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Differences in feeding adaptations in intertidal and subtidal suspension-feeding gastropods: studies on *Crepidula fornicata* and *Crepipatella peruviana*

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Abstract Suspension-feeding organisms living in the intertidal zone experience reduced feeding times associated with periodic aerial exposure. The potential morphological and physiological adaptations to this reduced feeding time were investigated for two closely related gastropods, *Crepidula fornicata* and *Crepipatella peruviana*. Intertidal *C. fornicata* had heavier gills than subtidal conspecifics, a difference mediated by larger gill surface areas and greater numbers of gill filaments among intertidal individuals of a given size. In contrast, the gills of intertidal and subtidal *C. peruviana* were morphologically indistinguishable. Despite relatively larger food-collecting organs, individuals of *C. fornicata* from the intertidal zone had clearance rates (CR) that were not significantly different from those of subtidal conspecifics. In contrast, the CR of intertidal *C. peruviana* were significantly lower than those of subtidal conspecifics. The low CR of intertidal *C. peruviana* may be partially explained by significantly lower measured particle transport velocities across their gills. In the context of feeding, intertidal individuals of *C. fornicata* performed at least as well as subtidal conspecifics, resulting in a population whose adults were as large as those found subtidally. This suggests that *C. fornicata* has had a long interaction with the environmental heterogeneity associated with intertidal life. In contrast, intertidal

individuals of *C. peruviana* were on average smaller than subtidal individuals and may be stressed in the intertidal.

Introduction

The physical and ecological factors that control species' distributional ranges have recently received heightened attention due to anticipated climate change and an increased number of biological invasions (Sexton et al. 2009). Because species are usually distributed over large areas latitudinally, species range limits are most often studied on a broad geographic scale (e.g., Sagarin and Gaines 2002; Sorte and Hofmann 2004; Kuo and Sanford 2009). Such studies have been important for identifying potential biotic and abiotic limiting factors for a host of different species and their potential adaptations at range edges (e.g., Fawcett 1984; Zacherl et al. 2003; Lima et al. 2007; reviewed by Bridle and Vines 2007; Sexton et al. 2009). However, large distances separating central populations from those at range edges can make the study of limiting factors and adaptation difficult since a variety of different conditions (e.g., climate, temperature, salinity, wave action, available substrate, species composition, species interactions, and food sources) vary considerably.

The intertidal zone represents an abrupt spatial limit over very short distances for many marine organisms (Holt and Keitt 2005). Though some marine species are only found subtidally (e.g., Tomanek and Somero 1999; Collin 2000; Stillman and Somero 2000), and some are found chiefly in the intertidal zone (e.g., Connell 1972; Perez et al. 2009; Bourdeau 2011), a number of species are abundant in both areas (e.g., Dame 1972; Fletcher 1984; Saier 2002; Schaffmeister et al. 2006; Dong et al. 2011; Diederich and Pechenik 2013) and so experience a remarkable range of

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conditions over very short distances. Species whose populations extend from the intertidal zone (the upper edge of their range) into the adjacent subtidal zone can be studied in the context of range boundaries, but on a much smaller spatial scale. At high tide, intertidal organisms experience many of the same conditions that subtidal organisms do, as the two groups are often only meters apart, and a well-established gradient of stressors exists as one moves from the subtidal up through the intertidal zone (Menge 1976; Newell 1979; Denny 1985; Helmuth 1998). Thus, the limiting factors associated with aerial exposure in the intertidal zone and species' adaptations to those factors can be studied by investigating the characteristics of species whose members are living both intertidally and subtidally.

The gradients of stressors most closely associated with intertidal life are usually linked to environmental heterogeneity from aerial exposure: when compared to subtidal organisms, intertidal organisms experience periodic exposure to desiccation (e.g., Garrity 1984) and to hypoxia (e.g., Brinkhoff et al. 1983), rapid changes in salinity (especially in tide pools—e.g., Morris and Taylor 1983), and greater and more rapid temperature fluctuations (e.g., Diederich and Pechenik 2013). However, sessile suspension-feeding invertebrates, such as those investigated in the present study, are at an added disadvantage if they live intertidally, as they are unable to feed while exposed to the air.

A number of studies have documented differences in feeding organs or feeding strategies among some populations of marine invertebrates living in different conditions (e.g., Morton et al. 1957; Payne et al. 1995; Ito et al. 2002; Chaparro et al. 2004; Dutertre et al. 2007). For example, Newell et al. (1971) found that although the periwinkle *Littorina littorea* only feeds while submerged, periwinkles living high in the intertidal zone compensated for shorter feeding times with quicker radular rasping rates when compared to those of periwinkles living in the low intertidal zone. Similarly, Drent et al. (2004) found that gill-to-palp ratios (which determine particle sorting efficiency) of the deposit feeding clam, *Macoma balthica*, were flexible and depended upon the grain size of the material that the clams were feeding on. In general, intertidal grazers typically change their feeding activities depending on the duration of aerial exposure (Newell et al. 1971; Zeldis and Boyden 1979; Little 1989; Little et al. 1991; Santini et al. 2004, but not always, e.g., Underwood 1984), but the situation is not as clear for suspension-feeders (Morton et al. 1957; Griffiths and Buffenstein 1981; Widdows and Shick 1985; Bayne et al. 1988; Kreeger et al. 1990; Charles and Newell 1997). At least some suspension-feeders have the ability to compensate for differences in water turbidity with flexibility in the sizes of their feeding organs (Payne et al. 1995; Honkoop et al. 2003; Drent et al. 2004; Dutertre et al. 2007).

The closely related calyptraeid gastropods *Crepidula fornicata* (native to the east coast of North America) and

Crepidatella peruviana (formerly *Crepidatella fecunda*, native to the Chilean coast) live both intertidally and subtidally (Gallardo 1979; Collin 2003; Diederich and Pechenik 2013). These gastropods eat by collecting particles from the water using their modified gill (ctenidium) and transporting those particles to a food groove, where they are concentrated, directed to the mouth (via the food groove in the neck), and ingested (Chaparro et al. 2002). Because *C. fornicata* and *C. peruviana* do not move as adults and have only limited mobility as juveniles (and as small males) (Conklin 1897; Chaparro et al. 2001a), individuals living at the upper edge of their intertidal range have less time to collect food than their subtidal conspecifics. Unless they have a mechanism that compensates for reduced feeding time, this could potentially limit their vertical distribution, especially if slower growth delays a potential escape in size from mortality in the intertidal zone (Gosselin and Qian 1997; Hunt and Scheibling 1997).

In this study, we investigated the gill morphology and feeding physiology of *C. fornicata* and *C. peruviana* that were exposed to reduced suspension-feeding time at their vertical range edge. We compared various allometric relationships of the gill among intertidal and subtidal individuals living only meters apart at the same field sites for both *C. fornicata* and *C. peruviana*. We then used laboratory-based clearance rate (CR) experiments to assess the extent to which any differences in gill morphology actually affected the rate at which these organisms cleared food particles from the water. In addition, the speed of particle transport across the gill was quantified for *C. peruviana* using endoscopic analysis. Finally, size frequency distributions were used to estimate maximum growth potential for both species in the intertidal and subtidal zones.

Materials and methods

Collection and maintenance of snails

For all experiments, specimens of *C. fornicata* were collected from Bissel Cove, Rhode Island, USA (41.549920, -71.430584), where they can be found both intertidally and subtidally in large numbers (Diederich and Pechenik 2013). Collections were made for studies of gill morphology on April 20, 2011 and for clearance rates (CR) on May 22, 2012. Adults (14–40 mm SL) were collected at low tide from approximately 0.5 m above (+0.5 m) the mean low lower water mark (MLLW) (hereafter, “intertidal”) and 1 m below (−1.0 m) MLLW (hereafter, “subtidal”), and transferred to the laboratory in aerated seawater. Specimens of *C. peruviana* (scientific name from the World Register of Marine Species, date accessed: December 3, 2014) were collected from Pelluco Beach in Puerto Montt

(−41.478820, −72.914508), Chile, where they can be readily found both intertidally and subtidally (personal observation C. Diederich, O. Chaparro). For both species, intertidal and subtidal individuals were physically separated by ~50 m. Collections were made for the gill morphology studies and clearance rate experiments on October 17, 2012 and for particle velocity experiments on January 18, 2013. Adults were collected at low tide from approximately +1 m above MLLW (hereafter, intertidal) and −1 to −2 m below MLLW (hereafter, subtidal), and transferred to the laboratory in aerated seawater. Both of these species are protandrous hermaphrodites and both brood embryos for several weeks prior to larval release. Brooding status was incorporated into the clearance rate experiments (see below).

All experiments with *C. peruviana* were conducted using females (shell length >26 mm), which use suspension-feeding exclusively to obtain food; smaller individuals (males and juveniles) can also use the radula as a major means of food collection (Navarro and Chaparro 2002; Montiel et al. 2005). Both male and female *C. fornicata* were included for studies, since this species actively suspension-feeds even as recently metamorphosed juveniles (Eyster and Pechenik 1988).

Gill morphology

For studies of gill morphology, all specimens ($N = 40$ intertidal and 40 subtidal *C. fornicata*; 40 intertidal and 40 subtidal *C. peruviana*) were rinsed in deionized water and immediately preserved in 10 % formalin (diluted with 0.5 μm filtered seawater) buffered with sodium borate. Gills were dissected and photographed under a stereomicroscope fitted with an ocular micrometer. The number of gill filaments (minimum length 1 mm) in each gill was subsequently determined. The gill and remaining tissue were then dried separately on pre-weighed foil at 60 °C for 48 h to determine gill and total dry tissue weight. Using photographs taken under a stereomicroscope and analyzed using ImageJ (version 1.43; National Institutes of Health, Bethesda, Maryland, USA) for *C. fornicata* and Image-Pro Plus for *C. peruviana*, the longest five gill filaments were measured from the base to the most distal section of the filament bulb to determine the maximum filament length for each individual; these filaments were adjacent to each other and nearly identical in size. Finally, the gill surface area was determined using image analysis software by tracing the area of the intact, excised gill of each specimen.

Clearance rates

For the clearance rate (CR) measurements, the experimental snails were cleared of all epibionts and maintained

individually on their original substrate in glass aquaria with aerated, 0.5 μm filtered seawater. For *C. fornicata*, ambient temperature was 20 °C (field site water temperature at collection time was 17.9 °C) and salinity was 28; for *C. peruviana*, ambient temperature was 12–14 °C (similar to field site water temperature at collection time) and salinity was 30. In order to avoid acclimation to laboratory conditions, all experiments were performed within 24 h of collection (Rising and Armitage 1969; Widdows and Bayne 1971; McMahon and Payne 1980). Individuals were not fed after collection and prior to experimentation, and intertidal and subtidal snails experienced identical conditions except that intertidal snails were exposed to air for 3 h (*C. fornicata*) or 6 h (*C. peruviana*) (these times correspond to typical aerial exposure times at the edge of the vertical distributions of these species, Diederich and Pechenik 2013, personal observation O. Chaparro) prior to experimentation to simulate low-tide conditions.

Each snail was placed in an individual aquarium; for *C. fornicata*, each aquarium ($N = 95$ total) contained 3 L of 0.5 μm filtered seawater at salinity of 30 and at 20 °C, and for *C. peruviana*, each aquarium ($N = 79$ total) contained 10 L of 0.5 μm filtered seawater at salinity of 30 and at 14 °C. Air was continuously bubbled into each aquarium to ensure adequate mixing and to maintain a sufficient supply of dissolved oxygen. Pure cultures of either *Dunaliella tertiolecta* (for *C. fornicata*) or *Isochrysis galbana* (for *C. peruviana*) were used as the food sources for the snails, and these microalgae were added to each aquarium to achieve initial concentrations of approximately 30,000 cells mL^{-1} (Mardones et al. 2013). Because we could not add microalgae and take samples from each aquarium simultaneously, the addition of microalgae (and sampling) was performed sequentially with ~1 min between aquaria. All times were recorded so that CR could be computed. After aerial exposure (intertidal only), individuals were allowed ~10 min in seawater before phytoplankton suspensions were added.

One milliliter water samples was taken from each aquarium at the start of the experiment, and cell concentrations were measured (in triplicate) using a model ZM (*C. fornicata*) or Z2 (*C. peruviana*) electronic particle counter (Beckman Coulter Electronics) (incurrent aperture diameter of 140 μm). Snails were then allowed to filter the microalgae from the water for 2–4 h before final concentrations were determined. Because of the staggered sampling approach, we recorded the time between samples, but this amount of time was not exactly equivalent for each individual. Pilot studies revealed this amount of time to be appropriate in order to detect a reduction in cell concentration without allowing too many cells to be grazed from the suspension. However, clearance rates are notoriously variable from individual to individual in *C. fornicata* and even within an individual over time (Newell and Kofoed 1977a).

In addition to measuring algal concentration in all experimental aquaria, an additional two (for *C. fornicata*) or six (for *C. peruviana*) control tanks were set up with microalgae but without snails to determine settling or growth rates of algal cells during the experimental period. The clearance rate of each individual was estimated following the approach of Coughlan (1969):

$$CR = V[(\text{Log}_e C_0 - \text{Log}_e C_t) - a]/t]$$

where V is the volume of suspension, C_0 is the initial concentration, C_t is the final concentration, a is the rate at which particle concentration changed in the control suspension, and t is the duration of the experiment. At the end of the CR experiments, all snails were then removed from their substrate to determine their brooding status, and dry tissue weights were determined (see above).

Particle transport velocity on the gill

The speeds at which particles moved along the gill filaments of intertidal and subtidal *C. peruviana* were measured using endoscopy (OLYMPUS model OTV-S4 endoscope, power source OLYMPUS model CLV-10). This method has previously proven successful for determining particle velocity in this and closely related species (Mardones et al. 2013; *C. fornicata*, Shumway et al. 2014). Freshly collected (see above) intertidal and subtidal snails were removed from their substrates and allowed to adhere to transparent plastic plates. A small hole (diameter 3 mm) was first drilled in each plate where the endoscope would later be inserted and particle velocities were measured after specimens were allowed to adhere securely to the plates for 24 h. This procedure was performed on more organisms than were actually used in the analysis (10 intertidal, 11 subtidal) because some of the snails moved slightly after being placed on the substrate and thus did not allow for accurate placement of the endoscope. To measure particle velocity, each snail was maintained in its own 1-L aquarium with seawater at salinity of 30 and at 14 °C. Individuals were fed *I. galbana* at approximately 30,000 cells mL⁻¹. The tip of the endoscope was inserted through the hole in the plastic substrate and into the pallial cavity of the organism until the gill could be visualized. Filming was initiated once snails began filtering, and then, a suspension of non-toxic bright orange particles (2–10 μm diameter, Chaparro et al. 2001b, 2002) was added to the water near the incurrent feeding stream. These particles are easy to visualize, and they move along the gill at the same speed as does *I. galbana* (Mardones et al. 2013). Videos were visualized on a Trinitron Sony monitor and recorded to VHS for the analysis of particle velocity. To determine particle velocity, the displacement of orange particles along the gill was measured between two points. In order to ensure that only

particles driven by ciliary filament actions (not water flow in the mantle cavity) were measured, only particles in very close contact with the gill were selected. The time elapsed was determined by stepping through the video frame by frame (NTSC format: 30 frames s⁻¹, Ward et al. 1991), and the distance travelled by the particles was determined using the width of the gill filaments as a reference (Ward et al. 1991; Beninger et al. 1992; Mardones et al. 2013). Gill filament widths were determined after the particle velocity experiments were finished by dissecting the gill out of each specimen and measuring the filament width with a dissecting microscope at 40X. The filaments that were measured for width were in close proximity to the location where the particle movements were recorded.

Maximum size

Maximum size (shell length, SL) was used to estimate the growth potential of snails in the intertidal and subtidal zones. For *C. fornicata*, intertidal ($N = 206$) and subtidal ($N = 203$) adult snails (>15 mm SL) were collected in the spring of 2011, 2012, and 2013, and the longest shell dimension of each organism was measured to the nearest 0.1 mm with calipers. For *C. peruviana*, intertidal ($N = 147$) and subtidal ($N = 91$) adult snails (>25 mm SL) were collected in spring 2012, and the longest shell dimension of each organism was measured to the nearest 0.01 mm with calipers. Starting at 15 mm for *C. fornicata* and 25 mm for *C. peruviana*, snails were grouped into 2-mm SL classes.

Statistical analyses

Normality and homogeneity of variances were confirmed using D'Agostino and Pearson omnibus normality tests and F tests to compare variances; all analyses were performed in GraphPad Prism version 4.0.

For the studies of gill morphology, the size of each snail needed to be accounted for before the gills of intertidal and subtidal snails could be compared. An information-theoretical approach was used to model selection based on biological hypotheses and previously used models (Burnham and Anderson 2002; Johnson and Omland 2004) to determine the model that best suited each data set. Linear ($y = ax + b$) and power ($y = ax^b$) models were compared using a corrected Akaike information criterion score (AICc) (Akaike 1973) (GraphPad Prism version 4.0). After the appropriate model was selected, regressions of each gill variable against the dry weight of the snail for intertidal and subtidal subpopulations were compared using either ANCOVA (when the best model was linear) or extra sum-of-squares F test (when the best model was nonlinear).

Clearance rates (CR) were standardized for organismal weight as they have been shown to increase as the snails grow (Navarro and Chaparro 2002). For both species, CR was standardized (CR_s) to one gram of dry tissue weight using the allometric exponent of 0.56 (Navarro and Chaparro 2002) to describe the relationship between CR and tissue weight for *C. peruviana*, which was achieved following Bayne et al. (1987):

$$CR_s = (1/W)^b CR_e$$

where W is the dry tissue weight of the individual, b is the allometric exponent 0.56, and CR_e is the experimentally determined clearance rate. This method of standardization has also been used successfully for *C. fornicata* (Barillé et al. 2006), and the exponent used is very close to the universal scaling exponent for weight and oxygen uptake in gastropods (0.58–0.62, Marsden et al. 2011). Comparisons of CR among treatments were made using two-way ANOVA. Using our methodology, clearance rate could be underestimated if too much of the algal suspension was grazed (>35 %, Mardones et al. 2013) during the experimental time, so we repeated the above analysis after excluding data points from organisms that cleared >35 % of the algal suspension and the results did not change.

The individuals of *C. peruviana* used for the particle velocity experiments differed little in SL (<12 mm range), and particle velocity was not correlated with snail size (linear regression of SL vs. particle velocity: intertidal, $r^2 = 0.04$, $F_{(1,8)} = 0.34$, $p = 0.58$; subtidal, $r^2 = 0.00069$, $F_{(1,9)} = 0.0063$, $p = 0.94$). Thus, particle velocities were not standardized to the size of each snail. The velocities of particles were averaged for each individual, and the data for intertidal and subtidal subpopulations were then compared using an unpaired, two-tailed t test.

Size frequency distributions of intertidal and subtidal populations within each species were compared using contingency table analyses (χ^2 tests).

Results

Individuals of *C. fornicata* and *C. peruviana* showed dramatically different patterns of gill morphology across the intertidal–subtidal boundary. In particular, all measures of gill morphology were more strongly correlated with individual size for *C. fornicata* than for *C. peruviana* (Figs. 1, 2, 3, 4; Table 1).

Intertidal *C. fornicata* had gills that were as much as 50 % heavier than those of subtidal members of the same species, with the differences being greatest among larger adults (Fig. 1; $F_{(1,76)} = 10.53$, $p = 0.001$). This difference was at least partially mediated by differences in surface area (Fig. 3; $F_{(1,76)} = 4.75$, $p = 0.032$), and the gills

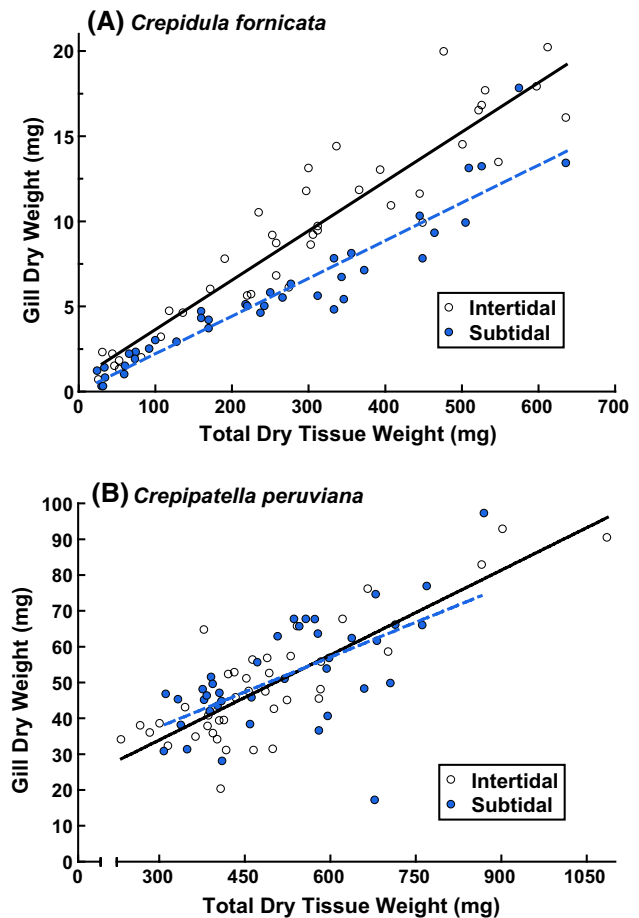


Fig. 1 Influence of habitat on the relationship between gill weight and total dry tissue weight for **a** *Crepidula fornicata* and **b** *Crepipatella peruviana*. Each point represents data from one individual. Detailed statistical information can be found in Table 1

of intertidal individuals had more filaments than those of subtidal individuals (Fig. 4; $F_{(2,76)} = 5.69$, $p = 0.0050$). The gills of the largest intertidal *C. fornicata* were about 80 % greater in surface area and about 30 % greater in the number of gill filaments than those of the largest subtidal members of the same species (Figs. 3, 4). The maximum lengths of the gill filaments, though, did not differ among intertidal and subtidal individuals (Fig. 2; $F_{(2,76)} = 0.95$, $p = 0.39$).

Unlike *C. fornicata*, however, the gills of intertidal and subtidal *C. peruviana* showed no significant differences in weight (Fig. 1; $F_{(1,76)} = 0.82$, $p = 0.37$ for slope; $F_{(1,77)} = 0.094$, $p = 0.76$ for intercept), maximum filament length (Fig. 2; $F_{(1,76)} = 1.45$, $p = 0.23$ for slope, $F_{(1,77)} = 0.0026$, $p = 0.96$ for intercept), surface area (Fig. 3; $F_{(2,76)} = 0.99$, $p = 0.38$), or number of filaments (Fig. 4; $F_{(2,76)} = 0.51$, $p = 0.61$).

Clearance rates for both intertidal and subtidal *C. fornicata* were highly variable. The range of CR for intertidal

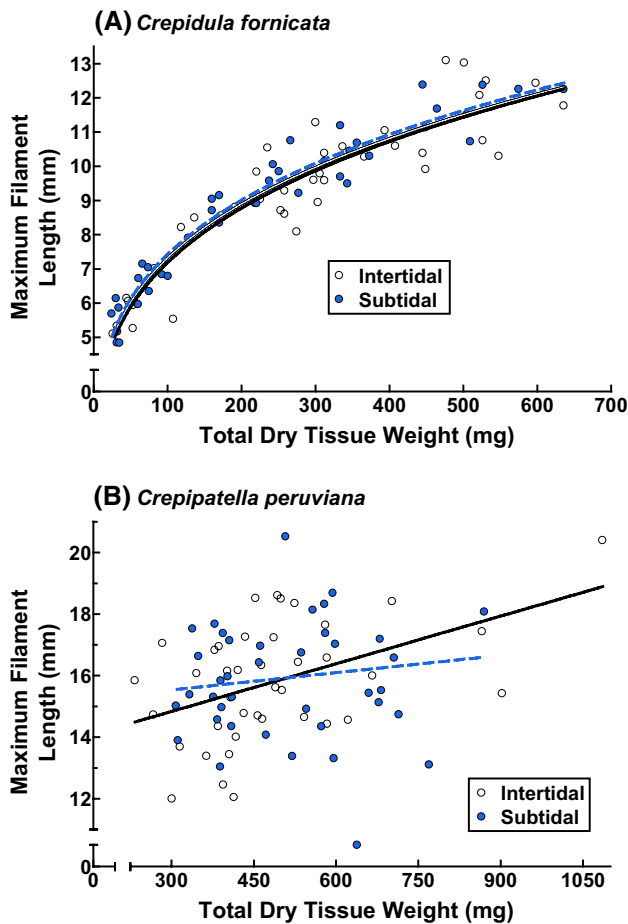


Fig. 2 Influence of habitat on the relationship between the maximum length of gill filaments and total dry tissue weight for **a** *Crepidula fornicata* and **b** *Crepipatella peruviana*. Each point represents data from one individual. Detailed statistical information can be found in Table 1

snails ($0.24\text{--}1.84\text{ L h}^{-1}\text{ g}^{-1}$) was somewhat greater than that for subtidal snails ($0.03\text{--}1.48\text{ L h}^{-1}\text{ g}^{-1}$). However, average CR did not differ significantly between intertidal and subtidal *C. fornicata* (Fig. 5; two-way ANOVA, $F = 1.87$, $p = 0.17$), and reproductive state (brooding vs. not brooding) also did not have a significant effect on CR (Fig. 5; two-way ANOVA, $F = 1.19$, $p = 0.28$; interaction, $F = 0.73$, $p = 0.40$). Conversely, intertidal *C. peruviana* had significantly lower clearance rates than subtidal *C. peruviana* (Fig. 5; two-way ANOVA, $F = 14.44$, $p = 0.003$). *Crepipatella peruviana* that were brooding had higher clearance rates than non-brooders (Fig. 5), though the difference in CR was not quite significant ($F = 3.25$, $p = 0.075$; interaction, $F = 0.029$, $p = 0.86$).

In *C. peruviana*, particles were transported across the gills of intertidal organisms significantly more slowly than those being transported across the gills of subtidal organisms (Fig. 6; $t_{19} = 2.38$, $p = 0.028$). Though particle

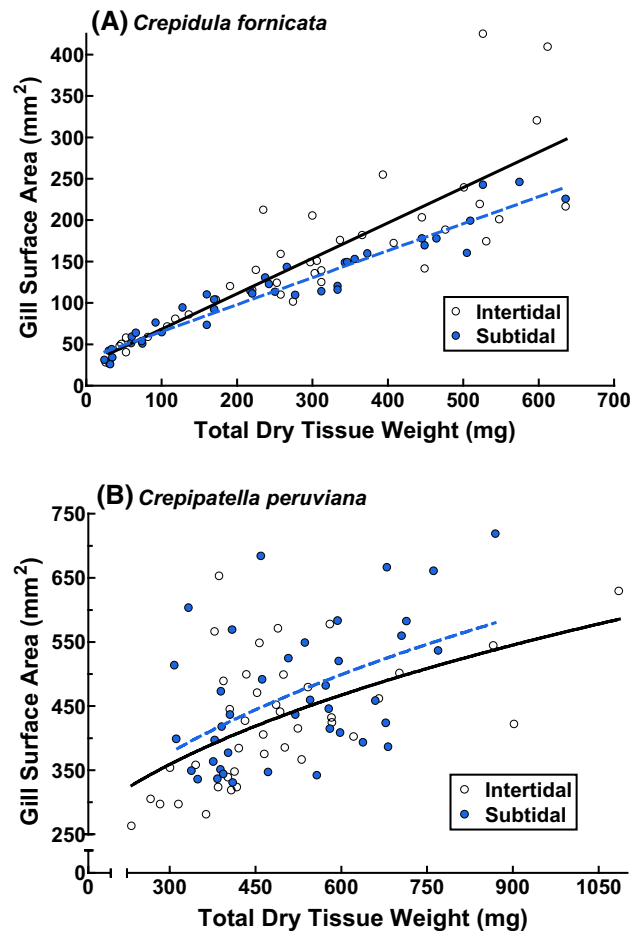


Fig. 3 Influence of habitat on the relationship between gill surface area and total dry tissue weight for **a** *Crepidula fornicata* and **b** *Crepipatella peruviana*. Each point represents data from one individual. Detailed statistical information can be found in Table 1

velocities across the gills of intertidal and subtidal *C. peruviana* varied widely (intertidal range = $42\text{--}307\text{ }\mu\text{m s}^{-1}$, subtidal range = $77\text{--}660\text{ }\mu\text{m s}^{-1}$), the average velocity of particles moving across gills of subtidal snails was $294.7 (\pm 164.8\text{ SD})\text{ }\mu\text{m s}^{-1}$, whereas the average velocity across gills of intertidal snails was only $153.3 (\pm 93.8\text{ SD})\text{ }\mu\text{m s}^{-1}$ (Fig. 6), $\sim 50\%$ slower than that for subtidal snails.

The size structures (SL) of intertidal and subtidal populations of *C. fornicata* differed significantly ($\chi^2 = 38.11$, $df = 14$, $p = 0.0005$), as there were generally more larger ($>27\text{ mm}$) intertidal individuals. However, members of both intertidal and subtidal subpopulations reached nearly identical maximum SL (44.6 mm subtidally, 43.3 mm intertidal). Conversely, *C. peruviana* attained a maximum SL of 66.2 mm in the subtidal zone, a length that was $\sim 34\%$ larger than that of intertidal *C. peruviana* (46.4 mm). The size structures of intertidal and subtidal populations of *C. peruviana* also differed significantly ($\chi^2 = 85.13$, $df = 20$, $p < 0.0001$), due principally to more large ($>45\text{ mm}$) subtidal individuals (Fig. 7).

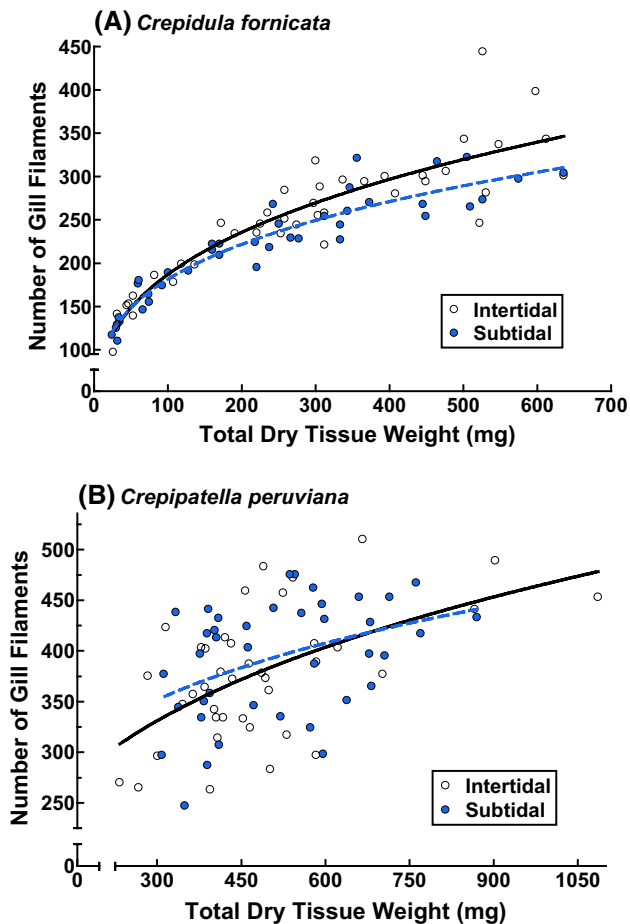


Fig. 4 Influence of habitat on the relationship between the number of gill filaments and total dry weight for **a** *Crepidula fornicata* and **b** *Crepipatella peruviana*. Each point represents data from one individual. Detailed statistical information can be found in Table 1

Discussion

Though *C. fornicata* and *C. peruviana* are closely related (Collin 2003) and have similar ecological niches, our results demonstrate that members of the intertidal range edge populations of these two species have responded very differently to the feeding disadvantages imposed by periodic aerial exposure. The gills of intertidal individuals of *C. fornicata* were considerably heavier than those of subtidal conspecifics, a difference mediated both by a larger overall gill surface area and a greater number of gill filaments. No such differences were found for *C. peruviana*: members of intertidal and subtidal populations of that species were morphologically indistinguishable for the gill parameters that we measured.

Morphological differences in the feeding organs of other conspecific suspension-feeders from different environments have previously been reported, mostly in bivalves (e.g., Franz 1993; Payne et al. 1995; Honkoop et al. 2003;

Drent et al. 2004; Dutertre et al. 2007, 2009; Yoshino et al. 2013). For example, Franz (1993) showed that *Geukensia demissa* mussels from Jamaica Bay, New York, living high in the intertidal zone had relatively larger gills than those living in the low intertidal.

In *C. fornicata*, the larger gills of intertidal organisms were not accompanied by a significant increase in clearance rate (CR) in our study; intertidal and subtidal *C. fornicata* fed at comparable rates. When data from intertidal and subtidal snails were pooled, the average CR was approximately $0.85 \text{ L h}^{-1} \text{ g}^{-1}$ for *C. fornicata*, which agrees with values of CR previously found for this species (Newell and Kofoed 1977a, b; Shumway et al. 2003; Barillé et al. 2006; Harke et al. 2011). Though the gill morphology data suggest a mechanism by which *C. fornicata* may compensate for reduced feeding time in the intertidal, our CR experiments were not able to detect any such compensation. Some suspension-feeders show considerable flexibility in feeding behavior (Bayne 2004), and compensatory increases in CR in response to aerial exposure have been found in some cases (Morton et al. 1957; Charles and Newell 1997; Marsden and Weatherhead 1999; Galimany et al. 2013); however, many suspension-feeders do not show increased CR or ingestion rates as compensation for aerial exposure in the intertidal zone (Griffiths and Buffenstein 1981; Widows and Shick 1985; Bayne et al. 1988; Kreeger et al. 1990). For example, Kreeger et al. (1990) found that *Geukensia demissa* mussels held under intertidal conditions (50 % exposure time) did not compensate for reduced feeding time with an increased ingestion rate when compared to mussels held in subtidal conditions. Charles and Newell (1997) confirmed these results, but did find increased CR in mussels held under conditions simulating a much higher tidal level (75 % exposure). Though we did not detect CR compensation in intertidal *C. fornicata*, it is important to note the high variability in CR among individuals in our experiments, which may have prohibited us from detecting meaningful compensation in this species; high variability in feeding rate has been found for this species before (Newell and Kofoed 1977a). Though other filter feeders may periodically stop feeding while submerged (e.g., Cranford et al. 2011), it is unknown what would cause *C. fornicata* to perform in this way while under water in ideal conditions (e.g., normal salinity, oxygen, and temperature, and no predators).

In our study, pooled data for clearance rates of *C. peruviana* also fell within the expected range determined by previous studies (Navarro and Chaparro 2002; Mardones et al. 2013). However, intertidal *C. peruviana* had a significantly lower average CR than subtidal *C. peruviana*, contrary to what we found for *C. fornicata*. Since gill morphologies did not differ among intertidal and subtidal *C. peruviana*, it was surprising to find such a dramatic

Table 1 Summary statistics for different aspects of *Crepidula fornicata* and *Crepidatella peruviana* gills regressed against total dry tissue weight

Figure	Species	Gill parameter	Model equation (difference in AICc) ^a	Intertidal and subtidal comparison	Location	a (95 % CI)	b (95 % CI)	r ² (p) ^b
1a	<i>Crepidula fornicata</i>	Weight (mg)	$a + bX$ (0.079)	ANCOVA $F_{1,76} = 10.53$, $p = 0.001$	Intertidal	0.74 (−0.48–1.98)	0.029 (0.025–0.033)	0.88 (<0.0001)
					Subtidal	0.0099 (−0.69–0.71)	0.022 (0.019–0.025)	0.91 (<0.0001)
2a	<i>Crepidula fornicata</i>	Maximum filament length (mm)	$a*b^X$ (38.97)	F test $F_{2,76} = 0.95$, $p = 0.39$	Intertidal	1.90 (1.42–2.38)	0.29 (0.25–0.33)	0.86
					Subtidal	2.06 (1.77–2.35)	0.28 (0.25–0.30)	0.94
3a	<i>Crepidula fornicata</i>	Surface area (mm ²)	$a + bX$ (1.932)	ANCOVA $F_{1,76} = 4.75$, $p = 0.032$	Intertidal	25.60 (−5.40–56.61)	0.43 (0.34–0.52)	0.71 (<0.0001)
					Subtidal	32.88 (24.18–41.57)	0.33 (0.30–0.35)	0.93 (<0.0001)
4a	<i>Crepidula fornicata</i>	Number of filaments	$a*b^X$ (22.24)	F test $F_{2,76} = 5.69$, $p = 0.005$	Intertidal	40.30 (25.45–55.15)	0.33 (0.27–0.40)	0.81
					Subtidal	47.68 (37.89–57.47)	0.29 (0.25–0.33)	0.90
1b	<i>Crepidatella peruviana</i>	Weight (mg)	$a + bX$ (1.34)	ANCOVA $b, F_{1,76} = 0.82$, $p = 0.37$ $a, F_{1,77} = 0.094$, $p = 0.76$	Intertidal	10.26 (1.01–19.50)	0.079 (0.061–0.097)	0.68 (<0.0001)
					Subtidal	18.17 (3.74–32.60)	0.065 (0.038–0.092)	0.39 (<0.0001)
2b	<i>Crepidatella peruviana</i>	Maximum filament length (mm)	$a + bX$ (0.55)	ANCOVA $b, F_{1,76} = 1.45$, $p = 0.23$ $a, F_{1,77} = 0.0026$, $p = 0.96$	Intertidal	13.29 (11.60–14.98)	0.0052 (0.0019–0.0084)	0.21 (<0.0028)
					Subtidal	14.97 (12.52–17.43)	0.0019 (−0.0027–0.0064)	0.018 (0.41)
3b	<i>Crepidatella peruviana</i>	Surface area (mm ²)	$a*b^X$ (0.64)	F test $F_{2,76} = 0.99$, $p = 0.38$	Intertidal	41.05 (−6.63–88.72)	0.38 (0.19–0.57)	0.31
					Subtidal	37.51 (−18.50–93.51)	0.40 (0.17–0.64)	0.23
4b	<i>Crepidatella peruviana</i>	Number of filaments	$a*b^X$ (1.46)	F test $F_{2,76} = 0.51$, $p = 0.61$	Intertidal	64.80 (8.41–121.20)	0.29 (0.15–0.43)	0.30
					Subtidal	104.7 (1.05–208.30)	0.21 (0.054–0.37)	0.16

^a As compared to the competing model (only power and linear models were compared)

^b Test for zero slope. Linear models only

difference in CR between those two groups. Moreover, the difference was not in the direction that we had initially anticipated. Our endoscopic results indicate that intertidal individuals started to collect phytoplankton immediately upon immersion. Thus, clearance rates of intertidal individuals were not artificially low because of a reluctance of these snails to begin feeding after they were submerged. We found that brooding individuals of *C. peruviana* had faster clearance rates than non-brooding individuals, and to nearly the same degree as was found by Mardones et al. (2013); this trend was observed among intertidal and subtidal individuals.

Assuming that decreased particle velocity across the gill surface also reflects a reduced capacity of the gill cilia to collect food, the slower CR for intertidal individuals of *C. peruviana* could be in part due to a decreased particle velocity along the gills of intertidal individuals. Slower particle velocity could be the result of reduced ciliary beat frequency on the gills of intertidal *C. peruviana*, something that could be examined in a future study. Overall, the particle transport velocities found in this study were slower than those previously found in *C. peruviana* (~1,400 $\mu\text{m s}^{-1}$, Chaparro et al. 2002). However, our experiments were performed at cooler temperatures than in Chaparro et al.

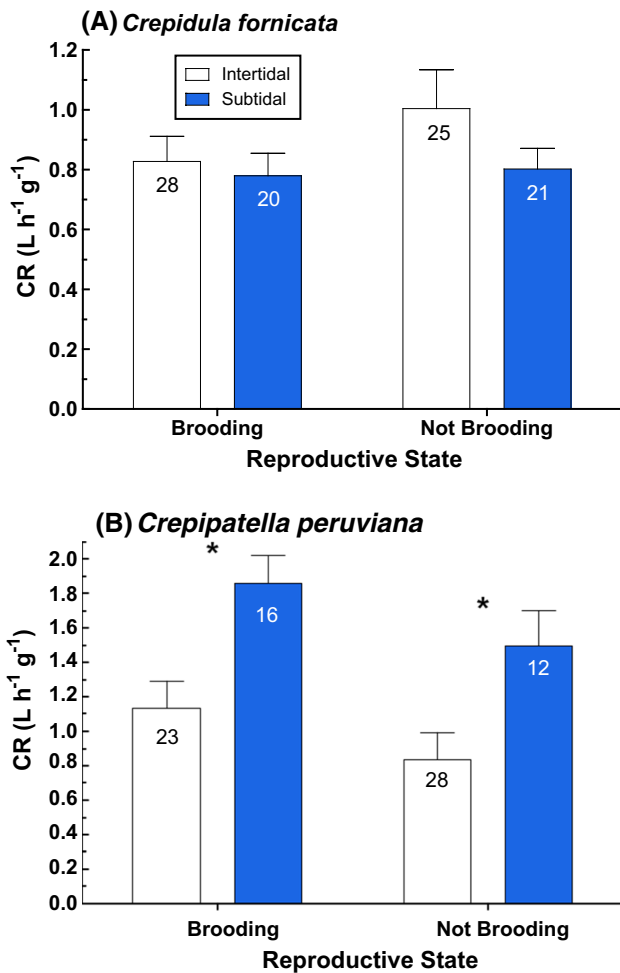


Fig. 5 Clearance rates of intertidal and subtidal **a** *Crepidula fornicata* and **b** *Crepipatella peruviana*. Sample size is indicated in each bar; error bars represent SEM. Asterisks denote significant differences in CR between intertidal and subtidal individuals, two-way ANOVA, $p < 0.05$

(2002), and *C. peruviana* in our study were first removed from their substrates and transferred to plastic plates, both of which may have contributed to the slower particle velocities that we found.

The intertidal zone is a particularly stressful place to live (e.g., Brinkhoff et al. 1983; Morris and Taylor 1983; Garrity 1984; Petes et al. 2007; Harley et al. 2009; Miller et al. 2009; Diederich and Pechenik 2013) for sedentary marine organisms, and physiological stress has previously been associated with reduced performance (i.e., feeding rate) in some marine invertebrates (Abel 1976; Menge 1978; Widows et al. 1981; McCormick et al. 1998). The pattern of CR and particle velocity transport across the gill in addition to the pattern of size distribution (subtidal > intertidal) in *C. peruviana* suggests that intertidal individuals could be stressed in relatively poor physiological condition. Individuals of *C. peruviana* may of course have physiological adaptations for maximizing energy gain in the intertidal zone that we did not quantify but should be studied further. Energetic compensation for aerial exposure time in other species has been linked to a number of other processes not explored here, including changes in metabolic rate, gut passage time, and absorption or assimilation efficiency (Griffiths 1981; Kreeger et al. 1990; Charles and Newell 1997; Marshall and McQuaid 2011). Additionally, clearance rate and condition index may not be tightly coupled for some species: suspended *Crassostrea virginica* oysters with smaller gills and lower CR than bottom oysters were actually found to have higher condition indices (Comeau 2013).

If larger gill size in intertidal *C. fornicata* is driven by adaptive plasticity, what mechanisms might control such a change? Like the compensatory feeding of the mussel *Geukensia demissa* (Charles and Newell 1997, see above), *C. fornicata* may experience a threshold shore level above which

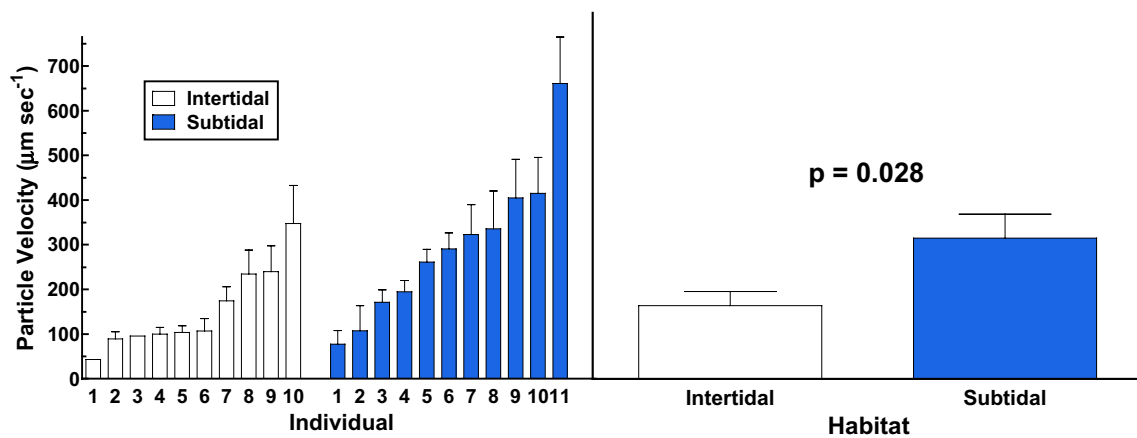


Fig. 6 Rate (+SEM) at which intertidal and subtidal *Crepipatella peruviana* moved particles across the gill toward the food groove. Mean particle velocities along the gills of each individual are shown

in the left panel, and mean particle velocities of all individuals grouped by habitat are shown in the right panel (result of unpaired *t* test is shown above the bars)

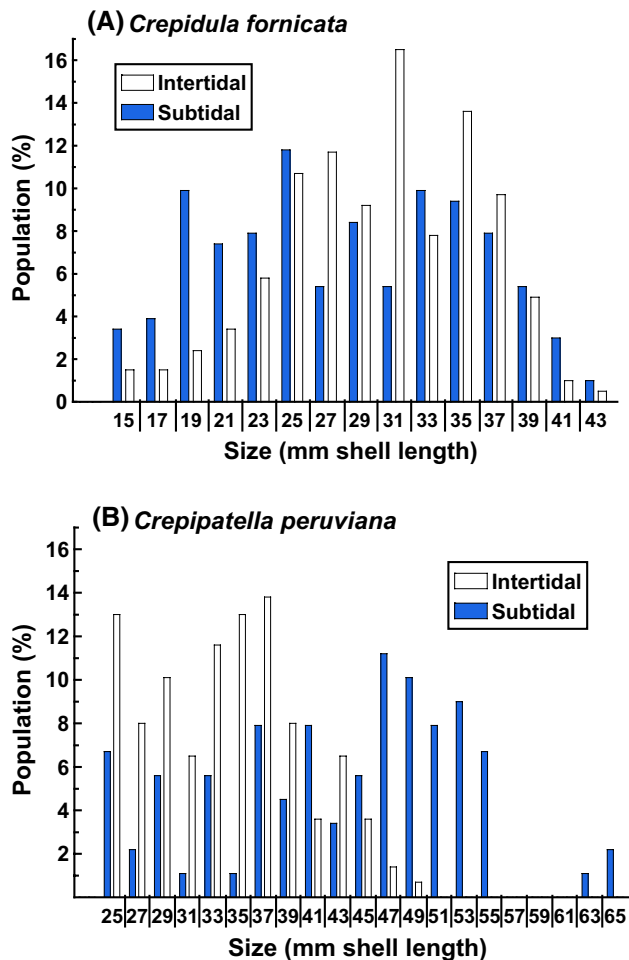


Fig. 7 Size distributions for intertidal and subtidal individuals of **a** *Crepidula fornicata* collected from Bissel Cove in Narragansett Bay, RI, USA, and **b** *Crepipatella peruviana* collected from Puerto Montt, Chile. Numbers on the x-axis represent the lower end of each size class (15 = 15–17 mm). **a** Frequency distributions of intertidal ($N = 206$) and subtidal ($N = 203$) subpopulations are significantly different ($\chi^2 = 38.11$, $df = 14$, $p = 0.0005$), though the snails reach similar maximum sizes. **b** Frequency distributions of intertidal ($N = 147$) and subtidal ($N = 91$) subpopulations are significantly different ($\chi^2 = 85.13$, $df = 20$, $p < 0.0001$), with subtidal individuals reaching a maximum size 34 % greater than intertidal individuals

it is advantageous to have a relatively larger gill. However, intertidal individuals of *C. fornicata* are usually relegated to the mid- to low intertidal zone (Diederich and Pechenik 2013), and even short bouts of aerial exposure may trigger a shift in resource allocation toward growing relatively larger gills. It is interesting that intertidal *C. fornicata* had larger gills but similar CR when compared to subtidal conspecifics, while intertidal *C. peruviana* had reduced CRs relative to those of subtidal individuals despite no difference in gill sizes. Individuals of *C. fornicata* may have a longer history of association with the environmental heterogeneity found in the intertidal zone. Indeed, *C. fornicata* is also relatively

eurythermal (Diederich and Pechenik 2013) and tolerant of long periods of aerial exposure (Hoagland 1984), traits necessary for intertidal life, though intertidal individuals in some areas may be living close to their thermal maximum (Diederich and Pechenik 2013). As it relates to feeding, the intertidal *C. fornicata* in our study may be better equipped to cope with the disadvantages associated with aerial exposure than those of *C. peruviana*. This may help to explain the ability of intertidal *C. fornicata* to attain sizes equivalent to those of subtidal snails, while intertidal *C. peruviana* did not seem to grow to be as large as subtidal *C. peruviana*.

Our studies highlight the value of investigating organisms of the same species from intertidal and subtidal zones in the context of range boundaries. At a single field site, some organisms will experience conditions associated with “central” (subtidal) populations, while conspecifics only meters away can be characterized as experiencing “range edge” conditions (intertidal). Additionally, abiotic conditions in intertidal and subtidal areas may be nearly identical when the tide is in, and when the tide is out, the suite of abiotic conditions that change is both easily measurable (time emersed, temperature, water lost, etc.) and well characterized (Newell 1979; Denny 1985; Helmuth 1998; Helmuth and Hofmann 2001).

Finally, our results may have implications for the relative success of these species as it relates to their potential for invading new areas. In fact, *C. fornicata* is an extremely successful invasive species along European coastlines (and other areas, Blanchard 1997), though they are not always found intertidally in the invaded area, while *C. peruviana* has not been found outside its native range. While the repeated importation of *C. fornicata* into European waters (e.g., on oyster shipments, Blanchard 1997) caused their initial introduction, the reasons for its remarkable success as an invasive species are less clear (Dupont et al. 2006; Viard et al. 2006; Blanchard 2009; Bohn et al. 2012). When viewed in the context of habitat colonization, the ability of *C. fornicata* to perform well in the stressful living conditions that characterize the intertidal zone may be contributing to their relative abilities to invade new areas.

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