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The effect of water temperature and velocity on barnacle growth: Quantifying the impact of multiple environmental stressors $\stackrel{\circ}{\approx}$



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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 $(32 \pm 1 \text{ and } 34 \pm 1 \text{ cm s}^{-1};$ mean \pm SE) and warm temperatures (16.81 \pm 0.05 °C) experienced higher growth compared to individuals at low velocities (1 \pm 1 cm s⁻¹) and temperatures (13.67 \pm 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;

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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

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

$$E_{\rm P} = E_{\rm C} - E_{\rm R} - E_{\rm F},\tag{1}$$

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

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

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 Download English Version:

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