

Latitudinal variation in larval development of coral reef fishes: implications of a warming ocean

I. M. McLeod^{1,2,3,4,5,*}, M. I. McCormick^{1,2}, P. L. Munday^{1,2}, T. D. Clark⁵,
A. S. Wenger^{1,2}, R. M. Brooker^{1,2,6}, M. Takahashi¹, G. P. Jones^{1,2}

¹College of Marine and Environmental Sciences, ²ARC Centre of Excellence for Coral Reef Studies,

³Estuary and Coastal Wetland Ecology Laboratory, and ⁴TropWATER (Centre for Tropical Water and Aquatic Ecosystem Research), James Cook University, Townsville, QLD 4811, Australia

⁵AIMS@JCU and Australian Institute of Marine Science, Townsville, QLD 4810, Australia

⁶School of Biology, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA

ABSTRACT: Latitudinal gradients in water temperature may be useful for predicting the likely responses of marine species to global warming. The ranges of coral reef fishes extend into the warmest oceanic waters on the planet, but the comparative life-history traits across their full latitudinal range are unknown. Here, we examined differences in early life-history traits of 2 coral reef fishes, the damselfish *Pomacentrus moluccensis* and the wrasse *Halichoeres melanurus*, among 8 locations across 21° of latitude, from northern Papua New Guinea (2.3°S) to the southern Great Barrier Reef (23.3°S). Water temperature during larval development ranged between 25.6 and 29.8°C among sites, with the warmest sites closest to the equator. Recently settled juveniles were collected and otolith microstructure was analysed to estimate pelagic larval duration (PLD), daily growth, and size at settlement. Latitudinal comparisons revealed a non-linear relationship between temperature and each of PLD, larval growth and size at settlement. PLD declined with increasing temperature up to approx. 28 to 29°C, above which it stabilised in *P. moluccensis* and increased in *H. melanurus*. Larval growth increased with increasing temperature up to approx. 28 to 29°C before stabilising in *P. moluccensis* and decreasing in *H. melanurus*. Size at settlement tended to be highest at mid-latitudes, but overall declined with increasing temperature above 28.5°C in both species. These results indicate that the thermal optima for growth and development is reached or surpassed at low latitudes, such that populations at these latitudes may be particularly vulnerable to global warming.

KEY WORDS: Climate change · Growth rate · Life history plasticity · Latitudinal comparison · Lemon damselfish · Pelagic larval duration · Tail-spot wrasse · Thermal reaction norm

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INTRODUCTION

There is an urgent need to better understand how organisms respond to changing temperatures as overwhelming evidence for rapid global warming accumulates (Bopp et al. 2013, IPCC 2013). The latitudinal ranges of some marine and terrestrial species are shifting poleward in response to increasing tem-

peratures (Hickling et al. 2006, Chen et al. 2011, Poloczanska et al. 2013). Tropical species are predicted to be among the most sensitive to global warming as they already experience high temperatures, with relatively little seasonal change (Tewksbury et al. 2008). Yet, many tropical species are distributed over a broad latitudinal range and their responses to the gradient in temperatures across

their range can provide clues as to how they will respond to a markedly warmer climate (Deutsch et al. 2008, Dillon et al. 2010, Sunday et al. 2011). In particular, establishing the relationships between latitude and critical life-history traits will assist in defining the thermal reaction norm (*sensu* Angilletta 2009) for these traits and indicate how close populations are to their thermal limits.

The persistence of populations in a changing climate will be constrained by their most vulnerable life stages or reproduction (Pankhurst & Munday 2011). For many marine fish species it is the small pelagic larval life stage that is the most vulnerable to environmental stressors such as temperature changes (Pankhurst & Munday 2011, Pörtner & Peck 2011). The larval stage is critically important for dispersal and connectivity among adult populations (Cowen & Sponaugle 2009, Jones et al. 2009). Since mortality rates are extremely high during this life phase (Leis 1991, Peck et al. 2012), small changes in larval growth, developmental, or survival rates could have large impacts on adult population dynamics. For example, Lo-Yat et al. (2011) documented a severe reduction in larval supply to the adult reef fish population in French Polynesia associated with abnormally warm waters during an El Niño event. Therefore, identifying temperature effects on fish larvae is essential to predict the impacts of climate warming on marine fish populations and fisheries.

In the tropics, reef-building corals appear to be close to their thermal maxima and episodes of mass coral bleaching in response to extreme temperatures are predicted to become more common as the oceans continue to warm (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2007). However, we are only beginning to understand how coral reef fishes will respond to temperature change. To predict future responses to temperature change it is critical to define the thermal reaction norms (the shape of the relationship between a particular trait and temperature). Thermal reaction norms typically exhibit a dome-shaped relationship, where rates increase with temperature up to an optimal level (thermal optimum) then decrease gradually with further increases in temperature (Pörtner & Farrell 2008, Tewksbury et al. 2008). However, most research to date has shown that the thermal reaction norms for growth of larval fishes tend to be approximately linear until an upper lethal temperature is reached (Sponaugle & Cowen 1996, Rombough 1997). Meta-analyses (Houde 1989, Laurel & Bradbury 2006), experiments (McCormick & Molony 1995, Green &

Fisher 2004) and field studies (Meekan et al. 2003, Sponaugle et al. 2006) have indicated that larval growth rates generally increase with increasing temperature. Additionally, within the temperature range currently experienced by reef fishes, warmer years generally appear to favour recruitment for a variety of coral reef fishes (Meekan et al. 2001, Wilson & Meekan 2002, Cheal et al. 2007). Based on this knowledge, it is predicted that climate warming could have positive outcomes for coral reef fish larvae because enhanced growth will lead to faster metamorphosis and less time spent in the dangerous pelagic environment (O'Connor et al. 2007). However, mortality rates may be higher and larvae may be smaller at settlement, which may counter this effect.

Many species of coral reef fishes are distributed across a large latitudinal range from the equator to subtropical waters (Jones & McCormick 2002). Indeed, many span temperature ranges that are actually greater than the projected increase in ocean temperature by the end of the century (Munday et al. 2008). With a few notable exceptions (Booth & Parkinson, 2011, Takahashi et al. 2012), there is little information on intraspecific latitudinal variation in important early life-history traits of tropical fishes across their distribution range. Few studies of larval fish development in relation to temperature have included populations at latitudes close to the equator, which may be particularly sensitive to global warming (Sunday et al. 2011, Rummer et al. 2014). Indeed, recent research has indicated that in the warmest waters close to the equator (Takahashi et al. 2012), abnormally warm water during El Niño events (Lo-Yat et al. 2011) or elevated temperatures in line with ocean-warming predictions (McLeod et al. 2013) are associated with slower larval growth and reduced survival. However, no studies have examined the thermal responses of existing populations of larval fishes over their entire latitudinal range, which would provide a means to gauge the shape of their thermal reaction norms. Leis et al. (2013) emphasised the urgent need for more studies investigating latitudinal and temperature effects on larval life history traits to improve understanding of connectivity and dispersal patterns, inform fisheries management and conservation, and predict climate-driven changes to marine systems.

Larval fishes exhibit 3 interrelated developmental traits that have a bearing on successful recruitment to the adult populations and will likely respond to changes in temperature: larval growth, pelagic larval duration (PLD) and size at settlement. Increased

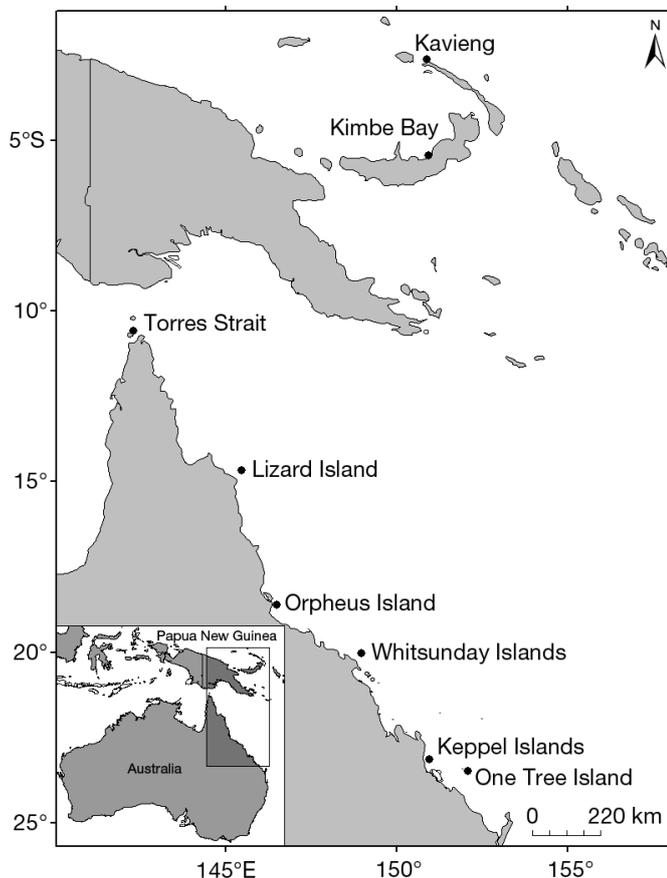


Fig. 1. Location of study sites where *Pomacentrus moluccensis* and *Halichoeres melanurus* were sampled in Eastern Australia and Papua New Guinea: One Tree Island (23°30'S, 152°04'E), Keppel Islands (23°10'S, 150°57'E), Whitsunday Islands (20.03°S, 148°57'E), Orpheus Island (18°37'S, 146°29'E), Lizard Island (14°40'S, 145°27'E), Torres Strait (10°34'S, 142°18'E), Kimbe Bay (5°25'S, 150°56'E) and Kavieng (2°36'S, 150°52'E)

growth rates are likely to lead to reduced PLD because there are strong negative correlations between growth rates and PLD, with fast-growing larvae often exhibiting shorter larval duration (Houde 1989, McCormick & Molony 1995, Sponaugle & Cowen 1996, Green & Fisher 2004). The relationship between growth rates and PLD will influence size at settlement (Sponaugle et al. 2006), which is important because a larger size at settlement can be associated with increased growth and survival after settlement (Sogard 1997).

The relationship between developmental temperature and size at settlement of coral reef fishes generally follows the 'developmental temperature-size rule' (Atkinson 1994) with a larger settlement size at lower temperatures (McCormick & Molony 1995, Radtke et al. 2001, Green & Fisher 2004,

Sponaugle & Grorud-Colvert 2006). The relationship between larval life-history traits and temperature has mostly been studied in laboratory experiments, or using temporal variation in temperature within a single location or region, and few studies have examined relationships among larval life-history traits across the entire latitudinal temperature range of a species.

The aim of this study was to examine the effects of a temperature gradient on key early life-history traits of 2 coral reef fishes across their entire latitudinal range in the southern hemisphere. We sampled recently settled juveniles of the yellow damselfish *Pomacentrus moluccensis* and the tail-spot wrasse *Halichoeres melanurus* from 8 locations that spanned 21° latitude, from the southern Great Barrier Reef (GBR) to within 2° of the equator in northern Papua New Guinea (PNG; Fig. 1). Pelagic larval duration, pre-settlement growth rates, and size at settlement were estimated by examining the microstructure of otoliths (ear bones), which exhibit daily rings and settlement marks. The variations in these traits were examined in relation to the average water temperatures experienced by the larvae during development to determine if the reaction norms were linear among latitudes, as suggested by existing experimental and observational studies, or if there is a shift in the shape of the reaction norm at higher temperatures close to the equator.

MATERIALS AND METHODS

Study species and collection

The yellow damselfish *Pomacentrus moluccensis* (Pomacentridae; Bleeker, 1853) and the tail-spot wrasse *Halichoeres melanurus* (Labridae; Bleeker, 1851) are common in shallow coral reefs in the Western Pacific (Randall et al. 1990, Green 1998). *P. moluccensis* lay demersal eggs during a reproductive season from October to March on the GBR (Milicich et al. 1992, Booth et al. 2000), and throughout the year in equatorial regions such as northern PNG (Srinivasan & Jones 2006). *H. melanurus* is a broadcast spawner with a reproductive season ranging from December to February at Lizard Island in the northern GBR (Green 1998), to year-round in equatorial regions (Srinivasan & Jones 2006). Previous estimates suggest that *P. moluccensis* and *H. melanurus* have free-swimming pelagic phases lasting 15 to 23 d (Wellington & Victor 1989, Bay et al. 2006a) and 20 to 24 d (Victor 1986), respectively.

To investigate variation in larval traits in relation to latitude and water temperature, newly settled individuals (*P. moluccensis*: <25 mm total length [TL]; *H. melanurus*: <30 mm TL) were collected from the reef using hand nets and clove oil anaesthetic from 8 and 7 locations respectively, spanning a latitudinal gradient of 21° from near the equator in PNG to the southern GBR (Fig. 1). Samples were collected from 2009 to 2013, at times when young recruits were available and collection was logistically possible. After capture, fish were euthanized on ice and TL was measured to the nearest 0.1 mm using callipers.

Otolith preparation and analysis

A pair of otoliths (sagittae) were extracted from each fish, cleaned in distilled water and stored dry. A transverse cross-section through the nucleus of one otolith was prepared as described by Wilson & McCormick (1997). Each sectioned otolith was viewed through a compound microscope, using immersion oil at 200 to 400× magnification, and 1 to 6 digital images were taken, depending on the size of the otolith. If >1 image was taken, images were merged using Adobe Photoshop v.6. The otolith radius, the longest distance from the core to the settlement mark, and the hatch ring radius were measured from the merged photograph using image analysis software (ImageJ v.1.45s, National Institutes of Health).

The settlement mark of *P. moluccensis* was characterised by a sudden decline in daily ring increment widths (Type I transition mark; Wilson & McCormick 1999). The settlement mark of *H. melanurus* was characterised by a wide band (Type II transition mark; Wilson & McCormick 1999). For *H. melanurus* we interpreted the inner edge of the transition band to indicate settlement, corresponding to the time at which settling larvae began metamorphosis, and the outer edge of the band as corresponding with the completion of metamorphosis as described by Victor (1982).

The number of daily increments from the nucleus to the settlement mark was counted to estimate PLD for *P. moluccensis*. For *H. melanurus* we added 2 d to the count of pre-settlement increments to account for the time between fertilisation and deposition of daily increments, as being typical of wrasse species (Victor 1982, Cowen 1991). The number of days post-settlement was estimated by counting the number of rings after the settlement mark. Blind

counts of daily increments were conducted twice. A third blind count was conducted when the error between the first 2 counts was >10%. When the closest 2 of the 3 counts differed by >10% the slide was rejected (N = 11). When slides were accepted, an average of the 2 counts was used for further analysis.

Daily rings have previously been validated for *P. moluccensis* (Brunton & Booth 2003). We assumed otolith growth rings were daily for *H. melanurus* because (1) daily growth rings have been validated for the congeneric species *H. miniatus* (Munday et al. 2009) and *H. bivittatus* (Victor 1982), and (2) in a pilot study we established there was a strong linear correlation ($r^2 = 0.87$) between the number of days post-hatch and the TL of 190 juvenile *H. melanurus* (11.6 to 27.7 mm TL; I. M. McLeod unpubl. data, see Supplement at www.int-res.com/articles/suppl/m521/p129_supp.xls). TL (mm) at settlement of newly settled juveniles was back-calculated following the biological intercept method developed by Campana & Jones (1992), using the equation:

$$L_S = L_C + (O_a - O_c) \times (L_c - L_0) \times (O_c - O_0)^{-1} \quad (1)$$

where L_S is length at settlement, L_C is length at capture, L_0 is length at age zero, O_a is otolith radius at settlement, O_c is otolith radius at capture, and O_0 otolith radius at hatch. L_0 was taken to be 2.5 mm for *P. moluccensis* (Fisher 2005) and 1.62 mm for *H. melanurus* (estimated as the mean larval size at hatching of 2 congeneric species, *H. poecilopterus* and *H. tenuispinnis*; Kimura et al. 1998). When hatch rings were not clear enough to measure accurately (N = 53 among species) the mean hatch ring diameter calculated for the particular species and location was used. Independent sample *t*-tests showed that there were no significant differences in any of the performance variables tested between the fish with measured otolith radiuses at hatch and those with estimated otolith radiuses at hatch. Average pre-settlement growth rates (mm d^{-1}) were calculated by dividing the estimated changes in TL of each fish by their individual PLD. The date of settlement of individual fish was estimated by subtracting post-settlement age (days) from the sample collection date, plus 5 d of metamorphosis for *H. melanurus*. The estimate of 5 d was used because (1) this is the mean number of days for metamorphosis to complete for the congeneric species *H. bivittatus*, and (2) it was possible to discern several (usually 5) faint increments making up the transition band in some otoliths.

Water temperature data

Historical temperature data (2004–2012; Fig. 2) for sites except Kavieng were obtained from 2 subtidal temperature loggers at 0.5 to 10 m depth at each site (accessed from the Australian Institute of Marine Science website: <http://data.aims.gov.au/seatemp>, downloaded 1 February 2013). Historical temperature data (2004–2012) for Kavieng were obtained from the Integrated Global Ocean Services System satellite sea surface temperatures taken in 1° latitude/longitude grids near Kavieng (2.5°S, 150.5°E). The time period 2004–2012 was chosen for the long-term averages because that time period had the most complete data available. Water temperature during the PLD for each fish was calculated as the mean temperature for the site, between the individual estimated hatching date and settlement date. Because there were no temperature data available for when the fish collected from Torres Strait were in their pelagic larval stage, the mean temperature during the same days of the year (2004–2012) in the Torres Strait was used. Because of the differences in the timing of sampling, the average (mean \pm SE) temperature experienced by larvae at locations did not always reflect what would be expected along the latitudinal gradient.

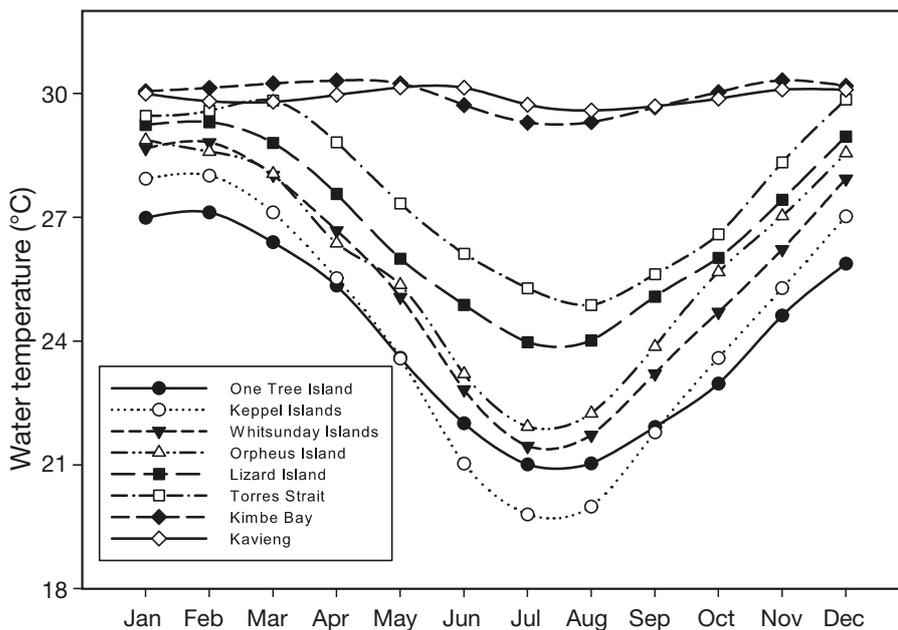


Fig. 2. Monthly average water temperature (2004–2012) at the study sites: One Tree Island, Keppel Island, Whitsunday Islands, Orpheus Island, Lizard Island, Torres Strait, Kimbe Bay and Kavieng (see Fig. 1 for locations)

Statistical analysis

ANOVA was used to compare mean PLD, pre-settlement growth rates, and settlement size among locations. Assumptions of homogeneity of variance and normality were examined using residual analysis. Tukey's tests were used to distinguish any significant difference among means found through ANOVA. Variation in early life history traits in relation to temperature and among latitudes was analysed using quadratic regression analysis of the mean values of each trait for each site. Because we predicted that temperature would have a greater effect than site and we were most interested in the effects of temperature on early life history traits among locations rather than at specific sites, site was not included in the regression model. SPSS Statistics v.21 (IBM) was used for all statistical analyses.

RESULTS

Pelagic larval duration

Pelagic larval duration ranged from 16 to 24 d for *Pomacentrus moluccensis* and 19 to 27 d for *Haliichoeres melanurus*. Despite high levels of variability within locations, PLDs were significantly different among latitudes (Tables 1–3). Developmental temperature explained 44% of the variation in *P. moluccensis* PLD and 34% of the variation in *H. melanurus* PLD among latitudes. Latitudinal variations in PLD exhibited curvilinear relationships with water temperature (Fig. 3a,b). *P. moluccensis* PLDs were longest at the Whitsunday Islands where larvae experienced the coolest developmental environment and shortest at Torres Strait and northward where developmental temperatures were $>28.5^{\circ}\text{C}$ (Fig. 3a). *H. melanurus* PLDs were longest at Orpheus Island where larvae experienced the coolest developmental environment and shortest at Lizard Island where developmental temperatures were $\sim 29^{\circ}\text{C}$ (Fig. 3b). Thus, temperatures

Table 1. *Pomacentrus moluccensis*. Mean (\pm SE) water temperature that larval fish were exposed to, and pelagic larval duration (PLD), growth rate and settlement size (total length) of sampled populations. Homologous subgroups as differentiated using Tukey's tests are displayed by the capital letters after the performance variable values

Location	Sampling month	n	Water temp. ($^{\circ}$ C)	Latitude ($^{\circ}$ S)	PLD (d)	Growth rate (mm d^{-1})	Settlement size (TL, mm)
Kavieng	Aug 2011	39	29.8 \pm 0.02	2.36	18.3 \pm 0.20 (A)	0.67 \pm 0.01 (A)	12.1 \pm 0.12 (A)
Kimbe Bay	Oct 2009	31	28.4 \pm 0.01	5.25	18.6 \pm 0.15 (AB)	0.67 \pm 0.01 (A)	12.4 \pm 0.12 (AB)
Torres Strait	Dec 2011	28	28.2 \pm 0.09	10.34	18.0 \pm 0.20 (A)	0.69 \pm 0.01 (A)	12.3 \pm 0.13 (ABC)
Lizard Island	Jan 2011	37	29.7 \pm 0.02	14.40	19.1 \pm 0.17 (BC)	0.63 \pm 0.01 (B)	12.0 \pm 0.09 (ABCD)
Orpheus Island	Dec 2009	30	26.2 \pm 0.06	18.37	20.4 \pm 0.19 (DE)	0.62 \pm 0.01 (B)	12.6 \pm 0.13 (CD)
Whitsunday Islands	Nov 2010	43	25.6 \pm 0.05	20.03	21.8 \pm 0.19 (F)	0.58 \pm 0.01 (C)	12.7 \pm 0.12 (CD)
Keppel Islands	Jan 2010	29	28.0 \pm 0.04	23.10	19.8 \pm 0.22 (CD)	0.68 \pm 0.01 (A)	13.4 \pm 0.12 (DE)
One Tree Island	Feb 2013	24	27.0 \pm 0.09	23.30	21.4 \pm 0.27 (EF)	0.61 \pm 0.01 (BC)	13.0 \pm 0.17 (E)

Table 2. *Halichoeres melanurus*. Mean (\pm SE) water temperature that larval fish were exposed to, and pelagic larval duration (PLD), growth rate and settlement size (total length) of sampled populations. Homologous subgroups as differentiated using Tukey's tests are displayed by the capital letters after the performance variable values

Location	Sampling month	n	Water temp. ($^{\circ}$ C)	Latitude ($^{\circ}$ S)	PLD (d)	Growth rate (mm d^{-1})	Settlement size (TL, mm)
Kavieng	Aug 2011	39	29.8 \pm 0.01	2.36	23.7 \pm 0.18 (A)	0.55 \pm 0.01 (A)	10.55 \pm 0.08 (A)
Kimbe Bay	Oct 2009	26	28.9 \pm 0.03	5.25	22.4 \pm 0.18 (B)	0.59 \pm 0.02 (B)	10.66 \pm 0.12 (A)
Torres Strait	Dec 2011	32	28.5 \pm 0.08	10.34	21.8 \pm 0.24 (B)	0.59 \pm 0.01 (B)	10.74 \pm 0.14 (A)
Lizard Island	Feb 2011	21	28.7 \pm 0.02	14.40	21.7 \pm 0.28 (B)	0.63 \pm 0.02 (C)	11.00 \pm 0.23 (AB)
Orpheus Island	Dec 2009	31	26.1 \pm 0.01	18.37	25.3 \pm 0.20 (C)	0.53 \pm 0.01 (A)	11.49 \pm 0.15 (BC)
Whitsunday Islands	Mar 2012	19	28.0 \pm 0.11	20.03	24.3 \pm 0.29 (A)	0.59 \pm 0.01 (B)	11.76 \pm 0.15 (C)
Keppel Islands	Jan 2010	22	28.0 \pm 0.02	23.10	23.3 \pm 0.23 (A)	0.61 \pm 0.02 (BC)	11.78 \pm 0.20 (C)

around 28.5 to 29.0 $^{\circ}$ C appear to be optimal for minimising PLD in these species.

Larval growth

Average daily growth ranged from 0.48 to 0.81 mm d^{-1} for *P. moluccensis* and 0.45 to 0.77 mm d^{-1} for *H. melanurus*. Despite high levels of variability within locations, growth rates were significantly different among latitudes (Tables 1–3). Latitudinal variation in larval growth was best described by a curvilinear relationship with water temperature (Fig. 3c,d). *P. moluccensis* larval growth was slowest at the Whitsunday Islands where larvae experienced the coolest developmental environment and fastest at Torres Strait where developmental temperatures were \sim 29 $^{\circ}$ C (Fig. 3c). *H. melanurus* larval growth was slowest at Orpheus Island where larvae experienced the coolest developmental environment and fastest at Lizard Island where developmental temperatures

Table 3. Results of ANOVA comparing early life-history traits of *Pomacentrus moluccensis* and *Halichoeres melanurus* among populations sampled. PLD: pelagic larval duration

Life-history trait	df	F	p
<i>P. moluccensis</i>			
PLD	7, 263	52.4	< 0.001
Growth rate	7, 263	13.0	< 0.001
TL at settlement	7, 263	22.7	< 0.001
<i>H. melanurus</i>			
PLD	6, 191	35.4	< 0.001
Growth rate	6, 191	15.2	< 0.001
TL at settlement	6, 191	14.6	< 0.001

were \sim 28.5 $^{\circ}$ C (Fig. 3d). Temperature explained 28.9% of the variation in *P. moluccensis* growth and 39.6% of the variation in *H. melanurus* growth among latitudes. Temperatures around 28.0 to 29.0 $^{\circ}$ C appear to be optimal for maximising growth rates in these species.

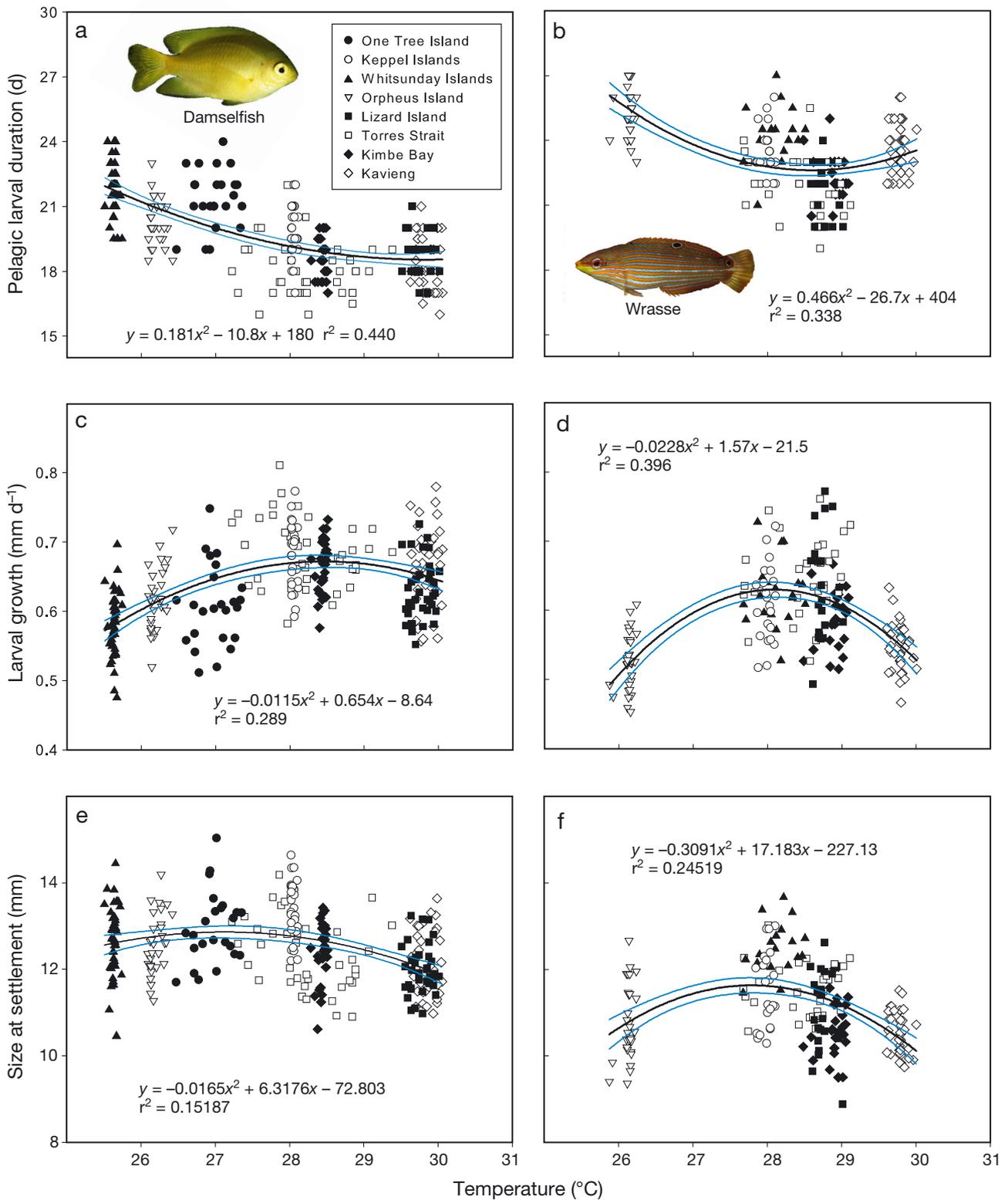


Fig. 3. (a,b) Pelagic larval duration, (c,d) pre-settlement growth rates, and (e,f) total length at settlement of *Pomacentrus moluccensis* (left panels) and *Halichoeres melanurus* (right panels), in relation to mean water temperature during larval development at 8 locations: One Tree Island, Keppel Islands, Whitsunday Islands, Orpheus Island, Lizard Island, Torres Strait, Kimbe Bay, and Kavieng. Figure shows the statistical outputs of the regressions, regression lines and 95 % confidence intervals of the regression model

Settlement size

Size at settlement ranged from 10.45 to 15.03 mm TL for *P. moluccensis* and 8.88 to 14.00 mm TL for *H. melanurus*. Temperature explained 15.2 and 24.5% of the variation in size at settlement of *P. moluccensis* and *H. melanurus*, respectively. Despite high levels of variability within locations, size at settlement was significantly different among latitudes and changed in a curvilinear manner with temperature (Tables 1–3, Fig. 3e,f). Size at settlement was highest at moderate temperatures and latitudes, and generally declined above 28.5°C. The smallest *P. moluccensis* sizes at settlement were found in Kavieng and Lizard Island and the largest at the Keppel Islands (Table 1, Fig. 3e). The smallest *H. melanurus* sizes at settlement were found in the PNG sites of Kavieng and Kimbe and the largest at the Keppel and Whitsunday Islands (Table 2, Fig. 3f).

DISCUSSION

The potential impacts of global warming across latitudes remain poorly understood. In this study, we showed that the latitudinal patterns of PLD, larval growth and size at settlement of 2 coral reef fish species were significantly correlated with water temperature. Among latitudes the thermal reaction norms for PLD, larval growth rate, and settlement size were non-linear, with the major shift in the relationships between temperature and all 3 traits occurring at 28 to 29°C. The decrease in growth rates at the warm sites closer to the equator contrasts with predictions of previous studies that suggested linear increases in growth rate across the natural thermal range. Curvilinear responses to temperature are a general indication of thermal thresholds and optima for fitness-related traits (Pörtner & Farrell 2008, Angilletta 2009). The slower growth and development rates in warmer waters close to the equator suggest that those populations may be already living at temperatures beyond the optimum for these traits.

The thermal optimum for growth and development of the 2 coral fishes in this study appears to be around 28 to 29°C; above these temperatures, the thermal optimum may be exceeded. The observed positive correlations between growth rate and temperature, and negative correlation between PLD and temperature up to 28.5°C, are consistent with previous studies on larval coral reef fishes (McCormick & Molony 1995, Wilson & Meekan 2002, Meekan et al. 2003, Green & Fisher 2004, Takahashi

et al. 2012). Sponaugle et al. (2006) found a linear relationship between growth and temperature in the coral reef wrasse *Thalassoma bifasciatum*, but recruitment declined above 28.5°C, suggesting a thermal threshold had been reached. Takahashi et al. (2012) found a linear increase in the larval growth of *Pomacentrus moluccensis* with increasing temperature (25.4 to 29.3°C) during the breeding season (November to February) at Lizard Island. However, developmental temperatures were higher at Lizard Island when samples were collected for the present study (29.7°C mean), and *P. moluccensis* larval growth rates were lower than the maximum growth rates found by Takahashi et al. (2012), indicating that optimal temperatures for growth might have been surpassed at this location when temperatures increased above 29.3°C. Additionally, experimental evidence was provided by McLeod et al. (2013), who raised larval *Amphiprion percula* at current day temperature and an elevated temperature (+3°C) and found very limited capacity for extra growth when abundant food was provided, and severely reduced growth at the elevated temperature when food was restricted. Interestingly, a recent study into the effects of temperature on the larval development of a tropical echinoderm *Acanthaster planci* showed that development rates, normal development and larval size were optimal at a similar temperature, 28.7°C (Lamare et al. 2014).

Increased water temperature is expected to accelerate physiological processes in larvae, provided temperatures do not exceed the thermal optima for this life stage (Munday et al. 2008). Larval coral reef fishes can have exceptionally high rates of aerobic metabolism (Nilsson et al. 2007, McLeod et al. 2013) during this period of rapid growth and ontogenetic development, which have been shown to increase with elevated temperatures for a larval coral reef damselfish (McLeod et al. 2013). Elevated routine metabolic rate and therefore energy use at higher temperatures may leave less energy available for growth, especially if food supplies are low or digestive capacity is limited, and this may have contributed to the lower growth rates in the warmest waters in the present study.

The observed dome-shaped patterns of the relationship between larval traits and temperature may be explained in part by local adaptation of northern populations. There is ample evidence of within-species temperature-dependant physiological responses of early life history traits. However, the actual effects in nature might be minimised through adaptation of key traits. The high levels of gene flow in

coral reef fishes, including *P. moluccensis*, between latitudes on the GBR (Doherty et al. 1995, Bay et al. 2006b, Jones et al. 2010) might limit the potential for local adaptation. In contrast, strong genetic structure has been described between populations of coral reef fish species in Kimbe Bay (and presumably Kavieng) and the GBR (Messmer et al. 2005, Jones et al. 2010), possibly as a result of landmasses serving as a barrier to larval dispersal. The isolation of these northern populations may have facilitated regional adaptation to the thermal environment, and consequently a different temperature dependency. However, in the present study there was little difference in the relationship between temperature and early life history traits among populations from the GBR and the northern PNG sites. There is potential for an interaction of epigenetic effects with genes and location, with environmental factors affecting the expression of genes only regionally even though all populations have the same genes. It is not possible to assess this tentative hypothesis using the current data set, but it offers an intriguing opportunity for further research. Despite the potential for local adaptation there is evidence for a species-wide optimal temperature for growth and development.

Local environmental factors other than temperature no doubt also contributed to the observed differences in larval traits among locations. In larval fishes, the process of growth reflects the interaction of an individual's developmental physiology with a range of physical and biological factors (Bergenius et al. 2005), such that location-specific environmental factors apart from developmental temperature can have important effects. Prolonged larval development can be associated with poor environmental conditions, such as reduced food or sub-optimal temperatures, so that it takes longer for the larvae to reach a state where they are developmentally prepared for metamorphosis (McCormick & Molony 1992, 1995, Green & Fisher 2004, McLeod et al. 2013). Other physical factors apart from temperature or food supply can also have important effects on larval development. For example, wind speed and direction determine small-scale turbulence in the water column and may indirectly influence how larvae encounter and capture prey (Bergenius et al. 2005), turbidity levels can have important effects on feeding success (Peck et al. 2012), and excess turbidity can delay larval development (Wenger et al. 2014). Variation in solar radiation and along-shore wind, but not developmental temperature, accounted for the majority of the variability in larval growth of a coral reef surgeonfish *Acanthurus chi-*

rugus at San Blas archipelago in Panama (Bergenius et al. 2005). Hydrodynamic regimes are also likely to vary among latitudes (Leis et al. 2013). Few studies exist of the effects of physical oceanographic processes on latitudinal differences in dispersal. However, there is a general pattern of increasing wind and eddy forming currents in mid to high latitudes and this may also be the case for high-latitude tropics (Leis et al. 2013). Variation in physical oceanic processes may influence availability of planktonic food for larvae and their interaction with suitable settlement habitat, and this may influence larval development and duration. The magnitude of influence of other environmental factors apart from temperature cannot be answered with the current data set, but this is an intriguing subject for future studies. Differences in these environmental factors undoubtedly influenced the rates of growth and development measured in the present study; yet despite this, temperature-related patterns in growth and development were evident.

Larval body size at settlement was highly variable at all sites and weakly correlated with temperature. Most (75 to 85%) of the variability in size at settlement was due to site-specific differences other than developmental temperature. Size at settlement likely depends on complex, site-specific interactions among temperature, food supply, oceanographic processes, predation, and availability of suitable settlement habitat. Despite the weak correlation between temperature and size at settlement in the present study, the patterns generally followed the prediction of the 'developmental temperature-size rule' with smaller sizes being present at elevated temperatures closer to the equator. Size at settlement for both species tended to decline at the warmest temperatures. Sponaugle et al. (2006) suggest that the negative correlation between settlement size and water temperature, also found in previous studies (McCormick & Molony 1995, Radtke et al. 2001, Green & Fisher 2004), is related to the length of time spent in the pelagic environment, with slow-growing larvae in cooler water settling at larger size because they spend more time in the planktonic stage. However, this hypothesis relies on there being adequate food supply to fuel this growth. Size at settlement may reflect trade-offs between spending longer in the dangerous pelagic environment, and settling too small or with poor body condition with consequent negative effects on post-settlement survival. The absence of differences in size at settlement among the GBR sites as predicted by the temperature-size rule might reflect

differing food levels or other site-specific environmental factors.

Settlement size plays an important role in influencing the mortality rates of recently settled juvenile fish, which is estimated to be as high as 25% on the first day after settlement (McCormick & Hoey 2004). A larger size at settlement may offer some survival advantages (Sogard 1997, Perez & Munch 2010). However, larger size at settlement does not always lead to higher survival because the optimal settlement size may be dependent on site-specific biological factors, including the composition and abundance of predatory species and the types and availabilities of habitat (Levin 1994, McCormick 1994). For example, Grorud-Colvert & Sponaugle (2011) showed that survival rates of a coral reef wrasse *Thalassoma bifasciatum* were higher at smaller settlement sizes. Size-selective mortality could have influenced the patterns of size at settlement found in this study because recently settled fish may have been selectively predated upon before capture. As ocean temperatures increase with global warming it could be expected that larval fish will metamorphose and settle at smaller sizes in the future but the consequences of this change are currently unknown.

The thermal reaction norms for important larval traits were broadly similar for the 2 study species from different families with different breeding modes (benthic egg laying vs. broadcast spawner). The fact that they are similar over such an extensive latitudinal range implies that both species are thermal generalists. They may be more resilient to thermal variation than thermal specialists that have smaller geographic ranges centred on the equator (Calosi et al. 2010). Our results contrast to those of Booth & Parkinson (2011) who showed that the PLD of 2 species of *Chaetodontidae* (butterflyfish) was similar across 23° of latitude. However, the closest site to the equator in their study was at Lizard Island (14.4°S), thus it is unknown if the PLDs of the 2 species of *Chaetodontidae* follow a similar pattern of increasing PLDs closer to the equator as was found in the present study. Further research into variation in the relationship between larval traits and temperature among species will be important for predicting the impacts of climate warming on fish communities and their associated fisheries.

O'Connor et al. (2007) present a unified model for the temperature dependence of larval development in marine animals based on a meta-analysis of published laboratory studies. Recent studies have used the results of this meta-analysis to predict that PLDs will be reduced and larval survival will increase in a

warming ocean, influencing connectivity and dispersal patterns (e.g. Munday et al. 2009, Kendall et al. 2013, Underwood et al. 2013). Our findings have new implications for predicting the consequences of global change on marine species. They strongly suggest that there may be latitudinal variation in the impacts of ocean warming on larval coral reef fishes, with populations closer to the equator at particular risk. We predict that coral reef fish larvae at high latitudes are likely to grow faster and settle earlier with small increases in ocean temperature (as predicted by existing models), but at lower latitudes the thermal optimum may be exceeded with global warming leading to slower growth and extended PLD. However, further research into other species will be required to assess the generality of these predictions.

Climate change models predict an increase in global sea surface temperatures of 2.2 to 3.8°C by the end of the 21st century under 'business as usual' scenarios of carbon emissions (Bopp et al. 2013). This may take many populations closer to the equator up to their thermal limit, and those currently at their limit may be severely impacted by changes in larval development and survival. Similar latitudinal variation in vulnerability patterns have been described for terrestrial ectotherms, suggesting that many populations close to the equator are already living towards the upper edge of their thermal limits, and will be highly vulnerable to a changing climate.

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