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MOVEMENT AND MICROHABITAT USE OF INTERTIDAL SNAILS DURING ACTIVE SUMMER MONTHS

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MOVEMENT AND MICROHABITAT USE OF INTERTIDAL SNAILS DURING ACTIVE SUMMER MONTHS

by

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ABSTRACT

Understanding how animals move provides insight into biological interactions between trophic levels, behavioural ecology of species, population dynamics, and biodiversity conservation in a changing climate. Habitat selection is a way for snails to avoid predators and unsuitable environmental conditions, locate food, and find mates. Using radio frequency identification technology we determined: 1) if snail motility was affected by a passive integrated transponder tag, 2) the extent of snail dispersal, daily distance travelled, and directionality over the active summer period, 3) the frequency in which intertidal gastropods *Nucella lamellosa*, a predator, and *Lirabuccinum dirum*, a scavenger, use different microhabitats at low tide, 4) if snail movement or use of sheltered microhabitats was affected by tidal amplitude, daily maximum air temperature, or precipitation, and 5) if body condition was sacrificed for movement. *Nucella lamellosa* and *Lirabuccinum dirum* differed significantly in their dispersal, directionality, microhabitat use, and exposure at low tide, but did not differ in their daily distance travelled. Snail movement and exposure were not influenced by tidal amplitude, maximum daily air temperature, or total daily precipitation. Daily distance travelled did not impact snail growth over the summer, but there was a positive relationship between *L. dirum* dispersal and growth. This study found that *N. lamellosa* and *L. dirum* have inherently different patterns of movement and microhabitat use, perhaps due to differences in food source, but likely due to a combination of abiotic and biotic interactions.

Thesis Supervisor: Dr. Louis Gosselin

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INTRODUCTION

Motility in animals is important because it provides insight into biological interactions between trophic levels (Rochette and Dill 2000), behavioural ecology of species (Owen-Smith et al. 2010), population dynamics (Morales et al. 2010), and biodiversity conservation in a changing climate (Franklin 2010). Studying daily movement and dispersal can elucidate the roles that energy allocation, feeding preference, predation, and microhabitat use play in the ecology of intertidal invertebrates.

Intertidal species are faced with the evolutionary decision to adapt behaviourally and physiologically to either obtain food from high intertidal elevations or compete with the multitude of species in the lower regions of the intertidal zone. While competition for resources is lessened in the upper part of the intertidal zone, physiological stress, especially desiccation, peaks in that zone as higher parts of the intertidal zone receive more sun exposure, warmer summer temperature, and drier conditions than lower parts (Harley 2008; Hayford et al. 2018). For invertebrates with extensive locomotive abilities, daily movement between the upper and lower intertidal zone grants them access to resources not available to species restricted to lower elevations (Hayford 2018). Slow locomotion restricts the use of upper parts of the intertidal zone because of the risk imposed by desiccation, so slow-moving snails must remain in lower parts of the intertidal zone (Hayford et al 2018) unless they have evolved a high degree of physiological tolerance of desiccation, temperature extremes, and ultraviolet radiation.

Habitat selection is another way snails avoid predators and unsuitable environmental conditions, locate food, and find mates (Dill 1987; Jordan et al. 1997; Jones and Boulding 1999; Chapperon and Seuront 2013; Moisez et al. 2020). According to Jones and Boulding (1999) and Moisez et al. (2020), adult snails prefer topographically complex habitats, which allow individuals to avoid weather stress and predators. Selection of suitable habitats may be influenced by various abiotic and biotic factors, such as substrate temperature or predator and prey relationships, resulting in different preferred habitats for species with different ecologies (Moisez et al. 2020). Structurally complex microhabitats that provide cryptic spaces for motile invertebrates to hide are common in the intertidal zone of the west coast of British Columbia, and include filamentous algae, clusters of mussels, barnacles (Gosselin and Chia 1995), sand, empty shells (McLeod 2016), and bare rock

(Moisez et al. 2020). We hypothesize that snails seek microhabitats that provide protection from predators and desiccation, so should often be found hidden under available microhabitat features such as rocks, sand, or empty shells.

Although cryptic microhabitats provide protection and shelter from adverse conditions, long periods spent hiding in these microhabitats can result in adverse consequences. Hiding in topographically complex habitats allows snails to avoid stressors but limits the time they spend foraging and finding mates, forcing them to trade reproduction and self-maintenance for protection (Jones and Boulding 1999). Determining how often snails are hidden in cryptic microhabitats rather than in exposed positions will help us understand this trade off. Furthermore, by driving snails toward sites commonly used for reproduction, behaviours such as homing have evolved to facilitate resource allocation and mating (Chelazzi et al. 1990; Erlandsson et al. 1999; Fratini et al. 2001).

Members of the *Nucella* genus lack planktonic larvae and instead fertilization is internal, with females laying egg capsules in complex intertidal microhabitats (Marko 2004). In *Nucella ostrina*, it takes two to four months for juveniles to hatch and once they do, they travel less than 5 m from their initial position, even as adults (McLeod 2016). It is therefore crucial that mature snails select habitats for egg-laying that protects egg capsules and juveniles from desiccation and predators. Once hatched, juveniles crawl from their capsule to protective microhabitats to avoid predators and desiccation (Gosselin and Chia 1995). Ideal snail habitat must also provide food and resources for adults. Adult *Nucella* are predacious, and their primary food source are the barnacle *Balanus glandula* and the mussel *Mytilus trossulus*, nonmotile animals that live mostly at high intertidal elevations on the west coast of North America (Hayford et al. 2018). The intertidal snail *Lirabuccinum dirum,* however, is a scavenger (Neilsen and Gosselin 2011), and therefore relies on different food allocation mechanisms than *N. lamellosa*. As a scavenger, *L. dirum* depends on the abundance of prey, the abundance of predators of that prey, and the mortality rate of these prey (Neilsen and Gosselin 2011). It is therefore of interest to monitor microhabitat use of *N. lamellosa* and *L. dirum* in the field to determine if adults of these species exhibit different microhabitat type preferences associated with their different foraging strategies. Specifically, we expect to find snails more often in microhabitats that contain their preferred food source.

Ectotherms can regulate their body temperature by exploiting the topographical complexity of their habitat (Bogert 1949). The rocky intertidal is one of the most stressful environments, subject to daily changes in tide height, ambient air temperature, and precipitation (Harley 2008). To understand how ectothermic organisms behave in response to changes in air temperature, we must consider whether movement and microhabitat selection are influenced by high summer temperatures (Kearney et al. 2009). Ectothermic animals have desiccation resistant behaviours such as movement into protective microhabitats that allow them to shelter during stressful conditions (Jones and Boulding 1999; Chapperon and Seuront 2010). Intertidal snails can actively select cooler microhabitats when the intertidal zone experiences high temperatures, and can move faster to avoid desiccation (Chapperon and Seuront 2010). These preferred microhabitats are often more sheltered from direct sunlight and cooler than exposed microhabitats (Chapperon and Seuront 2010). If *N. lamellosa* and *L. dirum* actively seek sheltered microhabitats for protection from desiccation and elevated temperature during low tides, then we expect their movement and use of cryptic microhabitats to increase during summertime periods of elevated air temperatures.

Demographic field studies of intertidal invertebrates have predominantly used mark-recapture techniques (Gibbons and Andrews 2004; Henry and Jarne 2007; Kovach and Tallmon 2010). This approach makes it possible to quantify differences in individual movement and survival and allows researchers to comparatively identify how individuals use microhabitats (Kovach and Tallmon 2010). Classically, researchers marked snail shells with paint, ink, or plastic numbered tags (Gosselin 1993; Gibbons and Andrews 2004; Henry and Jarne 2007). Limitations of the classic mark-recapture experimental method include the inefficiency of relocating small animals, the inability to locate individuals hidden in cryptic microhabitats and the need to disturb microhabitats to reveal hidden snails, the possible effects on life-history traits, and tag loss (Hale et al. 2012). It is also possible for tags to become broken or illegible due to environmental exposure, making data collection more tedious and less effective (Gibbons and Andrews 2007). Although radio frequency identification (RFID) technology has been used extensively in studies of vertebrates, it has only recently been incorporated into snail dispersal research (McLeod 2016; Hayford 2018). When determining which tagging method in mark-recapture studies is best, their impact on animal survival and life-history traits, tag retention rate, and detectability in field conditions must all be considered. Hale et al. (2012) suggested that RFID technology is superior to classic methods of visual tagging because there is lower impact on snail visibility to predators, better tag retention, and greater detectability. The ability to detect snails that would otherwise be hidden under different types of complex microhabitats is important, as we aim to infer the preferred microhabitats of *N. lamellosa* and *L. dirum*. Given that RFID makes it possible to locate snails that are not visible without disturbing the microhabitats, RFID was employed in this study.

The purpose of this study was to examine the movements and microhabitat use of two intertidal gastropods, *N. lamellosa* and *L. dirum*, in their natural habitat. Specifically, we aimed to determine: 1) if snail motility is affected by a passive integrated transponder (PIT) tag attached to their shell, and the effectiveness of RFID technology in studying intertidal snail behavior and ecology, 2) the extent of snail dispersal, daily distance travelled, and directionality over the active summer period, 3) the frequency in which *N. lamellosa* and *L. dirum* use natural microhabitats at low tide, 4) if snail movement or use of sheltered microhabitats are affected by tidal amplitude, daily maximum air temperature, or precipitation, and 5) if snail growth varies as a function of the extent of snail movement.

METHODS

Location and species used in study

This study examined two intertidal gastropod species, *Nucella lamellosa* and *Lirabuccinum dirum.* The study was carried out in Barkley Sound, on the west coast of Vancouver Island, and at the Bamfield Marine Science Centre. The location of the field experiment, as well as the source of all collected snails, was Grappler Inlet (48.83°N, -125.12°W). The site consists of a flat bench at an intertidal height of 1.3-1.6 m above mean lower low water, and is composed mainly of small rocks, pebbles, sand, and silt.

Effect of PIT tags on snail motility

An initial experiment was carried out in late June 2022 to determine if PIT tags attached to the shell affects the motility of these snail species. The tags selected for this study were 12 mm HDX PIT tags (Oregon RFID, Portland, USA), as these tags function well in marine habitats and have not been found to hinder motility in other intertidal snail species (McLeod 2016; Hayford et al. 2018). PIT tags were attached to the dorsal part of snail shells using Gorilla® Super Glue Gel (Fig. 1). The gel was allowed to harden in air for 2 h, then the snails were submerged in a tank with flowing seawater in the Bamfield Marine Science Center laboratory.

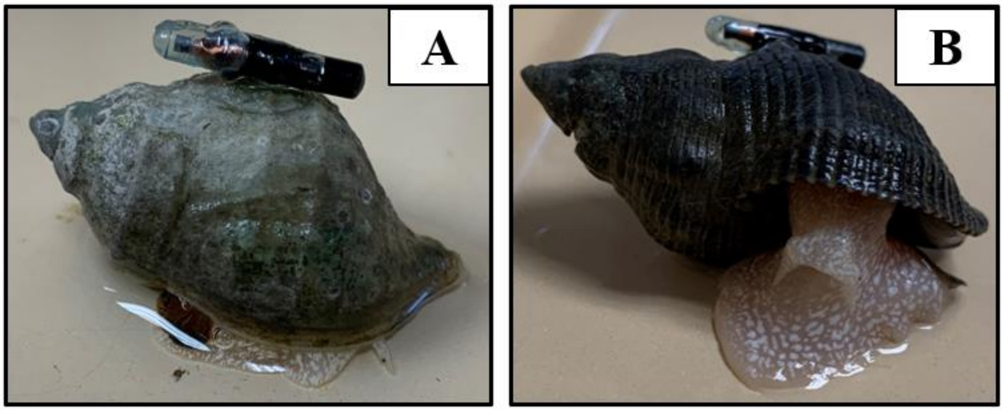

Figure 1. *Nucella lamellosa* (A) and *Lirabuccinum dirum* (B) with 12-mm HDX PIT tags glued to dorsal shell.

To determine if snail motility was affected by the presence of a PIT tag on their shell, the motility of 10 tagged snails of each species was then compared to the motility of 10 untagged snails of the same species. A 4 x 4 cm grid was drawn onto the underside of a clear, plastic tank placed inside a sea table. The tank was filled with flowing seawater and a video camera suspended 95 cm above the tank, facing the grid, was connected to a computer. Black curtains were hung around the sea table to block the view of external light and movements in the room, preventing disturbances that might affect snail behaviour (Fig. 2A). Each snail was placed inside the clear tank in the center of the grid (Fig. 2B). An individual 6 min video was recorded for each of the 40 tagged and untagged snails. Recordings started only after a snail began moving from its initial position on the bottom of the tank. Snail motility was analyzed, using the software OBS Studio, by measuring the total distance each snail moved, the distance dispersed from starting position to its position after 6 min, and the directionality of each snail using the grid. Directionality was calculated as total distance travelled divided by dispersal, where dispersal is the linear distance travelled by each snail.

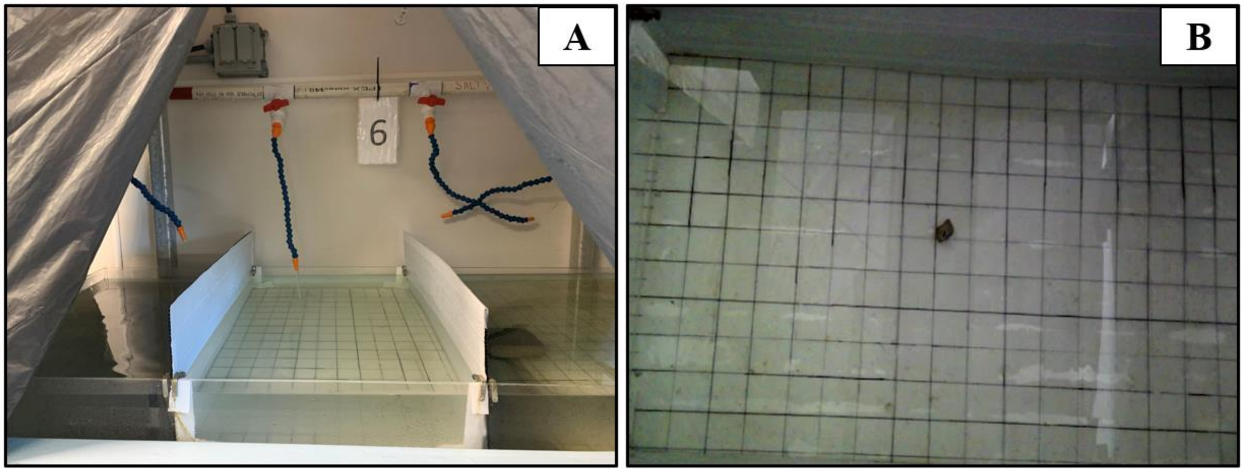

Figure 2. Motility experiment set up in a sea table (A). Videocam view of PIT tagged *N. lamellosa* placed on the center of the grid (B).

Movement of snails in the intertidal zone during active summer months

Use of RFID technology to locate snails in the field

From late June to mid August, the position of tagged snails at the Grappler Inlet site was repeatedly determined by triangulation, in which the distance of each snail was measured relative to three permanent locations at the margin of the field site. Each of the three triangulation locations (T1, T2, and T3) was marked by a screw drilled in a large rock or a rocky outcrop (Fig. 3). A total of 44 *N. lamellosa* and 44 *L. dirum* were collected from Grappler Inlet and transferred to the laboratory, and the body weight and length of each snail were recorded. A PIT tag was then attached to each snail so they could be repeatedly located in the field during the summer. On 17 June, 22 snails of each species were released at location 1, and on 18 June, 22 snails of each species were released at location 2 (Fig. 3). Snails were subsequently detected using a handheld RFID reader with detachable antenna that detected the PIT tag.

Once detected, the location of each snail was determined using triangulation, to an accuracy of ~2 cm. Given that intertidal snails may require a day or two to readjust to their environment after being transported (McLeod 2016), movement during the first 2 d after release were not used in the calculations of dispersal or distance travelled.

For the next 53-56 d, the position of each snail as well as the microhabitat occupied by the snail at low tide were recorded, searching for snails from location 1 and location 2 on alternate days (Fig.

3). This meant that tagged snails were detected every second day, tide permitting. On days when the low tide was higher than 1.3 m, most or all of the Grappler field site remained covered by water at low tide, and the RFID reader could not detect tagged snails. During these periods of 4-5 d, approximately every 2 weeks, movement and microhabitat data were not collected.

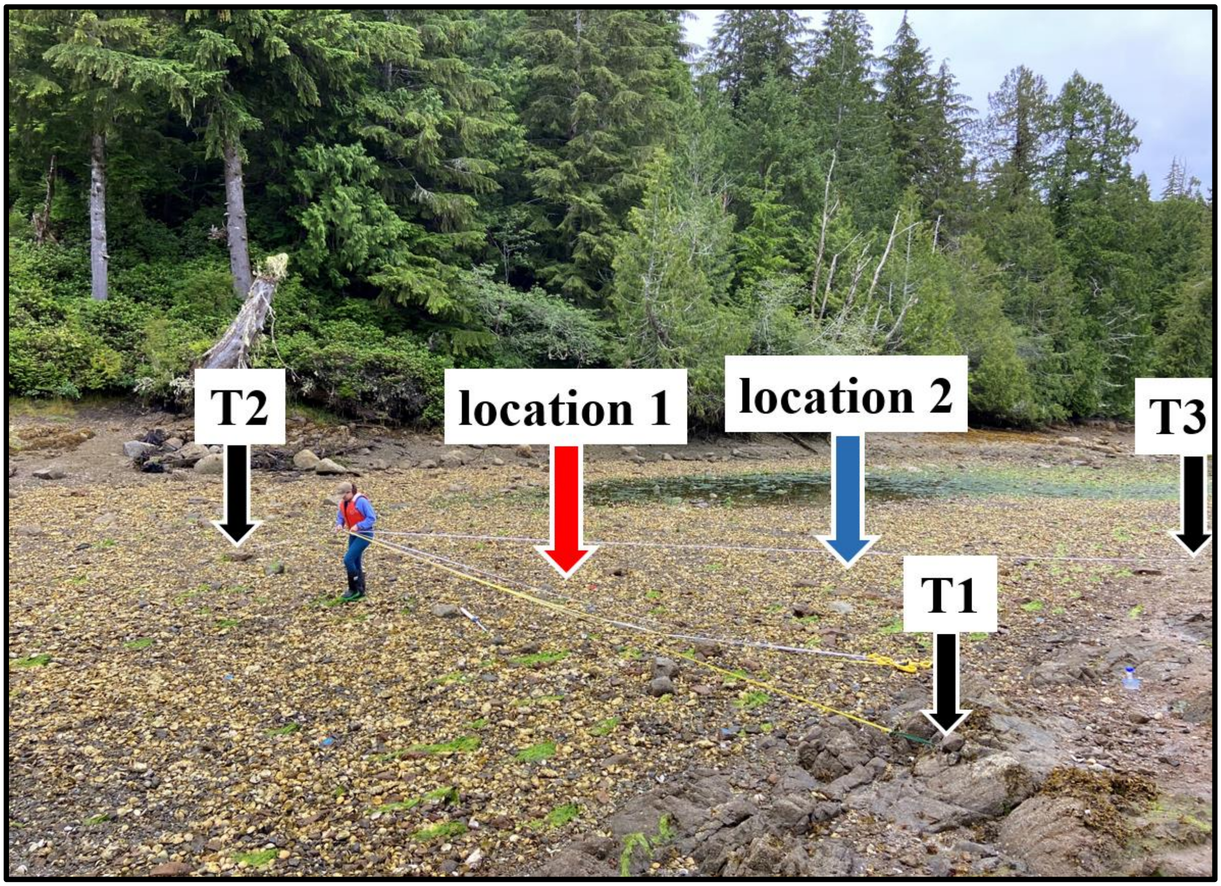

Figure 3. Grappler field site with arrows indicating snail outplanting locations 1 and 2, as well as triangulation locations T1, T2, and T3.

<u>Determination of snail coordinates</u>

The distance travelled by each snail over 2 d intervals was calculated by comparing the previous and current positions of the snail. When a snail was detected, the coordinates of the snail were determined by measuring the distance of the snail from triangulation positions T1, T2, and T3, using three 30 m measuring tapes. The natural microhabitat was not disturbed during these surveys; if a snail detected with the RFID reader was hidden (not visible, e.g., under a rock or shell), the snail was recorded as hidden and left as is. If a detected snail was visible, distances were measured from T1, T2, and T3 to the center of the PIT tag on the snail's shell. However, if the detected snail was hidden, distances were measured from T1, T2, and T3 to the center of the detection zone of the RFID antenna; the detection zone is the circular area around a PIT tag in which the RFID antenna detects the tag, and consisted of a radius of ~15 cm around a PIT tag. The coordinates of a snail were then calculated using triangulation (Appendix A).

Dispersal distance

Determining the greatest distance travelled away from the starting point was achieved by calculating the linear distance travelled by each *N. lamellosa* and *L. dirum* during the summer study period using the initial and final coordinates of the snail:

$$dispersal\ distance = \sqrt{(x_f - x_i)^2 + (y_f - y_i)^2} \qquad (4).$$

In equation 4, the variables x_i and x_f represent the x-coordinates of the initial and final position of a snail, respectively. The variables y_i and y_f represent the y-coordinates of the initial and final position of a snail, respectively. This equation was used in the determination of dispersal distance for 20 tagged snails of each species. The positions of these snails were recorded in the intertidal zone at the Grappler Inlet site on June 19 – 20 and then again in the last week of the study (August 13 – 15).

Daily distance travelled

Determining the distance travelled per day by *N. lamellosa* and *L. dirum* was done by calculating the total distance each snail travelled during the study period, and then dividing that distance by the number of days the snail was monitored in the study:

$$daily\ distance\ travelled = \frac{\sum\sqrt{(x_c - x_p)^2 + (y_c - y_p)^2}}{N} \qquad (5).$$

The variables x_c and x_p represent the x-coordinates of the current position of a snail and its position 2 d prior, respectively. The variables y_c and y_p represent the y-coordinates of the current position of a snail and its position 2 d prior, respectively. N is the number of days a snail was part of the study between June 19 and August 15. This equation was used in the determination of distance travelled per day for 20 tagged snails of each species from June 19 – 20 to the last week of the study (August 13 – 15).

Directionality

Directionality was a measure of the convolutedness of the path travelled by snails over the summer. The directionality of *N. lamellosa* and *L. dirum* was calculated using the following equation:

$$directionality = \frac{(dispersal\ distance/N)}{daily\ distance\ travelled} \qquad (6).$$

A direct (linear) travel path from initial position to final position at the end of the summer will have a directionality value close to one; the lower the directionality value below one, the more convoluted the travel path.

Microhabitat use during low tide

Availability of microhabitat types in the field

To determine the availability of different microhabitat types to snails at the field site, the percent cover of five microhabitat types was determined in a transect survey. The microhabitats present at the Grappler field site were small rock, large rock, shell, sand, and rockface. Small rocks were defined as having a diameter <10 cm, whereas large rocks had a diameter ≥10 cm. The shells present at the site included oyster, mussel, and clam shells. Sand was composed of fine rock and shell fragments. The rockface microhabitat (Fig. 4) was present only along the southeast side of the field site, and consisted of sloped, barnacle-encrusted rock that had deep crevasses (Fig. 4B) and ridges in which snails could hide.

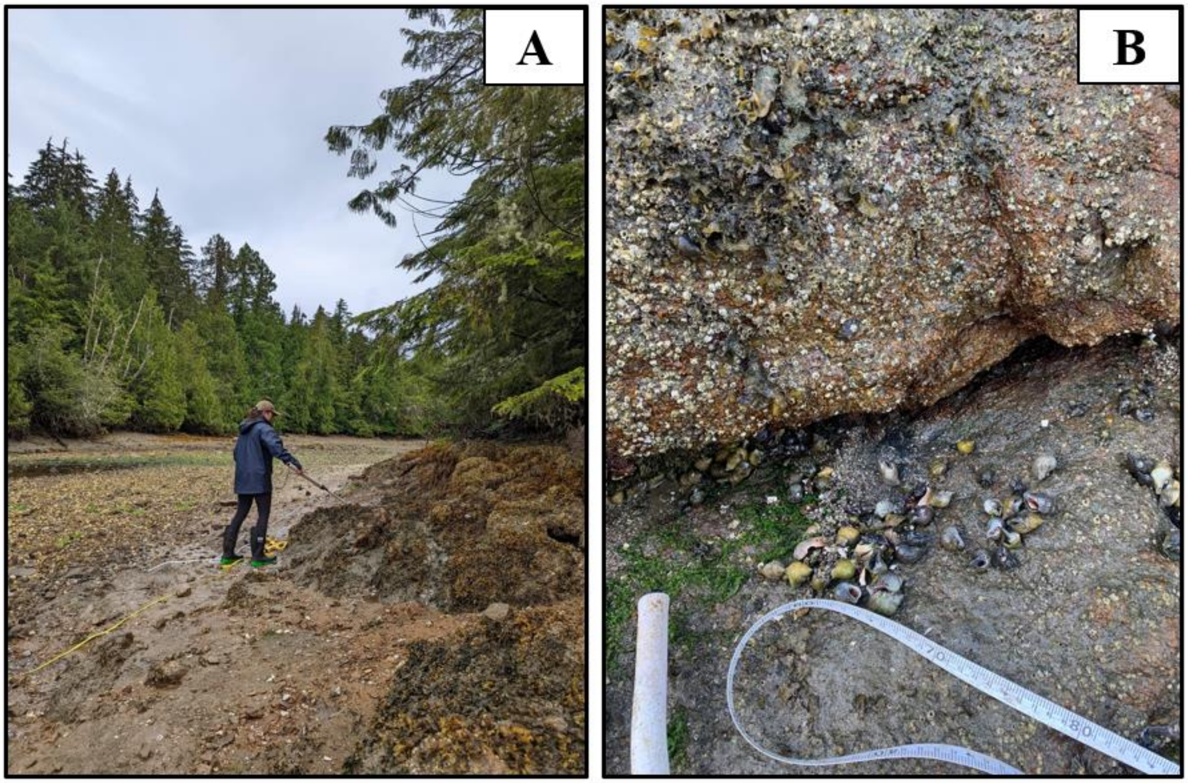

Figure 4. The sloping rockface of the Grappler field site (A) and a deep crevasse within the rockface where snails could hide (B).

To estimate the percent cover of each of the five microhabitat types at the Grappler site, a large section of the intertidal bench (a 12x18 m area) was marked into a grid of 54 2x2 m sections. Then, the percent cover of each microhabitat type was determined within the bottom left quarter (1x1 m quadrat) of every 2x2 m section. The percent cover of each of each microhabitat was estimated within a 1x1 m quadrat frame bearing vertical and horizontal strings that divided the quadrat area into a grid of four hundred 5x5 cm squares; two observers independently estimated the percent coverage of each microhabitat type, then agreed on a best estimate.

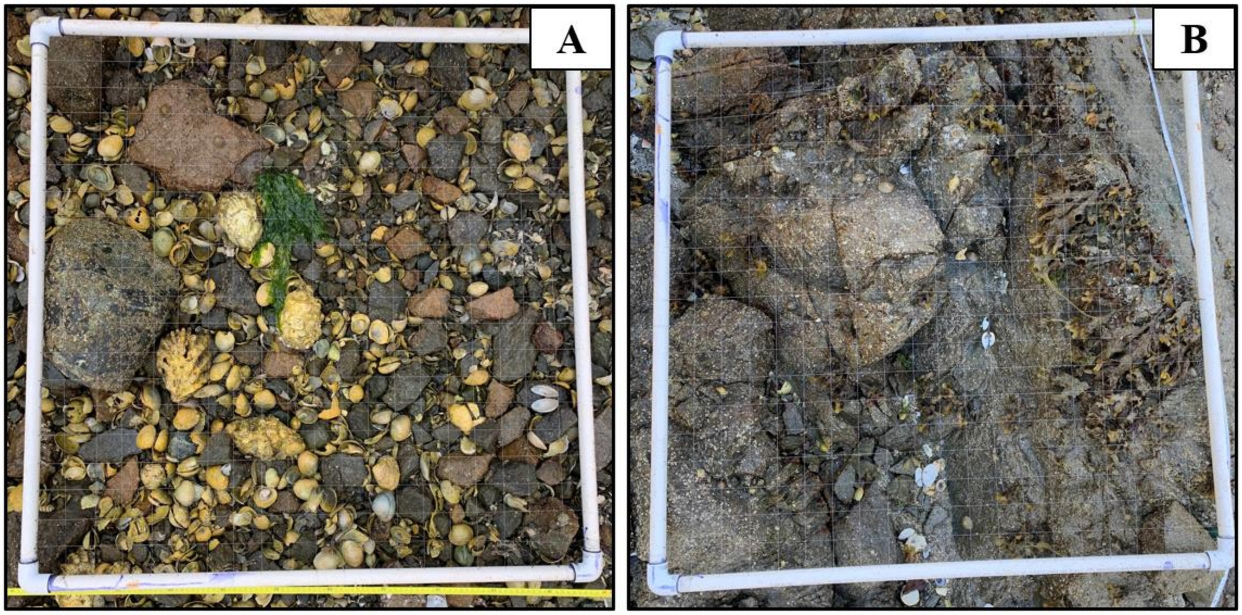

Figure 5. Microhabitats available to snails in the Grappler inlet intertidal zone, excluding the rockface (A). The rockface available to snails in the Grappler inlet intertidal zone (B). Both A and B feature the 1 by 1 m square used in the microhabitat survey.

Microhabitat use by snails

To determine if predatory *N. lamellosa* and scavenging *L. dirum* use certain microhabitat types more than others, the last microhabitat occupied by snails detected during the last two weeks of the study, August 1 – 15 (25 *N. lamellosa* and 30 *L. dirum*), was recorded. Use of the final microhabitat in which the snails were found ensured that snails had as much time as possible to find and occupy their preferred microhabitat.

Snail exposure

Snail exposure at low tide, defined as whether a snail could be seen by the observer or was fully hidden within natural microhabitat, was recorded for every snail every time it was located with the RFID reader throughout the study period (June 19 to August 15). Snails that were visible when detected were recorded as exposed, whereas snails not visible when detected were recorded as hidden. The instances that a snail was hidden when detected was expressed as a proportion of the total times detected.

Relationship between environmental factors affecting snail exposure and movement

Factors affecting snail exposure

To determine if environmental factors influenced snail exposure, the daily proportion of 44 snails of each species that were exposed at low tide was correlated with tidal amplitude, maximum daily air temperature, and total daily precipitation. Tidal amplitude for each day was determined based on hourly tide height data obtained from the historical data archive for Bamfield Station 8545 (Fisheries and Oceans Canada 2023). Maximum daily air temperature and total daily precipitation from June 19 to August 15 were retrieved from historical Ucluelet climate data archive (Government of Canada 2023).

Factors affecting snail movement

To determine if environmental factors influence snail movement, the average distance travelled by 44 *N. lamellosa* and 43 *L. dirum* in 2 d was correlated with tidal amplitude on the first day of the 2 d period, maximum temperature on the first day of the 2 d period, and total precipitation over the 2 d period. There were 30 d from June 19 to August 15 that *N. lamellosa* were detected in 2 d intervals. These 2 d periods did not occur during occasions when low tide was higher than 1.3 m. For *L. dirum*, there were 32 d that fit these criteria.

Relationship between summertime growth and movement

To determine if the growth of adult snails might be related to the extent to which they move during the summer, the body weight of 20 *N. lamellosa* and 20 *L. dirum* was measured upon collection in mid-June using a scale accurate to 0.01 g, and then again at the end of the data collection period on August 15. The relationship between change in body weight during the study period and distance travelled and dispersal by the snail during that period was then examined.

RESULTS

Effect of PIT tags on snail motility

Tagged (n=10) and untagged (n=10) *Nucella lamellosa* did not differ significantly in terms of total distance travelled (Welch's two tailed, two-sample t-test: $t_{0.05(17)}$=0.09, p=0.933), dispersal from starting point ($t_{0.05(17)}$=-0.56, p=0.584), or directionality ($t_{0.05(17)}$=0.70, p=0.492) (Fig. 6 A-C). The same was also the case in *Lirabuccinum dirum*, with no significant difference in total distance travelled ($t_{0.05(17)}$=0.56, p=0.583), dispersal ($t_{0.05(17)}$=0.52, p=0.611), or directionality ($t_{0.05(15)}$=-0.77, p=0.453) of tagged (n=10) and untagged (n=10) snails (Fig. 6 D-F).

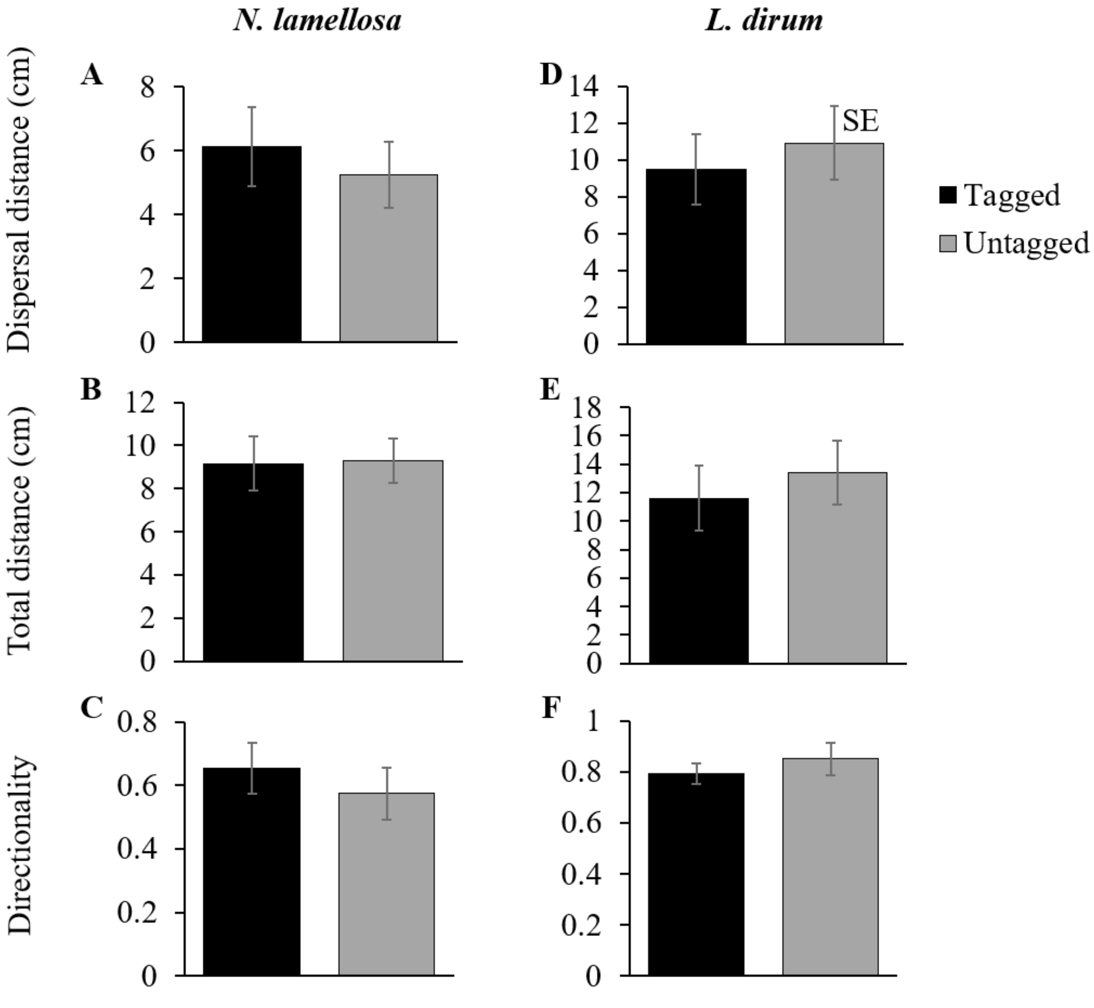

Figure 6. Average dispersal, total distance travelled, and directionality of 10 tagged and 10 untagged *N. lamellosa* (A, B, C) and *L. dirum* (D, E, F) over 6 min. A directionality value of 1 indicates a linear path; smaller values indicate an increasingly convoluted path.

Movement of snails in the intertidal zone during active summer months

During the first 2 d after snails were released (June 17 – 19), *L. dirum* (n=20) moved 35 ± 8 cm (average ± SE) each day, whereas the same snails travelled only 19 ± 2 cm per day during the rest of the study period (June 19 – August 15), a difference that was significant (paired t-test: $t_{0.05(19)}=-5.48$, $p \leq 0.001$). During the first 2 d after snails were released (June 17 – 19), *N. lamellosa* (n=20) moved 30 ± 4 cm each day, whereas the same snails travelled 27 ± 7 cm per day during the rest of the study period (June 19 – August 15), a difference that was not significant ($t_{0.05(19)}=-0.38$, p=0.710). Given the different movement behaviour during the first 2 d in *L. dirum*, as was also previously observed in *N. ostrina* (McLeod 2016), movement and microhabitat use data from the first 2 d after returning snails to the field site were not included in any of the following analyses, for both species. During the study period, the average daily distance travelled by *N. lamellosa* did not differ significantly from *L. dirum* (Welch's two-sample, two-tailed t-test: $t_{0.05(21)}=1.21$, p=0.239) (Fig. 7A). With regards to dispersal distance over the study period, *N. lamellosa* dispersed significantly farther than *L. dirum* ($t_{0.05(34)}=4.39$, $p \leq 0.001$) (Fig. 7B). Finally, the travel path of *N. lamellosa* was also significantly more linear than that of *L. dirum* ($t_{0.05(34)}=3.56$, p=0.001) (Fig. 7C).

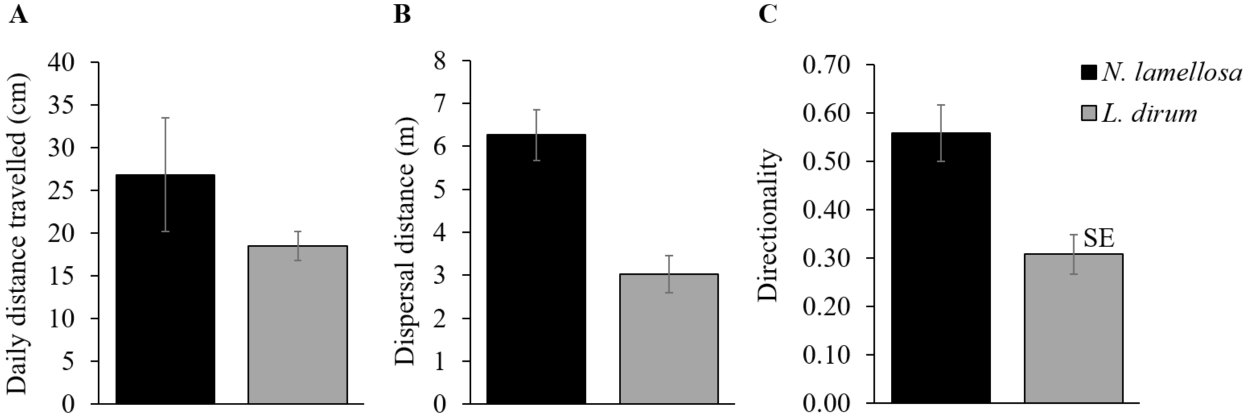

Figure 7. Average daily distance travelled (A), dispersal (B), and directionality (C) of *N. lamellosa* (n=20) and *L. dirum* (n=20) snails at the Grappler field site over 53-56 days, summer 2022. Directionality value of 1 indicates most linear path.

Microhabitat use during low tide

Microhabitat use by snails

On the intertidal bench at the Grappler Inlet field site, small rock was the most abundant microhabitat, followed by shell microhabitat, large rocks, sand, and rockface (Fig. 8).

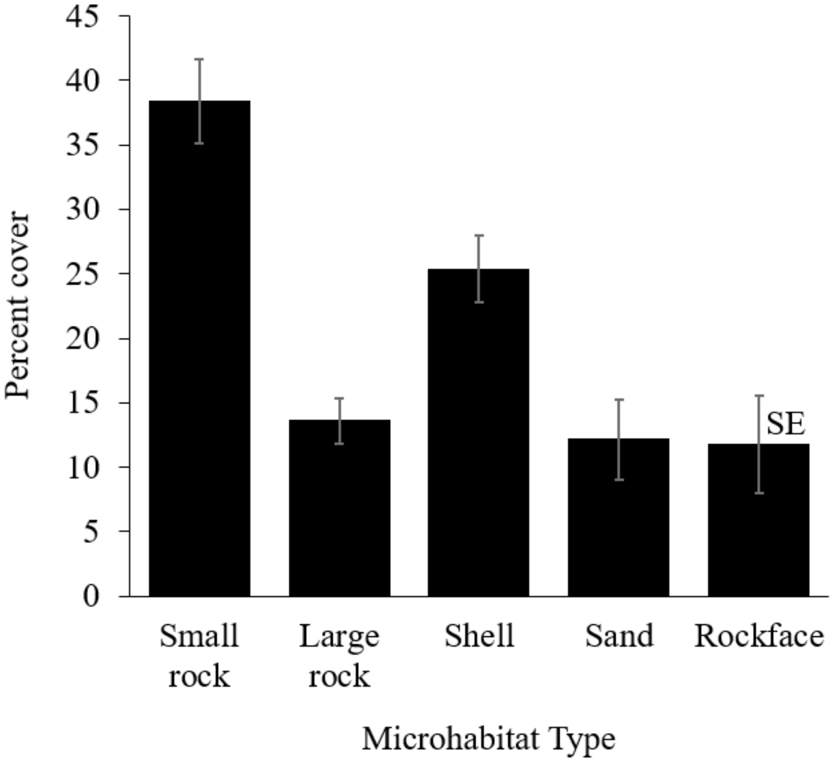

Figure 8. Average percent cover (n=54) of small rock, large rock, shell, sand, and rockface within a 12 x 18 m section of the Grappler field site.

The log-likelihood ratio for goodness of fit test with William's correction (Zar 2010) was used to compare the frequency of individuals of a species in each microhabitat type that would be expected if they were distributed entirely according to microhabitat availability, with the observed frequency of individuals of that species found in each microhabitat from August 1 – 15. The observed and expected frequencies of *N. lamellosa* in these microhabitat types differed significantly ($G_{adj}=14.010$, $\chi^2_{0.01(4)}=13.277$, $p<0.01$). The 25 *N. lamellosa* located in the last two weeks of the study were more frequent on rockface microhabitat, and less frequent among small and large rocks, than was expected based on microhabitat availability (Fig. 9A).

The observed and expected frequencies of *L. dirum* in these microhabitat types differed significantly ($G_{adj}=10.652$, $\chi^2_{0.025(3)}=9.348$, $p<0.025$). The 30 *L. dirum* located in the last two weeks of the study were more frequent in small rock microhabitat, and less frequent among large rocks, than was expected based on microhabitat availability (Fig. 9B).

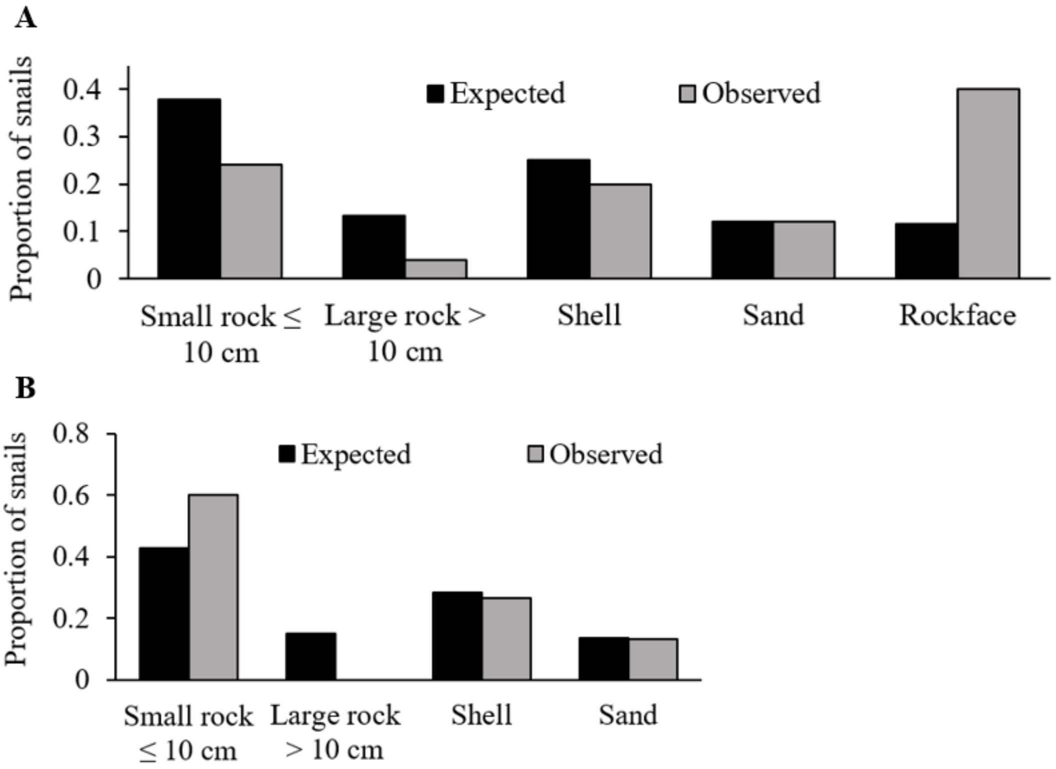

Figure 9. Expected and observed proportion of 25 *N. lamellosa* (A) and 30 *L. dirum* (B) in each microhabitat from August 1 – 15 based on availability of each microhabitat type.

Snail exposure

Individual *N. lamellosa* were hidden during almost 40% of the low tides, whereas *L. dirum* were hidden during more than 80% of the low tides during the study period (Fig. 10). *L. dirum* were hidden significantly more often than *N. lamellosa* (Welch's two-tailed two-sample t-test: $t_{0.05(84)}=-10.37$, $p\leq0.001$).

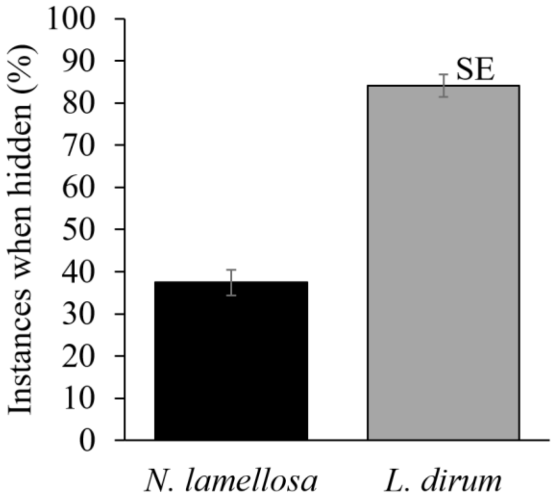

Figure 10. Proportion of instances (%) when *N. lamellosa* (n=44) and *L. dirum* (n=44) were detected but not visible (hidden under rocks, shells, sediment) at low tide from June 19 – August 15.

Relationship between environmental factors affecting snail exposure and movement

Factors affecting snail exposure

Multiple linear regression was used to determine if the daily proportion (arcsine transformed, Zar 2010) of 44 *N. lamellosa* and 44 *L. dirum* that were hidden at low tide from June 19 to August 15 varied as a function of tidal amplitude, maximum daily temperature, or total daily precipitation, using the statistics software Minitab®. For *N. lamellosa*, the regression was not statistically significant ($R^2 = 0.115$, $F_{(3,34)} = 1.47$, $p = 0.239$); tidal amplitude ($\beta = -0.0761$, $p = 0.168$), maximum daily temperature ($\beta = -0.01291$, $p = 0.174$), and total daily precipitation ($\beta = -0.00041$, $p = 0.954$) were not significantly related to the exposure of *N. lamellosa* at low tide. The same analysis for *L. dirum* was also not statistically significant ($R^2 = 0.0494$, $F_{(3,34)} = 0.59$, $p = 0.627$); tidal amplitude ($\beta = 0.0331$, $p = 0.637$), maximum daily temperature ($\beta = 0.0148$, $p = 0.224$), and total daily precipitation ($\beta = 0.00584$, $p = 0.528$) were not significantly related to the exposure of *L. dirum* at low tide.

Factors affecting snail movement

Multiple linear regression was used to determine if the distance traveled by *N. lamellosa* and *L. dirum* every 2 d from June 19 – August 15 varied as a function of tidal amplitude, maximum air temperature, or total precipitation, using the statistical software Minitab®. For *N. lamellosa*, the regression was not statistically significant ($R^2 = 0.1313$, $F_{(3,26)} = 1.31$, $p = 0.292$); tidal amplitude ($\beta = -0.394$, $p = 0.064$), maximum air temperature ($\beta = -0.0081$, $p = 0.792$) and total precipitation ($\beta = 0.0109$, $p = 0.520$) were not significantly related to the distance travelled by *N. lamellosa* in 2 d. The same analysis for *L. dirum* was also not statistically significant ($R^2 = 0.0267$, $F_{(3,28)} = 0.26$, $p = 0.856$); tidal amplitude ($\beta = -0.003$, $p = 0.986$), maximum air temperature ($\beta = -0.0024$, $p = 0.917$), and total precipitation ($\beta = -0.0110$, $p = 0.401$) were not significantly related to the distance travelled by *L. dirum* in 2 d.

Relationship between summertime growth and movement

The body mass (including shell) of 20 tagged *N. lamellosa* increased from 5.04 ± 1.67 g (average ± STD) in mid-June to 5.07 ± 1.59 g in mid-August, for an average growth in body mass of 1.43 ± 6.06 %. Final body mass was not significantly different from initial body mass (paired t-test: $t_{0.05(19)} = -0.59$, $p = 0.282$), indicating no consistent growth trend across *N. lamellosa*. The body mass (including shell) of 20 tagged *L. dirum* increased from 3.82 ± 1.09 g in mid-June to 4.09 ± 1.01 g in mid-August, for an average growth in body mass of 7.40 ± 3.75 %. Final body mass was significantly larger than the initial body mass (paired t-test: $t_{0.05(19)} = -9.38$, $p < 0.001$), indicating a significant growth trend across *L. dirum*.

For both snail species, simple linear regressions were used to determine if snail growth was related to the average distance travelled per day or to summertime dispersal distance. Growth was not significantly related to daily distance travelled in *N. lamellosa* ($R^2 = 0.0421$, $F_{(1,18)} = 0.79$, $p = 0.385$) (Fig. 11A), or in *L. dirum* ($R^2 = 0.0303$, $F_{(1,18)} = 0.56$, $p = 0.463$) (Fig. 11B). Growth of *N. lamellosa* was also not statistically related to dispersal ($R^2 = 0.0017$, $F_{(1,18)} = 0.03$, $p = 0.865$) (Fig. 11C), but growth did increase significantly with dispersal distance in *L. dirum* ($R^2 = 0.1980$, $F_{(1,18)} = 0.56$, $p = 0.049$) (Fig. 11D).

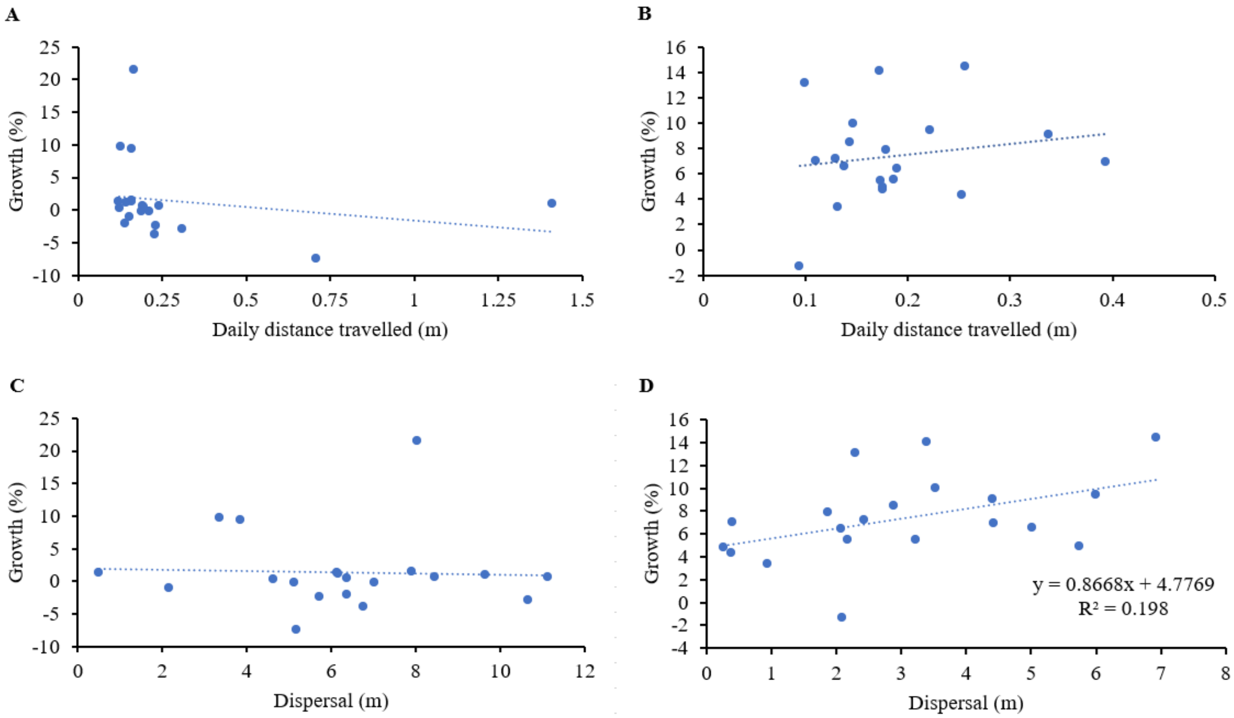

Figure 11. Fitted line plots of daily distance travelled as a predictor of (A) 20 *N. lamellosa* and (B) 20 *L. dirum* percent growth over the summer. Fitted line plots of dispersal as a predictor of (C) 20 *N. lamellosa* and (D) 20 *L. dirum* percent growth over the summer.

DISCUSSION

Effect of PIT tags on snail motility

Stress from capturing, handling, and tagging animals is known to impact their behaviour and thus can influence the results of behavioural studies (Dickens et al. 2009). In particular, tagging invertebrates with PIT tags can result in unreliable movement responses due to the added weight and resulting energy cost of the monitoring device (Wilson et al. 2011). The 12 mm HDX PIT tags used in this study weighed ~1.0 g (McLeod 2016), which increased the weight of the snails in this study by ~3.5%. This increase nevertheless conformed to the recommendation that tags remain below 4% of the body weight of an animal (Theuerkauf et al. 2007), supporting the hypothesis that these tags might not have much impact on the movements of the snails. This hypothesis was confirmed by the laboratory motility experiment, which found no detectable effect of PIT tags on either the amount or pattern of motility of adult *Nucella lamellosa* and *Lirabuccinum dirum*. A limitation of this study is that it is not known if PIT tags affected snail movement in the structurally complex intertidal zone by snagging on rocks and vegetation.

Movement of snails in the intertidal zone during active summer months

Dispersal has important consequences for survival and fecundity, including the ability of a disperser to locate food, protective microhabitats, and mates (Bowler and Benton 2005; Doligez and Pärt 2008). *N. lamellosa*, a muricid gastropod that hatches from a benthic egg capsule as a crawl-away juvenile and feeds on benthic invertebrates that are generally abundant in the intertidal zone, was expected to disperse minimally from its initial position at the start of the summer (Gosselin and Chia 1995). In contrast, much of the ecology and juvenile development of *L. dirum* is unknown (Nielsen and Gosselin 2011), but previous studies have observed or proposed that the dispersal of intertidal snails in general is minimal (Gosselin and Chia 1995; Pardo et al. 2004; Chapperon and Seuront 2013; McLeod 2016). Dispersal of the two species in the present study, however, differed considerably. Although living in the same environment and recorded over the same period of time, *N. lamellosa* dispersed ~52% farther than *L. dirum*. In addition, compared to the average summertime dispersal distance of 1 m in the intertidal predatory snail *N. ostrina* (McLeod 2016), the average dispersal of *N. lamellosa* (6.3 m) and *L. dirum* (3.0 m) recorded in the present study were substantially greater than in *N. ostrina*. It is not clear why *L. dirum* do not disperse as far as *N. lamellosa*, but the more limited dispersal of *L. dirum* might be attributed to a higher density of resources and mates. *N. lamellosa* may also be driven to disperse farther because of competition for resources with other predatory snail species such as *N. ostrina*, or with other non-gastropod species such as crabs and seastars. The greater dispersal of *N. lamellosa* may have been due to searches for microhabitats such as rockface crevasses or the sides of large rocks, that they require for attaching egg capsules.

Despite the potential ecological benefits of dispersal, movements are energetically costly (Bowler and Benton 2005) and gastropod predators and scavengers can not feed while crawling. Additionally, animals that disperse farther may be exposed to greater variations in temperature and desiccation, causing stress and requiring physiological and behavioural adaptations to deal with these stressors (Doligez and Pärt 2008). However, this study found that the growth of *N. lamellosa* and of *L. dirum* over the summer were not correlated with their daily distance travelled, nor was it related to dispersal distance in *N. lamellosa*. Dispersal and daily movements may nevertheless influence the population dynamics and intertidal ecology of *N. lamellosa* and *L. dirum*. For instance, dispersing farther can expose animals to greater predation risk (Stamps et al. 2005). During periods of travel, snails are more exposed and are thus more likely to be detected by predators. The present study exemplified this risk in that, by the end of the study period, 39% of studied *L. dirum* were missing, whereas 52% of studied *N. lamellosa* were missing, which might indicate increased mortality in the species with higher dispersal.

Dispersal also has evolutionary implications (Slatkin 1987; Johnson and Gaines 1990; Bowler and Benton 2005; Doligez and Pärt 2008). Given that dispersal is a determinant of gene flow (Slatkin 1987; Bowler and Benton 2005), and that the embryonic and larval stages of both species take place entirely within a benthic egg capsule (i.e., no larval dispersal), the crawling dispersal of adult snails in this study suggests, first, that *N. lamellosa* would have greater potential for gene flow than *L. dirum*, and second, that both species would have greater gene flow than *N. ostrina*. Through the spread of alleles, local populations with greater gene flow may benefit from reduced inbreeding depression (Johnson and Gaines 1990). Although there are ecological and adaptive consequences of crawling dispersal, the overall dispersal and gene flow of *N. lamellosa* and *L. dirum* may depend not only on summertime crawling dispersal, but also on occasional longer-distance drifting dispersal in the water column by rafting on algae or logs (Gosselin and Chia 1995).

Daily animal movements are important for obtaining resources (Swingland and Greenwood 1983), locating mates (Duvall and Schuett 1997), avoiding predators (Day and Branch 2002), and finding sheltered microhabitats (Gosselin and Chia 1995). Understanding how much an animal moves in a day allows inferences to be made about the time and energy it allocates to movement and the ecological implications of these movements. It is expected that the energy an animal gains from consuming food is generally greater than the energy used to move (Swingland and Greenwood 1983). Snails should therefore move only as far as food availability and energetic constraints permit and only when a new food source is needed, a mate or capsule deposition site need to be found, predation is imminent, or desiccation stress forces snails to seek sheltered microhabitats. *L. dirum* travelled on average 19 cm per day during the summer, which exceeded the expected travel distance of a previous study of adult *N. ostrina* in a wave-exposed intertidal environment (McLeod 2016), but was less than the 27 cm travelled per day by *N. lamellosa*. It is possible that movements by *L. dirum* and *N. lamellosa* at the wave-sheltered Grappler Inlet site were less hindered by wave action than at wave-exposed sites, or these two species may need to travel farther each day at the Grappler site to obtain food, locate mates, avoid predators, or seek shelter.

L. dirum was less directional in its movements than *N. lamellosa*, the travel path of *L. dirum* being ~45% more convoluted than in *N. lamellosa*. The directness of travel displayed by *N. lamellosa* was surprising given that previous research has suggested intertidal snails travel non-directionally, resulting in limited dispersal (Pardo et al. 2004; Chapperon and Seuront 2013; McLeod 2016). The intertidal herbivorous gastropods *Littorina saxatilis* and *Nerita atramentosa* likely distribute and use habitats based on food availability and temperature, therefore directionality could be influenced by substrate temperatures and food odours (Pardo et al. 2004; Chapperon and Seuront 2013). The mechanism responsible for the difference in directionality between *N. lamellosa* and *L. dirum* is unclear, but since the movement patterns of other intertidal snail species can be driven by the density and distribution of preferred food sources (Chapperon and Seuront 2013), it is possible that the species in this study reacted to food odours in their environment. Thus, the differences in movement between predatory *N. lamellosa* and scavenging *L. dirum*, as well as microhabitat use described below, could be due to differences in food preferences.

Microhabitat use during low tide

Predation as well as desiccation during low tide are the main sources of mortality of intertidal snails (Gosselin and Chia 1995). Mechanisms to avoid these stressors should therefore include shelter-seeking behaviours in suitable microhabitats, especially at low tide when desiccation and heat are most stressful. During low tide, intertidal snails should shelter in microhabitats that are in close proximity to food items. Of the microhabitats available at the Grappler field site by the end of the study, *N. lamellosa* were located on the rockface more than other microhabitat types during low tide. *L. dirum*, however, were most often located among small rocks, and never used the rockface microhabitat. The main food source of *N. lamellosa* are barnacles, which are located high in the intertidal zone on exposed rockfaces, whereas dead invertebrates, the main food source of *L. dirum*, might often end up lower in the intertidal, resting on the flat intertidal bench under small and large rocks. The difference in microhabitat use may reflect their different feeding preferences: *N. lamello*sa higher in the intertidal zone on surfaces where barnacles are common, and *L. dirum* in lower microhabitats where animals are most likely to die, for example due to reduced salinity

(Nielsen and Gosselin 2011), and also where water movement and gravity are most likely to deposit dead organisms. This difference in microhabitat use could be due to a response by these snail species to food odours (Chelazzi et al 1990; Chapperon and Seuront 2013). The more time a snail spends in sheltered microhabitats, the less time is spent seeking food sources (Jones and Boulding 1999; Moisez et al. 2020), resulting in a trade-off that requires snails to risk exposure for some time to obtain food before seeking shelter. For predatory *N. lamellosa*, the time spent hidden in sheltered microhabitats was ~55% less than in the scavenger *L. dirum*.

Environmental factors affecting snail exposure and movement

Tide cycles can influence the behaviour of intertidal snails. For instance, at low tide, snails may avoid high shore areas and exposed locations, whereas at high tide, snails may be able to access food in such high risk areas (Hayford et al. 2018). In the present study, however, tidal amplitude was not a predictor of movements in *N. lamellosa* or *L. dirum* over summer months, or of selected resting site (exposed or hidden) during low tide. Temperature during low tide can be a stressor for intertidal snails, especially when air temperatures are high during the day (Kearney et al. 2009; Chapperon and Seuront 2010). Snails were therefore expected to move less and be hidden more often when maximum daily temperatures were high. Maximum daily air temperature, however, did not seem to influence *N. lamellosa* and *L. dirum* movement or exposure, possibly because microhabitats used at low tide are selected by snails while still submerged, and thus when snails have not yet experienced the low tide aerial conditions. Finally, we considered the possibility that daily precipitation could influence the movement and exposure of snails. When it rains, the seawater in shallow inlets such as Grappler Inlet becomes diluted, especially during low tide in the intertidal zone. While it is plausible that the movement and exposure of snails could be influenced by varying amounts of precipitation, our study did not find evidence to support this. The movement and exposure of *N. lamellosa* and *L. dirum* did not seem to be affected by these environmental factors, suggesting that a broad range of summertime weather conditions do not significantly impact short-term snail decisions regarding exposure and movement.

Relationship between summertime growth and movement

Daily movement did not seem to impact snail growth. During the 57 d field study period, only *L. dirum* significantly increased in body weight. One explanation for this difference between species could have been that *N. lamellosa* travelled farther from their initial position, possibly to find food, mates, and egg capsule laying sites, thereby depleting energy that could have been allocated toward growth. Another explanation could be that the initial position of *N. lamellosa* at the start of the study was lacking in barnacles, their preferred food source, so *N. lamellosa* had to travel further to find more abundant food. Although both species of snail used in the present study were large adults and thus were expected to experience modest growth, the lack of growth in *N. lamellosa* was unexpected. This could have been due to the physiological stress of living at higher intertidal heights (Hayford et al. 2018). Further studies should determine the relationship between *N. lamellosa* and *L. dirum* body mass and desiccation stress at different intertidal heights.

While the growth of *L. dirum* was unrelated to the daily distance travelled, growth was positively correlated with dispersal distance. The farther *L. dirum* dispersed, the greater their resulting body condition at the end of the summer. Snails that dispersed farther may have had greater access to food than snails that stayed closer to their initial position, resulting in more energy available for growth.

Effectiveness of the tagging methodology

The effectiveness of RFID technology to track snail movement and microhabitat use is an important consideration for future intertidal snail studies (Hale et al. 2012). PIT tags did not perceptibly hinder the motility of snails in this study, so use of these tags could be a reliable approach for studying the ecology of intertidal gastropods in their natural habitat. RFID allowed the detection even of hidden snails without microhabitat disruption. Because snails and their microhabitats remained undisturbed after the initial collection, tagging, and return to the field, this study likely presents a more accurate record of movement and microhabitat use than studies using traditional tagging methods. PIT tags were similar in colour to the snail shells they were attached to, so visual predators were not signaled to the location of a tagged snail by bright tags. There were, however, limitations to using RFID in the intertidal zone. If a snail was covered by more than 8 cm of dense debris or water, the RFID reader could not detect the PIT tag. Some snails could not be detected on certain days but were likely present, hidden under a layer of sediment or water. The proportion of snails that were hidden at low tide was therefore likely even higher than reported in this study. Finally, the area at the field site that was monitored daily was larger than in previous snail studies, something that was possible due to the triangulation method used here. The study area was not constrained by a pre-set grid, so snails could be tracked even if they dispersed farther than expected, which was the case for *N. lamellosa* and *L. dirum*.

Conclusion

This study revealed that *N. lamellosa* and *L. dirum* disperse much farther during the active summer months than expected. Likewise, *N. lamellosa* display a surprising directness of travel over the summer. These species have different patterns of movement and microhabitat use, perhaps due to differences in food source, but likely due to a combination of abiotic and biotic interactions. Despite some limitations, RFID appears an effective tool for studying the movement of intertidal snails without disturbing their microhabitats. Although tidal amplitude, maximum daily air temperature, and daily precipitation did not seem to influence snail movement or exposure, further research should explore the impact of other environmental parameters such as wave action, predator abundance, or availability of preferred food on movement and microhabitat use by *N. lamellosa* and *L. dirum* during their active summer months.

LITERATURE CITED

Bogert CM. 1949. Thermoregulation in reptiles, a factor in evolution. Evolution. [accessed 2023 Apr 10]; 3(3): 195-211. https://onlinelibrary.wiley.com/doi/10.1111/j.1558-5646.1949.tb00021.x. doi: 10.1111/j.1558-5646.1949.tb00021.x.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Reviews. [accessed 2023 Apr 10]; 80, 205–225. https://onlinelibrary.wiley.com/doi/epdf/10.1017/S1464793104006645. doi: 10.1017/S1464793104006645.

Chapperon C, Seuront L. 2010. Behavioural thermoregulation in a tropical gastropod: links to climate change scenarios. Glob Chan Biol. [accessed 2023 Apr 10]; 17(4): 1740-1749. https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2010.02356.x. doi: 10.1111/j.1365-2486.2010.02356.x.

Chapperon C, Seuront L. 2013. Temporal shifts in motion behaviour and habitat use in an intertidal gastropod. Jour Mar Biol Assoc UK. [accessed 2023 Apr 10]; 93(4):1025-1034. https://www.researchgate.net/publication/236029165_Temporal_shifts_in_motion_behaviour_and_habitat_use_in_an_intertidal_gastropod. doi:10.1017/S0025315412000756.

Chelazzi G, Della Santina P, Parpagnoli D. 1990. The role of trail following in the homing of intertidal chitons: a comparison between three Acanthopleura spp. Mar Biol. [accessed 2023 Apr 10]; 105: 445-450. https://link.springer.com/content/pdf/10.1007/BF01316316.pdf.

Day EG, Branch GM. 2002. Influences of the sea urchin *Parechinus angulosus* (Leske) on the feeding behaviour and activity rhythms of juveniles of the South African abalone *Haliotis midae* Linn. J Exp Mar Biol Ecol. [accessed 2023 Apr 18]; 276(1-2): 1-17. https://www.sciencedirect.com/science/article/pii/S0022098102002046. doi: 10.1016/S0022-0981(02)00204-6.

Dickens M J, Delehanty DJ, Romero LM. 2009. Stress and Translocation: Alterations in the Stress Physiology of Translocated Birds. Proc Biol Sci. [accessed 2023 Apr 10]; 276(1664): 2051–2056. http://www.jstor.org/stable/30245021.

Dill LM. 1987. Animal decision making and its ecological consequences: The future of aquatic ecology and behaviour. Can J Zool. [Accessed 2022 Apr 10]; 65(4):803-811. http://www.nrcresearchpress.com/doi/abs/10.1139/z87-128. doi: 10.1139/z87-128.

Doligez B, Pärt T. 2008. Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. J Anim Ecol. [accessed 2023 Apr 18]; 77: 1199-1211. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2656.2008.01446.x. doi: 10.1111/j.1365-2656.2008.01446.x

Duvall D, Schuett GW. 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. Anim behav. [accessed 2023 Apr 18]; 54(2): 329-34. https://www.sciencedirect.com/science/article/pii/S0003347296904182. doi: 10.1006/anbe.1996.0418.

Erlandsson J, Kostylev V, Rolan-Alvarez E. 1999. Mate search and aggregation behaviour in the Galician hybrid zone of Littorina saxatilis. J Evol Biol. [accessed 2023 Apr 10]; 12(5): 891-896. https://onlinelibrary.wiley.com/doi/full/10.1046/j.1420-9101.1999.00087.x. doi: 10.1046/j.1420-9101.1999.00087.x.

Franklin J. 2010. Moving beyond static species distribution models in support of conservation biogeography. Div Dist. [accessed 2023 Apr 10]; 16(3): 321-330. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1472-4642.2010.00641.x. doi: 10.1111/j.1472-4642.2010.00641.x.

Fratini S, Cannicci S, Vannini M. 2001. Feeding clusters and olfaction in the mangrove snail Terebralia palustris (Linnaeus) (Potamididae: Gastropoda). J Exp Mar Biol Ecol. [accessed 2023 Apr 10]; 261(2): 173-183. https://www.sciencedirect.com/science/article/pii/S0022098101002738. doi: 10.1016/S0022-0981(01)00273-8.

Gibbons WJ, Andrews KM. 2004. PIT Tagging: Simple Technology at Its Best. BioScience. [accessed 2022 Apr 19]; 54(5):447–454. https://doi.org/10.1641/0006-3568(2004)054[0447:PTSTAI]2.0.CO;2.

Gosselin LA. 1993. A method for marking small juvenile gastropods. J Mar Biol Assoc UK [accessed 2023 Apr 16]; 73: 963-966. https://faculty.tru.ca/lgosselin/publications/gosselin_1993_jmbauk_73_963-966.pdf.

Gosselin LA, Chia FS. 1995. Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. Mar Ecol Prog Ser. [accessed 2022 Apr 19]; 128:213-223. https://www.int-res.com/abstracts/meps/v128/p213-223/. doi: 10.3354/meps128213.

Hale JR, Bouma JV, Vadopalas B, Friedman CS. 2012. Evaluation of Passive Integrated Transponders for Abalone: Tag Placement, Retention, and Effect on Survival. J Shell Res. [accessed 2022 Apr 19]; 31(3):789-794. doi: https://doi.org/10.2983/035.031.0324.

Harley CDG. 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Mar Ecol Prog Ser. [accessed 2023 Apr 10]; 371: 37-46. https://www.int-res.com/articles/meps2008/371/m371p037.pdf. doi: https://doi.org/10.3354/meps07711.

Hayford HA, O'Donnell MJ, Carrington E. 2018. Radio tracking detects behavioral thermoregulation at a snail's pace. J Exp Mar Biol Ecol. [accessed 2022 Apr 10]; 499: 17-

25. https://www.sciencedirect.com/science/article/pii/S0022098117302526?via%3Dihub. doi: 10.1016/j.jembe.2017.12.005.

Henry PY, Jarne P. 2007. Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. Invert Biol. [accessed 2022 Apr 19]; 126(2):138-153. https://onlinelibrary.wiley.com/doi/10.1111/j.1744-7410.2007.00084.x. doi: 10.1111/j.1744-7410.2007.00084.x.

Howard WE. 1960. Innate and Environmental Dispersal of Individual Vertebrates. Am Mid Nat. [accessed 2023 Apr 18]; 63(1): 152–161. https://www.jstor.org/stable/2422936. doi: 10.2307/2422936.

Johnson ML, Gaines MS. 1990. Evolution of Dispersal: Theoretical Models and Empirical Tests Using Birds and Mammals. An Rev Ecol Syst. [accessed 2023 Apr 18]; 21: 449–480. http://www.jstor.org/stable/2097033. doi: 10.2307/2422936.

Jones KMM, Boulding EG. 1999. State-dependent habitat selection by an intertidal snail: The costs of selecting a physically stressful microhabitat. J Exp Mar Biol Ecol. [Accessed 2022 Apr 10]; 242(2):149-177. https://www.sciencedirect.com/science/article/pii/S0022098199000908. doi: https://doi.org/10.1016/S0022-0981(99)00090-8.

Jordan F, Bartolini M, Nelson C, Patterson PE, Soulen HL. 1997. Risk of predation affects habitat selection by the pinfish lagodon rhomboides (linnaeus). J Exp Mar Biol Ecol. [Accessed 2022 Apr 10]; 208(1):45-56. https://www.sciencedirect.com/science/article/pii/S0022098196026561. doi: https://doi.org/10.1016/S0022-0981(96)02656-1.

Kearney M, Shine R, Porter WP. 2009. The potential for behavioural thermoregulation to buffer “cold-blooded” animals against climate change. PNAS. [accessed 2023 Apr 10]; 106(10): 3835-3840. https://www.pnas.org/doi/full/10.1073/pnas.0808913106. doi: https://doi.org/10.1073/pnas.0808913106.

Kovach RP, Tallmon DA. 2010. Strong influence of microhabitat on survival for an intertidal snail, Nucella lima. Hydrobiologia. [accessed 2022 Apr 19]; 652:49–56. doi: 10.1007/s10750-010-0317-5.

McLeod AJ. 2015. Snail trails: Use of new technology to discover how far intertidal sanils disperse and where they live. TRU Honours Thesis.

Moisez E, Spilmont N, Seuront L. 2020. Microhabitats choice in intertidal gastropods is species-, temperature- and habitat-specific. J Therm Biol. [accessed 2023 Apr 10]; 94:102785. https://www.sciencedirect.com/science/article/abs/pii/S030645652030557X#preview-section-abstract. doi: 10.1016/j.jtherbio.2020.102785.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT. 2010. Building the bridge between animal movement and population dynamics. Phil Trans R Soc B. [accessed 2023 Apr 10]; 365(1550): 2289-2301. https://www.jstor.org/stable/25699249. doi: 10.1098/rstb.2010.0082.

Neilsen TV, Gosselin LA. 2011. Can a scavenger benefit from environmental stress? Role of salinity stress and abundance of preferred food items in controlling population abundance of the snail Lirabuccinum dirum. J Exp Mar Biol Ecol. [Accessed 2022 Sept 24]; 410: 80-86. doi: https://doi.org/10.1016/j.jembe.2011.10.017.

Owen-Smith N, Fryxell JM, Merrill EH. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philos Trans R Soc Lond B Biol Sci. [accessed 2023 Apr 10]; 365(1550): 2267-78. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2894968/. doi: 10.1098/rstb.2010.0095.

Pardo LM, Johnson LE. 2004, Activity and shelter use of an intertidal snail: effects of sex, reproductive condition and tidal cycle. J Exp Mar Biol Ecol. [accessed 2023 Apr 10]; 301(2): 175-191. https://www.sciencedirect.com/science/article/pii/S0022098103004994#BIB47. doi: 10.1016/j.jembe.2003.09.017.

Rochette R, Dill LM. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. J Exp Mar Biol Ecol. [Accessed 2022 Apr 10]; 253(2):165-191. https://www.sciencedirect.com/science/article/pii/S0022098100002537. doi: https://doi.org/10.1016/S0022-0981(00)00253-7.

Slatkin M. 1987. Gene flow and the geographic structure of natural populations. Science. [accessed 2023 Apr 10]; 236(4803): 787-792. https://www.jstor.org/stable/1699930.

Stamps JA, Krishnan VV, Reid ML. 2005. SEARCH COSTS AND HABITAT SELECTION BY DISPERSERS. Ecology. [accessed 2023 Apr 18]; 86: 510-518. https://esajournals.onlinelibrary.wiley.com/doi/10.1890/04-0516. doi: 10.1890/04-0516.

Swingland IR, Greenwood PJ. 1983. The ecology of animal movement. Ox Clar Press. [accessed 2023 Apr 18]. https://www.researchgate.net/profile/Graham-Pyke/publication/260599391_Animal_movements_An_optimal_foraging_approach/links/61ade3ea50e22929cd4e9c85/Animal-movements-An-optimal-foraging-approach.pdf.

Theuerkauf J, Rouys S, Chatreau C. 2007. Mortality of radio-tracked wild rats in relation to transmitter weight and resilience of transmitters in relation to their design. J Roy Soc NZ. [accessed 2023 Apr 10]; 37(3): 85-90. https://www.tandfonline.com/doi/epdf/10.1080/03014220709510538?src=getftr.

Vuza DT, Chiţu S, Svasta P. 2010. An RFID tag simulator for the FDX and HDX protocols. IEEE 16th Int Symp Design Tech Elect Pack (SIITME). [accessed 2022 Apr 10]: 53-58. https://ieeexplore.ieee.org/abstract/document/5653722/authors#authors. doi: 10.1109/SIITME.2010.5653722.

Want R. 2006. An introduction to RFID technology. IEEE Per Comp. [accessed 2022 Apr 19]; 5(1):25-33. https://ieeexplore.ieee.org/abstract/document/1593568. doi: 10.1109/MPRV.2006.2.

Wilson CD, Arnott G, Reid N, Roberts Dai. 2011. The pitfall with PIT tags: marking freshwater bivalves for translocation induces short-term behavioural costs. Anim Behav. [accessed 2023 Apr 10]; 81(1): 341-346. https://www.sciencedirect.com/science/article/abs/pii/S0003347210004057?via%3Dihub. doi: 10.1016/j.anbehav.2010.10.003.

Zar JH. 2010. Biostatistical analysis. 5th ed. New Jersey: Pearson.

[GC] Government of Canada. 2023. Historical Data; [updated 2023 Jan 31; accessed 2023 Mar 12]. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

[DFO] Department of Fisheries and Oceans Canada. 2023. Tides, currents, and water levels; [updated 2023 Apr 5; accessed 2023 Mar 12]. https://www.tides.gc.ca/en/stations/08545/2022-06-19?tz=PDT&unit=m.

APPENDIX A

Field site information

At the site, a right triangle was delineated by three screws drilled into rock, the distances between each screw measured. From screw one (T1) to screw two (T2), the distance was 12.34 m, from T2 to screw three (T3), the distance was 18.35 m, and from T3 to T1, the distance was 13.60 m. When considered as points on a graph, T1 is located at (0 m, 0 m), T2 at (0 m, 12.34 m), and T3 at (13.6 m, 0 m). These three points formed a right triangle that stood as the basis for triangulation measurements (Fig. 3). Directionally, T1 was the origin, T2 pointed west from the origin, and T3 pointed north.

Triangulation equations

Snail coordinates were calculated using three distance measurements in the following triangulation equation:

$$y = \frac{{x_1}^2 - {x_2}^2 + {y_1}^2 - {y_2}^2 - {d_1}^2 + {d_2}^2}{-2(y_2 - y_1)} \qquad (1),$$

where y is the y-coordinate of a snail's position. The variables d_1 and d_2 correspond to the distances between a detected snail and T1 and T2, respectively. The variables x_1 and x_2 represent the x-axis coordinates of T1 and T2, and y_1 and y_2 represent the y-axis coordinates of T1 and T2, respectively. The coordinates of these two triangulation locations were T1 (0, 0) and T2 (0, 12.34) and thus the equation was simplified as:

$$y = \frac{-152.28 - {d_1}^2 + {d_2}^2}{-24.68} \qquad (2).$$

Once y was calculated, it was used to find x, the x-coordinate of a snail's position using a distance measurement from T3:

$$x = \frac{2y(y_3 - y_2) + {x_2}^2 - {x_3}^2 + {y_2}^2 - {y_3}^2 - {d_2}^2 + {d_3}^2}{-2(x_3 - x_2)} \qquad (3),$$

where d_3 is the distance of a detected snail to T3 and x_3 and y_3 are the x-axis and y-axis coordinates of T3. Using equations 2 and 3, the coordinates (x, y) of each snail were determined every second day.

APPENDIX B

Benefits of RFID technology

Recent radio frequency identification technology (RFID) has provided a way to overcome some of these mark-recapture limitations (Hale et al. 2012). RFID can identify distant or obscured objects if they have an integrated tag. RFID can be programmed to distinguish many different individualized tags and can obtain information about environmental factors and the individual tagged (Want 2006). Tagged animals are equipped with a passive integrated transponder (PIT) tag that, coupled with an RFID reader, can detect the location of the individual (Gibbons and Andrews 2004). PIT tags can vary in size, though the microchip is only 10 to 14 mm in length and two mm in diameter before the protective glass casing is added (Gibbons and Andrews 2004). The glass case is important to prevent tissue irritation and to protect the PIT microchip from eroding in or on the tagged organism, preventing negative effects that could lead to mortality of the organism and failure of the PIT tag itself (Gibbons and Andrews 2004; Want 2006). Using a gel epoxy adhesive to attach the PIT tag to the dorsal exterior of a snail's shell is the most proven method of tagging success (Hale et al. 2012; McLeod 2016). Similar to a barcode, PIT tags acts as unique identifiers for each tagged individual (Gibbons and Andrews 2004; Hale et al. 2012). RFID technology can be utilized in both an active and passive manner. While active PIT tags need to be connected to an outside power source such as a battery or power outlet, passive tags do not (Want 2006). Two types of PIT tags are commonly produced and used in mark-recapture studies. Active, or full duplex (FDX) tags, and passive, or half duplex (HDX) tags differ in their method of communication with the RFID reader (Vuza et al. 2010). FDX tags emit a signal to the reader while the reader collects that signal and sends its own to the tag. HDX tags must be charged by the reader before they emit a signal back (Vuza et al. 2010). HDX tags work well in field studies involving mobile, shelled invertebrates because they have an indefinite operational life and can be adhered to hard surfaces (Gibbons and Andrews 2004; Want 2006). This tag type is good for studies in the intertidal zone, because it is resistant to transmission noise due to highly conductive seawater, allowing researchers to locate and identify snails covered by a layer of seawater (Hayford et al. 2018). Any hesitation toward using PIT tags in invertebrate research has been due to assumed negative effects on mobility, microhabitat access, and foraging. However, these possible negative effects have not been observed in studies of snails or abalone equipped with PIT tags (McLeod

2016; Hale et al. 2015). When used in mark-recapture studies, PIT tags allow researchers to efficiently identify small, camouflaged animals as well as those that are hidden in complex habitats such as mussel beds or rocky terrain (Gibbons and Andrews 2004; McLeod 2016).

APPENDIX C

Statistical analysis

Welch's two-sample t-test does not require that samples have equal variances. Welch's t-test calculates degrees of freedom based on: $df = (s_1^2/n_1 + s_2^2/n_2)^2$ / { [$(s_1^2/n_1)^2 / (n_1 - 1)$] + [$(s_2^2/n_2)^2 / (n_2 - 1)$] }.

Required Permits

Due to the nature of this study and the location of our field site, several permits were required. The BMSC Animal Use Protocol for Invertebrates other than Cephalopods was submitted to BMSC. A License to Fish for Experimental, Scientific, Educational or Public Display Purposes was obtained from the Department of Fisheries and Oceans. To conduct research on the traditional lands of the Huu-Ay-Aht First Nations, a Heritage Investigation Permit was also obtained.