

RESEARCH ARTICLE

The energetic costs of living in the surf and impacts on zonation of shells occupied by hermit crabs

Guillermina Alcaraz^{1,*}, Brenda Toledo² and Luis M. Burciaga²

ABSTRACT

Crashing waves create a hydrodynamic gradient in which the most challenging effects occur at the wave breaking zone and decrease towards the upper protected tide pools. Hydrodynamic forces depend on the shape of the submerged body; streamlined shapes decrease drag forces compared with bluff or globose bodies. Unlike other animals, hermit crabs can choose their shell shape to cope with the effects of water flow. Hermit crabs occupy larger and heavier shells (conical shape) in wave-exposed sites than those used in protected areas (globose shape). First, we investigated whether a behavioral choice could explain the shells used in sites with different wave action. Then, we experimentally tested whether the shells most frequently used in sites with different wave action reduce the energetic cost of coping with water flow. Metabolic rate was measured using a respirometric system fitted with propellers in opposite walls to generate bidirectional water flow. The choice of shell size when a large array of sizes are available was consistent with the shell size used in different intertidal sites; hermit crabs chose heavier conical shells in water flow conditions than in still water, and the use of heavy conical shells reduced the energetic cost of coping with water motion. In contrast to conical shells, small globose shells imposed lower energy costs of withstanding water flow than large globose shells. The size and type of shells used in different zones of the rocky shore were consistent with an adaptive response to reduce the energetic costs of withstanding wave action.

KEY WORDS: Energetics, Gastropod shell, Hydrodynamics, Oxygen consumption, Waves, Intertidal

INTRODUCTION

The rocky shores are challenging marine environments where organisms face extreme levels of several factors that vary along a gradient (Gaylord, 2007). While biotic factors such as competition and predation play the primary roles in shaping the distribution of populations in relatively wave-protected habitats of the upper intertidal, it is hydrodynamic forces that most limit their distributions at wave action sites of the lower intertidal shores (Benedetti-Cecchi and Trussell, 2013; Blamey and Branch, 2009; Menge, 1978).

Hermit crabs are unusual in that their shells are not produced by their own bodies, but rather, are scavenged from the environment.


Thus, the characteristics of the shells they occupy depend both on their preferences and on the availability of shells in their habitat. On the one hand, if there are many shells available, hermit crabs can choose the shape and size of their shell in ways that are apparently adaptive (Hazlett, 1995; Mima et al., 2003), and shell preferences are likely a constitutive behavioral trait (Hazlett, 1995). Optimizing choice of shell morphology confers different advantages depending on the main biotic and abiotic selection pressures. For example, hermit crabs can minimize the effects imposed by biotic and abiotic factors of rocky intertidal shores – the most important of which include predation, temperature, desiccation and wave exposure (Kemp and Bertness, 1984; Trussell, 1997, 2000) – by using shells of different sizes and morphologies (Hazlett, 1981; Mima et al., 2003; Taylor, 1981; Turra and Leite, 2001). On the other hand, if shells are highly limited, hermit crabs can be forced into ‘best of a bad job’ scenarios in which they must accept whatever relatively suitable shell becomes available. It may be more feasible for crabs to choose a habitat that will be more adequate for the shell they have been able to acquire, rather than choosing the shell based on their preferred habitat. Either shell choice based on habitat or habitat choice based on shell occupation can lead to zonation in shell use (e.g. Bach and Hazlett, 2009).

Several hermit crab species have a well-established pattern of shell types occupied along the intertidal gradient (e.g. *Clibanarius antillensis*; Argüelles-Ticó et al., 2010). This zonation in shell use may be explained by variation of biotic and abiotic factors (e.g. Scully, 1979; Turra and Denadai, 2002; Turra and Leite, 2001). Previous studies have shown that the hermit crab *Calcinus californiensis* most frequently occupies shells with a globose shape (with a low aspect ratio) in wave-protected tide pools, where predation risk is high (e.g. *Nerita scabricosta*; Fig. 1A,B), while a lower proportion of crabs occupy *N. scabricosta* in wave-exposed sites (Arce and Alcaraz, 2011). At the same time, *C. californiensis* frequently uses shells with a conical shape (with tall spires and high aspect ratio) in sites exposed to wave action (e.g. *Stramonita biserialis*; Fig. 1A,B). Additionally, the conical *S. biserialis* shells occupied by *C. californiensis* in the wave-exposed site are relatively large (heavy, loose fitting), while crabs in the protected tide pools use relatively small shells of this species (light, tight fit; Arce and Alcaraz, 2011). The use of large and heavy shells has been suggested as an adaptive strategy in conditions with high water flow (Reese, 1969; Hahn, 1998) and high predatory pressure (Arce and Alcaraz, 2013; Mima et al., 2003). However, shells that are larger than optimal may also negatively impact growth rate (Alcaraz et al., 2015), brood size (Hazlett et al., 2005), foraging rate (Alcaraz and García-Cabello, 2017) and escape velocity (Alcaraz and Arce, 2017) of *C. californiensis* and other hermit crab species.

The cost of dealing with water flow in a given shell is determined by how the shell is affected by water acceleration, as well as lift and drag forces (Statzner, 2008). Acceleration depends on the volume of water displaced by the individual, but is generally small compared

¹Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México 04510, México.
²Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México 04510, México.

*Author for correspondence (alcaraz@ciencias.unam.mx)

 G.A., 0000-0002-5485-0671; B.T., 0000-0003-1478-9463; L.M.B., 0000-0003-4094-3663

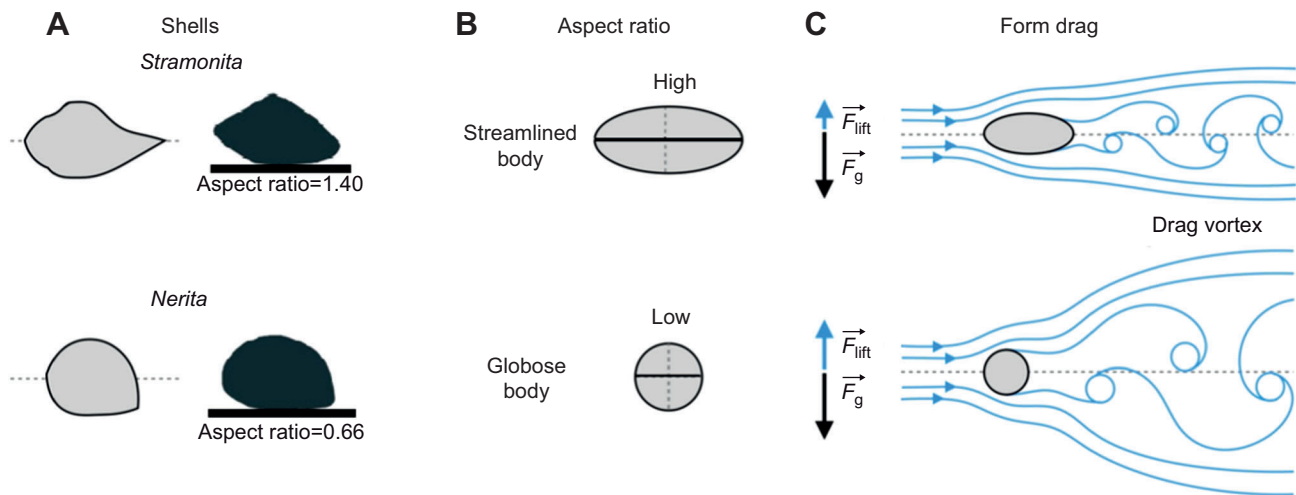


Fig. 1. Streamlined and globose bodies and their relationship with hydrodynamic forces. (A) Dorsal (light gray) and lateral (dark gray) outlines of *Stramonita biserialis* and *Nerita scabricosta* shells, the mean aspect ratio of these shells appear in below the shells (data from shells used in this study). The shells are shown with the longitudinal axis aligned parallel to the direction of the prevailing flow as this is the orientation that shells take by the effect of hydrodynamic forces. (B) Major (solid line) and minor axes (dotted line) of shapes with high a low aspect ratio. (C) Flow patterns and wakes (vortices) generated over a streamlined body and globose body; the arrows indicate the direction and the magnitude of the lift force (blue arrow) and the apparent mass of both shell species. \vec{F}_{lift} , lift force; \vec{F}_g , gravity force.

with lift and drag forces among relatively small animals (less than approximately 1.5 cm in shell height; Denny, 1989, 2000). Lift force acts upward in opposition to gravity, so that animals must avoid losing the grip on the substrate (Ditsche and Summers, 2014; Vogel, 2005). Lift force is caused by a difference in pressure between the top and bottom of a body, which is generated by differences in water speed (velocity squared); this force is proportional to the projected area of the body perpendicular to the flow (Denny, 1987; Denny and Gaylord, 2010). Additionally, gravity acts on body mass, resulting in a downward force that opposes the lift force; the weight of a body immersed in water decreases by a fraction of its weight with respect to the air depending on its density (apparent mass; Webb, 2007; Fig. 1C). Drag force pushes the animal across the surface and is proportional to water speed and to the projected area in the direction of flow. Drag force strongly depends on the object's shape: globose (bluff) bodies experience greater drag than streamlined bodies of equal projected area (Denny and Gaylord, 2010). Globose shells generate more flow separation (a separated boundary layer) over a substantial part of their surface, creating larger wakes and a lower pressure zone downstream (unsteady flow forces) than streamlined shapes (Ditsche and Summers, 2014; Vogel and Labarbera, 1978; Fig. 1C). Lift is the dominant force for shapes with a low aspect ratio (Denny and Blanchette, 2000). Some authors have suggested that the use of a heavy shell could help hermit crabs to avoid being dislodged from the substrate, because mass (gravity) opposes lift forces (e.g. Bach and Hazlett, 2009; Garcia and Mantelatto, 2001; Hahn, 1998; Reese, 1969).

Orientation is an important response to reduce the effects of the water flow (Alexander, 1990; Nishimoto and Herrnkind, 1978; Verhaegen et al., 2019; Warburton, 1976), and its benefit strongly depends on the shape of the shells (Verhaegen et al., 2019). The reduction of the cross-sectional area (exposed to the flow) resulting from flow orientation is higher for conical shells, with a higher aspect ratio, than for globose shells (Nagle, 1967). While crabs are walking, the longest axis of the shell is angled with respect to the direction of movement as a consequence of the position of the shell aperture (Chapple, 2012). However, as in other animals (e.g. snails,

bivalves, limpets, decapods), during the strong moments of water flow, hermit crabs stop walking, grip the substrate, and allow the longitudinal axis of the shell to align parallel to the direction of the prevailing flow by the effects of drag and lateral forces (i.e. because that alignment minimizes the strength of these forces; e.g. Denny and Blanchette, 2000; Nagle, 1967; Verhaegen et al., 2019; Warburton, 1976; Weissburg et al., 2003).

Zonation may be due to effects induced by the long-term energetic cost associated with exposure to hydrodynamic forces that are not strong enough to immediately dislodge organisms (Siddon and Witman, 2003). We hypothesized that if streamlined shapes and increased mass decrease the effect of hydrodynamic forces, then the energy cost of remaining gripped to the substrate will be lower for hermit crabs in heavy *S. biserialis* shells than those in light *N. scabricosta* shells. We had two main aims in this study: (1) to assess whether the pattern of shell size used by *C. californiensis* in wave-protected and wave-exposed sites is consistent with the shell species and size that would minimize hydrodynamic forces; and (2) to measure the energetic cost of remaining gripped to the substrate in hermit crabs occupying shells of different sizes (small and large) and shapes (globose and conical) under different hydrodynamic conditions to determine whether these two factors match shell occupation and preference under water flow conditions.

MATERIALS AND METHODS

Shell use in wave-protected and wave-exposed sites

We collected *Calcinus californiensis* Bouvier 1898 hermit crabs occupying *Nerita scabricosta* and *Stramonita biserialis* shells in two areas with different levels of exposure to wave action along the rocky shore of Troncones, Guerrero, Mexico. This part of the study generated data similar to those published in a previous study (Arce and Alcaraz, 2011), but it was important to confirm that the previously observed pattern of shell use occurs in the specific population of *C. californiensis* used to conduct the lab experiments.

We collected crabs along lines parallel to the shore. Wave-protected sites were shallow rock pools relatively close to the shore (± 5 m from the highest tide mark) with a mean maximum water speed of 1.0 cm s^{-1} (range from 0.1 to 2.0 cm s^{-1}). All of the sites

were submerged even during lowest tide. Wave-exposed sites were established according to the water speed, estimated as the mean of the highest speeds reached in each wave cycle (uprush and wash back) over 5 min, as described by Argüelles et al. (2009). The wave-exposed sites were approximately 25 m from the shore (± 9 –13 m from the lower limit of the wave-protected site); the mean maximum speed of this site was 57.3 cm s^{-1} (range from 22 to 160 cm s^{-1}). Water speed was measured once during the sampling using a flow meter (Global Water, FP211; precision $\pm 0.1 \text{ cm s}^{-1}$) as close as possible to the substrate from which the crabs were collected.

Hermit crabs were collected by hand during low tide by four searchers on April 2015. Four 10 min searches were conducted at wave-exposed and wave-protected sites. The hermit crabs were collected from the two sites at the same time by two searchers in each. At the end of each 10-min period, the collectors swapped sites, where they collected crabs for the next 10 min period. Immediately after collection, the hermit crabs were placed in individual containers (0.05 liters) and transported to the laboratory.

At the end of each experimental phase, the crabs were removed from their shells by gently heating the apex using a mini hot glue gun (10 W). The hermit crabs were weighed using a plate balance (OHAUS, $\pm 0.01 \text{ g}$) and shield length was measured using a digital caliper ($\pm 0.01 \text{ mm}$). The sex of the hermit crabs was determined by identifying the position of the genital pores (Mantelatto et al., 2009). Only males were used in the analysis to avoid biasing results by using females in different reproductive stages and differences in shell preference (Argüelles et al., 2009; Suárez-Rodríguez et al., 2019). The shells were dried (48 h, 60°C), weighed, and measured for length (longest dimension along the coiling axis) and width (widest dimension perpendicular to the coiling axis in the plane of the aperture; Bourdeau, 2009). All experiments were conducted during April and May 2015. At the end of each part of the study, the crabs were returned to the collecting site.

Statistics

For all continuous parameters, means \pm s.d. are given. The mass of the *N. scabricosta* and *S. biserialis* shells occupied by the hermit crabs in the wave-protected and exposed sites was compared by a two-way ANCOVA, using as factors the shell species and the site type. As our goal was to compare the mass of the shell occupied independent of the hermit crab's size, we used the hermit crab mass as a covariate. We performed a *post hoc* Scheffé test to determine which shell species/site type combinations differed from each other. Data normality was tested using the Shapiro–Wilk's *W*-test, and the homoscedasticity of variances was tested using Bartlett's test. Statistical analyses were conducted using Statistica 10.

Shell size preference

Crab capture and maintenance

We determined the size preference for *S. biserialis* ($n=66$) and *N. scabricosta* ($n=33$) shells under two water flow conditions (still water and bidirectional water flow). We captured hermit crabs occupying *N. scabricosta* and *S. biserialis* shells during low tide on the rocky shore at Troncones. Even though the water flow environment can influence the shell size preference, the crabs had to be collected in protected tide pools owing to the low number of crabs in *N. scabricosta* in wave crashing areas (Arce and Alcaraz, 2011). The hermit crabs were transported to the Laboratory of Ecophysiology at Mexico City and kept in individual containers for 24 h at similar conditions to those recorded in the field (still water; 27°C , a salinity of 35 PSU, and a natural photoperiod).

Experimental systems

The trials were conducted in a rectangular experimental chamber ($12 \times 10 \times 8 \text{ cm}$; 0.96 liters). The longer walls were made of solid polycarbonate sheets and the shorter ones of 0.5 mm mesh. A clear acrylic lid was used to close the chamber. The chamber was submerged in a larger container ($35 \times 20 \times 20 \text{ cm}$; 14 liters) with a thermostat to control temperature and aeration. Two pumps (JBJ OceanStream kit, OS-101K) were placed into the container at opposite sides of the experimental chamber to push water through the mesh. The water pumps were connected to an adjustable cycle timer (Ocean Pulse Wavemaker) that activated the pumps alternately every 10 s, simulating the bidirectional water flow in Troncones. The maximum water speed reached in the working area was $24 \pm 2 \text{ cm s}^{-1}$, which was measured using frame-by-frame video analysis of suspended particles (Riisgård and Larsen, 2010). The water speed was relatively slow compared with the mean water speed recorded at the wave-exposed sites. The timing of alternating the direction of the water flow was based on observations on the rocky shore of Troncones during the collection periods. We used the same experimental setup to test shell preference in still water conditions, except the pumps were turned off.

Experimental design and trial procedure

The hermit crabs occupying *N. scabricosta* and *S. biserialis* were haphazardly assigned to two different experimental treatments: still water and bidirectional water flow. Half of the hermit crabs collected in *N. scabricosta* ($n=9$) shells were assigned to the condition of still water and the other half of the animals were assigned to the water motion treatment ($n=9$). Similarly, half of the hermit crabs occupying *S. biserialis* shells were assigned to the still water condition ($n=16$) and the other half to the flow condition ($n=17$). The disparity in sample size was due to the differences in the number of hermit crabs occupying these shell species in the field. The hermit crabs were tested in the same shell species in which they were collected (*N. scabricosta* or *S. biserialis*) to avoid biases associated with previous experience (Alcaraz and Kruesi, 2009).

The hermit crabs were caged in individual enclosures with 20 empty shells of various sizes within a shell adequacy index (SAI; Asakura, 1995) of 0.5 to 1.5. The SAI indicates the quality of the shell occupied by the hermit depending on its body size; this value quantifies the deficit or surplus in the size of the shell currently occupied by a hermit crab relative to the preferred shell size when a large array of shell sizes is available (Hazlett et al., 2005; Vance, 1972). In the present study, the SAI was calculated as the ratio of the mass of the shell currently occupied by the crab divided by the mass of the preferred shell size (Asakura, 1995). In each trial, we placed four shells that fitted with the preferred shell size for the hermit crab ($\text{SAI}=1.0 \pm 10\%$); a similar number of tight ($\text{SAI}<1$) and loose ($\text{SAI}>1$) shells were offered to the crab, with the shell mass spaced as evenly as possible. The SAI was calculated for each crab from the equation previously estimated for *N. scabricosta* and *S. biserialis* shells (Arce and Alcaraz, 2012), and the range of 0.5 to 1.5 SAI was chosen based on records of shell sizes occupied the wild (Alcaraz and Arce, 2017; Alcaraz and García-Cabello, 2017).

We used different sets of shells according to the hermit crab's size. We used undamaged shells that did not have epibionts to avoid biases associated with the cost and benefits of these factors (Pechenik et al., 2001; Williams and McDermott, 2004). We used shells that had been previously occupied by hermit crabs in the field; the shells were rinsed with clean seawater before offering them to the hermit crabs. We attached a plastic hair claw (hair clip with interlocking teeth connected by a spring) to the shell the hermit

originally occupied to motivate the crab to leave it and swap to one of the empty shells offered. The crabs were left in the enclosure to choose among the shells for 24 h. The shell occupied by the crab after 24 h was considered the preferred one; for *C. californiensis* this period is long enough to choose an adequate shell size (Arce and Córdoba-Aguilar, 2018). The hermit crabs were removed from the tank. The crab and the chosen shell were weighed and measured as previously described. Shell mass was used as a measure of size because it is the variable that best explains the relationship between crab size (mass) and shell size (Arce and Alcaraz, 2012). Each crab was tested only once. At the end of the experiments the crabs were returned to the capture site.

Statistics

The mass of the *S. biserialis* and *N. scabricosta* shells preferred in still water and bidirectional water flow was compared by a two-way ANCOVA, with the shell species and the water flow condition as factors. The mass of the hermit crab was used as the covariate to assess the shell size preference independently of crab size. Multiple comparisons (Scheffé test) were used to assess which shell species and water condition combinations differed from each other. The normality of the data and homogeneity of variances were tested using the Shapiro–Wilk's *W*-test and Bartlett's test, respectively.

Energetic cost of coping with bidirectional water flow

Crab capture and experimental design

We measured the energetic cost of coping with bidirectional water flow (simulated waves) in hermit crabs occupying *N. scabricosta* and *S. biserialis* shells of two different shell sizes: small shells (tight fit, light) and large shells (loose fit, heavy). The hermit crabs occupying *N. scabricosta* ($n=12$) and *S. biserialis* ($n=13$) shells were collected on the rocky shore of Troncones. The crabs were transported to the laboratory and acclimated in individual containers (0.5 liters) for 15 days at a temperature of 27°C, salinity of 35 UPS, and 12 h:12 h light:dark photoperiod. The hermit crabs were fed daily with sinking pellets (New Life Spectrum, 3 mm).

After the acclimation period, the hermit crabs were randomly assigned to two different experimental groups based on the toss of a coin. Half of the hermit crabs occupying *N. scabricosta* shells were initially given a shell 50% smaller than their preferred size, while the other half were given a shell 50% larger than their preferred size. Similarly, half of the hermit crabs occupying *S. biserialis* shells were initially given a shell 50% smaller than their preferred size, while the other half were given a shell 50% larger than their preferred size. The criteria used to set a shell fit were based on data recorded for *C. californiensis* in the field (SAI ~0.5–1.5; Alcaraz and Arce, 2017; Alcaraz and García-Cabello, 2017). The mass of the shells given to each crab was calculated using the equations that describe the shell mass preferred as a function of the body mass of the crabs in still water (present study). We used this equation because the hermit crabs were collected and acclimated in still water. The body mass was preliminarily estimated by measuring the length of the left chela without removing the crabs from the shell to minimize stress. Crab mass (y) was predicted using the equation: $y=0.08x-0.14$, where x is chela length ($R^2=0.64$, $P<0.01$; Toledo, 2016). The same individual was tested for oxygen consumption in a small and a large shell within 7 days. We tested half of the crabs first in a small shell and then in a large shell, while the other half of the crabs were tested first in a large shell and then in a small shell in order to control for the order of the treatments. The assignment of hermit crabs to the trial order was random; the hermit crabs in different shell species were tested at random based on the toss of a

coin. The hermit crabs were tested in the same shell species in which they were collected.

The hermit crabs were offered an empty shell of the assigned size (small or large). We attached a hair claw to the shell offered to motivate the crab to swap to the shell offered (Arce and Alcaraz, 2012). The hermit crabs were acclimated to their new shell for 7 days in individually labeled containers (1 liter) submerged in the main reservoir with the same conditions previously described. After this period, the crabs were tested for oxygen consumption. Once the rates of oxygen consumption were measured in crabs occupying the first shell size assigned (a small or a large shell), the hermit crabs were offered a new shell of the other size. The crabs were acclimated to the new shell for 7 days, and then they were tested again to measure their rates of oxygen consumption. Hermit crabs that molted during this period ($n=5$) were not considered for the analysis.

Oxygen consumption measurements

The crabs were not fed for 24 h to minimize post-absorptive effects (Rosenfeld et al., 2015). The trials were conducted at 35 PSU, in a room with temperature controlled at 27°C. The metabolic rate was measured using a semi-closed respirometric system (Cech, 1990) using a 0.15 liter respirometric chamber (8.4×3.5×5 cm) fitted with propellers in their farther walls (Fig. 2). The hermit crabs were placed in the respirometric chamber at 08:00 h. The water of the respirometer was systematically renewed using water flowing from the upper container every 30 min. We measured the dissolved oxygen concentration continuously for periods of 30 min. To measure oxygen consumption, the water flow with the upper container was suspended. The propellers remained turned on at low speed (~60 rpm min⁻¹) during the refreshing periods and the metabolic measurements (to circulate the water). The standard metabolic rate (SMR) was estimated using the oxygen consumption measured from 11:00 to 12:00 h because of the low activity displayed by the crabs at this time (Alcaraz and Kruesi, 2012). The oxygen consumption measured from 13:00 to 14:00 h was used to calculate the energetic cost of coping with the bidirectional water flow [resting metabolic rate (RMR)].

The metabolic rate of the crabs exposed to the bidirectional flow was measured at a time at which the animals were active (14:00 to 15:00 h; Alcaraz and Kruesi, 2012) in the respirometric chamber fitted with propellers. The propellers pushed the water toward pipes (2.2 cm length) and a screen to reduce the level of turbulence. The respirometer was divided into two horizontal sections by a plate placed 2 cm from the main floor. The upper section was the working area (3.0×3.0×5.0 cm); it received water flow from the propeller. The lower section facilitated the water circulation flowing from the upper working area. The propellers were connected to a voltage-regulated motor that generated a maximal water flow in the working area of 24.4±1.9 cm s⁻¹; this water speed was moderate compared with the speeds crabs experience in the wave-exposed sites. The motors were connected to a timer that alternated the water flow coming from each side intermittently, simulating the bidirectional cycles of surge and backwash flow over periods of 10 s; the voltage was calibrated to generate the desired water speed in the working chamber. The water speed stabilized approximately 2 s after starting the propeller movement and then remained stable for the next 8 s. The water speed was measured by frame-by-frame video analysis of suspended particles (Riisgård and Larsen, 2010); it was checked every day. An optical oxygen sensor was placed in an opening in the lid of the respirometer. Two openings with valves in the lid functioned as water inlet and outlet, which refreshed the

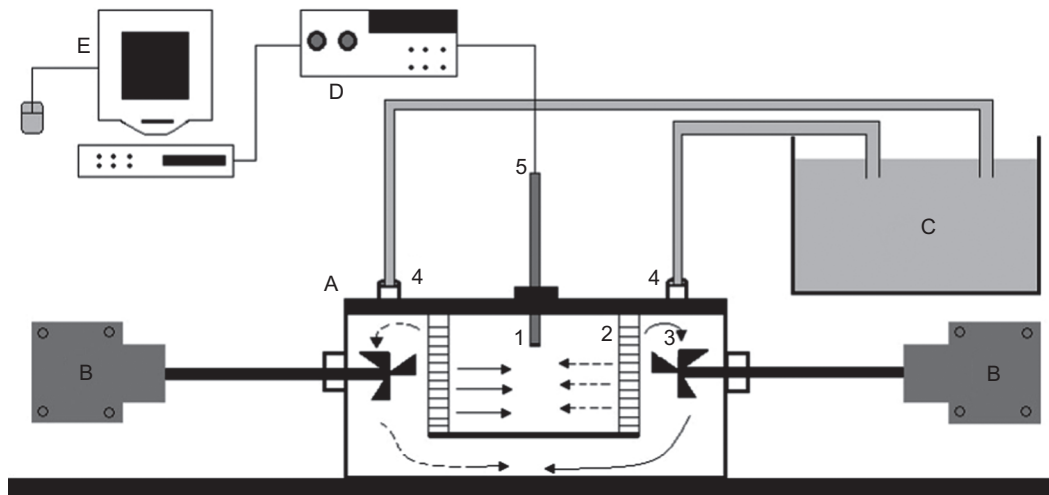


Fig. 2. Experimental system used to measure the energetic cost of withstanding bidirectional water flow. The schematic shows: (A) the respirometric chamber with its working area (1), screen (2), propeller (3), water inlet and outlet (4), and optical oxygen sensor (5); (B) voltage-regulated motors; (C) main water tank; Witrox 4; and (E) computer.

respirometer with aerated water coming from the main container (Fig. 2, 20 liters). The water in the respirometric chamber was renewed after each metabolic measurements.

The oxygen concentration was continuously measured using a fiber optic oximeter and a mini oxygen sensor (Witrox 4, Loligo Systems). The slope of the oxygen concentration with time yielded the oxygen consumption rate. An empty chamber was used as the control for each trial; these values were subtracted from the metabolic measures of the crabs (Cech, 1990). The cost of coping with the bidirectional water flow was calculated as the difference between the rate of oxygen consumption of the crab exposed to the water flow and the metabolic rate in still water. At the end of the experiments, the hermit crabs were sexed, weighed and measured as before. Only males were considered for the analysis.

Shell shape and size descriptors

The aspect ratio of the shells was calculated as shell length (longest dimension along the coiling axis) divided by shell width (widest dimension perpendicular to the coiling axis in the plane of the aperture; Bourdeau, 2009). We measured the surface area projected onto the substratum and the surface area exposed to the water flow of the shells used on the experiment as these parameters are standard shape measures for gastropods (Trussell, 1997; Trussell et al., 1993) and are critical for determining drag and lift forces in gastropod shells (Rilov et al., 2004). We traced the maximum projected surface area on the substrate and the surface area exposed to the water flow considering that the longest axis of the shell was oriented toward the water flow; we chose this orientation because this is the direction that the shell situates with respect to the water flow (present study; Verhaegen et al., 2019). The surface area projected onto the substratum was estimated by taking a photograph (Casio Exilim EXF1) of the shell placed aperture-down on a glass in a horizontal plane. The photograph was taken from underneath the glass, thus, with the shell aperture oriented parallel to the camera lens placed at 20 cm from the glass (Trussell, 1997). The area was calculated using computerized image analysis. The surface area exposed to the water flow was estimated by placing the shells centered 20 cm from the camera lens with the longest anteroposterior axis oriented perpendicular to the camera. For *S. biserialis* shells, the shell apex pointed toward the camera; however, for the *N. scabricosta*

shells, the longest anteroposterior axis does not correspond to the apex face. The areas of the shells (nearest 1 mm²) were estimated using the image analysis software ImageJ (National Institutes of Health, Bethesda, MD, USA).

Statistics

In order to validate the use of the chela size as a predictor of a crab's body mass before removing the crab from its shell, we compared the mass of the hermit crabs calculated from the chelae length (equation) to the mass of the same individual on a balance (determined after the crab had been removed from its shell) using a Student's *t*-test for paired samples. A one-way ANOVA was used to compare the actual body mass of the hermit crabs tested in shells of *S. biserialis* and *N. scabricosta*.

We compared the SMR of the hermit crabs using a repeated-measures ANOVA; shell species was used as a fixed factor and shell size was used as the repeated measure. A similar analysis was used to compare the RMR. The cost of coping with the bidirectional water flow for the hermit crabs occupying *N. scabricosta* and *S. biserialis* shells of different sizes were compared using a repeated-measures ANOVA; we used the shell species (*S. biserialis* and *N. scabricosta*) as the treatment effect (fixed factor) and the shell size as the repeated-measures factor (two levels: small and large shells). We also examined the combined effect of the shell species occupied and the shell sizes (interaction between the treatment and repeated measures) on the energetic cost of withstanding the bidirectional water flow. Planned comparisons (unequal *N* HSD test) were used to compare the energetic cost of withstanding the bidirectional water flow of the hermit crabs occupying: (1) small versus large *N. scabricosta* shells, (2) small versus large *S. biserialis* shells, (3) small *N. scabricosta* shells versus small *S. biserialis* shells, and (4) large *N. scabricosta* shells versus large *S. biserialis* shells.

The mass of the *S. biserialis* and *N. scabricosta* shells given to the hermit crabs in the different shell size treatments were compared using a two-way ANOVA with shell species and size of the shell occupied (small and large) as factors. The surface areas exposed to the water flow and the projected surface area onto the substratum of the two shells in still water and bidirectional flow conditions were compared using a two-way ANOVA. The shell species and the water

flow condition were used as factors, and separate analyses were conducted for each measurement. The aspect ratio of the *S. biserialis* and *N. scabricosta* shells used in the four treatments was compared using a one-way ANOVA. The differences between the shells of the different treatments were compared through Scheffé tests. The normality of the data and homogeneity of variances were tested as described before. Statistical analyses were performed using Statistica 10.

Animal welfare note (ethical regulation)

This study complies with the legal requirements of our country and international ethical standards. The hermit crab used (*Calcinus californiensis*) is not an endangered or protected species. We strictly followed the requirements from the official register of the Department (Ecología y Recursos Naturales; Facultad de Ciencias, UNAM) in SAGARPA (Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación) for animal capture (no. DF00000208).

RESULTS

Shell size occupied in wave-protected and wave-exposed sites in the field

The mass of the hermit crabs did not differ between sites (protected: mean=0.22±0.01; exposed: mean=0.21±0.01; ANOVA, $F_{1,120}=0.77$, $P=0.38$), though the crabs in *S. biserialis* shells (mean=0.25±0.01) were larger than the ones using *N. scabricosta* shells (mean=0.19±0.02; ANOVA, $F_{1,120}=9.25$, $P=0.01$). The hermit

crabs occupied *S. biserialis* and *N. scabricosta* shells of different mass at the wave-protected and wave-exposed sites (ANCOVA, $F_{1,120}=13.13$, $P<0.001$; Fig. 3A,B). The hermit crabs occupied larger *S. biserialis* shells (heavier with loose fit) at the wave-exposed site than at the wave-protected site (Scheffé test, $P<0.001$, Fig. 3A). However, the size of *N. scabricosta* shells occupied at the wave-protected and wave-exposed sites did not differ ($P=0.96$, Fig. 3B). *Stramonita biserialis* shells were heavier than *N. scabricosta* shells (ANOVA, $F_{1,120}=63.06$, $P<0.001$). The mass of the shells covaried with crab body mass ($F_{1,120}=265.74$, $P<0.001$).

Shell size preference

The mass of the hermit crabs did not differ between flow conditions (static: mean=0.39±0.03; flow: mean=0.41±0.03; ANOVA, $F_{1,99}=0.10$, $P=0.75$), though the crabs in *S. biserialis* shells (mean=0.45±0.03) were larger than the ones using *N. scabricosta* shells (mean=0.35±0.02; ANOVA, $F_{1,99}=5.22$, $P=0.02$). The shell mass preference differed in still water compared with bidirectional water flow conditions for crabs occupying both *S. biserialis* and *N. scabricosta* shells (ANCOVA, $F_{1,97}=114.75$, $P<0.001$; Fig. 3C, D). The hermit crabs occupying *S. biserialis* shells preferred larger shells (heavier with looser fit) in bidirectional water flow than in still water (Scheffé test, $P<0.001$; Fig. 3C). In contrast, the hermit crabs tested in *N. scabricosta* shells preferred smaller shells in bidirectional water flow than in still water ($P<0.001$; Fig. 3D). The *S. biserialis* shells were heavier than *N. scabricosta* shells in

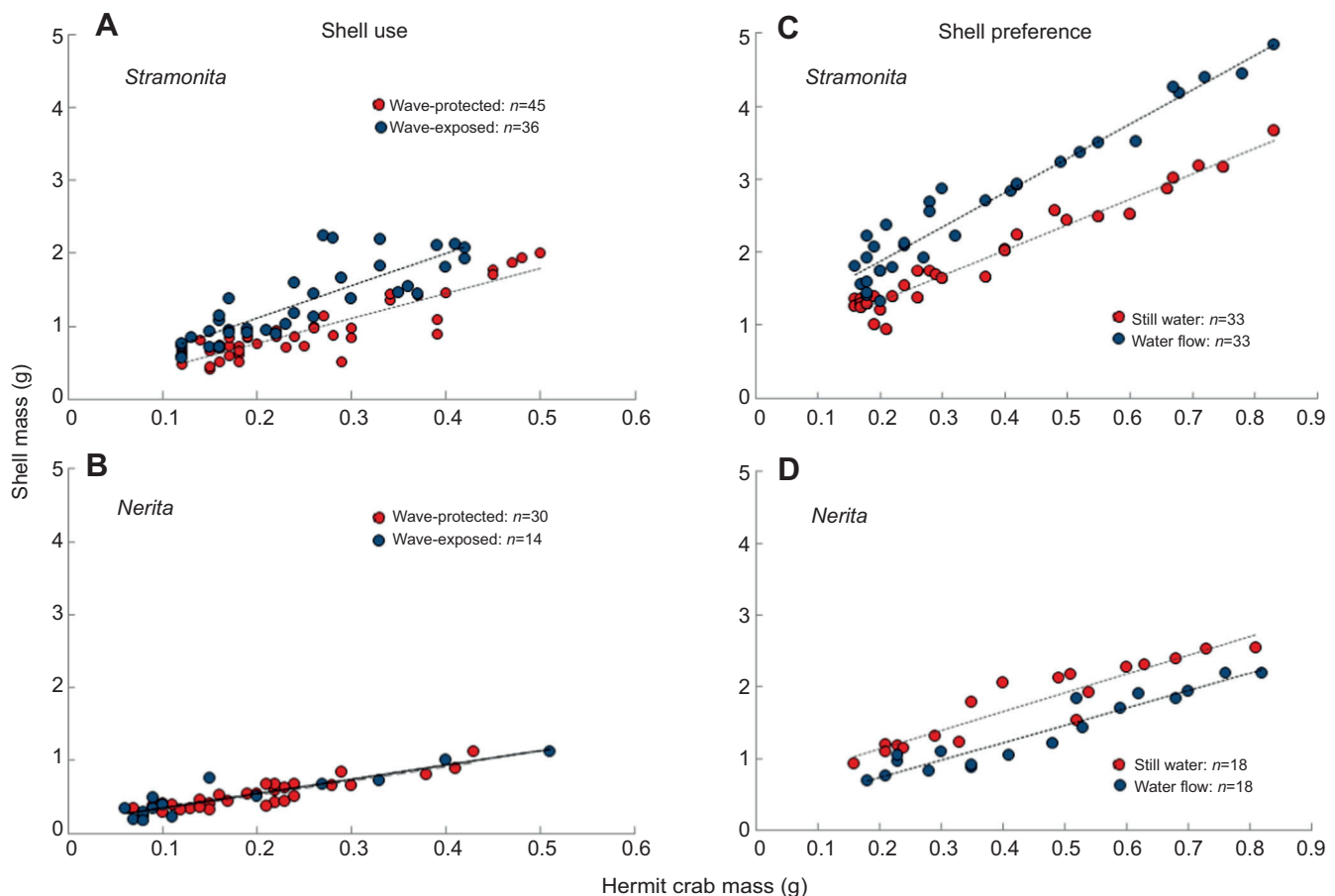


Fig. 3. Mass of *S. biserialis* and *N. scabricosta* shells occupied and preferred in different flow conditions. Mass of *S. biserialis* (A) and *N. scabricosta* (B) shells occupied in the wave-protected (red) and the wave-exposed sites (blue) in the field, and mass of *S. biserialis* (C) and *N. scabricosta* (D) shells chosen in the laboratory tests under still water (red) and bidirectional water flow (blue) conditions ($P<0.05$; two-way ANCOVA).

both flow conditions (ANCOVA, $F_{1,97}=311.90$, $P<0.001$). As expected, shell mass covaried with crab body mass (ANOVA, $F_{1,97}=700.50$, $P<0.001$).

Energetic cost of coping with bidirectional water flow

The body mass of the hermit crabs estimated by measuring chelae length was not significantly different from mass estimated using a balance plate (t -test, $t_{23}=0.51$, $P=0.62$); this validates the estimation of the body mass before removing the crab from its shell. The hermit crabs tested in *S. biserialis* (0.41 ± 0.09 g) and *N. scabricosta* (0.37 ± 0.11 g) shells had similar body mass (ANOVA, $F_{1,21}=1.24$, $P=0.28$). Both SMR and RMR were similar among hermit crabs occupying large and small shells of both species (repeated-measures ANOVA, SMR: $F_{1,21}=0.54$, $P=0.47$; RMR: $F_{1,21}=0.60$, $P=0.45$; Fig. 4A). However, the energetic cost of coping with the bidirectional water flow was influenced by the shell size (small and large; repeated-measures ANOVA, $F_{1,21}=5.31$, $P=0.03$; Fig. 4B), but not by shell species ($F_{1,21}=0.13$, $P=0.71$). The effect of shell size on the energetic costs to withstand the bidirectional water flow was opposite in *S. biserialis* compared with *N. scabricosta* shells (significant treatment \times repeated measures interaction, $F_{1,21}=29.32$, $P<0.001$). Hermit crabs occupying *S. biserialis* shells used 84% more energy when using small shells compared with crabs occupying large *S. biserialis* shells

(repeated-measures ANOVA, $P=0.003$; Fig. 4B). In contrast, among crabs using *N. scabricosta* shells, the crabs using large shells spent more energy than the crabs in small shells ($P=0.04$). The crabs in small *S. biserialis* shells spent more energy during the water flow trials than the crabs occupying small *N. scabricosta* shells ($P=0.004$; Fig. 4B). The crabs did not walk during the trials; rather, they gripped the substrate and allowed the longest axis of the shell to align parallel to the water flow direction. None of the crabs lost grip during the trials.

The *S. biserialis* shells had a higher aspect ratio than *N. scabricosta* shells (ANOVA $F_{1,42}=1308.2$, $P<0.001$). The mass of the small (tight fit) and large (loose fit) shells of *S. biserialis* and *N. scabricosta* given to the hermit crabs were different (ANOVA, $F_{1,42}=45.03$, $P<0.001$; Fig. 5A), the *S. biserialis* shells being heavier than *N. scabricosta* shells in the both flow conditions (ANOVA, $F_{1,42}=84.22$, $P<0.001$; Fig. 5A). The *N. scabricosta* shells had a larger area projected onto the substratum and a larger surface area exposed to the water than *S. biserialis* shells ($F_{1,42}=20.5$, $P<0.001$; $F_{1,42}=11.9$, $P<0.001$, respectively), independent of shell size (small or large). The large shells of both shell species had an area projected onto the substratum approximately twice that of the small shells ($F_{1,42}=474.8$, $P<0.001$; Fig. 5B). Similarly, large shells had a surface area exposed to the water flow nearly twice as large as that of the small shells ($F_{1,42}=164.5$, $P<0.001$; Fig. 5C).

DISCUSSION

The distribution pattern of shell species and size occupied by *C. californiensis* in the rocky intertidal shore, as well as shell preference, is consistent with the shell characteristics that reduce the energetic costs of withstanding wave action. The large *S. biserialis* shells occupied with the highest frequency in the wave-exposed sites minimize the cost of coping with water flow. As has been previously reported (Arce and Alcaraz, 2011), *C. californiensis* occupied *S. biserialis* shells that were 72% heavier at the wave-exposed than in the wave-protected sites, and *S. biserialis* were heavier than *N. scabricosta* shells (independent of crab size). Even though the force due to gravity decreases in submerged bodies as a consequence of buoyancy (Ditsche and Summers, 2014), the difference in mass between different submerged bodies results in differences in the net hydrodynamic forces acting on them (Denny, 1987; Martinez et al., 1998). The heavier the gastropod shell, the lower the net effects of hydrodynamic forces, and therefore, the less energy required to overcome water flow.

The lower energetic cost paid by the crabs using large *S. biserialis* shells compared with small *S. biserialis* shells (~80%) shows the relevance of mass in the effects of wave action. Some researchers have suggested that the use of heavy shells at wave-action sites can be explained by the advantages conferred to the occupants to overcome the hydrodynamic stress (e.g. Argüelles et al., 2009; Barnes, 2005; Bertness, 1980; Garcia and Mantelatto, 2001). Particularly, Hahn (1998) states that *Calcinus seurati* inhabiting hydrodynamically active sites occupy heavier shells of *Thais* sp. (*Stramonita*) than those from still-water sites. Similarly, Reese (1969) suggests that the use of relatively large and heavy shells might help *Calcinus elegans* avoid being washed away from the substrate. Hermit crabs can increase the relative mass of their shells by using a larger shell of the same species (loose fit, as in this study), shells of different species which have thicker walls (Arce and Alcaraz, 2013), encrusted shells (epibionts; Williams and McDermott, 2004), or shells that are damaged so that part of the structure is unusable (broken) but the part of the shell that the crab occupies is of the appropriate size, increasing the mass to shell

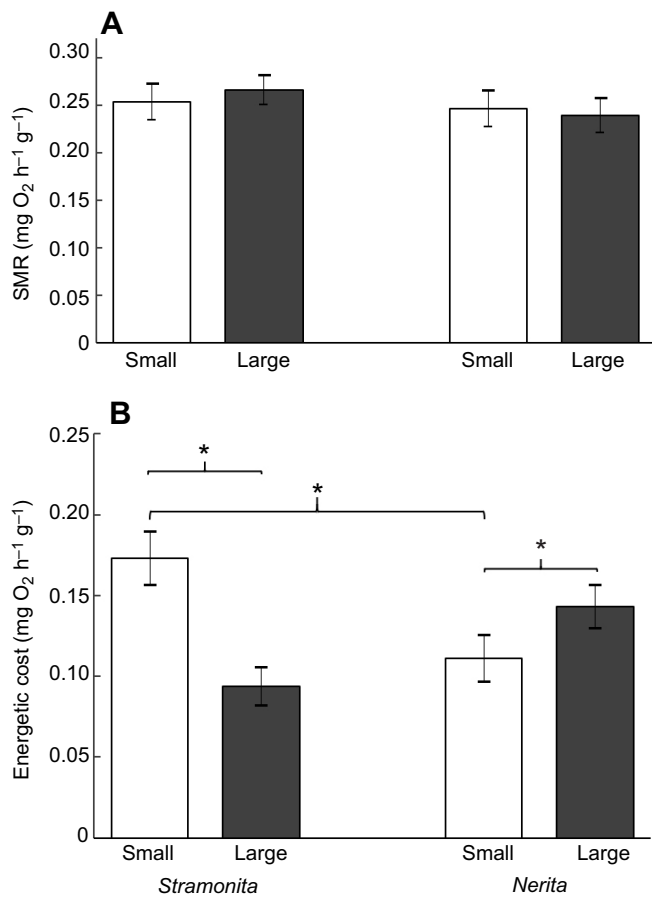


Fig. 4. Effect of using different size and shell species on the SMR and the cost of gripping the ground. Standard metabolic rate (A) and energetic cost to cope with bidirectional water flow (B) of hermit crabs occupying small shells (tight fitting; white bars) and large shells (loose fitting; gray bars) of *S. biserialis* ($n=11$) and *N. scabricosta* ($n=12$). Means \pm s.e.m. are shown. Statistically significant differences are indicated with asterisks ($*P<0.05$; repeated-measures ANOVA).

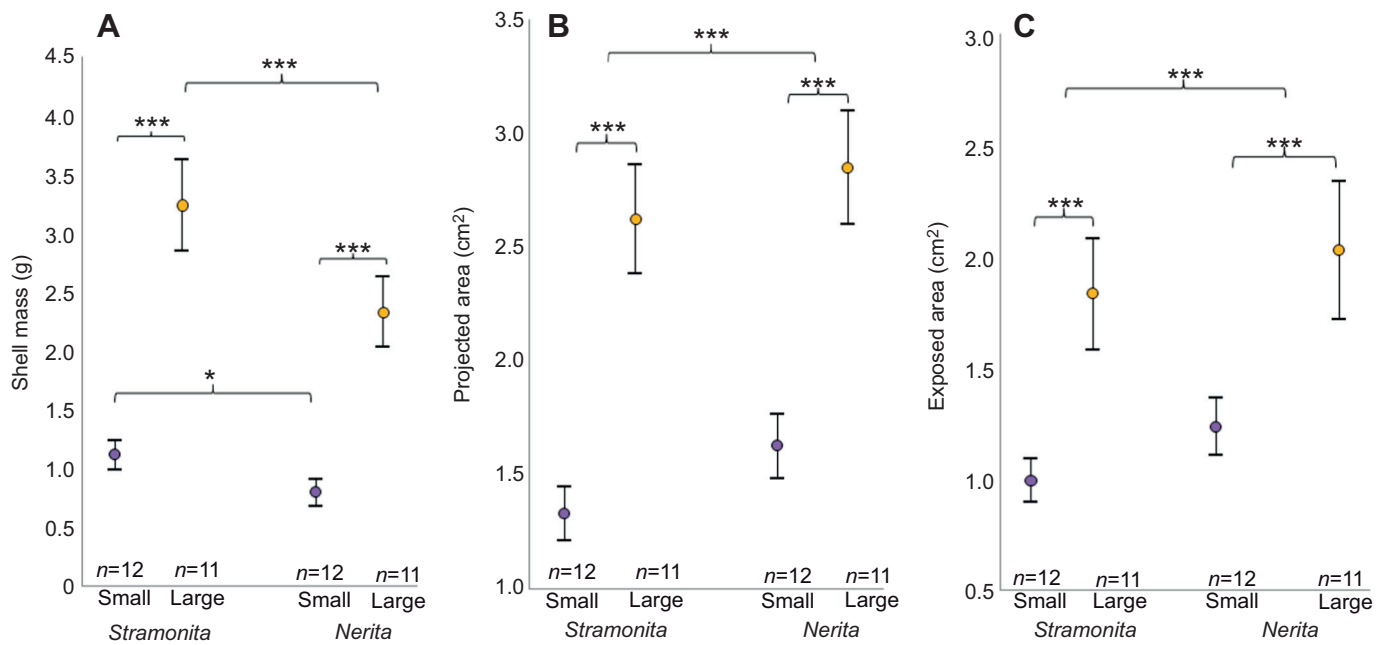


Fig. 5. Shape and size descriptors of the shells used to measure the energetic cost of coping with bidirectional water flow. Shell mass (A), projected surface area onto the substrate (B), and surface area exposed to water flow (C) of hermit crabs occupying small (tight fitting, purple) shells and large (loose fitting, yellow) *S. biserialis* and *N. scabricosta* shells. Statistically significant differences are indicated with asterisks (* $P < 0.05$, *** $P < 0.001$; unequal N HSD). Means \pm s.e.m. are shown.

internal volume ratio (Alcaraz and Kruesi, 2012). Our study demonstrates the advantages of using heavy shells (with a loose fit) in coping with hydrodynamic forces from an energetic perspective. The use of shells that are heavier than the preferred size can be costly because it elevates lactate levels in the hemolymph (encrusted shells; Briffa and Elwood, 2005), and can have negative effects on foraging (Alcaraz and García-Cabello, 2017), locomotion (Alcaraz and Arce, 2017), body growth (Alcaraz et al., 2015) and reproduction (Hazlett et al., 2005); however, as far as we know, none of these disadvantages have been identified under flow conditions, which may change the cost–benefit balance in favor of heavier shells.

Although the use of large rather than small *S. biserialis* shells reduced the energetic cost of coping with water flow, the effect was inverted when crabs used *N. scabricosta* shells, where the use of large shells increases the cost. The nerites (*N. scabricosta* and *N. funiculata*) are significantly lighter (at equivalent internal volumes) than any of the other shells commonly used by hermit crabs (Bertness, 1981). In addition to being lighter than *S. biserialis* shells, *N. scabricosta* shells also have a larger area exposed to the flow and larger projected surface area to the substrate compared with *S. biserialis* shells, independent of the size of the crab. The use of large shells of either of the two species increases the mass that acts opposite to the direction of the lift force. However, the surface areas exposed to flow and the projected surface area to the substrate, and thus the magnitude of the hydrodynamic forces, also increase with shell size (Rilov et al., 2004). A large *N. scabricosta* shell has greater mass than a small one, but much less mass than a large *S. biserialis* shell. At the same time, a large *N. scabricosta* shell has a larger surface area exposed to flow and projected area to the substrate than a large *S. biserialis* shell. In other words, the relationship between mass increase and size increase is more favorable hydrodynamically in *S. biserialis* shells than in *N. scabricosta* shells. *Nerita scabricosta* and *S. biserialis* shells

also differ in their internal architecture. *Nerita scabricosta* shells are low-spined, with a large internal space that lacks the spiral structure characteristic of most shells (columella; Vermeij, 1978). In contrast, *S. biserialis* shells are spired with a well-defined columella (Price, 2003). Thus, in addition to the mass and shape differences between these two species, *N. scabricosta* lacks a columella to which the hermit crab can wrap its abdomen around (Chapple, 2002), which might increase the cost of gripping the ground as the shells increase in size.

Additionally, by minimizing the surface area exposed to flow, the magnitudes of the hydrodynamic forces are reduced (Boller, 2006; Warburton, 1976). During the flow experiments, the hermit crabs' shells oriented with the longest axis in the direction of flow, as has been described in wave simulating tanks for gastropods, bivalves, limpets and decapods (Denny and Blanchette, 2000; García-March et al., 2007; Verhaegen et al., 2019; Weissburg et al., 2003). This orientation enables animals to expose the smallest front area and the longest profile in the flow direction, which reduces the effect of hydrodynamic forces (Nishimoto and Herrnkind, 1978; Verhaegen et al., 2019). However, the relative advantages of shell orientation depends on the shell type used, being more important for crabs using *S. biserialis* owing to its longer profile compared with *N. scabricosta* (see Fig. 1A). Even so, the cost of coping with flow did not depend on the shell shape alone. We hypothesized that the conical *S. biserialis* shells, with a streamlined shape, would have a smaller wake that would decrease the energy required to cope with the flow compared with *N. scabricosta* shells, which have a globose shape. However, the crabs using small *S. biserialis* shells, which are rarely found in wave-exposed areas, paid the highest energetic cost to cope with the water flow. Our data showed that the energetic cost of facing the bidirectional water flow is set by the interaction of shell mass and shape, not by shape alone. Verhaegen et al. (2019) describe a similar interaction between shape, size and orientation on the drag forces on freshwater snails.

The use of globose shells in wave-protected pools and conical shells in wave-exposed areas has been described for several species. For instance, in hydrodynamically active sites, *Clibanarius antillensis* occupies conical shells (e.g. *Cantharus*, *Engina* and *Stramonita*) much more frequently than globose shells (e.g. *Nerita*, *Natica* and *Polinices*; Argüelles et al., 2009). *Calcinus elegans* moves toward the intertidal and heavy surge conditions when occupying conical shells (*Nassarius papillosus*), but stay in protected tide pools when occupying non-hydrodynamic shells, such as irregularly shaped worm shells (*Serpulorbis variabilis*) or egg-shaped cowrie shells (*Cypraea capurserpentis*; Bach and Hazlett, 2009). Additionally, 90% of *C. elegans* withstand fast water currents when in conical shells, but only 20% avoid being dislodged by the same water regime when using worm or cowrie shells (Bach and Hazlett, 2009). This pattern of shell shape is not restricted to hermit crabs; it is also evident in the zonation of gastropod species along the intertidal gradient. Gastropods with high aspect ratios are commonly distributed in the upper intertidal (Lam, 2002). Notably, the globose-shaped gastropods *Lunella coronata* and *Nerita albicilla* seek refuges with slow water velocity (edges and corners), while the snails with streamlined forms crawl upstream in the flumes (Lam, 2002). Shell shape is also relevant for freshwater snails in which individuals with globular shells experience higher lift and drag forces than those with more streamlined shell forms when exposed to unidirectional water flow (20 to 100 cm s⁻¹; Verhaegen et al., 2019). Still, the use of globose and conical shells in different sites of the intertidal cannot be explained by the gastropod distribution along the gradient, mainly because of the high mobility of hermit crabs (Alcaraz and Arce, 2017; Benvenuto et al., 2003) and their ability to move within the short distance between the wave breaking zone and the tide pools in Troncones, as is also described by Bach and Hazlett (2009) for *C. elegans*.

Hydrodynamic forces play a strong role in determining where organisms can potentially live on rocky shores; however, the interplay of waves with other abiotic (e.g. temperature) and biological factors (e.g. predation pressure), ultimately determines the zonation in the subtidal zone (a part of the shore that is always submerged; Benedetti-Cecchi and Trussell, 2013; Connell, 1972). Neither hydrodynamics nor predation pressure explains the use of *N. scabricosta* shells in wave-protected tide pools. Nerites provide weak protection against peeler and crusher predators compared with conical shells (e.g. *Stramonita* and *Cantharus*; Alcaraz and Arce, 2017; Arce and Alcaraz, 2013). Even so, *C. californiensis* use *N. scabricosta* in protected tide pools where predation is more intense (Bertness and Cunningham, 1981; Menge, 1978). The use of *N. scabricosta* shells in the upper intertidal might be explained by its abundance and advantages conferred by its low weight (Bertness, 1981), which favor foraging, growth and the performance of precopulatory behavior compared with the relatively heavier conical shells (Alcaraz et al., 2015; Alcaraz and García-Cabello, 2017; Hazlett, 1995). The occupancy of *N. scabricosta* shells of the same size in the wave-protected and -exposed sites, even though the use of smaller *N. scabricosta* shells decreases the cost of dealing with water flow, suggests that the crabs occupying *N. scabricosta* shells stay in the lower intertidal only for short periods. The small number of crabs in *N. scabricosta* shells and other globose-shape shells inhabiting the wave-exposed areas supports this idea (e.g. Argüelles et al., 2009; Bach and Hazlett, 2009).

In this study, we tested only males. The ovigerous females of *C. californiensis* and other hermit crab species occupy wave-exposed areas with higher frequency than males (Arce and Alcaraz, 2011; Argüelles et al., 2009), and males and females prefer different

shell species (Suárez-Rodríguez et al., 2019); therefore, future studies are needed to assess potential differences in benefits and cost of different shell shapes and sizes for females in general, and ovigerous females in particular. Additionally, we used a relatively low water speed compared with the speed faced by animals living in these areas, and shell shape may have a stronger influence on the costs of counteracting hydrodynamic forces at higher water speeds than at the one we used. However, more experiments are required to test this assumption.

Hermit crabs commonly occupy a tight shell, which has been widely explained as a consequence of low shell availability (Vance, 1972), because small shells can be unfavorable for body growth, fecundity and protection from predators (e.g. Bertness and Cunningham, 1981; Fotheringham, 1976). However, the use of small shells can also favor escape speed (Alcaraz and Arce, 2017) and the energy required to deal with hydrodynamic stress when they are globose shape. Our results highlight the fact that the use of tight shells is not necessarily adverse for the hermit crabs, and in some environmental or biotic conditions, small shells may favor the individual's performance. The use of a non-preferred shell species (in this case *N. scabricosta* shells) may be a 'best-of-a-bad-job' strategy, which then leads crabs to choose the least disadvantageous shell size to minimize the cost of coping with wave action. Independently of the mode by which the crabs acquire a new shell (exploitation, vacancy chains, negotiation or fighting; Peres et al., 2018), it is likely that in the wild, hermit crabs in *N. scabricosta* shells move to the wave-protected tide pools, where the costs of the globose shell are minimized, until a more preferred shell becomes available. Similarly, individuals of *C. elegans* occupying egg-shaped cowrie and worm shells (non-preferred) remain in tide pools until they obtain a conical shell (preferred type), after which they move out of tide pools and stay on subtidal coral heads (Bach and Hazlett, 2009).

Finally, the phenotypic adaptations of sessile organisms to wave action have been widely assessed. However, few studies have estimated the adaptations of animals that use locomotor appendages to live under wave exposure (Lau and Martínez, 2003). Some of these studies have assessed the hydrodynamic forces affecting locomotion (e.g. speed and gaits), critical levels for dislodgement (e.g. Lau and Martínez, 2003; Martínez et al., 1998), hydrodynamic morphology of the carapace (Blake, 1985), and aggregation of individuals as a strategy to reduce drag forces (e.g. Bill and Herrnkind, 1976). However, as far as we know, this is the first study to measure the energetic cost of coping with bidirectional water flows in a marine animal. Our research supports the idea that long-term energy costs of living in wave-action sites have a critical role in the distribution of mobile animals in the intertidal, as has been suggested by Siddon and Witman (2003).

Acknowledgements

We thank Dr Karla Kruesi for her technical assistance. We thank Dr Ricardo Méndez-Fragoso and Dr Karla Kruesi for their comments to the manuscript and Dr Lynna Kiere for English editing. We thank the Posgrado en Ciencias del Mar y Limnología, U.N.A.M. and Consejo Nacional de Ciencia y Tecnología (CONACyT) for support to B.T. and L.M.B.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author contributions

Conceptualization: G.A., L.M.B.; Methodology: G.A., B.T., L.M.B.; Formal analysis: G.A., L.M.B.; Investigation: G.A., B.T., L.M.B.; Resources: G.A.; Writing - original

draft: G.A., B.T., L.M.B.; Writing - review & editing: G.A., L.M.B.; Supervision: G.A.; Project administration: G.A.; Funding acquisition: G.A.

Funding

This work was supported by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica, PAPIIT IN-216418.

Data availability

Data are available from the figshare digital repository (<https://doi.org/10.6084/m9.figshare.12328424.v1>).

References

- Alcaraz, G. and Arce, E.** (2017). Predator discrimination in the hermit crab *Calcinus californiensis*: tight for shell breakers, loose for shell peelers. *Oikos* **126**, 1299-1307. doi:10.1111/oik.03742
- Alcaraz, G. and García-Cabello, K. N.** (2017). Feeding and metabolic compensations in response to different foraging costs. *Hydrobiologia* **787**, 217-227. doi:10.1007/s10750-016-2965-6
- Alcaraz, G. and Kruesi, K.** (2009). The role of previous shell occupancy in the wild on laboratory shell choice by the hermit crab *Calcinus californiensis*. *Mar. Freshw. Behav. Physiol.* **42**, 55-62. doi:10.1080/10236240802663564
- Alcaraz, G. and Kruesi, K.** (2012). Exploring the phenotypic plasticity of standard metabolic rate and its inter-individual consistency in the hermit crab *Calcinus californiensis*. *J. Exp. Mar. Biol. Ecol.* **412**, 20-26. doi:10.1016/j.jembe.2011.10.014
- Alcaraz, G., Chávez-Solis, C. E. and Kruesi, K.** (2015). Mismatch between body growth and shell preference in hermit crabs is explained by protection from predators. *Hydrobiologia* **743**, 151-156. doi:10.1007/s10750-014-2029-8
- Alexander, D. E.** (1990). Drag coefficients of swimming animals: effects of using different reference areas. *Biol. Bull.* **179**, 186-190. doi:10.2307/1541768
- Arce, E. and Alcaraz, G.** (2011). Shell use by the hermit crab *Calcinus californiensis* at different levels of the intertidal zone. *Sci. Mar.* **75**, 121-128. doi:10.3989/scimar.2011.75n1121
- Arce, E. and Alcaraz, G.** (2012). Shell preference in a hermit crab: Comparison between a matrix of paired comparisons and a multiple-alternative experiment. *Mar. Biol.* **159**, 853-862. doi:10.1007/s00227-011-1861-x
- Arce, E. and Alcaraz, G.** (2013). Plasticity of shell preference and its antipredatory advantages in the hermit crab *Calcinus californiensis*. *Can. J. Zool.* **91**, 321-327. doi:10.1139/cjz-2012-0310
- Arce, E. and Córdoba-Aguilar, A.** (2018). The right choice: predation pressure drives shell selection decisions in the hermit crab *Calcinus californiensis*. *Can. J. Zool.* **96**, 454-459. doi:10.1139/cjz-2017-0023
- Argüelles, A., Álvarez, F. and Alcaraz, G.** (2009). Shell architecture and its relation to shell occupation by the hermit crab *Clibanarius antillensis* under different wave action conditions. *Sci. Mar.* **73**, 717-723. doi:10.3989/scimar.2009.73n4717
- Argüelles-Ticó, A., Álvarez, F. and Alcaraz, G.** (2010). Shell utilization by the hermit crab *Clibanarius antillensis* Stimpson 1862 (Crustacea: Anomura) in intertidal rocky pools at Montepio, Veracruz, Mexico. *Trop. Zool.* **23**, 63-73.
- Asakura, A.** (1995). Sexual differences in life history and resource utilization by the hermit crab. *Ecology* **76**, 2295-2313. doi:10.2307/1941703
- Bach, C. E. and Hazlett, B. A.** (2009). Shell shape affects movement patterns and microhabitat distribution in the hermit crabs *Calcinus elegans*, *C. laevimanus* and *C. latens*. *J. Exp. Mar. Biol. Ecol.* **382**, 27-33. doi:10.1016/j.jembe.2009.10.009
- Barnes, D. K. A.** (2005). Body and resource size at the land-sea interface. *Mar. Biol.* **146**, 625-632. doi:10.1007/s00227-004-1451-2
- Benedetti-Cecchi, L. and Trussell, G. C.** (2013). Intertidal rocky shores. In *Marine Community Ecology and Conservation* (ed. M. D. Bertness, J. F. Bruno, B. R. Silliman and J. J. Stachowicz), pp. 202-225. Sinauer Associates.
- Benvenuto, C., Sartoni, G. and Gherardi, F.** (2003). Foraging behaviour of the hermit crab *Clibanarius erythropus* in a Mediterranean shore. *J. Mar. Biol. Assoc. United Kingdom* **83**, 457-461. doi:10.1017/S0025315403007331h
- Bertness, M. D.** (1980). Shell preference and utilization patterns in littoral hermit crabs of the bay of Panama. *J. Exp. Mar. Biol. Ecol.* **48**, 1-16. doi:10.1016/0022-0981(80)90002-7
- Bertness, M. D.** (1981). The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). *Crustaceana* **40**, 197-205. doi:10.1163/156854081X00598
- Bertness, M. D. and Cunningham, C.** (1981). Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Mar. Biol.* **50**, 213-230. doi:10.1016/0022-0981(81)90051-4
- Bill, R. G. and Herrnkind, W. F.** (1976). Drag reduction by formation movement in spiny lobsters. *Science* **193**, 1146-1148. doi:10.1126/science.193.4258.1146
- Blake, R. W.** (1985). Crab carapace hydrodynamics. *J. Zool.* **207**, 407-423. doi:10.1111/j.1469-7998.1985.tb04940.x
- Blamey, K. L. and Branch, G. M.** (2009). Habitat diversity relative to wave action on rocky shores: implications for the selection of marine protected areas. *Ann. Zool. Fennici* **19**, 645-657. doi:10.1002/aqc.1014
- Boller, M. L.** (2006). The hydrodynamic effects of shape and size change during reconfiguration of a flexible macroalga. *J. Exp. Biol.* **209**, 1894-1903. doi:10.1242/jeb.02225
- Bourdeau, P. E.** (2009). Prioritized phenotypic responses to combined predators in a marine snail. *Ecology* **90**, 1659-1669. doi:10.1890/08-1653.1
- Briffa, M. and Elwood, R. W.** (2005). Metabolic consequences of shell choice in *Pagurus bernhardus*: Do hermit crabs prefer cryptic or portable shells? *Behav. Ecol. Sociobiol.* **59**, 143-148. doi:10.1007/s00265-005-0020-0
- Cech, J. J., Jr** (1990). Respirometry. In *Methods for Fish Biology* (ed. C. B. Schreck and P. B. Moyle), pp. 335-356. American Fisheries Society.
- Chapple, W. D.** (2002). Mechanoreceptors innervating soft cuticle in the abdomen of the hermit crab, *Pagurus pollicarus*. *J. Comp. Physiol. A Neuroethol. Sensory Neural Behav. Physiol.* **188**, 753-766. doi:10.1007/s00359-002-0362-2
- Chapple, W.** (2012). Kinematics of walking in the hermit crab, *Pagurus pollicarus*. *Arthropod Struct. Dev.* **41**, 119-131. doi:10.1016/j.asd.2011.11.004
- Connell, J. H.** (1972). Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* **3**, 169-192. doi:10.1146/annurev.es.03.110172.001125
- Denny, M. W.** (1987). Lift as a mechanism of patch initiation in mussel beds. *J. Exp. Mar. Biol. Ecol.* **113**, 231-245. doi:10.1016/0022-0981(87)90103-1
- Denny, M.** (1989). A limpet shell shape that reduces drag: laboratory demonstration of a hydrodynamic mechanism and an exploration of its effectiveness in nature. *Can. J. Zool.* **67**, 2098-2106. doi:10.1139/z89-299
- Denny, M. W.** (2000). Limits to optimization: fluid dynamics, adhesive strength and the evolution of shape in limpets. *J. Exp. Biol.* **203**, 2603-2622.
- Denny, M. W. and Blanchette, C. A.** (2000). Hydrodynamics, shell shape, behavior and survivorship in the owl limpet *Lottia gigantea*. *J. Exp. Biol.* **203**, 2623-2639.
- Denny, M. W. and Gaylord, B.** (2010). Marine ecomechanics. *Ann. Rev. Mar. Sci.* **2**, 89-114. doi:10.1146/annurev-marine-120308-081011
- Ditsche, P. and Summers, A. P.** (2014). Aquatic versus terrestrial attachment: water makes a difference. *Beilstein J. Nanotechnol.* **5**, 2424-2439. doi:10.3762/bjnano.5.252
- Fotheringham, N.** (1976). Effects of shell stress on the growth of hermit crabs. *J. Exp. Mar. Biol. Ecol.* **23**, 299-305. doi:10.1016/0022-0981(76)90027-7
- Garcia, R. B. and Mantelatto, F. L. M.** (2001). Shell selection by the tropical hermit crab *Calcinus tibicen* (Herbst, 1791) (Anomura, Diogenidae) from Southern Brazil. *J. Exp. Mar. Biol. Ecol.* **265**, 1-14. doi:10.1016/S0022-0981(01)00321-5
- García-March, J. R., Pérez-Rojas, L. and García-Carrasco, A. M.** (2007). Influence of hydrodynamic forces on population structure of *Pinna nobilis* L., 1758 (Mollusca: Bivalvia): the critical combination of drag force, water depth, shell size and orientation. *J. Exp. Mar. Biol. Ecol.* **342**, 202-212. doi:10.1016/j.jembe.2006.09.007
- Gaylord, B.** (2007). Hydrodynamic forces. In *Encyclopedia of Tidepools and Rocky Shores* (ed. M. W. Denny), pp. 276-278. University of California Press.
- Hahn, D. R.** (1998). Hermit crab shell use patterns: response to previous shell experience and to water flow. *J. Exp. Mar. Biol. Ecol.* **228**, 35-51. doi:10.1016/S0022-0981(98)00002-1
- Hazlett, B. A.** (1981). The behavioral ecology of hermit crabs. *Annu. Rev. Ecol. Syst.* **12**, 1-22. doi:10.1146/annurev.es.12.110181.000245
- Hazlett, B. A.** (1995). Behavioral plasticity in crustacea: why not more? *J. Exp. Mar. Biol. Ecol.* **193**, 57-66. doi:10.1016/0022-0981(95)00110-7
- Hazlett, B. A., Rittschof, D. and Bach, C. E.** (2005). The effects of shell size and coil orientation on reproduction in female hermit crabs, *Clibanarius vittatus*. *J. Exp. Mar. Biol. Ecol.* **323**, 93-99. doi:10.1016/j.jembe.2005.03.002
- Kemp, P. and Bertness, M. D.** (1984). Snail shape and growth rates: Evidence for plastic shell allometry in *Littorina littorea*. *Proc. Natl. Acad. Sci. USA* **81**, 811-813. doi:10.1073/pnas.81.3.811
- Lam, K. K. Y.** (2002). Escape responses of intertidal gastropods on a subtropical rocky shore in Hong Kong. *J. Molluscan Stud.* **68**, 297-306. doi:10.1093/mollus/68.4.297
- Lau, W. W. Y. and Martínez, M. M.** (2003). Getting a grip on the intertidal: flow microhabitat and substratum type determine the dislodgement of the crab *Pachygrapsus crassipes* (Randall) on rocky shores and in estuaries. *J. Exp. Mar. Biol. Ecol.* **295**, 1-21. doi:10.1016/S0022-0981(03)00276-4
- Mantelatto, F. L., Scelzo, M. A. and Tudge, C. C.** (2009). Morphological and morphometric appraisal of the spermatophore of the southern hermit crab *Isocheles sawayai* Forest and Saint Laurent, 1968 (Anomura: Diogenidae), with comments on gonopores in both sexes. *Zoologischer Anzeiger A J. Comp. Zool.* **248**, 1-8. doi:10.1016/j.jcz.2008.06.002
- Martinez, M., Full, R. and Koehl, M.** (1998). Underwater punting by an intertidal crab: a novel gait revealed by the kinematics of pedestrian locomotion in air versus water. *J. Exp. Biol.* **201**, 2609-2623.
- Menge, B. A.** (1978). Predation intensity in a rocky intertidal community - Relation between predator foraging activity and environmental harshness. *Oecologia* **34**, 1-16. doi:10.1007/BF00346237
- Mima, A., Wada, S. and Goshima, S.** (2003). Antipredator defence of the hermit crab *Pagurus filholi* induced by predatory crabs. *Oikos* **102**, 104-110. doi:10.1034/j.1600-0706.2003.12361.x
- Nagle, J. S.** (1967). Wave and current orientation of shells. *J. Paleontol.* **37**, 1124-1138. doi:10.1306/74D71848-2B21-11D7-8648000102C1865D

- Nishimoto, R. T. and Herrnkind, W. F.** (1978). Directional orientation in blue crabs, *Callinectes sapidus* Rathbun: escape responses and influence of wave direction. *J. Exp. Mar. Biol. Ecol.* **33**, 93-112. doi:10.1016/0022-0981(78)90001-1
- Pechenik, J. A., Hsieh, J., Owara, S., Wong, P., Marshall, D., Untersee, S. and Li, W.** (2001). Factors selecting for avoidance of drilled shells by the hermit crab *Pagurus longicarpus*. *J. Exp. Mar. Biol. Ecol.* **262**, 75-89. doi:10.1016/S0022-0981(01)00284-2
- Peres, P. A. S., Ferreira, A. P. and Leite, F. P. P.** (2018). Expanding the "shell exchange market" hypothesis for clustering behavior in intertidal hermit crabs: mating and tide as proximate factors. *J. Exp. Mar. Biol. Ecol.* **500**, 100-104. doi:10.1016/j.jembe.2017.12.019
- Price, R. M.** (2003). Columellar muscle of neogastropods: muscle attachment and the function of columellar folds. *Biol. Bull.* **205**, 351-366. doi:10.2307/1543298
- Reese, E. S.** (1969). Behavioral adaptations of intertidal hermit crabs. *Integr. Comp. Biol.* **9**, 343-355. doi:10.1093/icb/9.2.343
- Riisgård, H. U. and Larsen, P. S.** (2010). Particle capture mechanisms in suspension-feeding invertebrates. *Mar. Ecol. Prog. Ser.* **418**, 255-293. doi:10.3354/meps08755
- Rilov, G., Benayahu, Y. and Gansith, A.** (2004). Life on the edge: do biomechanical and behavioral adaptations to wave-exposure correlate with habitat partitioning in predatory whelks? *Mar. Ecol. Prog. Ser.* **282**, 193-204. doi:10.3354/meps282193
- Rosenfeld, J., Van Leeuwen, T., Richards, J. and Allen, D.** (2015). Relationship between growth and standard metabolic rate: measurement artefacts and implications for habitat use and life-history adaptation in salmonids. *J. Anim. Ecol.* **84**, 4-20. doi:10.1111/1365-2656.12260
- Scully, E. P.** (1979). The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. *J. Exp. Mar. Biol. Ecol.* **37**, 139-152. doi:10.1016/0022-0981(79)90091-1
- Siddon, C. E. and Witman, J. D.** (2003). Influence of chronic, low-level hydrodynamic forces on subtidal community structure. *Mar. Ecol. Prog. Ser.* **261**, 99-110. doi:10.3354/meps261099
- Statzner, B.** (2008). How views about flow adaptations of benthic stream invertebrates changed over the last century. *Int. Rev. Hydrobiol.* **93**, 593-605. doi:10.1002/iroh.200711018
- Suárez-Rodríguez, M., Kruesi, K. and Alcaraz, G.** (2019). The shadow of the shell: a cue for a new home. *J. Mar. Biol. Assoc. United Kingdom* **99**, 1165-1169. doi:10.1017/S0025315419000122
- Taylor, P. R.** (1981). Hermit crab fitness: the effect of shell condition and behavioral adaptations on environmental resistance. *J. Exp. Mar. Biol. Ecol.* **52**, 205-218. doi:10.1016/0022-0981(81)90037-X
- Toledo, B. M. E. R.** (2016). Consecuencias del oleaje sobre la preferencia de conchas de gasterópodos y sus costos energéticos en el cangrejo ermitaño *Calcinus californiensis* PhD thesis, Universidad Nacional Autónoma de México, Mexico City, Mexico.
- Trussell, G. C.** (1997). Phenotypic plasticity in the foot of an intertidal snail. *Ecology* **78**, 1033-1048. doi:10.1890/0012-9658(1997)078[1033:PPITFS]2.0.CO;2
- Trussell, G. C.** (2000). Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*. *Evol. Ecol. Res.* **2**, 803-822.
- Trussell, G. C., Johnson, A. S., Rudolph, S. G. and Gilfillan, E. S.** (1993). Resistance to dislodgement: habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Mar. Ecol. Prog. Ser.* **100**, 135-144. doi:10.3354/meps100135
- Turra, A. and Leite, F. P. P.** (2001). Shell utilization patterns of a tropical rocky intertidal hermit crab assemblage: I. The case of Grande Beach. *J. Crustac. Biol.* **21**, 393-406. doi:10.1163/20021975-99990140
- Turra, A. and Denadai, M. R.** (2002). Substrate use and selection in sympatric intertidal hermit crab species. *Brazilian J. Biol.* **62**, 107-112. doi:10.1590/S1519-69842002000100013
- Vance, R. R.** (1972). The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology* **53**, 1075-1083. doi:10.2307/1935419
- Verhaegen, G., Herzog, H., Korsch, K., Kerth, G., Brede, M. and Haase, M.** (2019). Testing the adaptive value of gastropod shell morphology to flow: a multidisciplinary approach based on morphometrics, computational fluid dynamics and a flow tank experiment. *Zool. Lett.* **5**, 1-13. doi:10.1186/s40851-018-0119-6
- Vermeij, G. J.** (1978). *Biogeography and Adaptation: Patterns of Marine Life*. Harvard University Press.
- Vogel, S.** (2005). Living in a physical world III. Getting up to speed. *J. Biosci.* **30**, 303-312. doi:10.1007/BF02703667
- Vogel, S. and Labarbera, M.** (1978). Simple for tanks research and teaching. *Bioscience* **28**, 638-643. doi:10.2307/1307394
- Warburton, K.** (1976). Shell form, behaviour, and tolerance to water movement in the limpet *Patina pellucida* (L.) (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **23**, 307-325. doi:10.1016/0022-0981(76)90028-9
- Webb, P.** (2007). Buoyancy. In *Encyclopedia of Tidepools and Rocky Shores* (ed. M. W. Denny), pp. 118-120. University of California Press.
- Weissburg, M. J., James, C. P., Smee, D. L. and Webster, D. R.** (2003). Fluid mechanics produces conflicting constraints during olfactory navigation of blue crabs, *Callinectes sapidus*. *J. Exp. Biol.* **206**, 171-180. doi:10.1242/jeb.00055
- Williams, J. D. and McDermott, J. J.** (2004). Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *J. Exp. Mar. Biol. Ecol.* **305**, 1-128. doi:10.1016/j.jembe.2004.02.020