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Daily and seasonal spatial behaviour of waved whelk *Buccinum undatum*: implications for fishery management and restoration

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Abstract

Many marine invertebrate fisheries are vulnerable to overexploitation and require conservation measures to ensure their sustainability. In recent years, landings of waved whelk *Buccinum undatum* (Linnaeus, 1758) have fallen considerably along the coasts of the St. Lawrence (Canada), dropping by up to 76% in some fishing areas. Local overfishing may be explained, in part, by the species' oviparous reproduction, which limits larval dispersion and population interactions. Using a 2-year long-term acoustic telemetry study, we tracked 20 individuals to assess their general movement behaviour and potential to disperse within an area. Tagged individuals displayed considerable daily movements (from a mean of 2 to 16 m/h), with no sensible differences between day and night. Both speed and habitat usage potential (HUP) varied among seasons, most likely due to the species' reproductive cycle: HUP was significantly larger during the breeding season of May (4570 m^2) and June (2779 m^2) than in the preceding winter months (1046 m^2). Although some individuals moved over a considerable depth range, we did not observe seasonality over the bathymetric gradient of the area. Overall, the species' restricted HUP limits individual dispersal, resulting in very poor connections between neighbouring populations and making *Buccinum undatum* vulnerable to local overfishing.

Key words: acoustic telemetry, fishery management, movement ecology, *Buccinum undatum*, Gastropoda, overfishing

1. Introduction

Locomotion is of great importance as an evolutionary strategy to enable animals to actively interact with their environment (Shaw 2020), influencing myriad ecological and evolutionary processes including connectivity among communities, range expansions, invasions, and population persistence (Allen et al. 2018). Recent advances in marine GPS-tracking, passive acoustic technologies, and fine-scale remotely sensed data now enable simultaneous quantification of individuals interactions with conspecifics and the landscape (Michelot et al. 2021; Costa-Pereira et al. 2022; Redaelli et al. 2022). Such information has improved our knowledge on multiple ecological aspects of oceans and marine organisms, although many features remain unexplored.

To address such deficiencies of observations, a growing number of studies have shown that modern acoustic telemetry may be used to understand the movement of many benthic invertebrate species to quantify their natural behaviour and to contribute to fisheries management (Hussey et al. 2015). Acoustic telemetry has proven its effectiveness to monitor the functioning of various fisheries, providing essential information to enhance their comprehension and the efficacy of restoration efforts (Crossin et al. 2017; Lavoie et al. 2022; Hewitt et al. 2023). Tracking systems generate short and long-term data on habitat usage to identify habitat-specific behaviours and determine areas of great ecological value (Crossin et al. 2017; Morse et al. 2018). They also provide information on fisheries interactions, addressing important questions relating to populations dynamics and connectivity between local communities (Lavoie et al. 2022; Sclafani et al. 2022; Lees et al. 2023).

The knowledge provided by these technologies allows scientists to better assess the status of fisheries resources and provide scientific advice to managers. Many marine invertebrate fisheries are highly vulnerable to local overfishing (Coates et al. 2013; Alati et al. 2020; Giglioli et al. 2021), requiring conservation measures to ensure their sustainability. For example, after observing that predatory whelks (i.e., *Busycotypus canaliculatus* (Linnaeus, 1758) and *Busycon carica* (Gmelin, 1791)) were attracted to newly planted scallop aggregations and therefore potentially negatively affecting local restoration efforts, Sclafani et al. (2022) recommended an approach to restore overexploited seabeds. Likewise, Konzentisch and Evans (2020) proposed limiting captures of the tropical queen conch *Lambis lambis* (Linnaeus, 1758) given the species' poor dispersion capacity and related high sensitivity to localised overexploitation.

Among molluscs, it is a common perception that gastropods represent slow-moving animals that undertake relatively limited displacements by gliding on a mucus-covered muscular foot (Coates et al. 2013; Konzewitsch and Evans 2020). However, acoustic telemetry reveals behaviours that track their daily and seasonal needs, with gastropods being able to cover considerable distances relative to their body size (Stieglitz and Dujon 2017; Konzewitsch and Evans 2020; Schlaff et al. 2020). For example, the predatory marine gastropod *Charonia tritonis* (Linnaeus, 1758) can cover up to 234 m/day to prey on crown-of-thorns starfish *Acanthaster planci* (Linnaeus, 1758) along the Great Barrier Reef, whelks doubling their covered distances during the night (Schlaff et al. 2020). Recent observations also suggest some seasonal mobility adaptations for a given species' life cycle and environmental conditions. In an Indian Ocean atoll, the mean habitat usage potential (HUP) of *Lambis lambis* was three times greater during the tropical summer relative to the preceding months (Konzewitsch and Evans 2020). In our focal species, the waved whelk *Buccinum undatum* (Linnaeus, 1758), a mark-recapture study estimated that individuals displayed mostly nocturnal activity, covering appreciable distances and move relatively quickly when stimulated by a baited trap (30–50 linear m/day; Himmelman 1988). However, mark-recapture methods do not provide information on total and seasonal displacements, making exploratory behaviours over study areas difficult to interpret and potentially underestimate the general mobility of individuals (Cote et al. 2019; Florko et al. 2021).

Along North Atlantic coasts, waved whelk *Buccinum undatum* constitutes an international fishery of great commercial value (Pêches et Océans Canada 2022*a*, 2022*b*). In the Gulf of St. Lawrence (Canada), however, regional whelk landings have declined substantially since 2017, with catch per unit effort of many fishing zones being between 3% and 49% lower than their historical median from 2002 to 2018 (Pêches et Océans Canada 2022*a*). According to local authorities, the status of an increasing number of *Buccinum undatum* stocks in the St. Lawrence is "concerning", with estimates predicting that they are unable to support long-term fishing effort (Pêches et Océans Canada 2022*a*). To conserve the regional community structure, the current conservation status of various populations requires a better understanding of the species' biology and ecology (Ashfaq et al. 2019; Borsetti et al. 2020; Pêches et Océans Canada 2022*a*). In particular, the species is characterized by delayed sexual maturity (i.e., 5–6 years) for both sexes and an oviparous reproduction strategy with internal fecundation, females laying eggs on hard structures found over the seabed from which developed larvae hatch (Martel et al. 1986; Ashfaq et al. 2019). The lack of a pelagic larval form has been hypothesized to define the isolation of single populations, potentially limiting their dispersal and perennity (Ashfaq et al. 2019). In this regard, a palaeoecological study found that risk of local extinction of gastropods may be related to life history traits that result in low colonization ability (Neubauer and Georgopoulou 2021). Acoustic telemetry could provide valuable information on the movement ecology of *Buccinum undatum*, yielding evidence of long-term population connectivity and persistence.

Using a 2-year acoustic telemetry array at a site on the North coast of the St. Lawrence (or *Magtogoek* following the First Nations' name), our study aims to provide more accurate information on the daily and seasonal movement of the marine gastropod *Buccinum undatum*. Our goal is to assess the animal's spatial behaviour and evaluate the effect of seasonal variability on its distribution. We assessed specific features of its mobility over the seabed, including the total travelled distance, day/night speed of displacement and their HUP across seasons. Together, this should allow the potential interconnectivity between neighbouring whelk populations to be better understood to evaluate the vulnerability of the species to localised overfishing.

2. Materials and methods

2.1. Study area

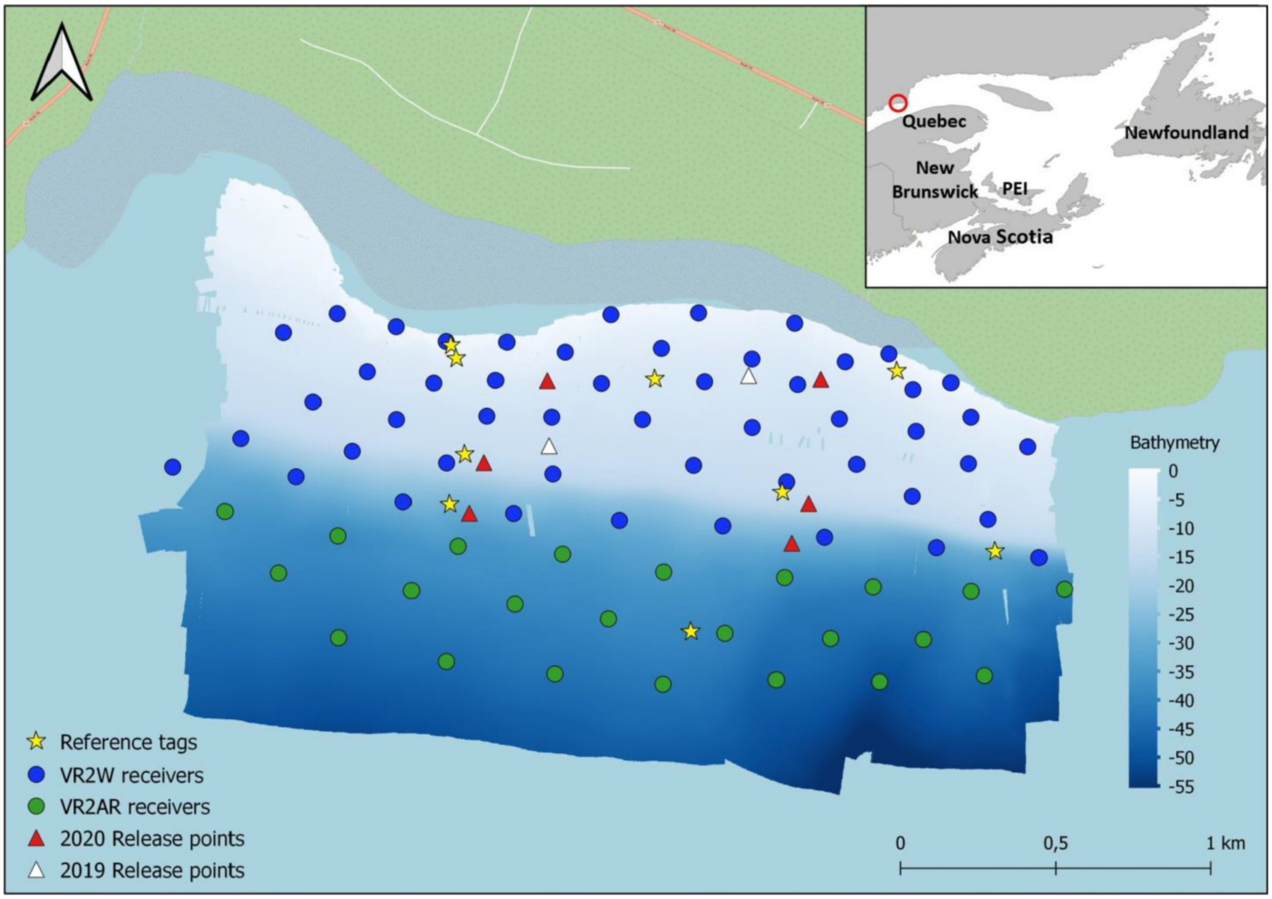
To investigate *Buccinum undatum* mobility patterns, we deployed an acoustic telemetry array in the Petite baie de Saint-Nicolas near Godbout, on the north shore of the St. Lawrence (N 49.302, W −67.685; Fig. 1). The entire area has a typical sub-arctic climate, with long, harsh winters and short, cool summers. This strong seasonality is reflected in the marine environment, where bottom waters cool down considerably during the winter/spring months (−1.2 °C) and then warm up during the summer (up to 16.9 °C at 13 m depth, Fig. 2). The substrate of the study site is characteristic from areas where *Buccinum undatum* is typically found along the St. Lawrence coasts (i.e., mixed substrate/rocks, sand, and gravel).

The bay displays a slight and regular slope down to a depth of 15 m, and then drops off to 50 m (Fig. 1). The regularity of the bottom and the strong seasonality make it an excellent study site for using acoustic telemetry to observe seasonal migrations of benthic species occupying the area.

2.2. Receiver array

Our study was done over 2 years and two types of receivers were deployed: VR2W and VR2AR (Innovasea, Canada). VR2W receivers were situated in shallower areas, whereas VR2AR

Fig. 1. Location of the receiver array during the 2020/2021 monitoring season within the study area of Petite baie Saint Nicolas, Quebec, Canada. Blue points are VR2W receivers, green points are VR2AR receivers, and yellow stars are reference tags deployed within the area. Release points of whelks *Buccinum undatum* in August 2019 are represented by the white triangles and October 2020 by the red triangles. The bathymetry of the study area is also shown. The base map is from OpenStreetMap (OSM). The bathymetric map was provided by CIDCO (Centre Interdisciplinaire de Développement en Cartographie des Océans). The map projection is in NAD83 (North American 1983 Datum) and the geographic coordinates are in UTM (Universal Transverse Mercator).



with an acoustic release system were deployed in areas that were too deep to dive (Fig. 1).

The first year of observations covered the period from August 2019 to July 2020 and included 26 receivers (18 VR2AR and 8 VR2W). In October 2019, 6 more VR2W receivers were added to the original array. From June 2020 to October 2021, the first array was enlarged with 36 VR2W and 5 VR2AR receivers (Fig. 1). Our array covered an area of approximately 2.7 × 2 km. Receivers were spaced approximately 500 m apart across most of the array; this distance was reduced to 50–100 m along the shallow shoreward edge of the array. Range tests across different depths at the site were used to assess detection efficiencies and determine receiver spacing. As signal detection was lower in shallow water, distances between receivers were reduced in the shallower part of the study area.

The VR2AR acoustic receivers and HOBO temperature loggers recorded temperature to monitor seasonal and daily variations within the study site. All records were used to create a thermal array so that every whelk location could be paired with specific temperatures.

2.3. Tagged animals

Animals from two main sites separated by approximately 1 km were used to assess subpopulation connectivity. In each site, three sampling points were defined as a function of study area depth (Fig. 1). Animals were collected by scuba divers, brought to the surface and transmitters glued to the shells using epoxy glue (Lepage Ultra superglue$^{\text{TM}}$; Fig. 3). Handling was limited as much as possible and tagging was done immediately following collection. Animals were kept in containers for a period of 15–30 min to allow the glue to fully set and then divers returned them to the same location on the bottom from where they were collected. As the tagging procedure may alter the natural behaviour of tagged animals, we only consider data collected after the first 24 h (see also Stieglitz and Dujon 2017; Cote et al. 2019; Lavoie et al. 2022).

V9-1x and V9-2x acoustic tags were used (Innovasea; tag dimensions of 9 × 24 mm with a weight in water of 2 g) and programmed to emit a signal at a frequency of 69 kHz every 120/140 and 180/300 sec, respectively. Batteries in tags have an estimated autonomy of 672 days for V9-1x tags and 912

Fig. 2. Temperatures experienced by tracked waved whelks *Buccinum undatum* all over the monitoring period. Temperature values were directly related to the position of each individuals over the study area. Summer months of June, July, and August show a great thermal variability, while winter months show constant cold temperatures.

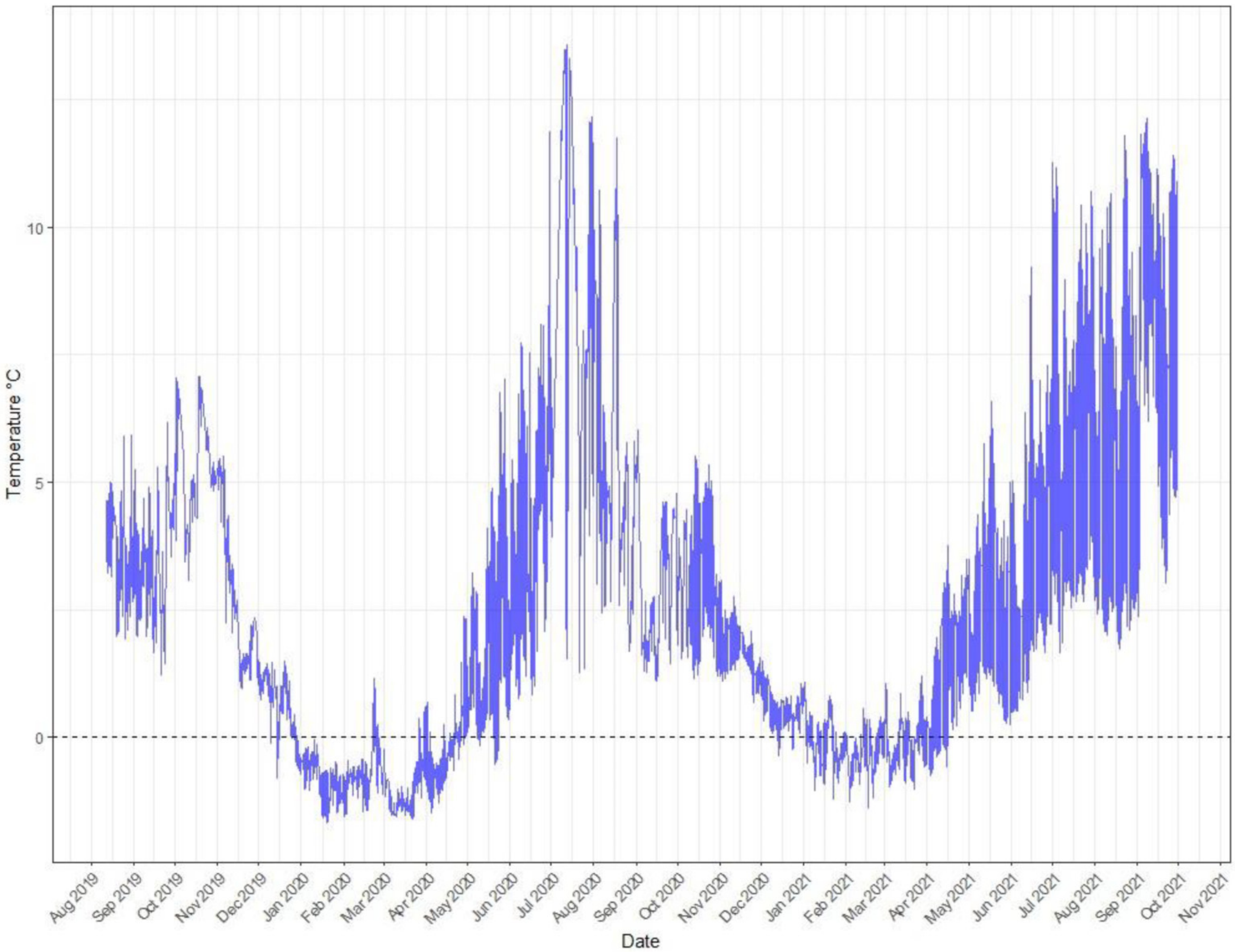


Fig. 3. Picture of acoustic V9-1x tag on waved whelk *Buccinum undatum* attached with epoxy glue on the upper part of the shell—© K. A. MacGregor.

Table 1. Data summary of the 20 retained tagged waved whelks *Buccinum undatum* with shell length at the time of tagging, No. of tracking days for each individual, spatial metrics, and habitat usage potential.

Tag ID	Length (cm)	Release zone	Date of first detection	Date of last detection	No. of days	% Retention rate				Tot. trav. dist. (km)	Net dist.(m)	HUP (m^2)
						2019/2020	2020/2021					
						T1	T2	T3	T4			
21	8.5	East	12/08/2019	15/10/2021	790	79.4	78	51	37	48.303	257	37 171
24	8.8	East	12/08/2019	17/10/2021	790	70.7	80	54	50	66.347	86	8054
25	8.5	East	13/08/2019	16/10/2021	790	77.2	87	59	58	220.062	345	209 949
27	9.1	East	12/08/2019	28/05/2020	291	88.4				10.083	239	7872
40	7.5	East	12/08/2019	05/07/2020	324	92.1				15.770	93	5542
42	7.6	East	12/08/2019	05/07/2020	324	90.9				14.240	94	5984
69	9.1	West	11/10/2020	15/10/2021	370			57	66	86.072	352	38 793
70	8.6	West	11/10/2020	15/10/2021	370			54	41	5.677	553	15 005
71	9.1	West	11/10/2020	15/10/2021	370			60	47	56.661	60	13 000
72	9.2	West	11/10/2020	14/10/2021	369			70	67	110.984	585	78 522
73	8.9	West	11/10/2020	15/10/2021	370			48	59	69.879	381	40 229
78	9.4	West	11/10/2020	14/10/2021	369			50	57	69.117	330	29 114
81	8.2	West	11/10/2020	31/05/2021	232			54	39	35.690	381	34 603
82	8.2	West	11/10/2020	15/10/2021	370			60	55	74.658	304	18 032
83	7.4	East	13/10/2020	30/07/2021	290			33	37	11.939	267	10 777
93	9	East	10/10/2020	09/10/2021	364			62	37	63.775	533	44 771
4	7.4	East	10/10/2020	15/10/2021	371			53	41	29.604	143	15 280
15	8.2	East	10/10/2020	31/05/2021	233			50	55	39.099	123	5539
44	7.9	East	13/10/2020	31/08/2021	322			41	37	32.155	205	23 976
46	7.9	East	13/10/2020	31/07/2021	291			30	46	19.411	63	9698

Note: Percent of retention rate columns indicate the proportion of detections that were maintained after filtration to calculate spatial metrics. 95% kernel habitat usage potential (HUP) is reported. Dates are given as dd/mm/yy.

days for V9-2x tags. This allowed us to follow animal movements over long time periods (>1 year). In August 2019, 16 animals were initially tagged; 36 further individuals were then tagged in July 2020.

During the tagging procedure, the Canadian Council on Animal Care guidelines were followed and permits for field and observational work were granted by Fisheries and Oceans Canada of the government of Canada.

2.4. Data filtering and quality control

Fine-scale positioning data were provided by Innovasea after analysis of the raw receiver detection logs and included a measure of positioning error for stationary and synchronization tags (HPE: horizontal positioning error). Data collected from fixed-location synchronization tags of receivers were used to establish an acceptable error threshold to filter the dataset and assess the quality of positioning data (see also Meckley et al. 2014; Florko et al. 2021).

The four datasets resulting from August 2019 to October 2021 (T1, T2, T3, and T4) were characterised by different distributions of HPE values. To maintain consistency between the four datasets, we filtered the data using threshold HPE values that corresponded to similar errors in metres. In particular, the T1 dataset going from August 2019 to July 2020 showed an error of 7.24 m (HPE 20); the T2 dataset going from July 2020 to October 2020 showed an error of 14.14 m (HPE 8); the T3 dataset going from October 2020 to May 2021 showed an error of 16.9 m (HPE 4); the T4 dataset going from May 2021 to October 2021 showed an error of 15.02 m (HPE 3).

Of the 16 individuals tagged in 2019, we retained 6 individuals that presented a sufficiently high number (>50%; mean proportion of detections retained 72%) of locations with HPE values less than 20 (Table 1). Of the 36 individuals tagged in 2020, we retained 14 individuals that presented a sufficiently high number (>50%) of localisations with an HPE value of less than 8–4–3 (T2–T3–T4; Table 1). The remaining individuals were considered to have lost their transmitters or presented a considerable number of detections with significant errors and were thus excluded from subsequent analyses.

After this initial filtration based on HPE values, we applied a second filter based on maximum biologically possible speeds to eliminate positions considered to be incorrect (Fig. S1). We thus calculated movement speeds for every step and eliminated all points representing steps where whelks would have had to travel at speeds > 25 m/h. This speed was selected by means of analysis of a series of baited camera videos at our study site in which *Buccinum undatum* were never observed to exceed 20 m/h, despite the attraction by bait.

A series of V9 and V13 reference tags (Innovasea; transmission delays of 540/660 and 500/700 sec, respectively) were deployed over our study area to validate whelk habitat usage (Fig. 1). Tags were at fixed positions on moorings over the whole study period. The related data provides a general idea of the potential measurement errors that could occur over specific times of the year. Before undertaking the analysis of habitat usage, reference tag datasets were filtered using the same parameters used for tags deployed on animals to compare between tags.

2.5. Calculation of behavioural metrics

2.5.1. Total and net travelled distances

We calculated Euclidean distances to sum the consecutive travelled distances between successive locations determined through X and Y coordinates calculated for each whelk to define the total travelled distance. In addition, we calculated the total net travelled distance for each animal considering the distance between the first and the last recorded location of the study period, thus estimating a drift potential of individuals from their release point.

2.5.2. Standardised speed

As observations were not homogeneously distributed over the day (with only a few hours per day covered by recordings), a standardised speed of displacement was calculated from the recorded travelled distance (metres) over the related time of the observation (hours). Standardised speeds (m/h) were then calculated over day and night periods to assess potential variation between the two light regimes. To observe any seasonal patterns, the resulting standardised speed was used to evaluate variation in movement between night and day over different months of the study period.

To assess diel behaviour of *Buccinum undatum*, standardised speeds were sorted into two light regimes based on the hours of sunset/sunrise: day hours are between sunrise and sunset and night hours are between morning and evening nautical twilight. Python package "ephem 4.1.4" (Rhodes 2011) for performing high-precision astronomy computations was used to determine sunrise/sunset hours of each day of the year at the study site.

2.5.3. Habitat usage potential calculation

The HUP for each individual was estimated using the kernel method to create a utilisation distribution (KUD; Van Winkle 1975; Worton 1989) to describe the probability that an animal can be found in a given location. Of the available analytical methods, Börger et al. (2006) found that the kernel method was the most unbiased home range estimator across sampling regimes and was also more robust to relatively small sample sizes. KUD estimation using a bivariate normal kernel density estimate with a reference bandwidth smoothing parameter for 95% KUD has been used to calculate the home ranges of many species with a 50% KUD often considered to be the "core area" of space use by individuals (Konzewitsch and Evans 2020). Since the concept of home ranges is difficult to apply to mobile benthic marine animals which tend not to display fidelity to certain sites or coherent usage patterns at the time-scales considered (without considering the habitat use of the larval life stage), we used the term HUP instead of "home range" and "core area". We thus calculated the HUP of individuals as the area (m^2) of the 95% KUD. We also calculated the HUP area for each month of the study period to evaluate potential seasonal behavioural changes.

Table 2. Equations used in statistical analyse.

$\text{Standardised speed} \sim \mathbf{M} + \mathbf{Y} + \mathbf{DN} + \mathbf{T} + \mathbf{R} + \mathbf{M{:}T} + (1\mid \textit{Individual})$	(1)
$\text{HUP} \sim \mathbf{M} + \mathbf{Y} + \mathbf{T} + \mathbf{R} + \mathbf{M{:}T} + (1\mid \textit{Individual})$	(2)

Note: Fixed effects are in bold (month (M), year (Y), day and night period (DN), temperature (T), release area (R) and interaction between month, and temperature (M:T)), while random effect is in italic. See Section 2.6 for details. HUP, habitat usage potential.

To examine connections and any subsequent mixing between groups of individuals released in the western and eastern parts of the bay (Table 1), we calculate the total HUP of each group as well as the percentage of overlap during the study period.

2.5.4. Depth preference

A detailed bathymetric map of the study site was provided through a collaboration with CIDCO (Centre Interdisciplinaire de Développement en Cartographie des Océans), who undertook a multibeam survey in 2019. We matched the coordinates of each detection with the depth from the bathymetric map, and then calculated an average depth for individuals for each month of the study period to evaluate depth shifts over the bathymetric gradient.

2.6. Statistical analyses

Standardised whelks' speeds and variations in HUP were analysed using linear mixed models (LMMs) including different explanatory variables in addition to a single random effect (Table 2). LMMs allow considering intra-individual variability by including a random effect for each individual and include fixed effects to assess the impact of different variables on measures. Two models were generated for each of the two considered behavioural parameters (i.e., standardised speed and HUP; Table 2) and the significance of each factor was assessed within the model (Table 3).

Among different fixed effects at our disposal, only factors expected to affect whelks' movement were selected to be included in the models (such as period of the year and day, thermal conditions, and release area; Table 2). The interaction between the period of the year (i.e., month) and temperature (see Table 2) was used to assess potential variations in the relationship between whelks' movement and thermal conditions over seasons. The size of the individual was tested on the two models and found to be not significant. Due to our restricted sampling range (limited to larger individuals from 7.4 to 9.4 cm; Table 1), the size factor was thus removed from the models.

Model fit was graphically validated after residuals inspection (see Figs. S2 and S3) and HUP values were log-transformed to approximate normality of residuals. Factor interactions did not create significant problems with multicollinearity and thus remained in the final models (Fig. S4). All analyses were conducted using R (version 4.2.2; R Core Team 2022) using the packages "lme4" (Bates et al. 2015) and

Table 3. Outputs from linear mixed models considering the influence of different fixed factors (i.e., month, year, temperature, release area, and interaction between month: temperature) on the individuals' standardised speed and habitat usage potential (HUP) over the study period.

Stand. speed	β	SE	χ^2	Df	*P*-value
Month			765.51	11	**< 0.001**
Year	0.43	0.18	6.07	1	**0.013**
DayNight	1.37	0.10	176.08	1	**< 0.001**
Temperature	0.11	0.08	0.002	1	0.964
Release area	– 3.08	0.91	11.43	1	**< 0.001**
Month: Temperature			97.32	11	**< 0.001**
HUP	β	SE	χ^2	Df	*P*-value
Month			42.35	1	**< 0.001**
Year	– 0.03	0.21	0.01	1	0.899
Temperature	0.3	0.15	1.2	1	0.273
Release area	0.64	0.26	6.07	1	**0.013**
Month: Temperature			10.84	11	0.456

Note: The variances of the random effect "Individual" were 7.89 and 0.21 for stand. speed and HUP, respectively. Significant effect (*P*-value < 0.05) is indicated in bold. HUP was log-transformed to approximate normality of residuals.

"car" (Fox and Weisberg 2018) to get the significance of the test. A significance *P*-value of 0.05 was used for all analyses.

3. Results

3.1. Inter-individual variability in travelled distances and habitat usage potential

Of the 2019 tagged whelks, three were followed for approx. one year (from August 2019 to July 2020), while three other individuals were detected during the entire study period (from August 2019 to October 2021; Table 1). Of the 2020 tagged whelks, 14 were successfully detected from 232 to 371 days (from October 2020 to October 2021; Table 1).

Mobility varied greatly among individuals, showing high inter-individual variability of movements. Over single days (24 h), whelks were able to move between a mean of 449.7 m/day (±15.2 standard error (SE); tag No. 72) and 61.1 m/day (±4.1; tag No. 81). Several individuals showed a maximal daily travelled distance up to 600 m (tag No. 25, 69, 72, 73, 93), while they did not move in some days (i.e., less than 1 m travelled distance). All tracked individuals showed a mean daily net travelled distance of 8.2 m/day (±0.39) all over the study period, with maximal values between 30 and 90 m/day.

Of the tagged whelks, tag No. 25 travelled the greatest total distance (220 km) over 790 monitoring days, with others moving over a mean total distance of 45.23 km (±6.82), although over different monitoring periods (see Table 1). The large discrepancy in linear movements among individuals was reflected in HUP values, with tag No. 25 exploring a total area of 209 900 m^2 compared to others with a mean HUP of 23 261.15 m^2 (±4326.38; Table 1). Overall, there was a great inter-individual variability in HUP, with some individuals exploring large areas (>100 000 m^2; e.g., tag No. 25, 72, 83) compared to others (<10 000 m^2; e.g., tag No. 15, 24, 42; Table 1).

The mean total net travelled distances of all individuals was 269.75 m (±36.86) from their release point (maximum of 585 m of tag No. 72; Table 1), further indicating that the dispersal potential of individuals remains limited to a restricted area. As a consequence, there was no overlap of HUP (i.e., 0% overlapping) between the two groups released in the east and west parts of the study area during the entire study period.

3.2. Standardised speed

Over the entire study period, there was great inter-individual variability in standardised speed (variance of random effect: 7.89), with whelks moving between a mean of 15.85 m/h (±0.34 SE; tag No. 72) and 5.11 m/h (±0.25; tag No. 83) over the study period. During the day, whelks moved a mean of 10.15 m/h (±0.09), while they moved a mean of 11.32 m/h (±0.09) during the night. Standardised speed varied by month ($P < 0.001$), with an increasing trend during summer months in both day and night periods (Table 3; Fig. 4). Whelks moved a mean of 12.99 m/h (±0.24) and 13.2 m/h (±0.25) in June and July compared to a mean of 8.36 m/h (±0.18) and 9.25 m/h (±0.2) in December and January, respectively (Fig. 4). While this seasonal pattern was marked for some individuals, it was unnoticeable for other whelks that showed only a few months of increased speed or a year-round consistent pattern of mobility (Fig. 5).

The effect of temperature on standardised whelk speeds was a function of months (significant interaction between months and temperature, $P < 0.001$; Table 3). Speed increased as a function of temperature in March, April, and May, the predicted standardised speed increasing by a mean of 0.61 m/h (±0.04) each 1 °C (Fig. 6). In all other months (except November), this positive relationship was not observed, with summer months showing constant standardised speeds despite increasing temperatures (Fig. 6).

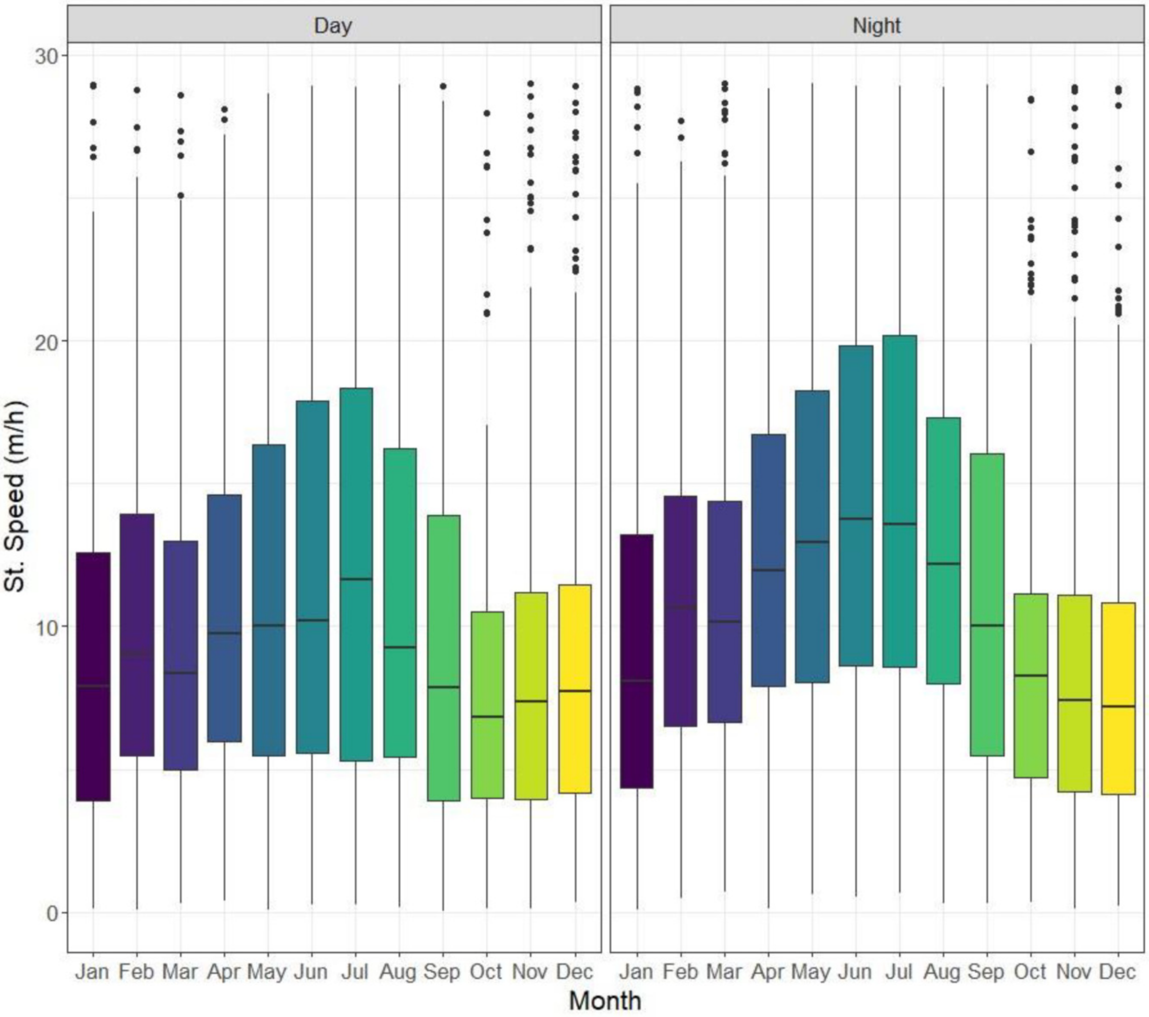
The release area also showed a significant effect on whelks mobility ($P < 0.001$; Table 3), with individuals from the west site showing a mean standardised speed of 12.66 m/h (±0.1) compared to a mean of 9.57 m/h (±0.07) in the east site.

3.3. Seasonality of habitat usage potential (HUP)

HUP varied significantly among months ($P < 0.001$), with the proportion of explored area by whelks increasing during May and June (Table 3; Fig. 7). In this period, whelks explored an average area that was 60.8% and 82.2% larger than previous and following months, respectively. Mean HUP in May and June corresponded to 4570.6 m^2 (±1407.26 SE, $n = 20$) and 2779.27 m^2 (±611.18, $n = 22$) compared to those in April (2438.45 $m^2 \pm 811.76$, $n = 21$) and July (1159.9 $m^2 \pm 215.95$, $n = 19$). The lowest mean HUP was observed in January (1046.31 $m^2 \pm 231.22$, $n = 20$), followed by July and September (1247.38 $m^2 \pm 276.67$, $n = 16$).

Both temperature and the interaction between temperature and month did not have significant effect on HUP

Fig. 4. Seasonal variations in the standardised speed of waved whelks *Buccinum undatum* over day and night periods over different months of the year. Of note, the great inter-individual variability of recorded speeds.



(Table 3). The release area had a significant effect on whelks mobility ($p = 0.013$), with individuals from the west site showing a mean HUP of 2488.53 m^2 (±277.54) compared to a mean HUP of 1724.13 m^2 (±237.88) in the east site.

3.4. Depth preference

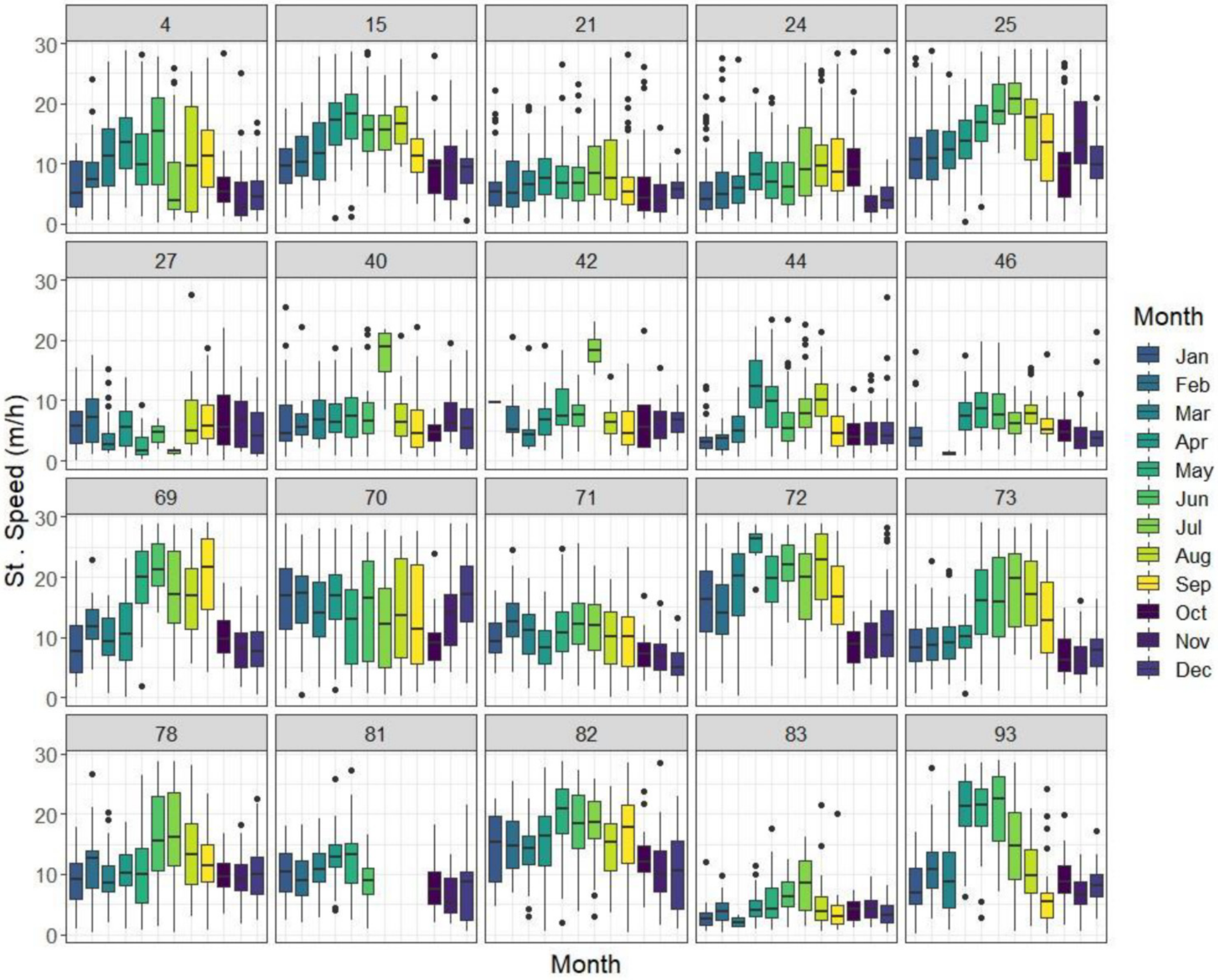
Although some individuals moved over a considerable range of depths during the study period (up to 25 m), no variation in seasonal movements was observed over the bathymetric gradient of the area. Tag No. 25 showed the greatest bathymetric gradient from October 2019 to March 2020, moving from 12.5 to 41 m (Fig. 8). In contrast, several individuals remained at depths similar to their release point throughout the entire year (Fig. 8). The minimum recorded depth was 6.3 m (tag No. 46), while the maximum was 41 m (tag No. 25).

4. Discussion

Our study shows that *Buccinum undatum* displays considerable spatial and temporal variation in behaviour, covering great distances over the year although occupying a relatively small area of the surrounding space. Standardised speeds show that individuals move an average of 5 to 16 m/h during both day and night, allowing animals to explore appreciable portions of the habitat within which they live over the year. The magnitude of travelled distances and HUP are similar to the mobility reported for other gastropods. The tropical giant triton *Charonia tritonis* shows a 95% kernel home range average of 1170 m^2, with an observed maximum of 1788 m^2 over 16 tracking days (Schlaff et al. 2020). In an estuarine habitat in Mexico, the queen conch *Lobatus gigas* (Linnaeus, 1758) exhibited a kernel home range average of 8045 m^2 over 6 months, with the greater amplitude up to 18 500 m^2 (Stieglitz and Dujon 2017). When compared to the same time frame as previous studies, it is evident that *Buccinum undatum* can cover similar areas as tropical gastropods, although some individuals (e.g., tags No. 69 and 72) are observed to travel much greater distances in late spring, demonstrating a greater ability to disperse during this period.

The high inter-individual variability observed in the present study has also been observed for other marine gastropods. Stieglitz and Dujon (2017) suggest that variation of

Fig. 5. Seasonal variation in standardised speed for each tracked waved whelk *Buccinum undatum* over different months of the year. Of note, individuals show a great inter variability of the response, with some whelks showing a marked seasonal pattern, while others showing relatively constant pattern all over the year.

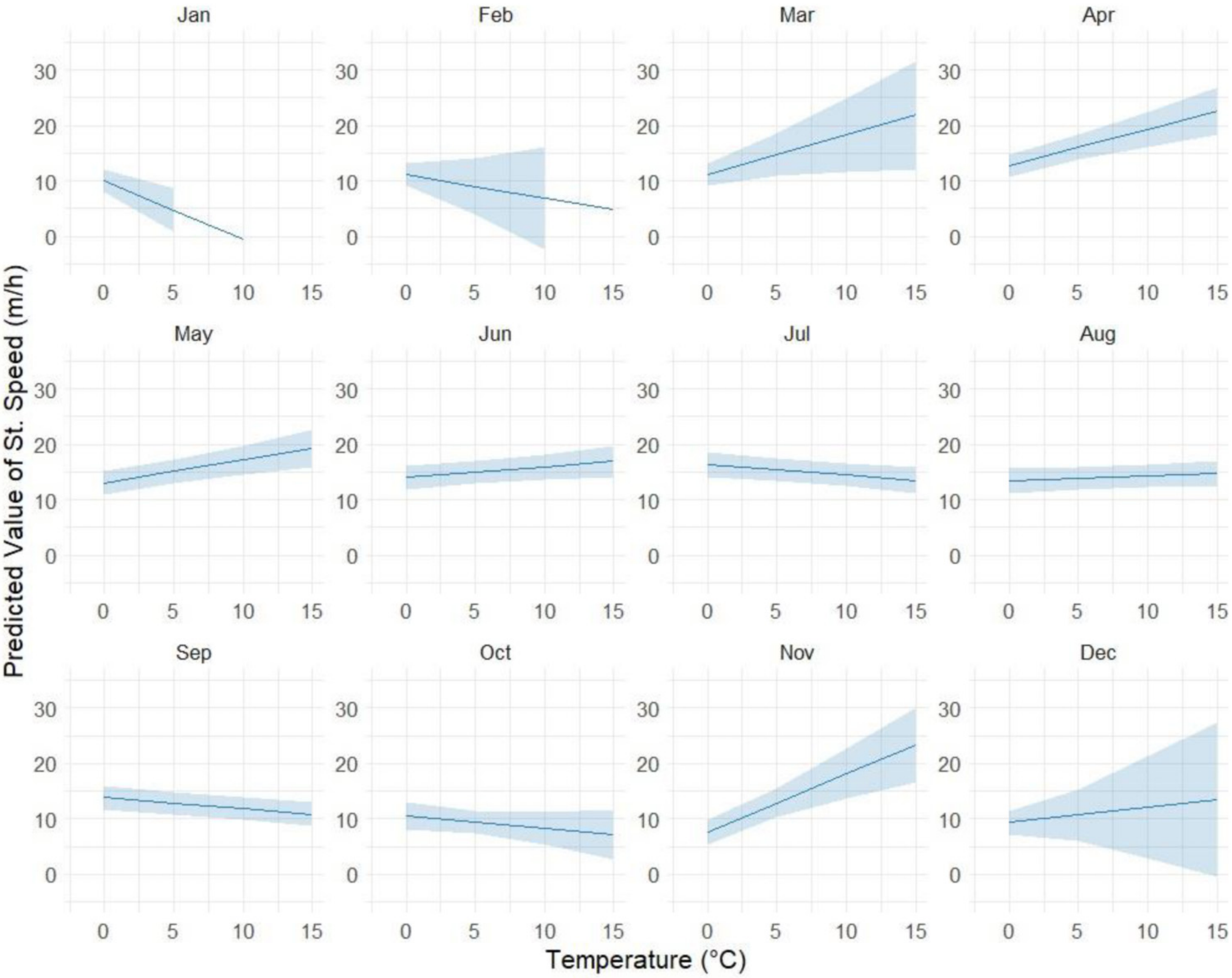


mobility is related to the age of the individuals, with older *Lobatus gigas* moving greater distances than younger ones. In our case, we tagged a very small size range of animals (limited to "large" individuals from 7.9 to 9.4 cm) and thus do not observe a correlation between movement and animal length (and thus age). Variation could also be related to the sex of animals, although this was not determined and thus was not included in our analysis. The observed variations in HUP between the two main release areas could be related to either the individual's sex or the type of substrate in the respective sites.

Although Himmelman (1988) estimated that individuals displayed mostly nocturnal activity, our data show that waved whelks move both the day and night. The statistical differences revealed by our analysis are likely not biologically significant, with only a mean of 1.2 m/h between the two light regimes over the entire study period. The movement of *Buccinum undatum*, however, clearly changes across seasons, increasing speed of displacement and covering greater areas from the late spring (May to June) compared to the rest of the year. Himmelman and Hamel (1993) and Martel et al. (1986) suggested a seasonality of spatial and feeding behaviours for the species. In particular, the proportion of actively feeding individuals increased from late autumn to early spring, with stationary whelks being more frequent on sandy bottoms during the winter (Martel et al. 1986; Himmelman and Hamel 1993). Our results show that *Buccinum undatum* appears to move over a limited area during the cold winter season, most likely in search of food, as Martel et al. (1986) found that 40%–60% of whelks had food in their stomachs during the winter and early spring (and only 0%–8% in summer).

Through the months of May and June, the species shows an increased HUP, likely due to reproductive needs. Indeed, Martel et al. (1986) used histological analysis of the reproductive organs to suggest that the mating season of *Buccinum undatum* on the north coast of the Gulf of St. Lawrence begins in mid-May, reaches a peak in June, and terminates in July. Most of our individuals displayed about twice the HUP during May and June than they did during the previous and following months. As *Buccinum undatum* has separate sexes and

Fig. 6. Predicted values of standardised speed according to our first model concerning the interaction between month and temperature. Note that although the model includes temperatures of up to 15 °C, these values cannot be reached during the winter months within our study area. The present figure illustrates the eventual existing relationship between mobility potential of waved whelks *Buccinum undatum* and temperature.

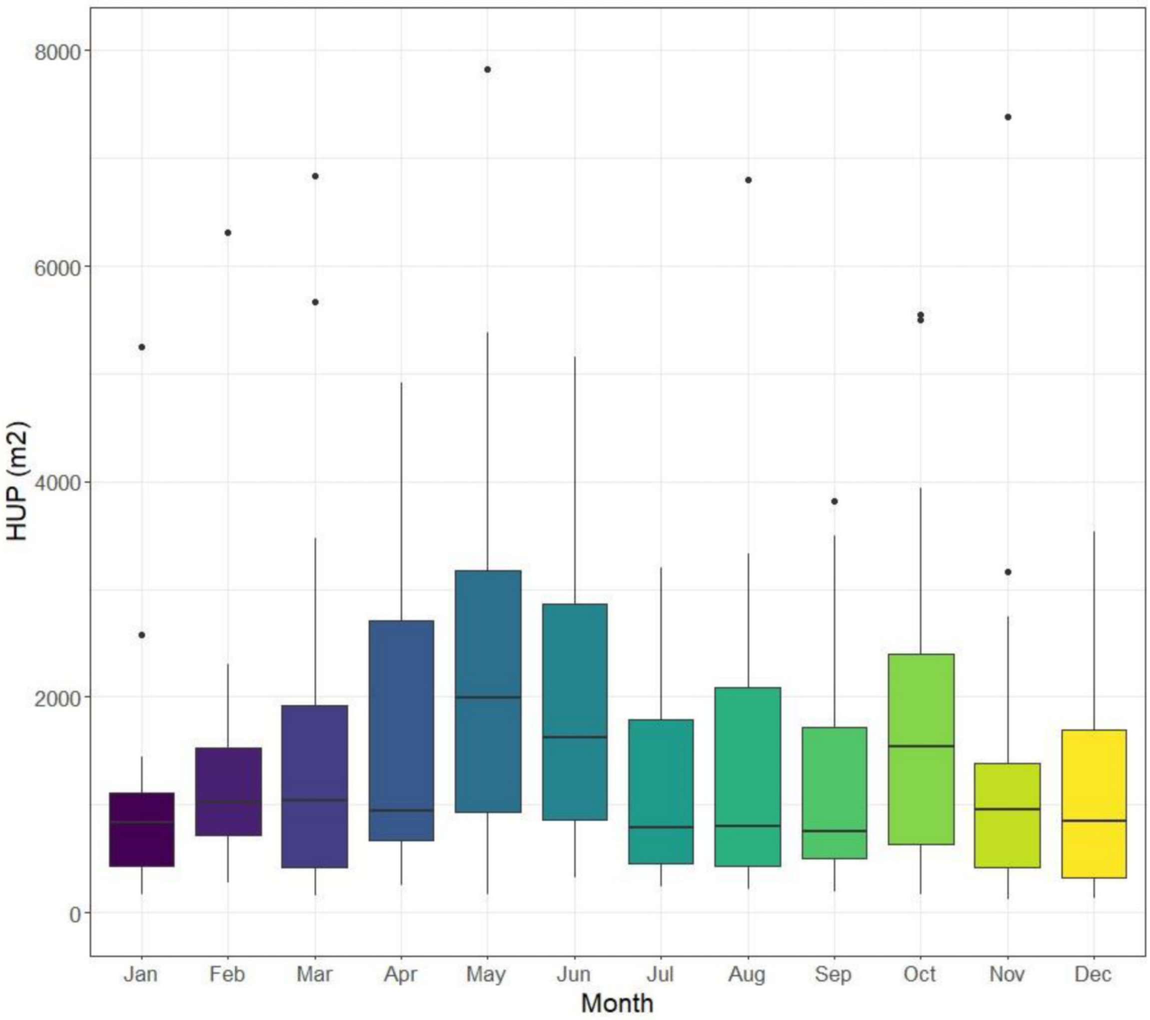


internal fertilization, the greater travelled distances during the spring would enhance the chances of encountering conspecifics for reproduction, with sexually mature females releasing pheromones to attract males (Martel et al. 1986).

Following mating in the spring, we observed a marked decrease in HUP in July, although speed was sustained. The reduced HUP relative to previous months suggest a considerable behavioural change, with individuals exploring lower portion of areas while maintaining their mobility potential when moving. Through direct observations of the seafloor, Martel et al. (1986) identified this period as the time when females laid most of their eggs, with a peak between mid-June and mid-July. A single female *Buccinum undatum* can lay a large quantity of eggs over large boulders or stripes of brown algae on the seabed (on average 140 capsules containing ∼2700 eggs), the production of which is thought to require a considerable time and energy. Egg-laying, indeed, is a very slow process, where females remain in the same spot for several days (pers. observation), inducing a notable decrease in HUP. The increased variability in speed during June and July could be explained by the different strategies used by the sexes, with females becoming extremely sedentary during spawning and males continuing to move after mating.

The results suggest that temperature can only partially explain the seasonal mobility of waved whelks. In this regard, we observe a positive relationship between speed and temperature in the months of March, April, and May where the temperatures shift from negative to positive values (mean temperature of −0.2, 1.16, and 2.75 °C, respectively). As Borsetti et al. (2020) suggest that the reproductive cycle of waved whelks is closely related to temperature, the increasing temperatures observed during the spring may represent a starting signal for mobility of individuals before the breeding season. In all other months (except November), however, this trend is not observed, highlighting the presence of other explanatory factors, including the biological aspects of the species (see above).

Fig. 7. Seasonal variations in habitat usage potential (m^2) of waved whelks *Buccinum undatum* over different months of the year. Of note, the lower variability of winter month compared to spring/summer months.

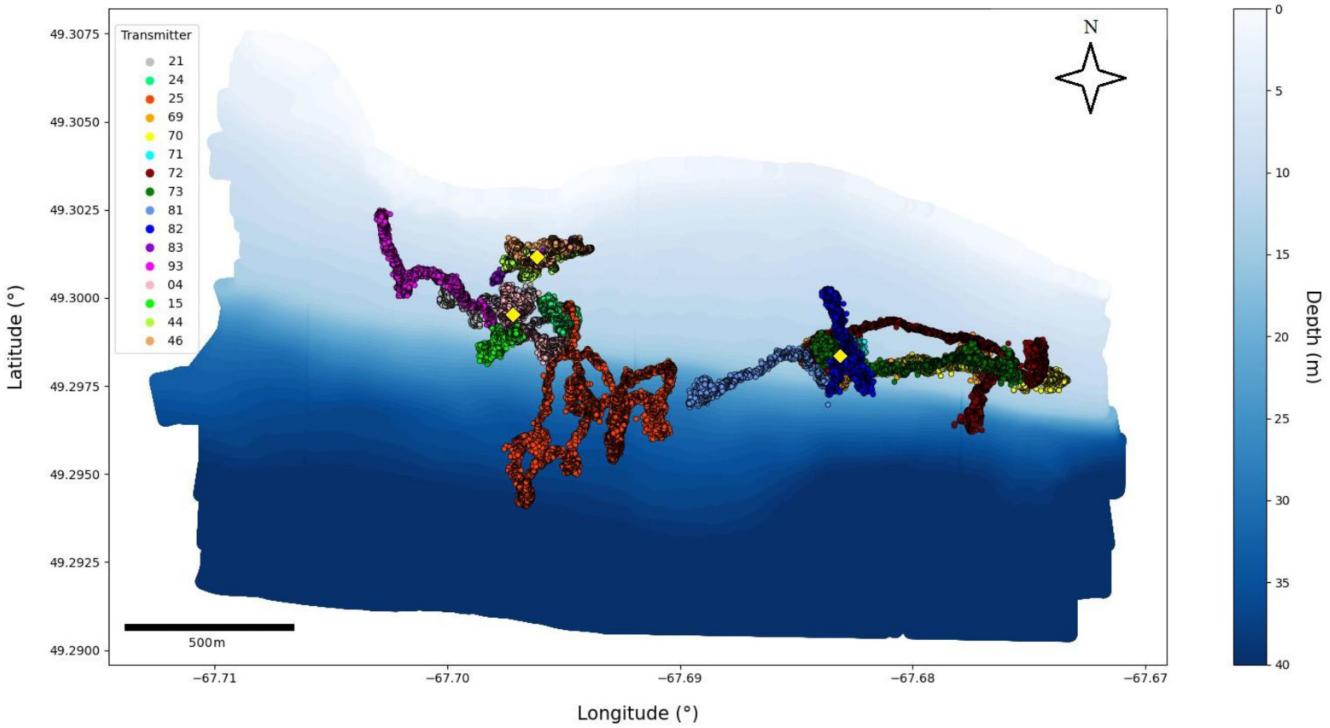


Although several benthic invertebrates perform seasonal migrations to deeper waters during the winter on North American coasts (Goldstein and Watson 2015; Cote et al. 2019), this was not evident for *Buccinum undatum*, which showed a lack of migratory patterns leading up to the cold season. None of our tracked animals followed a depth gradient across the study period, remaining at relatively constant depths between 10 and 30 m and never exceeding 41 m (although the species can be found at 1000 m depth; Borsetti et al. 2018).

Given the absence of extensive seasonal migrations and relatively limited HUP, the dispersal of *Buccinum undatum* individuals is somewhat restricted. For example, animals with tags NO. 21, 24, and 25 never travelled beyond the limits of the acoustic telemetry array through the 790 days study period, showing a maximum HUP of 209 900 m^2 (tag n °25). Although the two release regions were only 1 km apart, there was no interaction between the two groups of tagged individuals during the entire study period, with no overlap between the areas explored by single animals. Observing important phenotypic differences in relatively close subpopulations (dozens to hundreds of kilometres) along the coast of Nova Scotia, Ashfaq et al. (2019) suggested that local populations may be genetically distinct due to spatial isolation. In addition to the limited dispersion of adults, *Buccinum undatum* does not have a pelagic larval stage, limiting connectivity between populations, as pelagic larvae are considered one of the main means of exchange between benthic communities (Treml et al. 2015; Demmer et al. 2022). Ashfaq et al. (2019) and Borsetti et al. (2018) also suggested that animals in their study site were vulnerable to overexploitation, highlighting the importance of evaluating the spatial scale of individual movements in these benthic communities.

Our long-term acoustic telemetry study highlights that exchanges between *Buccinum undatum* populations may be very limited even at large temporal scales as this species moves over largely restricted spatial scales. The limited spatial scale of movements could result in local populations being vulnerable to overfishing. This issue has come to light in the St. Lawrence due to the overexploitation of several populations caused by their easy capture (up to 400 individuals in a single baited-trap following a 24 h soak; Himmelman

Fig. 8. Recorded location of all 2020 tagged individuals from October 2020 to October 2021 with respect to bathymetry of the Petite baie de Saint-Nicolas. Tags (No. 21/24/25) show displacements from August 2019 to October 2021. The yellow diamonds represent the east and west main release points of the tracked individuals of waved whelks *Buccinum undatum* during the study period.



1988). In the Quebec region alone, catches fell an average of 32% between 2017 and 2021, with a decline of 76% in some areas. Catches per unit of effort (CPUE) are declining sharply, decreasing by up to almost 50% and seriously threatening the perennity of the resource in several local fisheries (Ashfaq et al. 2019; Pêches et Océans Canada 2022*a*). The Newfoundland and Labrador commercial whelk fishery has steadily dwindled since 2011 (the mean annual CPUE have decline in some areas from 16.9 to 13.2 km/trap between 2018 and 2020), causing several fishermen to retire from the practice (Pêches et Océans Canada 2022*b*). The important ecological and economic consequences of the loss of this resource requires major conservation efforts to protect local populations.

The species' vulnerability to local extinctions and the strong potential for local adaptation suggest that regional management of whelk populations will have a better chance of ensuring the sustainability of the fishery. The current fishing season runs from early April to September (Pêches et Océans Canada 2022*a*), potentially removing gravid females and severely limiting the species' breeding efforts. Because the peak of the reproductive season is expected to stretch from the beginning of May to the end of July, we recommend shifting the *Buccinum undatum* fishing season from August to October/November as marketable individuals stay in the same area throughout the year, remaining a constantly available resource for fisheries. In areas where the resource has vanished, targeted restocking operations could be performed to take advantage of the species' limited dispersal potential. In fact, their sedentary nature could ensure effective repopulation over areas of interest. Several recent studies have demonstrated the validity of this method for restoring benthic communities in previously highly exploited areas (Cau et al. 2019; Giglioli et al. 2021). Given their low mortality upon capture (Ashfaq et al. 2019), any restocking of *Buccinum undatum* would likely have a positive impact on local subpopulation dynamics.

Information of a species' dispersal potential determined through acoustic telemetry studies, coupled with knowledge of biological life cycles can determine the success of management efforts in communities of ecological and economical interest. Indeed, the characteristics we observed for *Buccinum undatum* (i.e., limited habitat utilisation potential leading to possible population fragmentation) have also been observed for other benthic species (Stieglitz and Dujon 2017; Konzewitsch and Evans 2020; Schlaff et al. 2020), suggesting that conservation measures developed for one species could be adapted for other cases where movement and life-history are similar. As dispersal and colonization ability are often inversely correlated to local risk of extinction (Kotiaho et al. 2005; Neubauer and Georgopoulou 2021), area-specific telemetry studies may be used to improve the long-term management of fishery stocks. An increasing number of species are known to display complex behaviours that vary as a function of biological and ecological factors. Research on the various facets of dispersal of benthic marine invertebrates is recommended to increase awareness of the potential vulnerability of specific marine species to local overfishing.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2024-0056.

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