

# Thermal tolerance of the nektonic puerulus stage of spiny lobsters and implications of ocean warming

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**ABSTRACT:** Recent recruitment declines in important spiny lobster fisheries worldwide have triggered conjecture about negative impacts of anthropogenically induced environmental change on their long-lived planktonic larval life stages. Puerulus larvae are the critical transitional stage between pelagic larval development and coastal juvenile recruitment and may be particularly sensitive to environmental change due to immature cardiorespiratory capacity and exceptional energy demands associated with shoreward migration. We measured *Sagmariasus verreauxi* pueruli energy metabolism and defined their thermal tolerance, which are considered against published coastal recruitment data and spatially explicit ocean warming scenarios. The upper threshold of the thermal optimum window (upper pejus temperature range) was defined by the temperature optimum for aerobic scope. Within the upper pejus temperature range, pueruli had diminished aerobic capacity for physiological performance and used more of their finite lipid reserves to support an amplified metabolism. Sea surface temperatures at the northern extent of their natural range already reach the upper pejus range, and monitoring settlement data from the wild indicated that fewer puerulus successfully recruit during hot seasons in this area. Our study provides some evidence that physiological thermal tolerance constraints are already limiting post-larval recruitment. Predicted increases in water temperatures for their rapidly warming habitat will amplify the thermal challenge experienced by pueruli and may result in large shifts in lobster distribution and significant re-shuffling of species assemblages, creating challenges for sustainable natural resource management.

**KEY WORDS:** Ecophysiology · Larvae · Metabolism · Recruitment · Climate change · *Sagmariasus verreauxi* · Temperature

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## INTRODUCTION

Immature anatomy and physiology and the complexity of larval life strategies of highly fecund marine species makes them sensitive to environmental change. Small changes in success during the larval stages can greatly impact population dynamics, and accordingly, ocean warming is expected to have a major effect on the distribution and abundance of marine species through the influence on post-larval recruitment (Pörtner & Peck 2010). The pelagic larval life cycle of spiny lobsters (family Palinuridae) is

among the longest of any marine invertebrate and can last for up to 2 yr (Phillips et al. 2006a), making patterns in coastal recruitment particularly vulnerable to climate change. Spiny lobster larvae settle in shallow inshore waters as pueruli, which are a lecithotrophic transitional stage between pelagic phyllosoma larval development and benthic juveniles (Fitzgibbon et al. 2014). Shoreward migration involves active swimming and includes diurnal migration through the water column, which presents a substantial energetic challenge (Jeffs et al. 1999, 2005, Fitzgibbon et al. 2014). The duration of the

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puerulus stage in the wild is largely unknown, and in culture, it has been shown to be highly temperature-dependent, ranging between 12 and 40 d (Matsuda et al. 2001, Phillips et al. 2006a, Fitzgibbon et al. 2014). Considerable seasonal fluctuations in pueruli recruitment can occur related to oceanic conditions, influencing productivity, which impacts the capacity of the planktotrophic phyllosoma to accumulate energy reserves, as well as advective physical processes, which may impede the migration to shore (Caputi et al. 2010). Recently, there has been a disturbing global trend for unprecedented puerulus recruitment failure in some of the world's largest lobster fisheries (Ehrhardt & Fitchett 2010, Linnane et al. 2010, 2013, Feng et al. 2011). In several of these fisheries, egg production has remained stable, implying that large-scale environmental factors may be influencing larval performance, and some have suggested links to climate change (Pecl et al. 2009, Caputi et al. 2010, 2013, Johnson et al. 2011, Saunders et al. 2012, Fitzgibbon et al. 2014).

Environmental temperature has strong and systematic impacts on biological processes at all levels of organization, from cells to ecosystems, and is arguably the most influential environmental factor affecting the distribution and abundance of marine ectotherms (Harley et al. 2006, Richardson 2008, Dell et al. 2014). The thermal physiology of species or specific life stages plays a dominant role in determining geographical boundaries of species populations. An understanding of thermal responses can therefore be valuable in forecasting species' vulnerability to environmental change (Pörtner & Knust 2007, Pörtner & Farrell 2008, Pörtner 2010). Oxygen and capacity-limited thermal tolerance theory (OCLTT) hypothesizes that the mismatch between the oxygen demand and oxygen supply to the tissues is the first mechanism restricting performance at the limits of the thermal tolerance window of marine organisms (Pörtner 2001, Pörtner & Knust 2007). According to the OCLTT, oxygen supply to the tissues is best within the optimal temperature range, which lies between the lower and upper pejus temperatures, which are less extreme than the critical limits and represent thermal transitions that are more ecologically relevant (Frederich & Pörtner 2000, Pörtner & Peck 2010).

The thermal tolerance of aquatic organisms is not uniform throughout development and may be reduced during the early and late life stages (Pörtner & Farrell 2008). Limited thermal tolerance occurs in larvae due to immature cardiorespiratory development and high energy demands. Lobster pueruli have both

underdeveloped oxygen delivery capacity and exceptionally high energy demands associated with inshore migration, making them a potentially thermally limited bottle neck within the spiny lobster life cycle (Fitzgibbon et al. 2014). The physiological thermal tolerance window of pueruli of any species has not been examined; however, studies of the preceding phyllosoma stages demonstrate that lobster larvae become increasingly sensitive to high water temperatures, particularly during the final stages before metamorphosis to pueruli (Matsuda & Yamakawa 1997, Fitzgibbon & Battaglene 2012b).

Lipids accumulated during the phyllosoma phase are the principle energy source used to fuel shoreward transport (Jefferies et al. 1999, Phillips et al. 2006b, Limbourn & Nichols 2009). While pueruli have evolved several energy-saving mechanisms, including reduced basal metabolism and limited aerobic scope, many may be unable to fuel the journey or arrive at settlement with insufficient energy reserves to support post-settlement survival (Phillips et al. 2006b, Fitzgibbon et al. 2014). The effect of temperature on puerulus energy substrate use has not yet been examined; however, suboptimal temperature can alter the substrate use of phyllosoma to fuel the energy requirements (Bermudes & Ritar 2004). Evaluation of the quotient of oxygen consumption and ammonia-nitrogen excretion rates (O:N ratio) provides a useful assessment of physiological stress as it presents a measure of the integration of physiological functions and gives some indication of the catabolic balance between the energy substrates (Johns 1981, Bermudes & Ritar 2004).

Extreme temperatures may also affect the metabolic pathways used to fuel energetic costs. High temperatures can influence both the magnitude and duration of anaerobic metabolism of aquatic animals, and at extreme temperatures, elevated oxygen consumption rates after anaerobic activity, termed excess post-exercise oxygen consumption (EPOC), can increase to levels beyond the recovery capability of the animal (Brett 1964, Lee et al. 2003, Zeng et al. 2010). The EPOC represents the amount of oxygen required to restore tissue and cellular homeostasis after exhaustive activity and can be used to assess the magnitude of anaerobic performance, aerobic fitness, and recovery rate of aquatic animals (Lee et al. 2003, Zeng et al. 2010).

Among Palinurid lobsters, the eastern rock or packhorse lobster *Sagmariasus verreauxi* provides a particularly important subject for elucidating species response to climate change because it populates one of the fastest-warming regions in the southern hemi-

sphere (Johnson et al. 2011, Hobday & Pecl 2013). *S. verreauxi* occur in the water off the east coast of Australia (28° S to 42° S) and the north island of New Zealand, where ambient temperatures can range between approximately 12 and 28°C (Montgomery et al. 2009). Based on climate change models, sea surface temperature in waters off south-eastern Australia could increase by 1.5 to 3°C by the year 2070, making it one of several global warming hot spots around the world (Lough et al. 2012, Hobday & Pecl 2013).

We hypothesize that physiological thermal constraints of the puerulus stage limit the geographic distribution and abundance of post-larval recruitment of spiny lobsters. The study aimed to (1) establish the thermal tolerance of *S. verreauxi* based on OCLTT, (2) establish if thermal tolerance constraints could explain recent low recruitment in several fisheries worldwide, and (3) investigate pueruli thermal constraints under projected global warming scenarios that will underpin forecasts of the influence of ocean warming on spiny lobster fisheries. The study used measurements of aerobic capacity and aspects of energy use (O:N ratio and EPOC) to define the physiological thermal tolerance of pueruli. We examined temperature-acclimated pueruli to best reflect thermal response to chronically warming oceans.

## MATERIALS AND METHODS

### Experimental animals

Captive broodstock *Sagmariasus verreauxi* were maintained at the Institute for Marine & Antarctic Studies (IMAS), Hobart, Australia. Larval hatching occurred from 3 females, and phyllosoma were cultured to the final instar as described by Fitzgibbon & Battaglene (2012a,b). Individual final instar (Instar 17) phyllosoma were randomly removed from mass culture and placed into replicated 2 l cylindrical vessels which received flow-through filtered seawater at 5 exchanges per hour where the phyllosoma were observed daily for metamorphosis. After metamorphosis, individual pueruli were maintained for 5 or 6 d at 21°C before the water temperature was changed to the treatment temperature. Pueruli were then acclimated to the treatment temperatures for 2 to 3 d before sampling for respiratory experiments. The age of the pueruli at sampling was from 7 to 9 d post metamorphosis (mean =  $7.9 \pm 0.2$  d,  $n = 24$ ), which is within the stable intermoult phase of the moult cycle of *S. verreauxi* pueruli (Fitzgibbon et al. 2014).

### Experimental design

We examined the effects of 6 water temperatures, 15, 18, 21, 24, 27, and 30°C, which span the range of temperatures throughout the species' current natural geographical range and under a predicted global warming scenario. The metabolism of 4 independent pueruli was examined per temperature. Wet weight of pueruli was  $0.29 \pm 0.02$  g, and carapace length was  $10.1 \pm 0.2$  mm ( $n = 24$ ).

### Respirometry

Pueruli oxygen consumption rates were measured within an automated twin chamber intermittent flow-through respirometer system composed of two 19 ml glass micro-respiration chambers with internal diameter of 22.2 mm and a length of 45 mm (CH10650, www.loligosystems.com). A twin channel peristaltic pump was used to continuously circulate water at a rate of  $10 \text{ ml min}^{-1}$  through the chambers and past an oxygen sensor where dissolved oxygen was recorded and logged every 20 s by a fibre optic oxygen microsensor meter (OXY-4 mini, www.preSens.de), interfaced with a laptop computer. A second twin channel peristaltic pump was used to introduce new water from an external water bath at  $14 \text{ ml min}^{-1}$ . This pump was connected to a digital recycler timer, which was programmed to turn on and off in 10 min cycles; alternating the chambers between closed and flow-through cycles every 10 min allowed a pueruli oxygen consumption rate measurement every 20 min. The respirometer chambers were submerged within a water bath that received seawater at a rate of 6 exchanges per hour from a 20 l insulated sump, which was heated from 15°C to the treatment temperatures ( $\pm 0.2^\circ\text{C}$ ) by a thermostatically controlled immersion heater. Air delivered through an aquarium air stone maintained dissolved oxygen in the external water bath at 100% saturation. The water bath housing the chambers was enclosed in a black box to exclude light and external stimuli, and dissolved oxygen within the respiratory chambers never fell below 85% saturation during oxygen consumption rate measurements. Following each experiment, the respirometer system was sterilized with a  $1 \text{ mg l}^{-1}$  solution of sodium hypochlorite, rinsed with fresh water, and air dried. Evaluation of oxygen consumption rates and metabolic states was similar to that described by Fitzgibbon et al. (2014). Individual pueruli were placed into the respirome-

ter chamber in the late afternoon, and oxygen consumption was logged overnight for 16 h, during which time approximately 48 individual measurements of each pueruli routine metabolic rate were obtained (Fig. 1). From these 48 measurements, standard metabolic rate (SMR) was defined as the mean of the lowest 10% of the oxygen consumption rate recordings (5 recordings), and routine metabolic rate (RMR) as the average of all recordings (Fig. 1). Pueruli were then removed from the respirometer and swam till exhausted by encouraging pueruli by hand to swim along a 4 m long channel for 10 min. Pueruli would typically become exhausted and non-responsive to stimuli by hand before the 10 min was completed. The protocol was maintained to keep in time with the open cycle of the respirometer system, allowing for immediate oxygen consumption measurement once the animal was placed back in the chamber. Three pueruli EPOC rates were recorded at 10, 30, and 50 min post-exhaustion. Active metabolic rate (AMR) was defined as the maximum EPOC recording, which was typically the first recording after exhaustive exercise. Duration of EPOC was determined as the time when EPOC fell to levels that were not significantly different from pre-exhaustion RMR levels. Puerulus aerobic scope was determined by subtracting the SMR from the AMR. Immediately after respiratory measurements, pueruli were re-

moved from the chambers, carapace length (CL) was measured using a projector microscope, and wet weight (WW) was recorded after drying the pueruli with paper towel. Oxygen demand of the respirometer system with the pueruli removed was then recorded for 1 to 2 h as a measure of background respiration.

### Ammonia-nitrogen excretion

Ammonia-nitrogen excretion rates of pueruli were determined in respirometer chambers during the final oxygen consumption rate measurements of both RMR and EPOC protocols, representing the routine and active metabolic states for ammonia-nitrogen excretion, respectively. For these measurements, the respirometer system closed-cycle duration was manually extended for 50 min to allow the accumulation of ammonia. Respiratory chamber water was immediately collected in acid-washed glass vials, a small drop of chloroform was added to inhibit bacterial growth, and the samples were stored at  $-18^{\circ}\text{C}$  for later analysis. The ammonia-nitrogen concentration was determined spectrophotometrically using the salicylate-hypochlorite method in which indophenol blue is produced by the reaction of ammonia with salicylate and hypochlorite (Bower & Holm-Hansen 1980). Ammonia-nitrogen excretion rates were also corrected for background levels of ammonia (background levels were generally below detectable limits) and expressed as  $\mu\text{g NH}_4\text{-N g}^{-1} \text{ dry weight (DW) h}^{-1}$ . Atomic O:N ratios were determined as the quotient of simultaneous measurements of oxygen consumption rate ( $\text{mmol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ) and ammonia excretion recordings ( $\text{mmol NH}_4\text{-N g}^{-1} \text{ DW h}^{-1}$ ).

### Seawater temperature data

Seawater temperatures were described using BRAN2p1 (Bluelink ReANalysis v. 2.1), a 3-dimensional multi-year ensemble optimal interpolation reanalysis applied to a global ocean general circulation model (Oke et al. 2008, Schiller et al. 2008). Data were extracted for the years 1992 to 2007, focusing on the months coinciding with the highest reporting of *S. verreauxi* puerulus settlement (September to January) (Montgomery & Craig 2005). Daily sea surface

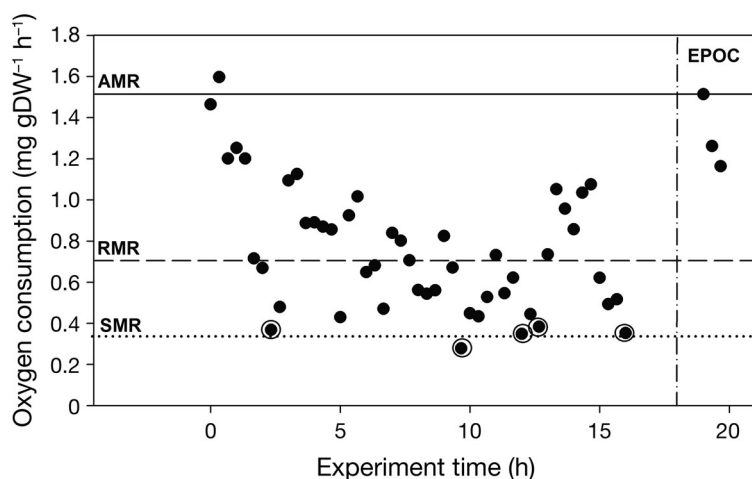


Fig. 1. Example of a single respiration trial for *Sagmariasus verreauxi* pueruli (Trial 1 at  $21^{\circ}\text{C}$ ), which demonstrates metabolic state determination. Dotted line represents the standard metabolic rate (SMR) as the mean lowest 10% of recordings (circled dots). Dashed line indicates the routine metabolic rate (RMR) as the average of all recordings (dots). Measurements made after the vertical dashed and dotted line represents excess post-exercise oxygen consumption rate (EPOC) recordings. Solid line represents the active metabolic rate (AMR), which was defined as the maximum EPOC recording. DW: dry weight

temperature estimates are produced by the BRAN model at a horizontal resolution of  $1/10^\circ$ . These data were extracted for a domain encompassing the East Coast of Australia ( $10^\circ\text{S}$  to  $45^\circ\text{S}$ ,  $140^\circ\text{E}$  to  $160^\circ\text{E}$ ). Furthermore, mean daily temperature values from a shelf and shelf break domain off Sydney Harbour ( $33^\circ$  to  $34^\circ\text{S}$ ,  $151.5^\circ$  to  $152.5^\circ\text{E}$ ) were calculated to generate a single, daily time series of sea surface temperature (SST). The same approach was taken to produce an average time series of SST in the region east of Coffs Harbour ( $30^\circ$  to  $31^\circ\text{S}$ ,  $153.1^\circ$  to  $154.1^\circ\text{E}$ ). The Sydney region represents the peak post-larval settlement region, while Coffs Harbour is considered the northern extent for *S. verreauxi* puerulus settlement (Montgomery & Craig 2005).

### Puerulus recruitment data

Recruitment data for the seasons 1995–96 to 2002–03 at the Sydney and Coffs Harbour regions were obtained from Montgomery & Craig (2005) and represent a standardized mean of *S. verreauxi* pueruli and early-instar juvenile recruits per settlement collector during the September to January settlement period. At each location, 3 replicate seaweed type collectors were sampled every 4 wk during the first quarter of the lunar month, and the numbers were summed to give the total number of recruits per collector per year at each site (Montgomery & Craig 2005).

### Ocean warming scenarios

To estimate future SST in the regions of interest as well as more broadly across the eastern seaboard of Australia, we used an ensemble analysis of climate change models, focusing on 2 future Special Report on Emissions Scenarios (SRES: A2 and A1FI). Models used in the analysis were produced for the Intergovernmental Panel on Climate Change Third Assessment Report (IPCC 2007) and accessed via OzClim ([www.csiro.au/ozclim/home.do](http://www.csiro.au/ozclim/home.do)) (Ricketts & Page 2007, Hobday 2010). Changes are expressed to a baseline Global Climate Change Model (GCM) field for the years 1990 to 2000, such that absolute change is determined by adding the change to the baseline. Within OzClim, we used the mean SSTs from an ensemble of 9 GCMs for each SRES scenario and month in the years 2050 and 2100 interpolated to the same spatial resolution ( $10\text{ km}$ ) as used for the historical SSTs produced using the BRAN2p1 product.

### Statistical analysis

Oxygen consumption rates of pueruli were determined by applying linear regressions to the rate of decline of dissolved oxygen concentration over the final 9 min of each 10 min respirometer closed cycle period. On occasion when linear regression coefficients were  $R^2 < 0.96$ , data for that period were excluded from analysis (accounted for  $<4\%$  of measurements). Mean recorded levels of background respiration accounted for 21.9% (SD = 8.7%,  $n = 26$ ) of recorded oxygen consumption rate measurements and were subtracted. Mass-specific oxygen consumption rates expressed as  $\text{mg O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ . Pueruli DW was approximated as 22% of the recorded wet mass of individuals based on the average moisture content of intermoult *S. verreauxi* (Fitzgibbon et al. 2014).

Exponential regressions were fitted to raw data to describe the relationship between pueruli SMR and RMR with temperature, with ANOVA used to test for significance. Regressions for SMR and RMR were not extended past  $27^\circ\text{C}$  due to the failure of the exponential relationship at  $30^\circ\text{C}$ . Quadratic polynomial regression and ANOVA were used to test the significance of the relationship between AMR and aerobic scope with temperature. Optimum temperature ( $T_{\text{opt}}$ ) for aerobic scope was calculated as the maximum zero solution to the first derivative of the quadratic regression. Two-way ANOVA was used to test the effect of metabolic state (routine or active) and temperature on either nitrogen excretion or the O:N ratio, and Tukey's B posteriori analysis was used to assess the differences among factors. Two-tailed independent *t*-tests were used to test the difference between EPOC and pre-exhaustion RMR. Statistics were performed with SPSS 16.0 for Windows. Values are given as means  $\pm$  SE, and significance levels were set at  $p < 0.05$ .

## RESULTS

### Metabolic rates and aerobic scope

Between 15 and  $27^\circ\text{C}$ , *Sagmariasus verreauxi* pueruli SMR and RMR increased exponentially with temperature (Fig. 2a, Table 1). At  $30^\circ\text{C}$ , pueruli SMR and RMR fell to  $>1$  SE below the projected exponential regression fitted to the data from 15 to  $27^\circ\text{C}$ . The decoupling of the exponential relationship of SMR with temperature indicates that the upper critical temperature ( $T_c$ ) was reached from 27 to  $30^\circ\text{C}$ . A sig-



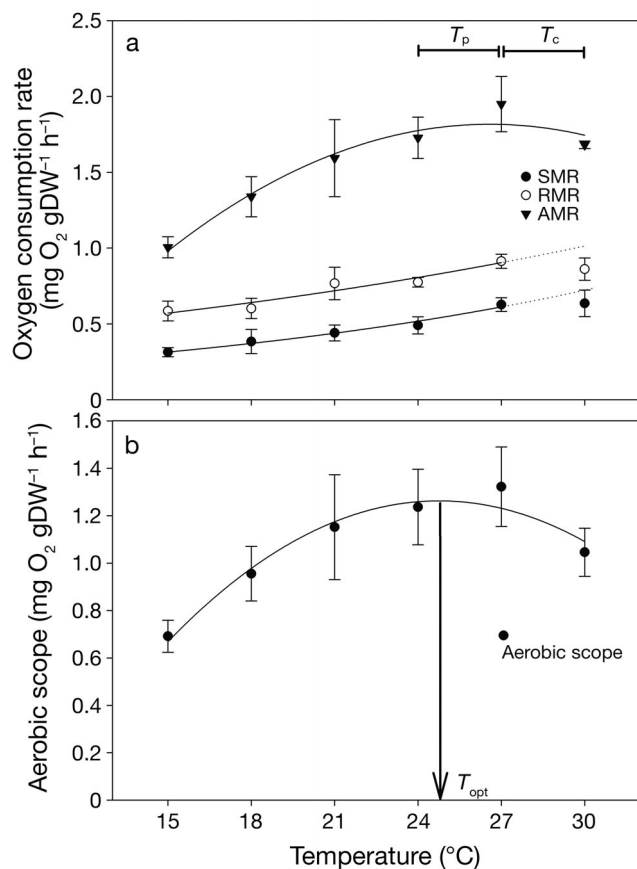


Fig. 2. Effect of temperature on the (a) standard (SMR), routine (RMR), and active (AMR) metabolic rates and (b) aerobic scope of *Sagmariasus verreauxi* pueruli. Values are means  $\pm$  SE (n = 4). Details on regression lines through data are shown in Table 1. Arrow specifies the temperature optimum (T<sub>opt</sub>) for aerobic scope. T<sub>p</sub> and T<sub>c</sub> indicate the pejus and critical temperature ranges, respectively. DW: dry weight

nificant quadratic polynomial regression described the effects of temperature on pueruli AMR. Maximum levels of AMR were recorded at 27°C, and AMR declined sharply at 30°C AMR. The influence of temperature on pueruli aerobic scope was best described by a significant quadratic relationship (Fig. 2b, Table 1). Peak pueruli aerobic scope, as represented by the T<sub>opt</sub>, was recorded at 24.9°C, indicating that the upper pejus range of *S. verreauxi* pueruli was reached from 24 to 27°C. At 30°C, the aerobic scope was considerably reduced.

### Ammonia-nitrogen excretion

Pueruli ammonia-nitrogen excretion was affected by temperature, being significantly elevated at 30°C within the critical temperature range (Fig. 3a, Table 2). Ammonia-nitrogen excretion of pueruli was

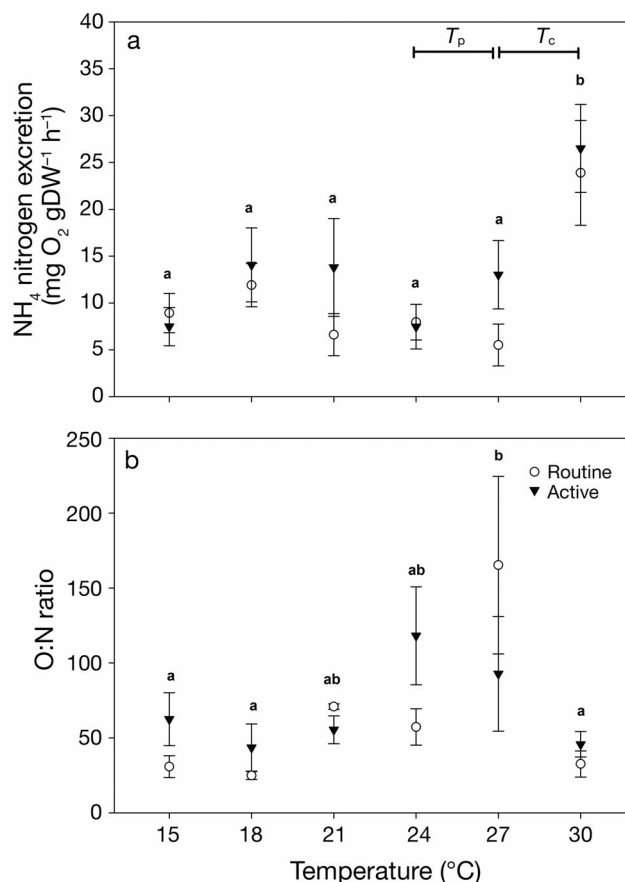


Fig. 3. Effect of temperature on the (a) ammonia-nitrogen excretion and (b) oxygen:nitrogen ratio (O:N ratio) of *Sagmariasus verreauxi* pueruli during routine and active metabolic rate measurement. Values are means  $\pm$  SE (n = 4). Different superscripts indicate significant differences (2-way ANOVA, Tukey's B post hoc, p < 0.05) of the combined data of O:N ratio recorded at both metabolic states (routine and active) relative to temperature (Table 2). T<sub>p</sub> and T<sub>c</sub> indicate the pejus and critical temperature ranges, respectively. DW: dry weight

not affected by metabolic state, and there was no significant interaction between temperature and metabolic state. Puerulus O:N ratio was affected by temperature, being greater at 27°C within the pejus temperature range (Fig. 3b, Table 2). There was no significant effect of metabolic state or any significant interaction between temperature and metabolic state.

### Pueruli EPOC rates

Increasing temperature amplified the duration of EPOC (Fig. 4). At 15°C, EPOC returned to levels that were not significantly different from pre-exhaustion routine metabolic levels within 30 min (2-tailed t-test,

Table 1. Details of exponential regressions ( $y = ae^{bx}$ ), describing the relationship between temperature ( $^{\circ}\text{C}$ ) and standard and routine metabolic rates (SMR and RMR, respectively;  $\text{mg O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ), and quadratic regressions ( $y = ax^2 + bx + c$ ), describing the relationship between temperature ( $^{\circ}\text{C}$ ) active metabolic rate (AMR;  $\text{mg O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ) and aerobic scope ( $\text{mg O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ ) of *Sagmariasus verreauxi* pueruli presented in Fig. 2. \*Regression statistically significant (ANOVA)

	Temperature range ( $^{\circ}\text{C}$ )	<i>a</i>	<i>b</i>	<i>c</i>	$R^2$	df	<i>F</i>	<i>p</i>
SMR	15–27	0.137	0.055	–	0.54	19	21.18	<0.001*
RMR	15–27	0.322	0.038	–	0.48	19	16.56	<0.001*
AMR	15–30	–2.582	0.330	–0.006	0.54	23	12.44	<0.001*
Aerobic scope	15–30	–2.563	0.309	–0.006	0.38	23	6.30	0.007*

Table 2. Results of 2-way analysis of variance conducted to assess the effects of temperature and metabolic state (routine or active) on *Sagmariasus verreauxi* pueruli ammonia-nitrogen excretion and O:N ratio (see Fig. 3). \*Regression statistically significant (ANOVA)

Response variable	Source of variation	df	<i>F</i>	<i>p</i>
Ammonia-nitrogen excretion	Temperature ( <i>T</i> )	5	7.312	<0.001*
	Metabolic state ( $\text{MO}_2$ )	1	2.139	0.152
	$T \times \text{MO}_2$	5	0.589	0.709
	Error	36		
O:N ratio	Temperature ( <i>T</i> )	5	4.467	0.003*
	Metabolic state ( $\text{MO}_2$ )	1	0.186	0.669
	$T \times \text{MO}_2$	5	1.791	0.139
	Error	36		

df = 6,  $t = -1.820$ ,  $p = 0.119$ ). At 18 and  $21^{\circ}\text{C}$ , post-exhaustion oxygen consumption levels returned to routine levels within 50 min (2-tailed  $t$ -test, df = 6,  $t = -2.214$ ,  $p = 0.069$  and  $t = -2.285$ ,  $p = 0.062$ , respectively). At temperatures  $\geq 24^{\circ}\text{C}$ , EPOC did not fall to pre-exhaustion levels within the experimental period (2-tailed  $t$ -test, df = 6,  $t = -4.093$ ,  $p = 0.006$ ,  $t = -9.577$ ,  $p = <0.001$  and  $t = -9.981$ ,  $p = <0.001$  for 24, 27 and  $30^{\circ}\text{C}$ , respectively).

### SST and ocean warming scenarios

In the Sydney region, there was no significant relationship between recruitment, as measured by mean numbers of pueruli and early instar juveniles on settlement collectors, and temperature (Fig. 5a). Recruitment at the northern extent of the settlement range at Coffs Harbor was negatively related to water temperature (Fig. 5b).

Average SST in the  $1^{\circ} \times 1^{\circ}$  domain adjacent to Sydney varied by approximately  $2^{\circ}\text{C}$  and remained  $>1$  SD below the upper pejus temperature range for all years assessed (1993 to 2006). When considering ocean warming scenarios, the average temperatures

increased by approximately  $3^{\circ}\text{C}$  by 2050, to the boundary or within the pejus temperature range, and maximum temperatures exceeded the pejus range by  $>1^{\circ}\text{C}$ . The projected temperature in 2100 indicates that the average SST will reside at the upper boundary of the pejus range, with the upper limit of the standard deviation exceeding the pejus temperature range (Fig. 5c). Moreover, in 2100, maximum SST will exceed the pejus range by  $>4^{\circ}\text{C}$ .

Average SST in the  $1^{\circ} \times 1^{\circ}$  domain adjacent to Coffs Harbour was within 1 SD of the pejus temperature range for 10 of the 14 historical years assessed (1993 to 2006), and maximum temperatures were within the pejus range for all years. However, the degree of ocean warming is not predicted to be as great in this area relative to the Sydney domain (Fig. 6); hence, the slower water temperature increase in

2050 is predicted to increase the maximum temperature to approximately  $28.3^{\circ}\text{C}$ , similar to the temperature predicted off Sydney, but again significantly warmer than the pejus range of *S. verreauxi* puerulus. A similar scenario to the predictions for the Sydney domain are predicted in 2100 for the area adjacent to Coffs Harbour, with maximum temperatures exceeding the pejus range by approximately  $3^{\circ}\text{C}$  (Fig. 5d).

When the lower end of the pejus temperature range is considered ( $24^{\circ}\text{C}$ ), the optimum temperature range (15 to  $24^{\circ}\text{C}$ ) is maintained across a relatively broad expanse of the coast during the recruitment season, from approximately  $30^{\circ}\text{S}$ , adjacent to Coffs Harbour, to  $37^{\circ}\text{S}$ , adjacent to the south coast of New South Wales (Fig. 7a). When the 2050 (SRES: A1FI) warming prediction is added to the 2004 example, the northern extent of the optimum temperature range shifts southward to approximately  $31^{\circ}\text{S}$ , close on the shelf, but offshore, the warm tongue of water associated with the East Australian Current (EAC) has a greater influence increasing the proportion of days outside the optimum temperature range. The southern extent of the optimum temperature range against the coast does not shift dramatically further south. In general, the

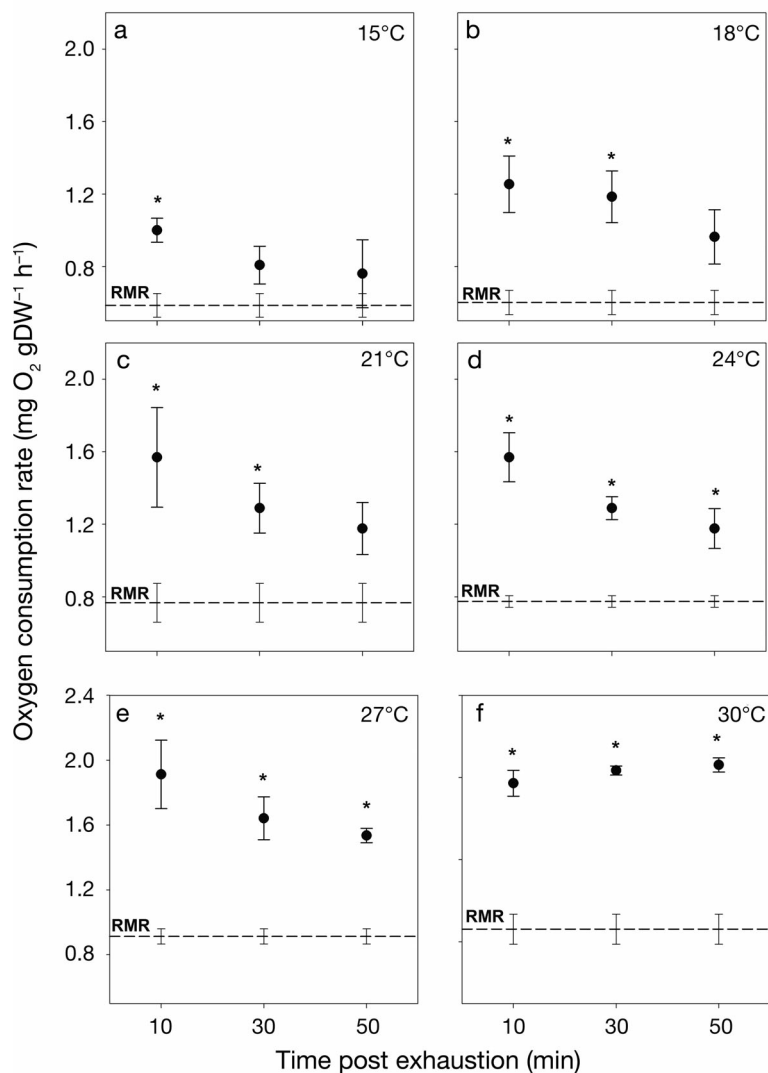


Fig. 4. Mean ( $\pm 1$  SE;  $n = 4$ ) excess post-exercise oxygen consumption rate (EPOC) of *Sagmariasus verreauxi* pueruli at (a) 15°C, (b) 18°C, (c) 21°C, (d) 24°C, (e) 27°C, and (f) 30°C. Dashed line represents the pre-exhaustion routine metabolic rate (RMR). Asterisks (\*) indicate significant differences (2-tailed independent *t*-test,  $p < 0.05$ ) between post-exhaustion oxygen consumption and pre-exhaustion RMR. DW: dry weight

spatial domain where the percentage of days did not exceed 30% outside the optimum temperature range is more restricted than the 2004 example (Fig. 7b). With the addition of the 2100 (SRES: A1FI) warming scenario to the 2004 example, the optimum temperature range had shifted dramatically southward, with the northern extent of the zone in which the optimum temperature range was not exceeded on >30% of days estimated at approximately 37°S, while the southern extent was as far south as 45°S, south of Tasmania. Again, the spatial range where the optimum range of temperature was not exceeded on >30% of the days considered was smaller than in both the 2004

and 2050 examples, and the tongue of warm water extending from the EAC has a significant effect on reducing the proportion of days within the optimum temperature range at both the Coffs Harbour and Sydney domains of interest (Fig. 7c).

When the upper end of the pejus temperature range is considered (27°C), the optimum temperature range (15 to 27°C) is maintained across a much large expanse of the coast during the recruitment season—extending from approximately 20° to 40°S in 2004 (Fig. 7d). As the climate projection scenarios are added for 2050 and 2100, a contraction and poleward shift of the spatial region that has a high proportion of days within the optimum temperature range is predicted. The effect is far less dramatic than when the lower end of the pejus temperature range is considered. Even for 2100, it is predicted that a large area of the Tasman Sea will remain thermally optimal for *S. verreauxi* recruitment albeit over a broader area of the southeastern seaboard of Australia, including Tasmania.

## DISCUSSION

Our findings indicate that *Sagmariasus verreauxi* pueruli at their equatorward extent of settlement are already living at their thermal maximum and suggest that physiological thermal tolerance constraints may be limiting post-larval recruitment. The upper pejus range was from 24 to 27°C and was characterized by the maximum of aerobic scope ( $T_{\text{opt}} = 24.9^\circ\text{C}$ ) and increased O:N ratio, indicating a greater dependence on lipids as an energy substrate. From 1993 to 2006, maximum water temperatures at the northern extent of their natural range consistently reached the pejus temperature range, with puerulus recruitment negatively correlated to the average temperature within the months September to January. Further increases in water temperatures predicted for 2050 and 2100 far exceed the optimal temperature range of this critical and challenging stage of the lobster life cycle and are likely to lead to a contraction in the geographical range at the equatorward boundary, with predicted temperature increases in 2100 likely to more broadly affect the



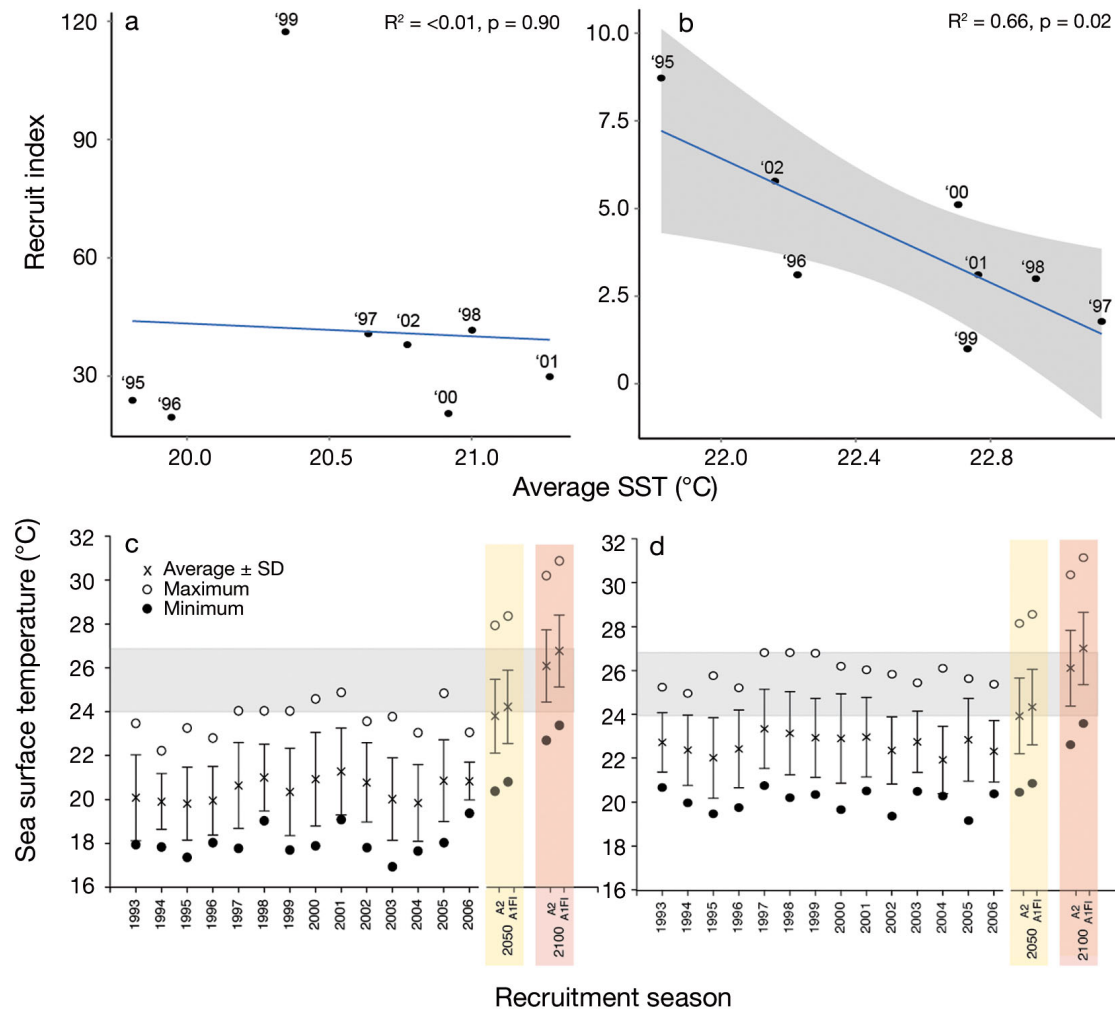


Fig. 5. Linear relationship between the *Sagmariasus verreauxi* recruitment index (Montgomery & Craig 2005) and average sea surface temperatures (SST) for (a) the Sydney ( $y = -3.25x + 108.28$ ) and (b) the Coffs Harbour ( $y = -4.43x + 103.93$ ) regions of New South Wales, Australia. Grey shading represents 95 % confidence limits; numbers above points indicate survey year. Note different scales on the y-axis for (a) and (b). Maximum, minimum, and average SSTs for seasons 1993–1994 to 2006–2007 as well as projected temperature for 2050 and 2100 (based on the months September to December and January), using both SRES A2 and A1FI, for (c) Sydney and (d) Coffs Harbour regions of New South Wales. The grey shading in (c) and (d) represents the pejus temperature range for *S. verreauxi* pueruli

distribution and abundance of pueruli on the east coast of Australia.

#### Physiological response of pueruli to water temperature

The standard metabolic rate of exothermic organisms typically increases exponentially with temperature within the thermal tolerance window, which is set between the lower and upper critical temperatures (Pörtner et al. 2005, Schröder et al. 2009, Storch et al. 2011). Determination of the exponential phase of temperature-dependent SMR has previously been

used to indicate the critical tolerance limits of larval crustaceans (Storch et al. 2011). From 27 to 30°C, the exponential relationship of pueruli temperature-dependent SMR failed, indicating that the critical tolerance limits were reached. We examined the respiratory response of pueruli at 3°C increments so were unable to define the exact upper critical limit which falls between 27 and 30°C. Beyond the critical temperature tolerance limit, a systemic decrease in oxygen levels results in the organism resorting to anaerobic metabolism where life is not sustainable (Pörtner 2010). There was little evidence to suggest that the lower pejus threshold was exceeded by the minimum temperature examined (15°C).

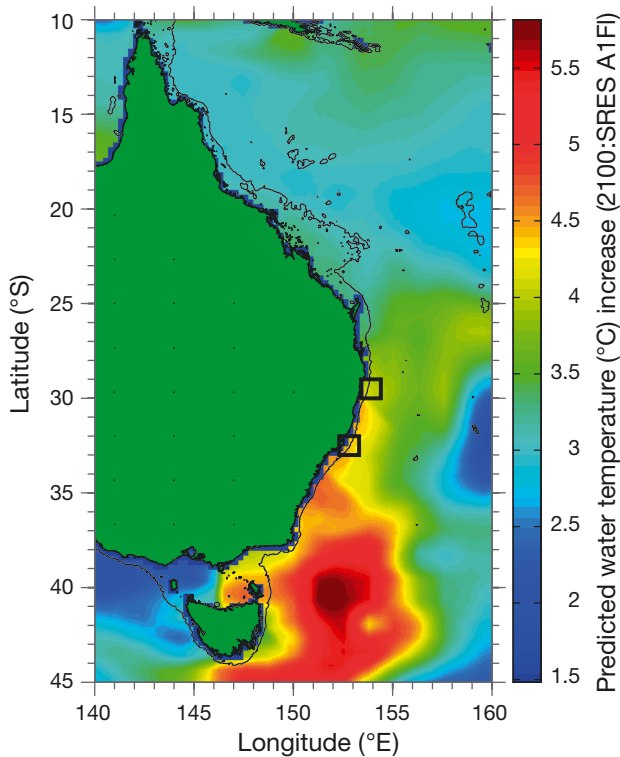


Fig. 6. Example of the predicted ocean warming off the east coast of Australia in 2100 under the A1FI SRES. Northern black box is the domain off Coffs Harbour; southern black box is the domain off Sydney. Black lines indicate the 200 m isobaths

Thermal performance curves describing the relationship between temperature and aerobic scope have proved useful for elucidating thermal adaptation in both terrestrial and aquatic endotherms and to a large extent have been consistent with OCLTT (Eliason et al. 2011, Healy & Schulte 2012). The maximum aerobic scope of pueruli, as determined by the  $T_{opt}$ , was from 24 to 27°C, indicating that the upper pejus temperature was within this range. Beyond the pejus temperatures, the animal's progressively reduced capacity to supply sufficient oxygen to the tissues results in reduced aerobic scope, and the organism may need to engage compensatory mechanisms that divert energy from performance parameters that correlate with fitness (Mark et al. 2002, Pörtner et al. 2006).

Evaluation of the atomic ratio of oxygen consumed versus nitrogen excreted can elucidate energy substrate use, with an O:N ratio below 16 indicating protein-dominated catabolism, while a value above 60 corresponds to lipid-dominated metabolism (Corner & Cowey 1968, Mayzaud & Conover 1988). At the upper pejus temperature range, the O:N ratio of pueruli was significantly increased resulting from high levels

of oxygen consumption accompanied by low levels of nitrogen excretion, indicating an increased reliance on lipid metabolism to support both basal and active metabolism (Corner & Cowey 1968, Mayzaud & Conover 1988). Crustacean larvae typically display a shift toward protein-oriented metabolism under sub-optimal temperature (Johns 1981, Agard 1999, Bermudes & Ritar 2004). The apparent increased lipid catabolism of pueruli at the upper pejus temperature range likely relates to the high availability of stored lipid reserves supporting the lecithotrophic life stage. Increased lipid catabolism at the upper pejus temperature range will place further pressure on limited energy reserves, a crucial factor affecting successful recruitment of spiny lobsters (Jefferies et al. 1999, Phillips et al. 2006b, Limbourn & Nichols 2009, Fitzgibbon et al. 2014). With further heating to the critical temperature range, pueruli demonstrated a reduced O:N ratio, largely attributed to a significant increase in nitrogen excretion, demonstrating reliance on protein metabolism. A shift toward protein-oriented metabolism in response to heat stress has previously been observed with the phyllosoma of spiny lobsters and some teleosts (Bermudes & Ritar 2004, Glencross & Bermudes 2011). Pueruli do not typically catabolize high levels of protein to support energy requirements during the intermoult phase, but protein may be important in the synthesis of the exoskeleton in the moult to first instar juvenile (Limbourn & Nichols 2009, Fitzgibbon et al. 2014).

Following exhaustive exercise, *S. verreauxi* pueruli had a well-defined EPOC, demonstrating a significant anaerobic capacity most likely from within the large white muscle fibers that facilitate tail-flipping as an escape response (Calinski & Lyons 1983, Wells et al. 2001, Jimenez et al. 2008). Anaerobic activity can be considerably more energetically expensive than aerobic activity and represents a large proportion of total energetic costs of strenuous activity in some aquatic organisms (Lee et al. 2003). Our results suggest that anaerobically supported retreat swimming associated with predator avoidance imposes considerable energetic cost. The duration of EPOC of *S. verreauxi* pueruli increased with temperature, which is similar to observations with teleosts and demonstrates greater metabolic capacity (Brett 1964, Lee et al. 2003, Zeng et al. 2010). However, this greater metabolic capacity is coupled with longer recovery requirements, which could make the animals more susceptible to subsequent predator encounters. The thermal effect on predator-prey interactions such as these are important for the overall climate change impact and response (Dell et al. 2014).

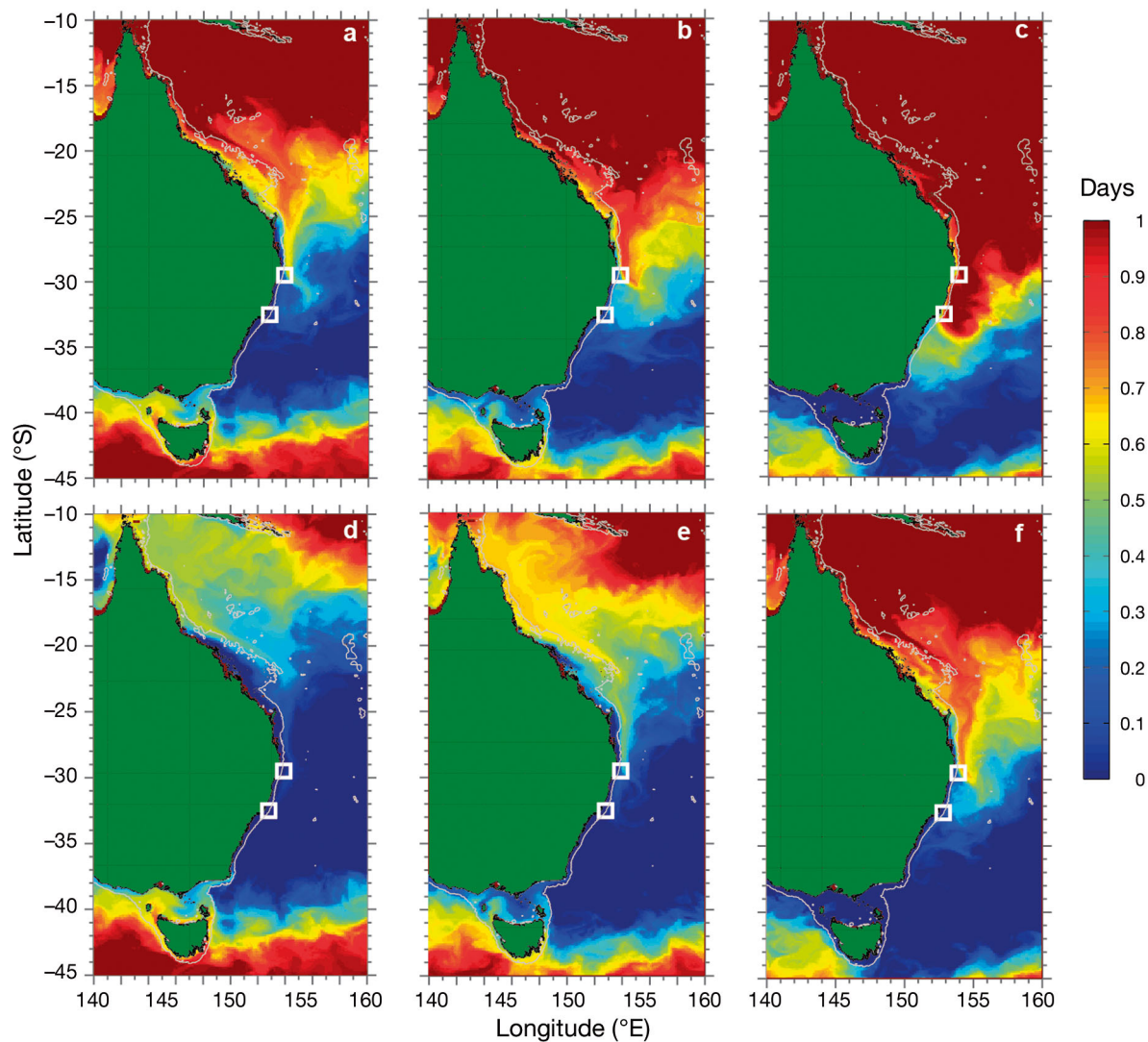


Fig. 7. Proportion of days outside the optimum temperature range of *Sagmariasus verreauxi* pueruli across the months September to January (the settlement period of *S. verreauxi* pueruli). (a–c) Lower estimate of the upper pejus limit of the optimum temperature range (15 to 24°C); (d–f) the higher estimate of the upper pejus limit of the optimum temperature range (15 to 27°C). (a,d) Example from a historical period (2004); (b,e) scenario based on spatial ocean warming of SRES A1FI added to baseline temperature data from the 2004 example for 2050; (c,f) same warming scenario for 2100. The northern white box is the domain off Coffs Harbour, and the southern white box is the domain off Sydney. Grey lines indicate the 200 m isobaths

### Optimum thermal range of pueruli

We found no evidence that the thermal optimal zone of pueruli is reduced compared to other larval life stages. The optimum thermal range for *S. verreauxi* pueruli (15 to 27°C) is within the range found optimal for the culture of early and mid-phyllsoma stages, which is achieved at 23°C (Fitzgibbon & Battaglene 2012b). Optimum temperature for growth of late-stage phyllsoma leading up to metamorphosis to pueruli displayed a downward shift to 21°C,

suggesting a reduced thermal tolerance range for this stage (Fitzgibbon & Battaglene 2012b). Studies of kelp crab *Taliepus dentatus* demonstrate an ontogenetic shift in thermal tolerance through the larval stages, with the megalopae having the narrowest tolerance window compared to the preceding zoea stages (Storch et al. 2011). Storch et al. (2011) suggested that the megalopae may have a smaller thermal window because of their larger size, as OCLTT predicts that temperature-dependent aerobic limits are experienced earlier by larger individuals. To our

knowledge, lobsters of the families Palinuridae and Scyllaridae have the largest larvae of any decapod crustacean, which is likely to amplify the challenges of balancing oxygen supply and demand. The final phyllosoma stages are larger than pueruli, with mass lost in the morphological transformation of metamorphosis and due to lecithotrophy (Fitzgibbon & Battaglene 2012b). Late-stage phyllosoma also have less advanced cardiorespiratory anatomy compared to pueruli as they do not possess branchial chambers and have rudimentary gills (Kittaka et al. 1997). Although the flattened form of phyllosoma assists cutaneous respiration, it is likely that meeting the oxygen demands for these exceptionally large larvae makes them particularly vulnerable to heat stress and may explain their apparent reduced thermal tolerance compared to the smaller early phyllosoma stages and pueruli (Matsuda & Yamakawa 1997, Fitzgibbon & Battaglene 2012b).

#### **Effect of oceanic water temperature on puerulus recruitment**

Puerulus recruitment of *S. verreauxi* is negatively correlated to average SST in the equatorward extent of their range, where SSTs commonly reach the upper pejus range. This is not the case in the mid-range, where temperatures typically remain below the upper pejus range. The finding provides some evidence of a plausible mechanistic effect between physiological thermal tolerance limits and recruitment. The data do need to be interpreted with caution, and we acknowledge that the correlation examined seasonal averages and it is unclear if settlement was inhibited during specific periods of warm water temperatures that exceeded the optimum range. A similar trend was observed with southern rock lobster *Jasus edwardsii*, for which monthly pueruli recruitment was negatively related to water temperature in the warmer northern region of their range, on the east coast of Tasmania, but not further south, which adds support to the possible link between thermal tolerance and recruitment patterns (Johnson et al. 2011). All the drivers for settlement of spiny lobsters are not completely understood and could be related to seasonal variation in oceanic currents and productivity (Johnson et al. 2011). For example, stronger southward penetration of the east Australian current may act to deliver *S. verreauxi* larvae further south, resulting in reduced recruitment in the north on years with higher than average seawater temperatures.

#### **Effect of predicted climate change-induced warming of ocean waters on *S. verreauxi* pueruli**

Further rises in temperature predicted for 2050 and 2100 are likely to affect local populations through a negative influence on the ability of pueruli to recruit to coastal populations across their current distribution. This negative effect of predicted temperature increases has also been reported for the oceanic larval phase of some teleosts (Tracey et al. 2012). The degree to which acclimation or genetic adaptation might protect lobster populations from climate change is unclear. Additionally, further research is required to determine the magnitude and distribution of phenotypic plasticity for environmental tolerance. However, studies with copepods reared at high temperatures for several generations suggest that crustaceans may have limited potential for adaptation to climate change (Kelly et al. 2012). Other species and life stages of spiny lobsters may be more vulnerable to environmental change than *S. verreauxi*. *S. verreauxi* inhabit the thermally broad mid-latitudes and thus are theoretically more likely to adapt to environmental change than species which have evolved in more thermally stable or constrained environments, such as the tropics (Nguyen et al. 2011). Furthermore, *S. verreauxi* exist on a latitudinally extended coastline and so are able to shift their distribution further poleward, a trend which is already occurring (Johnson et al. 2011, Last et al. 2011). For many other locations, for example, past the southern tip of Tasmania (where there is no suitable inshore reef habitat until Antarctica), a poleward shift in geographic distribution is not physically possible for species that find themselves in warming waters beyond their thermal optima.

Ocean warming in south-eastern Australia has already been linked to shifts in distribution of several dozen species (Ling et al. 2009, Pitt et al. 2010, Last et al. 2011). Moreover, predicted temperature increases in global warming 'hotspots', such as the south-eastern coast of Australia, will most likely lead to continued and significant re-shuffling of species assemblages, with subsequent challenges for sustainable natural resource management (Hobday & Pecl 2013). With ocean temperature a major driver of the distribution, abundance, phenology, and life-history of marine species (Harley et al. 2006, Byrne et al. 2011), understanding the mechanistic relationship between ocean temperature and the physiological scope of species will be crucial to predict and adapt to the effects of climate change on the marine environment.



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