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The effect of water temperature and velocity on barnacle growth: Quantifying the impact of multiple environmental stressors ☆

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ABSTRACT

Organisms employ a wide array of physiological and behavioral responses in an effort to endure stressful environmental conditions. For many marine invertebrates, physiological and/or behavioral performance is dependent on physical conditions in the fluid environment. Although factors such as water temperature and velocity can elicit changes in respiration and feeding, the manner in which these processes integrate to shape growth remains unclear. In a growth experiment, juvenile barnacles (*Balanus glandula*) were raised in dockside, once-through flow chambers at water velocities of 2 versus 19 cm s^{-1} and temperatures of 11.5 versus 14 °C. Over 37 days, growth rates (i.e., shell basal area) increased with faster water velocities and higher temperatures. Barnacles at high flows had shorter feeding appendages (i.e., cirri), suggesting that growth patterns are unlikely related to plastic responses in cirral length. A separate experiment in the field confirmed patterns of temperature- and flow-dependent growth over 41 days. Outplanted juvenile barnacles exposed to the faster water velocities (32 ± 1 and 34 ± 1 cm s^{-1}; mean ± SE) and warm temperatures (16.81 ± 0.05 °C) experienced higher growth compared to individuals at low velocities (1 ± 1 cm s^{-1}) and temperatures (13.67 ± 0.02 °C). Growth data were consistent with estimates from a simple energy budget model based on previously measured feeding and respiration response curves that predicted peak growth at moderate temperatures (15 °C) and velocities (20–30 cm s^{-1}). Low growth is expected at both low and high velocities due to lower encounter rates with suspended food particles and lower capture efficiencies respectively. At high temperatures, growth is likely limited by high metabolic costs, whereas slow growth at low temperatures may be a consequence of low oxygen availability and/or slow cirral beating and low feeding rates. Moreover, these results advocate for approaches that consider the combined effects of multiple stressors and suggest that both increases and decreases in temperature or flow impact barnacle growth, but through different physiological and behavioral mechanisms.

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1. Introduction

Body size is an important trait that has direct implications for a species' abundance and distribution. Size can affect physiological and ecological processes including metabolic activity, feeding rate and reproductive success (Davies, 1966; Peters, 1986). Indeed, the effects of environmental conditions on an organism's growth and development can lead to habitat-related clines in body size (e.g., latitude, elevation; Chown and Klok, 2003; Angilletta et al., 2004;

Verberk and Atkinson, 2013; Verberk et al., 2011). For many marine species, body size is an important determinant of food web dynamics, reproductive output, and population density (Cohen et al., 1993; Levitan, 1991; Marquet et al., 1990; Sebens, 1981). In the intertidal zone, body size often correlates with environmental gradients in water temperature and flow (Denny et al., 1985; Trussell, 2000). The potentially interactive effects of multiple environmental variables on growth, however, remain less well understood (Todgham and Stillman, 2013).

For benthic suspension feeders that procure resources from the water column, growth is potentially influenced by conditions in the fluid environment (e.g., temperature and flow). Indeed, temperature-body size correlations in marine invertebrates can be positive (Berke et al., 2013), negative (temperature-size rule; Irie and Fischer, 2009), or unimodal (Schöne et al., 2002). Temperature can affect growth through changes in physiology and the viscosity of seawater (Podolsky, 1994). Verberk and Atkinson (2013) further

Table 1
Growth responses for marine suspension feeders. "+"=higher growth with increasing temperature or velocity, "−"=lower growth with increasing temperature or velocity, Unimodal=a single peak at an optimal temperature or velocity and None=no relation. NR=not reported. Values in brackets are peak velocities/temperatures.

Organism	Velocity (cm s^{-1})	Relation	Temperature (°C)	Relation	Source
Various corals	NR	NR	18–26	Unimodal (26 °C)	Jokiel and Coles (1977)
Alcyonium siderium	10–20	+	NR	NR	Sebens (1984)
Anthopleura elegantissima	NR	NR	5–25	Unimodal (5–10 °C)	Sebens (1980)
Argopecten irradians	0.2–12.8	Unimodal (0.76 cm s^{-1})	14–27	NR	Kirby-Smith (1972)
A. irradians	0–15	Unimodal (1–6.5 cm s^{-1})	18–23	NR	Cahalan et al. (1989)
Placopecten magellanicus	0.5–23.5	Unimodal (2–6 cm s^{-1})	2–12	NR	Wildish et al. (1987)
Crassostrea gigas	NR	+	10–23	Variable	Malouf and Breese (1977)
Crassostrea virginica	1–8	Unimodal (4.2 cm s^{-1})	21 ± 0.3	NR	Grizzle et al. (1992)
Mercenaria mercenaria	1–8	Unimodal (2.2 cm s^{-1})	21 ± 0.3	NR	Grizzle et al. (1992)
Mya arenaria	0.1–6	+	1.5–16	NR	Emerson (1990)
Mytilus trossulus	1–40	−	16.5–17.0	NR	Ackerman and Nishizaki (2004)
M. californianus	1–40	−	16.5–17.0	NR	Ackerman and Nishizaki (2004)
M. californianus	NR	NR	~10–13	+	Menge et al. (2008)
Pseudochitinopoma occidentalis	2–15	−	NR	NR	Eckman and Duggins (1993)
Membranipora membranacea	2–15	−	NR	NR	Eckman and Duggins (1993)
Balanus glandula	2–15	None	NR	NR	Eckman and Duggins (1993)
Semibalanus cariosus	2–15	None	NR	NR	Eckman and Duggins (1993)
Pollicipes polymerus	2–15	None	NR	NR	Eckman and Duggins (1993)
B. cretanus	2–15	Unimodal (8 cm s^{-1})	NR	NR	Eckman and Duggins (1993)

suggest that O_2 availability may actually be lower at colder temperatures due to lower O_2 partial pressure, which ultimately may serve to limit body size. The effects of water velocity on growth are similarly equivocal as the relationship between flow and growth in benthic marine invertebrates can be positive, negative or unimodal (Table 1). Moreover, interactive effects of temperature and flow may influence growth through simultaneous changes in physiology and mass transport. For instance, increased temperatures may lead to high metabolic demand, whereas higher water velocity will increase the exchange gases and nutrients that sustain metabolism. Regardless, it remains uncertain how simultaneous changes in multiple environmental stressors may, or may not, affect growth in benthic marine invertebrates (Crain et al., 2008; Todgham and Stillman, 2013).

Although growth rates have been measured or estimated for many barnacles species (Bertness et al., 1998; Sanford et al., 1994; Thiyagarajan et al., 2003), evidence linking growth to changing environmental conditions remains largely correlative. For instance, growth in Balanus glandula is known to follow a seasonal pattern, with highest growth in the spring, when planktonic food is abundant, and lower growth rates in the fall and winter (Barnes, 1955; Moore, 1934; Wethey, 1983). Semibalanus balanoides at high flow sites had higher growth rates than individuals at low flow sites (Crisp, 1960; Sanford et al., 1994). Similarly, Sanford and Menge (2001), found that barnacle growth was highest at sites with high wave-exposure during periods of elevated water temperatures. Plastic changes in cirral morphology, the appendages used to acquire food, have also been documented in barnacles, with increased water motion leading to shorter cirri (Arsenault et al., 2001). Although such correlative patterns suggest a link between growth and environmental conditions, little experimental evidence exists to test these relationships.

Energy budget models, based on quantitative experiments, can generate predictions about growth under different environmental conditions. Their value lies, in part, in their ability to generate predictions about how a species will respond to novel environmental conditions that may not exist today (Kearney and Porter, 2009). Such predictions, however, require careful measurement of physiological responses like feeding and respiration under a range of environmental conditions. For barnacles, we have recently developed response curves for feeding and respiration as a function of both temperature and velocity (Nishizaki and Carrington, 2014a,

2014b), allowing for predictions of growth in the barnacle, Balanus glandula. In this study, we aim to measure barnacle growth responses to different water temperatures and velocities to test our model predictions.

Specifically, we compare the model outcomes to results from a pair of growth experiments that examine the effects of water temperature, velocity and their interaction on barnacle growth. In the first experiment, barnacle growth rates were measured in a dockside experiment where water temperatures and velocities were controlled. In second experiment, growth rates were measured for juvenile barnacles outplanted in the field at three sites.

2. Materials and methods

2.1. Model predictions

Energy available for barnacle growth was estimated from feeding and respiration data collected over different temperatures and velocities (Nishizaki and Carrington, 2014a, 2014b). The total barnacle energy budget (E_{TOT}; J day^{-1}) was calculated as (Wu and Levings, 1978)

$$E_P = E_C - E_R - E_F, \tag{1}$$

where E_P is the energy available for somatic growth (J day^{-1}), E_C is the rate of energy gained from consumption (J day^{-1}), E_R is the rate of energy used for respiration (J day^{-1}), and E_F is the rate of energy loss to fecal production. Values of E_F were calculated by multiplying E_C by 1 – the assimilation efficiency for Balanus glandula (92.5%, not including dissolved organic matter; Wu and Levings, 1978). We have omitted any term for the energy lost to molting because they contribute less than 2% to the overall barnacle energy budget (Wu and Levings, 1978). The rate of energy gained from consumption was calculated as

$$E_C = C \times TSM \times CS \times Q, \tag{2}$$

where C is the relative capture rate (% of maximum capture rate), which is temperature and flow dependent as measured by Nishizaki and Carrington (2014a), TSM is the total suspended matter concentration measured from the Friday Harbor Laboratories dock (g L^{-1}), CS is the caloric content of suspended material in seawater (11,427 J g^{-1}; Platt and Irwin, 1973) and Q is the volume of water

that moves through an area the size of the cirral net (L day^{-1}) based on water velocity, cirral length and the proportion of time that the cirri are exposed to the water column based on beating behaviors specific to each water temperature and velocity (Nishizaki and Carrington, 2014a).

The rate of energy used in respiration can be calculated as

$$E_R = R \times OC, \tag{3}$$

where R is the temperature- and flow-dependent respiration rate (L O_2 day^{-1}) as measured by Nishizaki and Carrington (2014b) and OC is the oxycaloric value of 4800 cal L O_2^{-1} (Crisp, 1971).

To account for the diversion of energy from somatic growth to reproductive production, we incorporate a minimum threshold energy to classify reproductively active barnacles,

$$E_{thresh} = \max(E_P)0.159, \tag{4}$$

based on the observation that no barnacle less than 15.9% the size of the largest barnacle (basal area) in our experiments was found to have developed gonads. The energy for production was then calculated as

For $E_P \geq E_{thresh}$

$$E_P = E_{thresh} + ((1 - 0.123) \times (E_P - E_{thresh}))$$

assuming that 12.3% of available energy was diverted to reproduction (Wu and Levings 1978), barnacles that did not reach reproductive maturity remain as

For $E_P < E_{thresh}$

$$E_P = E_P$$

2.2. Barnacle growth in dock mesocosm experiment

Experiments were conducted at the Friday Harbor Laboratories of the University of Washington (FHL-UW) on San Juan Island, WA, USA. To examine the influence of water temperature and velocity on growth, juveniles settled on plates were raised under different thermal and flow conditions in a dockside experiment from July 19 to August 25, 2011. Fresh seawater was drawn off the FHL-UW floating dock, from a depth of 1 m below the surface using a 2800 GPH submersible bilge pump (Rule Industries, Gloucester, MA, USA) fitted with a mesh (pore size 2 cm $\times$ 2 cm) over the inlet. Water was transported via a 5 cm diameter PVC pipe into one of two header tanks (180 L; 65 cm height; 60 cm diameter). The water in one of the tanks was heated with seven 38 cm 1000 W submersible heating elements (Biotherm 1000 W Titanium Heating Element, Blueline Aquatics, San Antonio, TX, USA), and the other tank was left unheated. Both tanks were wrapped in 5 cm thick foil and fiberglass insulation (SP55, Frost King, Mahwah, NJ). Each header tank emptied via a 5 cm diameter bottom standpipe into a 5 cm PVC manifold that supplied four raceways (total of 8 raceways; Fig. 1). Each raceway measured 5 cm width 150 cm length 3 cm depth and flow in each raceway was controlled with a 5 cm diameter PVC ball valve preceding the entrance end. At the exit end of the raceway, a 3 cm tall spillover gate was placed to maintain sufficient water depth to cover the barnacle plates. The raceways were shaded with 0.32 cm plywood covered in reflective mylar thermal blankets (Primacare, Dallas, TX, USA).

Temperatures were monitored in all eight raceways by a vacuum-sealed Thermocron iButton datalogger (Maxim Integrated/Dallas Semiconductor, San Jose, CA, USA), every 15 min for the duration of the experiment. Water velocities directly over the barnacle plates were measured every week by timing the downstream movement of fluorescein dye. Five measurements were made over each plate every week and small adjustments with the ball valve were made to maintain water velocities. Water velocities
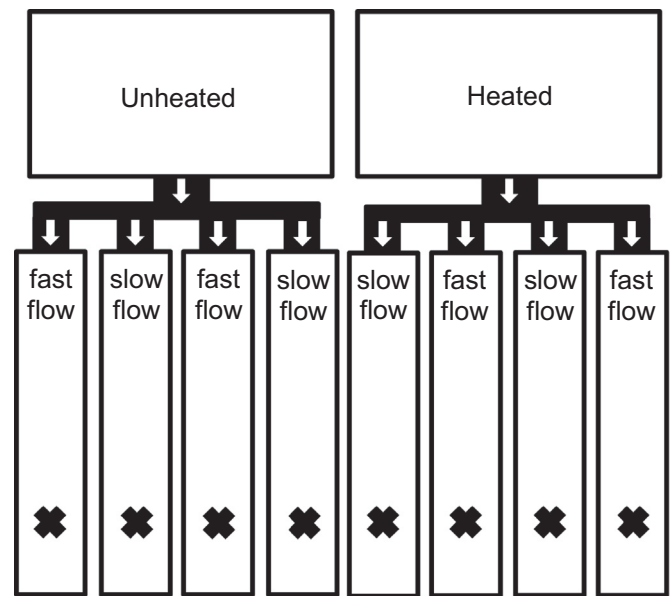

Fig. 1. Raceways used to assess barnacle growth in response to water temperature and velocity. Arrows indicate direction of water flow and the location of barnacle plates are indicated by the "$\times$" symbols.

and temperatures were chosen to include conditions that elicited physiological and behavioral responses (Nishizaki and Carrington, 2014a, 2014b), and were tightly controlled throughout the experiment (19.1 $\pm$ 0.7 and 2.0 $\pm$ 0.1 cm s^{-1} and 11.5 $\pm$ 0.2 and 14.1 $\pm$ 0.4 °C, respectively; means $\pm$ SE; $N=6$ weeks for velocities and $N=3550$ samples every 15 min for temperatures).

Barnacles were settled on 10 cm $\times$ 10 cm PVC plates covered on one side with SafetyWalk Tape® (Product number 7740, 3M Company, Saint Paul, MN, USA) to provide adequate surface rugosity for settlement. The plates were set out under the FHL-UW dock in April, 2011 and once barnacles had settled (July, 2011), each plate was cut in half, to produce a 5 cm $\times$ 10 cm plate. At the beginning of the experiment, barnacles were thinned to ensure that individuals were of similar size among plates (basal area=1.53 $\pm$ 0.07 mm^2 with no statistical differences among plates). Plates were photographed weekly to measure the basal area (mm^2) often individual barnacles on each plate for five weeks. Growth rates were based on the change in basal area over the entire length of the experiment.

At the end of the experiment, the ten barnacles on each plate were dissected to separate any gonadal material from the body. Gonad and barnacle body were both dried at 60 °C in a drying oven for 48 h and weighed. As cirral morphology is known to undergo plastic responses to flow (Arsenault et al., 2001), the length of the sixth cirrus was also measured at the end of the experiment with a dissection microscope equipped with a CoolPix 995 digital camera (Nikon Inc., Tokyo, Japan). All images were processed using ImageJ software (v.1.45s; NIH, Bethesda, MD, USA).

2.3. Barnacle growth in the field

A second experiment measured growth rates of barnacles that were outplanted in the field at sites of varying water temperatures and velocities. Growth rates were monitored at Argyle Creek on San Juan Island, WA, USA (a marine research preserve, 48.52°N, 123.01°W), which feeds into a saltwater lagoon that fills at high tide and empties during low tide. As such, the creek experiences a range of water velocities and temperatures due to its tidal interactions with the lagoon.

Juvenile barnacles were settled onto Safety-Walk plates as described above. Plates were placed, uncut (10 cm × 10 cm) at two sites within Argyle Creek. The two sites, separated by 20 m, were chosen as representative of two different flow regimes (fast and slow). At each site, three concrete blocks (40 cm × 19 cm × 4 cm) were deployed amongst the bottom cobble and arranged to span the creek width. On each block, two barnacle plates were fastened for a total of 6 plates per site. Barnacles were also outplanted to a nearby (250 m) floating dock on the ocean side of the creek that experiences relatively slow water velocities. Two plates were attached to the left and right side of the dock at approximately 20 cm depth below the surface. Barnacles were continuously submerged throughout the experiment. Since block effects of plates and concrete blocks were not significant (ANOVA *p*-values from 0.12 to 0.45), individual barnacles were considered replicates.

Water temperatures at each site were monitored throughout the experiment using Tidbit v2 temperature probes sampling every 15 min (Onset Computers, Bourne, MA, USA). Water velocities were measured via three methods. First, water velocities were measured at high frequency over nine hours to quantify variation throughout the tidal cycle using an Acoustic Doppler Velocimeter (ADV; Nortek, Norway). The ADV was deployed on July 23, 2011, and made three measurements at each site once an hour. Measurements were made 1 cm above the substratum and sampled at 25 Hz. Weekly measurements were also made at the sites using a Marsh–McBirney flowmeter (model 523, Frederick, MD). From June 29 to August 9, water velocities were measured at the three sites 5 cm above the substratum. Relative water motion at each site was also estimated indirectly from mass loss of standard Plaster of Paris spheres (45 cm diameter; Nishizaki and Ackerman, 2007) over 24 h (spheres deployed at 17:00 on June 7, 2011 and collected at 17:00 on June 8, 2011).

Food concentration was measured both hourly over one tidal cycle and weekly over the course of the experiment by filtering water sampled at the site. 1 L seawater samples were run through glass GF/C Whatman filters and placed in a 60 °C drying oven (Model 255G, Fisher Scientific, Hampton, New Hampshire, USA) for 48 h to measure total dry weight using an electronic analytical balance (Sartorius 1602 MP8-1, $\pm$ 0.1 mg; Göttingen, Germany). Filters were then placed in a muffle furnace (Omegalux, LMF-3550) at 500 °C for 12 h and weighed again to procure organic/inorganic ratios.

2.4. Analysis

The effect of water temperature and velocity on barnacle size (e.g., shell, body and gonad) were analyzed with two-way ANOVAs. Proportional data were arcsin-square root transformed before using ANOVA. Where the assumptions of the general linear model could not be met, non-parametric Kruskal–Wallis tests were employed. For the mesocosm experiment, Student *t*-tests were run to determine if there were any differences between two raceways in a given treatment. For the field experiment, ANOVA was used to confirm similarity among plates within each site. Cirral lengths were analyzed using ANCOVA, using $\log_{10}$ transformed data to meet test assumptions. Dry body weight was used as a covariate as differences in growth were expected among the treatments and cirral length is known to vary with body size (Arsenault et al., 2001; Crisp and Maclean, 1990). To remove body-size effects, the least-squares mean cirral length was calculated for a standard body mass for each treatment using ANCOVA according to the methods of Marchinko and Palmer (2003). If the slopes of each treatment were not significantly different, the least-squares means for each treatment was plotted against water temperature and velocity. For all parametric tests, where significant differences were found, pairwise comparisons were made using Bonferroni

post-hoc tests. Differences in environmental conditions (i.e., temperature, velocity, dissolution rate, and seston concentration) among field sites were assessed using ANOVA or Kruskal–Wallis tests when the assumptions of the GLM were not satisfied. All analyses were conducted with SPSS v.19 (IBM Corporation, Chicago, IL).

Temperature coefficients (Q_{10}) describing the magnitude of change in growth with increasing temperature were calculated for the mesocosm experiment,

$$Q_{10} = \left(\frac{G_2}{G_1}\right)^{(10/(T_2-T_1))}, \qquad (5)$$

where G_1, G_2 are growth rates (mm^2 day^{-1}) measured as the change in basal area between the beginning and end of the experiment and T_1, T_2 are corresponding temperatures (°C).

2.5. Predicted versus measured growth

The measured growth rates of barnacles from the mesocosm experiment were compared to the predictions of the energy budget model. Barnacle growth was assessed at four temperature–velocity combinations (11.5 °C/2 cm s^{-1}, 11.5 °C/19 cm s^{-1}, 14 °C/2 cm s^{-1} and 14 °C/19 cm s^{-1}). Dry mass of body, shell and gonad were summed and regressed against the predicted energy for production (J day^{-1}).

3. Results

3.1. Model predictions

Model predictions estimated from respiration and feeding rates are presented in Fig. 2A. Barnacles at 2 cm s^{-1} were predicted to have low levels of energy available for production at both 11.5 °C and 14 °C (8.65–18.44 J day^{-1} respectively; Fig. 2B). In contrast, barnacles at 19 cm s^{-1} had more energy available for production at both 11.5 and 14 °C (12.32 and 22.32 J day^{-1}).

3.2. Barnacle growth in dock mesocosm experiment

Basal area growth was lowest in the low temperature-low flow treatment (1.0 $\pm$ 0.1 mm^2 day^{-1}; Fig. 3A), intermediate for both the low temperature-high flow treatment and the high temperature-low flow treatment (1.4 $\pm$ 0.1 mm^2 day^{-1} for both), and highest at the high temperature-high flow treatment (1.5 $\pm$ 0.1 mm^2 day^{-1}). Growth rates were significantly higher at faster velocities ($F_{(1,76)} = 4.086$, $p < 0.050$) and high temperatures ($F_{(1,76)} = 16.872$, $p < 0.001$). There was also a significant interaction between velocity and temperature ($F_{(1,76)} = 4.798$, $p < 0.050$); Q_{10} for barnacles at 2 and 19 cm s^{-1} were 3.3 and 1.2, respectively.

At low velocities (2 cm s^{-1}), dry body masses were lower at 11.5 °C compared to 14 °C (1.2 $\pm$ 0.1 × 10^{-3} g to 1.6 $\pm$ 0.2 × 10^{-3} g; Fig. 3B). Masses were higher at 19 cm s^{-1} and again increased from 11.5 °C to 14 °C (1.8 $\pm$ 0.1 × 10^{-3} g to 2.7 $\pm$ 0.4 × 10^{-3} g). Dry body mass was significantly affected by flow (Mann–Whitney *U*, $p < 0.001$) and temperature (Mann–Whitney *U*, $p < 0.001$).

Dry shell masses at the end of the experiment were lowest for the low temperature-low flow treatment (0.05 $\pm$ 0.01 g; Fig. 3C). Shell mass was higher at both the low temperature-high flow and high temperature-low flow treatments (0.07 $\pm$ 0.01 g and 0.08 $\pm$ 0.01 g respectively). Masses were highest in the high temperature-high flow treatment (0.09 $\pm$ 0.01 g). Shell mass was significantly influenced by both water velocity ($F_{(1,76)} = 4.074$, $p < 0.050$) and temperature ($F_{(1,76)} = 10.167$, $p < 0.003$). The interaction was not significant ($F_{(1,76)} = 0.001$, $p = 0.999$).
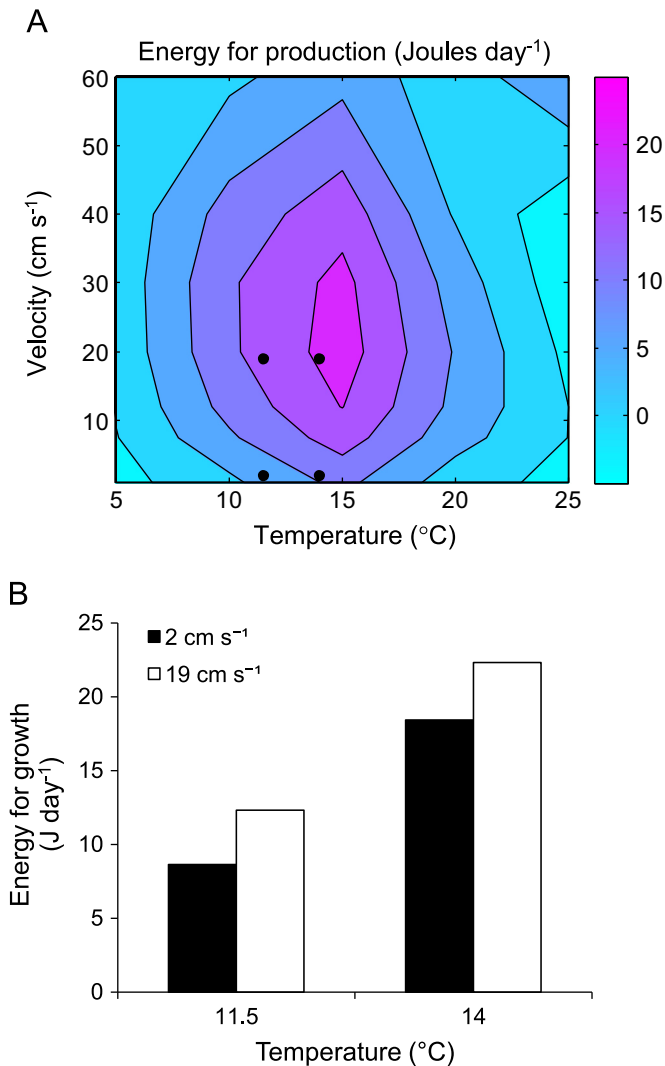
A

B

Fig. 2. Model predictions for barnacle growth. (A) Predicted energies available for production for *Balanus glandula* as a function of water temperature and velocity. Contour lines represent intervals of 5 J and black circles indicate environmental conditions used in the mesocosm experiment and (B) predicted energies available for production under conditions matched to the mesocosm experiment, based on Joules gained from measured feeding rates (Nishizaki and Carrington, 2014a) and respiration rates (Nishizaki and Carrington, 2014b) under different water velocities and temperatures.

In our experiments, more barnacles produced eggs in the high velocity-high temperature treatment (90%) compared to all other treatments (25–70%; Fig. 3D). At low velocities (2 cm s^{-1}) gonad mass increased from 11.5 °C to 14 °C ($1.9 \pm 0.6 \times 10^{-3}$ g to $2.6 \pm 0.6 \times 10^{-3}$ g). At 19 cm s^{-1}, gonad masses were higher and increased from 11.5 °C to 14 °C ($2.7 \pm 0.8 \times 10^{-3}$ g to $7.2 \pm 1.2 \times 10^{-3}$ g respectively; Fig. 3D). Gonad mass was significantly influenced by both water velocity ($F_{(1,76)} = 5.117$, $p < 0.030$) and temperature ($F_{(1,76)} = 4.583$, $p < 0.040$).

Cirral lengths were longer under slow water velocities and warmer water temperatures ($F_{(1,75)} = 147.04$, $p < 0.001$ and $F_{(1,75)} = 125.89$, $p < 0.001$ respectively; Fig. 4).

3.3. Barnacle growth in the field

Water temperatures at the slow flow site near the ocean (13.67 ± 0.02 °C) were 23% lower compared to the intermediate (16.81 ± 0.05 °C) and fast flow sites (16.87 ± 0.05 °C; Fig. 5A). Significant differences were found among all three sites

($F_{(2,11520)} = 1689$, $p < 0.001$) with post-hoc tests indicating that the slow site was significantly cooler than the intermediate and fast sites.

Throughout the tidal cycle, water velocities were higher at the intermediate and fast flow sites (0.32 ± 0.01 m s^{-1} and 0.34 ± 0.01 m s^{-1} respectively) compared to the slow site (0.01 ± 0.01 m s^{-1}; Fig. 5B). Consistent differences among the sites were found at all times tested (for all times $p < 0.001$ from ANOVA, $N=3$), with post-hoc tests indicating that each site was significantly different from the other two. Weekly measurements made over the duration of the experiment also indicated that water velocities at the slow site were slower (0.01 ± 0.01 m s^{-1} averaged over all days), than the intermediate and fast sites (0.83 ± 0.21 m s^{-1} and 1.09 ± 0.22 m s^{-1} respectively; Fig. 5C). Consistent differences in weekly velocities existed among the sites (Fig. 5C; Kruskal–Wallis test, $p < 0.001$; $N=8$ sample days). Similarly, dissolution rates were significantly higher at the intermediate and high flow sites (40 ± 1 and 63 ± 3%) compared to the low flow site (2%; Fig. 5D; Kruskal–Wallis test, $p < 0.005$; $N=6$ spheres).

Although there were fluctuations in seston concentration on a daily time scale (6.4–27.7 mg L^{-1}), there were no significant differences among the three sites ($F_{(2,12)} = 36.552$, $p = 0.993$; Fig. 6A). Likewise, over the month-long duration of the experiment, seston concentrations at the three sites varied from 6.6 to 17.1 mg L^{-1} (Fig. 6B), but no difference in concentration was found among the three sites (Kruskal–Wallis tests, $p = 0.359$; $N=5$). The organic fraction of seston ranged from 25% to 48% over the duration of the experiment, but no significant differences were found among the three sites. ($F_{(2,12)} = 1.133$, $p = 0.354$; Fig. 6C).

Barnacle basal areas increased throughout the field deployment from 6.01 ± 0.27 mm^2 to 40.05 ± 1.20 mm^2 (> 500% increase; Fig. 7). Although barnacle growth varied among sites (high flow site > intermediate site > slow site), these differences were not significant (Fig. 7; Kruskal–Wallis tests, $p = 0.165$).

Cirral lengths at the slowest site were significantly longer (30%) than those found at the intermediate and fast sites (Fig. 8; ANCOVA, $p < 0.001$).

3.4. Predicted versus measured growth

Barnacle growth rates from the mesocosm experiment correlated well with the energy available for production as predicted by the model (Fig. 9; slope $= 2.353$; R^2 of 0.84, $p = 0.081$). Residuals indicated faster growth than predicted for both treatments at 14 °C and slower growth than predicted for both 11.5 °C treatments.

4. Discussion

Our model of barnacle growth, based on measured respiration and feeding rates, suggests that peak rates should occur at moderate water temperature (15 °C) and velocities (20–30 cm s^{-1}; Fig. 2). Barnacles at slow velocities should experience lower growth, due to lower encounter rates with suspended food particles, whereas at high velocities, barnacles experience lower capture efficiencies, which also reduces their potential for growth (Nishizaki and Carrington, 2014a). At low temperatures, limited O$_2$ availability and feeding activity may combine to depress growth. For extremely warm temperatures, high metabolic demand can impose similar limits on growth (Nishizaki and Carrington, 2014b). These predictions provide a comparison for barnacle growth data collected in the mesocosm and field experiments.

Basal area growth rates in the outdoor mesocosms ranged from 1.0 to 1.5 mm^2 day^{-1} and 0.4 to 1.5 mm^2 day^{-1} in the field transplant experiments (Figs. 3A and 7). In both experiments,
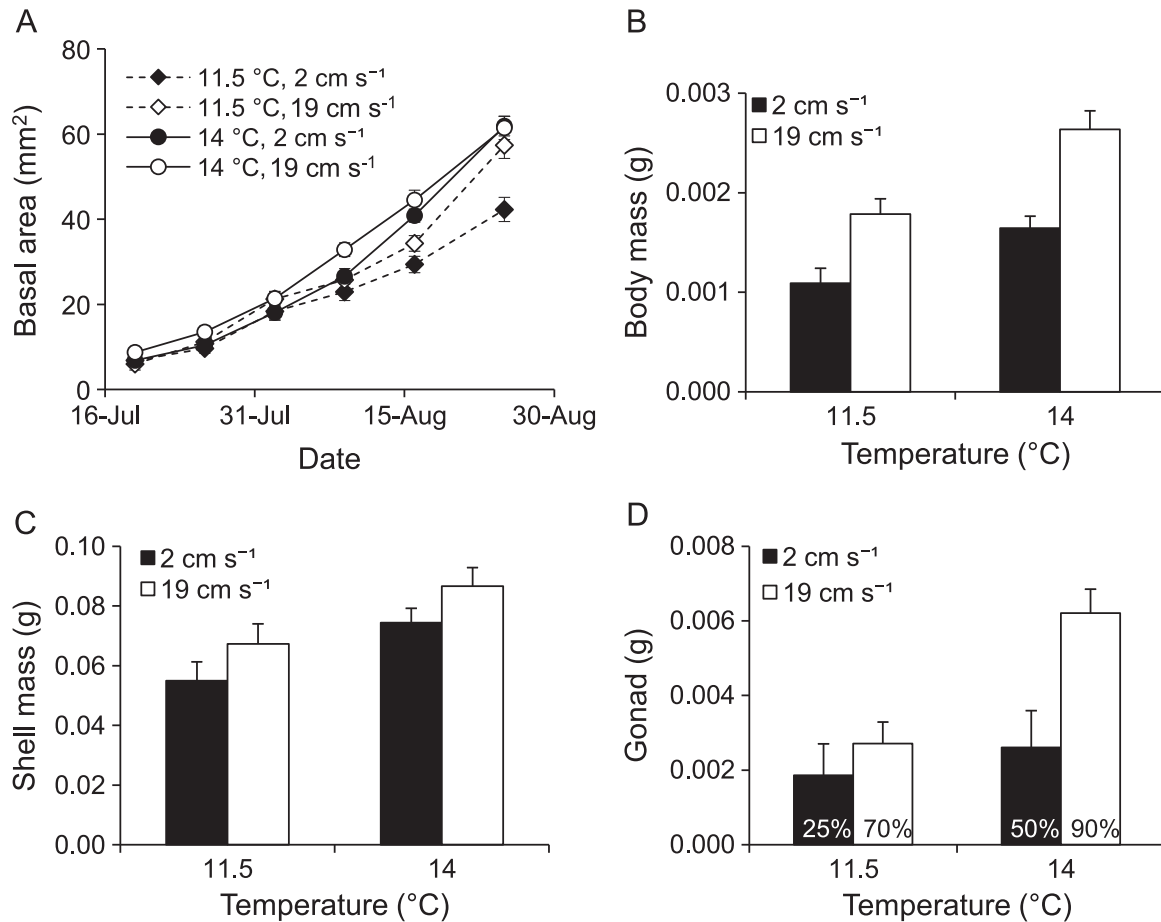
Fig. 3. Barnacle growth in response to water temperature and flow in the dock mesocosm experiment. Changes in (A) basal area, (B) dry body mass, (C) shell mass and (D) gonad mass over time for barnacles grown in different water velocities (2 and 19 cm s^{-1}) and temperatures (11.5 or 14 °C). Percentages in plot D represent the proportion of barnacles that were found to have reproductive material at the end of the experiment. All measurements made at the conclusion of the dockside experiment. $N=20$ barnacles, error bars represent standard error.
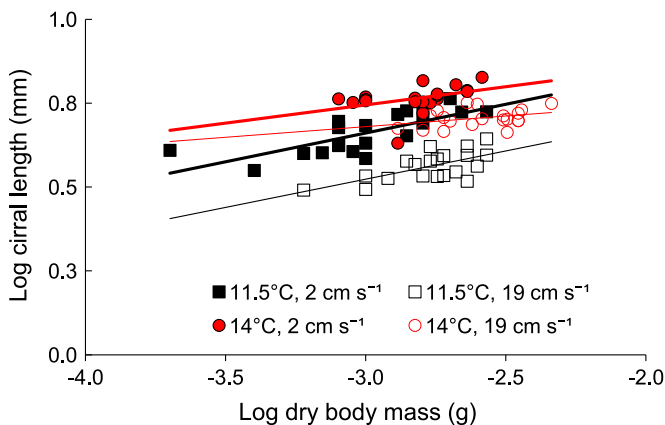
Fig. 4. Log–log comparison of cirral length versus dry body mass for barnacles as a function of temperature and flow in the dock mesocosm experiment. Each point represents an individual barnacle. Fitted lines represent 11.5 °C (black lines), 14 °C (red lines), 2 cm s^{-1} (thick lines) and 19 cm s^{-1} (thin lines) and differences in slope were not significant (ANCOVA, $p=0.409$). $N=20$ barnacles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increased barnacle growth was associated with higher water temperatures and velocities (Figs. 3A and 6). In addition, cirral lengths in both the mesocosm and the field were reduced at higher velocities (Figs. 4 and 8).

In the mesocosm experiment, barnacles experienced greater growth under warmer temperatures (14 °C versus 11.5 °C) and faster velocities (19 cm s^{-1} versus 2 cm s^{-1}), consistent with model predictions (Fig. 2A). At 2 cm s^{-1}, there was a positive relationship between temperature and growth ($Q_{10}=3.3$), consistent with other intertidal ectotherms that report Q_{10} values between 2.0 and 4.1 (Dame, 1972; Green and Hobson, 1970). In contrast, temperature had much less impact on growth at 19 cm s^{-1} ($Q_{10}=1.2$), possibly due to higher food availability (Nishizaki and Carrington, 2014a), that buffered the thermal response (Schneider et al., 2010). In addition, generally limited O_2 delivery at low flows (Nishizaki and Carrington, 2014b) may lead to increased growth as temperature and O_2 availability rise (Verberk and Atkinson, 2013). Conversely, fast flows that deliver higher levels of O_2 may buffer any effects of temperature. In the field, barnacles tended to grow larger at sites with higher temperatures (17 °C versus 14 °C), though these differences were not significant.

Highest growth was observed in our experiments at temperatures that were nearly optimal based on model predictions (14 °C in mesocosm and 17 °C in field), and may reflect patterns of thermal sensitivity for both feeding and respiratory activity. At low temperatures, cirral activity and ingestion increases up to 15–20 °C and decreases at temperatures ≥ 25 °C (Anderson and Southward, 1987; Nishizaki and Carrington, 2014a). Respiration rates, meanwhile, increase from low to intermediate temperatures (5–20 °C), and remain high through 25 °C (Nishizaki and Carrington, 2014b). Although such high temperatures were only briefly seen at midday in Argyle Creek, future increases in water temperature may reduce growth at the two warm sites (e.g., high respiration and decreasing
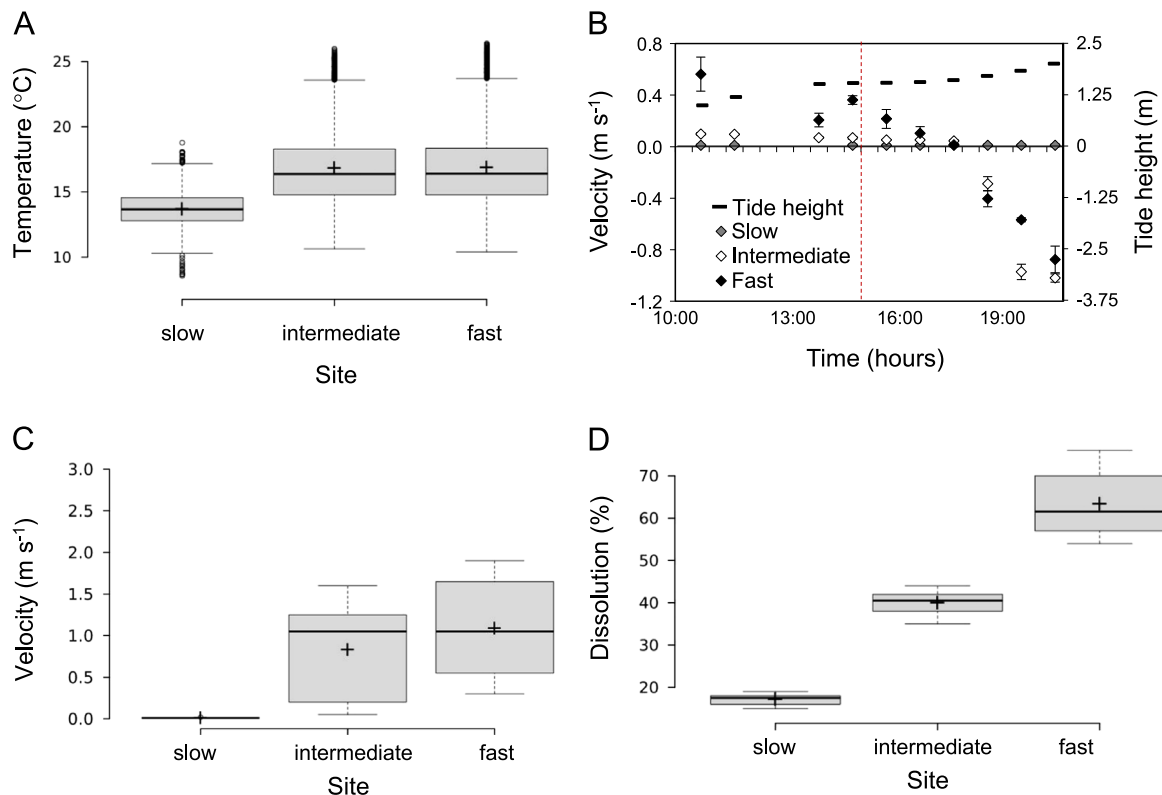
Fig. 5. Physical conditions at Argyle Creek. (A) Water temperatures at three field sites located at Argyle Creek, WA, USA. Boxplot center lines show the medians; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots; crosses represent sample means. $N = 3845$ sample points. (B) water velocities at three sites through tidal cycle. Hatched line depicts tide height and the red line delineates the change in direction of water flow at the site (e.g., ebb versus flood tide), (C) water velocities at sites measured weekly with Marsh–McBirney flowmeter and, (D) dissolution rate of Plaster of Paris spheres. $N = 6$ spheres, error bars represent standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

feeding), while increasing growth at the cool site.

Faster water velocities in the mesocosm experiments led to significantly higher barnacle growth (Fig. 3). In the field experiment, barnacle growth tended to be higher at the fast velocity site, though differences among sites were not significant (Fig. 7). In contrast to our results, Eckman and Duggins (1993) found that *Balanus glandula* growth rate was relatively insensitive to changes in water velocity from 2 to 16 cm s^{-1}. Those experiments ran from June until the end of November, and it is possible that slow growing barnacles caught up to faster growing barnacles by the end of the season if larger barnacles divert proportionally more energy towards reproductive production and away from growth. A lack of reproductive output data, however, prevents more detailed comparison.

At low flows (< 5 cm s^{-1}), increasing velocity increases the rate of food delivery (Nishizaki and Carrington, 2014a; Taghon et al., 1980), O$_2$ availability, and respiration rate up to some limit (Nishizaki and Carrington, 2014b). At high velocities, water motion will impose mechanical forces that may damage cirri (Marchinko, 2007) or make them less effective. Thus, growth rates should be optimal at intermediate water velocities.

Barnacles exposed to slower water velocities had longer cirri compared with individuals grown under faster flows. This flow-dependent response is consistent with the findings for a number of barnacle species (Arsenault et al., 2001; Marchinko and Palmer, 2003), and do not explain the observed differences in barnacle growth. Whereas, cirri were longest under slow velocities, both encounter rate and growth rate were lowest under slow flows. Cirral lengths were also slightly longer (14%) at 14 °C compared to 11.5 °C, possibly reflecting the need for increased oxygen ventilation or particle capture at elevated temperatures (Nishizaki and

Carrington, 2014b). Longer cirri may facilitate respiration as they serve both as a surface for gas exchange and as a means of increasing flow (Anderson, 1994). In the field, velocity differences were much larger than in the mesocosm and are likely to have driven the observed differences in cirral length.

In the mesocosm experiment, barnacles under the high temperature and high velocity treatment were predicted to have more energy available for production. Although body and shell growth was higher under these conditions, there was also a notable increase in reproductive output (Fig. 3D). Bertness et al. (1991) suggest that larger barnacles produce proportionally more reproductive material, which appears consistent with these results. Switching of energy reserves from somatic growth to gonad production in mature barnacles may contribute to differences between shell and body mass (Fig. 3A–C).

Results from the mesocosm and field experiments provide complimentary tests of the growth model. Barnacle growth in the mesocosm matched closely with the predictions of the energy budget model (Fig. 9). Barnacles at 14 °C grew faster than predicted, whereas barnacles at 11.5 °C grew more slowly than predicted (Fig. 9). Temperatures and velocities in the mesocosm experiment were chosen based on predictions based on established physiological and behavioral responses (Nishizaki and Carrington, 2014a; Nishizaki and Carrington, 2014b). From the response surface in Fig. 2A, it is clear that treatments chosen without such knowledge would likely yield incomplete, and difficult to interpret results. Depending on the treatments chosen, results could suggest a negative relationship between temperature/velocity and growth, opposite responses to each factor, or no effect for one or both factors. Our field experiment, however, served as a test of the model for barnacles in their natural habitat. Not surprisingly, both
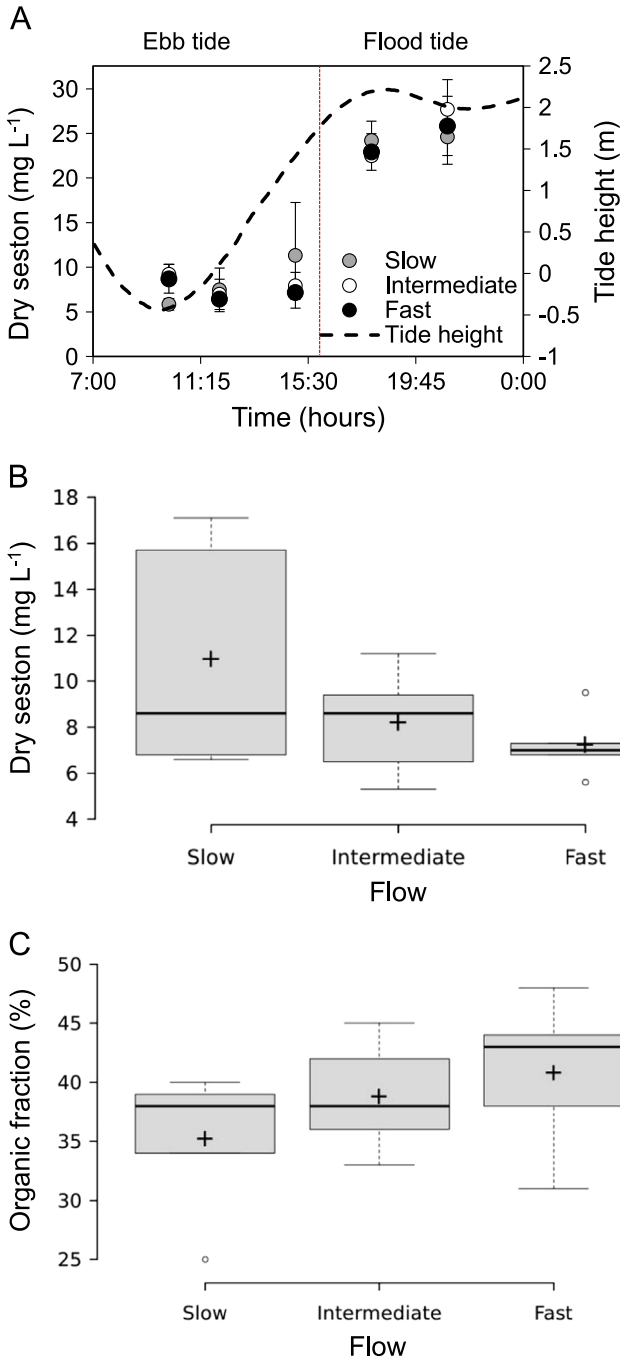
A

B

C

Fig. 6. Seston concentrations at field sites located at Argyle Creek, WA, USA. (A) Dry seston measured through tidal cycle. Hatched line depicts tide height and the red line delineates the change in direction of water flow at the site (e.g., ebb versus flood tide), error bars represent standard error, (B) dry mass of seston at three field sites over the duration of the growth experiment, and (C) organic fraction over the duration of the experiment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature and velocity were more variable in the field compared to the mesocosm. Although field growth generally conformed to model predictions, increased environmental variability limited our certainty when matching theoretical and experimental data. Regardless, when these results are taken together, it is reasonable to conclude that temperature and flow are two important mechanisms underlying barnacle growth.

These results demonstrate that water temperature and velocity affect the growth of the barnacle, *Balanus glandula*. Peak growth rates are predicted for intermediate water temperatures (15 °C)
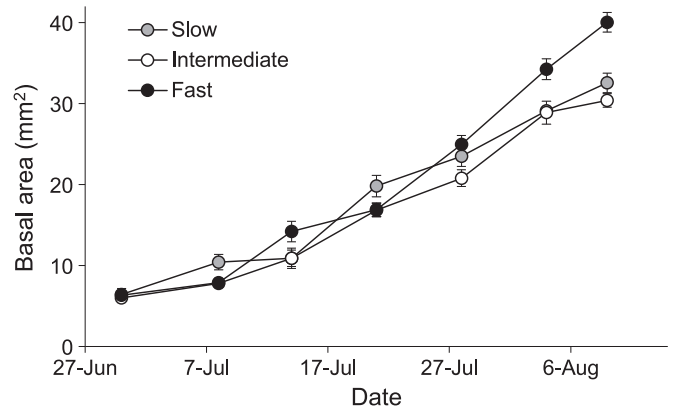

Fig. 7. Growth of barnacles outplanted in the field. Symbols represent mean basal area ± standard error for barnacles outplanted at one of three sites of varying water flow (slow, intermediate and fast). $N=60$ barnacles for fast and intermediate, $N=40$ for slow.
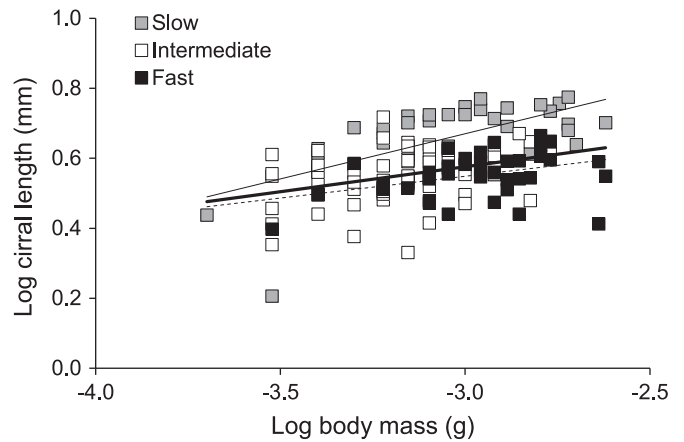

Fig. 8. Cirral lengths from barnacles at the end of field deployment. Log–log relationships of cirral length as a function of dry body mass for the slow ($N=40$, thin line), intermediate ($N=60$, dark line) and fast flow ($N=60$, hatched line) sites. Each point represents an individual barnacle. Differences in slope were significant (ANCOVA, $p < 0.001$), with body mass having a greater effect on cirral length on barnacles at the slow site.
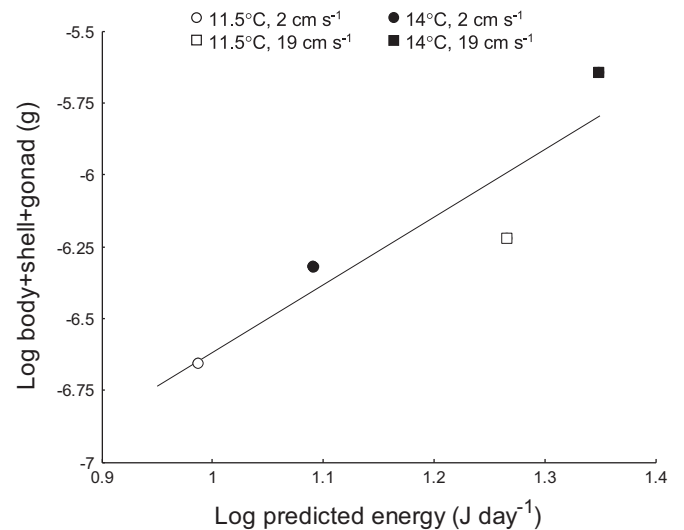

Fig. 9. Comparison of predicted energy for production versus measured barnacle growth in mesocosm experiment. Growth was assessed at 11.5 °C (open symbols), 14 °C (filled symbols), 2 cm s^{-1} (circles) and 19 cm s^{-1} (squares).

and velocities (20–30 cm s^{-1}), whereas reduced growth is predicted at extreme temperatures and velocities, each due to a different physiological or behavioral responses in respiration or feeding. Growth rates from both experiments conform well to model predictions calculated from temperature- and flow-dependent feeding and respiration rates (Fig. 9; R^2=84%). The model, however, overestimates growth at 11.5 °C and underestimates it at 14 °C. These results demonstrate the efficacy of models to predict the effect of multiple environmental stressors on growth when rooted in a mechanistic understanding of physiological and behavioral performance.

Acknowledgements

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