



OXYGEN CONSUMPTION IN RELATION TO BODY SIZE, WAVE EXPOSURE, AND CIRRAL BEAT BEHAVIOR IN THE BARNACLE *BALANUS GLANDULA*

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ABSTRACT

Barnacle feeding and respiration depend on the activity of feeding appendages known as cirri. We measured the oxygen consumption of individuals of the acorn barnacle *Balanus glandula* Darwin, 1854 to determine how changes in beating behavior, body size, and cirrus length affected energy demand. Respiration rates increased exponentially with body mass to the 0.66 power. Respiration rates did not differ significantly among pumping, normal, and fast beats, even though these beats involve different levels of cirral and opercular activity. Finally, barnacles from a location of high water motion exhibited significantly shorter cirri and lower oxygen consumption for a given body size than those from calmer waters.

KEY WORDS: *Balanus glandula*, cirral beat, Cirripedia, metabolic scaling, respiration

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INTRODUCTION

The barnacle *Balanus glandula* Darwin, 1854 is a common rocky-shore intertidal species along the Pacific coast of North America from Mexico to Alaska (Morris et al., 1980) and has recently been introduced to South America and Japan (Geller et al., 2008). Like all free-living cirripedes, *B. glandula* uses modified leg appendages, known as cirri, to feed and circulate water for respiration (Crisp and Southward, 1961; Anderson and Southward, 1987; Davenport and Irwin, 2003). Barnacle activity involves a number of distinct behaviors, from solely opening and closing the operculum to complex cirral beats in which the cirri may emerge from the operculum, and completely unfurl and furl before retracting (Crisp and Southward, 1961). The type of behavior often varies with water flow, food supply, and temperature (Anderson and Southward, 1987). Although much is known about how cirral beating rate varies with body size in barnacles (Anderson and Southward, 1987; Crisp and Maclean, 1990), less is known about how body size, cirrus length, or behavior affects respiration rates.

The rate of oxygen consumption is commonly used to infer metabolic energy use in heterotrophic organisms because these organisms use oxygen in respiration to release energy via the Krebs cycle. The relationship between respiration and body mass is usually exponential, of the form $R = aM^b$ (Glazier, 2005). Here R is the respiration rate ($\mu\text{mol O}_2 \cdot \text{min}^{-1}$), M is body mass (g dry weight), a is a constant and b is the scaling (or allometric) exponent. Respiration should generally increase with body mass, as larger

organisms need more energy; thus, b is usually positive but is commonly less than 1, meaning that while larger animals use overall more oxygen per individual than small animals they use less oxygen per unit body mass. The two most commonly cited values of b are $2/3$ and $3/4$. The $2/3$ value has been justified on the grounds that respiration should scale with the surface area of the respiratory surface, and area generally scales to the $2/3$ power of body mass (Glazier, 2005). The argument for a $3/4$ scaling exponent is based on the geometry of circulatory systems (Brown et al., 2004). However neither model has overwhelming support, as a recent review by Glazier (2005) found that values for invertebrates ranged from -1.20 to $+2.05$. Previous studies of barnacles have found exponents ranging from 0.658 to 0.827 (Barnes and Barnes, 1959; Prasada Rao and Ganapati, 1969; Wu and Levings, 1978).

The rate of oxygen consumption might vary with barnacle behavior if there are differences in the energetic costs of different behaviors. Crisp and Southward (1961) identified six behaviors in balanoid barnacles: closed, testing, pumping, normal beat, fast beat, and extension. Each behavior involves a different combination of opercular and cirral activity, each which involves combinations of muscular activity and hydraulic pressure from the movement of haemocoelic fluids (Anderson, 1994). In the case of opercular movement, the opercular plates are held closed by the contraction of several sets of opercular plate muscles. The relaxation of these muscles, combined with muscle contractions of the mantle tissue, push that fluid into the body and opercular valves,

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open the operculum (Anderson, 1994). Cirral extension is begun by additional contraction of the mantle tissue, which pushes fluid into the prosoma. The prosoma rotates apically and contraction of prosomal muscles push fluid into the thorax and cirri, causing the cirri to unfurl. Cirral furling is accomplished by contraction of cirral muscles that push fluid back into the prosoma and ultimately into the mantle (Anderson, 1994). Thus, the greater the level of opercular or cirral movement in a particular beating behavior the greater the likely energetic cost of the behavior.

The closed behavior should use the least oxygen of any behavior, as the plates are fully closed with no water exchange outside the barnacle (Crisp and Southward, 1961). Next least should be testing, which occurs when a barnacle's operculum repeatedly opens and closes. Some movement of the prosoma and thorax may occur, but the cirri rarely protrude (Crisp and Southward, 1961). Pumping is characterized by rhythmic movement of the operculum and slight protrusion of furled cirri (Anderson and Southward, 1987). Thus pumping beat should require greater energy than testing or closed, as it involves a greater level of activity. Normal beat is similar to pumping beat, but the barnacle's cirri fully unfurl and furl, making it likely to be the most energetically costly of all behaviors. In fast beat, opercular movements are reduced and the cirri move more rapidly moving cirri than in normal beat. Also, the cirri do not retract fully into the mantle cavity between beats, as they do in normal beat. Lastly, extension occurs when the cirri remain protruded without any rhythmic movement (Crisp and Southward, 1961). These last two behaviors involve less opercular and cirral movement than normal beat, and thus should be less energetically costly to produce than a normal beat. However, their energy use relative to testing and pumping is difficult to predict.

One additional factor that may influence respiration rates is cirrus length. Barnacles from areas with high water motion generally have shorter cirri than those from calmer waters (Marchinko, 2007). Higher water motion brings a greater food (and oxygen) supply than calm water, but also greater pressure-drag on the cirri. Smaller cirri are less vulnerable to damage and deformation when feeding (Marchinko and Palmer, 2003; Marchinko, 2007; Neufeld and Rankine, 2012) and are thought to be an adaptation to high water flow. Longer cirri are thought to be advantageous in food-limited calmer water because they allow the processing of larger volumes of water per beat, but no one has yet looked at the energy costs associated with beating these different-sized cirri. All else being equal, a longer cirrus should take more energy to beat.

In this study, we examined the effects of body size, beating behavior, and cirral phenotype on the oxygen consumption rate of *B. glandula* collected from two locations in Newport Bay, California and maintained in the laboratory. We also examined the relationship between opercular diameter and dry tissue mass in both freshly collected barnacles and those maintained in a laboratory environment to determine whether laboratory culturing affected dry tissue weight.

METHODS AND MATERIALS

Animal Collection and Storage

Individuals of *B. glandula* anchored to mussels were collected from Pirates Cove, just inside the entrance of Newport Bay, Orange County, CA, USA (33°35'41.73"N, 117°52'42.12"W) on multiple occasions. Individuals were collected on mussel shells (*Mytilus californianus* and *Mytilus galloprovincialis*) attached to rocky benches or jetties. All barnacles were collected from a wave-sheltered region in the north end of the cove, with the exception of individuals designated as "wave-exposed," which came from farther south, on or near the jetty at the mouth of Newport Bay.

Animals were transported on ice to the W.M. Keck Science Center (Claremont, CA, USA), where all experiments were performed. Mussels were immediately shucked and all mussel tissue was removed. Mussel valves with barnacles were maintained in 280-liter recirculating tanks with natural seawater at $16 \pm 1^\circ\text{C}$. Water quality was monitored semi-weekly and seawater was replaced as needed. Animals were acclimated for at least one week prior to respirometry.

Barnacles were feed 2-3 times weekly with nauplii of *Artemia* spp. (INVE Aquaculture Nutrition, Salt Lake City, UT, USA), hatched 48-72 hours prior to feeding. During feedings, animals were submerged in separate 10-gallon tubs for 8-15 hours. Concentrations of nauplii were high enough to prevent depletion by the end of a feeding session.

For experiments, individual barnacles were excised from the mussel shells using a pair of cutting pliers (model Nos. 338 and 437, Channellock, Meadville, PA, USA) to cut a circle through the mussel shell around the barnacle. A short "leash" of fishing line was attached to the excised mussel shell with hot-melt glue, which enabled the barnacle to be suspended in the respirometry chamber.

Experimental Parameters

Size and Mass Measurements.—Opercular diameters were measured to the nearest 0.01 mm as the largest diameter along the inside of the operculum (Palmer, 1980) using the inside jaws of a pair of digital vernier calipers (Digimatic Caliper model CD-6" CX, Mitutoyo America, Aurora, IL, USA). To calculate dry tissue mass, individual barnacles were dried for 48 hours at 60°C and then ashed for 4 hours at 400°C . Ash-free dry mass was calculated as the difference between the two measurements. Cirrus length measurements were made by dissecting out the prosoma from the shell and photographing the cirri under a dissecting microscope. The length of the sixth cirrus was measured using the segmented line tool in ImageJ (W. S. Rasband, U.S. National Institutes of Health, Bethesda, MD, USA), following the curve through the center of the ramus.

Oxygen Measurements.—Oxygen levels ($\mu\text{mol} \cdot \text{l}^{-1}$) were measured using a fluorescence-based optical sensor system (Neofox system; Ocean Optics, Dunedin, FL, USA). The sensor was calibrated daily in filtered seawater ($0.45 \mu\text{m}$) into which air had been bubbled for at least 12 hours. Measurements were made in an airtight chamber consisting of a 28 ml shell vial capped by a No. 3 rubber stopper (Fig. 1), filled with aerated, filtered seawater. The sensor was inserted through a hole in the stopper and sealed with modeling clay. A layer of black plastic was glued to the bottom of the vial to eliminate any reflection from the oxygen sensor, ensuring an accurate oxygen reading. For small barnacles, the volume of the chamber was reduced by filling the bottom of the vial with hot-melt glue. The chamber was equipped with a 10×3 mm spin bar and placed on a stir plate (Isotemp 11-100-49SH, Fisher Scientific, Waltham, MA, USA) to keep the water well mixed during measurements. To control temperature, the chamber was placed in the cavity of a 50 ml jacketed beaker (Kimble Chase-Kontes Glass, Vineland, NJ, USA). The beaker was connected to a circulating water chiller (AC200-A25U, Thermo Fisher Scientific, Waltham, MA, USA), which kept the chamber temperature at $16 \pm 0.25^\circ\text{C}$. The space between the exterior of the chamber and the interior of the beaker was filled with additional filtered seawater to maximize thermal conductance. To measure the water volume inside the chamber, the chamber, stir bar, and stopper were weighed dry before each run and then again at the end of the run when the barnacle and sensor had been removed, but not the water. The water volume was calculated as the difference between the two mass measurements divided by the density of seawater, calculated from the water's salinity and temperature. This was used to convert the respiration measurements from $\mu\text{mol} \cdot \text{l}^{-1} \cdot \text{min}^{-1}$ to $\mu\text{mol} \cdot \text{min}^{-1}$ for each barnacle. Trials lasted a maximum of 30 minutes and the seawater in the vial was replaced anytime the concentration of oxygen decreased to less than 90% of saturation. Individuals were run through repeated trials to maximize

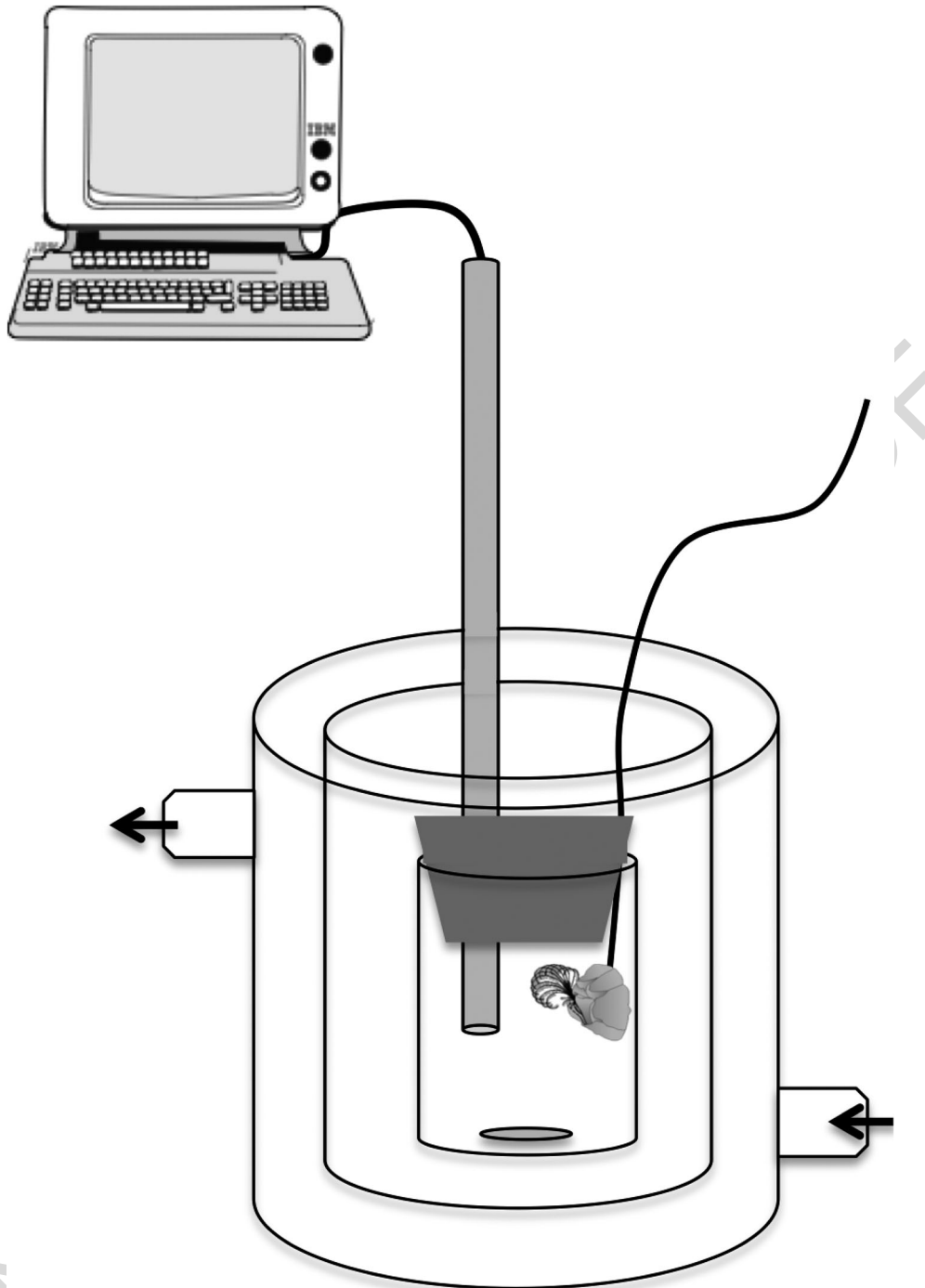


Fig. 1. Respirometry chamber. The barnacle is suspended on a leash of fishing line inside a 25-ml clear glass scintillation vial, filled with $0.45\ \mu\text{m}$ filtered seawater and capped with a rubber stopper. The sensor, which measures both oxygen and temperature, is inserted through a hole in the stopper, and the hole is sealed with modeling clay. A stir bar in the bottom of the chamber keeps the water mixed during measurements. For temperature control, the chamber is placed inside a 50-ml clear glass-jacketed beaker that is connected to a circulating water chiller, and filled with filtered seawater to a level above the vial.

observations. A behavior had to be exhibited continuously for a minimum of 1 minute for the respiration rate to be used.

Behavior was observed by eye and noted continuously throughout each trial. We consistently observed four of the six behaviors described by Crisp and Southward (1961): closed, pumping, normal beat, and fast beat. Testing was difficult to distinguish from closed, and extension was rarely seen. Barnacles sometimes alternated between two behaviors, particularly between closed and normal beat and between fast beat and extension. We excluded these observations.

Statistical Analyses.—All analyses were completed in JMP v.8 for Macintosh (SAS, Cary, NC, USA). All models were tested for normality and homogeneity of errors. To determine the relationship between opercular diameter and tissue mass, and to explore whether laboratory rearing affected mass, we compared dry weight and opercular diameter of two groups of 25 barnacles collected on the same day. One group was processed within 24 hours while the other was maintained in the lab for 30 days before processing. The regression equation tested was: $\log_{10}(\text{dry weight}) = \log_{10}(\text{operculum diameter}) + \text{group} + \log_{10}(\text{operculum diameter}) \times$

group. There was one outlier in this model that affected both normality and homoscedasticity of errors; however, excluding the outlier did not change the significance of the effects tests, so it was left in.

To determine the effect of operculum diameter on respiration rates, a regression was run on 31 barnacles for which normal-beat data were available. The barnacles were sampled in three different months: August 2011 ($n = 12$), February 2012 ($n = 8$) and April 2012 ($n = 11$). The regression equation was $\log_{10}(O_2) = \log_{10}(\text{Operculum}) + \text{season} + \log_{10}(\text{Operculum}) \times \text{season}$. To compare the oxygen consumption of different behaviors, replicate measurements of each behavior were averaged for each individual barnacle that showed at least two of the four target behaviors (closed, normal beat, pumping, or fast beat). The regression equation was $\log_{10}(O_2) = \log_{10}(\text{Operculum}) + \text{behavior} + \log_{10}(\text{Operculum}) \times \text{behavior}$, with barnacle identity included as a random variable.

To determine whether barnacles collected from the rock jetty had shorter cirri than those farther inside the bay, we used an ANCOVA with operculum diameter as the covariate. The equation was: Cirrus length = Operculum + population + Operculum \times population. Because cirri length and operculum diameter are both length measurements, we did not test for an exponential relationship. To determine whether barnacles from the rock jetty had lower oxygen consumption during normal beat at a given operculum diameter, we used an ANCOVA with operculum length as the covariate. The equation was: $\log_{10}(O_2) = \log_{10}(\text{Operculum}) + \text{population} + \log_{10}(\text{Operculum}) \times \text{population}$.

RESULTS

Overall, dry mass increased with operculum diameter, with an exponent of 2.8322 ± 0.2631 SE ($F_{1,1} = 115.9258$, $p < 0.0001$, Fig. 2). There was no significant difference between the exponents of field-collected and laboratory-maintained barnacles (interaction $F_{1,1} = 0.0021$, $p = 0.96$), but slightly different multipliers (group $F_{1,1} = 9.4373$, $p = 0.0036$). The barnacles that were maintained in the laboratory for 30 days had significantly greater mass than freshly collected barnacles. According to the regression model, a 4.1 mm barnacle increased from roughly 9.55 mg to 13.44 mg dry tissue mass over the 30 days. A sizeable number of barnacles in the laboratory-maintained group contained gonad tissue, although this wasn't quantified.

The respiration of barnacles undergoing normal beat increased with operculum diameter, with an exponent of 1.8533 ± 0.3608 ($F_{1,1} = 15.808$, $p = 0.0005$). This was calculated after excluding the interaction term between season and diameter, which was not significant (interaction $F_{2,2} = 0.1565$, $p > 0.8$). Neither were there differences in intercepts among seasons (season $F_{2,2} = 1.4229$, $p = 0.26$),

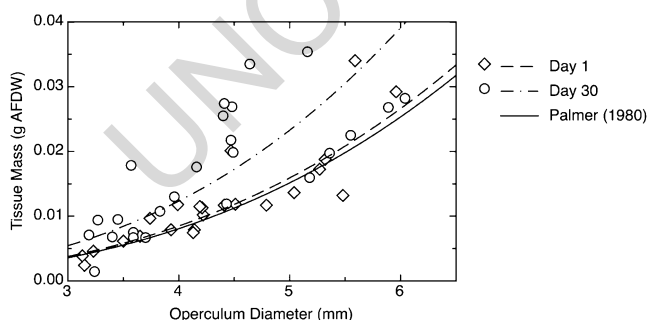


Fig. 2. *Balanus glandula* tissue dry-mass (ash-free dry weight) in relation to operculum diameter. Day 1 barnacles were processed 1 day after field collection. Day 30 barnacles were maintained in the laboratory for 30 days before measurements. See text for the regression model that produced the two dashed lines. The solid regression line is based on an equation reported by Palmer (1980) for *B. glandula* collected from Washington State.

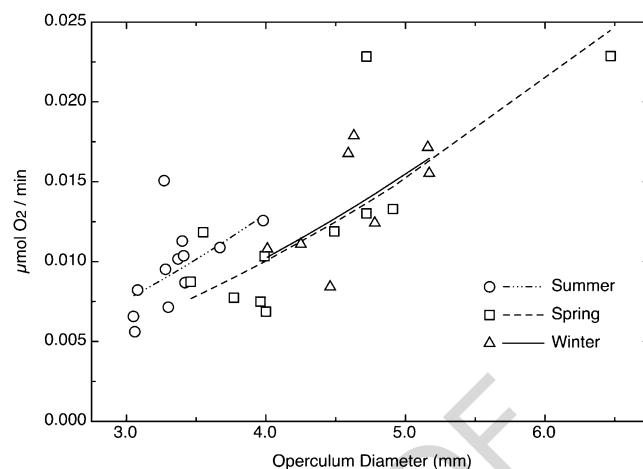


Fig. 3. Aquatic oxygen consumption of *Balanus glandula* collected during three different seasons. Regression equations are plotted for a model that included separate intercepts for each season, but a single slope. See text for full model details.

yet when plotted (Fig. 3) the summer group tended to have slightly higher respiration rates at a given diameter than the other two. Pooling the intercept term across seasons led to a smaller scaling exponent (1.3667 ± 0.2415) and a lower r^2 (0.52 vs. 0.58), thus separate intercepts were retained in the final model.

Average-sized barnacles (operculum diameter 3.86 mm) engaged in either pumping, normal, or fast beating consumed oxygen at rates of roughly 0.0100-0.0105 $\mu\text{mol}/\text{min}$ (Fig. 4), while closed barnacles consumed roughly an order of magnitude less ($F_{3,3} = 165.8669$, $p < 0.0001$). This was significantly less than the other three behaviors (Tukey-HSD, $p < 0.05$), but no other behaviors differed. There were no significant differences among behaviors in the scaling exponent of the relationship between diameter and oxygen consumption ($F_{3,3} = 1.132$, $p = 0.35$). After excluding the interaction term between behavior and the scaling exponent, the pooled scaling exponent was 1.8666 ± 0.3422 ($F_{1,1} = 28.0799$, $p < 0.0001$).

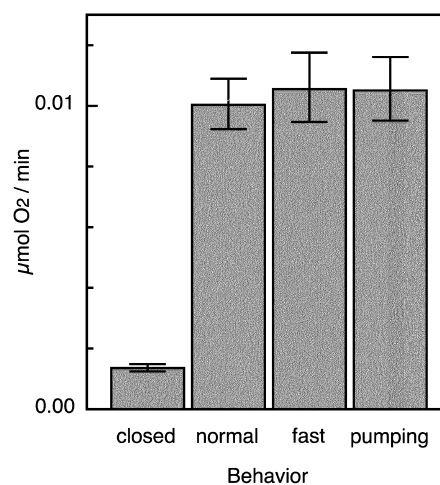


Fig. 4. Aquatic oxygen consumption for *Balanus glandula* as a function of cirral beating behavior. See text for description of behaviors. Rates are least-squared means (\pm SE) for a 3.86 mm operculum.

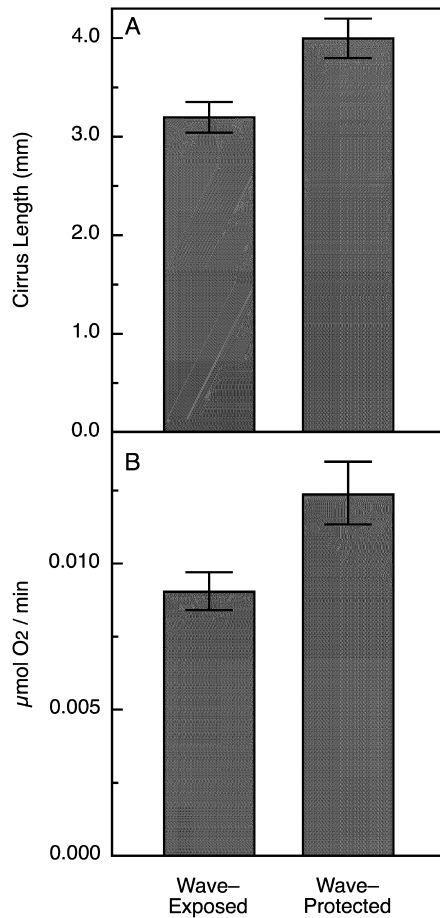


Fig. 5. Differences in (A) cirri length and (B) oxygen consumption under normal beat for barnacles collected from the jetty near the mouth of the bay (Wave Exposed) and in a nearby cove (Wave Protected). Cirrus lengths are least-squared means (\pm SE) for a 4.4 mm operculum. Oxygen consumption rates are the least-squared means (\pm SE) for a 4.5 mm operculum.

Barnacles from the sheltered population had significantly longer cirri than those from the wave-exposed jetty (Fig. 5A), roughly 0.80 mm longer for a 4.4 mm operculum diameter ($F_{1,1} = 10.3642$, $p = 0.0057$). There was no difference in the slope of the linear relationship between cirrus length and operculum diameter between the two groups ($F_{1,1} = 0.2186$, $p = 0.65$), although the overall relationship was positive (slope = 0.7209 ± 0.2357 , $F_{1,1} = 9.3543$, $p = 0.0038$). The wave-protected barnacles also used significantly more oxygen per minute ($F_{1,1} = 7.5571$, $p = 0.0112$, Fig. 5B), roughly 37% more for a 4.5 mm operculum diameter. The exponent for the respiration-operculum diameter relationship did not differ significantly between wave-protected and wave-exposed barnacles ($F_{1,1} = 0.0218$, $p = 0.8839$), averaging 1.6990 ± 0.3772 ($F_{1,1} = 20.2883$, $p = 0.0001$).

DISCUSSION

The results of this study confirm previously reported allometric relationships among length, mass, and respiration in *B. glandula*. They also provide two new insights into the effects of beating behavior and cirrus length on oxygen consumption. First, there was little difference in oxygen con-

sumption among pumping, normal, and fast-beating behaviors. This was surprising given the differences in opercular and cirral activity associated with each behavior. Second, the smaller cirri found in wave-exposed barnacles were energetically less costly than the longer cirri of wave-protected individuals, when individuals of similar operculum diameter were compared. While previous work on cirral plasticity has emphasized hydrodynamic forces and food supply as underlying explanations for cirral length, this is the first study to identify energetic cost differences.

The regression calculated between operculum diameter and dry tissue mass (ash-free dry weight) was nearly identical to one originally reported by Palmer (1980) for a Washington State population of *B. glandula* (Fig. 2). In both cases, the scaling exponent was approximately 2.8, which is reasonably close to the expected exponent of 3 for a length-mass relationship. Barnacles kept in the laboratory for 30 days did not show any signs of suffering from their experience. Instead, this group had a significantly greater dry mass per unit operculum length than those collected from the field. Some of the mass increase appears to be due to increased reproductive tissue, although the exact amount was not quantified. It is unclear whether this extra mass would influence oxygen consumption, as Wu and Levings (1978) found that *B. glandula* ovarian tissue and egg masses consumed 1-2 orders of magnitude less oxygen per milligram than body tissue.

The respiration regression analysis revealed that oxygen consumption scaled to length to a power of roughly 1.86. Given that mass scaled to length to a power of 2.8, this translates to a respiration-mass exponent of 0.66. Additional estimates of the exponent from the behavior and cirri length analyses were similarly calculated as 0.67 and 0.61, respectively. These values are all close to the predicted 2/3 value based on allometric scaling. They are also very similar to the value of 0.666 ± 0.016 which we calculated for *B. glandula* from a regression equation reported by Wu and Levings (1978). And they are also within the range of other reported scaling exponents for other balanoid barnacles (0.658 to 0.827: Barnes and Barnes, 1959; Prasada Rao and Ganapati, 1969). But they are lower than the other commonly accepted rate of 0.75 (Brown et al., 2004; Glazier, 2005).

The relatively low exponent of 0.66 might reflect decreases in the energetic costs of respiration with increasing body size. In balanomorph barnacles, the frequency of beating declines with increasing body mass to the -0.1 to -0.35 power (Anderson and Southward, 1987; Crisp and Maclean, 1990). Because the volume of water processed per beat increases with the square of cirral length (Anderson and Southward, 1987), larger animals can process as much water or more water per beat, allowing for slower beating rates. Beating is likely a large component of energy use during respiration and so a lower frequency of beating in larger animals should reduce energy consumption. Individual beat rates were not counted in this study, so it is unclear exactly how much beat rate changes with body size in this population of *B. glandula*.

There was also a slightly higher rate of oxygen consumption during normal beat for barnacles measured in the sum-

mer, as opposed to the winter or spring. While this difference was not statistically significant, pooling across seasons led to a poorer overall fit of the normal beat regression model. One possible explanation is that either metabolism or mass may vary seasonally. The difference is unlikely to be related to seasonal variation in reproductive mass, as southern California barnacles generally spawn in the winter and spring, and gonad tissue is nonexistent in the summer (Hines, 1978). All animals were laboratory acclimated to the same temperature of 16°C before use and were fed at roughly the same frequency, so they should be physiologically quite similar. The difference may simply reflect the small sample size and limited overlap in size between the summer group and the other two groups.

The results also suggest that an individual barnacle does not change its respiration rate by changing its beating behavior. There were no significant differences in oxygen consumption among the different beating behaviors, with the exception of the difference between 'closed' and all other behaviors. This is surprising given the differences in cirral and opercular activity that occur with these different behaviors (Crisp and Southward, 1961). For the three behaviors we observed, we originally hypothesized that both pumping and fast beat would be less energetically costly than normal beat. Pumping beat lacks the motions related to furling and unfurling the cirri, and thus should require less energy. Fast beats are similar to normal beats except both the cirral and opercular movements are shallower, which should reduce energy costs. Yet, normal beats tended to show lower oxygen consumption than fast or pumping (approximately 0.0005 $\mu\text{mol}/\text{min}$ less for a 3.6 mm barnacle), although this was not statistically significant. In this study, we did not count the number of beats, and it is possible that if oxygen consumption were adjusted to a per-beat basis, differences would emerge. For example, fast beats in *B. glandula* generally occur 2 to 2.5 times more often per second than pumping or normal beats, which tend to be very similar in frequency (S. Gilman, unpublished data). This means that the similar rates of energy consumption per minute for fast and normal beating would translate into roughly 60% less energy consumed per beat during fast beating, which is consistent with our hypothesis.

Finally, consistent with prior studies of *B. glandula* (Marchinko and Palmer, 2003; Li and Denny, 2004), we found that barnacles collected from an area with high water motion, the jetty at the mouth of Newport Bay, had significantly shorter cirri lengths for a given opercular diameter than those sampled from the inside of the bay. Shorter cirri are thought to be an adaptation to avoid damage under high water motion (Marchinko, 2007); but, their greater diameter and musculature has led to the suggestion that they might require more energy to beat (Neufeld and Rankine, 2012). Yet we found that, for a given operculum diameter, the shorter, wave-exposed cirri are less costly to beat. For example, a 4.5 mm barnacle undergoing normal beat consumed roughly 37% more oxygen per minute with long cirri than with short cirri. Because these measurements were made on field-collected individuals, we cannot conclusively attribute the difference in respiration to the plasticity of cirrus length. This result could be strengthened by measuring both cirrus

length and respiration on individuals that were reciprocally transplanted to each habitat for a period long enough to cover several molts. Nevertheless, if the longer cirrus phenotype is more energetically costly, long cirri must have some benefit in calm water in order for barnacles to maintain them. The most commonly suggested explanation is that longer cirri catch more food in calmer waters (Marchinko and Palmer, 2003); however, clearance rates have never been estimated for either of *B. glandula*'s two cirrus types.

In summary, the results of this study show that the scaling relationships for length vs. mass and mass vs. oxygen consumption in *B. glandula* generally match expected allometric relationships. We also found that oxygen consumption increased with cirrus length, when body size was held constant. In contrast, there was surprisingly little difference in oxygen consumption rates among the different types of cirral beats studied. It is unlikely that the energetic costs of these beats are really identical, given the different patterns of cirral and opercular activity involved in each behavior. However, this study only measured oxygen consumption per minute, and it seems likely that the number of beats per minute differs among the behaviors. This would be a fruitful area for future studies.

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