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Future ocean temperature impacting the survival prospects of post-larval spiny lobsters

Luvia Lorei García-Echauri [a,*], Geoffrey Liggins [b], Paulina Cetina-Heredia [c], Moninya Roughan [c], Melinda A. Coleman [d], Andrew Jeffs [a,e]

[a] Institute of Marine Science, The University of Auckland, Auckland, 1010, New Zealand
[b] NSW Department of Primary Industries, Sydney Institute of Marine Science, Mosman, New South Wales, 2088, Australia
[c] Regional and Coastal Oceanography Laboratory, School of Mathematics and Statistics, UNSW Australia, Sydney, Australia
[d] Department of Primary Industries, NSW Fisheries and National Marine Science Centre, Coffs Harbour, New South Wales, Australia
[e] School of Biological Sciences, University of Auckland, Auckland, 1010, New Zealand

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ABSTRACT

Spiny lobster post-larvae undertake an extensive migration from the open ocean to the coast, during which time their swimming is fueled solely by energy reserves accumulated through their preceding larval phase. We assessed the influence of future ocean temperatures on the swimming behavior and energy use of migrating post-larvae of *Sagmariasus verreauxi,* by experimentally swimming post-larvae for up to 6 days at three temperatures and measuring the lipid and protein used, and observing their time spent actively swimming. Increasing the temperature from 17 °C to 23 °C doubled the energy utilized by post-larvae while swimming, while also reducing the time they spent swimming by three times. Therefore, increasing ocean temperatures appear to greatly affect the energetic cost and efficiency of shoreward migration of post-larvae in this lobster species, with the potential to markedly impact post-larval recruitment into coastal populations under future scenarios of ocean warming.

1. Introduction

Ocean temperatures are increasing (Hansen et al., 1997; Levitus et al., 2000), with the oceans in the Southern Hemisphere heating four times faster than in the Northern Hemisphere (Wijffels et al., 2016). These increases in temperature have wide ranging impacts on marine organisms, such as shifts in species distribution and abundance (Greenstein and Pandolfi, 2008; Johnson et al., 2011; Southward et al., 2005), changes in phenology (Edwards and Richardson, 2004), reduction in ocean productivity (Behrenfeld et al., 2006; Polovina et al., 2008), changes in geographic range, increases in the susceptibility, severity and prevalence of diseases (Harvell et al., 2002) and shortening of larval durations, which can negatively affect larval dispersal, mortality, connectivity and recruitment (Connor et al., 2007; Green and Fisher, 2004; Tong et al., 2000; Whalan et al., 2008).

Spiny lobsters are unusual in that they have an extended oceanic larval phase that can last well over a year in some species (Bradford et al., 2015; Goldstein et al., 2019; Lesser, 1978; Montgomery and Craig, 2005) and whose dispersal may be particularly susceptible to changing ocean temperatures (Cetina-Heredia et al., 2015). The phyllosoma larvae of spiny lobsters grow markedly in size during their pelagic larval phase and gradually accumulate considerable energetic reserves by feeding on a wide range of macro-zooplankton, including, cnidarians, chaetognaths, crustaceans, and fish larvae (Connell et al., 2014; Jeffs, 2007; O'Rorke et al., 2013; Saunders et al., 2012; Suzuki et al., 2008; Wang et al., 2014). For example, from egg hatch until the end of the 18 month larval phase in the Australasian red spiny lobster, *Jasus edwardsii*, the dry biomass of the larvae increases by more than an order of magnitude, and the proportion of lipid in relation to total larval body mass increases more than six fold from 5% to over 33% (Phleger et al., 2001). The accumulated reserves are used for fueling the active migration towards the coast by the subsequent non-feeding post-larval or puerulus stage (Kough et al., 2014; Phillips and McWilliam, 1986; Phillips and Olsen, 1975). The metamorphosis into a puerulus occurs at a wide range of distances offshore and newly metamorphosed pueruli start their migration to shore with widely varying levels of accumulated energy reserves (Booth and Chiswell, 2005; Jeffs et al., 2005). This ultimately results in the migrating pueruli arriving on the coast with highly variable remaining energetic reserves which is thought to greatly affect their prospects for establishing as benthic juveniles (Fitzgibbon

* Corresponding author. 23 Symonds St, Auckland, 1010, New Zealand.
E-mail address: lgar433@aucklanduni.ac.nz (L.L. García-Echauri).

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et al., 2014a). This process has been postulated as the likely cause of significant reductions in the recruitment of the three largest spiny fisheries in the world that are collectively worth well in excess of US$1 billion in catches annually.

Indirect measurements of the energetic cost of migration have found that pueruli of *P. cygnus* use 1.6 J km^{-1} (Phillips et al., 2006), and experimental swimming of pueruli of *J. edwardsii* found they use 96 J per day (García-Echauri and Jeffs, 2018), but these results do not provide information on how swimming pueruli respond to changes in temperature.

Pueruli are believed to use chemical and physical cues to migrate directly toward coastal settlement habitats (Goldstein and Butler, 2009; Hinojosa et al., 2016; Stanley et al., 2015) but their swimming behavior while migrating onshore is largely unknown. Short term observational experiments tracking pueruli swimming in situ in experimental chambers held near the surface of the ocean found that they swim towards the coast, during both day and night (Kough et al., 2014). They have been observed to exhibit rheotaxis (directed movement towards the current), to use non-visual cues, such as chemical and sound cues, to orient themselves (García-Echauri and Jeffs, 2018; Hinojosa et al., 2016, 2018) and to use water currents and onshore winds to aid their shoreward migration (Calinski and Lyons, 1983; Caputi and Brown, 1993; Phillips and Pearce, 1997; Acosta and Butler, 1999; Caputi et al., 2010; Linnane et al., 2010). However, it is unclear how much of their time is spent swimming. Understanding swimming behavior of pueruli and how it is influenced under future scenarios of ocean warming is key for incorporating into effective models for predicting settlement.

One of the fastest warming ocean regions in the world is in southeastern Australia (Cai et al., 2005; Oliver and Holbrook, 2014; Wu et al., 2012), within which is the natural range of the eastern rock lobster, *Sagmariasus verreauxi*. In this region the mean sea surface temperature is projected to increase by 2 °C by 2050 compared to the average temperature for 1990–2000 under the A1B scenario (Hobday and Lough, 2011; Oliver and Hoolbrook, 2014).

Cultured pueruli have their peak aerobic scope at 24.9 °C with an upper temperature pejus of between 24 and 27 °C (Fitzgibbon et al., 2014b) while temperatures above this are critical and result in poor oxygen supply to tissues (Pörtner, 2010). Within the range of 15–27 °C the standard metabolic rate and routine metabolic rate in pueruli increase exponentially with temperature, and pueruli of *S. verreauxi* in the northern end of their settlement regions are already subjected to their thermal maximum (Fitzgibbon et al., 2014b). These metabolic measures suggest that regional increases in water temperature will make the onshore migration of pueruli more energetically costly, potentially resulting in fewer pueruli retaining sufficient energetic reserves to survive through settlement and establish into the coastal population as benthic juveniles.

Therefore, the aim of this research is to determine how increases in water temperature affect the swimming behavior in pueruli, and how it affects the amount of energy used by migrating pueruli of *S. verreauxi*, measured as the amount of lipid and protein reserves that are catabolized. We predicted that at warmer temperatures pueruli will spend more energy when swimming, and that the time spent by pueruli on swimming will be reduced due to the greatly elevated energetic demands.

2. Materials and methods

2.1. Study area and sampling

Recently arrived pueruli (i.e., stage I and II, sensu Booth, 2001) of *S. verreauxi* were collected from pueruli collectors deployed at two sites on the coast of New South Wales, in Sydney and Ulladulla (Phillips and Booth, 1994), deployed by the New South Wales Department of Primary Industries (as in Montgomery and Craig, 1997) in Australia. The collectors were cleared at monthly intervals shortly after new moon from September to November in both 2015 and 2016. Seawater temperatures during pueruli collection ranged from 17 to 20 °C. Immediately after collection pueruli were held in ambient seawater and transferred to the nearby aquarium facilities at the Sydney Institute of Marine Science. In total, 428 wild pueruli were collected for experiments from 12 separate collection events.

2.2. Swimming experiments

Wild pueruli are very difficult to capture in large numbers simultaneously because of their cryptic behavior and low natural abundance. Hence, it was necessary to rely on smaller numbers of pueruli collected at multiple occasions from two sites (i.e., Ulladulla and Sydney) over a two-year period (i.e., September to November for both 2015 and 2016). Consequently, it was not possible to adopt an orthogonal experimental approach for each cohort of pueruli collected at any one monthly sampling event due to insufficient replication across the number of experimental treatments required for this study. Therefore, an iterative experimental approach was adopted, with pueruli from a single collection event being allocated to increasingly more treatments, if the number of captured animals allowed sufficient replication for each successive treatment.

The pueruli obtained from each collection event were allocated to one of three experimental treatments: control, swimming, or holding. Control pueruli were frozen immediately upon collection, their biochemical composition was analysed, and this value was used to determine the initial energetic condition of the pueruli, while the remaining living pueruli were subjected to the remaining experimental treatments, i.e., swimming, or holding.

Pueruli used for holding and swimming experiments were kept in the experimental conditions for either 3 or 6 days, and at either 17, 20 or 23 °C. The pueruli from each month's collection event were used in iterative experiments, each with a limited range of temperature treatments due to the highly constrained numbers of post-larvae available at any one collection event as outlined previously (Table 1).

Pueruli in the holding treatment were kept in aquaria that were supplied with continuously flowing filtered seawater but did not recreate pelagic conditions and allowed pueruli to adopt a reptant lifestyle consistent with their behavior following settlement into coastal habitats.

Pueruli were held for 3 or 6 days to measure the rate of energy used after settlement, and at 17, 20 and 23 °C to compare the energetic demand at current and future ocean temperatures.

For the swimming treatment, small cylindrical kreisel tanks with a slow rotating flow (0.15–0.17 m s^{-1}) of filtered seawater (UV and 5 μm) were used to re-create pelagic conditions by maintaining pueruli in continuous suspension (see description of tank design and operation in García-Echauri and Jeffs, 2018). Pueruli were swum for 3 or 6 days to calculate the rate of energy used while swimming, and at 17, 20 and 23 °C to compare the energetic demand at current and future temperatures.

The behavior of each puerulus in the kreisel tank was observed once every half hour during the day and every 3 h at night, and the behavior at that time point was recorded. The recorded behavioral categories were: swimming, clinging onto the walls of the tank, drifting with the water current, and clinging onto other pueruli whilst drifting together as "clumps". If a puerulus was holding on to the walls of the tank or another puerulus at the time of observation they were gently detached by nudging with a cable tie. The number of pueruli was kept to four or less per tank in an effort to reduce clinging behavior, which would be unlikely to occur when individuals are highly dispersed in the ocean pelagic environment.

The aquaria for the swimming and held experiments were kept in continual darkness, with behavioral observations made under dim red light, since pueruli are thought to remain out of the photic zone in the wild (Phillips et al., 2006b). When each respective experimental period ended, the pueruli were removed from their swimming or holding tanks

Table 1
Differences in mean morphological and biochemical parameters of control pueruli sampled from two sites in New South Wales, Australia, with 12 different sampling events. Different superscript letters indicate statistical differences in means within columns ($P < 0.05$). (Syd = Sydney, Ulla = Ulladulla, CL = Carapace length, DW = Dry weight, TL = Total lipid, TP = Total protein, Expt = experimental). The column marked "Experimental groups" indicates the control pueruli for which there were no differences in morphological or biological parameters and therefore could be combined for subsequent analyses of results of experimental treatments of pueruli.

Site	Date	n	CL	DW	TL	TP	Expt Group
Syd	9/2015	24	9.8 ± 0.1^{a}	$71.2\ 1.9^{a}$	6.5 ± 0.5^{a}	26.5 ± 1.3^{a}	1
Ull	9/2015	4	9.9 ± 0.1^{a}	77.2 ± 0.7^{a}	7.1 ± 0.9^{a}	30.2 ± 1.9^{abc}	1
Syd	10/2015	5	10.3 ± 0.3^{ab}	79.5 ± 8.7^{ab}	9.2 ± 3.0^{abc}	30.8 ± 3.4^{abc}	1
Ull	10/2015	16	10.2 ± 0.1^{ab}	78.2 ± 2.5^{ab}	7.8 ± 0.6^{ab}	25.3 ± 2.8^{ab}	1
Syd	11/2015	4	10.4 ± 0.2^{ab}	83.3 ± 5.4^{abc}	5.4 ± 1.0^{ab}	24.7 ± 4.9^{abc}	1
Ull	11/2015	6	10.3 ± 0.2^{ab}	86.9 ± 3.1^{abc}	8.3 ± 1.1^{abc}	32.9 ± 3.3^{abc}	1
Syd	9/2016	17	9.9 ± 0.1^{ab}	76.9 ± 2.3^{a}	7.0 ± 0.7^{a}	33.1 ± 2.5^{abc}	1
Ull	9/2016	18	10.0 ± 0.1^{a}	77.2 ± 2.3^{a}	7.2 ± 0.8^{a}	33.1 ± 1.8^{abc}	1
Syd	10/2016	19	10.1 ± 0.1^{ab}	79.7 ± 2.5^{b}	9.51 ± 1.1^{bc}	37.9 ± 2.5^{bc}	2
Ull	10/2016	26	10.4 ± 0.1^{bc}	89.1 ± 2.5^{c}	10.8 ± 0.6^{bce}	34.9 ± 1.1^{c}	2
Syd	11/2016	20	10.5 ± 0.1^{c}	92.3 ± 2.3^{c}	12.8 ± 1.7^{d}	38.2 ± 2.0^{c}	3
Ull	11/2016	27	10.6 ± 0.1^{c}	91.2 ± 1.7^{c}	10.2 ± 0.6^{de}	36.1 ± 1.7^{c}	3

and immediately frozen for later biochemical analyses.

2.3. Biochemical analyses

The carapace length (CL) of each puerulus was measured, before being lyophilized and weighed to determine their dry weight (DW). Total lipid (TL) of each puerulus was determined using a modified Bligh and Dyer (1959) protocol. The residual puerulus tissue was then used for total protein (TP) determination, using a Micro BCA protein assay (Thermo Scientific, Rockford, Illinois, USA) (Walker, 1994). The quantity of lipid used by each puerulus whilst undergoing their experimental treatment (i.e., swimming or holding for 3 or 6 days) was estimated by subtracting their measured TL from the mean TL of the control pueruli at capture. The same approach was also used to estimate protein use. The biochemical measures of lipid and protein expenditure were converted to estimates of total biochemical energy (joules) by using widely accepted calorific equivalents (Winberg, 1971). Comparing the total joules spent by pueruli in each treatment standardizes the energy used by experimental animals regardless of whether it has been sourced from lipid or protein. The total lipid and total protein results are also presented to explain the differential use of substrates depending on the state of the energetic reserves, and the results in joules explain the total energy used in the treatments at different temperatures.

2.4. Statistical analyses

Statistical analyses of the biochemical results were performed using GraphPad Prism version 7.00, and the behavioral results were analysed with R (R Core Team, 2016).

To determine if pueruli collected at different times and from two sites were similar in size and energy content from the outset, statistical comparisons were made of the measures of morphological and biochemical parameters of the control pueruli from each sampling event. Hence, two-way ANOVAs were used to compare each of the parameters for the control pueruli (i.e., CL, DW, TL and TP), using collection site and date as factors. If the controls from pueruli collected at different times were equivalent for all the morphological and biochemical parameters then it provided confidence that these animals had a similar nutritional condition from the outset of their use in the experimental treatments. If so, then the experimental data for those collections were combined into a single group and subsequently analysed together with the confidence they had a similar starting size and nutritional condition (Table 1).

For each group a one-way ANOVA was used for comparing each of the four morphological and biochemical parameters of experimental pueruli (i.e., CL, DW, TP, and TL) from all of the possible treatment combinations; control, holding, and the completed experimental combinations of the six available for both swimming and holding (i.e., for 3 or 6 days at 17, 20 or 23 °C). Where an ANOVA revealed significant overall differences among the means a multiple comparisons test was performed to identify differences among pairs of means, using a Tukey-Kramer test to correct for error inflation caused by multiple comparisons. Prior to analyses the equality of variance of the data was confirmed with a Brown–Forsythe test, and normality of the data with a D'Agostino-Pearson test. If the normality test failed, data transformations were performed. If data transformations did not normalize the data then a Kruskal Wallis test was used as a non-parametric alternative for the analyses.

For each group, the amount of lipid and protein used by pueruli in swimming or holding treatments was calculated by subtracting the TL or TP at the end of the experimental interval (i.e., 3 or 6 days, at 17, 20 or 23 °C) from the mean TL or TP of the control pueruli for the same group at capture, with the resulting differences providing an estimate of the biochemical substrate catabolized during the experimental treatment. A one-way ANOVA was then used to determine if there were differences among the treatments for each of the estimates for catabolized TL and TP. For each group, the lipid and protein catabolized at each temperature, length of experiment, and type of activity (swimming or holding) was then standardized to lipid and protein utilization per day by dividing by the experimental duration in days (i.e., 3 or 6 days) and compared with a one-way ANOVA.

To calculate total energy spent by pueruli in each treatment, the estimates of the lipid and protein spent by each individual were transformed into joules using standard conversion factors for lipid and protein (Winberg, 1971) and then added together. The joules spent by pueruli belonging in all groups was then compared among all treatments with a one-way ANOVA.

A logistic regression model was used to identify differences in swimming behavior at different temperatures, with swimming behavior expressed as a binomial dependent variable (i.e., swimming or not swimming) with experimental temperature (i.e., 17, 20 or 23 °C), diurnal period (i.e., periods of day and night at collection site), and number of days swimming used as categorical independent variables (i.e., predictor variables). The behaviors of drifting, clinging to the walls, and clinging to another puerulus, were also fitted to the binomial models in a similar manner. To analyze swimming behavior, pueruli were pooled into the same groups used for the biochemical comparisons to ensure similar starting condition of pueruli. Within groups the different collection dates were analysed with estimated marginal means tests and compared with Tukey's test to determine if there were further behavioral differences between the pueruli from different collection dates, despite their physical similarities. Since the model tests the overall

proportion of pueruli displaying a behavior, observations from pueruli in the 3 day swimming experiment were pooled with those from pueruli in the 6 day swimming experiment. For the swimming experiments at 23 °C, the first 2 days were used to acclimate the pueruli by gradually raising the temperature to the experimental temperature of 23 °C.

All means are reported with their accompanying standard errors.

3. Results

3.1. Morphometric and biochemical results

Control pueruli were highly variable in their morphometric and biochemical measurements among the different collection dates and locations (Table 1).

The comparison of the four morphological and biochemical parameters among the control pueruli collected at different sites and dates enabled them to be combined into three groups for which the pueruli had similar starting size and nutritional condition (Table 1). The combined data for these three groups were used for subsequent comparisons of the experimental results within the groups.

3.2. Experimental group 1 (N = 215)

The DW of pueruli from the control and all treatments ranged from 44.1 to 114.9 mg (Table 1), with no difference between any combination of treatments and the control ($F_{(8, 202)} = 1.3$, $P = 0.22$) with an overall mean of 76.36 ± 0.81 mg.

Overall there was a significant difference in the mean TL among experimental treatment combinations ($F_{(7, 207)} = 6.52$, $P < 0.0001$), with control pueruli having higher TL than pueruli swum for 6 days at 20 and 23 °C ($P < 0.0001$ and $P = 0.004$ respectively), and higher TL than pueruli held for 6 days at 23 °C ($P < 0.0001$) (Fig. 1 A).

There was an overall significant difference in the TP among experimental treatment combinations ($H = 30.78$, $P < 0.0001$), with TP being higher in control pueruli than for pueruli swum for 6 days at 20 and 23 °C ($P = 0.001$, $P = 0.0002$ respectively), and pueruli held for 6 days at 23 °C ($P = 0.001$) (Fig. 1 B).

3.3. Experimental group 2 (N = 71)

Group 2 had the smallest sample size of only 74 animals over seven different treatment combinations (Table 2). There were no differences in DW, TL or TP between control and treatments ($F_{(8, 62)} = 1.0$, $P = 0.44$; $H = 12.93$, $P = 0.11$; $H = 5.41$, $P = 0.71$ respectively) although there was a general trend for the results of all experimental treatments to be lower than their corresponding controls (Table 2, Fig. 2A and 2B).

Table 2
The set of experimental treatments included in each experimental group. Experimental pueruli were divided into three groups by comparing the morphological and biochemical parameters of control pueruli that were sampled immediately after their collection from the wild.

Treatment	Groups
Held 3 days at 17 °C	1
Held 6 days at 17 °C	1
Held 3 days 20 °C	2, 3
Held 6 days 20 °C	2, 3
Held 3 days 23 °C	2, 3
Held 6 days 23 °C	1, 2, 3
Swum 3 days at 17 °C	1
Swum 6 days 17 °C	1
Swum 3 days 20 °C	2, 3
Swum 6 days 20 °C	1, 2, 3
Swum 3 days at 23 °C	2, 3
Swum 6 days at 23 °C	1, 2, 3

3.4. Experimental group 3 (N = 94)

The mean DW of pueruli was different among experimental treatment combinations ($F_{(8, 77)} = 2.47$, $P = 0.02$) (Table 2). DW was the greatest in pueruli held for 3 days at 23 °C, averaging 94.01 mg ± 4.36 mg, followed by control pueruli averaging 91.68 mg ± 1.37 mg, and was smallest in pueruli held and swum for 6 days at 20 °C. Control pueruli had greater DW compared to experimental pueruli: swum 6 days at 20 °C, held for 6 days at 20 °C and held for 6 days at 23 °C ($P = 0.01$, $P = 0.008$, and $P = 0.03$ respectively). Pueruli held at 23 °C for 3 days had greater DW compared to pueruli held 6 days at 20 °C and pueruli swum for 6 days at 20 °C ($P = 0.02$ and $P = 0.03$ respectively) (Fig. 3).

There were overall differences in the mean (square root transformed) TL, in pueruli of among the experimental treatments ($F_{(8, 85)} = 9.39$, $P < 0.0001$), with the control pueruli having higher TL compared to pueruli swum for 6 days at 20 and 23 °C ($P < 0.0001$) as well as when compared to pueruli held for 3 days at 20 °C ($P = 0.0002$) and held 6 days at 20 and 23 °C ($P = 0.0001$ and $P = 0.004$ respectively) (Fig. 3A). There were no differences in the TP of pueruli from the different treatments ($H = 8.18$, $P = 0.42$) (Fig. 3B).

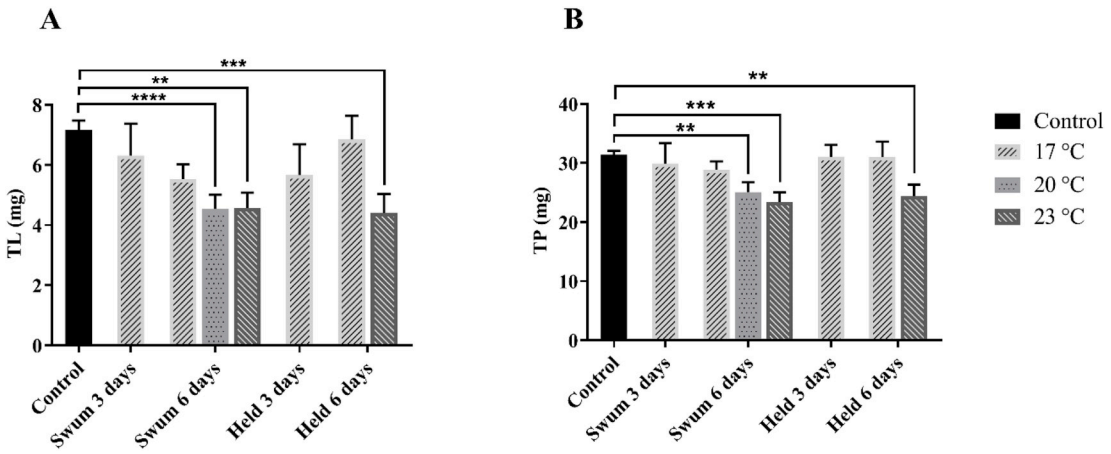

Fig. 1. Mean TL (A -Total lipid) and TP (B - Total protein) of pueruli from experimental group 1, with data for pueruli that were swum and held for 3 and 6 days at 17 °C, swum for 6 days at 17, 20 and 23 °C, and held for 6 days at 17 and 23 °C, asterisks represent statistical differences between pairs of treatments (****P ≤ 0.0001, ***P ≤ 0.001, **P ≤ 0.01).

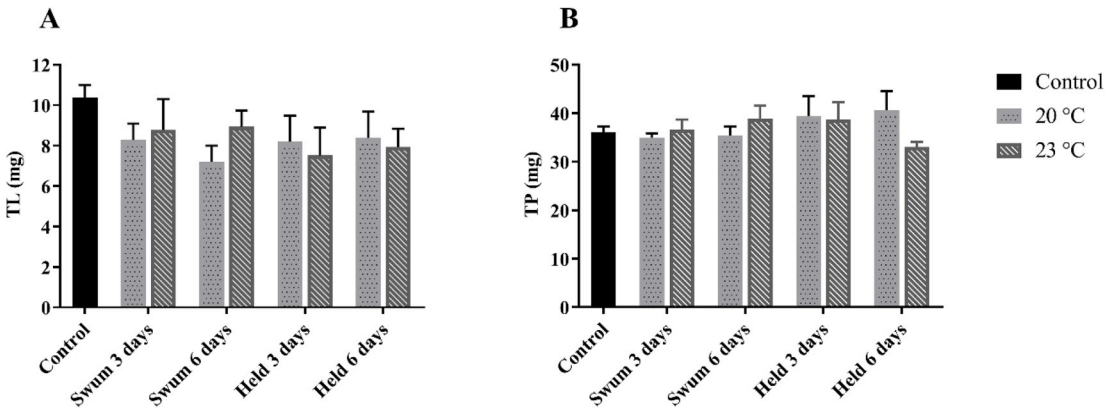

Fig. 2. Mean TL (A - Total lipid) and TP (B - Total protein) of pueruli from experimental group 2, with data for pueruli that were swum and held for 3 and 6 days at 20 and 23 °C.

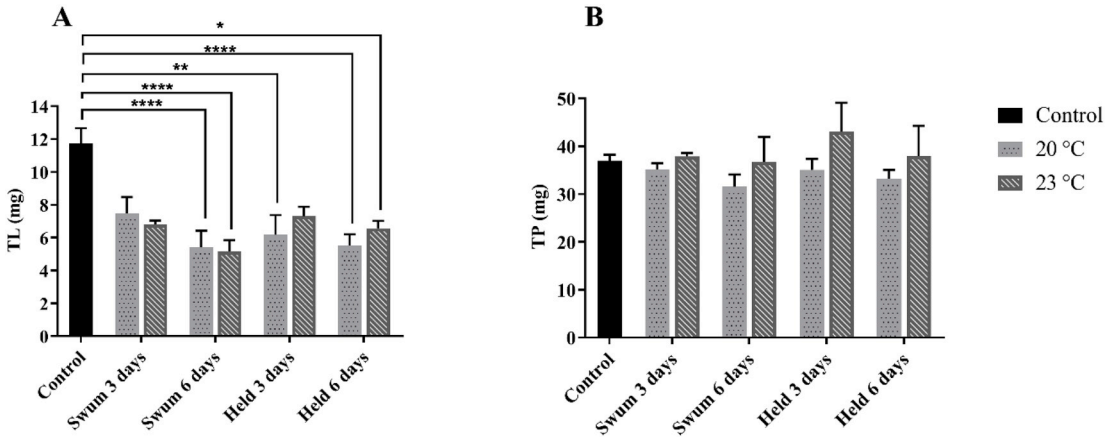

Fig. 3. Mean TL (A - Total lipid) and TP (B - Total protein) of pueruli from experimental group 3, with data for pueruli that were swum and held for 3 and 6 days at 20 and 23 °C. Asterisks represent statistical differences between pairs of treatments (****P ≤ 0.0001, ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05).

3.4.1. *Energy spent*

Since there was no difference in lipid and protein concentration among control and treatments in group 2, they were excluded from the energetic analyses. This represented 71 out of 380 samples.

The total energy spent in each treatment was calculated by adding the equivalent in joules of the lipid and protein spent in group 1, and only the lipid for group 3, since this group did not spend a significant amount of protein (Fig. 3). In group 1 the total joules spent was lower in pueruli swum or held for 3 and 6 days at 17 °C compared to pueruli swum or held for 3 and 6 days at 20 and 23 °C ($F_{(6,\ 179)} = 13.06$, $P < 0.0001$, Table 3), in group 3 there was no difference in the joules spent among treatments ($F_{(7,\ 39)} = 1.29$, $P = 0.28$, Table 3). Comparing the joules spent in matching treatments between groups 1 and 3 failed to identify any differences ($F_{(5,\ 118)} = 0.77$, $P = 0.57$) (Table 3).

Table 3
Mean energetic expenditure in joules spent per day by pueruli from group 1, and 3 for swimming or being held for 6 days at 17, 20 and 23 °C. Letters in superscript represent differences in means among treatments within columns, P > 0.05.

Temperature	Treatment	Group 1	Group 3
17 °C	Swimming	23.1 ± 3.2[a]	N/A
20 °C	Swimming	42.4 ± 3.7[b]	32.6 ± 1.5[a]
23 °C	Swimming	48.6 ± 3.6[b]	41.8 ± 6.7[a]
17 °C	Held	3.8 ± 7.8[a]	N/A
20 °C	Held	N/A	29.3 ± 3.8[a]
23 °C	Held	45.6 ± 4.3[b]	41.0 ± 4.3[a]

3.5. *Behavioral observations*

Group 1

For group 1 the behavioral observational data could only be collected for the experiments at 17 °C due to logistical constraints. During the swimming experiment at 17 °C the pueruli over 3 days and 6 days combined spent a high proportion of time swimming or drifting (Table 4). During the day pueruli would swim significantly less than during the night (Fig. 4).

Group 2

In group 2 there was no difference in the proportion of time spent swimming or clinging to other pueruli between the 20 °C and 23 °C treatments, but at 23 °C pueruli spent more time drifting and less time clinging to the walls of the tank, compared to pueruli at 20 °C (Table 4). Overall in group 2 the time spent swimming was less than in group 1 at 17 °C.

At 20 °C during the day the mean proportion of time spent swimming

Table 4
Proportion of time spent performing the 4 behaviors observed during the swimming experiments by pueruli from groups 1, 2, and 3 at 17, 20, and 23 °C.

	Group 1	Group 2		Group 3	
Temperature	17 °C	20 °C	23 °C	20 °C	23 °C
Swim	36.9 ± 0.7	27.7 ± 1.0	27.9 ± 1.5	31.0 ± 1.3	12.6 ± 1.8
Cling	22.3 ± 0.6	32.4 ± 1.1	24.9 ± 1.4	32.9 ± 1.3	9.8 ± 1.6
Drift	37.8 ± 0.7	24.4 ± 1.0	31.9 ± 1.6	34.9 ± 1.4	77.1 ± 2.3
Clinging to pueruli	0.3 ± 0.2	15.6 ± 0.2	15.2 ± 1.2	1.1 ± 0.3	0.6 ± 0.4

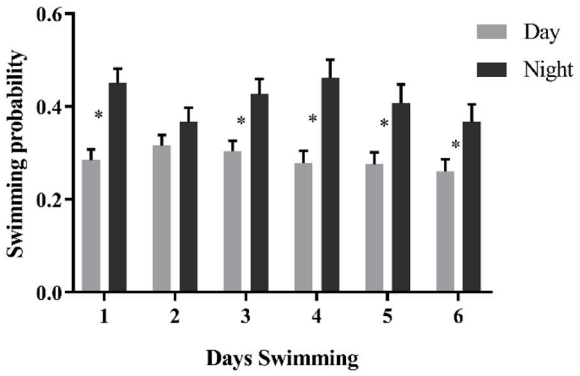

Fig. 4. Proportion of time spent swimming by pueruli for each successive day of the experiment for group 1 at 17 °C. Asterisks represent significant differences between day and night measurements on the same day ($P < 0.05$).

was 26.5% ± 1.3% and during the night was 32.4% ± 1.7%. Pueruli swam significantly more during the night than during the day at 20 °C during day 1 and 2 of the experiment, and at 23 °C on the fifth day of the experiment (Fig. 5).

Group 3

In group 3 there was almost a 20% reduction in time spent swimming and the time spent clinging to the tank at 23 °C compared to 20 °C, at 23 °C pueruli spent the majority of the time drifting in the tank (Table 4).

At 20 °C during the day pueruli swam more during the night throughout the experiment, at 23 °C there was not a clear trend of preference between daytime or nighttime swimming (Fig. 6). Pueruli at 20 °C were 3.1 times more likely to be swimming compared to pueruli at 23 °C ($P < 0.0001$).

There was no difference in the proportion of time pueruli spent on each of the four different behaviors between groups 2 and 3 in swimming experiments at 20 °C ($P = 0.11$), but at 23 °C the pueruli from group 3 were 3.73 times less likely to be swimming than in group 2 ($P < 0.0001$).

4. Discussion

The behavior and energetics of swimming pueruli was studied at different temperatures to understand how ocean warming can affect the survival and settlement of *S. verreauxi.* The shoreward migration of the post-larvae of *S. verreauxi* occurs in a fast warming ocean region (Wu et al., 2012), and since *S. verreauxi* are metabolic conformers, increases in seawater temperatures should represent corresponding increases in metabolic rate. This would increase their energetic cost to reach coastal settlement sites, potentially reducing the amount of lobsters with sufficient energetic reserves to complete the migration, with the potential to recruit in coastal lobster populations.

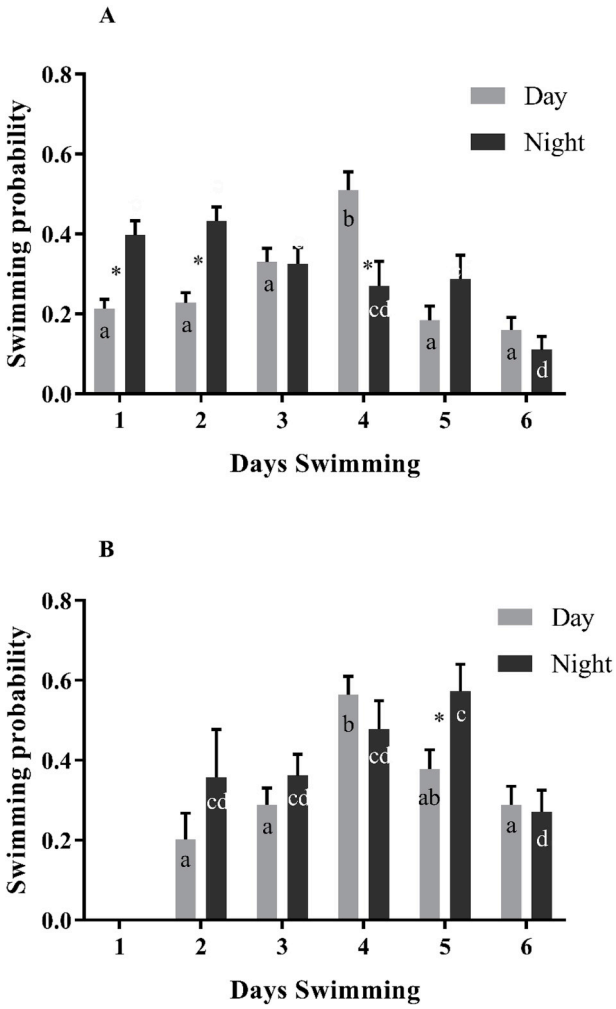

Fig. 5. Proportion of time spent swimming by pueruli for each successive day of the experiment for group 2 at 20 °C (A) and 23 °C (B). Letters in bars indicate differences among means during the day or night ($P \leq 0.05$). Asterisks represent differences between day and night measurements on the same day ($P \leq 0.05$). The temperature was slowly raised during 1.5 days to reach 23 °C, therefore there are no data of pueruli swimming at 23° on day 1.

4.1. Lipid and protein use

Migrating pueruli primarily use lipid to fuel their swimming (Jeffs et al., 2001; Jeffs et al., 1999; Jeffs et al., 2001b; Jeffs et al., 2002; Limbourn et al., 2008; Limbourn and Nichols, 2009) and start using protein once lipid reserves become depleted (Fitzgibbon et al., 2014a). Control pueruli in group 3 had the greatest starting levels of lipid (12.8%) and protein (40.3%) and pueruli in this group subsequently spent more lipid than pueruli in groups 1 and 2 during both swimming and holding treatments at all temperatures. Pueruli in group 3 did not

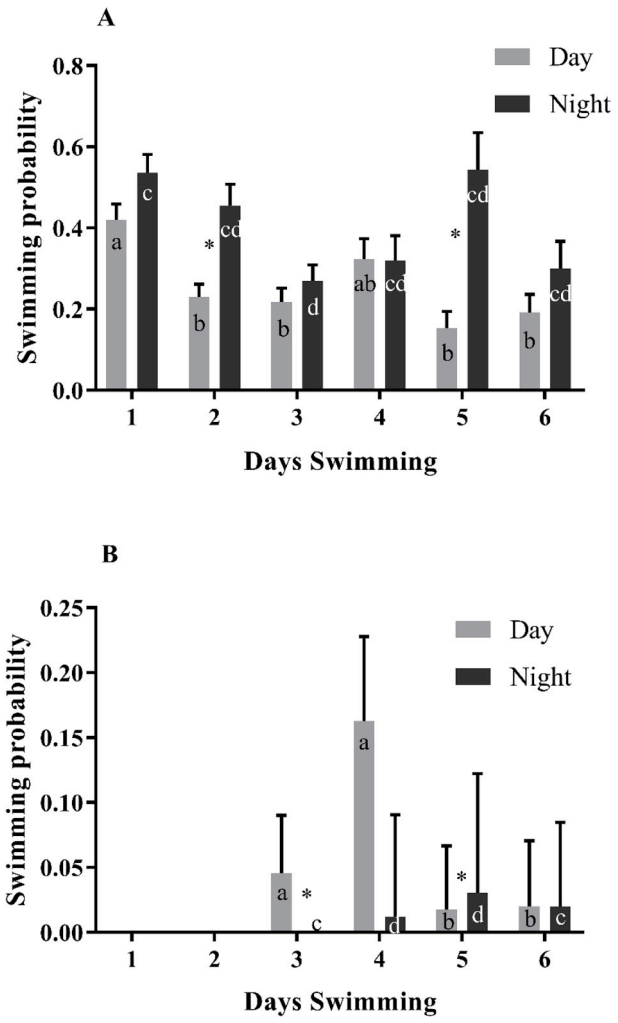

Fig. 6. Proportion of time spent swimming by pueruli for each successive day of the experiment for group 3 at 20 °C (A) and 23 °C (B), scaling in graph B is smaller to show data, but the night observations data on day 3 are too small to show on the graph. Letters in bars indicate differences among means either during the day or night ($P \leq 0.05$). Asterisks represent differences between day and night measurements on the same day ($P \leq 0.05$). The temperature was slowly raised during 2 days–23 °C, therefore there are no data of pueruli swimming at 23° on day 1 and 2.

use protein during these treatments at any of the temperatures tested. Control pueruli in group 1 had a mean TL of 9.3% (DW). Pueruli from this group had 7.2% lipid or more at the end of the treatments at 17 °C (swum and held for 3 and 6 days) and did not spend protein during the experiments. However, in treatments at 20 °C and 23 °C, pueruli with lower TL of 5.7%–6.0% also had low protein levels (swum for 6 days at 20 °C, and swum or held for 6 days at 23 °C) consistent with a switch to the catabolism of protein once the pueruli had reached between 7.2% and 6.0% of remaining lipid. This would also be consistent with the 6.5% lipid concentration in juveniles of *S. verreauxi* reaching their nutritional point of no return (García-Echauri et al., 2019). Pueruli in group 3 at the end of all treatment combinations had from 5.9% to 7.8% lipid and had not used significant amounts of protein. It could be that pueruli from the treatment with 5.9% lipid (swum 6 days at 23 °C) had only recently reached the critical lipid concentrations and were starting to catabolize protein, but their protein use was insufficient to be detected by the statistical analyses given the high level of overall variability in biochemical measures from pueruli. This explanation would seem plausible, as the total energy spent in joules between groups 1 and 3 was similar when swimming or held at the same experimental temperature. Group 2 did not provide results with statistical significance, this could have been because this relatively small group had a higher variability in the initial energetic conditions at arrival making it even more difficult to detect differences among the limited replication for individual treatments.

A minimum of 5% lipid of body mass has been suggested as essential for meeting requirements for structural and biochemical functioning for krill (Hagen et al., 2001). This minimum is consistent with the apparent threshold in pueruli of *S. verreauxi* when they appear to switch from catabolizing lipid to protein. The effect of temperature on the amount of lipid used in the different treatments was not detected in group 1, since lipid was being spared, but these effects are evident in the protein used. In contrast, in group 3 the effect of temperature was seen in the lipid used, but not in protein content, because of this it is necessary to analyze the total joules spent in each treatment. These differences in the results among the different experimental groups also highlight the high variability in the biochemical condition of pueruli arriving to the coast at different times and locations.

Pueruli in holding treatments used the same amount of lipid and protein as those swimming for the same duration at the same temperature, in group 1 at 23 °C and in group 3 at 20 and 23 °C. It is likely that the development toward first instar juvenile was suppressed in pueruli that continued swimming in the experimental flumes, in comparison to the pueruli that were in reptant holding conditions where development toward first instar juvenile appeared to be accelerated (pers. obs.). Extensive morphological changes are required for the moult to first instar juvenile (Abrunhosa and Kittaka, 1997; Lemmens and Knott, 1994; Nishida et al., 1990), which are also likely to require substantial rearrangement of body protein, and the extensive use of remaining energy reserves at a similar rate to that measured for swimming pueruli.

4.2. Energy spent swimming

Wild pueruli in group 1 had a daily average use of 23.12 J ± 3.22, 42.38 J ± 3.66 J, and 48.60 J ± 3.57 J when swimming at 17, 20 and 23 °C respectively, using a combination of lipid and protein. The difference in joules spent swimming was significant when comparing 17 °C with both 20 and 23 °C treatments but not between 20 and 23 °C.

Pueruli in group 3 used 32.56 J ± 1.46 J per day when swimming at 20 °C and 41.78 J ± 6.65 J when swimming at 23 °C, in both cases using only lipid, although these means were not different. Experimental measures of energy using similar experimental methods in swimming pueruli of *J. edwardsii* found that they consumed 63.2 J per day of lipid and 26.9 J per day of protein at 19–22 °C, (i.e., total of 91 J per day) (García-Echauri and Jeffs, 2018) which is considerably higher than measured for pueruli of *S. verreauxi* at a range of temperatures in this current study. However, the body mass of *J. edwardsii* pueruli is approximately double that of *S. verreauxi* and their physical body dimensions are larger, which would greatly increase the hydrodynamic drag during active swimming and would readily explain the greater energy use by pueruli of this species.

4.3. Swimming behavior

The clinging behavior observed in the experimental pueruli is believed to be a settlement seeking behavior (Kittaka, 1990; Kittaka and Ikegami, 1988; Kittaka and Kimura, 1988) and may be a consequence of the wild pueruli being removed from collectors where they had already begun to adopt a reptant clinging behavior. The behavior of pueruli clinging to one another has also been reported for *P. argus* (Calinski and Lyons, 1983), where pueruli would clump in groups up to 50–60 individuals when captured and held together. In this experiment, clinging behavior was discouraged in order to maintain an experimental situation that approximated pelagic conditions, and to prevent the initiation of settlement behavior. The opportunity to cling and the experimental nudging of clinging pueruli may have interfered with the estimations of

other behaviors. Clinging was observed for 10–33% of the time among the various treatments, however, in the pelagic environment where there is no substrate on which to cling, it is likely that this time would have been spent swimming or drifting.

When swimming behavior in pueruli decreased the drifting behavior increased. Comparing the proportion of pueruli drifting in group 1 at 17 °C and group 3 at 23 °C, drifting went from 37.8% to 77.1%, while the clinging behavior decreased or only increased in small percentages (clinging to tanks 22.3% to 9.9%, clinging to other pueruli 0.3%–0.6% from 17 to 23 °C respectively). The drifting behavior has also been previously observed in pueruli of *P. argus* in an experimental field situation (Kough et al., 2014). Drifting by pueruli in the experimental tanks in this current study could also reflect a resting period needed to recover after the use of anaerobic metabolism to support elevated energetic demands (Ellington, 1983; Jensen et al., 2013), which can explain the significant reduction in pueruli swimming behavior and corresponding increase in drifting behavior observed at 23 °C. Oxygen stress has been observed to decrease swimming activity with a concomitant increase in hovering behavior in krill larvae (Kils, 1982). Likewise, in fish larvae, drifting behavior has been proposed as an effective means of saving energy when subjected to strong currents (Hogan and Mora, 2005). Drifting could also be used as passive transport, by relying on currents or Stoke's forces to assist pueruli in their migration toward the coast (George, 2005; Jeffs et al., 2005).

In the swimming experiments wild pueruli would swim to match the speed of the current in the tanks while continuously displaying rheotaxis, as previously seen in *J. edwardsii* (García-Echauri and Jeffs, 2018). In this study, although pueruli were not continuously active, they would swim both during the day and night periods, as has also been observed in the wild (Kough et al., 2014; Phillips and Olsen, 1975). However, pueruli tended to spend a greater proportion of time swimming during the night as has also been observed in fish larvae (Champalbert and Castelbon, 1989; Fisher and Bellwood, 2003; Forward et al., 1996), but in some experimental groups of pueruli this difference was not maintained throughout the duration of the experiment. Phyllosoma have an endogenous circadian rhythm for moulting (Matsuda et al., 2003), and an endogenous circadian vertical migration that persists for at least 6 days when placed in complete darkness (Ziegler et al., 2010), this diurnal behavior in phyllosoma is thought to be mediated by the eyestalk. Pueruli are likely to also have an endogenous circadian pattern for swimming, that persisted during the experiments. The swimming experiments in this study were performed in darkness, and there is evidence that fish larvae can adjust their circadian patterns of swimming to the timing of artificial lighting (Champalbert and Castelbon, 1989), so it is possible that day and night differences observed in the swimming pattern of pueruli may not be representative of pueruli in the wild. It has been reported that fish larvae swim less after settlement (Leis et al., 2011) therefore, it is also possible that the experimental use of pueruli from collectors that have already completed a migration to coastal settlement habitat may under represent the swimming capabilities of pueruli, compared to newly metamorphosed pueruli in the pelagic environment.

4.4. Effect of increased temperatures on pueruli migration

The development of phyllosoma larvae of *S. verreauxi* could benefit from increases in ocean temperature because their optimal development temperature is at 23 °C (Fitzgibbon and Battaglene, 2012), and although changes in ocean circulation associated with this increase in temperature are expected to reduce the successful transport of larvae, the developmental benefits outweigh the anticipated reduction in larval dispersal (Cetina-Heredia et al., 2015). Other studies have found that increasing temperatures causes *J. edwardsii* phyllosoma to develop faster, producing smaller larvae that would store less energetic reserves (Tong et al., 2000). Even if warmer oceans do not increase mortality during the phyllosoma stage, it could cause them to develop more rapidly into pueruli with lower energetic reserves available for migration to coastal settlement sites.

For a puerulus of *S. verreauxi* to swim 1 km at 17 °C it would require on average about 4.5 J and take around 4.7 h, while at 20 °C it would require 10.6 J and take 6 h, and at 23 °C about 24 J and about 14.7 h, based on the estimates of the time spent swimming, the swimming speed, and the rate of energy being used, from experimental results from groups 1 and 3. The pueruli of *J. edwardsii* have been estimated to use 91 J per day when migrating onshore based on the same experimental methods as this current study and taking into consideration both lipid and protein (García-Echauri and Jeffs, 2018) (i.e., 15, 22 and 57 J in 4, 6 and 15 h respectively). Indirect estimations have calculated that pueruli of *J. edwardsii* use 5.7 J km^{-1} (Jeffs et al., 1999) and *P. cygnus* uses 1.6 J km^{-1} when crossing the continental shelf, but with the aid of currents and wind (Phillips et al., 2006). The estimates of the distances capable of being swum by pueruli of *S. verreauxi* in this study are calculated, without the assistance or hindrance of physical processes.

The increment in temperature from 17 to 23 °C doubles the energy used by pueruli and reduces the average time spent actively swimming by three times. Therefore, increasing water temperature could be expected to greatly prolong the shoreward migration of pueruli, increasing the chances of predation, ultimately reducing the number of pueruli that reach the coast because of an energetic shortfall, or that arrive with insufficient reserves to subsequently successfully transition to benthic juveniles.

This study appears to confirm the potential negative effects that warming oceans can have on the recruitment of spiny lobsters, and particularly for *S. verreauxi*, a species that is distributed in a hot spot for ocean warming.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Luvia Lorei García-Echauri: Methodology, Validation, Formal analysis, Investigation, Writing - original draft, Visualization. **Geoffrey Liggins:** Conceptualization, Methodology, Resources, Writing - review & editing, Project administration. **Paulina Cetina-Heredia:** Writing - review & editing. **Moninya Roughan:** Writing - review & editing, Supervision, Funding acquisition. **Melinda A. Coleman:** Writing - review & editing. **Andrew Jeffs:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - review & editing, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.104918.

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