

Elevated temperature restricts growth potential of the coral reef fish *Acanthochromis polyacanthus*

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Received: 3 March 2008 / Accepted: 16 May 2008 / Published online: 5 June 2008
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Abstract In order to test the effect of temperature variation on the growth of a common coral-reef fish, *Acanthochromis polyacanthus*, juveniles, sub-adults and adults were reared on either high or low food rations at temperatures corresponding to the long-term (14 year) minimum, average and maximum summer sea-surface temperatures (26, 28 and 31°C respectively) at Orpheus Island, Great Barrier Reef, Australia. Both temperature and food supply affected the growth of juvenile and adult *A. polyacanthus*. Individuals grew more on high food rations, but growth declined with increasing temperature. Importantly, at 31°C, the growth of juveniles and adults on the high food ration was nearly identical to growth on the low food ration. This indicates that the capacity for growth is severely limited at higher ocean temperatures that are predicted to become the average for Orpheus Island within the next 100 years as a result of rapid climate change.

Keywords Climate change · Temperature · Growth · Food supply

Introduction

Rapid climate change over the next 50–100 years is predicted to cause an increase in average sea-surface temperatures (Guinotte et al. 2003; IPCC 2007), leading to significant impacts on important life history characteristics of marine fishes, such as growth rates, developmental schedules and reproductive output (Wood and McDonald 1997; Munday et al. 2008). The growth rate of fishes with an unlimited food supply generally increases with increasing temperature, up to an optimal temperature, after which it declines rapidly (Jobling 1997). However, food is rarely unlimited in the wild and growth of fish on a fixed ration is expected to decline with increasing temperature due to increased energetic demands from higher metabolic rate at higher temperatures. At high temperatures, growth rates of fish on high or low rations are expected to converge near zero as the thermal maximum for growth is approached (Jobling 1997). The impact of increasing sea temperatures on growth rates of marine fishes will, therefore, depend on how close populations are to their thermal optimum and maximum, and whether food is abundant or in short supply.

Although the effects of temperature and food supply on growth of temperate marine fishes have been studied in some detail (see Jobling 1997 for review; also, Buckley et al. 2004; Martell et al. 2005), much less is known about how growth rates of tropical marine fishes respond to temperature fluctuations (Munday et al. 2008). Because tropical species generally experience a narrower range of seasonal variation in sea temperature than temperate species, they may be expected to exhibit a reduced range of thermal tolerance and a more pronounced decline in growth once thermal optima are passed. This would make them particularly sensitive to increases in sea temperature as a result of rapid climate change.

Communicated by Biology Editor Dr Mark McCormick

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This study examined the interacting effects of temperature and food supply on the growth of a common coral-reef fish, *Acanthochromis polyacanthus* (Bleeker 1855). *A. polyacanthus* is an ideal species to examine the effects of temperature variation on growth because it exhibits genetic subdivision among populations at different locations on the Great Barrier Reef (GBR) (Doherty et al. 1994; Bay et al. 2006), and thus, is likely to exhibit relatively strong adaptation to local thermal environments. Local adaptation should increase the performance of individuals at the environmental conditions usually experienced, but might also make them more susceptible to rapid environmental change because gene variants that could prove useful under new conditions could have been selectively removed (Visser 2008). In order to test the effect of increased temperature on the growth of *A. polyacanthus*, juveniles, sub-adults and adults were reared at three different temperatures on either a high quantity or a low quantity diet. The rearing temperatures were chosen to represent the long-term average, minimum and maximum summer temperatures of the collection location (Orpheus Island, GBR). This experimental design was used to test if *A. polyacanthus* populations at Orpheus Island are living close to their optimal thermal range, whether growth was reduced at maximum summer temperatures and how food supply affected growth at the range of temperatures currently experienced. The experiment also enabled an investigation of how *A. polyacanthus* populations might be affected by rapid climate change, because the maximum temperature ($\sim 31^{\circ}\text{C}$) used in the experiment is likely to be experienced with increasing frequency on the GBR by the end of this century (Lough 2007).

Materials and methods

All fish were maintained at James Cook University's environmentally-controlled aquarium facility. Adult breeding pairs of *A. polyacanthus* were collected near Orpheus Island ($146^{\circ}29'\text{E}$, $18^{\circ}32'\text{S}$) on the central GBR during June and July 2005, approximately 3 months before the commencement of the experiment. Breeding pairs were housed in 70 l tanks supplied with a constant flow of aerated seawater at 28°C (range of $27.3\text{--}28.9^{\circ}\text{C}$) and fed twice daily with commercial fish-food flakes and INVE Aquaculture Nutrition 12/20 NRD pellets. Breeding pairs laid clutches of 400 to 700 eggs on the underside of a terracotta pot. Newly hatched juveniles were fed live *Artemia* nauplii at 2 ml^{-1} of the parental tank. One week after hatching, juveniles were transferred to separate 70 l tanks, where they were fed INVE Aquaculture Nutrition NRD larval pellets twice daily until required for the experiment.

All juveniles and sub-adults used in the growth experiment were offspring of the breeding pairs (above).

Adults used in the growth experiment were obtained from the Reef HQ aquarium in Townsville, where they experienced similar water temperature and day length to the central GBR. At the start of the experiment, 42 juveniles (73–92 days old), 42 sub-adults (220–235 days old) and 42 adults (2–4 years old) were randomly assigned to individual aquaria at one of six combinations of temperature (3 levels) and food supply (2 levels). Juveniles were randomly selected offspring from five parental breeding pairs and sub-adults were randomly selected offspring from three parental breeding pairs. Adults were progeny of *A. polyacanthus* at the Reef HQ Aquarium that were originally collected from the central GBR. Each aquarium had a constant flow of aerated sea water at one of three temperatures: 26°C (mean \pm sd = $26.1^{\circ}\text{C} \pm 0.25$), 28°C ($28.0^{\circ}\text{C} \pm 0.33$) or 31°C ($30.8^{\circ}\text{C} \pm 0.59$). These temperatures were chosen to reflect the minimum, average and maximum sea temperature recorded during the late spring–summer breeding season (Nov–Feb) at Orpheus Island over a 14-year period from 1992 to 2006 (Fig. 1). Lighting was set at 12 h light:12 h dark to simulate natural summer day length. Half of the fish in each temperature treatment were fed a high quantity of commercial fish pellets, sufficient to produce rapid growth and high body condition (high quantity diet) (Donelson et al. 2008). The other half were fed one third the amount of the same diet (low quantity diet). The volume of feed varied with ontogenetic stage (see below).

Twelve randomly selected juveniles and all sub-adults and adults were weighed (wet weight to nearest 0.01 g) before being transferred to individual grow-out aquaria. Juveniles were subsampled for weight estimates to limit the potential for procedure-related mortality to this relatively sensitive life-stage.

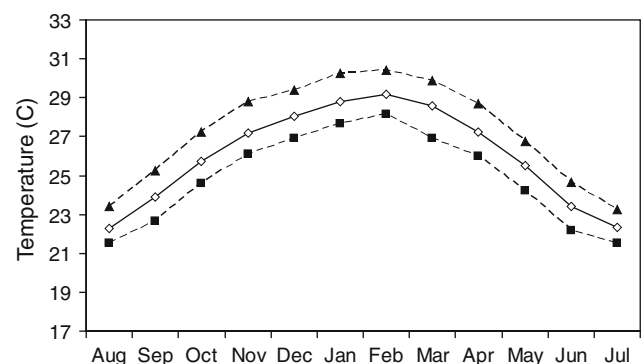


Fig. 1 Monthly average (\diamond), minimum (\blacksquare) and maximum (\blacktriangle) water temperatures at 9 m on the reef slope, Pioneer Bay, Orpheus Island between 1992 and 2006. Temperature was recorded at daily intervals by the James Cook University/Australian Institute of Marine Science weather station. Minimums and maximums are the minimum and maximum value for that month averaged over the period 1992–2006

Juveniles (average weight \pm SE: $0.51 \text{ g} \pm 0.07$) were housed in 2 l aquariums and fed approximately 2 mg of 200 micron NRD commercial fish-food pellets (protein $>55\%$, fat $>9\%$, and fibre $<1.9\%$) either twice a day (high quantity diet) or once a day, two out of every 3 days (low quantity diet). Sub-adults ($1.97 \text{ g} \pm 0.06$) were housed in 25 l aquariums and fed an alternating diet of 0.01 g of 12/20 NRD fish-food pellets and 0.01 g of Wardley Total Marine fish-food flake either twice a day (high quantity diet) or once a day, two out of every 3 days (low quantity diet). Adults ($42.5 \text{ g} \pm 1.37$) were housed in 28 l aquariums and fed an alternating diet of 0.1 g of 12/20 NRD fish-food pellets and 0.1 g of Wardley Total Marine fish-food flake either twice a day (high quantity diet) or once a day, two out of every 3 days (low quantity diet).

All fish remaining (4–6 in each treatment level) after 3 months were reweighed and growth was calculated as the difference between the start and finish weights. The average weight of the 12 juveniles measured at the start of the experiment was used as the starting weight for juveniles that were not individually weighed at the start of the experiment. A two-way factorial ANOVA followed by Tukey's post-hoc comparisons of means was used to test the effect of temperature and diet on growth for each ontogenetic stage.

Results and discussion

Both temperature ($F_{2,24} = 4.18$, $P = 0.03$) and food supply ($F_{1,24} = 16.14$, $P < 0.001$) had a significant effect on the growth of juvenile *A. polyacanthus*. Overall, growth was greater for individuals on the high quantity diet compared to the low quantity diet; however, growth declined with increasing temperature (Fig. 2a). The interaction between temperature and food was statistically non-significant ($F_{2,24} = 2.25$, $P = 0.13$), although the small sample sizes for each combination of temperature and food supply ($N = 5$) meant that the power to detect a significant effect was low (0.4). Nevertheless, there was a greater effect of temperature on growth for fish receiving the high quantity diet compared to those receiving the low quantity diet (Fig. 2a). The mean growth of individuals reared on the high quantity diet at 26°C was approximately three times that of individuals reared on the same diet at 31°C . In contrast, there was no difference in growth with increasing temperature for individuals reared on the low quantity diet (Fig. 2a).

Food supply ($F_{1,23} = 10.76$, $P = 0.003$), but not temperature, had a significant effect on the growth of sub-adult *A. polyacanthus*. There was no significant difference between low and high food diets for any single temperature (Fig. 2b); however, overall growth was higher on the high food diet ($7.73 \text{ g} \pm 0.48$) compared to the low food

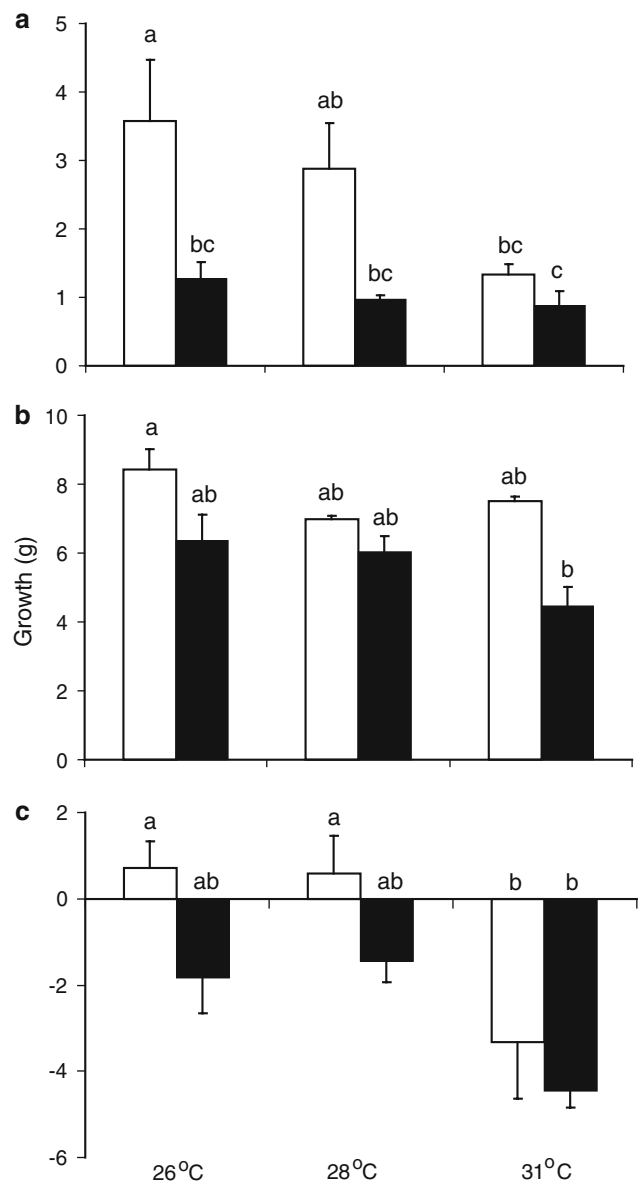


Fig. 2 Mean increase in weight \pm SE of (a) juvenile, (b) subadult and (c) adult *Acanthochromis polyacanthus* reared for 3 months at 26, 28 or 31°C on either a high (unfilled bars) or low (filled bars) quantity diet. Letters above bars indicate statistically similar means for each ontogenetic stage

diet ($5.61 \text{ g} \pm 0.43$). Both temperature ($F_{2,24} = 9.63$, $P < 0.001$) and food supply ($F_{1,24} = 6.92$, $P = 0.01$) had a significant effect on the growth of adult *A. polyacanthus*. Adults on the low quantity diet lost weight at all temperatures, indicating that this diet was insufficient to maintain a high body condition (Fig. 2c). On average, adults on the high quantity diet gained weight at 26°C and 28°C , but suffered a large decrease in weight at 31°C (Fig. 2c). Adults on the low and high quantity diet lost approximately 8% and 10% of their body weight, respectively, when reared at 31°C .

These results demonstrate that elevated water temperature had a significant effect on the growth of juvenile and adult *A. polyacanthus*. Lower growth rates at higher temperatures are expected when the food ration is fixed, because more energy is used for maintenance activities at higher temperatures, and, therefore, individuals would need to consume additional food to maintain growth rates (Jobling 1997). Importantly, these results suggest that the benefits of additional food supply on juvenile growth become diminished at higher temperatures in *A. polyacanthus*. The mean growth of juveniles on the high quantity diet at 31°C was no higher than that of juveniles reared on the low quantity diet at this temperature, in contrast to a large difference in growth between diets at 26°C. This demonstrates that the potential for growth is impaired at elevated water temperatures. Similarly, adults receiving a diet that was sufficient to increase their body weight at 26°C and 28°C experienced a substantial and significant decline in body weight at 31°C. At this temperature, the loss of condition on the high quantity diet was no different from that observed for fish on the low quantity diet. Growth of juveniles and adults was affected by temperature. In contrast, growth of sub-adults did not show a significant response to temperature, which suggests that sensitivity to temperature differs with ontogenetic stage.

The average summer sea temperature at Orpheus Island over the past 14 years has been between 28 and 29°C (Fig. 1). The average monthly-maximum sea temperature over the same time period was 30.5°C (hottest recordings = 31.8°C in Feb 2002). These results show that the growth performance of juvenile and adult *A. polyacanthus* declines markedly at the maximum sea temperatures experienced at this location. Although these maximums are only reached occasionally at present, this result has important implications for the capacity of *A. polyacanthus* to deal with rapid climate change. Average sea temperatures are predicted to increase by at least 1–3°C on the GBR over the next 50–100 years (Lough 2007) and 31°C is only 2–3°C above the long-term average summer sea temperature at Orpheus Island. Therefore, it is highly likely that temperatures near current-day maximums will become the average conditions experienced at Orpheus Island by the end of this century. *A. polyacanthus* on the central GBR will experience significantly reduced growth potential unless they acclimate or adapt to increasing sea temperature. In particular, individuals will be unable to take advantage of periods of high food supply to increase their growth or improve their body condition.

Reduced potential for growth of juveniles and adults at higher sea temperatures could have important long-term consequences for *A. polyacanthus* populations. Mortality rates of coral reef fishes are very high during the early juvenile phase (Almany and Webster 2006) and are often

size dependent (Sogard 1997; Jones and McCormick 2001). Slower growth at higher temperatures increases the mortality risk of juveniles because they remain in the vulnerable small size classes for longer. Reduced potential for growth could also affect the reproductive success of adults. *A. polyacanthus* in good body condition commence breeding earlier than individuals in poorer body condition, they have more reproductive bouts over the breeding season, each clutch contains a greater number of eggs (Thresher 1983; Donelson et al. 2008) and the newly hatched offspring are larger than offspring from parents in poor body condition (Donelson et al. 2008). Consequently, reduced capacity for adults to maintain their body condition at higher temperatures could lead to a persistent, long-term reduction in reproductive performance.

Food appears to be a limited resource for some reef fish populations (Jones and McCormick 2001), including those of *A. polyacanthus* (Thresher 1985). Even if more food was available, the results from this study show that individuals that increase their consumption rates still suffer a decline in growth if future temperatures exceed the local thermal optimum.

Genetic adaptation could moderate the effects of rapid climate change (Skelly et al. 2007). Many coral reef fishes have short generation times and some mid-latitude populations exhibit strong genetic connectivity with low-latitude populations already living at higher temperatures (Bay et al. 2006). Short generation times and gene flow from low-latitude populations might assist mid-latitude populations, such as those at Orpheus Island, adapt to increased temperature (Munday et al. 2008; Visser 2008). For *A. polyacanthus*, however, the relatively low levels of gene flow that are responsible for establishing genetic subdivision among populations will also reduce the capacity for populations of this species to adapt to increasing temperature by the flow of favourable genotypes from populations already living in warmer waters.

Acknowledgments We thank Reef HQ for supplying fish, JCU/ AIMS weather facility for the sea-temperature records, MARFU staff for assistance with the experiments and three anonymous reviewers for helpful comments on the ms.

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