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Underwater video reveals decreased activity of rocky intertidal snails during high tides and cooler days

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Abstract

Nearly all of our understanding of rocky inter-tidal ecology comes from studies conducted at low tide. To study inter-tidal organisms at high tide, we anchored waterproof digital GoPro® video cameras in wave-exposed tidepools and recorded the daytime movements of the black turban snail, *Tegula funebralis*, over the tidal cycle between May and August 2012 near Bodega Bay, California. Overall, snails moved more quickly and presumably foraged more during low tides and on days with warmer air and perhaps water temperatures. This is similar to other ectotherms that exhibit increased metabolic rates, movement and foraging in warmer conditions. Snails also moved less during flood and high tides, may have moved downward in tidepools at flood tides, and showed evidence of reduced activity on days with larger waves. This inactivity and refuge seeking may have been a strategy to avoid dislodgment by waves. Analysis of snail trajectories showed foraging bouts indicated by alternating zig-zagging and straight movement. There was no effect of temperature, wave height, or tidal phase on distribution of snail turning angles, suggesting that they may have foraged consistently but moved faster during warm conditions and low tides, thereby grazing a larger area. This is one of few direct recordings of inter-tidal organisms on wave-exposed rocky shores during high tide. The methods used here are easily transferable to other studies, which are needed to increase our understanding of behaviors that structure rocky shore communities during high tide.

KEYWORDS
animal movement, GoPro, rocky inter-tidal, tidal cycle, underwater video, wave exposure

1 | INTRODUCTION

Exposed rocky inter-tidal shores have long been a fruitful system for ecological studies, contributing substantially to ecological theory. However, nearly all observations on these wave-swept shores are conducted during low tide because shores are inaccessible during high tide. Our limited understanding of organisms during high tide has come primarily from indirect rather than direct observations. Such studies include trapping animals during high tide (Hunter & Naylor, 1993; Silva, Hawkins, Boaventura, Brewster, & Thompson, 2010), comparing changes between successive low tides (Chapperon & Seuront, 2009; Doering & Phillips, 1983; Pardo & Johnson, 2006), observing endogenous rhythms and other behaviors during constant conditions or simulated high tides in the laboratory (Morgan, 2007; Vieira et al., 2012), or simulating flow in the laboratory (Denny, 1989; Martone & Denny, 2008). Direct observations in wave-exposed environments at high tide are few and have been accomplished by suspending a researcher or video camera above incoming waves (Wara & Wright, 1964; Wright & Nybakken, 2007), by mounting a video camera in the inter-tidal (Burrows, Kawai, & Hughes, 1999; Miller, 2007; Robles, Alvarado, & Desharnais, 2001), and by listening to and recording rasps of gastropod radulae on surfaces (Kitting, 1979).

Timing of foraging by inter-tidal animals depends on their responses to environmental stresses at low tide, their resistance to dislodgement by waves at high tide and predation pressures that may change over the diel or tidal cycle. During high tide, incoming waves typically reduce activity of many sedentary invertebrates, such as seastars, sea urchins, some snails and some limpets, (Dayton, 1985; Menge, 1978; Miller, 1974; Pardo & Johnson, 2006; Wright & Nybakken, 2007). Other more mobile or firmly attached species typically increase activity during high tide, such as hermit crabs, brachyuran crabs, lobsters, fishes, mussels, some snails and some limpets (Hunter & Naylor, 1993; Morgan, 2007; Palmer, 1974; Robles et al., 2001; Silva et al., 2010). During low tide, inter-tidal invertebrates inhabiting exposed rock surfaces generally avoid desiccation and thermal stress by seeking shelter and decreasing activity (Garrity, 1984; Jones & Boulding, 1999; Marchetti & Geller, 1987). These conditions are less stressful in tidepools, so animals may actually utilize these wave-free periods to forage. The tidal cycle is superimposed onto the diel cycle, which exposes animals to the sun and warmth during the day and colder conditions at night. Further, daytime low tides expose organisms to visual aerial predators (e.g. birds), daytime high tides expose them to visual aquatic predators (e.g. fish), and nighttime exposes them to nocturnal predators at high and low tides (e.g. crabs and octopi). Thus, inter-tidal invertebrates should adjust their activities cyclically to minimize physiological stress, dislodgement and predation. However nearly all inter-tidal studies are conducted during daytime low tides, which is just one phase of this complex dual cycle.

To remedy one aspect of this gap in knowledge, we investigated the behavior of the black turban snail, *Tegula funebralis* (formerly *Chlorostoma funebralis* Bouchet & Rosenberg, 2015), during the daytime at low, flood and high tide. We conducted our investigations in Horseshoe Cove, which is adjacent to the Bodega Marine Laboratory in Northern California, USA (38°19′00.6″N, 123°04′15.8″W). *Tegula funebralis* occurs in high densities in the inter-tidal zone of rocky shores along the west of North America from Vancouver Island to Baja California where it grazes on microalgae and macroalgae (Ricketts, Calvin, Hedgpeth, & Phillips, 1985). *Tegula funebralis* is very tolerant of thermal stress and desiccation at low tide (Tomanek & Somero, 1999). The only direct observations of *T. funebralis* at high tide revealed that densities were greatest atop rocks at night and they declined in bright moonlight and large swell (Wara & Wright, 1964), and no observations of snails inhabiting tidepools throughout the tidal cycle have been documented.

To assess snail activity throughout the tidal cycle, we designed and fabricated two underwater camera mounts to deploy a digital underwater video camera in tidepools during low, flood and high tides. We used a nearby weather station to assess how temperature (air and seawater) and wave height affected snail activity during our camera deployments. We also deployed a depth and temperature logger in the tidepools (although not during camera deployment) for days at a time to measure the variation in water temperature in the tidepool microhabitats and to assess probable wave exposure over the tidal cycle.

2 | MATERIAL AND METHODS

2.1 | Video recordings

We used a GoPro® Hero 2 (www.GoPro.com) high-definition digital video camera to capture changes in behavior of the common herbivorous snail *T. funebralis* with tidal phase or daily weather conditions. We filmed snails in rocky inter-tidal tidepools during low, flood and high tides 10 times on nine dates between 25 May and 6 August 2012. Due to limited camera battery life (~4 hr), we were unable to capture ebb tides. We continuously recorded snail movements in three tidepools (6.402, 0.662 and 0.260 m^2 surface area) during the daytime as nighttime illumination may have altered snail behavior. Shore levels of the three tidepools were 1.37, 1.37 and 1.14 m above mean lower low water, which we determined with surveying equipment and United States Geological Survey geodetic benchmarks. A total of 29.5 hr of recordings was taken, ranging from 73 to 212 min and averaging 180 min. We tracked 198 snails, with 10–29 snails observed during each deployment. An example video at 20× speed is included in Appendix S1.

The GoPro digital video camera is affordable, rugged and versatile making it ideal for deployments in the wave-exposed rocky inter-tidal environment. We placed the camera in the stock dive housing and one modified using the Snake River Prototyping BlurFix Lens kit (http://www.snakeriverprototyping.com). Desiccant strips were installed in the housing to prevent condensation from forming while recording. The camera has a 170° wide-angle lens, 11-megapixel resolution and a small image sensor, which creates a large depth of field, causing all objects to be in focus. We recorded high-definition video (1,920 × 1,080 pixels) and used the optional GoPro battery Bacpac (www.GoPro.com) to extend battery life.

Depending on the topography of the tidepool, we deployed cameras in two ways to film snail activity on vertical rock surfaces inside tidepools just below the waterline (see Appendix S2 and Figures S1–S4 therein for design and fabrication of both camera mounts). The camera was deployed above one steep-sided tidepool using an inverted tripod design (Figure 1a). The tripod mount could be raised or lowered and oriented at any angle, making it more versatile for deep or irregular tidepools. The other two tidepools were larger and had flat surfaces, so we used a simpler detachable stainless steel plate mount to fasten the camera to the bottom of each tidepool (Figure 1b). Both camera mounts had to withstand direct impacts by large waves on the windy, wave-exposed Northern California coast. The camera was situated 0.25–1 m from the target (Figure 1c), although longer or shorter distances could be used depending on the size of organisms and clarity of the water. An object of known size was placed on the rock surface in the center of the field of view at the start of each video to standardize our distance measurements during video analysis.

2.2 | Image analyses

We used FINAL CUT PRO X software (Apple Inc., http://www.apple.com/final-cut-pro) to increase the video speed 20× and convert videos

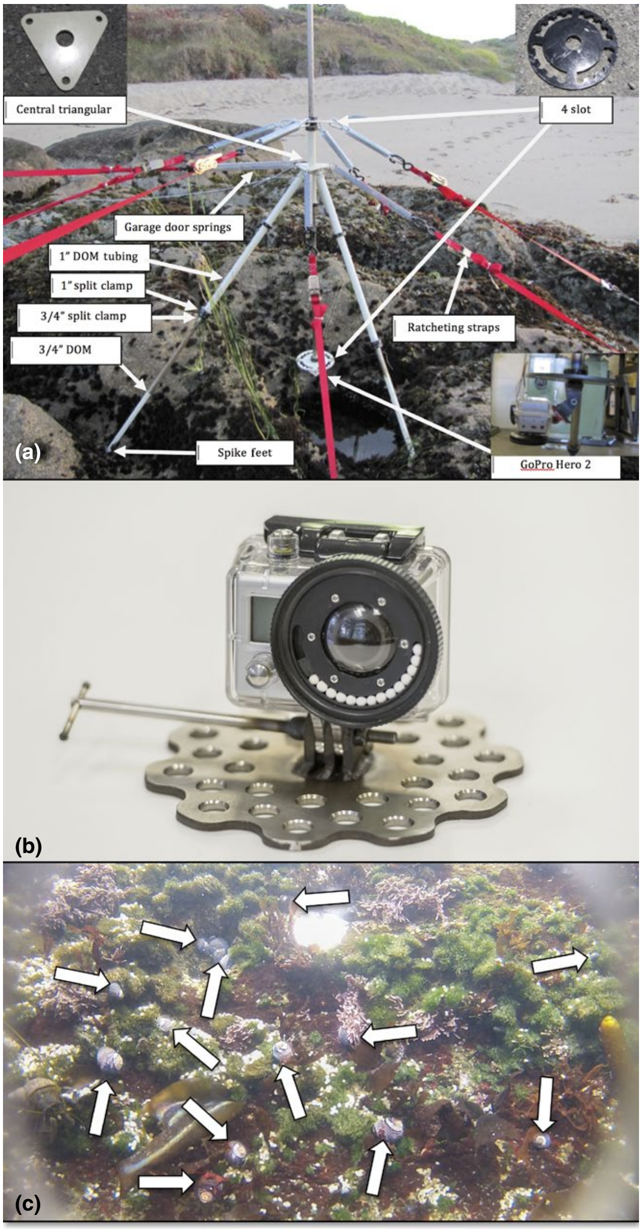

FIGURE 1 The (a) tripod mount and (b) bottom mount for a digital video camera used to record movement in tidepools at Horseshoe Cove, California, between 25 May and 6 August 2012. The camera on the tripod mount was submerged in the tidepool using a telescoping arm during deployment to capture the vertical wall of the steep-sided tidepool. See Appendix S2 and Figures S1–S4 therein for details on mount designs, components and fabrication. A still frame of a video (c) shows the underwater view of *Tegula funebralis* in an experimental tidepool

to image sequences. Then we imported images at 20-s intervals into IMAGEJ software as a stack (Rasband, 1997-2017). To track snail movements, we assigned numbers to each individual snail and manually tracked them between frames using the Manual Tracking plugin for IMAGEJ (https://imagej.nih.gov/ij/plugins/track/track.html) to determine their xy co-ordinates in cm. As snails were very abundant and we observed that handling them increased their movement (Gravem & Morgan, 2016), we decided not to mark individuals. Thus it is possible that some snails may have recurred on different days. However, this was likely rare because they were abundant, mobile and videos were taken days to weeks apart. To quantify overall speed and any movement upward or downward on shore, we calculated snail velocity and vertical velocity in cm/min for each 20-s interval as: velocity = $3 \times \sqrt{[(Y_t - Y_{t-1})^2 + (X_t - X_{t-1})^2]}$; vertical velocity = $3 \times (Y_t - Y_{t-1})$. To document zig-zagging and other feeding behaviors (Norton, Hawkins, Manley, Williams, & Watson, 1990), we calculated turning angle for each 20-s frame using R software (R Core Team, 2013) and the ltraj function in the ADEHABITATLT package (Calenge, 2006). Snail turning angle may indicate whether snails were foraging as indicated by zig-zagging or in transit as indicated by straight trajectories (Swingland & Greenwood, 1983). Turning angle was measured and graphed as positive for clockwise turns and negative for counter-clockwise turns. For analyses we used the absolute value of the turning angle so that low numbers were straight trajectories and large numbers were sharply angled trajectories. We noted only one occurrence of snail dislodgement. Foraging on drift algae would cause snails to stop moving while feeding and alter our interpretation of movement data, but this was not observed.

2.3 | Stresses over the tidal cycle

We assigned each video frame to low, flood and high tidal phases by first determining what time the tide should cover each tidepool based on its shore level using tide tables at 1-min resolution (http://tbone.biol.sc.edu/tide). This was the “predicted submergence”. From the animal’s point of view, flood tide begins before predicted submergence as the first wave peaks hit the tidepool and continues after the predicted submergence as wave troughs expose the tidepool. Thus, we defined flood tide as the 35 min before and after the predicted submergence. We chose 35 min based on our observation that bubbles from incoming waves always occurred in videos within the period 35 min before and after the predicted submergence. Changing wave heights during the videos likely extended or contracted the length of flood tide, but all videos were taken on days of fairly small significant wave height (mean daily significant wave height: 0.77–3.02 m.)

To determine (i) if ±35 min around predicted submergence was an appropriate time span for flood tide and to (ii) determine the potential wave and temperature stresses the snails may have experienced during the videos, we deployed a temperature and depth logger (HOBO U-20 Onset corporation) sequentially in each of the three tidepools for 5–7 days between 1 and 20 August 2013 and set recordings to 1-min intervals (Figure 2). Although these logger deployments were 1 year after the snail videos were taken, we deployed them during the same season (summer), in the same tidepools and at the exact locations of the video cameras. In addition, dates of video and logger deployments had similar ranges of mean daily swell heights (0.77–3.02 and 0.63–2.13 m, respectively), air temperatures (8.8–12.3 and 10.8–13.5°C, respectively) and water temperatures (8.6–11.3 and 9.9–12.6°C, respectively; data from http://www.ndbc.noaa.gov/accessed through the UC Davis Bodega Ocean Observing Node http://bml.ucdavis.edu/boon).

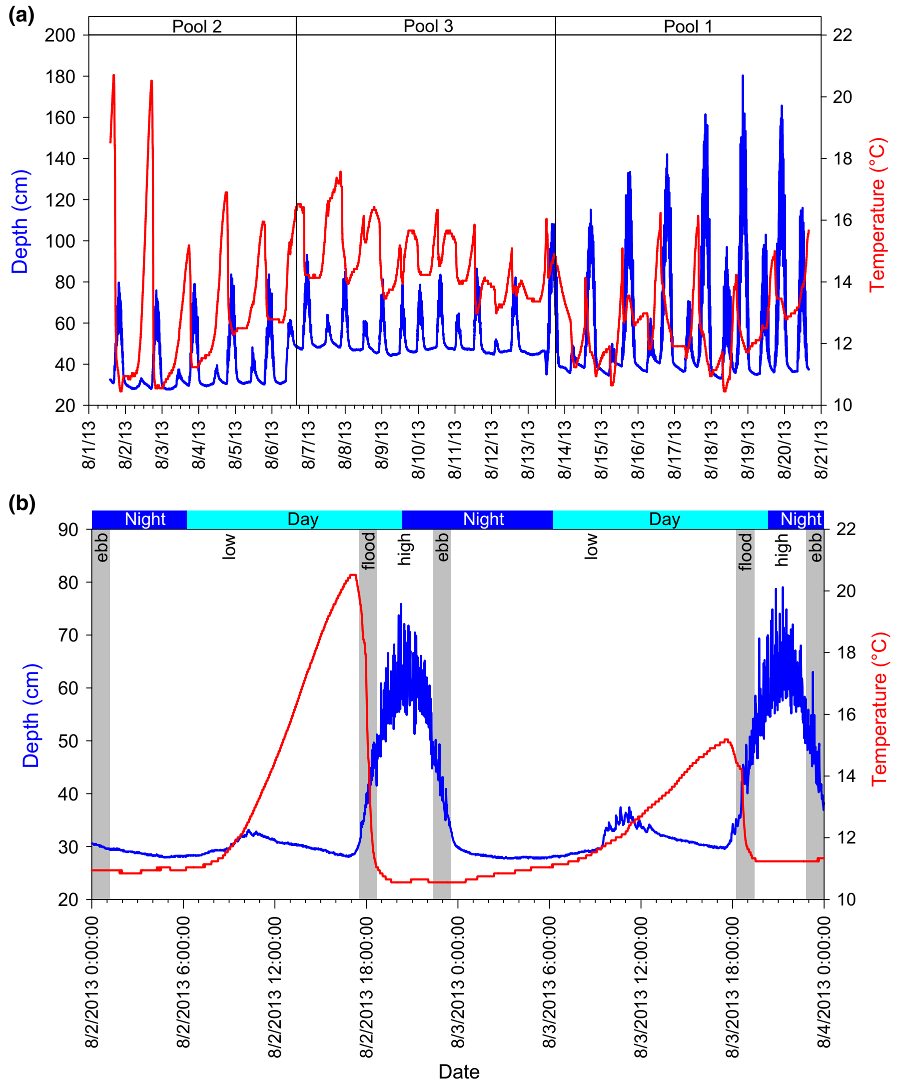

FIGURE 2 Water depths and water temperatures inside three experimental tidepools at the depth of the video cameras for 3 weeks (a) in summer 2013. Panel (b) zooms in on 2 days (Aug 2 and 3 2013) to illustrate the distinction between low, flood, high and ebb tides. The increasingly warm temperatures and shallow stable depth coincide with low tide. The sudden drops in temperature as depth increased indicates flood tide, which we defined as predicted submergence ±35 min using tide tables. Low stable temperatures and deep fluctuating depth indicate high tide. Decreasing depth but stable low temperature indicates ebb tide, which we defined as predicted emergence ±35 min using tide tables. The deployments in the tidepools happened to coincide with some very warm days (left side of (a)) and some days with fairly large waves (right side of (a))

While we cannot know what the actual temperature and wave conditions were during the videos, we can gain a view of the typical environmental fluctuations the snails experienced in each tidepool. Admittedly, the magnitudes of the fluctuations were likely different on the dates of video and logger deployments, but the general patterns among tidal phases were likely consistent. Most importantly, the logger deployments provide an estimation of the length of flood tide by showing how long the transition between low and high tide lasted. We predicted that low tide would show increasingly warm temperatures and low wave action (indicated by stable water depth), flood tide would show a sharp drop in water temperature and high wave action (indicated by deepening, fluctuating water depth), and high tide would have low stable water temperatures and high wave action (indicated by consistently deep and fluctuating water depth).

2.4 | Weather data

Although we have no direct measures of temperature and wave conditions that snails experienced at the scale of the tidepools during the videos, we used nearby weather stations to measure local weather conditions on the dates the videos were recorded. We obtained data for significant wave height (mean height of the highest ⅓ of waves), from a mooring located 1 km offshore, water temperature from a seawater intake pipe <50 m away at 4 m depth and air temperature from weather instruments <100 m away from the tidepools (Bodega Ocean Observing Node http://bml.ucdavis.edu/boon). The proximity of these instruments renders the majority of the weather data very accurate (i.e. the water temperature during high tide, air temperature, and among-day differences in wave exposure). However, the local scale topography could have somewhat altered the wave heights the tidepools were exposed to, and the size of the tidepools and length of emersion likely affected how warm the tidepools became during low tide. No rainfall occurred during the study. We then ran correlations between mean snail velocity (cm/min) and mean daily (i) significant wave height, (ii) air temperature and (iii) water temperature. As snail velocity was negatively correlated with wave height and positively correlated with both air and water temperatures (Figure 3, see Results for details), we then included these as co-variates in further analyses on tidal phase.

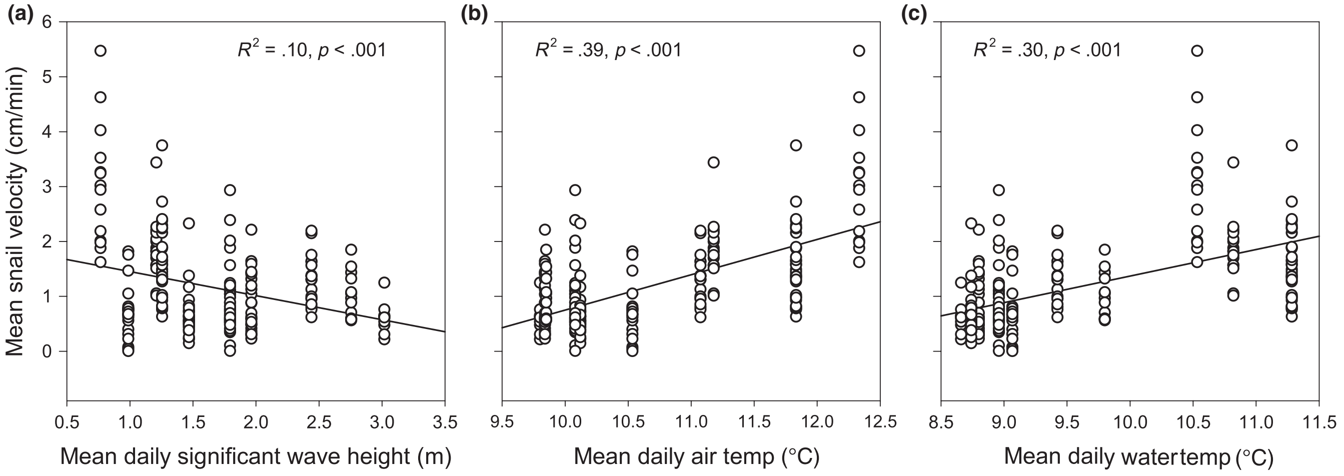

FIGURE 3 Correlations between mean velocities of individual *Tegula funebralis* from videos and mean (a) wave height, (b) air temperatures and (c) seawater temperatures taken at a nearby mooring during each video deployment

2.5 | Statistical analyses

We tested the effects of significant wave height, air temperature, water temperature and tidal phase (low, flood, high) on mean snail velocities, mean vertical velocities and mean absolute turning angle conducting analyses of co-variance (ANCOVAs) using the general linear model platform in JMP PRO 12 software (SAS Institute) followed by Tukey's post-hoc analyses. We used adjusted sums of squares (Type III) to test the importance of each factor having already considered the others. No transformations were necessary to meet model assumptions of normality and homogeneity of variance. Because the strong effects of weather on snail movement masked the effects of tidal phase in the figures, we ran identical ANCOVA models but removed tidal phase, and then used the model residuals as the response variable for our graphs. To further investigate whether the distributions of snail movements (residual velocity, residual vertical velocity and absolute turning angle) varied among tidal phases, we ran Kolmogorov–Smirnov tests between each of the three phases using the ks.test function in R.

3 | RESULTS

3.1 | Stresses over the tidal cycle

Overlays of temperature and depth fluctuations (Figure 2) in the tidepools demonstrated that our estimation of flood tide as 35 min around predicted submergence typically captured both the increase in water depth (high wave stress) and sudden drop in temperature as waves first washed over tidepools. Further, the end of flood tide coincided with a stabilization of water temperature indicating full mixing of tidepool volume with incoming seawater. Low tide typically exhibited an increase in water temperature during the daytime and very little water depth changes indicating little wave action. High tide typically showed fluctuating but high mean water depths, indicating high wave action, and low stable water temperatures.

3.2 | Weather conditions and snail behavior

As expected, mean snail velocity and significant wave height (Figure 3a; $r^2 = 0.10$, $F_{(1,226)} = 24.57$, $p < .001$, velocity = 1.891–0.438 × significant wave height) tended to be negatively related. Snail velocity was positively related to air (Figure 3b; $r^2 = 0.39$, $F_{(1,226)} = 147.14$, $p < .001$, velocity = −5.678 + 0.643 × air temperature) and water temperatures (Figure 3c; $r^2 = 0.30$, $F_{(1,226)} = 98.95$, $p < .001$, velocity = −3.458 + 0.483 × water temperature).

When testing each weather variable having considered the effects of the other two weather variables and tidal phase, we found a similar strong positive correlation of air temperature with mean snail velocity (Table 1; ANCOVA: $r^2 = 0.45$). However, we did not detect a relationship with wave height, but we detected a negative relationship with water temperature. This was surprising given the trends in Figure 3, and we suspect that tracking behavior over a larger range of wave heights and water temperatures would yield more discernible patterns. Snail vertical velocity was not correlated with any of the weather conditions (Table 1, ANCOVA: $r^2 = 0.03$).

3.3 | Tidal phase and snail behavior

Having already considered the three weather conditions, snails moved faster during low tide than flood or high tide (Figure 4a; Table 1; ANCOVA: $r^2 = 0.45$). The residual snail velocity distribution was also shifted toward faster velocities at low than flood or high tide (Figure 4b; Kolmogorov–Smirnov: Low vs. Flood: D = 0.35, $p < .001$, Low vs. High: D = 0.33, $p < .001$). Although tidal phase did not affect snail vertical velocity after having considered the effects of the three weather conditions (Figure 4c; Table 1; ANCOVA: $r^2 = 0.03$), the residual vertical velocity distributions indicated more downward movement during flood tide compared to low tide (Figure 4d; Kolmogorov–Smirnov: Low vs. Flood: D = 0.26, $p = .017$).

TABLE 1 Analyses of covariance using adjusted sums of squares (SS) testing the effects of wave height, air temperature, water temperature and tidal phase on mean velocity and vertical velocity of *Tegula funebralis*

	Mean velocity				Mean vertical velocity				Mean turning angle			
Term	*df*	SS	F	*p*	*df*	SS	F	*p*	*df*	SS	F	*p*
Significant wave height	1	<0.01	<0.01	.992	1	<0.01	0.03	.861	1	3,028	6.76	.010
Air temperature	1	18.56	47.81	<.001	1	0.62	1.98	.161	1	938	2.09	.149
Water temperature	1	1.83	4.70	.031	1	0.23	0.73	.393	1	278	0.62	.431
Tidal phase	2	8.65	11.13	<.001	2	0.83	1.34	.264	2	797	0.89	.412

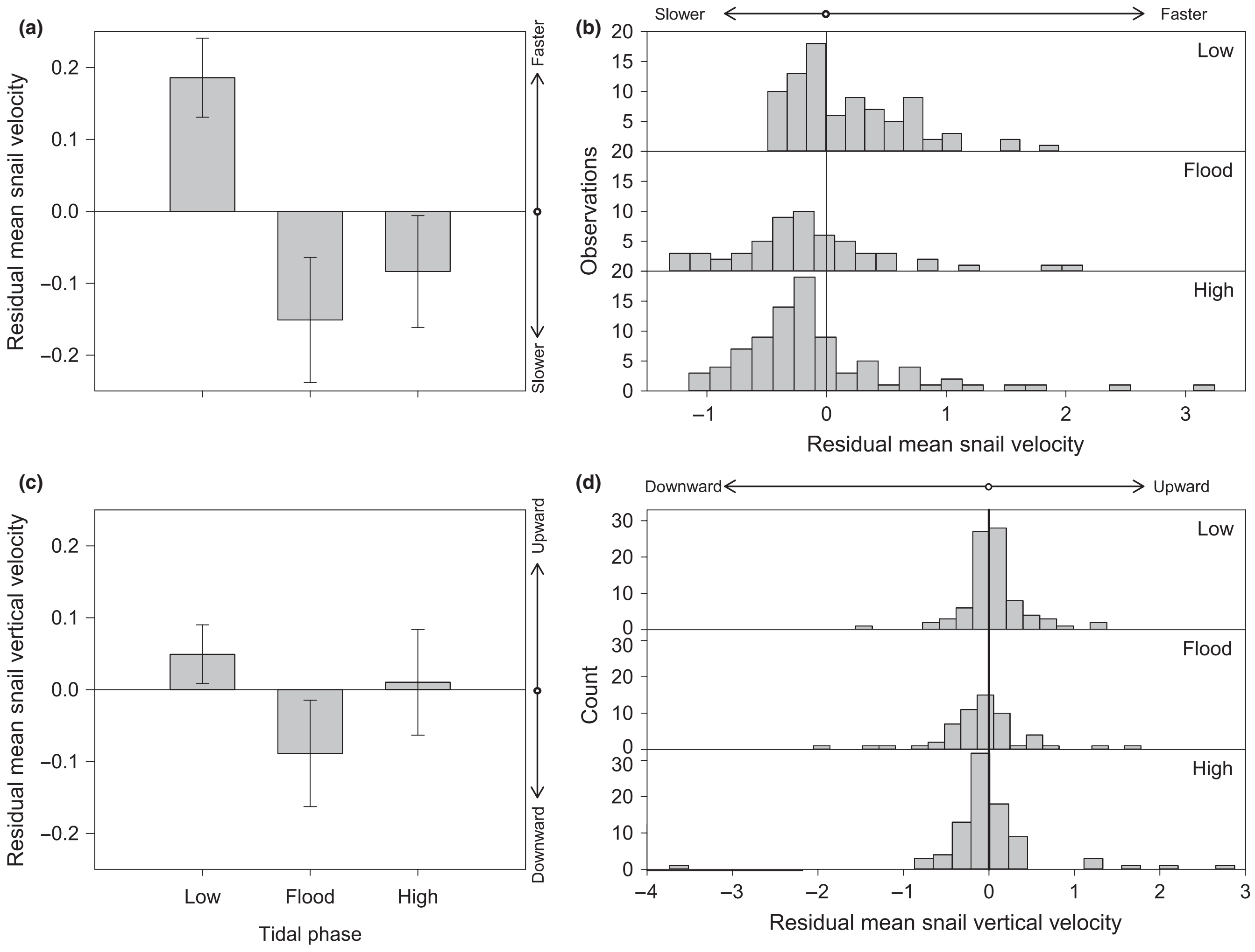

FIGURE 4 The means (a & c) and distributions (b & d) of individual *Tegula funebralis* velocities (a & b) and mean vertical velocities (c & d) among the tidal phases having already considered the effects of wave height, air temperature and water temperature on snail velocity. In (a) and (b), values greater (lower) than zero indicate faster (slower) than predicted velocities. In (c) and (d), values greater (lower) than zero indicate more upward (downward) movement than predicted

3.4 | Turning angle and snail trajectories

Mean snail turning angles were not affected by tidal phase (Figure 5; Table 1; Kolmogorov–Smirnov: D < 0.10, $p > .771$). Wave height was positively correlated with turning angle, but overall model fit was very low, so this result is not likely ecologically relevant (Table 1; ANCOVA: $r^2 = 0.04$).

By comparing snail movements in xy co-ordinate space (Figure 6a), it was clear that snails generally make clustered sharp turning angles with occasional short bursts of straight movement, indicating foraging,

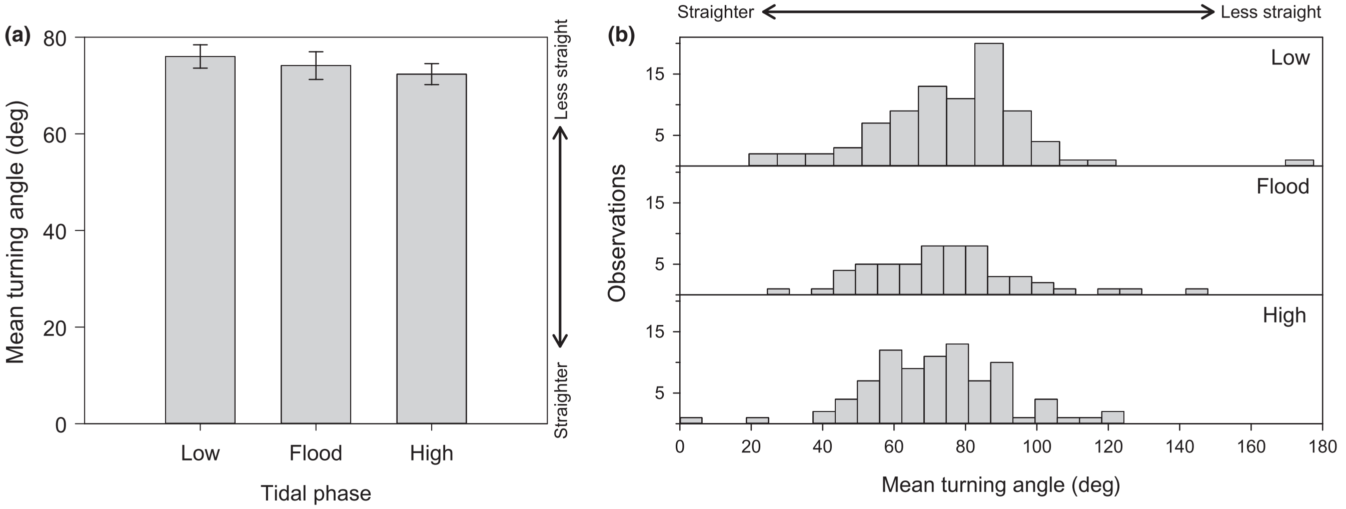

FIGURE 5 The mean (a) and distribution (b) of the absolute turning angles by *Tegula funebralis* among tidal phases. 0° indicates straight movement, 90° indicates a perpendicular turn and 180° indicates a reversal in direction

followed by relocation, then foraging (Swingland & Greenwood, 1983). By investigating turning angle (Figure 6b), it is clear that snails were repeatedly alternating between clockwise (positive values) and counterclockwise (negative values) sharp turns, again with occasional straight trajectories (near-zero values). Other snails exhibited generally straight paths, which indicate directed relocation or fleeing from a stimulus (Swingland & Greenwood, 1983), although these behaviors were much less common.

4 | DISCUSSION

4.1 | Increased activity at low tide and on warm days

Increased velocity during daytime low tide suggests that *T. funebralis* was active and perhaps foraging (Swingland & Greenwood, 1983). Similarly, we observed increased snail activity on days with warmer air and probably water temperatures. Although we did not measure tidepool water temperature directly during our study, the maximum daily tidepool water temperatures during low tide 1 year later were between 14.2 and 20.7°C compared to maxima between 11.0 and 16.6°C during high tide. Therefore, warmer tidepool water temperatures during low tides in our study were likely similar and promoted increased snail activity. Hence, increasingly warm water temperatures as low tide progressed and on warm days likely promoted grazing. In a previous study, feeding rates of *T. funebralis* were maximal at moderately warm water temperatures (15°C) and activity levels increased as water temperature rose to 23°C in the laboratory (Yee & Murray, 2004). Similarly, the thermal optimum, as measured by turning frequency in the laboratory, was around 20°C (Tepler, Mach, & Denny, 2011). Furthermore, heart rate increased with temperature until about 31°C in *T. funebralis*, after which it decreased rapidly (Stenseng, Braby, & Somero, 2005), as is typical when temperature extremes are reached. These studies corroborate our finding that snails are more active during warmer low tides compared to colder flood and high tides. However, they were not conducted in the same geographic area and local adaptation could result in slightly different physiological responses by our experimental snails (Gleason & Burton, 2013). Increased activity during warmer temperatures is a typical feature of ectotherms as their metabolism and muscle activity increases with temperature (Huey & Stevenson, 1979). Temperatures during our study apparently did not approach the extreme temperatures that are stressful for *T. funebralis* (Stenseng et al., 2005; Tomanek & Somero, 1999), because their activity levels did not decrease on the warmest days. We also saw no evidence of stress in the videos, although during heat waves at this site we have observed snails in tidepools upside down with their opercula closed. Our finding of increased activity during low tide and warm days is somewhat surprising as warm low tides are generally thought to be quite stressful for inter-tidal organisms. However, tidepools likely are a respite from this stress on most low tides (Garrity, 1984). Indeed, the lack of upward movement at low tide suggests that snails may have remained in tidepools to avoid much higher temperatures and desiccation outside of them. These stresses can be lethal, and *T. funebralis* and other gastropods outside of tidepools reduce movement and feeding while seeking refuge during low tide (Jones & Boulding, 1999; Marchetti & Geller, 1987; Wara & Wright, 1964; Yamane & Gilman, 2009). Thus, emersed and immersed *T. funebralis* may exhibit very different activity patterns over the tidal cycle.

4.2 | Decreased activity at flood and high tide and on wavy days

Snails in wave-exposed tidepools decreased activity during flood and high tide compared to low tide, and appeared to move downward at flood tide. Further, snail activity tended to decrease on days with larger waves. These behaviors indicate that snails may mitigate the risk of dislodgement from increasingly frequent and energetic waves during flood tide (Castilla, Steinmiller, & Pacheco, 1998). Strong turbulence

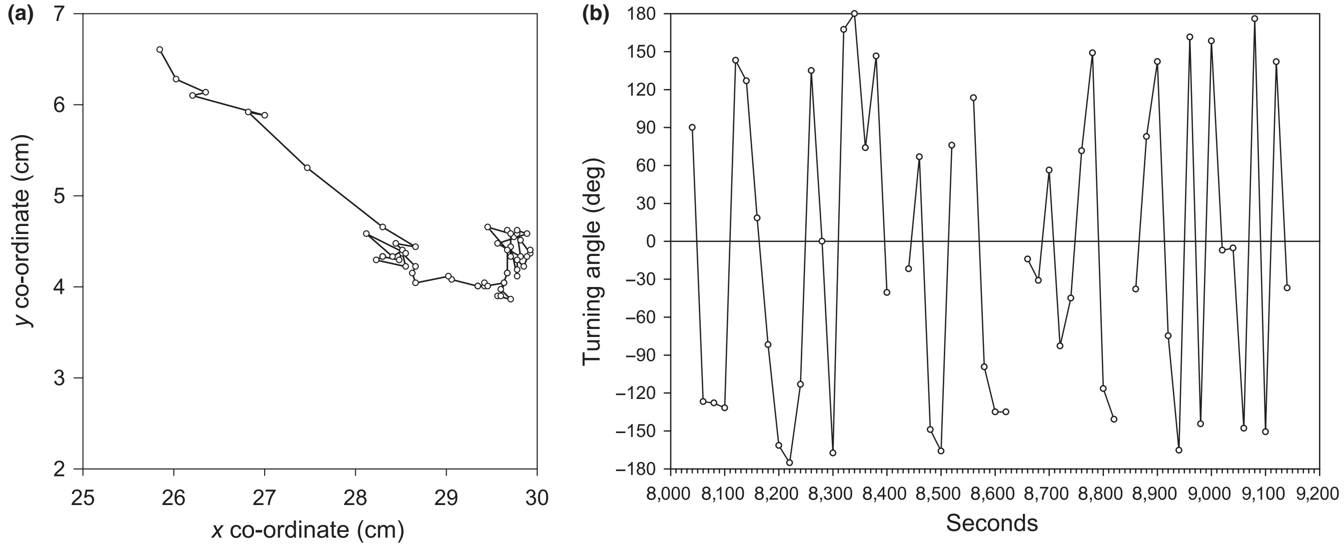

FIGURE 6 An example of an individual *Tegula funebralis* (a) trajectory and (b) turning angles during a low tide on 25 May 2012. Positive and negative values of turning angles in (b) indicate clockwise and counter-clockwise turns, respectively, and 0° indicates straight paths

may dislodge and kill *T. funebralis*, as it does periwinkle snails and limpets (Chapperon & Seuront, 2009; Denny & Blanchette, 2000; Miller, O'Donnell, & Mach, 2007; Pardo & Johnson, 2006; Wright & Nybakken, 2007). Larger waves prevent inter-tidal snails from returning to the upper inter-tidal zone after dislodgment (Miller et al., 2007), and they tend to seek shelter from waves during high tide (Pardo & Johnson, 2006). Thus, it is not surprising that *T. funebralis* decreased activity during flood and high tide and wavy days.

In laboratory studies, *T. funebralis* exhibited a pulse in downward movement when exposed to turbulence (Overholser, 1964), so the snails in our study may have exhibited a similar behavior by moving downward at flood tide. This is in contrast to an other study that has shown that tropical gastropods show a pulse in activity during flood tide on a sheltered rocky inter-tidal shore, which was attributed to decreased physiological stress coupled with temporarily low fish predation (Garrity, 1984). We did not find a pulse in velocity at flood tide, perhaps because the wave forces at this exposed site are much larger and the temperature stresses are lower than in protected tropical waters.

The observed patterns in *T. funebralis* behavior may have cascading effects on the inter-tidal community. *Tegula funebralis* primarily grazes benthic diatoms and some species of macroalgae (Aquilino, Coulbourne, & Stachowicz, 2012; Thornber, Jones, & Stachowicz, 2008), and it can affect both biomass and community structure of tidepool macroalgae by changing succession trajectories (Nielsen, 2001). Grazing by *T. funebralis* in tidepools also slows the growth of both micro- and macroalgae (Gravem, 2015). In other inter-tidal systems, gastropod density is negatively correlated with wave height, affecting the abundance and community structure of algae (Lauzon-Guay & Scheibling, 2009). Further, limpets assess when the risk of dislodgement is low enough to graze, affecting the abundance and community structure of algae (Wright & Nybakken, 2007). Overall, rhythms in foraging and other activities by inter-tidal species can affect the abundance and composition of species in tidepools and the exposed areas around them (Morgan, 2007).

4.3 | Foraging trajectories

Snails exhibited foraging trajectories by moving in a zig-zagging motion for minutes at a time then exhibiting occasional short linear movements followed again by zig-zagging. This type of trajectory is a typical foraging trajectory for grazing animals (Swingland & Greenwood, 1983). However, we did not observe a difference in mean turning angle or change in the turning angle frequency distributions among tidal phases or any strong correlation between turning angle and weather conditions. Therefore, snails may be foraging at all times, but warmer temperatures during warm days or low tide simply increase their velocity, presumably allowing them to graze a larger area.

5 | CONCLUSIONS

Tegula funebralis in tidepools suppressed activity and perhaps moved downward during daytime flood tide, and larger waves may have reduced activity. Increased activity during low tides and warm days suggests they utilize wave-free and warm periods to graze, probably in part because their metabolism increases. We developed an inexpensive, safe, and effective method for observing organisms during high tide, which is a gap in our understanding of exposed rocky shore communities. Although we focused on just one of the species recorded, the behaviors of other species were clearly visible, including abundant hermit crabs, limpets and sculpins. We also focused on velocities and trajectories over the tidal cycle, but many other behaviors could be observed both inside and outside tidepools using our methods, such as foraging, homing, mating, spawning, hatching and intra-specific and inter-specific interactions between predator and prey and competitors. We restricted our observations to daytime during spring and summer months, and further exploration of seasonal or diel changes in behavior are logical next steps. Our techniques are easily applied, opening the door to widespread investigations of rocky inter-tidal communities during the "other half" of the tidal cycle.

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