



Development in a warm future ocean may enhance performance in some species



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ABSTRACT

Understanding the capacity of organisms to cope with projected global warming through acclimation and adaptation is critical to predicting their likely future persistence. The vast majority of research on tropical species suggests they will be substantially negatively affected by future warming and have limited capacity to acclimate to changes. This study tested whether the spine cheek anemonefish, *Premnas biaculeatus*, has the capacity for developmental thermal acclimation of metabolic attributes and critical thermal maximum (CT_{max}) to increasing sea water temperature. Juveniles of *P. biaculeatus* exhibited high capacity for developmental thermal acclimation of aerobic physiology. Fish reared at +1.5 °C and +3.0 °C above present-day mean temperatures possessed enhanced performance across all testing temperatures (28.5 °C to 31.5 °C), i.e. overcompensation. Specifically, this occurred through increases in maximum oxygen consumption ($MO_{2Maximum}$) that resulted in elevations in both net and factorial aerobic scope. In addition, fish reared at +1.5 °C also exhibited a partial increase in critical thermal maximum (CT_{max}) by 0.5 °C, however no increase was observed in fish reared at +3.0 °C. Fish reared at +3.0 °C were significantly longer, heavier and in better condition than +0.0 °C present-day fish, suggesting that alterations to aerobic physiology correspond to enhancement of growth and condition as would be predicted with the oxygen and capacity limited thermal tolerance hypothesis. These results indicate that the acclimation to future warming may produce overall enhanced performance in some species. It also suggests that the developmental acclimation ability varies substantially between species within the same family and a greater understanding of promoted or reduced acclimation capacity will be critically important to predicting the impacts of climate change on coral reef systems.

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1. Introduction

Tropical ectotherms are expected to be one of the most sensitive groups of organisms to global warming since they have evolved in relatively stable thermal environments (Deutsch et al., 2008; Tewksbury et al., 2008). Studies investigating the response of current populations of tropical species to future increases in environmental temperature indicate they currently live close to their thermal optimum, and any future increases are likely to produce negative effects (Stillman, 2003; Deutsch et al., 2008; Tewksbury et al., 2008). This is especially true for marine fish, which exhibit significant declines in performance with only a few degrees temperature increase above current-day summer temperatures (Nilsson et al., 2009, 2010; Donelson et al., 2010; Rummer et al., 2014). For tropical marine species, average sea surface temperature is predicted to increase up to 3.0 °C by the end of the century (Lough, 2007; Hobday and Lough, 2011; Bopp et al., 2013; Collins et al., 2013). The longer term ability of organisms to respond to this

future temperature increase is currently poorly understood. However, the response will be directly linked to range shifts (Parmesan, 2006) as well as population and species persistence at present locations (Charmantier et al., 2008; Visser, 2008; Chevin et al., 2010; Somero, 2010).

Since most marine species are ectotherms, the response of marine organisms to elevations in environmental temperature will be largely determined by the impact temperature has on the rate of cellular processes (Fry, 1967; Hazel and Prosser, 1974; Clarke and Johnston, 1999; Burel et al., 1996), and the resulting effects on performance and behaviour (Sunday et al., 2011). For aquatic ectotherms, the ability for oxygen delivery to match increased oxygen demand has been proposed as the key determinant of performance and persistence of species with warming (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Eliason et al., 2011). Specifically, as environmental temperature increases above the thermal optimum, a greater rise in resting metabolic rate (minimum energy required at rest) occurs relative to maximum metabolic rate, reducing metabolic scope for aerobic activity (the difference between maximum and resting; Pörtner, 2002; Pörtner and Knust, 2007). This response is driven by the inability of the circulatory and ventilatory system to maintain the increase in oxygen demand under

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maximal activity (Pörtner, 2002). Changes in aerobic capacity are expected to directly reduce the ability for an individual to undertake non-essential activities, including swimming, foraging, growth and energy storage (oxygen and capacity limited thermal tolerance hypothesis: OCLTT; Pörtner, 2002; Pörtner and Peck, 2010). However, the generic application of the OCLTT theory to all species and ecosystems has recently come under scrutiny (Clark et al., 2013; Gräns et al., 2014; Norin et al., 2014). An alternate theory proposes that all physiological processes may not possess the same thermal performance and optimum (multiple performance multiple optima: MPMO), and consequently aerobic capacity will not govern all other higher level performance (Clark et al., 2013).

Many tropical ectotherms may already be living close to their critical thermal maximum (CT_{max}) (corals: Hoegh-Guldberg, 1999; lizards: Tewksbury et al., 2008; insects: Deutsch et al., 2008) and while this is not likely to be the case for tropical marine fishes (Mora and Ospina, 2001; Munday et al., 2008), it is yet to be tested for most species (exceptions Eme and Bennett, 2009). CT_{max} is often correlated with optimal performance temperatures (Huey and Bennett, 1987; Garland et al., 1991) and represents the point at which cellular stress occurs due to the inability of proteins to fold, and the integrity of cell membranes becomes compromised (Hazel and Williams, 1990; Hazel, 1995; Robertson and Hazel, 1997). Cell membranes are compromised due to the excess thermal energy breaking weak bonds. This causes proteins to lose their structural stability, destabilise and restrict hydrophobic interactions (Hazel and Williams, 1990; Hazel, 1995; Robertson and Hazel, 1997). In some fishes, CT_{max} and CT_{min} can increase or decrease relative to the environmental temperature through modification to membrane composition (Robertson and Hazel, 1997; Eme and Bennett, 2009).

When individuals experience environmental changes they can modify phenotypic traits (without genetic change) in relation to the conditions experienced (Fry, 1967; Randall et al., 2000; Woods and Harrison, 2002). When the environment alters directionally it is termed acclimation and can be divided into two classes: 1) developmental acclimation which encompasses permanent responses to the environment experienced in early ontogeny and 2) reversible acclimation which includes controlled responses in relation to daily or seasonal fluctuations in the environment (Angilletta, 2009). It is expected that reversible acclimation should be favoured when environmental variation is experienced within a generation, while developmental acclimation should be favoured when the environment varies between generations (Angilletta, 2009). In both cases there are energetic costs associated with modification of morphology, behaviour or physiology in relation to the altered environment (Hoffmann, 1995; Angilletta et al., 2003). It is the costs associated with acclimation that mean it will not always be observed to be beneficial (Leroi et al., 1994; Angilletta, 2009). Generally, it is believed that acclimation of thermal limits will occur more readily than alterations to optimal performance temperature (Angilletta, 2009).

Reversible acclimation is prevalent in temperate marine fishes and is able to occur on short time scales of only days to weeks (Guderley and Johnston, 1996; Barrionuevo and Fernandes, 1998; Beitinger and Bennett, 2000; Sandblom et al., 2014). In contrast, polar species require 2 to 4 times longer to complete acclimation of similar traits (Peck et al., 2014). To date research has found no evidence for reversible acclimation in tropical coral reef fishes as adults, possibly due to the reduced seasonal thermal variation experienced (Nilsson et al., 2009, 2010; Gardiner et al., 2010; Johansen and Jones, 2011). While evidence for reversible acclimation is lacking, developmental thermal acclimation has been observed when tropical fish develop from early life at elevated water temperatures (Donelson et al., 2011; Donelson and Munday, 2012; Scott and Johnston, 2012; Grenchik et al., 2013). Specifically, when fish are reared from hatching at elevated temperatures, their performance at these warmer temperatures is greater than other individuals from the same cohort that have been reared at current-day

temperatures and then tested at elevated temperatures later in life (Donelson et al., 2011; Donelson and Munday, 2012). In these cases only partial or perfect compensation has been observed (Donelson et al., 2011; Donelson and Munday, 2012).

The aim of this study was to test the capacity for developmental thermal acclimation in the spine cheek anemonefish, *Premnas biaculeatus*, to elevated water temperatures predicted to occur by 2100. Specifically, the research aimed to understand the capacity for acclimation of a range of physiological attributes including routine oxygen consumption ($MO_{2Routine}$), maximum oxygen consumption (MO_{2Max}), net aerobic scope, factorial aerobic scope and critical thermal maximum (CT_{max}). The relationship between aerobic physiology and higher-level performance traits, including growth and condition, was explored to determine the correspondence with the OCLTT or MPMO hypotheses.

2. Materials and methods

2.1. Study species and experimental design

The spine-cheeked anemonefish, *P. biaculeatus* (Bloch 1790), is a widespread coral reef fish throughout the Indo-Pacific. *P. biaculeatus* lay benthic eggs but larvae are pelagic for approximately the first two weeks of life. This reef fish species lives in monogamous pairs where the male is generally less than half the size of the female (Fishelson, 1998; Fautin and Allan, 1992). *P. biaculeatus* are protandrous hermaphrodites with a female dominant social structure (Fautin and Allan, 1992). Established pairs of *P. biaculeatus* were collected from Bramble Reef (18°24'S, 146°42'E) located in the central region of the Great Barrier Reef during June and July 2008. Breeding pairs were transported back to the James Cook University Research Aquarium Facility in Townsville and maintained in 60 L aquaria in a closed seawater system (>16,000 L) inside an environmentally controlled room. Pairs were maintained at the mean present-day ocean temperature for the collection location, which followed natural seasonal changes in water temperature (Australian Institute of Marine Science temperature loggers 6–8 m; <http://data.aims.gov.au/>; Donelson et al., 2011). During breeding, water temperature was maintained at the average summer ocean temperature for the collection location (28.5 ± 0.3 °C). Pairs were provided with aquaculture pellets ad libitum 4–5 times per day (INVE Aquaculture Nutrition NRD G12 pellets).

Pairs of *P. biaculeatus* were provided with half a terracotta pot as a shelter, which also provided a nest site for their benthic eggs. Offspring from 5 pairs that reproduced during the austral summer November 2008 to February 2009 were utilized for the current experiment. On the night of hatching (approximately 5–6 days post-laying), clutches were transferred to a 40 L closed-system aquaria and maintained at the average present-day temperature for the collection location with constant aeration. 60–70% of the water was exchanged once a day prior to feeding and the addition of green water (microalgae) in the morning. From hatching to 6 days post-hatching, larvae were fed *Brachionus* sp. rotifers at a rate of 8 individuals ml⁻¹. After 6 days-post hatching the amount of rotifers that were provided was reduced by 1 individual ml⁻¹ every day until day 12 when rotifers were ceased. In combination, newly hatched *Artemia* sp. nauplii were introduced at a rate of 1 individual ml⁻¹ per day, from 6 until 10 days post-hatching when they were provided at 5 individuals ml⁻¹ for the remainder of the larval period. Larvae settled at approximately 14 days post-hatching.

At settlement, sibling fish were placed into individual 60 L tanks (on a partially-closed >50,000 L system) and divided randomly into 3 temperature treatments: +0.0 °C (the present-day average for the collection location, following natural seasonal changes), +1.5 °C and +3.0 °C. These elevated temperatures are likely to be experienced by 2100 (Lough, 2007; Hobday and Lough, 2011; Bopp et al., 2013; Collins et al., 2013). Natural daylight was experienced by fish throughout the experiment. From 14 to 21 days post-hatching fish continued to be fed *Artemia* nauplii at a rate of 5 individuals ml⁻¹. After 21 days,

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