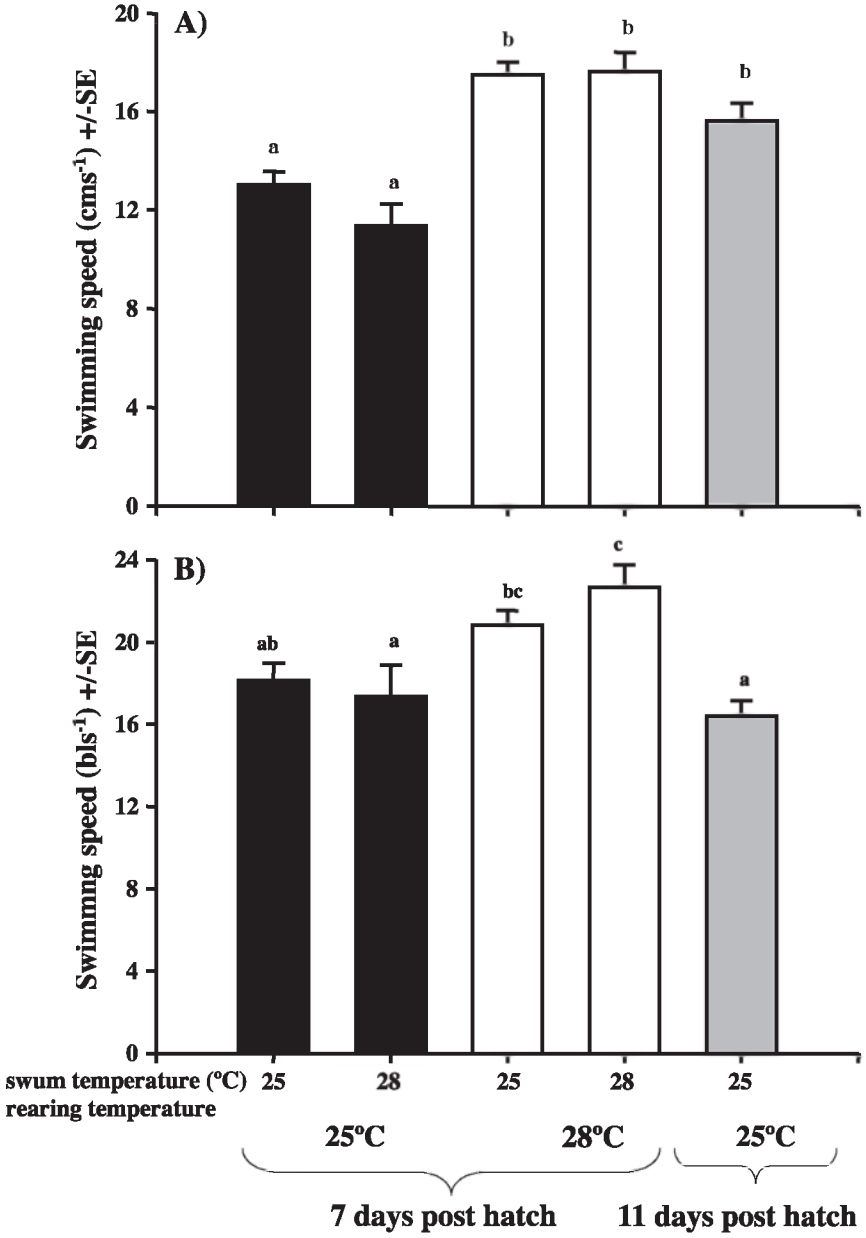

Fig. 3. Average swimming speed in centimetres per second (cm s^{-1}, A) and body lengths per second (bl s^{-1}, B) of 7-day-old fish reared at 25 °C (black bars) and 28 °C (white bars) and 11-day-old fish reared at 25 °C (grey bar). Letters above bars indicate significant subgroups. For larvae reared at 28 °C, 7-day-old fish represent 1 day prior to metamorphosis. For larvae reared at 25 °C, 11-day-old larvae represent 1 day prior to metamorphosis.

Within each rearing temperature, larvae swum at the two different temperatures were of similar size (Fig. 2).

3.3. Temperature effects on swimming speed

Temperature significantly affected the swimming performance of larvae among the five rearing/swimming temperature and age combinations identified in Fig. 1 (Table 2). At 7 dah, larvae reared at 28 °C were capable of maintaining significantly faster speeds (cm s^{-1}) than 7-day-old larvae reared at 25 °C, regardless of the temperature of the swimming experiment (Fig. 3A). However, when comparing larvae of similar developmental stage, i.e. premetamorphic larvae (7 days after hatching for 28 °C and 11 days after hatching for 25 °C), there was no significant difference in the U-crit swimming speeds achieved by larvae from each rearing temperature (Fig. 3A).

When U-crit is standardised for larval length (body lengths per second, bl s^{-1}), larvae aged 7 and 11 dah reared at 25 °C achieved slower critical swimming speeds than larvae 7 dah reared at 28 °C (Fig. 3B). While U-crit measured in absolute terms (i.e. cm s^{-1}) of premetamorphic larvae reared at 25 °C were similar to premetamorphic larvae reared at 28 °C, relative to their size their critical swimming speed was slower.

When larvae of the same age (7 dah) and from the same rearing temperature were exposed to short-term temperature change, there was no difference in their maximum sustained swimming speed (U-crit), for either absolute (cm s^{-1}) or relative (bl s^{-1}) speed (Fig. 3). Larvae reared at 28 °C and then exposed to 25 °C for 4 h and tested at this temperature did not achieve different U-crit than larvae maintained and tested at 28 °C (Fig. 3). Similarly, larvae cultured at 25 °C and then exposed to 28 °C for 4 h did not achieve different U-crit than larvae maintained and test at 25 °C (Fig. 3). Short-term temperature change had no immediate effect on U-crit, although long-term (rearing) temperature differences did.

4. Discussion

In the tropical reef fish species, *A. melanopus*, a small variation in temperature resulted in a large variation in growth, development and swimming performance. These factors individually are central to survival and dispersal for pelagic marine larvae, and in combination they are fundamental to replenishment of reef fish populations. A 3 °C reduction in rearing temperature decreased the growth, developmental rate and swimming speed in *A. melanopus* larvae. However, when multiple effects of decreased temperature were combined and developmental rate was factored in, reduced temperature resulted in presettlement larvae that were larger and capable of similar swimming speeds to larvae reared at 28 °C. While the differences in these three traits recorded at temperatures only 3 °C apart demonstrate a relatively large degree of plasticity in the larval phase of these fish in response to environmental variation, they also illustrate the importance of choosing the most appropriate endpoint for comparison. If this experiment only compared presettlement fish, then little effect of temperature on growth and swimming would be found. Conversely, if only size—and swimming—at absolute age were

compared, then the most parsimonious conclusion would be that lower temperature results in smaller, slower fish.

4.1. Ecological implications of response to temperature change

Our findings of an extended PLD coupled with decreased maximum swimming speed at lower temperature indicate that even small changes in temperature may substantially decrease the chance of survival for these reef fish larvae. It is during development in the pelagic environment that fish are the most susceptible to changes in temperature (Rombough, 1997). This stage also has the highest risk of mortality through predation or starvation (Bailey and Houde, 1989; Ferron and Leggett, 1994). Increased PLD increases the length of exposure of fish larvae to the high-risk pelagic environment, indirectly reducing probability of survival. Reduced swimming speed increases rates of predation (Miller et al., 1988) and influences the extent to which larvae can use active behaviour to modify their dispersal patterns, actively self-recruit or enhance recruitment success (Armsworth, 2001; Sponaugle et al., 2002). Replenishment of adult populations in many marine fishes occurs through a pelagic larval phase and reef fish larvae can potentially modify their patterns of dispersal during this phase using active swimming behaviour (Leis and McCormick, 2002). Swimming is also central in hunting and prey capture (Hunt von Herbing et al., 2001). The overall length of the larval phase is important to dispersal and the degree of connectivity among populations of marine fishes (Doherty et al., 1994; Riginos and Victor, 2001). Clearly, the diminished swimming performance and increased developmental time of larval *A. melanopus* in response to a decrease in temperature suggests that on coral reefs, small changes in temperature may have critical impacts on dispersal, recruitment and replenishment.

4.2. Temperature effects on swimming speed

The substantial effect of larval rearing temperature on maximum on swimming speed (U-crit) in *A. melanopus* larvae contrasts with another key finding from this study that temperature change in the immediate swimming environment did not significantly alter U-crit. Temperature change (excluding the viscous change normally associated with temperature) of the swimming test environment also did not affect the spontaneous or routine swimming activity in small larvae (9.6 ± 0.39 mm) of Atlantic herring (Fuiman and Batty, 1997). Any changes in water viscosity normally associated with decreased temperature had little effect on the swimming capability of these *A. melanopus* larvae (cf. Batty, 1984; Fuiman and Batty, 1997), although this change in viscosity may be negligible for tropical fish (Hunt von Herbing, 2002). Like most ectotherms, a fish body temperature equilibrates rapidly to its thermal environment (Taylor et al., 1997). Temperature-specific changes affect an ectotherm at the molecular and cellular level, but are associated with the whole organism adapting its energy consumption to prevailing conditions in the natural habitat (Wieser, 1973). That *A. melanopus* larvae achieved similar maximum swimming speeds (U-crit) in different swimming test water temperatures suggests that any short-term equilibration posed by the changed swimming temperature did not significantly override

the effects of the larval rearing environment. Short-term temperature change is moderated by immediate physiological or biochemical compensation of the animals to thermal change, within a thermal tolerance level (Schmidt-Nielsen, 1997). So while a long-term thermal difference during development affects the functional and developmental physiology of the animal, *A. melanopus* was able to compensate for short-term change and maintain the standard of its critical swimming performance.

The measured effects of rearing temperature on maximum sustained swimming speed of *A. melanopus* larvae are likely due to physiological or biochemical costs involved with adapting to the prevailing environmental conditions that were not measured in this study. Temperature changes can affect many of the structures that enable swimming in a developing larva. Decreased temperature can affect muscle development through reducing the rate of muscle growth and net food conversion efficiency (Hanel et al., 1996). Temperature directly influences myogenesis of the swimming muscles through a trade-off between hypertrophy and hyperplasia (Hanel et al., 1996) and reduces the rate of myofibril synthesis (Johnston et al., 2001) and number of myotomes (Hempel and Blaxter, 1961). Further, structures related to respiration develop more slowly in larvae raised at a lower temperature (Hunt von Herbing et al., 1996) and the rate of respiration, or metabolism is slower in lower temperatures (Wieser and Kaufmann, 1998). Any or all of these factors could be responsible for the reduced swimming speeds reached by larvae reared at lower temperatures.

4.3. Response relative to nontropical fishes

While it has been identified that there are differences in the response of tropical and temperate species to temperature changes throughout their development (Rombough, 1997; Hunt von Herbing, 2002), the magnitude of the change has not been previously described. Critical swimming speed was proportionally affected more per degree of temperature than in many temperate species; however, growth did not show a corresponding magnitude of change and PLD was affected less compared to temperate species (Table 3). Q_{10} values of the change in rate of swimming speed in response to temperature for temperate marine and freshwater fishes suggest that organisms from colder climates showed a smaller magnitude of change as indicated by smaller values of Q_{10} relative to our tropical species (Table 3; Hunt von Herbing, 2002). This response was predicted in a recent review on the importance of the physical properties of water to physiological function of the fishes, whereby increased temperatures may increase swimming efficiency due to a reduction in the kinematic viscosity in warm water (Hunt von Herbing, 2002).

Growth is a function of cellular activities, which are dictated by general physical laws. Therefore when temperature induced changes in growth are standardised for the degree of temperature change, similar patterns could occur across thermal ranges. The change in growth measured in *A. melanopus* ($Q_{10}=2.4$) was within the range found in other studies (Table 3), suggesting that the effect of temperature on growth rate is not greater in this tropical fish species compared to temperate regions. Growth and swimming speed show different magnitudes of response to temperature change relative to other organisms and to each other.

Table 3
Q_{10} values for three traits from the early life history of fishes reflecting the effect of a 10 °C increase in temperature on the rate of a given process

Species	Climate	Temperature change (°C)	Q_{10}	Reference
Developmental rate				
Amphiprion melanopus	trop	25–28	0.36	This study
Pseudopleuronectes americanus	temp	2–8	5.12	Laurence, 1975
Gadus morhua	temp	5–10	1.5	Hunt von Herbing et al., 1996
Brevoortia tyrannus	temp	15–20	1.83	
Brevoortia tyrannus	temp	20–25	1	Fitzhugh and Nixon, 1997
Critical swimming speed (bl s^{-1})				
Amphiprion melanopus	trop	25–28	2.74	This study
Clupea harengus U_{max}	temp	5–12	1.62	Johnston et al., 2001
Dicentrarchus labrax	temp	15–28	1.07 ± 0.13	Koumoundouros et al., 2002
Oncorhynchus nerka	temp fw	5–27	0.75 ± 0.26	Brett, 1967
Routine swimming				
Clupea harengus (TL 18.2 ± 1.8 mm)	temp	6–13	2.6* (2.2)[a]	Fuiman and Batty, 1997
Clupea harengus (TL 18.2 ± 1.8 mm)	temp	7–14	1.9* (1.4)[a]	Fuiman and Batty, 1997
Growth (mm day^{-1})				
Amphiprion melanopus	trop	25–28	2.4	This study
Channa striatus	trop/sub-trop	21.7–27	1.91	Qin and Fast, 1998
Achirus lineatus	sub-trop	24–28	1.66	Houde, 1974
Anchoa mitchilli	sub-trop	28–30	0.10	Houde, 1974
Anchoa mitchilli	sub-trop	24–28	1.67	Houde, 1974
Archosargus rhomboidalis	sub-trop	26–30	0.99	Houde, 1974
Hippoglossus hippoglossus	temp	5–8	5.3	Galloway et al., 1998
Clupea harengus	temp	10–8	0.8	McGurk, 1984
Clupea harengus	temp	8–6	1.25	McGurk, 1984
Menidia menidia	temp	17–28	4.03	Yamahira and Conover, 2002
Menidia menidia	temp	17–28	4.37	Yamahira and Conover, 2002
Anarhichas minor (eggs only)	temp	6–8	2.38	Hansen and Falk-Petersen, 2001
Anarhichas minor (eggs only)	temp	4–6	5.15	Hansen and Falk-Petersen, 2001
Morone americana	temp fw	17–21	2.68	Margulies, 1989
Morone americana	temp fw	13–17	6.42	Margulies, 1989
Perca fluviatilis	temp fw	15–20	4.79	Wang and Eckmann, 1994
Hybrid *Lepomis cyanellus* × *L. macrochirus*	temp fw	21–24	2.17	Mischke et al., 2001
Hybrid *Lepomis cyanellus* × *L. macrochirus*	temp fw	19–21	0.95	Mischke et al., 2001

All other values were calculated following $Q_{10}=[R_2/R_1]^{10/(T_2-T_1)}$, where T_1 and T_2 are the temperatures over which the change was recorded, R_1 is the rate of a process at T_1, and R_2 is the rate of the process at T_2.

[a] Corrected for viscosity.

* Denote Q_{10} values that were published in the cited reference.

4.4. Bigger is not necessarily better

The theoretical framework for development of fish larvae, based on temperate studies, suggests size is one of the central factors in survival and can manifest profound differences in success of larvae for recruitment (Miller et al., 1988) and survival (Houde, 1989). The 'bigger is better' and 'growth-mortality' hypotheses encapsulate the importance of size, whereby bigger larvae increase their chance at survival through increased ability to capture food and escape predation, (Anderson, 1988; Miller et al., 1988). For *A. melanopus*, decreased temperature reduced the absolute rate of growth and development. This resulted in smaller fish for absolute age although larger fish at settlement. These larger fish did not have better maximum sustained swimming speed, therefore would probably not have the predicted increased ability to capture food and escape predation (see Anderson, 1988; Miller et al., 1988). Size may infer better survival in an environment where competition is high (Coates, 1980; Booth, 1995) but 'bigger is better' theory becomes complicated when performance capabilities are examined. Our results suggest that under changed environmental conditions, bigger was not necessarily better as larvae raised at a lower temperature were bigger at metamorphosis but did not perform better in trials measuring critical swimming speed. Therefore the competitive advantage afforded to bigger larvae under stable conditions (e.g. Coates, 1980; Miller et al., 1988) is compromised under changed temperature conditions through decreased swimming performance. Decreased temperate also increased the time until metamorphosis in *A. melanopus*, which increases their time in the high-risk pelagic environment, further compromising the chances of survival for larvae raised at colder temperature, despite the fact they are bigger.

Given the decreased growth and development rates in response to lower temperature, it appears counterintuitive for larvae from the lower temperature treatment to be larger at metamorphosis. However, the reduction in absolute growth results in an increase in stage-specific growth because the time between intervals was increased (Atkinson, 1996). Similar relationships between the responses of growth and development to temperature change have been identified in organisms from nine phyla within four kingdoms (Atkinson, 1996).

5. Conclusions

Temperature has been considered as an influence on growth and survival of fishes for three decades (Houde, 1974); however, the implications for performance, development and plasticity are only recently being realised (Koumoundouros et al., 2002; Yamahira and Conover, 2002). Response to environmental changes must be considered within the context of an organisms normal environment, as thermal sensitivity is generally a reflection of field temperature and levels of local adaptation (e.g. van Berkum, 1986; Conover and Schultz, 1997). To date, many of the predictions regarding the biology and ecology of marine fish larvae come from models of temperate systems. These systems are characterised by large diurnal and seasonal fluctuations, and organisms that are presumably physiologically adapted to these local thermal regimes. The magnitude of the functional response in this tropical reef example suggests that using temperate models

to predict thermally induced recruitment could seriously underestimate the effect of small changes in the environment.

This paper is a significant first step in understanding how temperature changes manifest themselves on the development of tropical reef fish larvae. We concur with Conover and Schultz (1997) that bigger is not necessarily better, as size does not confer an advantage when performance is considered as well as growth in response to a change in temperature. Our results imply that temperature changes manifest themselves in a variety of ways in the pelagic larvae phase, and the different magnitude of response in growth, development and maximum achieved swimming speed emphasises the value of using measurements appropriate to the ecology of the organism. Future studies should consider performance and developmental attributes such as PLD and swimming speed and not just growth in measuring response to environmental change.

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