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Par

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Impacts acoustiques du trafic maritime sur les invertébrés marins benthiques vagiles des zones côtières subarctiques

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Avertissement

Nature rightly questioned never lies

Robert Mallet,

from A Manual of Scientific Enquiry, 1849

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Réalisation Scientifiques

Articles publiés

Uboldi T, MacGregor KA, Lavoie MF, McKindsey CW, Gendreau Y, Pettré J, Chauvaud L, Olivier F, Tremblay R (2025) Daily and seasonal spatial behaviour of waved whelk *Buccinum undatum*: implications for fishery management and restoration. Canadian Journal of Zoology 103: 1-14.

Byrro-Gauthier N, Uboldi T, Olivier F, Tremblay R, Chauvaud L, Mathias D, Lazure P, Frémont A, Meziane T, Chauvaud S, Winkler G (2025) "*Should I stay, or should I go*": anthropogenic noises disrupt early recruitment of subarctic invertebrates. Ecological applications (In press)

Articles en revision

Uboldi T, Byrro-Gauthier N, Bridier G, Jézéquel Y, Drolet D, Pettré J, Olivier F, Tremblay R, Chauvaud L (202X) Shipping noise alters the behaviour and habitat usage of waved whelks *Buccinum undatum* (Gasteropoda). Marine Pollution Bulletin

En préparation

Uboldi T, Lugo CJ, Riley C, Drolet D, Chauvaud L, Trembaly R, Olivier F (202X) Divergent effects of shipping noise on rock crab (*Cancer irroratus*) activity across circadian and seasonal cycles. Journal visé: *Animal Behaviour*

Communications orales

Conférence "Movement Ecology of Animals"

Juillet 2023 – Lucca, Italy

"Daily and seasonal spatial behaviour of *Buccinum undatum* along the sub-Arctic coastal system of the St. Lawrence gulf" – Présentation poster

Réunion Annuelle de la Société Québécoise pour l'Étude Biologique du Comportement

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"Marcher ou mourir : un potentiel de dispersion réduit révèle la tendance à l'extinction locale des populations de *Buccinum undatum*" – Présentation orale

Réunion annuelle de Ressouces Aquatiques Québec (RAQ)

Novembre 2023 – Québec, Canada

"Marcher ou mourir : un potentiel de dispersion réduit révèle la tendance à l'extinction locale des populations de *Buccinum undatum*" – Présentation orale

Réunion Annuelle de la Société Québécoise pour l'Étude Biologique du Comportement

Novembre 2024 – Montréal, Canada

"Some don't like it noisy: shipping noise alters the behaviour and habitat usage of waved whelks *Buccinum undatum* (Gasteropoda)" – Présentation orale

Réunion annuelle de Ressouces Aquatiques Québec (RAQ)

Novembre 2024 – Québec, Canada

"Some don't like it noisy: shipping noise alters the behaviour and habitat usage of waved whelks *Buccinum undatum* (Gasteropoda)" – Présentation poster

Conférence "World Aquaculture Society"

Mars 2025 – Nouvelle Orléans, USA

"Some don't like it noisy: shipping noise alters the behaviour and habitat usage of waved whelks *Buccinum undatum* (Gasteropoda)" – Présentation orale et poster

Séjours scientifiques à l'extérieur du laboratoire

Institut national de recherche en sciences et technologies du numérique

Centre de Rennes Bretagne Atlantique, Campus Universitaire de Beaulieu, 263 avenue du Général Leclerc, 35042 Rennes, France. 2023, encadré par Julien Pettré et Anne Helene Olivier. Traitement des données concernant les chapitres 1 et 2.

Autres communications

Rédaction de l'article "L'océan n'est pas un monde silencieux" dans le journal en ligne The Conversation. https://theconversation.com/locean-nest-pas-un-monde-silencieux-180537

Idéation et diffusion du podcast "C'est quoi la mer" en collaboration avec Horizon Open Sea Festival. Produit par La Stridente. https://soundcloud.com/lastridente/cest-quoi-la-mer

Rédaction du texte "Et si les bulots pouvaient nous entendre…" à l'occasion des 10 ans de participation du Québec à la Fête de la Science. En collaboration avec l'IFQM

Summary

Résumé de thèse en langue française

L'anthropophonie constitue un facteur anthropique majeur susceptible de moduler significativement le comportement de la faune marine, y compris celui des invertébrés. Des sources sonores telles que les battages de pieux, les échosondeurs, les prospections sismiques, les activités de pêche ainsi que l'intensification du trafic maritime ont démontré leur capacité à induire des altérations comportementales substantielles chez de nombreuses espèces d'invertébrés marins, avec des conséquences potentielles sur leurs fonctions écologiques au sein des écosystèmes. Malgré l'intérêt croissant porté à cette problématique, la compréhension des mécanismes comportementaux sous-jacents aux réponses au bruit anthropique reste lacunaire, et plusieurs interrogations fondamentales demeurent non résolues.

Dans le but de combler ces insuffisances, ce projet de doctorat s'articule autour de trois axes principaux visant à décrypter les specificités comportementales de deux espèces benthiques vagiles d'invertébrés marins — *Buccinum undatum* (Gastropoda) et *Cancer irroratus* (Malacostraca). L'étude portera sur leurs réponses comportementales face à l'exposition prolongée au bruit de navigation, à travers une approche combinée d'expérimentations contrôlées en laboratoire et d'observations *in situ*.

Dans le **Chapitre 1**, nous avons caractérisé le comportement spatial naturel du gastéropode *B. undatum* dans le golfe du St. Laurent, révélant des specificités comportementales substantielles aux échelles circadienne et saisonnière. Ce jeu de données a été obtenu grâce au déploiement d'un réseau de télémétrie acoustique sur une base pluriannuelle, qui a permis de décrire le mode de déplacement de cette espèce et de mettre en évidence une forte saisonnalité dans la mobilité individuelle. De plus, le potentiel limité d'utilisation de l'habitat restreint la dispersion des individus, entraînant de très faibles connexions entre populations voisines et rendant ainsi l'espèce particulièrement vulnérable à la surpêche locale.

S'appuyant sur ces connaissances, le **Chapitre 2** a utilisé des métriques spatiales et comportementales spécifiques à l'espèce pour évaluer l'impact potentiel du bruit des navires sur la mobilité et l'activité de *B. undatum*. Une expérience *in situ* a été menée dans la Baie de Miquelon, utilisant la télémétrie acoustique pour examiner les effets du bruit de navigation sur le comportement spatial de spécimens sauvages en environnement ouvert. Pour corroborer ces observations, des expériences complémentaires ont été réalisées en conditions contrôlées à l'aide d'accéléromètres. Dans l'ensemble, les résultats montrent qu'à différentes intensités et durées, le

bruit des navires affecte négativement les capacités locomotrices des gastéropodes, limitant ainsi leur potentiel de dispersion dans l'environnement.

Enfin, pour élargir l'étude à d'autres classes d'invertébrés marins benthiques vagiles, le **Chapitre 3** a examiné les effets de niveaux similaires de bruit maritime sur le comportement spatial de *C. irroratus* via la vidéoanalyse et l'accélérométrie. Un protocole expérimental a été développé afin de tenir compte des specificités comportementales de l'espèce en fonction des cycles circadiens et saisonniers. Les résultats indiquent que le bruit des navires a significativement impacté l'activité des crabes, mais uniquement dans la période de nuit au printemps, reflétant ainsi un effet modulé selon le facteur saisonnier.

Nos résultats sur *B. undatum* et *C. irroratus* confirment ainsi que l'exposition au bruit de navigation perturbe les spécificités comportamentales et la mobilité au cours des stades adultes de nombreuses espèces d'invertebrés marins, compromettant la dispersion individuelle dans l'environnement local, avec des implications directes pour la fitness des individus, susceptibles de réduire la connectivité des populations et d'affecter la structure des communautés à long terme.

Introduction

I Using animal behaviour as an ecological proxy

1.1 The arduous definition of animal behaviour

Although it is a common perception that science must rely on clearly defined concepts that are evident and consensual to the entire scientific community, there are today a multitude of core concepts that are still ambiguous in their basic definition. Biology itself can give a multitude of different definitions to life, cognitive science exists without a clear definition of cognition, and there is no clear consensus on the definition of psychology (Levitis et al., 2009). It is therefore not surprising that in behavioural biology there are different ways of defining behaviour in living organisms, and that these definitions can sometimes be inconsistent. Levitis et al. (2009) collected about 25 different operational definitions of behaviour among biologists engaged in behavioural research, finding *surprisingly widespread disagreement as to what qualifies as behaviour*. Researchers often based their views on intuitive understanding rather than on formal criteria, contradict themselves, each other and published definitions, indicating that they are using individually variable intuitive opinions. According to Baum (2013), the definition of behaviour changes as our understanding of behaviour changes, making a final definition impossible.

Based on a set of various definitions found in literature, Levitis et al. (2009) exposed a definition of behaviour that is still widely recognised today: behaviour is the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes (except for plants in which development, physiology and behaviour would go hand in hand, as suggested by Trewavas 2009). Baum (2013) add to this essential definition that behaviour must be also defined by its function, having in itself a specific purpose and representing a choice of the individual (or group). In other worlds, behaviour is generally assumed to involve an active movement in the physical space (relatively fast in time to differentiate from development), defined as the result of the processing of internal and external cues that are responsible for the organism's reactions, with the purpose of changing its temporary state facing a specific condition.

In this definition, external stimuli refer to any environmental factor that can cause some behavioural responses in the organism. These can include physical changes like temperature, light, and sounds, as well as interactions with other organisms like predator presence, food availability, and social interactions (Wilson et al., 2020). Aside from external cues, internal stimuli determined by the individual's genetics control the physiological states within the organism, also leading to phenotypic behavioural reactions (Horodysky et al., 2015). Konrad Lorenz, the father of behavioural biology,

first proposed in 1950 the idea that animal behaviour is defined by a combination of physiological, genetic and environmental factors.

For many behavioural biologists, indeed, the internal physiological state can be considered as a connection between the external living environment and animal behavioural response (Horodysky et al., 2015). Changing living conditions, trigger a number of physiological mutations, stimulating (or limiting) specific behaviours (Fig. 1). Usually, external stressors trigger a sequence of reactions in a precise order (Portz et al., 2006). First, fast physiological reactions occur through the release of substances that minimize the impact of stressors, rapidly adapting the organism to the new imposed conditions. This leads to secondary responses, which modify the internal functioning of the stressed animal, varying the composition of different metabolites within the body. Triggered by the body's momentary physiological state, tertiary responses that follow result in phenotypic changes in terms of growth and reproduction rate, resistance to diseases and behavioural responses with potential impacts on fitness (Portz et al., 2006; Fig. 1). Along this chain of events, the study of the relationship existing between the external condition and the associated behavioural reaction is called behavioural ecology.
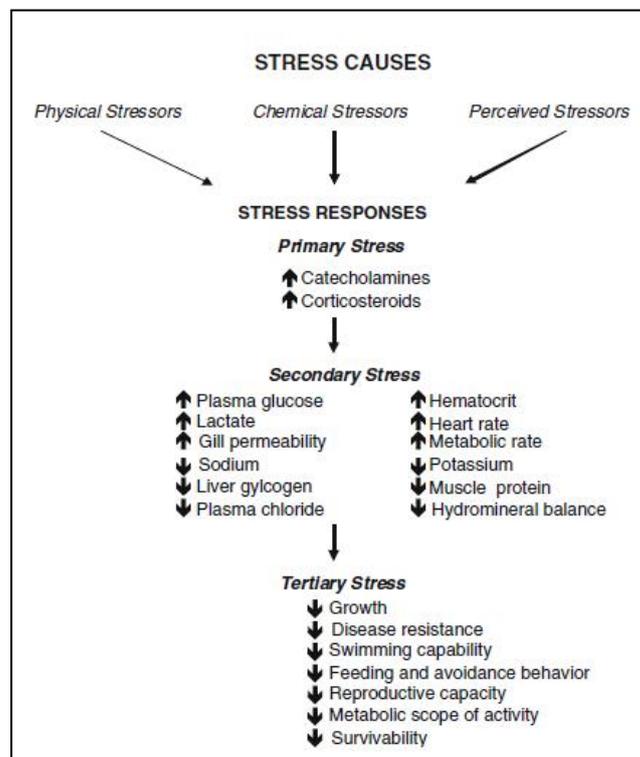
Figure 1: Typical sequence of stress responses of animals exposed to altered living conditions (Portz et al., 2006)

1.2 What is it the behavioural ecology?

Behavioural ecology is the study of how all living organisms, including humans, make decisions and behave in order to maximise their chances of survival and reproduction, taking into account factors such as food intake, resource defence, and environmental constraints (Davis et al., 2012). The aim of the behavioural ecology is to try to understand how an animal's behaviours is adapted to the environment, and, in the context of conservation, how it changes according to external stimuli imposed by human activities (Rahman and Candolin, 2022). As described above, the link between ecology and behaviour is very strong, as ecology defines the best behavioural strategy with which the organism responds to stimuli. This science allows asking a series of questions ranging from the motive to the consequences that drive a type of animal behaviour, combining a number of concepts relating to behavioural, ecological and evolutionary aspects (Davis et al., 2012).

Within their habitat, organisms continuously resort to a sequence of physiological and behavioural events according to the environment they experience along their life. In a natural pristine habitat, the environmental predictability allows animals to be synchronized with the natural conditions they experience (Riotte-Lambert and Matthiopoulos, 2019). In this way, environmental changes are perceived by the animal as transitional events that evolution has provided behavioural strategies to cope with (e.g., seasonal and/or vertical migrations). Overall, the environmental predictability enables animals to reduce the uncertainty of the environmental conditions they experience, adapting their behaviour accordingly to the experienced circumstances (Riotte-Lambert and Matthiopoulos, 2019). Human-induced changes, however, interrupt the typical environmental predictability, creating new conditions to which organisms are potentially poorly adapted, deeply affecting their sensory bubble. By changing the population density, the availability of prey and/or modifying the physical and chemical structure of the environment (e.g., global changes), the original environmental predictability can be dramatically lost and animal behaviour may lose many of its critical aspects (Wilson et al., 2020; Rahman and Candolin, 2022). Wilson et al. (2020) reviewed different human-induced changes in animal behaviour like: foraging strategies, communication, timing and distribution of activities, vigilance, rest, hygiene, breeding and parental care. The ecological consequences of animal behaviour alteration can be significant and varied, leading to cascading effects on species interactions, community structure, and ecosystem functions.

The intensity at which the anthropic disturbance occurs is also a crucial parameter in determining the magnitude of behavioural responses (Wilson et al., 2020). Commonly, the relationship between animal behaviour and anthropogenic disturbance exhibit nonlinear trends. In many cases, indeed, an

appreciable change in behaviour occurs only after the disturbance intensity is sufficiently high. In this case, an abrupt behavioural change arises when a certain threshold of tolerance has been exceeded. Alternatively, when altered behaviours are too costly to maintain, a gradual stabilisation to new habits is observed to adapt to the imposed conditions. It is also possible that the animal becomes accustomed to the disturbance of human activities, with a slow re-establishment of the habitual animal activities (Wilson et al., 2020; Fig. 2).
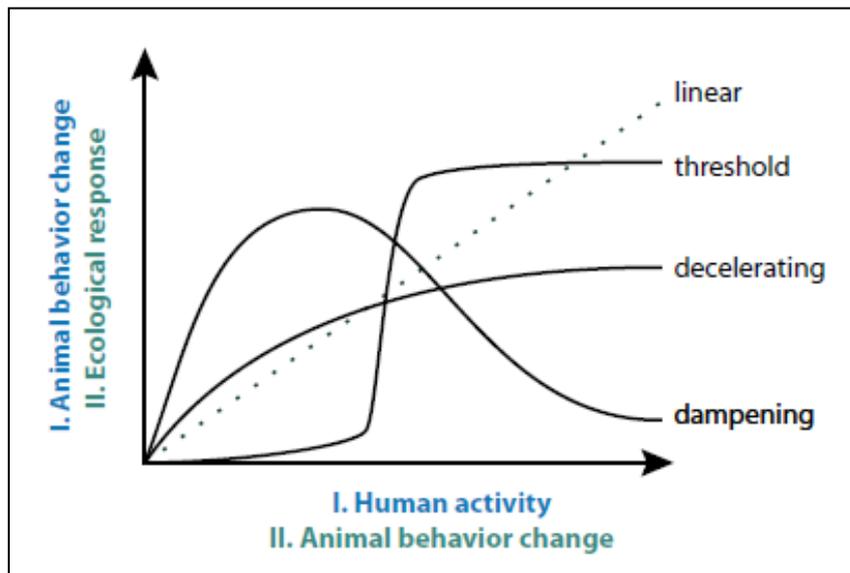
Figure 2: Examples of potential nonlinear relationships between human activities and animal behaviour (Wilson et al., 2020)

Among a large number of different factors, the environment is composed of a multitude of acoustic stimuli playing an active role in defining animal behaviour and ecology (Erbe et al., 2019; Duarte et al., 2021; Farina et al., 2021). Following the theory of the environmental predictability, organisms are deeply adapted to the soundscape of their living environment, relying on acoustic factors to adjust their behaviours and perform many of their living function (Farina et al., 2021; Erbe and Thomas, 2022). By introducing new uncompetitive noises, however, modern human activities break the soundscape predictability of the natural environment, potentially leading to critical changes in animal behaviour and ecology (Erbe et al., 2019; Di Franco et al., 2020).

II Sounds (… and noises) as a part of life

2.1 The contribution of geophony, biophony and anthrophony

Through millions of years of evolution, animals have evolved specific sensory bubbles that enables them to perceive the world (i.e., the *umwelt*; Uexküll, 1909). Among other factors, the living

environment is composed of a multitude of sounds and noises that can travel long distances at any time, crossing solid and liquid obstacles to reach the sensory bubble of many animal species. The acoustic component of our planet plays such an important role for life that it now appears as a new subject in the field of natural sciences: the soundscape ecology (Pijanowski et al., 2011). Indeed, planet Earth's soundscape is structured by a combination of different physical and biological interpreters that differs between geographical areas and living environments. Noises generated by abiotic events are the most represented within the natural soundscape, through noisy performances such as erupting volcanoes, wind, crashing waves, storms, fires, landslides, ice cracking... (Duarte et al., 2021). Such composition of acoustic elements generates what it is called as geophony, defining the overall soundscape of an environment (Fig. 3). Although geophony is often categorized as mere environmental noises, it has shaped the Earth's acoustic landscapes for billions of years, defining very important sonic implications to the evolution and adaptation of living species, resulting in essential ecological relationships (Farina et al., 2021).

Living organisms make their own contribution to the audible environment through biophony: a combination of sounds and noises produced by animals varying considerably in terms of acoustic propagation and frequency range, from chirping of birds to powerful cetacean calls (Duarte et al., 2021; Redaelli et al., 2022; Fig. 3). Animals have evolved extremely different organs of sense to perceive such elements of exceptional importance to life, as sounds can regulate many behavioural aspects of organisms in addition of making animal communication possible (Lillis et al., 2013; Miller et al, 2022). Sound plays a fundamental role in the survival and reproductive success of many animal species, constituting an essential tool for communication, orientation, defence, attracting partners and maintaining social cohesion (Hawkins and Poppers, 2017). In terrestrial environments, animals use it to demarcate territory, alert mates to danger or interact with the group, while in marine ecosystems, where light is often insufficient, sound becomes crucial for navigation, echolocation and long-distance communication (Erbe and Thomas, 2022).

The excellent physical propagation characteristics of sounds within the living environment make acoustic an excellent stimulus for biota, but also one pollutants of excellence (Aulanier et al., 2017; Jones et al., 2023). Recently, indeed, an important source of acoustic pollution has emerged as anthropophony (Fig. 3). Before the modern era, this source had a negligible contribution to the global sound scene. However, following the industrial revolution, anthropophony generated such great impact that it is now considered one of the most massive interpreters (Duarte et al., 2021; Bonnel et al., 2022). This source is often noisy, chaotic and uncompetitive compared to other natural sounds, being the result of all sorts of man-made machinery, to the point that it could be also

defined as technophony (Puppel, 2020). Anthropophony alters the sensory bubble of an undetermined number of terrestrial and marine animals, changing their behaviour and potentially their ecological functions (Drolet et al., 2016; Di Franco et al., 2020; Miller et al., 2022). The study by McClure et al. (2013) showed that the acoustic simulation of a crowded road could cause massive annoyance to various species of migratory birds, one-third of which did not stop in the area and the others spending less time in search of food. In crickets (*Gryllus bimaculatus*), acoustic noise can impair the accuracy of signal detection and processing, with experienced males living on highway edges decreasing their chirp rate in response to passing cars (Classen-Rodrìguez et al., 2021). In the marine environment, humpback whales (*Megaptera novaeangliae*) were observed to increase the amplitude of their vocalizations by 0.8 dB for every 1.0 dB increase in ambient noise, while vocalizing less frequently (Erbe et al., 2019). Fishes, like Arctic cod (*Boreogadus saida)*, modified their distributional range in a northern Canada bay because of the noise generated by commercial shipping, also altering their swimming behaviour (Ivanova et al., 2020).
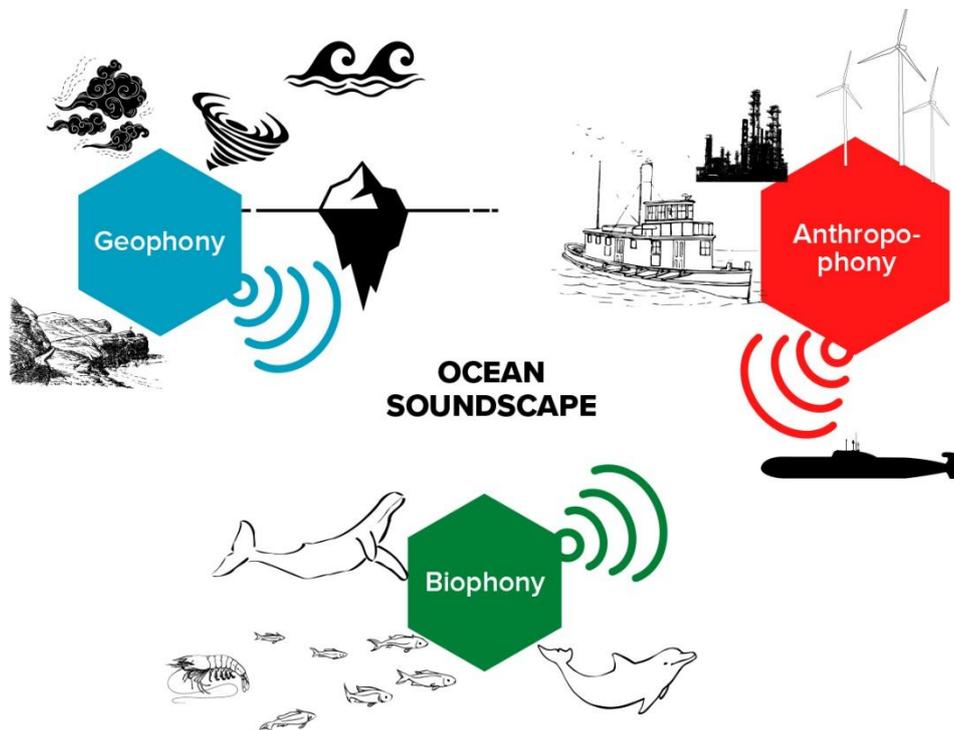
Figure 3: Examples of the three sources of an oceanic soundscape: anthropophony, biophony, and geophony (Rey-Baquero et al., 2021).

In recent years, increasing interest has also been devoted at the relationship between underwater acoustic and marine invertebrates, investigating the potential impacts of anthropophony on their life cycle (Di Franco et al., 2020; Solé et al., 2023). Overall, many studies agree that acoustic factors play an important role in defining the physiological and behavioural rhythms of several species of

marine invertebrates, being also greatly sensitive to noise pollution induced by human activities (Lillis et al., 2013; Charifi et al., 2017; Solé et al., 2023). A number of marine invertebrate species, indeed, evolved auditory organs that allow them to perceive soundwave propagation through the water column and sediment, mainly perceiving sounds at low frequencies at certain intensities.

2.2 Underwater basic acoustics

Sound vs *Noise: what's the difference?*

In the general conception, the etymology of the words "sound" and "noise" is often associated, both defined as any acoustic phenomenon perceived by a receiver. While sound is usually perceived as a pleasant stimulus, noise is usually perceived as annoyance (from the Latin word "nausea" meaning disgust and discomfort), although this definition is largely specie-specific. In physical terms, sound is typically characterized by a regular, periodic waveform, while noise consists of irregular, aperiodic fluctuations with no distinct frequency pattern (Fry, 1979). In this manuscript, we will use to the term "sound" to refer identifiable acoustic sources, while the term "noise" will refer to unwanted sounds that interfere with other sound of interest (see Hawkins and Popper, 2017).

Sound waves acoustic characterization

In acoustics, sound is described as a vibration that propagates in the form of mechanical waves, generating both pressure differential (compression *vs* rarefaction) and particle motion (Fig. 4). Due to the greater density and incompressibility of the liquid, soundwaves propagate faster in the water (about 1500 m/s) than in air (about 343 m/s), making the aquatic medium an excellent environment for sound propagation. In particular, the water density reduces energy loss especially at low frequencies soundwaves, which can travel long distances without significant attenuation. In the marine environment, the pressure and temperature of the water significantly influence the propagation of soundwaves, creating phenomena such as the 'sound channel'. Thus, sound propagates from the surface of the water column to the seabed, creating a complex propagation channel (Bonnel et al., 2022).
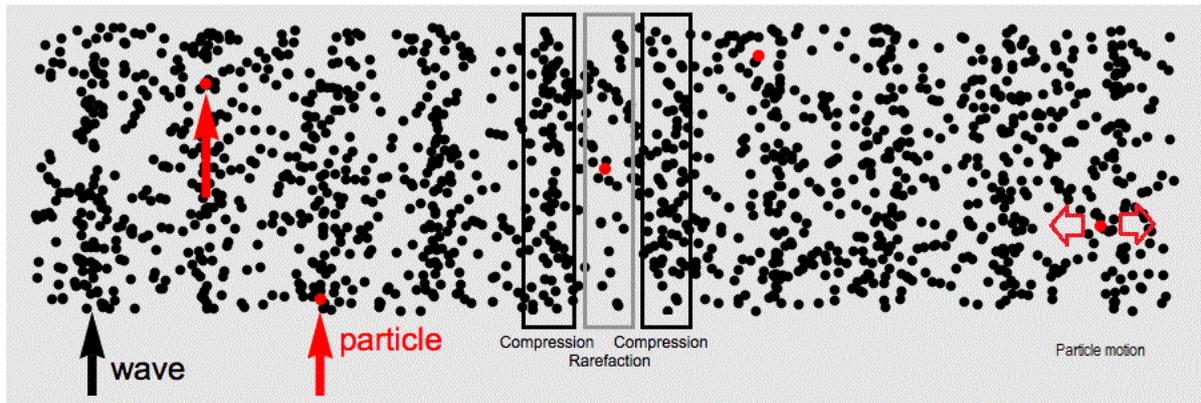
Figure 4: Sound propagation in the water medium showing wave behaviour and particle motion.

Sound propagation in the marine environment is attenuated to a certain extent depending on the geo-physical-acoustic properties of the water column and seabed. In acoustics, this loss of sound level during propagation in the environment is called transmission loss (TL), defining a certain sound level upon arrival at the receptor (received level, RL). The RL combines the intensity of the sound wave at the source (source level, SL) following some loss of intensity during propagation (TL), to which the ambient noise level (noise level, NL) is added. In underwater acoustics, while sound propagates uniformly in all directions following a spherical TL near to the source (I), the cylindrical TL prevails in shallow water where sound propagates as a cylindrical wave between the sea floor and the sea surface (II). According to the location of audio recording, these two formulas are used to calculate TL:

(I) $TL = 20 \times \log (\text{Distance})$

(II) $TL = 10 \times \log (\text{Distance})$

The Sound Pressure Level (SPL) can be described through the use of different units of magnitude that consider different aspects of sound wave propagation in the environment. The acoustic pressure is the most widely used component in the field of bioacoustics to calculate SPL. Acoustic pressure is described using the Pascal (Pa = N/m2), defining the force (Newton) per unit area perpendicular to the direction of propagation. The formula calculates SPL from the recorded acoustic pressure P (in Pascal) relatively to a referential pressure (1 µPa in the water):

$$SPL = 20 \log_{10} \left(\frac{P}{P_{\text{ref}}} \right)$$

SPL (i.e., acoustic pressure) is represented by means of a scale in decibels (dB), allowing a logarithmic representation of the acoustic pressure measurement. This is expressed as dB relative to 1 µPa (dB re 1 µPa), because 1 µPascal is the standard reference pressure used to ensure consistency in sound level comparisons within the aquatic environment. For example, a pressure of 10 µPa corresponds to a sound level of 20 dB re 1 µPa, while a pressure of 1 000 000 µPa corresponds to a level of 120 dB re 1 µPa.

Next to acoustic pressure, acoustic intensity is defined as the energy flow (Watt) per unit area perpendicular to the direction of propagation. It is described as the power per unit area carried by the acoustic pressure, and it is measured in watts per square meter (W/m²).

SPL can be calculated with different methods according to the sound characteristics. Duration defines the time for which a certain sound perturbation persists within the environment. There are impulsive sound perturbations, characterised by short, instantaneous sound pulses (such as pile driving and echolocation). In this case, the SPL is calculated by defining the difference between the maximum positive and maximum negative value of the sound signal in the time domain (peak to peak, Fig. 5):

$$SPL_{\text{peak-peak}} = 20 \log_{10} \left(\max \left(|p(t)| \right) - \min \left(|p(t)| \right) \right)$$

Similarly, it can be also calculated by defining the difference between the maximum positive and the equilibrium value of the sound signal (0-to-peak, Fig. 5):

$$SPL_{\text{peak}} = 20 \log_{10} \left(\max \left(|p(t)| \right) \right)$$

In contrast, there are continuous sound perturbations with acoustic signals that are more persistent in time (such as shipping noise and ambient noise). In this case, the SPL is defined as an energy average of the amplitude of the acoustic signal over time (root mean square, Fig. 5):

$$SPL_{\text{rms}} = 20 \log_{10} \left(\sqrt{\frac{1}{t} \int_0^t p(t)^2 \, dt} \right)$$

Another measurement, the SEL (Sound Exposure Level), expresses the dose of sound energy received over a duration t, and is therefore expressed in dB re 1 µPa²·s.

$$SEL = 10 \log_{10} \left(\int p(t)^2 \, dt \right)$$

The acoustic frequency describes the number of complete oscillations (cycles) of the sound wave per time unit (1 sec) and is described using the unit Hertz (Hz; Fig. 5). In general, the more cycles there are in a unit of time, the sharper the acoustic signal becomes (high frequency). Referring to human acoustic capabilities, sounds with frequencies below 20 Hz are called infrasound, sounds between 20 Hz and 20 kHz are called audible and sounds above 20 kHz are called ultrasound. To characterise a certain type of noise, one often calculates the intensity distribution of the acoustic signal according to certain sequences, defining an acoustic spectrum in dB re 1 $\mu Pa^2/Hz^{-1}$.
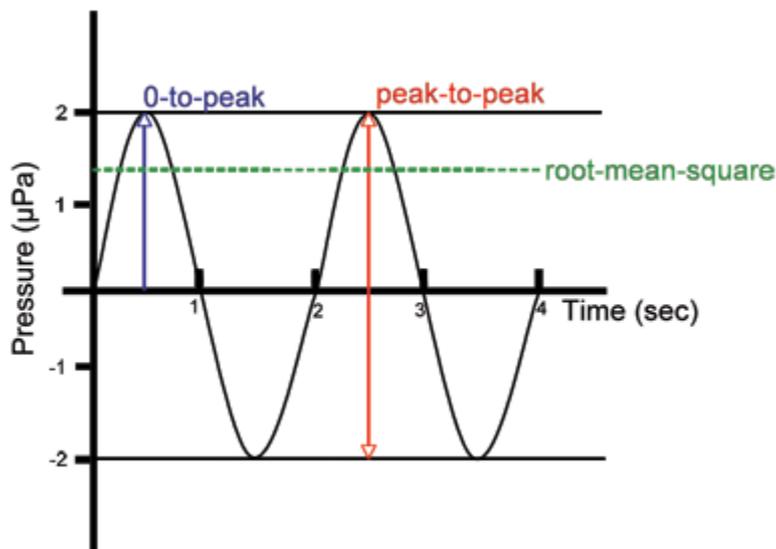
Figure 5: The most frequently employed acoustic parameters to consider when characterizing soundwaves, including: 0-to-peak, peak to peak and root mean square.

Sound waves also generate particle motion during its propagation (Fig. 4). Because acoustic propagation in a medium occurs through compression and rarefaction waves, this induces microscopic oscillations of particles around their equilibrium position. The particles move back and forth in a direction parallel to the propagation of the wave, but the propagating perturbation carries the energy of the sound wave. To calculate particle motion in the context of sound waves, we typically relate it to displacement (d in meters), velocity (u in m.s^{-1}), or acceleration (a in m.s^{-2}) of the particles in the medium. Particle motion is the acoustic component detected by certain aquatic animals, such as invertebrates, making it a central concept in marine bioacoustics (Hawkins and Popper, 2017).

2.3 Hearing systems in marine invertebrates

The hearing range of marine animals is a key determinant of their potential responses to different components of ocean soundscapes and their vulnerability to stressors of different sources of underwater noise (Duarte et al., 2021). Hearing thresholds have been measured in a number of marine species, although a complete understanding of hearing capabilities in all taxa remains generally poor (Houser et al., 2017; Popper et al., 2022; Solé et al., 2023). This is especially true in marine invertebrates, where hearing organs have only recently been described, with their functioning and hearing range being largely unknown (Solé et al., 2023).

By specific sensory organs, marine invertebrates are now recognised to perceive sound through particle motion (Hawkins and Popper, 2017; Solé et al., 2013). Crustaceans, molluscs, cnidarians (and many others) have evolved mechanoreceptors including statocysts and surface sensory hairs to detect gravity, acceleration and acoustic stimuli witin the water medium (Solé et al., 2023). Similarly to the fishes' inner ear (i.e., the otolith system), statocysts are internal organs containing dense, calcareous granules, usually called statolith (or statoconia; Fig. 6). When the soundwave hits the animal's body, the statolith moves, pressing against the sensory cilia over the internal wall of the statocyst, and finally generating a neuronal response to sound (Fig. 6).
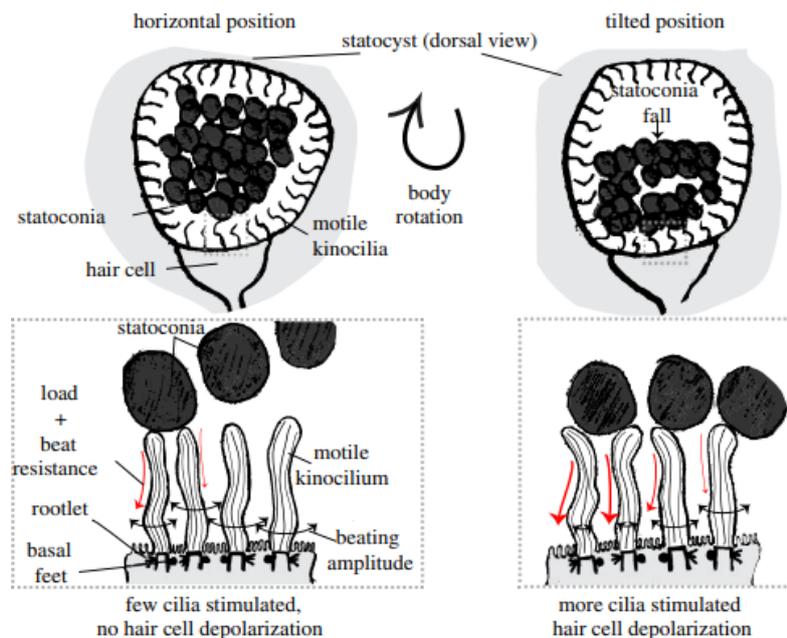
Figure 6: Functioning of internal statocyst. (Top left) Drawing of a mollusc statocyst in the resting position (i.e. with the animal in a horizontal position). View from the dorsal side. (Bottom left) Close-up view of a multiciliate capillary cell in resting position. (Top right) Upon tilting, the statoliths redistribute to one side, thus increasing the possibility of the cilia colliding with them.

(Bottom right) More cilia come into contact with the statocones. (Modified from Bezares-Calderòn et al., 2020).

In addition to statocysts, marine invertebrates possess epidermal detector systems to perceive water particle motion, known as hydrodynamic receptor systems, which are distributed along the external body surface and are considered functionally analogous to the lateral line system in fish (Solé et al., 2023). Furthermore, recent studies indicated that mollusc bivalves also have an abdominal sensory organ (ASO) that would be able to perceive the water particle motion caused by sound propagation (Zhadan et al., 2004). Such mechanoreceptor organ is found at the edge of the mantle and is composed of several small tentacles that include 4 million sensory cells (Bonnel et al., 2022; Fig. 7). In crustaceans, chordotonal organs are mechanoreceptors responsible for detecting mechanical stimuli such as vibrations, sound waves, body movement, and joint position. They are usually located in the appendages of antennal fragellum and walking legs and they compose the crustacean's auditory system beside internal statocysts and external sensory hair cells (Solé et al., 2023).
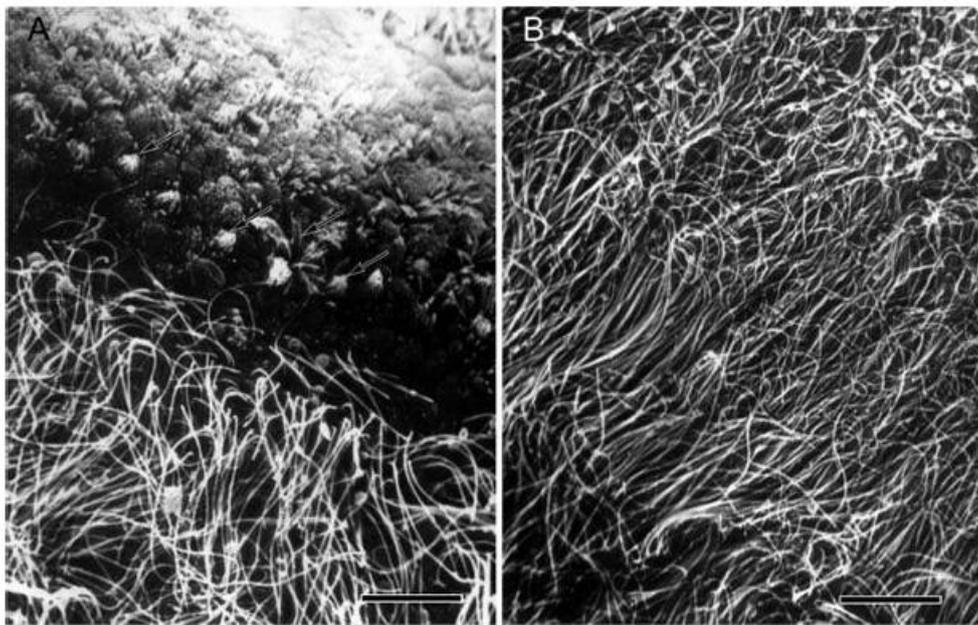
Figure 7: Ultrastructure of the surface of abdominal sense organ (ASO) of the scallop *Mizuhopecten yessoensis*. A) Scanning electron microscope image of the edge of the sensory epithelium. Arrows indicate multiciliar cells. Scale bar: 40 μm. B) Scanning electron microscope image of the central zone of the sensory epithelium. Scale bar: 40μm. (Zhadan et al., 2004).

Through the reported auditory systems, marine invertebrates can perceive a wide range of sound frequencies, most of them responding to very low frequencies, which cause the greater particle motion (Wale et al., 2021). In mollusc bivalves, Japanese oysters (*Crassostrea gigas*) were shown

to have maximum sensitivity from 10 to 200 Hz (Charifi et al., 2017) and the bivalve ASO is highly sensitive to waterborne vibrations in the range 20–1500 Hz (Solé et al., 2023). In Japanese and swifti scallops (*Mizuhopecten yessoensis* and *Chlanys swifti*), individuals of both species were sensitive to acoustic stimuli in the range of 30–1000 Hz, ASO being responsible of the directional sensitivity of soundwaves (Zhadan, 2005). Through tonal signals at frequencies within the range 5 to 410 Hz, blue mussels (*Mytilus edulis*) also reacted to substrate-borne vibrations generated by sound propagation within the sediment (Roberts et al., 2015).

Recent behavioural (including changes in ventilation rhythm) and electrophysiological studies also confirmed cephalopod sensitivity to low frequencies (Solé et al., 2023). In longfin squid (*Loligo pealeii*), responses were obtained between 30 and 500 Hz with the statocyst detecting the particle motion component of the emitted sound (Mooney et al., 2010).

In crustaceans, the American lobster (*Homarus americanus*) is known to sensibly react to low frequencies under 300 Hz, particularly between 80 and 100 Hz (Jézéquel et al., 2021). The prawn *Palaemon serratus* is sensitive to sounds with frequencies ranging between 100 and 3000 Hz, being able to hear sound of 500 Hz regardless of their size (Lovell et al., 2006). In snapping shrimps (*Alpheus richardsoni*), the auditory detection was most sensitive between 80 and 100 Hz (up to 1500 Hz) through statocysts (Dinh and Radford, 2021).

2.4 The relevance of underwater sounds for marine invertebrate

As sound waves can carry a large panel of information over relative long distances in the water environment, acoustic signals are now recognised to regulate the interactions between a growing number of marine invertebrate species, integrating animal communication beside chemical and visual cues (Di Franco et al., 2020; Jézéquel et al., 2020; Kühn et al., 2023). Furthermore, the soundscape of a certain environment can inform the animals about its characteristics, causing considerable changes in their behaviour (Lillis et al., 2013; Charifi et al., 2017; William et al., 2022). For such reasons, acoustic signals are of crucial importance for many living aspects of species, including different life stages of many marine invertebrates (Lillis et al., 2018; Filiciotto et al., 2019).

- Larval phase

Most marine invertebrate species display a bentho-planktonic life cycle including an initial pelagic larval form before evolving into a juvenile then an adult. Since larval settlement success partly

determines overall individual fitness (larval supply theory; Gaines and Roughgarden, 1985), early life stages must respond appropriately to environmental cues, including underwater acoustic signals.

A growing number of studies highlight that planktonic larvae of many species can perceive the underwater soundscape typical of their living environment to eventually settle on the most appropriate substrate (Lillis et al., 2013; Hinojosa et al., 2016; Anderson et al., 2021; William et al., 2022). For example, oyster larvae are more likely to settle in environments exposed to oyster reef sounds, suggesting the larvae react actively to specific soundscape stimulations (Lillis et al., 2013). Moreover, coral larvae orient themselves towards a low-frequency healthy reef soundscape, larval settlement begin twice as high in the proper acoustic environment (Lillis et al., 2018). In coastal water, underwater reef sound emissions were also observed to attract a significant proportion of post-larvae of southern rocky lobster compared to the control site (Hinojosa et al., 2016).

Although larvae show sensory organs that still have to develop during further stages, the sensory capacity of such planktonic stage is already well established (Williams et al., 2022). The ability of planktonic larvae to settle on appropriate environments via acoustic cues suggests a great capacity to decode the soundscape properties of their habitat, emphasising the importance of acoustic stimuli in defining the overall fitness from early life stages for several marine invertebrate species (Veillard et al., 2025).

- Adult phase

Within their habitat, marine invertebrates generate a large panel of intentional and/or involuntary sounds and noises during interactions (i.e., predation, territorial defence, social and sexual behaviour), locomotion and feeding activities (Solé et al., 2023). In some cases, species are supposed to actively respond to the geophony of their environment (Charifi et al., 2017), while others influence the soundscape through specific behaviours or by shaping the resident community involved in the local chorus (Radford et al., 2008; Lillis et al., 2014).

Although no behavioural functionality has yet been found, many bivalves generate puffing noise and sharp cracks with valve movements while expelling water and faeces from their inner cavity (Di Iorio et al., 2012; Coquereau et al., 2016). For example, *Mimachlamys varia* produced a transient sound when jumping (received level up to 125 dB re µPa), a rapid valve closure used by the scallop to move or turn to a desired position (Coquereau et al., 2016). In *Pecten maximus* coughing sounds ranges from 20 to 27 kHz, their acoustic characteristics being detected up to several tens of meters (Di Iorio et al., 2012).

In echinoderms, only sea urchins have been investigated, generating crackling sounds (from 800 Hz to 28 kHz) by stridulation of spines on hard bottoms while moving and by scraping kelp and microalgae while grazing (Solé et al., 2023). In New Zealand, groups of foraging endemic sea urchins (*Evechinus chloroticus*) considerably increased the ambient sound pressure levels at dusk compared to mid-day levels, contributing to the underwater chorus essential in assisting settlement for many other local species (Radford et al., 2008).

Beside the unintentionally produced noises, crustaceans use specific acoustic signals to exchange information about predation interactions, territorial defence, social and sexual behaviour (Kühn et al., 2023; Solé et al., 2023). By the collapse of cavitations bubbles during rapid claw closure, snapping shrimps cause one of the most ubiquitous and audible sound sources on coral reefs (from 2 to 200 kHz). Although this sound was initially considered as a simple consequence of the predation activity, snap rates are now recognised to play a fundamental role in the territorial behaviour of shrimps, with major ecological functions in the coral reef chorus (Au and Banks, 1998; Lillis and Mooney, 2018). Crustaceans also actively communicate via acoustic stimuli through stidulatory movements of their body components to produce creaky sounds. In the European lobster (*Homarus gammarus*), Jézéquel et al. (2020) denoted that individuals produced buzzing sounds during agonistic encounters through carapace vibrations to repel intra-specific competitors. When facing each other, competitors produced very low sounds, with peak frequencies varying between 100 and 200 Hz. Similarly, red swamp crayfishes (*Procambus clarkii*) produced acoustic signals to defend their territory against intraspecific competitors (Buscaino et al., 2012). The sound emitted by the European spiny lobster (*Palinurus elephas*) can be detected over kilometres underwater (up to 3 km; Jézéquel et al., 2020), covering fundamental behavioural functions. To reduce predation threats, spiny lobsters facing conger eels and octopus attacks produce high level of noises associated to their defensive behaviour (frequency range from 2 to 75 kHz; Buscaino et al., 2011). In zooplankton, northern krill (*Meganyctiphanes norvegica*) and copepods (*Calanus* spp.) produced sounds with frequencies from 87 to 3020 Hz, suggesting that acoustic could be used for intraspecific communication among individuals and maintain group cohesion (Kühn et al., 2023). Interestingly, sound emission is supposed to play a central role also during courtship behaviour of *Neohelice granulate* crabs, sounds being diffused during breeding periods, probably in a view to advertise the male presence to other competitors or to attract receptive females (Filiciotto et al., 2019).
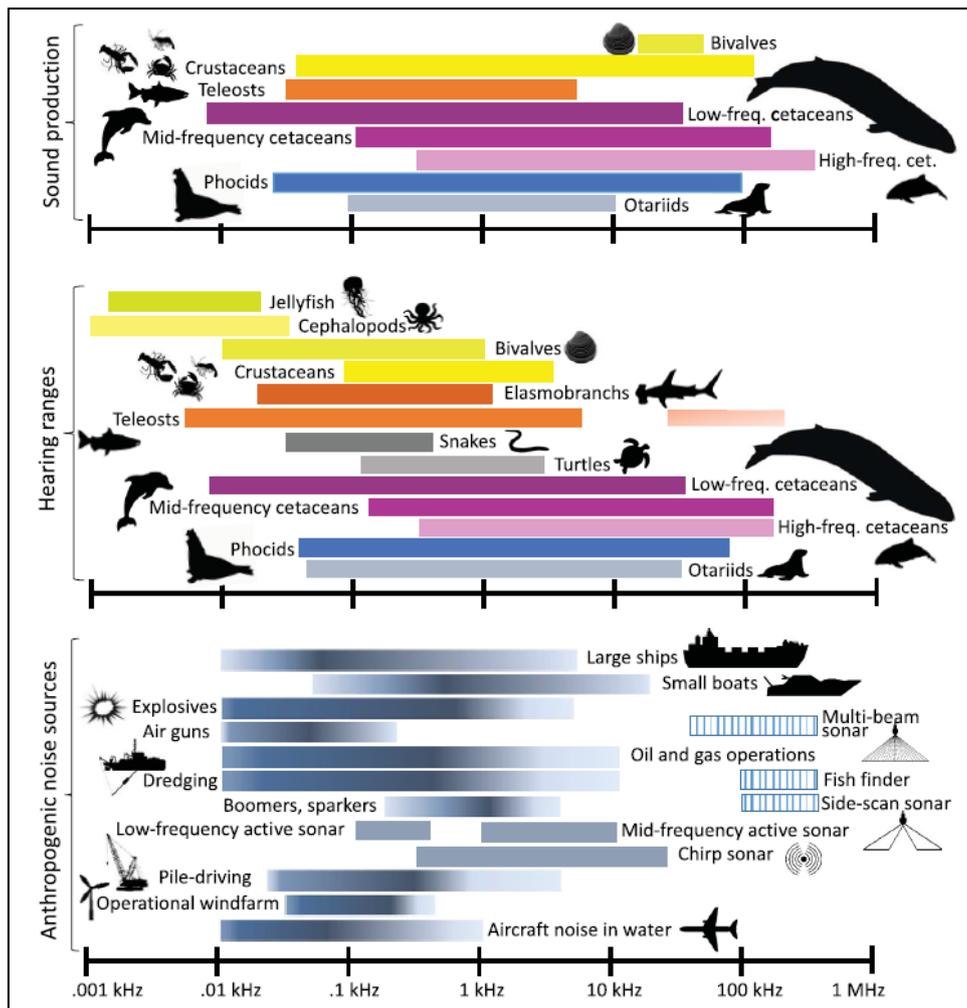
Figure 8: Animals' sound production and hearing ranges in the ocean soundscape characterized by a growing presence of anthropogenic noises (Duarte et al., 2021).

As reported in recent literature, a growing number of studies have focused on characterizing the sounds produced and perceived by various marine invertebrate species, with particular attention to their functions, intensity, and detectable frequency ranges (Charifi et al., 2017; Lillis and Mooney, 2018; Jézéquel et al., 2020; Fig. 8). In particular, there is increasing interest in understanding the relationship between the environmental soundscape and key biological functions in these species (Lillis et al., 2013; Radford et al., 2008; Charifi et al., 2017).

In the context of rising underwater acoustic pollution, further research is needed to assess whether the auditory sensitivities of marine invertebrates overlap with noise generated by human activities. Over the past few decades, indeed, elevated levels of anthropophony have significantly altered the acoustic properties of many marine ecosystems, substantially increasing sound intensity over large spatial scales and potentially causing significant behavioural disruptions across a broad range of marine animal taxa.

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III Introducing Anthropophony: an increasing relevant stressor for marine invertebrates

3.1 A general overview of the actual context of anthropophony in the oceans

Oceans' soundscape is determined by a combination of different physical and biological interpreters that marine animals use to interact with each other and satisfy their general needs. Nowadays, however, oceans are not exempt from anthropophony, as human activities such as urbanisation, shipping, seabed mapping and resource extraction add considerable noise to the aquatic environments modifying their natural soundscape (Duarte et al., 2021; Fig. 8).

Human-induced noises are present at all sound frequency levels in the seas, and it is now considered to be a major element of the 21st century pollution, appearing in a number of national and international regulations (e.g., US National Environment Policy Act and European Commission Marine Strategy Framework Directive; Wale et al., 2013). One of the most concerning issues of acoustic pollution is that noise easily disperses beyond the directly impacted areas, occupying very large portions of an environment. For instance, commercial shipping and seismic exploration generate low-frequency sounds (10 to 500 Hz) that can propagate over considerable distances as such acoustic waves are slightly absorbed by the water (Jones et al., 2023). Small coastal vessels and various engineering works generate medium frequencies (500 to 25 kHz), while echo-sounders emit higher frequencies disturbance (>25 kHz) to obtain high-resolution images of the seabed (Hildebrand, 2009). In general, not only frequency and sound pressure levels, but also the exposure periodicity is an important factor to consider when dealing with acoustic pollution (Di Franco et al., 2020). Acute exposures are usually short and sharp, typically originating from specific sources like pile driving and echo sounding, while chronic exposures are usually longer and result from an accumulation of several repetitive noises like shipping and windfarms (Charifi et al., 2017; Duarte et al., 2021).

Among other acoustic pollutants, human activities have witnessed a dramatic increase in the number of commercial ships cruising over the oceans in the last 50 years. Indeed, container traffic has improved by a factor of five since 1990 (McKenna et al., 2012) and, in some geographical areas, shipping noise has doubled since the 1960's, especially in the northern hemisphere where the most important economic forces are concentrated (Frisk, 2012). To date, commercial shipping has increased by 12 dB the general ambient noise and much of our oceans are currently affected by anthropogenic noises as low frequency acoustic waves propagates over large distances (Duarte et

al., 2021). This has contributed to a 32-fold increase in low-frequency noise along the major trade routes and noise emissions from ships are predicted to double every 11.5 years, although with large regional differences (Hildebrand, 2009; Jalkanen et al., 2022).

Some regions, indeed, are potentially more at risk of losing their original soundscape due to their strategical economic importance (Jalkanen et al., 2022). Because of the gradual melting of the summer ice in the Great North, new trade routes will be adjusted in accordance with the ice extent, changing the global noise dynamics of the Arctic (Aulanier et al., 2017; Hawkins and Popper, 2017; Halliday et al., 2020; Worcester et al., 2020). Ice clearance for extended periods during the summer will allow more commercial vessels to transit key naval corridors, such as the Canadian North-West Passage and the North-eastern Passage (also known as the Northern Sea Route NSR; Fig. 9). The Arctic Ocean could be particularly vulnerable to anthropogenic noise due to their strong historical and geographical isolation to this type of pollutant (Halliday et al., 2020).

While the Arctic regions will experience a critical shift in their soundscape in the near future, many areas already have a high rate of attendance by the world's commercial fleet. An an example, over 5000 cargo ships with 50 million tons of load transit each season (8 months) through the St. Lawrence seaway (Parrott et al., 2011; The geography of transport systems). Due to the important frequentation, shipping noise in this area was absent only 32% of the time and loud noise levels was present 42% of the season duration with a transit of many different types of vessels (Aulanier et al., 2017; data: 2013). Due to shipping passage, a substantial portion of the St. Lawrence estuary is now exposed to sound exposure levels (SEL_{30min}) exceeding 149 dB re 1 μPa^2.s [63 Hz one-third-octave band] over 75% of time (Gervaise et al., 2015), drastically altering its original soundscape.
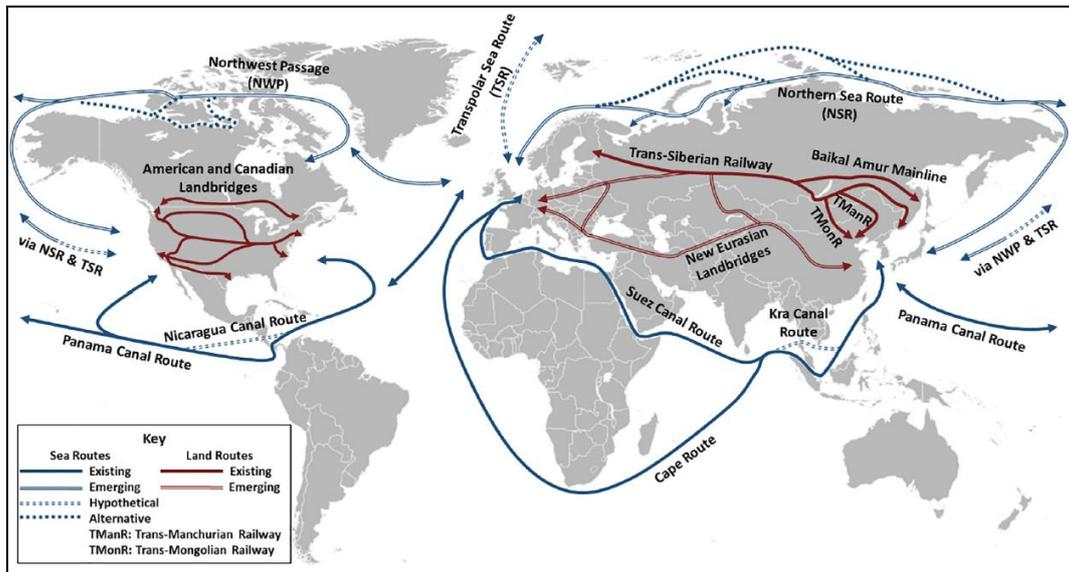
Figure 9: World map of existing and emerging major commercial routes (Theocharis et al., 2018).

These trading routes are frequented by a wide range of commercial vessels, which containerships, dry bulk and liquid tanker vessels contributes to the 75% of the underwater shipping noise source energy (Jalkanen et al., 2022). Each type of vessel has a different acoustic signature depending on its activity, the load carried, the type of propeller and the hull design. In an interesting study, McKenna et al. (2012) described and compared acoustic signatures from a variety of modern commercial ships (Fig. 10). For example, the typical noise of container ships and tankers is predominantly below 40 Hz, while the noise of bulk carriers is predominantly close to 100 Hz (McKenna et al., 2012). Despite such small differences, shipping noise is usually characterized by very low frequencies (i.e., below 200 Hz) with a pressure level ranging from 140 dB re $\mu Pa^2/Hz^{-1}$ for small fishing vessels to 195 dB re $\mu Pa^2/Hz^{-1}$ for fast-moving tankers (from 10 Hz to 1 KHz; Hildebrand, 2009).
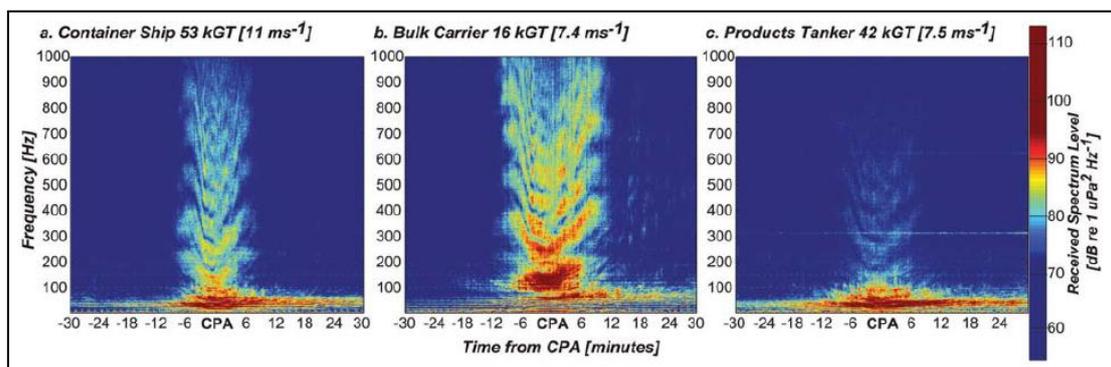
Figure 10: Received sound pressure levels during 1-h passages of three different ship-types (McKenna et al., 2012).

According to studies on the impact of noise on various marine species, such acoustic signatures can have significant effects on many organisms. In particular, a growing body of research highlights that shipping noise operates at frequencies and intensities that are detectable by numerous species, including aquatic invertebrates (Filiciotto et al., 2014; Wale et al., 2019; Charifi et al., 2017; Carter et al., 2020; Di Franco et al., 2020).

3.2 Influence of anthropophony on marine invertebrates

The amplitude of the impact of noise pollution on marine invertebrates varies depending on factors such as the source, frequency and intensity. Anthropophony from punctual noises-generating activities (i.e., pile driving, artificial sonar and seismic explosions) usually reveal of an extreme noise intensity, to the point of causing physical injuries in soft-body organisms, beside physiological and behavioural modifications (Solé et al., 2017; Solé et al., 2019; Jézéquel et al., 2022). In contrast, chronic noises generated by more diffused activities (i.e., commercial shipping, wind farms), generates acoustic pollution characterised by low frequencies and high persistence resulting in a long-lasting source of disturbance, potentially leading to long-term metabolic and behavioural responses (Wale et al., 2013; Filiciotto et al., 2016; Charifi et al., 2017).

Overall, an increasing body of research highlights the considerable effects of shipping noise across various life stage – larval, juvenile and adult – of numerous marine invertebrate species (Wale et al., 2013; Pine et al., 2016; Charifi et al., 2017; Carter et al., 2020; Doyle et al., 2020).

- Larval phase

As described above, the larval settlement phase in many marine invertebrates is influenced by a complex suite of environmental cues, among which the underwater soundscape plays a crucial role (Byrro-Gauthier et al., in press; Lillis et al., 2013). Natural acoustic signals, such as those produced by healthy reef habitats or biological sources (e.g., snapping shrimp, fish vocalizations), are known to guide larvae toward suitable settlement sites, thereby enhancing post-settlement survival and recruitment success (Lillis et al., 2018).

However, in the context of increasing anthropogenic noise—primarily from maritime traffic—both laboratory and field studies have shown that larvae can detect and respond to these novel acoustic stimuli (Byrro-Gauthier et al., in press; Jolivet et al., 2016; Veillard et al., 2025). Such responses may include altered swimming behaviour, delayed or premature settlement, and physiological stress, all of which can disrupt critical early life-history processes (Byrro-Gauthier et al., in press; Nedelec et al., 2014; Veillard et al., 2025). The masking of natural sound cues by anthropogenic

noise may also interfere with habitat recognition, leading to reduced settlement success or misdirected settlement in suboptimal environments. These disruptions have potential consequences for population dynamics, recruitment patterns, and the stability of benthic–pelagic coupling in marine ecosystems (Byrro-Gauthier et al., in press; Pine et al., 2012; Veillard et al., 2025).

- Adult phase

Highly persistent and low chronic frequency noises, affect many adult life aspects of several marine invertebrate species, such as mobility, interactions, feeding and sheltering behaviours (Di Franco et al., 2020; Solé et al., 2023).

Molluscs, especially bivalves, can perceive low-frequency chronic human-induced noises, at different sound pressure levels (Solé et al., 2023). Charifi et al. (2017) with an interesting valvometry study showed that the Pacific oyster (*Crassotrea gigas*) transiently closed their valves in response to frequencies in the range of 10 to <1000 Hz (with maximum sensitivity from 10 to 200 Hz) and that the minimum acoustic energy required to obtain a response was 0.02 m-s^{-2} at 122 dB$_{rms}$ re 1 μPa for frequencies ranging from 10 to 80 Hz. In sessile giant clams (*Tridacna maxima*) exposed to shipping noise (150 dB re 1 μPa), Doyle et al. (2020) found an increase of latency in shell closure (a potential anti-predator response). In the freshwater quagga mussels (*Dreissena rostriformis bugensis*), motorboat noises (up to 134 dB re 1 μPa from 0 to 64 kHz) increased the aggregation of exposed individuals, further influencing valve amplitude gaping and filtering behaviour (Turco et al., 2025). It is of great interest to note that clearance rate significantly changes when mussels are subjected to noise pollution: such process being reduced of 84% in response to shipping noise (150 dB re 1 μPa^2/Hz^{-1}) in *Mytilus edulis*, with considerable carry-over effects by weakening the role of mussels in the benthic-pelagic coupling (Wale et al., 2019; Fig. 11).
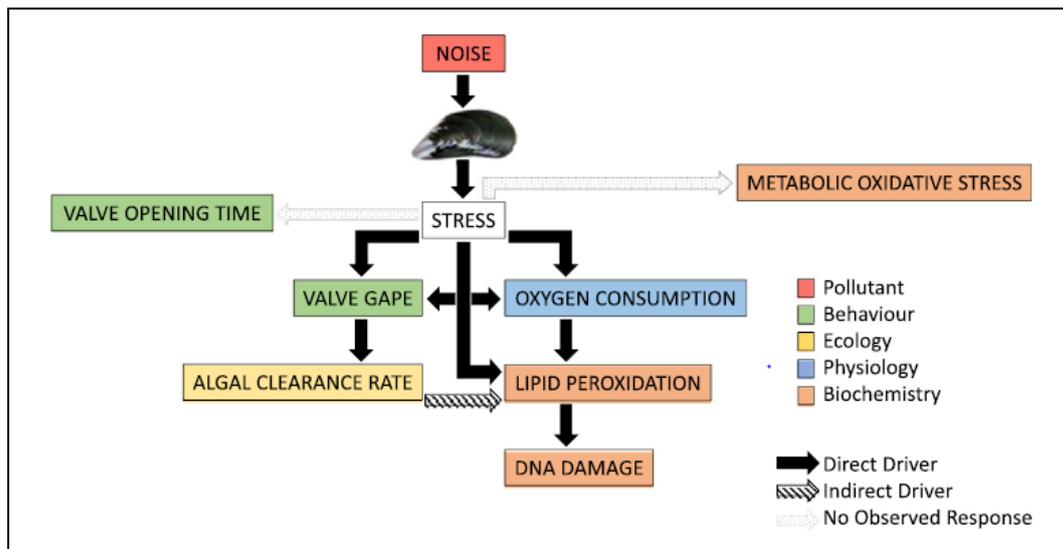
Figure 11: Example of the impacts of noisy conditions to physiological, behavioural and ecological aspect of the blue mussel (*Mytilus edulis*; Wale et al., 2019)

In crustaceans, Mediterranean spiny lobsters (*Palinurus elephans*) subjected to boat noise emissions (frequency band of 0.1–3 kHz; up to 120 dB re 1 µPa) showed increased locomotion activities and lower values of interactions, clearly indicating that lobsters tented to abandon their group of formation (Filiciotto et al., 2014). Interestingly, similar behaviours were recorded when animals were potentially subjected to imminent threats (predation) and under significant stress conditions. Similarly, Celi et al. (2013) have reported that specimens of *Procambarus clarkii* reduced the number of their encounters if exposed to acoustic stimuli (peak amplitude 148 dB re 1µPa at 12 kHz). Recent studies also demonstrate that shipping noise (from 120 to 130 dB re 1 µPa) increased the risk of starvation and predation for the shore crab *Carcinus maenas* (Carter et al., 2020; Wale et al., 2013). Camouflage is a primary defence to prevent predation but then animals must rely on other additional defences. In shore crab, noise was supposed to impair both camouflage and escape capacities, as individuals exposed to shipping noise were impaired in changing the shell coloration and less reactive to retreat to a simulated predator attack (Carter et al., 2020). In the European lobster (*Homarus gammarus*), the acoustic communication between conspecifics may be masked by chronic anthropogenic noises (118 dB re 1 µPa from 55 to 1000 Hz), individuals increasing their call rates in presence of shipping noise suggesting a vocal compensation (Jézéquel et al., 2021). Hermit crabs were also used in several researches as a model organism to investigate the effect of acoustic pollution on several behavioural patterns typical of the species. At different noisy intensity and frequencies (from 119 to 143 dB_{rms} re 1 µPa at 1000 Hz), hermit crabs significantly modified their locomotor activities, hiding latency facing predators and choosing shells more quickly as response to noise (Tidau and Briffa, 2019; Briffa et al., 2024).

The series of experiments highlight the high sensitivity of various classes of marine invertebrates to anthropogenic noise. Overall, the observed behavioural changes may trigger cascading ecological effects in local environments, potentially disrupting key ecosystem dynamics (Wale et al., 2019). In this context, evaluating the behavioural responses of animals to anthropophony is essential for anticipating its broader ecological consequences. Among the wide range of behavioural traits, mobility holds particular importance as an evolutionary strategy, allowing individuals to actively carry out essential ecological functions such as foraging, reproduction and habitat selection (Joo et al., 2020). Therefore, studying animal mobility in relation to noise might be especially relevant for understanding and defining the ecological impact of acoustic pollution in marine ecosystems.

IV Assessing marine invertebrates' movement ecology using biotelemetry tools

4.1 Mobility: an essential behavioural aspect to consider in marine invertebrates

Movement ecology explores how organisms—ranging from animals to plants and microorganisms—move through and interact with their environments (Joo et al., 2020). Mobility plays a critical role in many biological processes, including reproduction, gene flow, population connectivity, range expansions, and species persistence, thereby influencing fundamental evolutionary dynamics (Allen et al., 2018; Joo et al., 2020). Across taxa, animals have evolved diverse movement strategies to meet essential needs such as foraging, mating, and predator avoidance. These movement patterns are often shaped by environmental heterogeneity, as individuals seek favourable habitats in response to changing conditions (Allen et al., 2018; Riotte-Lambert and Matthiopoulos, 2019).

Repeated movements in relation to a defined spatial area often identify a characteristic movement pattern of an animal, with a particular significance for the individual (Lyons et al., 2013; Allen et al., 2018). The *home range* (or habitat usage potential) is usually defined as the area an individual traverses during its routine activities, while the *core area* refers to locations within that range used more intensively (Tomasevic & Marzluff, 2018). In several studies, kernel density estimators and utilization distribution (UD) are employed to provide a precise delimitation of the home range. Analytical tools such as the kernel method provides an estimate for the UD which give the probability that an animal is found at a given point in the space. Usually, the home range is defined as an area inside a contour enclosing a certain portion (i.e., 95%) of the total probability density of

the location, while the core area is defined within a lower percentage of space (i.e. 50%; Katajisto and Moilanen, 2006; Stieglitz and Dujon, 2017; Fig. 12).
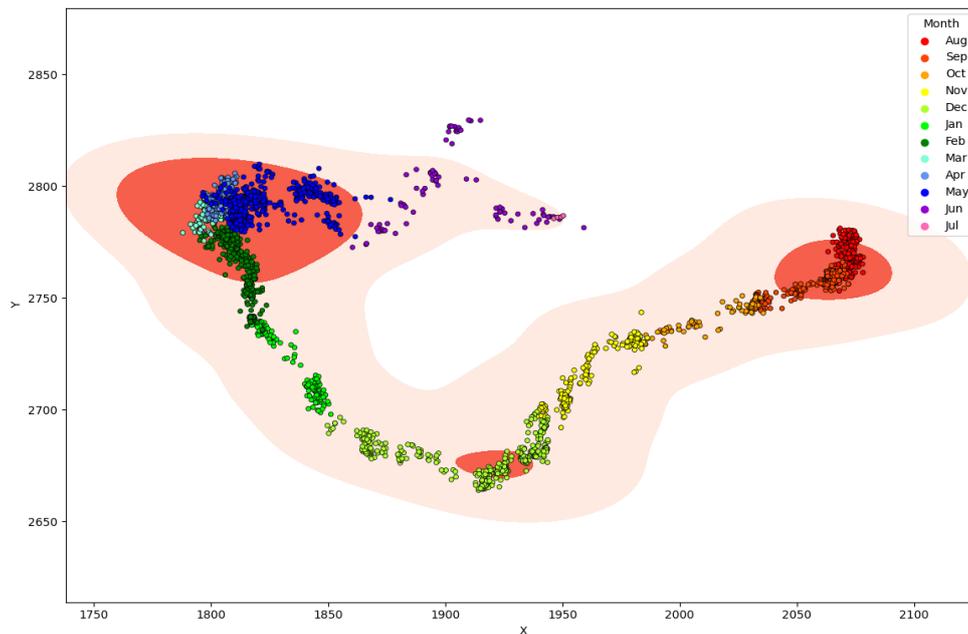
Figure 12: Monthly home range (light orange) and core area (dark orange) extent of a *Buccinum undatum* specimen along the coast of the St. Lawrence estuary (Canada).

Although defining concepts of mobility in animals with complex life cycles—such as marine invertebrates—remains challenging (Allen et al., 2018), recent studies highlight the remarkable plasticity in movement exhibited by several taxa. Their spatial patterns are shaped by both endogenous rhythms and environmental factors, including temperature, seasonality, light cycles, and human disturbances. For example, *Charonia tritonis*, a predatory gastropod, can travel over 200 metres per day, with increased nocturnal activity likely linked to prey availability (Schlaff et al., 2020). Similarly, *Homarus americanus* undertakes large-scale seasonal migrations between shallow coastal and deep offshore waters in response to temperature changes (Goldstein and Watson, 2015).

Environmental stressors also play a pivotal role in modulating invertebrate mobility. Predation pressure, for instance, can limit spatial exploration—as seen in American lobsters that reduce movement in the presence of Atlantic cod (McMahan et al., 2013). Concerning human-induced disturbance, light pollution altered the tidal and circadian activity of the amphipod *Americorchestia longicornis*, which shifts its behaviour under artificial illumination (Lynn et al., 2021).

Given this behavioural context, understanding how external factors—particularly anthropogenic disturbances like underwater noise—affect mobility is increasingly important. Changes in spatial behaviour, such as reductions in activity or displacement from preferred habitats, can have

cascading ecological consequences (Tucker et al., 2018; Wilson et al., 2020). As noise pollution intensifies in marine environments, studying how it alters mobility of marine invertebrates offers valuable insights into broader ecological disturbance.

4.2 The advantages of Acoustic Telemetry and Accelerometry

Benthic marine invertebrates' behaviour and mobility are difficult to study due to their complex-to-access underwater living habitats. As a result, most of the previously reported behavioural experiments about the effect of noise on marine invertebrates' behaviour imply controlled mesocosms (see Di Franco et al., 2020). However, investigating behavioural modifications can be tricky when experiments take place in an artificial environment: the simulated conditions themselves may affect the animal's state, unable to know whether or not the intended stressor is the cause of the observed mutations (Wilson et al., 2021; Matveev and McGaw, 2022). On the other hand, in the open environment direct observations of animal behaviours are only allowed for limited period of time though scuba diving and video recordings.

The study of benthic marine invertebrate behaviour and mobility becomes more viable since recent progress in biotelemetry that record movements within the natural habitat (Hussey et al., 2015; Cote et al., 2019). Remote monitoring of behaviour allows animals to be located and observed with virtually no limitations due to visibility, observer bias or geographical scale. Acoustic telemetry is a technology that allows information to be transferred through underwater soundwaves: a transmitter fitted on the animal sends a high-frequency acoustic signal that is picked up, decoded and timed by a set of acoustic receivers to locate a specific point in the space (Fig. 13). As sound waves propagate greatly in the water, acoustic telemetry can be used to transfer relatively complex information over long distances (Hussey et al., 2015). In this way, telemetry technologies can provide information on both small-scale habitat usage and large-scale migrations of a large panel of aquatic organisms. In literature, acoustic telemetry has been mostly used to assemble a large amount of accurate data concerning the trajectories drawn by pre-selected animals (Morse et al., 2018; Schlaff et al., 2021), in order to answer biological questions such as the size of a species' home range and/or travelled distances. However, such tools can also be used to assess and quantify the impact of stressors derived from human activities. Hellström et al. (2016) suggested that acoustic telemetry can be a valuable method within ecotoxicology to extrapolate information obtained in the laboratory to the natural environment, increasing our understanding of how behavioural responses observed in the laboratory translate into ecological consequences.
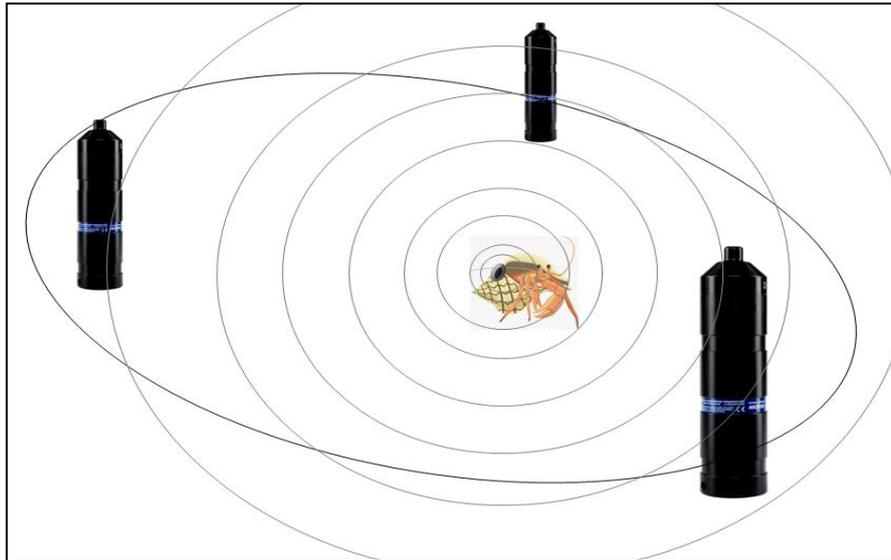
Figure 13: How acoustic telemetry works? Here, a transmitter emitting an acoustic signal perceived at different moments by the multiple receivers. By triangulating the received signal, it is then possible to define the position of the animal in the space.

Beside acoustic telemetry, accelerometry allows the observation of finer behavioural responses in many different species. Similarly to statocysts, accelerometers offer an electronic analogue capable of capturing continuous, high-resolution data on acceleration, posture and fine-scale-movements over time (Jolivet et al., 2015). In this way, it is possible to deduce specific animal behaviours, presence of stressors and estimate the energy expenditure (Brown et al., 2013). Stieglitz and Dujon (2017) showed that the use of a triaxial accelerometer allows significant additional information on the animal's movement behaviour. This is true especially for slow-moving benthic animals (e.g., gastropods), where positioning data alone might be not enough to define their behavioural characteristics (Stieglitz and Dujon, 2017).

Mobility, habitat usage and overall activity are very important factors in animal behavioural ecology, with critical consequences for the ecosystem functioning (Lundberg and Moberg, 2003). External factors, like human-induced pollutants, can change the mobility patterns of many animal species by influencing displacements within their natural habitat, potentially modifying the ecological role of movement (Filiciotto et al., 2014; Tucker et al., 2018; Lynn et al., 2021). Thus, biotelemetry technologies are greatly helpful for researchers that aim to study animal behaviour on both *in situ* and controlled experiments, assessing the great behavioural variability of marine invertebrates and potential alteration facing noise pollution.

V PhD's context and objectives

As previously introduced, anthropophony is emerging as a significant driver of behavioural change in marine fauna, including invertebrates. Pile driving, echo-sounders, seismic exploration, and the intensification of shipping traffic have been shown to substantially alter the behaviour of numerous marine invertebrate species, with potential repercussions for their ecological roles. Despite growing interest, the overall understanding of noise-induced behavioural changes remains limited, with many key questions still unresolved. Notably, the majority of studies addressing the effects of anthropogenic sound focus on only a few classes — primarily bivalves, cephalopods, and crustaceans — and rarely account for the temporal specifities of invertebrate behaviour. In particular, the behavioural responses of marine gastropods to acoustic pollution remain entirely absent from the scientific literature. Furthermore, most experimental studies on the impact of underwater noise have been restricted to short-term exposures (ranging from minutes to a few hours), mostly confined to controlled environments (laboratory experiences) and specific times of day and seasons (typically daylight hours during a single season). This narrow approach limits our ability to assess the real biological impacts of noise across varying circadian and seasonal cycles in marine invertebrates, limiting the complete understanding of the ecological consequences of anthropophony within the marine environment over the long period.

To address these knowledge gaps, this PhD project consist of three main chapters with the aims to explore the behavioural specificities of two marine invertebrate benthic vagile species — *Buccinum undatum* (Gastropoda) and *Cancer irroratus* (Malacostraca) — and to investigate their behavioural responses to anthropogenic noise using both *in situ* and controlled laboratory experiments over extended exposure times (Tab. 1).

In **Chapter 1**, we characterized the natural spatial behaviour of the gastropod *B. undatum*, revealing substantial behavioural specificities across both circadian and seasonal cycles. This dataset was obtained in collaboration with Chris McKindsey's team (DFO) through the deployment of a multi-year acoustic telemetry array in Petite Baie Saint-Nicolas, located along the northern coast of the Gulf of St. Lawrence. Building upon the knowledge acquired during this first chapter, in **Chapter 2**, species-specific spatial and behavioural metrics were subsequently employed to evaluate the potential impact of shipping noise on *B. undatum* mobility and activity. An *in situ* experiment was conducted in the Miquelon Bay, employing acoustic telemetry to assess the effects of shipping noise on the spatial behaviour of wild specimens in the open environment. To corroborate the field

observations, complementary experiments were performed under controlled conditions at the Institut Maurice-Lamontagne (IML) using accelerometry. To have an insight into other classes of benthic vagile marine invertebrates, the study was further extended in **Chapter 3** to examine the effects of similar shipping noise pressure levels on the spatial behaviour of *C. irroratus* through video recording and accelerometry. To this end, an experimental design was developed to account for the species' behavioural specificities in relation to both circadian and seasonal cycles.

Table 1: General description and main objectives of the three chapters included in the present PhD project.

Chapter n°	Considered species	Exposure time	Experimental setup	Objective
Chapter 1	*Buccinum undatum*	-	*In situ*	Assessing the spatial behaviour of a wild population of *B. undatum* over multiple circadian and seasonal cycles by a long-term acoustic telemetry monitoring study
Chapter 2	*Buccinum undatum*	10 days (*in situ*) + 2h (controlled)	*In situ* + Controlled	Assessing the impact of determined SPL_{rms} of shipping noise on the spatial behaviour of *B. undatum* via acoustic telemetry and accelerometry
Chapter 3	*Cancer irroratus*	2 days	Controlled	Assessing the impact of determined SPL_{rms} of shipping noise on the spatial behaviour of *C. irroratus* via accelerometry and video recordings

Chapter 1

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 two-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 *B. undatum* vulnerable to local overfishing.

Résumé

De nombreuses pêcheries d'invertébrés marins sont vulnérables à la surexploitation et nécessitent des mesures de conservation pour assurer leur durabilité. Ces dernières années, les débarquements de buccins *Buccinum undatum* (Linnaeus, 1758) ont considérablement diminué le long des côtes du Saint-Laurent (Canada), avec une baisse pouvant atteindre 76 % dans certaines zones de pêche. La surpêche locale peut s'expliquer en partie par la reproduction ovipare de l'espèce, qui limite la dispersion des larves et les interactions entre les populations. À l'aide d'une étude de télémétrie acoustique à long terme menée sur deux ans, nous avons suivi 20 individus afin d'évaluer leur comportement général en matière de déplacement et leur potentiel de dispersion dans une zone donnée. Les individus marqués ont montré des déplacements quotidiens considérables (de 2 à 16 m/h en moyenne), sans différence notable entre le jour et la nuit. La vitesse et le potentiel d'utilisation de l'habitat (PUH) variaient selon les saisons, très probablement en raison du cycle de reproduction de l'espèce : le PUH était nettement plus important pendant la saison de reproduction en mai (4570 m^2) et juin (2779 m^2) que pendant les mois d'hiver précédents (1046 m^2). Bien que certains individus se soient déplacés sur une profondeur considérable, nous n'avons pas observé de saisonnalité sur le gradient bathymétrique de la zone. Dans l'ensemble, le PUH restreint de l'espèce

limite la dispersion des individus, ce qui se traduit par des connexions très faibles entre les populations voisines et rend B. undatum vulnérable à la surpêche locale.

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; Giglioli et al. 2021; Alati et al. 2020), 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 *B. undatum* constitutes an international fishery of great commercial value (Pêches et Océans Canada 2022a, 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 2002-2018 (Pêches et Océans Canada 2022a). According to local authorities, the status of an increasing number of *B. 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 2022a). 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 2022a). 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 *B. undatum*, yielding evidence of long-term population connectivity and persistence.

Using a two-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 *B. 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 Material 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. 14). 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. 15). The substrate of the study site is characteristic from areas where *B. 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, then drops off to 50 m (Fig. 14). 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.
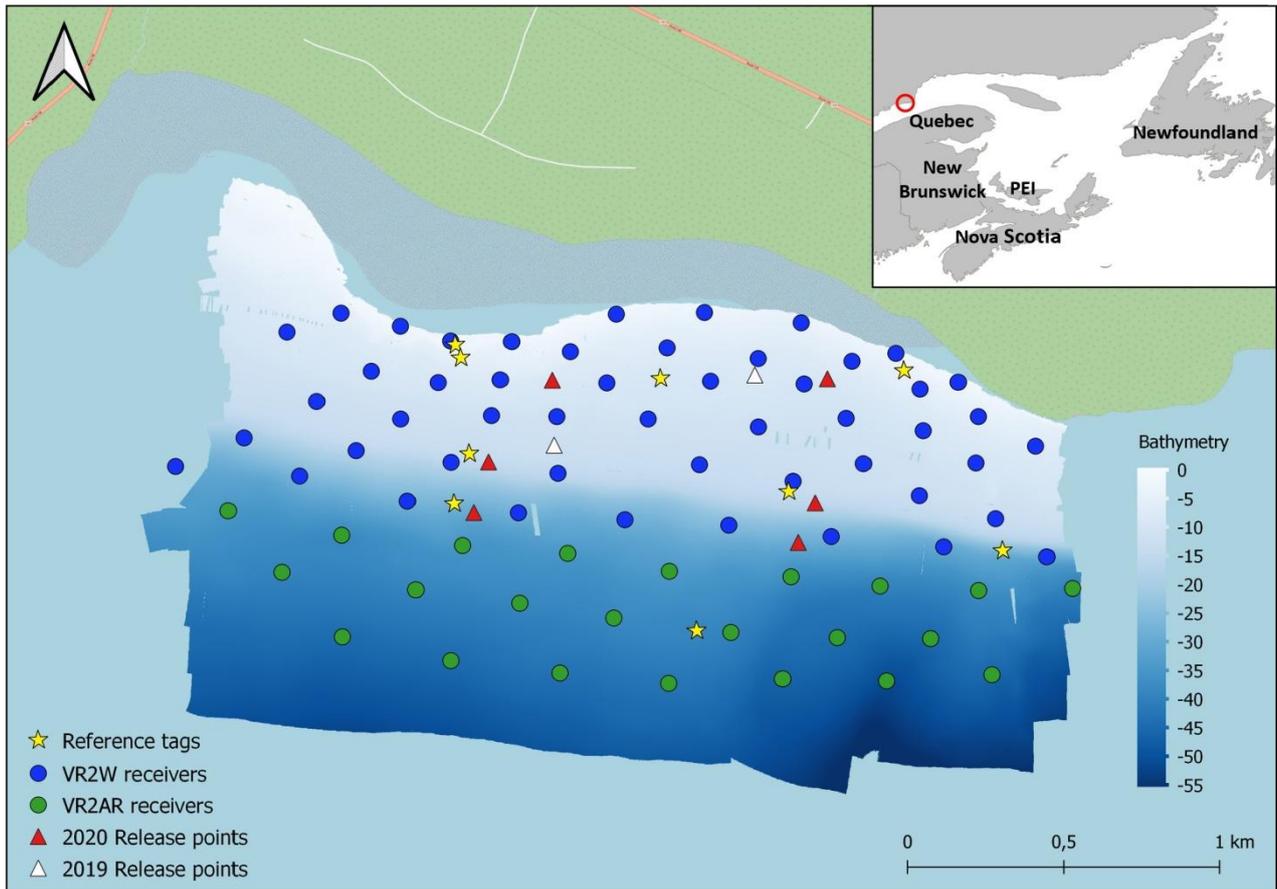
Figure 14: Location of the receiver array during the 2020/2021 monitoring season within the study area of Petite baie Saint Nicolas, Quebec, Canada. Blue points are VR2W receivers, green points are VR2AR receivers, and yellow stars are reference tags deployed within the area. Release points of whelks *Buccinum undatum* in Aug. 2019 are represented by the white triangles and Oct. 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).
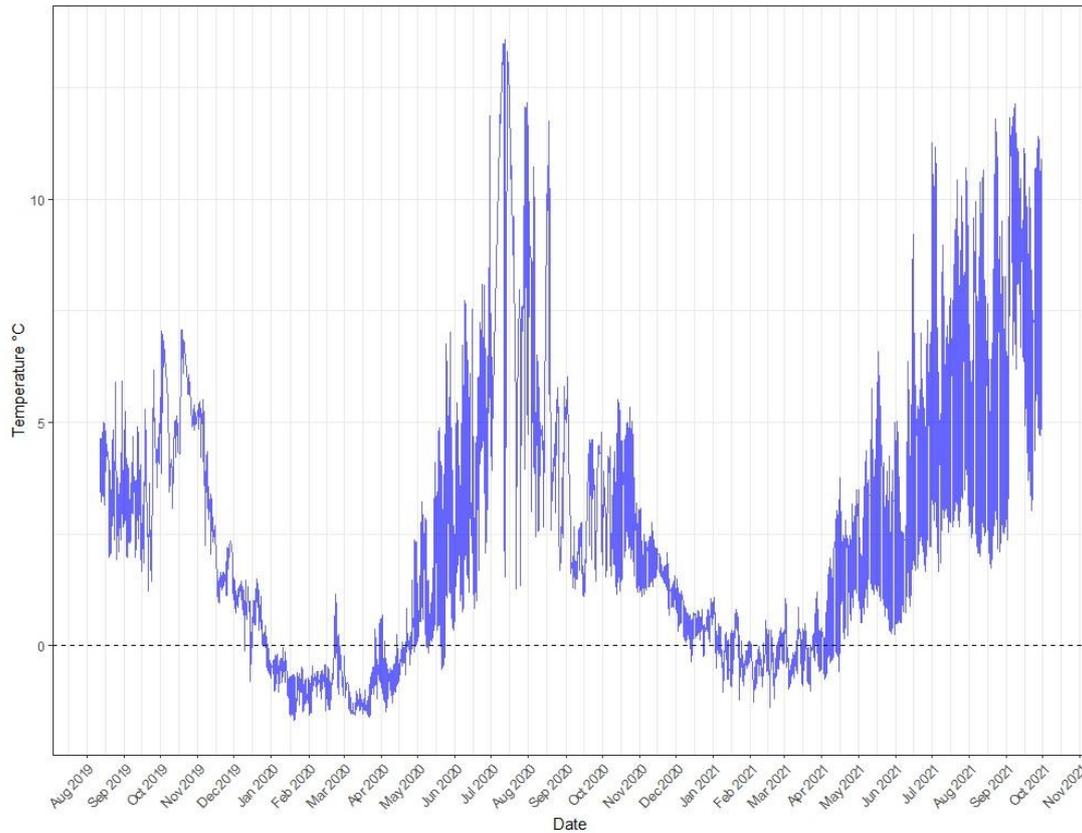
Figure 15: Temperatures experienced by tracked waved whelks *Buccinum undatum* all over the monitoring period. Temperature values were directly related to the position of each individuals over the study area. Summer months of June, July and August show a great thermal variability, while winter months show constant cold temperatures.

2.2 Receiver array

Our study was done over two years and two types of receivers were deployed: VR2W and VR2AR (Innovasea, Canada). VR2W receivers were situated in shallower areas, whereas VR2AR with an acoustic release system were deployed in areas that were too deep to dive (Fig. 14).

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. 14). Our array covered an area of approximately 2.7×2 km. Receivers were spaced approximately 500m apart across most of the array; this distance was reduced to 50-100m 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. 14). Animals were collected by scuba divers, brought to the surface and transmitters glued to the shells using epoxy glue (Lepage Ultra superglue^{TM}; Fig. 16). 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 minutes 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 hours (see also Stieglitz and Dujon 2017; Cote et al. 2019; Lavoie et al. 2022).

Figure 16: 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.

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 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 was 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 (Tab. 2). 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; Tab. 2). 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 > 25m/h. This speed was selected by means of analysis of a series of baited camera videos at our study site in which *B. undatum* were never observed to exceed 20m/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. 14). 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.

Table 2: Data summary of the 20 retained tagged waved whelks *Buccinum undatum* with shell length at the time of tagging, n° of tracking days for each individual, spatial metrics and habitat usage potential. % 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.

						% Retention Rate						
Tag ID	Length (cm)	Release zone	Date of first detection	Date of last detection	N° of days	2019/2020 T1	2020/2021 T2	T3	T4	Tot. Trav. Dist. (km)	Net Dist.(m)	HUP (m^2)
21	8.5	East	12/08/2019	15/10/2021	790	79.4	78	51	37	48.303	257	37171
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	209949
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	38793
70	8.6	West	11/10/2020	15/10/2021	370			54	41	5.677	553	15005
71	9.1	West	11/10/2020	15/10/2021	370			60	47	56.661	60	13000
72	9.2	West	11/10/2020	14/10/2021	369			70	67	110.984	585	78522
73	8.9	West	11/10/2020	15/10/2021	370			48	59	69.879	381	40229
78	9.4	West	11/10/2020	14/10/2021	369			50	57	69.117	330	29114
81	8.2	West	11/10/2020	31/05/2021	232			54	39	35.690	381	34603
82	8.2	West	11/10/2020	15/10/2021	370			60	55	74.658	304	18032
83	7.4	East	13/10/2020	30/07/2021	290			33	37	11.939	267	10777
93	9	East	10/10/2020	09/10/2021	364			62	37	63.775	533	44771
4	7.4	East	10/10/2020	15/10/2021	371			53	41	29.604	143	15280
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	23976
46	7.9	East	13/10/2020	31/07/2021	291			30	46	19.411	63	9698

2.5 Calculation of behavioural metrics

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.

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 *B. 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.

Habitat Usage Potential calculation

The habitat usage potential (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 analytic methods, Börger et al. (2006) found 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.

To examine connections and any subsequent mixing between groups of individuals released in the western and eastern parts of the bay (Tab. 2), we calculate the total HUP of each group as well as the percentage of overlap during the study period.

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 (LMM) including different explanatory variables in addition to a single random effect (Tab. 3). 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; Tab. 3) and the significance of each factor was assessed within the model (Tab. 4).

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; Tab. 3). The interaction between the period of the year (i.e., month) and temperature (see Tab. 3) 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; Tab. 2), the size factor was thus removed from the models.

Model fit was graphically validated after residuals inspection (see Fig. 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 'car' (Fox and Weisberg 2018) to get the significance of the test. A significance *P*-value of 0.05 was used for all analyses.

Table 3: Equations used in statistical analyse. 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.

Standardised Speed ~ **M** + **Y** + **DN** + **T** + **R** + **M:T** + (*1/Individual*)	[1]
HUP ~ **M** + **Y** + **T** + **R** + **M:T** + (*1/Individual*)	[2]

Table 4: 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 HUP over the study period. 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) are indicated in bold. HUP was log-transformed to approximate normality of residuals.

Stand. speed	*β*	*SE*	*χ²*	*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*	*χ²*	*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

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 Aug. 2019 to Jul. 2020), while three other individuals were detected during the entire study period (from Aug 2019 to Oct. 2021; Tab. 2). Of the 2020 tagged whelks, 14 were successfully detected from 232 to 371 days (from Oct. 2020 to Oct. 2021; Tab. 2).

Mobility varied greatly among individuals, showing high inter-individual variability of movements. Over single days (24h), whelks were able to move between a mean of 449.7 m/day ($\pm$ 15.2 standard error (SE); tag n° 72) and 61.1 m/day ($\pm$ 4.1; tag n° 81). Several individuals showed a maximal daily travelled distance up to 600 m (tag n° 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 ($\pm$ 0.39) all over the study period, with maximal values between 30 and 90 m/day.

Of the tagged whelks, tag n° 25 travelled the greatest total distance (220 km) over 790 monitoring days, with others moving over a mean total distance of 45.23 km ($\pm$ 6.82), although over different monitoring periods (see Tab. 2). The large discrepancy in linear movements among individuals was reflected in HUP values, with tag n° 25 exploring a total area of 209 900 m^2 compared to others with a mean HUP of 23 261.15 m^2 ($\pm$ 4326.38; Tab. 2). Overall, there was a great inter-individual variability in HUP, with some individuals exploring large areas (> 100 000 m^2; e.g., tag n° 25, 72, 83) compared to others (< 10 000 m^2; e.g. tag n° 15, 24, 42; Tab. 2).

The mean total net travelled distances of all individuals was 269.75 m ($\pm$ 36.86) from their release point (maximum of 585 m of tag n° 72; Tab. 2), 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 ($\pm$ 0.34 SE; tag n° 72) and 5.11 m/h ($\pm$ 0.25; tag n° 83) over the study period. During the day, whelks moved a mean of 10.15 m/h ($\pm$ 0.09) while they moved a mean of 11.32 m/h ($\pm$ 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 (Tab. 4; Fig. 17).

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. 17). 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. 18).
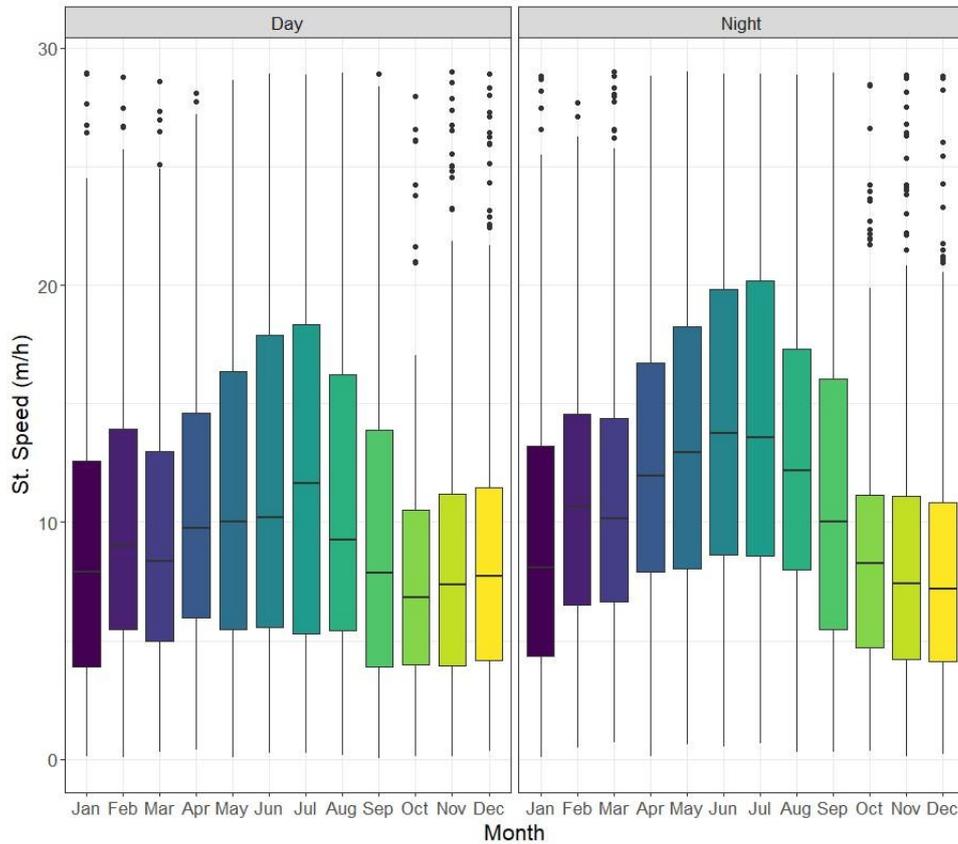
Figure 17: Seasonal variations in the standardised speed of waved whelks *Buccinum undatum* over day and night periods over different months of the year. Of note, the great inter-individual variability of recorded speeds.
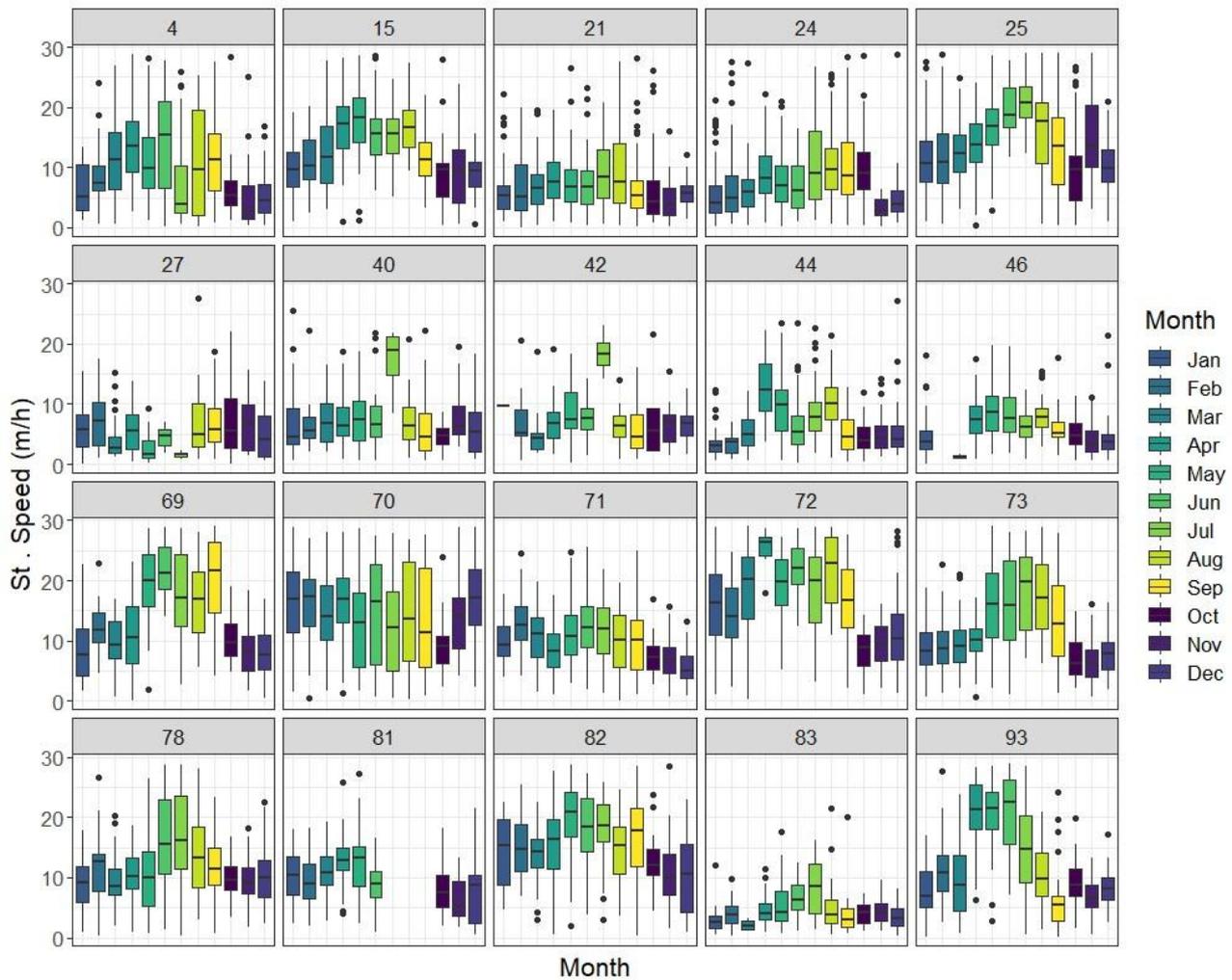
Figure 18: Seasonal variation in standardised speed for each tracked waved whelk *Buccinum undatum* over different months of the year. Of note, individuals show a great inter variability of the response, with some whelks showing a marked seasonal pattern, while others showing relatively constant pattern all over the year.

The effect of temperature on standardised whelk speeds was a function of months (significant interaction between months and temperature, $p < 0.001$; Tab. 4). 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 ($\pm$ 0.04) each 1°C (Fig. 19). In all other months (except November) this positive relationship was not observed, with summer months showing constant standardised speeds despite increasing temperatures (Fig. 19).

The release area also showed a significant effect on whelks mobility ($p < 0.001$; Tab. 4), with individuals from the west site showing a mean standardised speed of 12.66 m/h ($\pm$ 0.1) compared to a mean of 9.57 m/h ($\pm$ 0.07) in the east site.
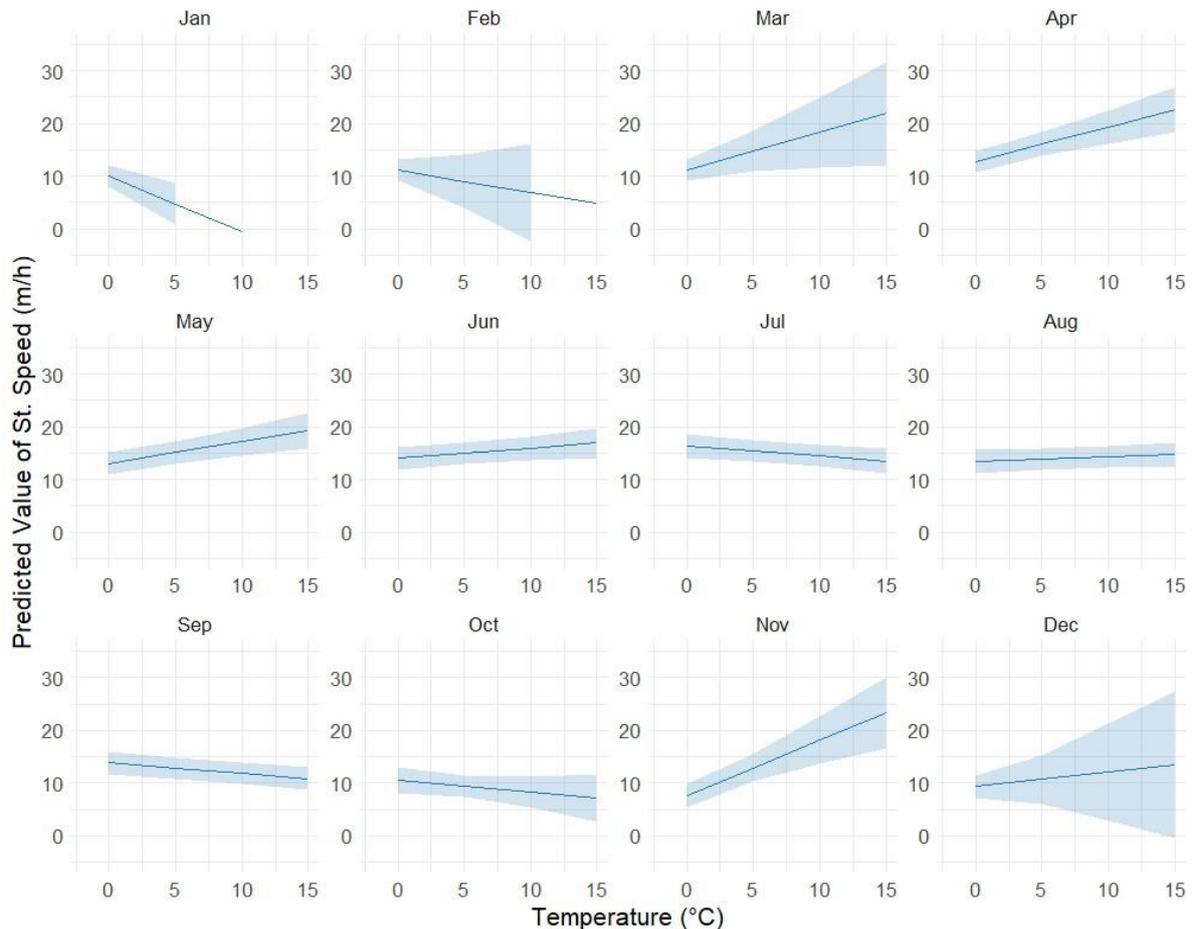
Figure 19: Predicted values of standardised speed according to our first model concerning the interaction between month and temperature. Note that although the model includes temperatures of up to 15°C, these values cannot be reached during the winter months within our study area. The present figure illustrates the eventual existing relationship between mobility potential of waved whelks *Buccinum undatum* and temperature.

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 (Tab. 4; Fig. 20). 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 ± 811.76, n = 21) and July (1159.9 m^2 ± 215.95, n = 19). The lowest mean HUP was observed in January (1046.31 m^2 ± 231.22, n = 20), followed by July and September (1247.38 m^2 ± 276.67, n = 16).

Both temperature and the interaction between temperature and month did not have significant effect on HUP (Tab. 4). 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.
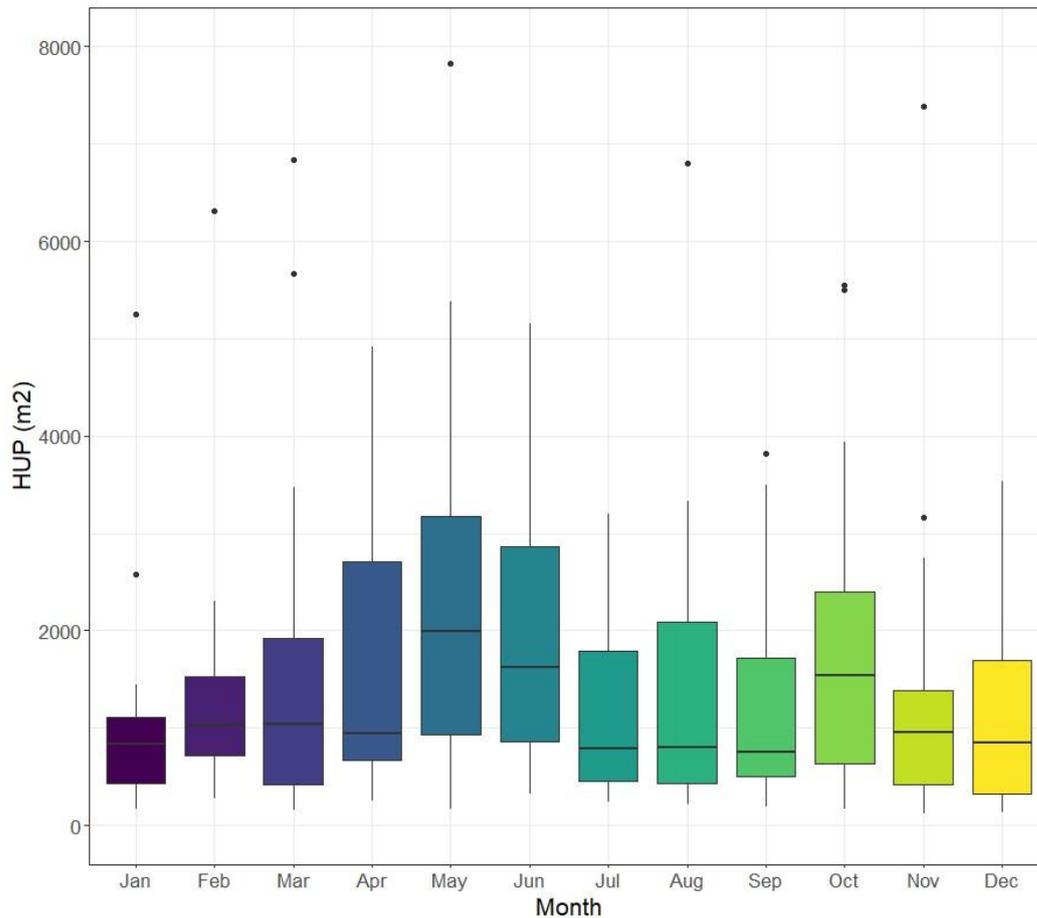
Figure 20: Seasonal variations in habitat usage potential (m^2) of waved whelks *Buccinum undatum* over different months of the year. Of note, the lower variability of winter month compared to spring/summer months.

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 n° 25 showed the greatest bathymetric gradient from October 2019 to March 2020, moving from 12.5 to 41 m (Fig. 21). In contrast, several individuals remained at depths similar to their release point throughout the entire year (Fig. 21). The minimum recorded depth was 6.3 m (tag n° 46), while the maximum was 41 m (tag n° 25).
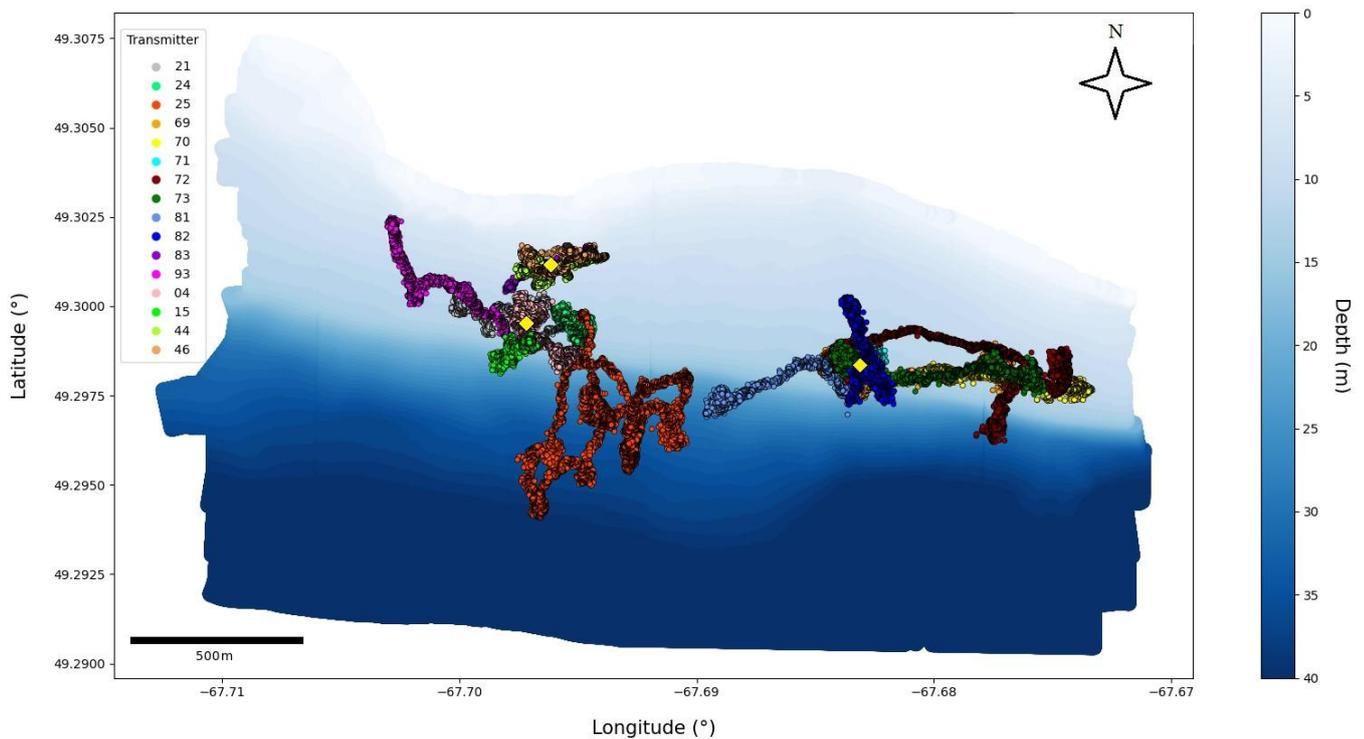
Figure 21: Recorded location of all 2020 tagged individuals from Oct 2020 to Oct 2021 with respect to bathymetry of the Petite baie de Saint-Nicolas. Tags n° 21/24/25 show displacements from Aug 2019 to Oct 2021. The yellow diamonds represent the east and west main release points of the tracked individuals of waved whelks *Buccinum undatum* during the study period.

4 Discussion

Our study shows that *B. 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 *B. undatum* can cover similar areas as tropical gastropods, although some individuals (e.g., tags n° 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 mobility is related to the age of the individuals, with older *L. 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 *B. 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 *B. 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 to 60% of whelks had food in their stomachs during the winter and early spring (and only 0 to 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 *B. 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 *B. undatum* has separate sexes and 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 *B. 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 temperature 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).

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 *B. 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 metres and never exceeding 41 metres (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 *B. undatum* individuals is somewhat restricted. For example, animals with tags n° 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 m2 (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, *B. 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 *B. 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 24h soak; Himmelman 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 2022a). 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 2022b). 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 2022a), 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 *B. 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 *B. 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 *B. 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.

5 Acknowledgements

Chapter 2

Shipping noise alters the spatial behaviour and habitat use of waved whelk (*Buccinum undatum*, Gastropoda)

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Abstract

Commercial shipping generates some of the most pervasive underwater anthropogenic noise. While impacts on marine mammals and fishes are well documented, effects on marine invertebrates - particularly gastropods - remain rare. Using both *in situ* and controlled experimental designs, we investigated the influence of a cargo ship noise on the spatial behaviour of the gastropod whelk *Buccinum undatum* across various spatiotemporal scales. By means of an underwater loudspeaker, we exposed two distinct acoustic telemetry arrays to contrasting shipping noise intensities (root-mean-square sound pressure levels (SPL_{rms}) of control/99.4 and 123.7 dB re 1 µPa) over a 10-day period to evaluate the effect of noise on mobility, habitat usage and distribution of wild specimens. To support these preliminary findings, individuals were exposed to different SPL_{rms} conditions (control/114.6, 122.5, 154.1 and 174.7 dB re 1 µPa) in a large tank to assess finer behavioural changes through accelerometry. Over the long term, field-exposed individuals showed significantly reduced speed of displacement and 21.1% lower daily covered distances. Whelks also exhibited 36.6% smaller habitat usage potential, although they did not display area avoidance from the polluted site. In laboratory, individuals exposed to the loudest SPL_{rms} were less active than other treatments, with 48.7% lower overall dynamic body acceleration and 34% shorter moving time. These results demonstrate that over different intensity and time scales, shipping noise negatively affects the locomotor capacity of gastropods, constraining their potential for dispersal in the environment.

Résumé

Le transport maritime commercial génère certains des bruits anthropiques sous-marins parmi les plus répandus. Si les impacts sur les mammifères marins et les poissons sont bien documentés, les effets sur les invertébrés marins, en particulier les gastéropodes, restent rares. À l'aide de dispositifs expérimentaux in situ et contrôlés, nous avons étudié l'influence du bruit des cargos sur le comportement spatial du gastéropode Buccinum undatum à différentes échelles spatio-temporelles. À l'aide d'un haut-parleur sous-marin, nous avons exposé deux réseaux de télémétrie acoustique distincts à des intensités de bruit de navigation contrastées (niveaux de pression acoustique moyens quadratiques (SPL_{rms}) de 99.4 et 123.7 dB re 1 µPa) pendant une période de 10 jours afin d'évaluer l'effet du bruit sur la mobilité, l'utilisation de l'habitat et la distribution des spécimens sauvages. Pour corroborer ces résultats préliminaires, les individus ont été exposés à différentes conditions SPL_{rms} (contrôle/114.6, 122.5, 154.1 et 174.7 dB re 1 µPa) dans un grand bassin afin d'évaluer les changements comportementaux plus fins à l'aide d'accéléromètres. À long terme, les individus

exposés sur le terrain ont montré une vitesse de déplacement significativement réduite et des distances parcourues quotidiennement inférieures de 21.1 %. Les buccins ont également montré un potentiel d'utilisation de l'habitat réduit de 36.6 %, bien qu'ils n'aient pas évité la zone polluée. En laboratoire, les individus exposés aux SPLrms les plus élevés étaient moins actifs que les autres groupes, avec une accélération dynamique globale du corps inférieure de 48.7 % et un temps de déplacement plus court de 34 %. Ces résultats démontrent qu'à différentes intensités et échelles de temps, le bruit des navires affecte négativement la capacité locomotrice des gastéropodes, limitant leur potentiel de dispersion dans l'environnement.

1 Introduction

Through millions of years of evolution, species have evolved their own sensory bubble that enables them to perceive the various elements that constitute the world (i.e., the *umwelt*; von Uexküll, 1909). In a natural pristine habitat, the environmental predictability allows animals to be synchronized with the conditions they experience (Riotte-Lambert and Matthiopoulos, 2019). Among other factors, the environment is composed of a multitude of sounds and noises determined by a combination of different physical and biological interpreters that enable organisms to perform their living functions (Charifi et al., 2017; Redaelli et al., 2022; Kühn et al. 2023). Nowadays, however, the predictability of the oceans' soundscape is changing dramatically, affecting the sensory bubble of an undetermined number of marine organisms (Di Franco et al., 2020; Solé et al., 2023). Anthropophony, indeed, is often noisy, chaotic and uncompetitive compared to natural sounds, resulting of all sorts of human activities (Duarte et al., 2021). Anthropic noise is considered a major element of the 21st century pollution, demonstrating a significant capacity of dispersion within the aquatic environment and encompassing a wide spectrum of frequencies (Worcester et al., 2020; Duarte et al., 2021). Among others, modern commercial shipping increased the general ambient noise of oceans and noise emissions (63 Hz 1/3 octave band from ships) are predicted to double every 11.5 years (Jalkanen et al., 2022). In some near-to-pristine Arctic regions, also, the proportion of shipping noise is predicted to largely increase by 34 to 44% in the next decades, with large-scale consequences for the Great North soundscape and ecology (Aulanier et al., 2017; Worcester et al., 2020).

A growing number of studies established that the pressure levels and frequency range typical of anthropophony can be detected by marine species (Duarte et al., 2021), leading to critical modifications in the animal behaviour and possible wider ecological issues across ecosystems (Wale et al., 2019; Di Franco et al., 2020; Ivanova et al., 2020; Solé et al., 2023). In particular, one of the most severe effects of noise pollution is the alteration of the animal activity and habitat usage (i.e., species distribution, territory delimitation; Ivanova et al., 2020; Sordello et al., 2020), potentially influencing myriads of ecological and evolutionary processes, including connectivity among communities, range expansions, invasions and persistence (Drolet et al., 2016; Allen et al., 2018). Nevertheless, these crucial behavioural aspects remain largely understudied, in part due to technical difficulties in quantifying the effect of marine noise on animal movement (Sordello et al., 2020). In this sense, acoustic telemetry and accelerometry could provide valuable information on the effects of acoustic pollution on the movement ecology of wild specimens, providing relevant evidence on potential long-term ecological consequences (see Ivanova et al., 2020).

Beside marine mammals and fishes, there is now evidence that anthropophony also negatively affect different classes of marine invertebrates (Duarte et al., 2021). Among others, molluscs can perceive acoustic stimuli through different sensory organs (i.e., statocysts, superficial receptors and flow detectors), actively reacting to a wide spectrum of noise frequencies through extensive behavioural changes (Wale et al., 2019; Di Franco et al., 2020; Solé et al., 2023). For instance, the pacific oyster *Crassostrea gigas* was observed to transiently close their valves in response to frequencies in the range of 10 to 1000 Hz, with maximum sensitivity from 10 to 200 Hz (Charifi et al., 2017). Shipping noise was also observed to induce more frequent colour changes and increased time swimming in the common cuttlefish, *Sepia officinalis*, with relevant interference in their acoustic sensory channel (Kunc et al., 2016). Despite in the last years an increasing attention was devoted to determine the sensitivity to noise in molluscs (especially bivalves and cephalopods), marine gastropods responses to acoustic pollution still remains rare in literature. This class of invertebrate, however, display the same "hearing" organs of other mollusc species (Solé et al., 2023), a wide range of behavioural patterns (Jolivet et al., 2015; Dujon et al. 2021) and different strategies of habitat usage (Stieglitz and Dujon, 2017; Uboldi et al., 2025) potentially affected by anthropophony.

Gastropods are usually considered as a class of slow-moving animals, performing relatively restricted displacements that define their spatial distribution within a certain habitat (Konzewitsch and Evans, 2020; Uboldi et al., 2025). Populations of waved whelk, *Buccinum undatum* (Linnaeus, 1758), were recently defined as very highly vulnerable to local extinction facing overfishing because of its restrictive life history strategies (i.e., late sexual maturation, internal fertilization, long life cycles and direct development) and limited dispersal potential of adult individuals (Ashfaq et al., 2019; MPO, 2022; Uboldi et al., 2025). The sedentary nature of the species, indeed, severely isolates neighbouring populations, showing low interconnectivity and reduced potential for colonizing new areas (Uboldi et al., 2025). Nonetheless, waved whelks show considerable daily displacements (from 2 to 20 m/h) and seasonal patterns of habitat usage essential to satisfy their general needs as feeding and reproduction (Martel et al., 1987; Uboldi et al., 2025). In this sense, a negative effect of shipping noise on individuals' mobility potential would add to populations' vulnerability, causing severe issues to their long-term resilience.

Because laboratory experiments can only provide partial answers to the effect of noise pollution on animal ecology (Filiciotto et al., 2014; Wale et al., 2019), we investigated the effect of shipping noise on *B. undatum* at different spatiotemporal scales. In a first field-based experiment, we established two distinct acoustic telemetry arrays exposed to contrasting noise pressure levels in a

remote sub-Arctic Bay, characterized by low maritime traffic, to assess the effect of shipping noise on *B. undatum* mobility, habitat usage and distribution directly in their living environment. To validate the preliminary findings obtained in the field, we exposed individuals to different shipping noise pressure levels in a large basin to assess finer behavioural changes through accelerometry. We finally relied on our field and lab observations to the biology of the species in order to have a clear overview of the potential ecological consequences resulting from this increasingly prevalent source of pollution.

2 Materials and Methods

2.1 Field experiment

2.1.1 Study area

The sub-Arctic Saint Pierre et Miquelon (StPM) archipelago is located at the entrance of the St. Lawrence Gulf along the southern coast of the Newfoundland Island (Canada, 46°50'N - 56°20'W). The archipelago is composed of three main islands, where St. Pierre hosts the majority of maritime activities of the region such as fishing, shipping and tourism. The Miquelon Bay, inversely, holds a reduced fleet of small boats and few commercial fishing vessels, showing a near-to-pristine acoustic environment with most hours of the day free of anthropogenic noise (see Byrro Gauthier et al., in press; Nguyen et al., 2021). Moreover, the trophic environment, mostly oligotrophic, is homogenous within the bay with organic matter and trophic markers remaining highly constant between various locations (Byrro Gauthier et al., in press). The extreme homogeneity of primary production, substrate type (i.e., sandy bottom) and bathymetry within the bay, allowed the establishment of two experimental sites, which soundscapes contrasted in relation to the distance from an underwater speaker emitting a cargo ship noise (Fig. 22, see below for details on the acoustic telemetry arrays).
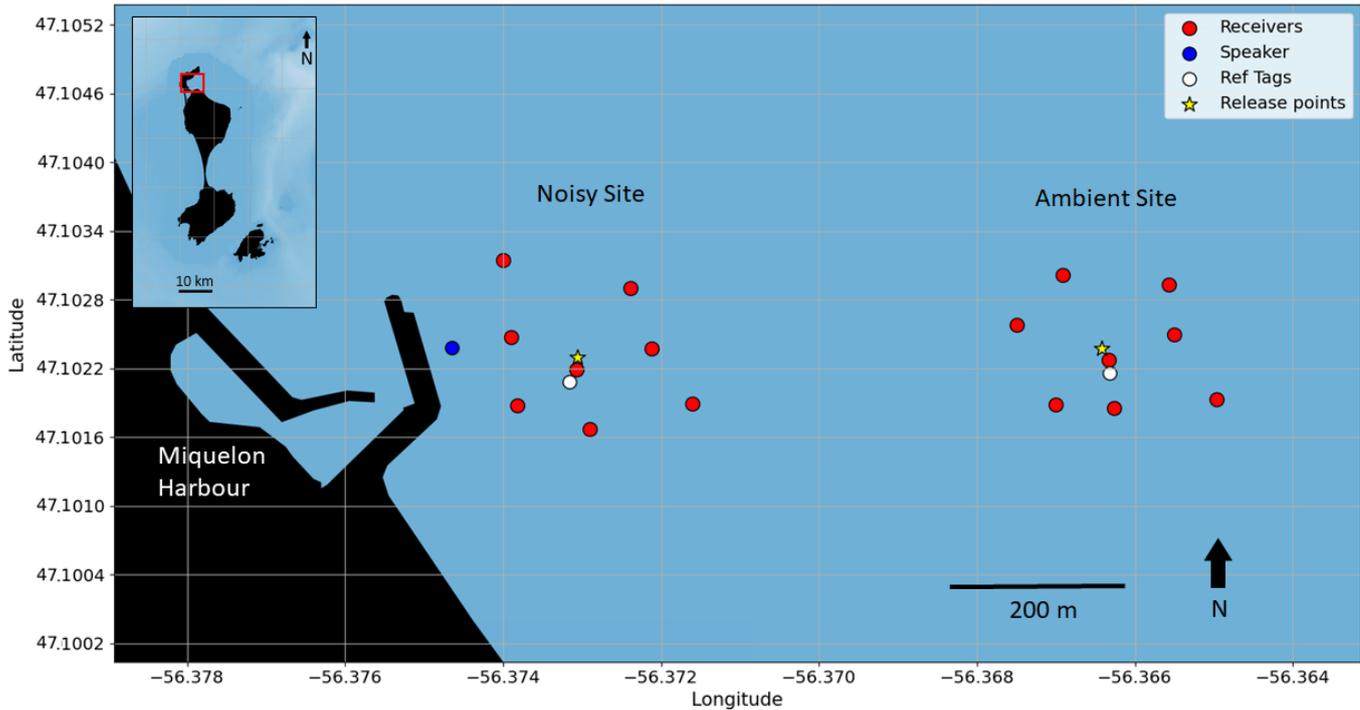
Figure 22: Map of the Saint Pierre et Miquelon's archipelago including a focus on the study area located in the Miquelon Bay showing the two acoustic telemetry arrays at different distance from the speaker. The centre of the noisy or the ambient sites were located at either 75 or 575m from the loudspeaker (blue dot), respectively.

2.1.2 Noise emission and characterization

Underwater soundscape was recorded on St. Pierre Island (46°46'44.90" N, -56°10'38.28"W) from November 2020 to April 2021 using a calibrated hydrophone (Aural-M2, Multi-Électonique, Rimouski, Canada). During such operation, the transit of the cargo ship "Nolhan Ava" (120 m length) was registered approximately 350 m from the hydrophone. From these recordings, a soundtrack of 1h20min was created, including 11 min of vessel noise (arrival of the ship), 39 min without vessel noise, another 8 min and 30 s of vessel noise (departure of the ship), and finally, 21 min and 30s without vessel noise. The vessel noise playbacks were broadcasted at the study site using an underwater loudspeaker (Lubell Labs®VC2C, Columbus, Ohio, USA; frequency range 50–1500 Hz), laid at 8 m depth from a dock (the speaker was cabled to the shore to allow continuous sound emissions). To monitor the natural soundscape and the sound pressure levels within the study area, we regularly deployed an acoustic recorder at the centre of the acoustic telemetry array of the noisy site (RTSYS-RESEA 320, Caudan, France; Hydrophone Colmar GP1516M, Sensitivity -172 dB re 1V/ μPa @ 5kHz, Bandwidth 3-75 KHz). The loudest vessel in the archipelago of St-Pierre-et-Miquelon was selected and looped to standardize exposure to

anthropogenic noise, as this approach avoided the complexities of replicating the variable acoustic landscape (e.g. day–night cycles, weekly re-creational peaks, and weather-driven fluctuations; see also Veillard et al., 2025).

Sound recording files (.wav) were first visualized over the entire frequency band by using the spectrogram view in Audacity® (Version 2.1.1; Audacity Team, 2015). Spectrograms were then computed to display a frequency range between 0 and 10 kHz to allow visual scanning and identification of the shipping noise. Using MATLAB (Version 9.1; 2016b), the playback soundtrack was cut into 8-min file sequences and the root mean square of the sound pressure level (SPL_{rms}) was calculated on each sequence over the 10–2000 Hz frequency band (SPL_{rms} [10–2000 Hz]). Acoustic analysis revealed that the 8-min sequences recorded at the noisy site during shipping noise emissions had a mean SPL_{rms} of 123.7 ± 0.7 dB re 1 µPa (mean ± standard error; Fig S5). The shipping noise emitted at the source (i.e., recorded at 3 m from the speaker) corresponded to a mean SPL_{rms} of 143.1 ± 0.7 dB re 1 µPa. The ambient noise had a mean SPL_{rms} of 99.4 ± 0.2 dB re 1 µPa (Fig. S5).

In underwater acoustics, while sound propagates uniformly in all directions following a spherical transmission loss (TL; $TL = 20 \times \log_{10}$ (Distance)) near to the source, the cylindrical TL ($TL = 10 \times \log_{10}$ (Distance)) prevails in shallow water where sound propagates as a cylindrical wave between the sea floor and the sea surface. To calculate the SPL_{rms} occurring at the centre of the ambient site (which was 500 m from the centre of the noisy site), the 'practical' TL ($TL = 15 \times \log_{10}$ (Distance)) was used, which falls between the predictions of the models described above (Coates, 1990). Therefore, we estimated that the SPL_{rms} of the shipping noise emissions at the ambient site was 83.5 dB re 1 µPa, which was lower than the ambient noise of the study area.

2.1.3 Acoustic telemetry arrays

Two different acoustic telemetry arrays were deployed at varying distances from the loudspeaker to create two contrasting sites relative to the soundscape – with or without shipping noise (Fig. 22). The noisy site was considered polluted because of its proximity to the acoustic emissions, whereas the ambient site had a natural soundscape specific to the bay (Fig. 22). Both arrays consisted of 8 VR2Tx receivers (Innovasea, Halifax) spaced between 25 and 125 m apart at 10 m depth. The receivers were positioned 1.5 m above the seabed by a 50 kg mooring connected with a surface buoy (Fig. S6). Nearby the central receiver of each site, a VEMCO reference tags (V9-1x) was deployed to assess precision of positional estimates during our study. The water temperature of the

two arrays was measured by receivers and remained stable at both sites throughout the study period (9.2 ± 0.2 °C and 8.6 ± 0.2 °C in noisy and ambient sites, respectively).

2.1.4 Tagged animals

Monitoring of *Buccinum undatum* mobility was carried out during the first half of July 2022 for a 10-day period. Out of a larger group of individuals maintained for 4 days in a suspended cage (i.e., without the possibility of feeding) at the Miquelon harbour, we collected a total of 10 individuals with similar shell length (93.8 ± 5.6 mm and 92.4 ± 4.8 mm for noisy and ambient sites, respectively; Tab. 5). For each site, five individuals were equipped with VEMCO transmitters (V9-1x / 69 kHz) with epoxy glue (Fig. S7) and then released by scuba divers around the central receiver of the acoustic telemetry array (see Fig. 22). The handling process of individuals lasted approximately 10 min. The Canadian Council on Animal Care guidelines were followed during tagging.

Table 5: Data summary of tagged waved whelks *Buccinum undatum* with shell length, n° of tracking days for each individual and the analysed spatial metrics. The percentage of retention rate columns indicate the proportion of detections retained after filtration at HPE 2 to calculate spatial metrics. 95 % kernel habitat usage potential (HUP) is reported.

Tag ID	Site	Length (cm)	N° days	Retention (%)	Tot n° Det.	Mean Speed (m/h)	Tot. Cov. Dist. (m)	Tot. Net Dist. (m)	Tot HUP (m²)
1	Noisy	10.3	10	79.4	4625	10.2	1827.7	2.5	37.9
2	Noisy	9	10	78.1	4733	11.6	2011.7	2.2	28.5
3	Noisy	9	10	80.2	5078	8.5	1394.4	10.2	29.6
4	Noisy	9.3	10	81.4	4583	8.8	1535.3	11.9	59.2
5	Noisy	9.2	10	77.1	4475	10.6	1817.6	15.8	67.9
6	Ambient	9.3	10	80.9	4911	10.5	1954.4	13.5	75.7
7	Ambient	9.9	10	85.4	4861	12.6	2278.8	3.3	30.7
8	Ambient	9.2	10	86.2	4892	9.8	1854.1	8.7	34.1
9	Ambient	8.7	10	83.6	4937	11.4	2146.2	33	182.9
10	Ambient	9	10	84.9	5200	12.3	2168.5	1.6	28.9

2.1.5 Horizontal Positioning Error evaluation and filtering

Fine-scale positioning data provided by Innovasea (Halifax) after analysis of the raw receiver detection logs includes a measure of horizontal positioning error (HPE) for stationary or synchronization tags. However, because HPE is unitless, we used the relationship between HPE and the distance of each detection from a calculated median position to establish acceptable error thresholds to filter the dataset (see also Uboldi et al., 2025). Data collected from fixed-location synchroniser tags of receivers were used to assess the quality of positioning data (Florko et al.,

2021). During the monitoring, a filtering HPE value equivalent to 2 was selected for both sites, which corresponded to a mean measurement error of 0.55 meters. The mean positioning error after filtering was 0.55 m, while individuals moved on average from 200 to 350 per day (see Result section 3.1), indicating that estimated movement distances were large relative to positioning error and thus biologically meaningful.

After filtering, 78.4 and 84.4% of detections were retained in noisy and ambient sites, respectively (Tab. 5). This value allowed us to balance the proportion of data excluded with the ability to calculate distances travelled with sufficiently high accuracy to allow comparisons between sites.

2.1.6 Calculation of behavioural metrics

Daily total and net covered distances

The daily total covered distance was calculated by adding the cumulative sum of Euclidean distances between successive locations determined by X and Y coordinates over 24h period. The daily net covered distance corresponded to the distance between the first and the last recorded location of the day. The direction (degree, °) of the total net covered distance between the first and last recorded location during the whole study period was also calculated to observe eventual mobility patterns of avoidance from the source of noise.

Speed

As observations were not uniformly distributed throughout the day, a standardised speed of displacement was calculated from the recorded travelled distance (meters) over the effective time of the observation (hours) in the 24h period. Then, to assess diel behaviour of *B. undatum*, speeds were also 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. Daily sunrise/sunset hours were determined by using Python package 'ephem 4.1.4'.

Steps length according to turning angles

Due to the high accuracy of the recorded locations, step lengths were also calculated to investigate possible variations in the individuals' trajectories quality. Step length was defined as the cumulative distance travelled between two sharp turns (i.e. a turning angle of more than 90° in either direction between two consecutive pairs of detections). The average of daily step lengths served as an indicator of the trajectory's quality generated by the tracked animal: longer steps indicate a linear trajectory, whereas shorter steps suggest a more sinuous trajectory.

Habitat Usage Potential calculation

The habitat usage potential (HUP) of each individual was estimated using the Kernel Utilization Distribution method (KUD; Worton, 1989). The utilization distribution describes the probability that an animal can be found in a given location and estimates the intensity of area use of the individual (Worton, 1989). Of the available analytic methods, Borger et al. (2006) found the kernel method was the most unbiased home range estimator across sampling regimes and was also more robust to relatively small sample sizes. In particular, KUD estimation using a bivariate normal kernel density estimate with a reference bandwidth smoothing parameter for 95% KUD is used to calculate the home ranges of many species. A 50% KUD is often considered to be the ''core area'' of space use by an individual (Konzewitsch and Evans, 2020). Here, we calculated the HUP of individuals considering the area (m^2) of the 95% KUD for daily and total study period.

Although KUD estimates can theoretically be affected by sample size (Borger et al., 2006), the number of detections in our dataset was high and relatively similar among individuals (Tab. 5). We therefore considered sampling effort unlikely to bias our results and did not include sample size as a covariate in the KUD model. We also recognize that KUDs can be influenced by temporal autocorrelation in location data (Borger et al., 2006). However, because our analyses focused on relative comparisons between sites and individuals rather than absolute home range estimates, and because detections were numerous and evenly distributed, we retained the KUD approach. This method is widely applied in movement ecology and allows direct comparability with previous studies.

2.2 Laboratory experiment

As it was not possible to carry out replicates in the field for logistical reasons, we conducted a laboratory experiment to validate the field observations. To isolate the sound factor, we thereby performed a tank-based experiment to assess the effect of different shipping noise levels on *B. undatum* behavioural activity over smaller spatial and temporal scales using accelerometry. To enable comparisons between the two experimental settings, we used SPL_{rms} comparable to those recorded in the field, as well as higher intensities (see below for details).

2.2.1 Animal maintenance and equipment attachment

Whelks were collected during the end of June 2023 by scuba divers at a site near the Maurice Lamontagne Institute in Mont Joli (Quebec, Canada). Upon arrival, animals were placed in holding tanks filled with filtered seawater coming from the same area. The seawater temperature and

salinity were 24/7 monitored, remaining constant for all the experiment. During the following weeks, individuals were fed with shrimp and herring once every four days. Prior to each trial, animals were fasted for 4 days to replicate the same fasting conditions used in the field experiment. No mortality events occurred during the holding period or experiments.

Individuals were separated in 24 sub clusters, each of which experienced a single treatment among the four predefined audio conditions. Thus, the four acoustic treatments were repeated six time (replicates). Each replicate consisted of three animals equipped with Axy 5 XS accelerometers (TechnoSmArt). Lego® were glued on shells with epoxy glue to allow accelerometers to be quickly attached just before the start of each trial (avoiding keeping the animal exposed to the air while the glue dries; Fig. S8). All tested individuals had similar shell lengths (i.e., 81 ± 11 mm).

2.2.2 Experimental setup

The experiment was conducted in a large tank of $3.5 \times 3.25 \times 1.3$ m (Vol = 14.8 m^3), allowing animals to move freely. The tank was filled with filtered seawater coming directly from the estuary. Seawater parameters (i.e., temperature and salinity) were measured with HOBO data loggers and remained constant during all trials (i.e., 9.02 ± 0.3 °C and 26.5 ± 0.2 psu, respectively).

Sound treatments included four conditions with five replicates: ambient room/control (SPL$_{rms}$ [10-2000 Hz] = 114.6 ± 0.6 dB re 1 µPa), low (SPL$_{rms}$ = 122.5 ± 0.2 dB re 1 µPa), intermediate (SPL$_{rms}$ = 154.1 ± 0.2 dB re 1 µPa) and high level of shipping noise (174.7 ± 0.6 dB re 1 µPa; Fig. S9). The shipping noise playbacks were the same as those used during the field experiment in the Saint Pierre et Miquelon archipelago, although only the arrival sequence (11 minutes) was broadcast in this experimental setup.

Trials were randomized between morning and afternoon to avoid bias determined by the period of the day. Prior to each trial, animals were positioned to acclimatize in a cage located at the center of the experimental tank. After 1 h acclimation, the cage was removed and animals were free to move during the remaining 2 h of experimentation. In noisy treatments, noise emissions started as soon as the acclimation cage was removed and shipping noise playbacks were broadcasted in a loop through the VR2C speaker. The speaker was suspended at 45 cm from the bottom, facing the whelks releasing point at 3m distance. At the end of each trial, the tank was completely emptied, the bottom cleaned and then refilled of water to avoid bias determined by the presence of potential residuals (i.e., feces or mucus) of previous individuals.

At the end of the experiment, individuals were frozen and stored at -20 °C before we broker the shell to identify the sex to detect potential sex-related response to noise.

2.2.3 Experimental and maintenance tanks characterization

In experimental tanks, sounds are usually distorted in the upper frequency bandwidth due to multiple resonant frequencies and reverberation against walls. We thus calculated the theoretical minimum resonant frequency of the experimental tank which was around 660 Hz (Akamatsu et al., 2002). Moreover, such physical effects as sound transmission loss induce complex sound propagation throughout the tank (i.e., expected highly spatially heterogeneous $SPL_{rms;}$ Duncan et al., 2016). This was not the case here, as SPL_{rms} followed a logarithmic decrease from the speaker up with minimum values at the tank walls (Fig. S10). Overall, SPL_{rms} values dropped by approximately 10 dB re 1 µPa from the speaker to the tank walls.

Experimental tank vibrations were assessed for the sole medium intensity treatment by using Axivity accelerometers (sampling frequency of 25 Hz – Range ±2 g) glued on the floor below and at 2.10 meters in front of the loudspeaker (i.e., the whelks release area). The root mean square particle acceleration level (PAL_{rms}) over the low frequencies [0-1000] Hz was calculated by combining triaxial data as the 3-D vector quantity. Under noise emission, accelerometers recorded below the loudspeaker and at the whelks' releasing area measured PAL_{rms} of 96.7 ± 0.3 and 85.5 ± 0.2 dB re 1 µm.s-2, respectively. In ambient room conditions, PAL_{rms} was equal to 85.9 ± 0.2 dB re 1 µm.s-2.

Whelks spent 26 days in maintenance tanks before beginning the trials. The tank room at the IML has several pumps, filtration systems and power generators, which may be very noisy when activated. The acoustics of the maintenance tanks were therefore quantified to assess potential acclimation to noise of individuals. The general SPL_{rms} [0-2000] within the maintenance tanks was 116.39 ± 1.6 dB re 1 µPa, which increased to 141.91 ± 1.1 dB re 1 µPa when the nearby power generator was operated (every 10 minutes for 5 minutes).

2.2.4 Calculation of behavioural metrics

Data from Axy 5 XS accelerometers were downloaded using 'X Manager' software (TechnoSmArt). Acceleration values were given in units of g, where g represents acceleration due to gravity (1 g = 9.81 m.s^{-2}). Accelerometers record movements simultaneously on the three axes as the relative change detected in gravitational acceleration. The Overall Dynamic Body Acceleration

(ODBA, in g), was calculated from tri-axial acceleration data as ODBA = |ax| + |ay| + |az| over the 2h of treatment. These data represented the acceleration recorded by the data logger owing to the dynamic movement of individuals during the trial.

Animals were considered to move when ODBA > 0.01 g for 1 sec (Dujon et al., 2021) and the overall time spent in motion was thus calculated by summing up all seconds where data points fitted that condition.

2.3 Statistical analysis

Field related data (i.e., daily total and net covered distance, speed and HUP) were analysed using linear mixed models (LMMs) including several explanatory variables in addition to a single random effect (Tab. 6). LMMs allow considering intra-individual variability by including a random effect for each individual and include fixed effects (Site, Day and interaction Site:Day) to assess their impact on measures. Four models were generated for each of the considered behavioural parameters (Tab. 6) and the significance of each factor was assessed within the model (Tab. 7). The influence of the day/night light regime on mobility was tested and found to be non-significant. Consequently, it was removed from the relative model and only average speed over 24h period was considered in the analysis. As animal size and water temperature were similar in both sites, they were not included in the models.

Two-ways permutational analyses of variance (PERMANOVAs) were performed on Euclidean dissimilarities of laboratory data (ODBA and moving time) to tests for significant differences across audio conditions and sex of individuals. As the sex factor was not significant, it was not retained for further analysis.

Linear mixed models fit was graphically validated after residuals inspection (Fig. S11 to S15) and the coefficient of covariation among fixed factors never exceeded a value of 0.3. As model assumptions were respected, full models were retained for the analysis. A p value < 0.05 was retained as statistically significant. All statistical analyses were conducted using R (version 4.2.2; R Core Team, 2022) with the packages 'lme4' (Bates et al., 2015). PERMANOVAS were performed using PRIMER® version 7 (Clarke and Gorley, 2015).

Table 6: Models used in statistical analysis for each of the considered behavioural parameter. Fixed effects are in bold (site (S), day (D) and interaction between site and day (S:D)), while random effect is in italic. See section 2.3 for details.

Daily Covered Distance ~ **S** + **D** + **S:D** + (1| *Ind*)	[1]
Speed ~ **S** + **D** + **S:D** + (1| *Ind*)	[2]
Daily Net Covered Distance ~ **S** + **D** + **S:D** + (1| *Ind*)	[3]
Step Length ~ **S** + **D** + **S:D** + (1| *Ind*)	[4]
HUP ~ **S** + **D** + **S:D** + (1| *Ind*)	[5]

Table 7: Outputs from linear mixed models considering the influence of different fixed factors (Site, Day and interaction Site:Day) on the considered behavioural parameters. Significant effect (P-value < 0.05) are indicated in bold.

Daily Cov. Distance [1]	β	*SE*	χ^2	*Df*	*P-value*
Site	14. 42	18.47	4.86	1	**0.028**
Day	12.36	2.14	33.51	1	**< 0.001**
Site : Day	4.04	2.98	1.83	1	0.175
Speed [2]	β	*SE*	χ^2	*Df*	*P-value*
Site	0.63	0.78	4.79	1	**0.029**
Day	0.51	0.09	32.73	1	**< 0.001**
Site : Day	0.16	0.13	1.7	1	0.192
Daily Net Cov. Distance [3]	β	*SE*	χ^2	*Df*	*P-value*
Site	0.3	1.31	3.57	1	0.058
Day	0.33	0.18	3.3	1	0.069
Site : Day	0.3	0.26	1.32	1	0.25
Step Length [4]	β	*SE*	χ^2	*Df*	*P-value*
Site	9.18	10.14	0.13	1	0.71
Day	0.69	0.91	0.57	1	0.45
Site : Day	-1.07	1.29	0.68	1	0.41
HUP [5]	β	*SE*	χ^2	*Df*	*P-value*
Site	5.32	4.91	3.97	1	**0.042**
Day	1.61	0.69	5.49	1	0.019
Site : Day	0.16	0.96	0.02	1	0.866

Results

3.1 Field experiment

All individuals were detected throughout the study period and remained within each of the predefined sites (Tab. 5; Fig. 23). To exclude any bias related to manipulation, displacements were analyzed over 7 days (from day 4 to 10; Fig. S16 and Tab. S1 for the whole 10 days period).

Over the considered 7 days, some behavioral parameters significantly differed between sites (Tab. 7). The mean daily covered distance was greater at the ambient site (mean 297.2 ± 8.7 m/day; $\pm$ standard error) than at noisy site (245.3 ± 8.5 m/day; $p = 0.028$; Tab. 7; Fig. 24, 25). Daily speed of displacement was also greater in the ambient site (12.4 ± 0.3 m/h) compared to the noisy site (10.2 ± 0.3 m/h; $p = 0.029$; Tab. 7; Fig. 24). Such reduced metrics recorded in the noisy site then reflected on the daily habitat usage potential (HUP), with individuals showing a greater mean daily HUP in the ambient site (18.4 ± 2.5 m^2/day) compared to the noisy site (12.9 ± 1.5 m^2/day; $p = 0.042$; Tab. 7; Fig. 24, 25).

Over the whole week, individuals from the noisy site covered a mean total distance of 1716.8 ± 110.9 m and a mean total HUP of 44.6 ± 8 m^2, while individuals from the ambient site covered a mean total distance of 2080.4 ± 76.9 m and a mean total HUP of 70.4 ± 25.4 m^2 (Tab. 5). By contrast, neither the mean daily net covered distance (mean $_{\text{Noisy-AmbientSite}} = 2.9 \pm 0.7$ m/day; $p = 0.058$) nor the mean step length (mean $_{\text{Noisy-AmbientSite}} = 71.4 \pm 2.9$ cm; $p = 0.71$) differed between sites (Tab. 7; Fig. 24), indicating the absence of changes in the trajectory quality. Overall, there was no clear tendency for whelks in the noise polluted site to move against the source of noise over the study period (Fig. 26).
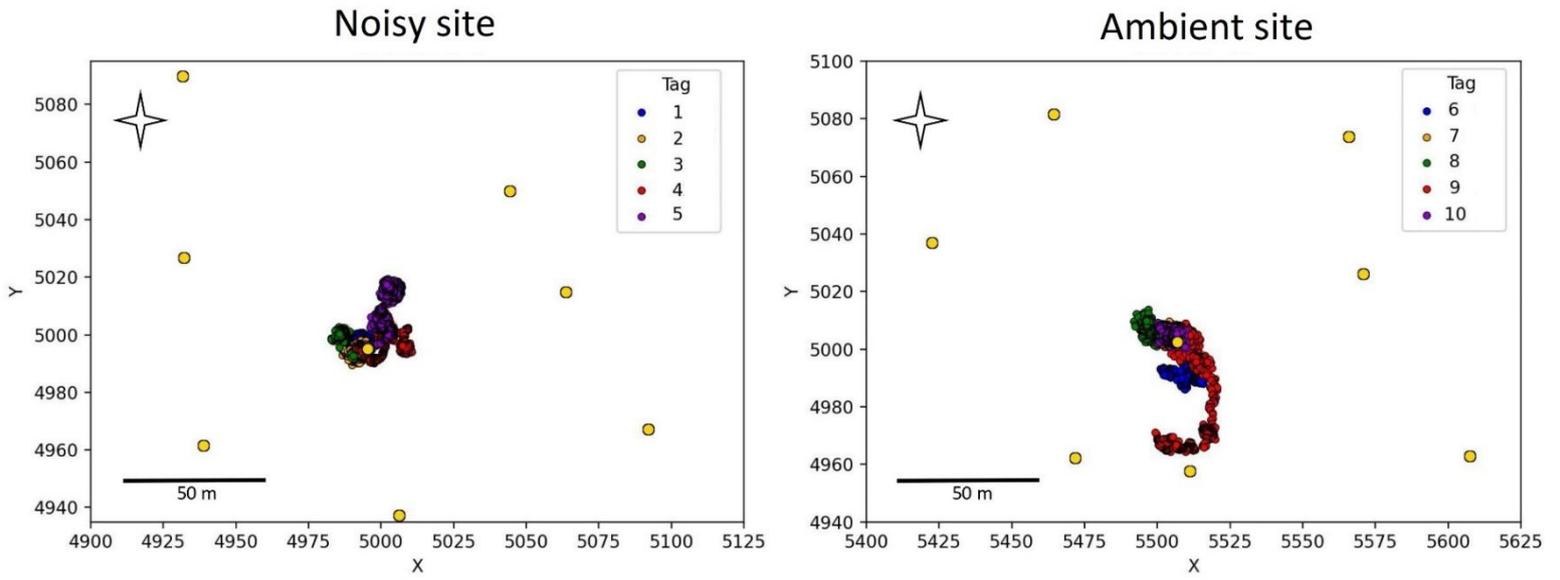
Figure 23: Maps of whelks' displacements over the 10 days study period in the noisy and ambient site. Acoustic telemetry receivers are indicated as bigger yellow points.

Figure 24: Predicted values of A) daily covered distance, B) speed, C) daily net covered distance, D) daily habitat usage potential (HUP) and E) step length according to the applied model in each site. Metrics and statistical comparison were calculated by excluding the first 3 days of experiment to avoid bias related to animal handling (Fig. S13, Tab. S1).

Fig. 25: Observed mean values of daily total covered distances and habitat usage potential (HUP) over one week in the noisy (red) and ambient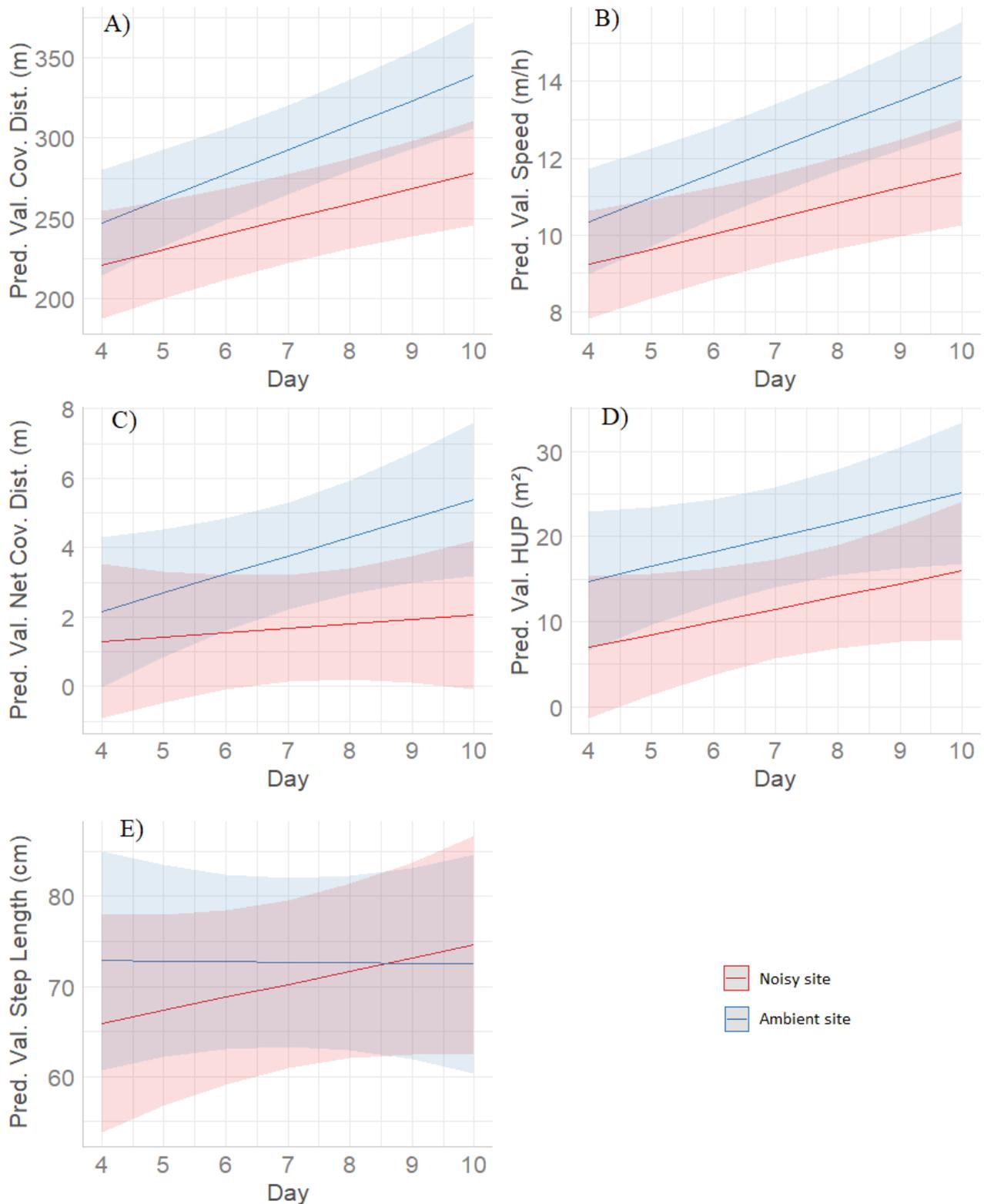 (blue) sites. Metrics and statistical comparisons were calculated by excluding the first 3 days of experiment to avoid bias related to animal handling (Fig. S16, Tab. S1).

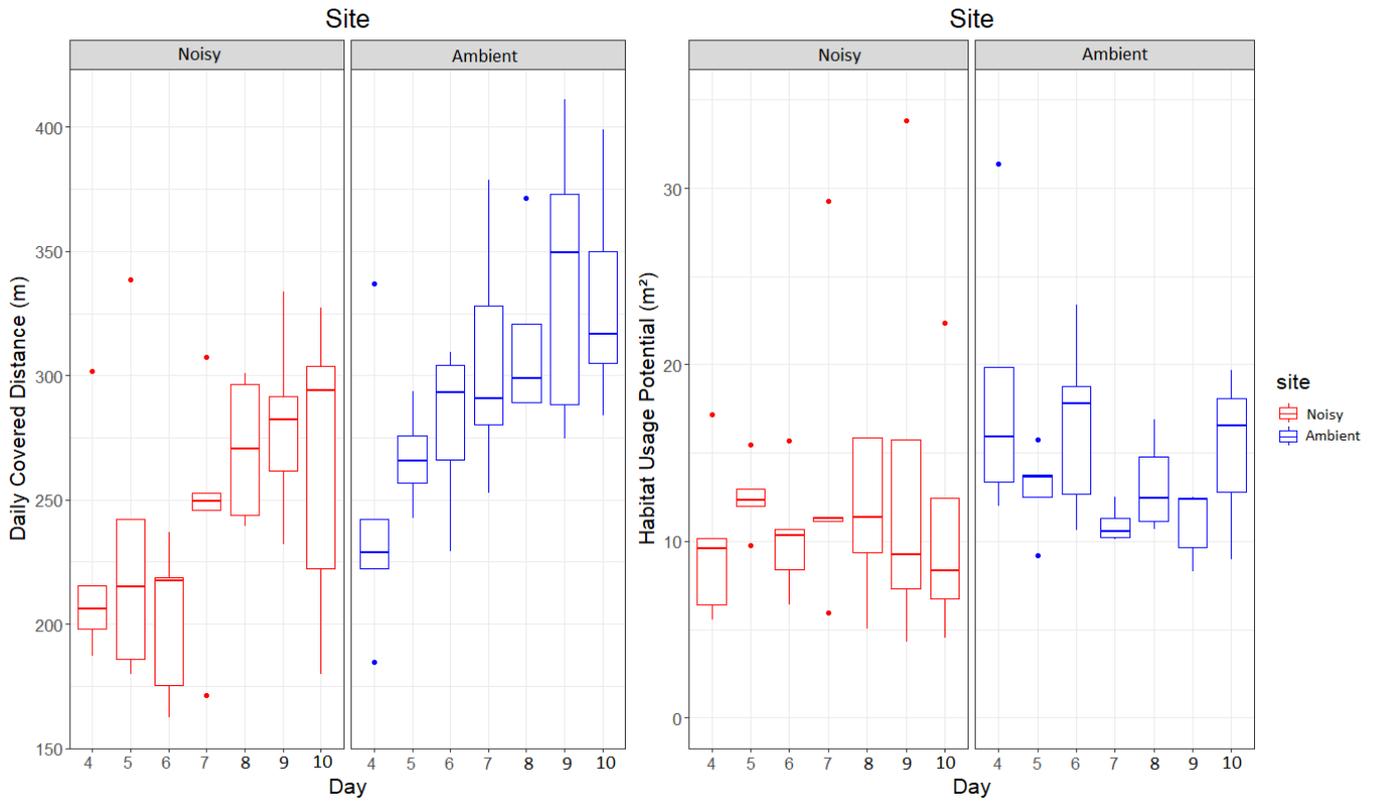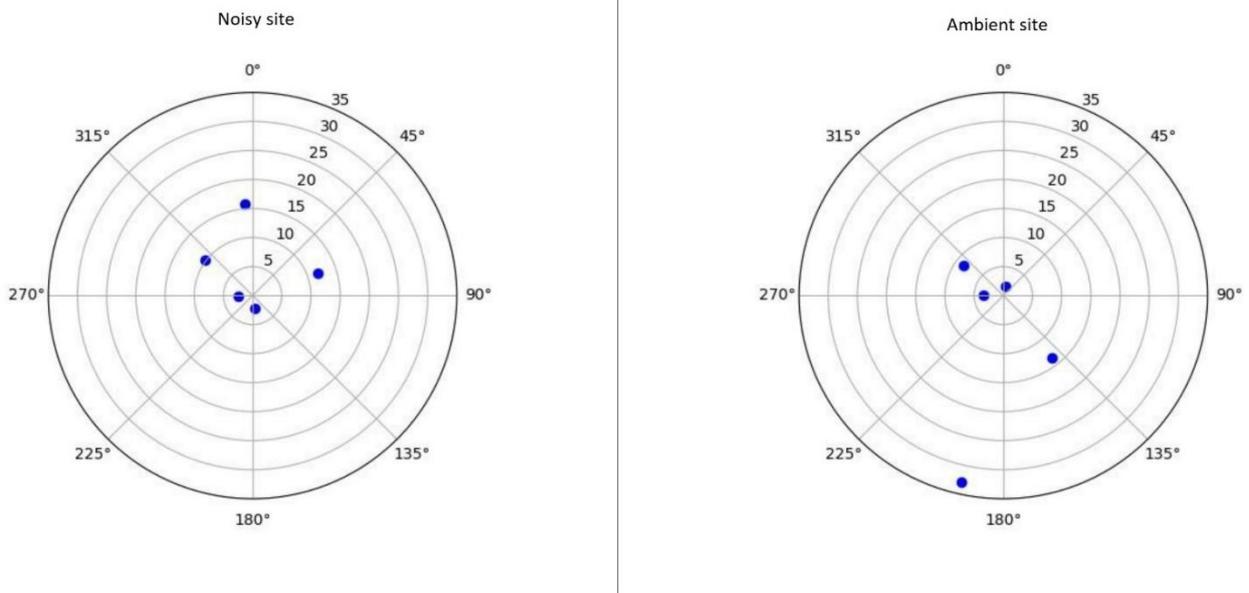Figure 26: Directions (°) of the total net covered distance (m) over one week. Individuals (blue points) from the noisy site did not move in the opposite direction of the source of noise (speaker located at 270° from the center of the noisy site).

3.2 Laboratory experiment results

The mean overall dynamic body acceleration (ODBA) varied among shipping noise treatments (PERMANOVA, $F_3 = 2.154$, $p = 0.04$; Fig. 26). ODBA calculated for individuals exposed to the loudest noise (0.019 ± 0.01 g) was ~ twice lower (pair-wise tests, $p < 0.035$) than compared to that of the other sound treatments (mean ODBA $_{control-low-medium} = 0.037 \pm 0.01$ g; $p > 0.836$; Fig. 27).

The mean moving time varied among shipping noise treatments (PERMANOVA, $F_3 = 3.255$, $p = 0.027$; Fig. 26). The time spent moving calculated for individuals exposed to the loudest noise (52.05 ± 11 min) was significantly lower (pair-wise tests, $p < 0.048$) than compared to that of the other sound treatments (mean moving time $_{control-low-medium} = 78.8 \pm 3.6$ min; $p > 0.836$; Fig. 27).
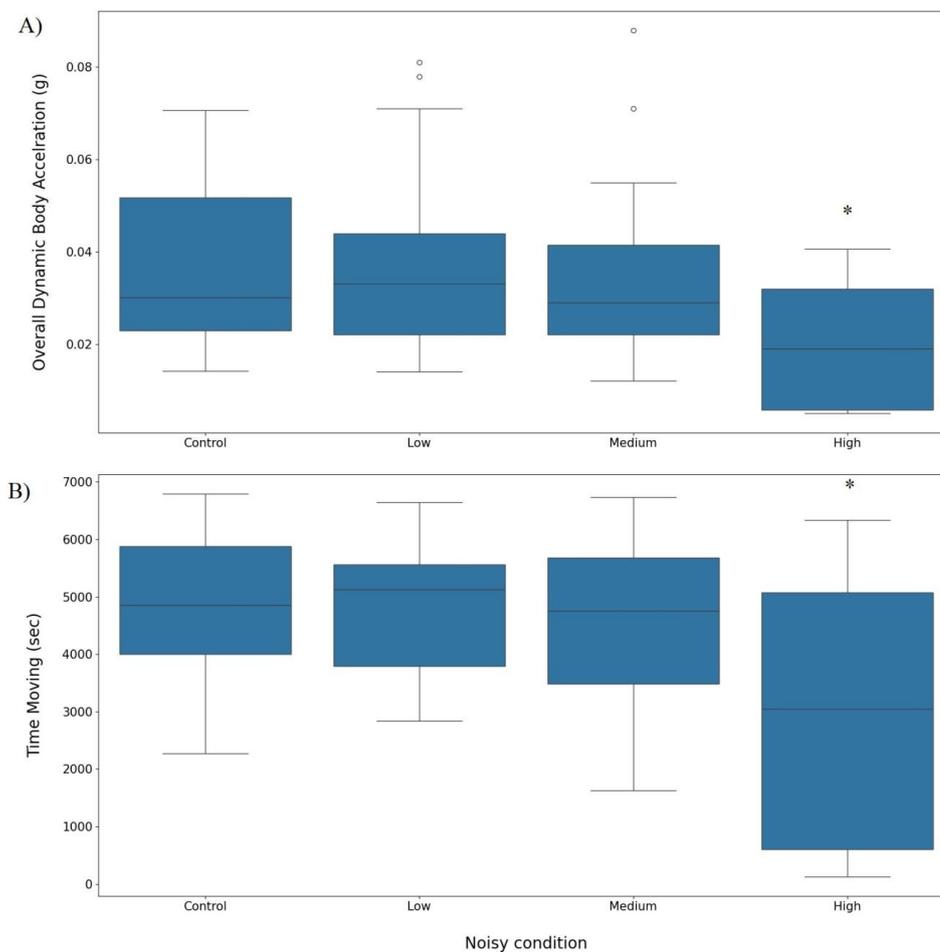

Figure 27: A) mean overall dynamic body acceleration of individuals and B) time spent moving over ambient noise (114.62 dB re 1 µPa), low (122.5 dB re 1 µPa), medium (154.1 dB re 1 µPa) and high (174.8 dB re 1 µPa) shipping noise conditions of all tested individuals. The asterisk stands for a p value < 0.05 according to PERMANOVAs analysis.

4 Discussion

Combining both field (acoustic telemetry) and laboratory (accelerometry) experiments, the present study demonstrates for the first time that a cargo ship noise can severely reduce the mobility and activity of the gastropod *Buccinum undatum,* without, however, a clear identification of a sound pressure level (SPL_{rms}) threshold controlling the behavioural responses (but see below).

In the field, movements of tracked whelks were significantly altered at a shipping noise SPL_{rms} threshold of 123.7 dB re 1 µPa, corresponding to a sound anomaly of +24 dB re 1 µPa when compared to the ambient soundscape. Such sound pressure level is frequently recorded along the main shipping lanes (McKenna et al., 2013) and in the proximity of commercial ports (Ivanova et al., 2020). Among other marine species, mollusks are known to be sensitive to similar sound pressure levels, leading to considerable behavioural changes (Charifi et al., 2017; Cones et al., 2023; Havlik et al., 2025). In their review, Cones et al. (2023) highlighted bivalves' behavioural responses for SPL_{rms} ranging from 138 and 143 dB re 1 µPa. In Charifi et al. (2017), the minimum acoustic energy required to elicit some valve responses in the Pacific oyster was equal to 122 dB re 1 µPa between 10 and 80 Hz. In gastropods, Solé et al. (2021) demonstrated substantial damages in statocysts of a freshwater gastropod species subjected to low frequency noise (from 5-400Hz) at high SPL_{rms} (157-175 dB re 1 µPa), only suggesting potential behavioural modifications. In a recent study, however, Havlik et al. (2025) showed substantial behavioural changes in wild *Lambis lambis* exposed to 130 dB re 1 µPa. In particular, boat noise treatments significantly decreased animals' activity, reducing the overall mobility and increasing the portion of individuals staying stationary over the seabed. Despite the limitation of lacking replication, which prevents movement metrics from being completely separated from site-specific variation, our field results suggest that prolonged exposure to $SPL_{rms} \geq 124$ dB re 1 µPa can induce considerable behavioural changes in the gastropod *B. undatum*. The altered behaviour found in *L. lambis* at similar SPL_{rms} (Havlik et al., 2025), further support the inference that the observed behavioural responses in *B. undatum* are related to noise exposure.

Furthermore, to address the lack of replication in the field, laboratory experiments were also performed to corroborate the field observations. These experiments partially confirmed the field results, as whelks exposed to shipping noise had a reduced mobility and activity in both open and controlled environments. However, in laboratory, whelks' behavioural changes were only evident at the highest noise pressure level of 175 dB re 1 µPa. The lack of observables responses for individuals under 122.5 and 154 dB re 1 µPa could relate on several origins. Firstly, in both

experiments, the initial animal manipulation (i.e., tag and release field procedure - but not the acoustic tag itself, see Fig. S4 - and the release in the laboratory tank) was supposed to affect the general mobility patterns of whelks. Therefore, animal manipulation during lab trials could mask the possible effect of noise over a short period among treatments except at ~175 dB re 1 µPa, this noise level overcoming the manipulation effect. Secondly, before trials, whelks were kept during 26 days in noisy maintenance tanks with sound pressure levels reaching up to ~142 dB re 1 µPa for 1/3 of time (when compressors and pumps were functioning). This could reveal an acclimation response to noise (here during the maintenance phase) which is still poorly reported in literature on marine invertebrates, although some recent studies suggest its potential for some bivalve and cephalopod species (Jézéquel et al., 2023; Solé et al., 2023). Usually, this noise acclimation leads to fewer behavioural reactions to noisy stimuli, decreasing their overall sensitivity threshold (Solé et al., 2023).

4.1 Acoustic telemetry survey considerations

The acoustic telemetry arrays revealed that whelks exposed to noise significantly reduced their daily displacements within their living environment, individuals covering 21.2% less linear distance in the polluted site compared to the pristine site. In particular, noise exposure resulted in a mean total loss of 350 m covered distance at the end of the 7-day study period. This is typically the daily distance of a wave whelk in the field (Uboldi et al., 2025), so it is reasonable to infer that individuals exposed to shipping noise have lost more than one day's journey time over the study period. When extrapolated to a longer period of time, individuals exposed to a constant underwater noise at similar sound pressure levels would lose more than a month's travel time over an entire year (but without taking into account possible acclimation).

One of the direct consequences of reduced mobility is the limited HUP of individuals exposed to noise. An animal travelling shorter daily distances is inclined to explore/exploit a limited portion of habitat at its disposal (Allen et al., 2018). In our case, ambient sound exposed individuals explored a significant larger area compared to shipping noise exposed animals, showing a higher daily HUP during most of the study period. The final HUP of individuals in the ambient noise condition was 36.6% larger than individuals exposed to noise. For a species such as *B. undatum* that usually shows a daily HUP of between 10 and 40 m^2 (Uboldi et al., 2025), the recorded average daily loss of 5 m^2 between sites represents a biologically significant decrease in their capacity to occupy the surrounding space.

No avoidance from the source of noise was observed during our work, suggesting that animals primarily reduce their mobility in noisy soundscape than actively moving away from the disturbance. Overall, wave whelk's responses to noise were mostly associated to changes of quantitative (i.e., daily covered distance, speed and daily HUP) rather than qualitative (i.e., daily net covered distance and step length) parameters of mobility. *Buccinum undatum* adults display a sedentary lifestyle within restricted areas even over successive years (Uboldi et al., 2025). In this study, individuals exposed to shipping noise maintained a reduced net covered distance and step length typical of their sedentariness, without increasing the linearity of their trajectory in the opposite direction to the noisy source. However, only a longer study period would allow to assess any escape events from the area beyond the 10 days predicted by our experimental setup.

4.2 Accelerometry survey considerations

The overall body acceleration (ODBA) reflects a combination of acceleration peak frequency and amplitude, and generally correlates well with speed (Shepard et al., 2008). Animals with a lower ODBA are thus supposed to be less active and mobile, covering lower distances over time (Bidder et al., 2012). Results of the laboratory experiments confirmed that the activity of individuals was reduced when exposed to shipping noise, supporting the field data (i.e. lower general mobility). Such results are in line with studies focusing on bivalves and gastropods exposed to shipping noise which activities usually decrease while the time they spend close increases (Charifi et al., 2018; Wale et al., 2019; Havlik et al., 2025). As an example, at 140–145 dB re 1 µPa shipping noise, the algal clearance rate of blue mussels is reduced by 84%, decreasing the valve open amplitude (Wale et al., 2019). Similarly, when exposed to acoustic pollution between 130 and 150 dB re 1 µPa, the pacific oysters spent more time closed and their valve and ventilation activities decreased (Charifi et al., 2018). Under 130 dB re 1 µPa, the gastropod *L. lambis* showed a Vector of Dynamic Body Acceleration (VeDBA) decreased by ~82.8% from ambient to boat noise treatment (Havlik et al., 2025). As the decreased activity is classical of a response to several stress sources (temperature peaks, blooms of toxic microalgae … see Haberkorn et al., 2011; Comeau et al., 2012), shipping noise, above a particular level, has a stressful behavioural effect in bivalves and gastropods (Charifi et al., 2018; Wale et al., 2019; Havlik et al., 2025). In this regard, gastropods such as *B. undatum* would also perceive shipping noise as a negative factor, exhibiting behavioural responses of reduced locomotor activity to mitigate its detrimental effect.

4.3 Potential ecological effect of shipping noise on *B. undatum*

In nature, organisms modify their behaviour continuously according to the presence of other species (e.g., predators or competitors) and specific environmental conditions (e.g., temperature, current, tide, feeding area, seasons...). In a natural pristine habitat, the environmental predictability allows animals to be synchronized with the natural conditions they experience (Riotte-Lambert and Matthiopoulos, 2019). In this way, the animal perceives environmental changes as transitional events that evolution has provided the strategies to cope with (e.g., seasonal migration). On the contrary, human-induced changes disrupt the typical environmental predictability and create new conditions to which organisms are poorly adapted, deeply affecting their natural behaviour (Wilson et al., 2020).

The HUP (or "home range") is the area where animals spend most of their time and perform their typical daily activities, such as feeding and mating (Tomasevic and Marzluff, 2018). When the movement of animals within their habitat is affected by an external factor, species-related functions are temporarily lost with ecological consequences for the population and ecosystem (Drolet et al., 2016). Reduced mobility could thereby affect the species' foraging activity, leading to potential food limitations for whelk individuals. From a broader perspective, *B. undatum* populations were recently characterized as highly vulnerable to local extinction due, in part, to their naturally low dispersal potential within the ecosystem (Uboldi et al., 2025). The need for long-term connectivity between neighbouring populations (also limited in part by the lack of a pelagic larval form) and the internal fertilisation typical of *B. undatum* make the resilience capacity of populations highly dependent on the mobility of single individuals (Ashfaq et al., 2019; Uboldi et al., 2025). In particular, individuals were observed to sensibly increase their HUP during the mating seasons of late spring along the St. Lawrence coast (Canada), probably to enhance the chances to meet a proper sexual partner (Uboldi et al., 2025). By reducing individual dispersal in the environment, shipping noise pollution could contribute to the depletion of the reproductive potential of the species, directly affecting the long-term population dynamics of the wave whelk. In order to confirm this hypothesis, however, it would be necessary to carry out monitoring over a longer time span that includes an entire breeding season and can assess the eventual presence of acclimatisation phenomena.

4.4 Assessing the effect of shipping noise in acoustically pristine habitats

Commercial shipping in the Arctic regions is considerably increasing during the last years and predicted to increase in the next decades (Aulanier et al., 2017; Worcester et al., 2020). Such remote regions were a long considered acoustically pristine habitats, characterized by the absence of anthropogenic noises year-round (Aulanier et al., 2017; Halliday et al., 2020). These ecosystems

could be particularly vulnerable to anthropogenic noise due to their strong historical and geographical isolation to this type of stress (Halliday et al., 2020). Even moderate input of anthropogenic noise can considerably change the soundscape of large areas, modifying the acoustic predictability to which local animals are accustomated. The National Oceanic and Atmospheric Administration (NOAA, 2018) established a behavioural disturbance threshold of 120 dB re 1 µPa for continuous noise in marine mammals (while 160 dB re 1 µPa for impulsive noises; see also Halliday et al., 2020). In Resolute Bay (Nunavut, Canada), Ivanova et al. (2020) found significant shift in Arctic cod home ranges in the area surrounding a vessel, where estimated noise pressure levels were near to 120 dB re 1 µPa. The present study confirms that a shipping noise anomaly of 123.7 dB re 1 µPa (+24 dB re 1 µPa compared to ambient noise) can restrict the mobility of a wild population of a benthic invertebrate species with potential cascading effects on its ecology in a near to pristine habitat. The ambient soundscape of the study region, indeed, is consistent with the remote western Canadian Arctic, where ambient sound levels (bands 50-1000 Hz) ranges from 90 dB to 110 dB re 1 µPa depending on wind speed (Halliday et al., 2021).

Overall, very few studies on the impact of anthropogenic noise in near-to-pristine and pristine environments have yet been carried out to be able to define a critical threshold of tolerance for resident animals. Now, it would be important to assess the impact of these stimuli within their natural living environments to consider the historical and local dynamics of noise in specific geographical areas.

5 Acknowledgements

Chapter 3

Divergent effects of shipping noise on Rock Crab (*Cancer irroratus*) activity across circadian and seasonal cycles

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Abstract

Underwater noise is now recognized as a major form of 21st-century pollution, with modern commercial shipping significantly increasing ambient noise along the coastal environment. Scientific research has highlighted serious concerns regarding the effects of noise exposure on marine invertebrates, revealing substantial physiological and behavioural changes. Current studies, however, primarily assess the impact of noise over short exposure periods (ranging from minutes to a few hours) and within specific, predefined time frames - typically daylight hours of a single season. This limitation hinders our ability to fully understand the long-term biological effects of anthropogenic noise on marine species. To address this gap, the present study investigates the impact of shipping noise (SPL_{rms} control/116 *vs* 145 dB re 1 µPa) on the mobility and activity of rock crabs (*Cancer irroratus*) over a relative extended period (48 hours), encompassing both day and night periods across two seasons (Spring *vs* Autumn). Activity levels varied significantly across times of day and seasons, crabs being more active at night and during Autumn. Shipping noise had a significant impact on crab activity, but only during the night-time in Spring, with individuals exhibiting a lower mean ODBA and reduced moving time than control. Additionally, we observed a strong handling effect during the first 24 hours, as crabs displayed heightened patrolling behaviour on Day 1, which gradually stabilized by Day 2. These results highlight that I) the effects of shipping noise on animal behaviour may vary according the biological condition of individuals, showing potential divergent effects across different phases of circadian and seasonal cycles and II) the importance of incorporating adequate acclimation and exposure periods in behavioural studies regarding noise pollution.

Résumé

Le bruit sous-marin est désormais reconnu comme une forme majeure de pollution du XXIe siècle, le transport maritime commercial moderne augmentant considérablement le bruit ambiant le long du littoral. La recherche scientifique a mis en évidence de graves préoccupations concernant les effets de l'exposition au bruit sur les invertébrés marins, révélant des changements physiologiques et comportementaux importants. Cependant, les études actuelles évaluent principalement l'impact du bruit sur de courtes périodes d'exposition (allant de quelques minutes à quelques heures) et dans des délais spécifiques et prédéfinis, généralement pendant les heures de jour d'une seule saison. Cette limitation nous empêche de comprendre pleinement les effets biologiques à long terme du bruit anthropique sur les espèces marines. Pour combler cette lacune, la présente étude examine l'impact du bruit des navires (SPLrms contrôle/116 vs 145 dB re 1 µPa) sur la mobilité et l'activité des

crabes de roche (*Cancer irroratus*) sur une période relativement longue (48 heures), couvrant à la fois les périodes diurnes et nocturnes sur deux saisons (printemps vs automne). Les niveaux d'activité variaient considérablement selon l'heure de la journée et la saison, les crabes étant plus actifs la nuit et en automne. Le bruit des navires a eu un impact significatif sur l'activité des crabes, mais uniquement pendant la nuit au printemps, les individus présentant une ODBA moyenne plus faible et un temps de déplacement réduit par rapport au groupe contrôle. De plus, nous avons observé un effet important lié à la manipulation au cours des premières 24 heures, les crabes affichant un comportement de patrolage accru le premier jour, qui s'est progressivement stabilisé le deuxième jour. Ces résultats soulignent que I) les effets du bruit des navires sur le comportement des animaux peuvent varier en fonction de l'état biologique des individus, montrant des effets potentiellement divergents selon les différentes phases des cycles circadiens et saisonniers, et II) l'importance d'intégrer des périodes d'acclimatation et d'exposition adéquates dans les études comportementales concernant la pollution sonore.

1 Introduction

Underwater noise is considered among the major elements of the 21st century pollution in the aquatic environment, encompassing a wide range of frequencies (Duarte et al., 2021). Among a large panel of noisy sources, modern commercial shipping considerably increased the general ambient noise of oceans, with acoustic emissions within the 63 Hz 1/3 octave band predicted to double every 11.5 years (Jalkanen et al., 2022). In recent years, a growing number of marine species were reported to be highly sensitive to the acoustic pollution produced by commercial shipping (Erbe et al., 2019; Ivanova et al., 2020; Solé et al., 2023). In particular, the scientific community revealed some serious issues about the noise exposure to marine invertebrates, leading to consistent physiological and behavioural modifications (Di Franco et al., 2020; Solé et al., 2023).

Among marine invertebrates, crustaceans are the most closely associated with underwater acoustics, being the only known subphylum that uses acoustic stimuli for intraspecific communication (Jézéquel et al., 2021; Solé et al., 2023). Particularly, crustaceans perceive low-frequency sounds through specialized mechanoreceptor systems composed of internal statocysts, external sensilla and chordotonal organs (Solé et al., 2023). Nowadays, an increasing number of scientific reports demonstrates that shipping noise leads to major behavioural changes in many species, affecting individual mobility (Filiciotto et al., 2014; 2016), foraging capacity (Wale et al., 2013), predator avoidance (Chan et al., 2010; Wale et al., 2013) and level of distraction (Tidau and Briffa, 2019; Tab. 8). Despite these crucial findings, the current body of research on the impact of chronic anthropogenic noises remains insufficient to reach a clear consensus about the exposure time and sound pressure levels that trigger the most damaging effects on crustacean behaviour (see Solé et al., 2023). In particular, the impact of shipping noise requires further investigation, as there is a significant gap in understanding how its effects may vary across animals' circadian and seasonal cycles (see Tab. 8).

Many species, indeed, undergo notable physiological and behavioural changes throughout different parts of the day (i.e., day *vs* night) and seasons (Goldstein and Watson 2015; Cote et al., 2019). For example, several species of shore crabs display heightened nocturnal activity to optimize specific survival strategies (Lynch and Rochette 2007; Rebach 1987; Silva et al., 2014), individuals of *Cancer magister* moving up to 1 km at night to increase foraging opportunities (Holsman et al., 2006). Many decapod species are also observed to adjust their seasonal behaviour to adapt to changing environmental conditions (Goldstein and Watson 2015; Cote et al., 2019). Among others, American lobsters (*Homarus americanus*) perform cyclical migrations over the eastern coast of

North America, moving to deeper waters during the winter and returning to the original areas in the spring (Goldstein and Watson 2015). Given the large behavioural variability within crustaceans, it is thus crucial to assess how noise influences species over divergent temporal scales, i.e., circadian and seasonal cycles.

Rock crabs (*Cancer irroratus*, Say 1817) exhibit significant behavioural changes in response to temporal cycles along the coasts of the Gulf of St. Lawrence (Canada). The species is mainly nocturnal to enhance predation success (Rebach, 1987; Barbeau et al., 1996), with some exceptions reported over its range of distribution (see Novak, 2004). Additionally, rock crabs undergo consistent seasonal migrations, moving across a considerable depth gradient throughout the year, which are influenced by various factors, including temperature and reproductive cycles (Comeau et al., 2012). Such behavioural shifts often results from major physiological changes that regulate the species' biological cycles, potentially leading to periods of increased vulnerability to external stressors that may affect the overall fitness. Indeed, vulnerability to environmental stressors usually depends largely on the individual's underlying physiological and behavioural state (Lam et al., 2022; Matveev and McGaw 2022).

The current scientific literature assesses the impact of shipping noise on very short periods of exposure (from minutes to a few hours) and on predefined periods of the day and year (only daylight hours of a specific season; Tab. 8). Moreover, most of the studies did not use standardized periods of acclimation, which can vary from few seconds to 1 hour before the start of experimental conditions (Tab. 8). Consequently, the present study aims to experimentally investigate the impact of shipping noise on the mobility and activity of rock crabs over a relative long period (48 hours) across different times of day (Day *vs* Night) and seasons (Spring *vs* Autumn). This allows a continuous monitoring of animals' behaviour over the experimental time, identifying periods of heightened sensitivity of rock crabs to shipping noise according to circadian and seasonal cycles.

Table 8: Acclimation, exposure times, day periods and experimental seasons employed in relevant studies about shipping noise effect on crustaceans' behaviour. (PSD, Power Spectrum Density)

Species	Accl. Time	Exp. Time	Day vs Night	Season (month)	Sound Pressure Levels	Effect	Refer.
Coenobita clypeatus	30 sec	30 sec	Day	October	98.1 dB re 1 µPa @ 1m	Distraction	Chan et al. 2010
Pagurus bernhardus	5 min	30 min	Day	-	165 dB re 1 µPa	Faster shell selection No difference in choosing the optimal shell size	Walsh et al. 2017
Pagurus bernhardus	20 min	20 min	Day	May - July	74.5 dB re 1 µPa *vs* 119 dB re 1 µPa at 1000 Hz	Changing in grouping behaviour	Tidau and Briffa 2019a
Pagurus bernhardus	5 min	20 min	Day	Nov. - January	119 *vs* 143 dB re 1 µPa	Disrupted shell choosing behaviour Shorter decision time	Tidau and Briffa 2019b
Homarus gammarus	-	1 h	Day	May - June	118. 4 dB re 1 µPa [55-1000Hz]; Max of 146.2 dB re 1 µPa	Acoustic masking Increased call rates Similar call duration	Jézéquel et al., 2021
Palinurus elephas	1 h	1 h	Day	May	PSD peaks up to 120 dB below 10 kHz	Higher values of mobility and speed No difference for Tail Flip Events	Filiciotto et al. 2014
Carcinus maenas	30 sec	7.5 min	Day	February *vs* May	103-108 *vs* 148-155 dB re 1 µPa	No difference in success finding food, time finding food, initial reaction to predator Difference in feeding, retreat to shelter, righting reflex No difference between cohorts (seasons)	Wale et al. 2013a
Carcinus maenas	-	15 min repeated 8 times at 48h intervals	Day	-	108-111 *vs* 148-155 dB re 1 µPa	Increased oxygen consumption	Wale et al. 2013b
Palaemon serratus	1 h	30 min	Day	-	PSD peaks up to 140 dB in the freq. band 0.1-3 kHz	Lower values of encounters Higher values of time spent outside shelter and resting No difference in tail flip and startle response event	Filiciotto et al. 2016

2 Materials and method

2.1 Acoustic characterization

To avoid potential confounding effects from using a broad range of noise sources, we focused solely on the noise emitted by a single source - the cargo ship *Nolhan Ava* (120 m length). This ensured that any observed behavioural changes in crabs could be directly linked to the vessel's acoustic characteristics, providing a clearer understanding about the impact of this category of noises on animal behaviour. Audio recordings were sampled on St. Pierre Island (46°46'44.90" N, -56°10'38.28" W) in 2021 using a calibrated hydrophone (Aural-M2, Multi-Électonique, Rimouski, Canada) located at 350 m from the ship's passage line. Playbacks were then re-emitted through an underwater speaker (Lubell Labs®VC2C, Columbus, Ohio, USA; frequency range 50–1500 Hz) placed in a large tank (3.5×3.25×1.3 m; Vol = 14.8 m^3) at 40 cm above the bottom in the facilities of the Maurice Lamontagne Institute (Mont Joli; Québec, Canada; 48° 38' 25.80 N 68° 09' 30.24 W).

In this study, treatments included two opposite sound conditions (Control *vs* Noisy). Each noisy sequence of shipping passage lasted for 11 minutes and were broadcasted in a loop over two experimental days (48 h). To assess the heterogeneity of noise within the tank, sound recordings were made over a 11 x 8 grid, 5 cm from the bottom (Fig. 28) with one acoustic recorder RTSYS-RESEA 320 (Caudan, France) equipped with the hydrophone Colmar GP1516M (Sensitivity -172 dB re 1V/ µPa @ 5kHz). Sound recording files (.wav) were first visualized over the entire frequency band by using the spectrogram view in Audacity® (Version 2.1.1; Audacity Team 2015). Spectrograms were then computed to display a frequency range between 0 and 10 kHz to allow visual scanning and identification of the shipping noise. Using MATLAB (Version 9.1; 2016b), the playback soundtrack was cut into 1-min file sequences and the root mean square of the sound pressure level (SPL$_{rms}$) was calculated on each sequence over the 0–2000 Hz frequency band (SPL$_{rms}$ [0–2000 Hz]).

Mean SPL$_{rms}$ of control condition corresponded to the ambient-room noise at 116.8 ± 0.6 dB re 1 µPa. By contrast, mean SPL$_{rms}$ of shipping noise conditions was equal to 145.5 ± 0.4 dB re 1 µPa, following a logarithmic decrease from the speaker to the tank walls (Fig. 28). Overall, SPL$_{rms}$ values dropped by approximately 10 dB from the speaker to the tank walls, with a maximum of 155.2 dB re 1 µPa nearby the speaker and a minimum of 134.8 dB re 1 µPa over the corners of the tank (Fig. 28).
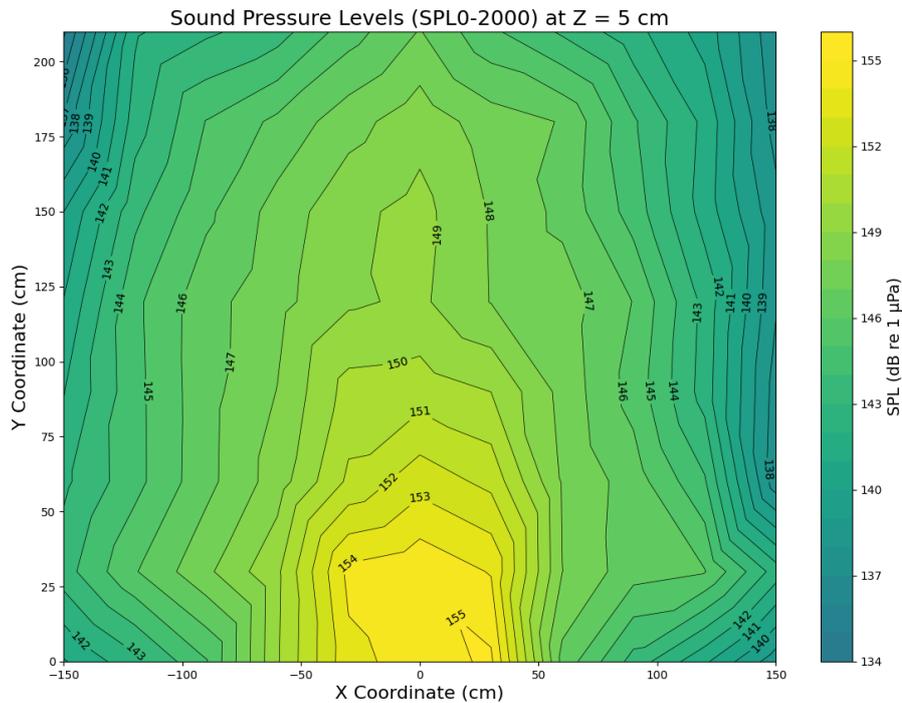
Figure 28: Propagation of the emitted shipping noise over the experimental tank for the 0–2000 Hz frequency band. Underwater speaker was located at coordinates (0 cm; 0 cm).

2.2 Animal choice, capture and maintenance

The crabs were caught directly from the St. Lawrence estuary (Quebec – Canada) in the proximity of the Maurice Lamontagne Institute (MLI) during two different seasons to prospect any behavioural change to be related to different physiological states of animals. A first experimental group of a total of 48 individuals was sampled in May 2024 (Spring). During this season, crabs returned to shallow waters after the winter period. A second experimental group of 36 individuals was sampled during the first weeks of October 2024 (Autumn) following reproductive season (Rondeau et al., 2014), just before crabs generally move to deeper waters to overwinter.

Individuals were collected at approximately 5m depth by using traps from the MLI docks, and only adult males were retained (limiting the experimentation to males because of their larger carapace easier to follow on video recordings). Upon arrival, animals were placed in holding tanks filled with filtered seawater inside the wetlabs, coming from the same area of capture. Individuals were separated in different subgroups, each of which would have experienced a different noise condition. All tested individuals had similar shell lengths (101.1 ± 1.2 mm in Spring *vs* 99.2 ± 1.2 mm in

Autumn). The seawater temperature and salinity were monitored seven day a week, 24 hours a day, and parameters remained constant for all the experiments (11.5 ± 0.3 °C and 26.1 ± 0.1 psu in Spring *vs* 10.3 ± 0.2 °C and 27.6 ± 0.3 psu in Autumn). During the following weeks, individuals were fed at satiety with blue mussels (*Mytilus edulis*) and herring (*Clupea harengus)* once every three days. No mortality events occurred during the holding periods or trials over the two experimental seasons.

Overall, crabs spent approximately 10 days in maintenance tanks before the beginning of the experiments. The tank room at the IML has several pumps, filtration systems and power generators, which may be noisy when activated. The acoustics of the maintenance tanks were therefore quantified during all the period and represented a mean SPL_{rms} [0-2000] of 128.6 ± 1.1 dB re 1 µPa.

2.3 Experimental setup

Experiments were conducted in a large tank allowing animals to move freely on a 4 cm thick layer of industrial pool sand (50 µm) rinsed before use. The tank was filled with filtered seawater coming directly from the estuary without temperature control. Seawater parameters (i.e., temperature and salinity) were measured with HOBO data loggers and remained constant during all trials (11.9 ± 0.3 °C and 26.2 ± 0.08 psu in Spring *vs* 10.5 ± 0.4 °C and 27.5 ± 0.1 psu in Autumn).

Each trial lasted a consecutive 48 hours (Day1 - Day2; from 9am on Day1 to 9am to Day3), allowing the crabs' behaviour to be examined over different periods of the day: two mornings (AM1 - AM2), two afternoons (PM1 - PM2) and two night periods (N1 - N2). A lighting system was put in place to reflect the realistic photoperiod that were encountered during the two seasons of experimentation. Because of the experiment's duration, water's chemical and physical parameters were quantified at the start and the end of each trial (Tab. S2).

After their transfer to the experimental tank, individuals were let to acclimatize for 1 hour (as Filiciotto et al., 2014 and 2016; Tab. 8). Then, in noisy treatments, shipping noise was played on a loop for the whole duration of the trial. A GoPro camera was installed over the tank to capture the whole surface in order to categorize crab displacement during daylight periods (AM and PM periods). To this end, each experimental group consisted of six animals tagged with various shapes on the top of their carapace to differentiate them in the video recordings. Among them, five individuals were additionally equipped with Axy 5 XS accelerometers (TechnoSmArt®), allowing to record crabs' activity also during the night periods. Accelerometers were set at 25Hz – 2 g and glued before the start of each trial on shells with epoxy glue. At the end of each trial, the tank was emptied and refilled with new water to restore the same starting conditions among replicates.

2.4 Calculation of behavioural metrics

2.4.1 Mobility: Covered Distance and Speed

All videos were analyzed to compile the crabs' x and y coordinates in each recorded frame (1 fps) by the use of Kinovea® video-tracking software. From these coordinates, it was possible to quantify the covered distance and the speed of displacement over a 45 minutes period of each of the pre-selected daylight study periods (AM1/PM1 - AM2/PM2). Video sampling was always done at the same hour of the day to avoid confounding effect related to the time of the day.

2.4.2 Activity: Overall Dynamic Body Acceleration and Moving Time

Data from Axy 5 XS accelerometers were downloaded using 'X Manager' software (TechnoSmArt). Acceleration values were given in units of g, where g represents acceleration due to gravity (1 g = 9.81 m.s^{-2}). Accelerometers record movements simultaneously on the three axes as the relative change detected in gravitational acceleration. The Overall Dynamic Body Acceleration (ODBA, in g), was calculated from tri-axial acceleration data as ODBA = |ax| + |ay| + |az| over 90 minutes of all the pre-selected study periods (AM1/PM1/N1 - AM2/PM2/N2). These data represented the acceleration recorded by the data logger owing to the dynamic movement of individuals during the trial. Coupling video and accelerometer recordings, animals were considered to move when ODBA > 0.1 g and the overall time spent in motion was thus calculated by summing up all seconds where data points fitted that condition. Activity sampling was always done at the same hour of the day to avoid confounding effect related to the time of the day.

2.4.3 Distribution over the tank surface

As there was a significant SPL loss from the speaker to the opposite side of the tank (Fig. 28), the distribution of crabs was analysed to assess the positions were crabs spent most of their time during the daylight periods (AM1/PM1 - AM2/PM2). To estimate the spatial distribution, positions of individuals were recorded every 5 minutes over a grid of 5 x 5 that covered the entire tank surface. The sum of the total number of positions recorded in each grid cell are shown in Fig. 31.

2.5 Statistical analysis

The behavioural parameters were analysed as a multivariate response matrix using permutational multivariate analysis of variance (PERMANOVA). The response matrix included covered distance, speed, ODBA and time moving, capturing different dimensions of crab behaviour.

An initial analysis included data from both experimental days to test for a general Day effect. Given the consistent and strong differences observed between days—likely reflecting disturbance or

acclimation effects (see Results 3.1.1; Fig. S17 and S18)—subsequent analyses focused exclusively on Day 2 to ensure behavioural stability and comparability. Within Day 2, PERMANOVAs were conducted to test the effect of Season on all behavioural parameters. Given the strong potential for biologically driven seasonal variation in crab behaviour, separate PERMANOVA models were subsequently constructed for Spring and Autumn. This seasonal division allowed for detailed investigation of noise-related behavioural changes within each seasonal context and enabled testing for season-specific interactions between sound exposure and the period of the day (AM, PM, N). Where significant main effects or interactions were found, pairwise comparisons were conducted with Bonferroni correction applied to control for multiple testing.

The difference in the spatial distribution of crabs within the experimental tank was analysed using analysis of variance (ANOVA), comparing different audio conditions and seasons. The assumption of normality was verified using the Shapiro-Wilk test, confirming that the data met the requirements for parametric testing.

A significance threshold of $p < 0.05$ was applied to determine statistically significant effects. All statistical analyses were conducted in R (version 4.2.2; R Core Team 2022) using the adonis2 function from the vegan package.

3 Results

3.1 Temporal effect

3.1.1 Manipulation effect in Day1 vs Day2

All tested parameters considerably changed from Day 1 to Day 2 in both treatments, highlighting marked behavioural differences between the two days (Fig. S17 and S18). The newly transferred animals showed marked patrolling behaviour along the edges of the experimental tank in Day1, reducing their mobility in Day2. In Spring, individuals reduced their mean covered distance by 91.6% and mean ODBA by 72.4% from Day1 to Day2. In Autumn, the mean covered distance decreased by 63.9%, and mean ODBA by 55.3% from Day1 and Day2.

Given the large behavioural difference reported between Day1 and Day2, we consider that Day1 behavioural parameters were altered by a manipulation effect. Therefore, we only present results from Day2, once the behavioural parameters were stabilized (see Fig. S17 and S18).

3.1.2 Seasonal effect

Because a triple interaction (pseudo-$F_{1,190}$ = 61.71, R^2 = 0.245, p = 0.001) was observed, a Permanova was performed by season to describe clearly the effect of noise treatment and period. In Spring, individuals moved a mean covered distance significantly lower than Autumn (4.06 m ± 2.4 vs 33.6 m ± 9.3, respectively), showing a reduced mean speed (0.17 m/min ± 0.09 vs 0.6 ± 0.2, respectively; Fig. 29). Similarly, the mean ODBA was lower in Spring compared to Autumn (0.08 g ± 0.01 vs 0.21 g ± 0.05, respectively) as well as the time spent moving (9.25 min ± 2.7 vs 34.9 min ± 6.3, respectively; Fig. 30).

3.1.3 Circadian effect

In Day2, both ODBA and time moving differed significantly across Periods (pseudo-$F_{2,189}$ = 7.48, R^2 = 0.073, p = 0.002), whereas covered distance and speed remained unchanged (pseudo-$F_{1,152}$ = 0.17, R^2 = 0.0011, p = 0.691; Fig. 29 and 30). In control conditions, crabs were more active during the night in both seasons (F = 7.81, R^2 = 0.175, p < 0.037), with ODBA and time moving higher than during the day (Fig. 30). In particular, the mean crab ODBA was equal to 0.08 g (± 0.01) during day in Spring, increasing to 0.14 g (± 0.02) during the night. Similarly, in Autumn, the mean crab ODBA was equal to 0.21 g (± 0.06) during day, increasing to 0.4 g (± 0.06) during the night.

3.2 Noise effect

3.2.1 Mobility and activity

The noise condition had no significant effect on covered distance and speed in either Spring (pseudo-$F_{3,78}$ = 0.14, R^2 = 0.0053, p = 0.981) or Autumn (pseudo-$F_{3,68}$ = 0.12, R^2 = 0.0055, p = 0.929; Fig. 29). However, in Spring, a significant interaction between audio condition and period of the day was detected for ODBA and time moving (pseudo-$F_{5,111}$ = 3.70, R^2 = 0.143, p = 0.006). Notably, post hoc comparisons revealed a significant difference between the noise treatment and control condition during the night period (F = 8.42, R^2 = 0.186, p = 0.030; Fig. 30), indicating that nighttime behavioural responses were particularly sensitive to noise exposure. In autumn, there was no significant interaction between noise exposure and time of day (pseudo-$F_{5,101}$ = 0.16, R^2 = 0.007, p = 0.11).

3.2.2 Crab distribution over the tank surface

Distribution over the tank did not change according to noise conditions (p = 0.81), neither to seasons (p = 0.84; Fig. 31). Crabs were mostly spotted at the corner as a consequence of their patrolling behaviour along the sides of the tanks (Fig. 4). No avoidance against the noise source was observed during the conditions.
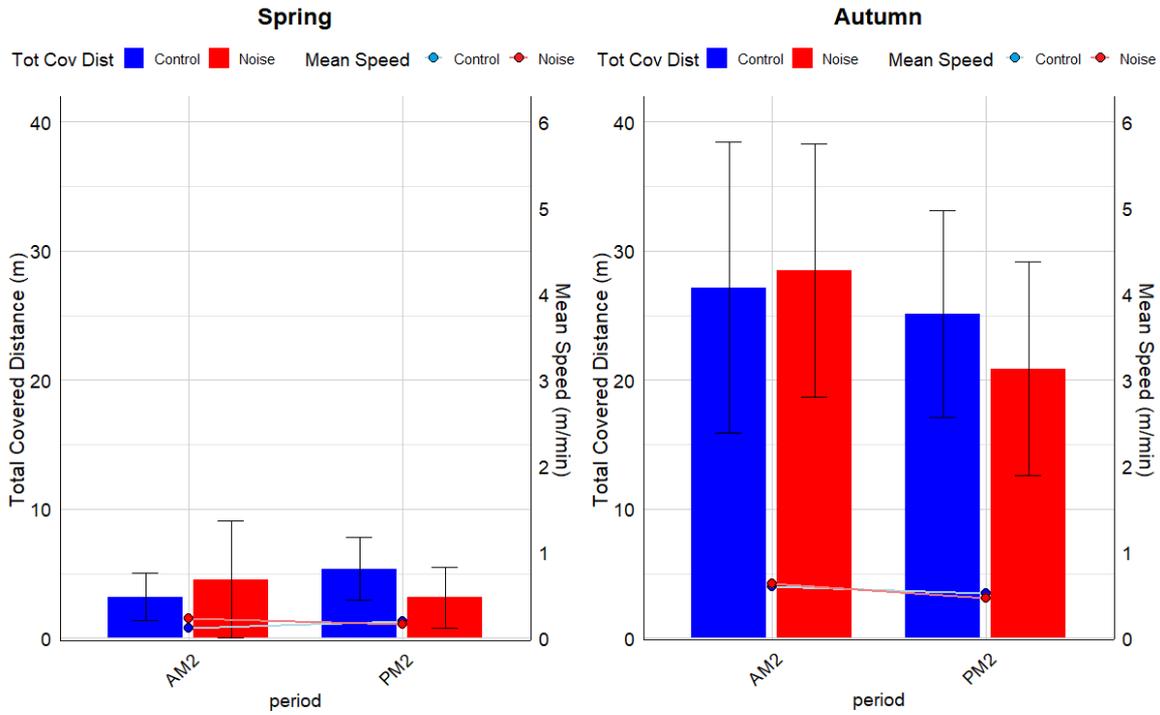
Figure 29: video recording related data showing the total covered distance (bars) and mean speed (lines) over different period of the day, seasons and audio conditions on Day2. Night periods were not analyzed by video recordings. Errors bars indicate the standard error of measure.
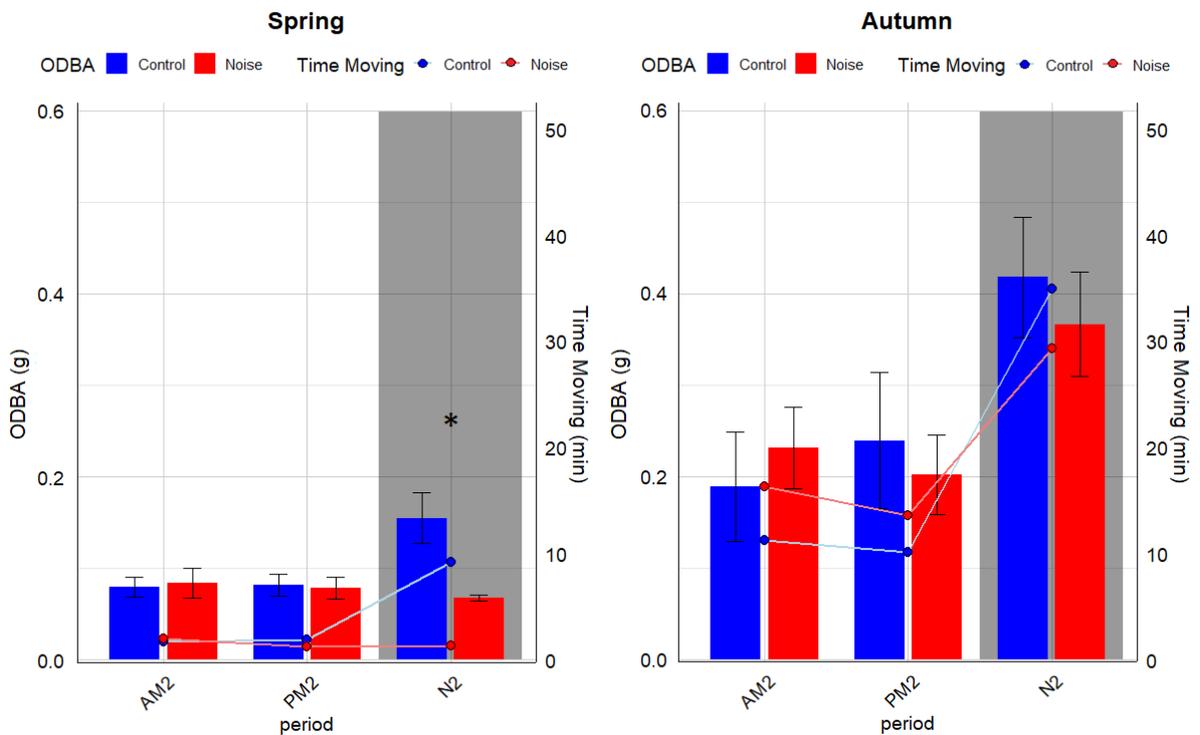
Figure 30: accelerometry related data showing the overall dynamic body acceleration (ODBA; bars) and moving time (lines) over different period of the day, seasons and audio conditions on Day2. Asterisk shows statistically significant difference between Noise conditions. Darker backgrounds identify night periods. Errors bars indicate the standard error of measure.
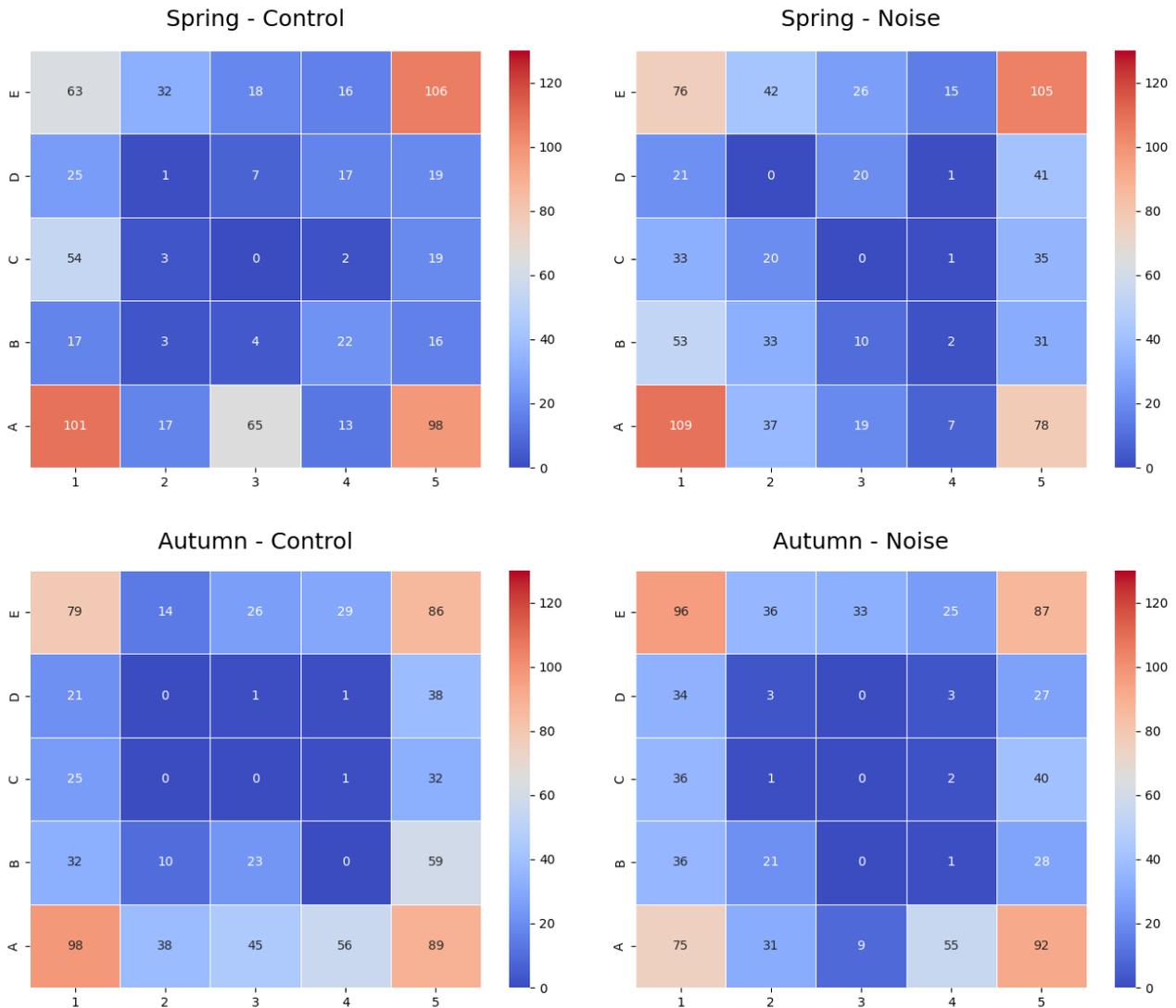
Figure 31: heat maps showing crab distribution over the tank surface in the different experimental audio conditions (Control *vs* Noise) and seasons (Spring *vs* Autumn). The number inside each cell represents the number of observations in which crabs occupied that specific cell.

4 Discussion

This study shows that exposure to shipping noise can lead to contrasting behavioural responses according to circadian and seasonal cycles. In particular, crabs appeared to be more active during the night in both seasons, with a significant effect of noise restricted to the nocturnal period of Spring. During Autumn, crabs were significantly more active, with no effect of noise during any of the analysed periods. The study also found that handling significantly influences the crabs' activity

over the first experimental hours, altering their behaviour and potentially influencing the effects of noise.

Over the first 24h, crabs' activity levels were higher immediately after transfer to the experimental tank, without any behavioural effect of shipping noise. In Matveev and McGaw (2022), acute stress response (increased metabolic rate and activity) also occurred after the transfer of *C. irroratus* between tanks, declining steadily over the next 12h. The same authors suggested a significant animal handling effect, highlighting that the introduction of individuals on a totally novel habitat may change their behavioural context. When reviewing the studies carried out on the effect of noise on crustacean behaviour, however, acclimatisation and exposure times did not consider this potential effect of handling. Filiciotto et al. (2014) observed behavioural changes just after 1 h of exposure (preceded by 1 h of acclimation; power spectrum peaks up to 120 dB re 1 µPa below 10 kHz), with European spiny lobsters showing reduced mobility, but not in the occurrence of tail flip events. After 7.5 min. exposure (preceded by 15-30 sec of acclimation), shore crabs (*Carcinus Maenas*) showed significant feeding and hiding behavioural changes according to shipping noise (148-155 dB re 1 µPa RMS), although there was no difference in success to find food and initial reaction to predator (Wale et al., 2013a). In Walsh et al. (2017), common hermit crabs showed faster shell selection after 30 minutes shipping noise exposure at 165 dB re 1 µPa (with 5 minutes acclimation to recover from handling; Tab. 8), but no difference in choosing the optimal shell size.

In the present work, crabs' behavioural responses did not differ between either control or noisy conditions during the first 24h, where activity levels were three times higher than during the next 24h. Such observations suggest that crabs were disturbed by the pre-trial manipulation and tank transferring, triggering patrolling behaviour and requiring 24 hours to return to stable activity levels. Similarly, Wilson et al. (2021) reported that handling on *Carcinus maenas* significantly increased oxygen consumption for up to 14 hours post-manipulation, recommending a minimum 12-hour acclimatisation period before commencing experimental procedures. Together, these findings underscore the importance of allowing sufficient acclimatisation time to ensure animals return to a stable behavioural state before assessing stress or behavioural responses. If not taken into account, indeed, cumulative or masking effects can occur when combined to noise exposure, potentially introducing bias into the final behavioural observations and leading to misinterpretation of the actual impact of the stressor.

When excluding handling effects, we noticed an important seasonal effect, with higher activity levels during the night (see also Rebach, 1987; Barbeau et al., 1996; although in Autumn,

individuals showed some mobility even during daytime). The month of May immediately follows the typically rough winter period in the Gulf of St. Lawrence, during which the crabs seem to go into partial quiescence with a reduction in their home range and moving to slightly deeper waters (McKindsey et al., data not published). This event of partial migration was confirmed by catches we made to collect individuals, with considerably reduced catches during the first days of May compared to following weeks (data not shown). The reduced activity of the crabs during Spring was further confirmed by video and accelerometers related data, as all analysed behavioural parameters were lower compared to Autumn. In Newfoundland, individuals of *C. maenas* showed a significant reduction in activity after long-term exposure to cold temperatures (2 °C), with crabs entering a dormant state (although not complete) and reducing feeding during the winter (Rivers et al., 2025). Thus, the observed reduction in *C. irroratus* activity may reflect the physiological stress induced by the cold and harsh winter conditions experienced in the Gulf of St. Lawrence in the preceding month. Low winter temperatures, indeed, usually trigger considerable changes in metabolism, immune system and osmoregulation in a great number of crab species, often resulting in a temporary metabolic disorder during the cold season (Ren et al., 2021). As a consequence, these suboptimal environmental conditions could place individuals of *C. irroratus* in a compromised physiological state, potentially heightening their vulnerability to additional stressors such as shipping noise.

Crabs were significantly more mobile and active in Autumn, as total covered distance increased by five times during the day, and the mean ODBA doubled during the night. This season follows the summer period in which the animals have presumably reached an optimal physiological condition due to the abundance of food in the shallow waters near the coast (Hanson et al., 2014). At warmer summer temperatures (12 °C), *C. maenas* were significantly more active, increasing their mobility and consuming more food (Rivers et al., 2025). According to data collected by McKindsey et al. (data not published), male crabs of *C. irroratus* also exhibited a significant increase in areas occupied during the month of October along the north coast of the St. Lawrence estuary, potentially for reproductive purposes. In this region, indeed, crabs' mating events occur from late summer to autumn, when females moult in October and November (Haefner 1976). Concerning the shipping noise influence, because no effects were found during this season, behavioural responses to noise exposure in crabs may vary according to temporal and physiological rhythms. According to our findings, indeed, the baseline condition of the animal seems to play an important role in defining the effect of noise on animal behaviour, with weakened individuals in Spring showing enhanced responses compared to individuals in a proper condition during Autumn.

In our original experimental setup, only adult males were selected due to their large carapace surface, easier to follow in video recordings with visual tags. In spring, however, gravid females were also frequently observed all over the sampling period. During this season, females carry on their abdomen a large number of fertilized eggs (4000 – 500 000 eggs depending on the individual size) from the previous year, hatching during the late spring (Haefner 1976). Given this important reproductive constraints, females may present weakened physiological states compared to males during the considered season, potentially showing wider behavioural reactions to shipping noise. Just as temperature changes have been shown to differentially influence the behaviour of gravid and non-gravid female crabs (Lam et al., 2022), it is plausible that noise may also exert varying effects depending on the individual's physiological state. By assuming that the basic physiological condition can influence the relationship between noise and animal behaviour, the hypothetical adverse energetic condition of females in spring could seriously damage the fitness of this sex. Future studies should implement the assessment of the relation between gravid females and shipping noise to highlights potential negative effects on the species' reproductive potential.

The nocturnal influence of noise in Spring could have significant effects on the species' basic functions. Although we did not directly measure the covered distances during this period, the reduced activity recorded via accelerometry could translate into a significant decrease in individual mobility (Bidder et al., 2012). In their natural habitat, crabs return to shallower waters in spring after a wintering in slightly deeper waters (McKindsey et al., data not published). It is therefore possible to suggest that individuals are prospecting new feeding grounds to find nourishment and restore their energetic reserves (Comeau et al., 2012; Hanson et al., 2014). By reducing mobility shipping noise could thus decrease the crabs' ability to find suitable food sources, and by cascade their overall fitness for the following seasons. Based on the present work, a SPL shipping noise of 145.5 dB re 1 µPa can affect the spatial behaviour of *C. irroratus* during the night period of the Spring season. Other crustaceans species were also observed to respond to similar shipping noise pressure levels (from 143 to 165 dB re 1 µPa; see Tab. 8). However, a great portion of the shoreline in the St. Lawrence Estuary is exposed to SPL_{rms} of lower intensity than those applied in our experimental setup (Gervaise et al., 2015), levels that may nonetheless be sufficient to affect the behaviour of local individuals. For example, the hermit crab (*Pagurus bernhardus*) was observed to behaviourally react to shipping noise SPL_{rms} starting from 119 dB re 1 µPa (Tidau and Briffa, 2019a; Tab. 8). Lobsters (*Homarus americanus*) significantly displayed a greater sensitivity at 80–120 Hz, with SPL_{rms} thresholds ranging between 99 and 107.5 dB re 1 µPa (Jézéquel et al., 2021b). It would therefore be interesting to assess whether lower SPL also have an effect on the behaviour

of the considered species, establishing a minimal noise threshold level triggering behavioural reactions in exposed animals. Furthermore, while this study was conducted over 48h, we believe that additional studies over an even longer period would be necessary to confirm our results. We suggest planning a monitoring program to observe crab behaviour over several consecutive nights during Spring to observe potential cumulative or acclimation events. To date, indeed, noise acclimation remains an underreported phenomenon in behavioural studies related to acoustic pollution, with most of the reported studies assessing the impact of anthropogenic noises over short periods of time. Whilst a short-term approach only allows punctual observations, longer exposures may reveal crucial complex behavioural responses to noise, inducing potential nonlinear relationships between anthropophony and animal behaviour.

5 Acknowledgements

Discussion

This thesis highlights several behavioural aspects of two marine invertebrate species - *Buccinum undatum* and *Cancer irroratus* - along with their respective responses to shipping noise, investigated through innovative experimental approaches. Overall, our findings emphasize the critical role of underwater anthropogenic noises in influencing the mobility of different classes of benthic vagile marine invertebrates, shipping noise affecting the spatial behaviour and dispersal of individuals with potential broader population-level consequences along the coastal environment.

I. Shipping noise alters *B. undatum* and *C. irroratus* behavioural strategies

An increasing number of marine invertebrate species are now recognized as exhibiting highly specialized behavioural adaptations in response to conditions imposed by the local environment. Abiotic factors such as light, temperature, current, salinity, and oxygen concentration have been shown to influence a wide range of behavioural traits related to the movement ecology of several species (Goldstein and Watson, 2015; Jolivet et al., 2015; Stieglitz and Dujon, 2017; Schlaff et al., 2020). Although the role of the underwater soundscape in shaping the behaviour of marine invertebrates remains relatively underexplored, growing evidences suggest that acoustic cues may also elicit critical behavioural responses contributing to the individual fitness (Lillis et al., 2013; Charifi et al., 2017; Solé et al., 2023).

The two considered species belong to animal classes - Gastropoda and Malacostraca – representing benthic marine invertebrates for which mobility correspond to a critical behavioural trait directly related to many other essential life aspects (Jolivet et al., 2015; Morse et al., 2018; Cote et al., 2019; Schlaff et al., 2020; but see also Chapter 1). Although the modes and metrics of locomotion differ considerably between species, both heavily rely on movements to locate food and sexual partners, escape predators, but also to actively respond to the large environmental heterogeneity characterizing their living habitat. Both *B. undatum* and *C. irroratus*, indeed, exhibited specie-specific highly specialized spatial behaviours in response to the conditions of the local environment (Chapter 1 and 3). This high degree of behavioural specialization resulted in distinct seasonal patterns, and in the case of the crabs, even circadian rhythms over different part of the day (Chapter 1 and 3). These mobility patterns represent adaptive behavioural strategies that have evolved as increasing individual fitness, enhancing resource acquisition, reproductive success and survival under specific environmental conditions.

Following the concept of the environmental predictability (see Riotte-Lambert and Matthiopoulos, 2019), the living habitat assumes a degree of stability to which animals adapted their behaviours over time. When human activities are involved, however, the natural rhythms are considerably

altered, losing the inherent consistency to animal behaviour (Wilson et al., 2020). In our case, anthropophony was found to disrupt the animals' usual mobility patterns, thereby reducing the dispersal potential of both considered species and compromising the biological and ecological functions served by movement, with potential final repercussion on the individual fitness (Chapter 2 and 3; Fig. 32). In particular, chronic noise pollution—such as that generated by shipping—is now increasingly recognised to alter the movement ecology across multiple life stages in many benthic–pelagic species, affecting both pelagic larvae and benthic adults, potentially altering population dynamics and community structures (Byrro-Gauthier et al., in press; Filiciotto et al., 2014; Jolivet et al., 2016; Kunc et al., 2016; Solé et al., 2023; Chapters 2 and 3; Fig. 32).

II. By altering animal spatial distribution, shipping noise has implications for local ecological dynamics

In marine invertebrates, biological traits like effective dispersal during planktonic larval stages and benthic adult phases are key factors shaping local populations (Allen et al., 2018; Chiu et al., 2023). Indeed, individual mobility supports core ecological processes, including gene flow, reproduction, connectivity, and habitat colonisation, allowing organisms to adapt to the environmental heterogeneity (Allen et al., 2018; Joo et al., 2020). By altering the anatomy, physiology and specific behavioural strategies of multiple ontogenetic stages of aquatic inverterbates, shipping noise may ultimately affect the dynamics of local populations, potentially leading to broader implications such as altered community structure and reduced ecosystem resilience along the coastal habitat (Kunc et al., 2016; Fig. 32).

Potential effect of shipping noise on larval dispersal

Recent studies defined specific anthropogenic sound pressure levels (SPL_{rms}) inducing delayed metamorphosis and increased metabolic costs, altering the survival and dispersal potential of marine invertebrates' larvae within the water column (Byrro-Gauthier et al., in press; Nedelec et al., 2014; Jolivet et al., 2016; Veillard et al., 2025).

In blue mussel (*Mytilus edulis*), shipping noise modified the life cycle of larvae by influencing their settlement and modulating their metabolism (Veillard et al., 2025). In particular, larvae exposed to high SPL_{rms} (151 dB re 1 μPa) had higher energy expenditures, resulting in decreased energy reserves. As a consequence, larvae where forced to settle without any positive settlement cue, or even in an unfavourable environment, potentially leading to increased larval mortality and consequences on the biodiversity of the local benthic community (Veillard et al., 2025). Likewise, Nedelec et al. (2014) also found that exposure to boat noise (no description of levels) reduced

successful development of the gastropod *Stylocheilus striatus* embryos by 21% and additionally increased mortality of larvae by 22%, suggesting potential broader population-level consequences. Studies on the gastropod *Bembicium nanum* also detected an increase in larvae swimming activity when organisms were exposed to anthropogenic noise (no description of levels) in the laboratory, potentially altering their settlement rate (Stocks et al., 2012). Chronic noises (up to 145 dB re 1 μPa) also delayed median time to metamorphosis and discouraged larval settlement in two common estuarine crabs, *Austrohelice crassa* and *Hemigrapsus crenulatus*, the researchers concluding that noise is likely to mask natural acoustic settlement cues (Pine et al., 2012).

These findings underscore the detrimental impact of shipping noise during one of the most sensitive phases of the marine invertebrate life cycle —larval settlement— suggesting potential consequences at a broader ecological scale. By analysing the larval community structure, Byrro-Gauthier et al. (in press) reported a marked decline in species diversity and evenness in response to shipping noise (140 dB re 1μPa².s) in the Saint Pierre et Miquelon archipelago, with noticeable shifts in community composition along the SPL_{rms} gradient. In particular, an increase in the abundance of *Mytilidae* and *Lacuna* sp. larvae was observed in collectors located near the source of vessel noise, while *Hitella arctica* presence decreased as SPL_{rms} increased (Byrro-Gauthier et al., in press). The same authors suggested that noise levels exceeding 140 dB re 1 μPa²·s could disrupt community structure and recruitment processes, highlighting the potential impact of anthropogenic noises on local population dynamics starting from the very early life stages of marine invertebrates.

Potential effect of shipping noise on adult dispersal

Beside larval dispersal, mobility of adult forms is also a fundamental ecological trait that supports key ecological features in many marine invertebrates' populations (Baird et al., 2012; Allen et al., 2018). This is especially true for benthic vagile species that, in many cases, can move substantial distances on the seafloor without site attachment, demonstrating a high variation in the strength and duration of displacements (Allen et al., 2018; Morse et al., 2018; Lavoie et al., 2022).

Numerous studies highlight the critical role of adult mobility in shaping population dynamics across the benthic environment. For example, in the Gulf of Mexico, amphipods associated with pen shells show marked differences in dispersal timing—some species disperse as adults, while others as juveniles—leading to varied patterns of recruitment and population structure (Munguia et al., 2007). Likewise, the European lobster (*Homarus gammarus*) and crawfish (*Palinurus elephas*) demonstrate contrasting adult movement behaviours: while lobsters exhibit strong site fidelity and

minimal displacement, crawfish engage in extensive seasonal migrations spanning hundreds of kilometers, resulting in differing levels of demographic connectivity (Ellis et al., 2023). Even in species without pelagic larval stages, such as the Antarctic amphipod *Orchomenella franklini*, genetic structuring over spatial scales indicates that adult movement, albeit limited, contributes meaningfully to gene flow (Baird et al., 2012). Similar trends are also observed in some marine gastropods species: along the North Pacific coast, *Monodonta labio* and *M. confuse* showed distinct genetic structures among neighbouring populations because of their different specie-specific mobility patterns (Chiu et al., 2023).

Overall, these examples underscore the critical role of dispersal in benthic marine invertebrates and how changes in mobility patterns can deeply affect ecological dynamics in the local environment. Although research on the impact of anthropogenic noise on benthic vagile invertebrate movement is still limited—mainly addressing crustaceans (see Solé et al., 2023; but Chapter 2)—existing studies consistently report significant alterations in locomotor activity (Filiciotto et al., 2014; Celi et al., 2015; Filiciotto et al., 2016; Briffa et al., 2024; see Introduction 3.2). Our results on *B. undatum* and *C. irroratus* further confirm that noise exposure disrupts mobility patterns across the adult life stages, compromising individual dispersal within the local environment, with direct implications for the invidivual fitness, potentially reducing populations connectivity and affecting community structure over the long term (Chapters 2 and 3; Fig. 32). Given the strong link between dispersal ability and population persistence (Kotiaho et al., 2005; Neubauer and Georgopoulou, 2021; see also Chapter 1), these findings emphasize that alteration in individuals' movement ecology due to anthropophony—both at the pelagic larval and benthic adult stages—can undermine the resilience and stability of local populations and several benthic communities along portions of coast regularly exposed to intense shipping passage. In particular, this may be especially true along new trading routes predicted to be established along the coasts of Arctic regions (Theocharis et al., 2018), where the morphology of the territory and the low adaptation to noise of local species may create shipping noise hotspots that could interfere with the regional ecological dynamics.
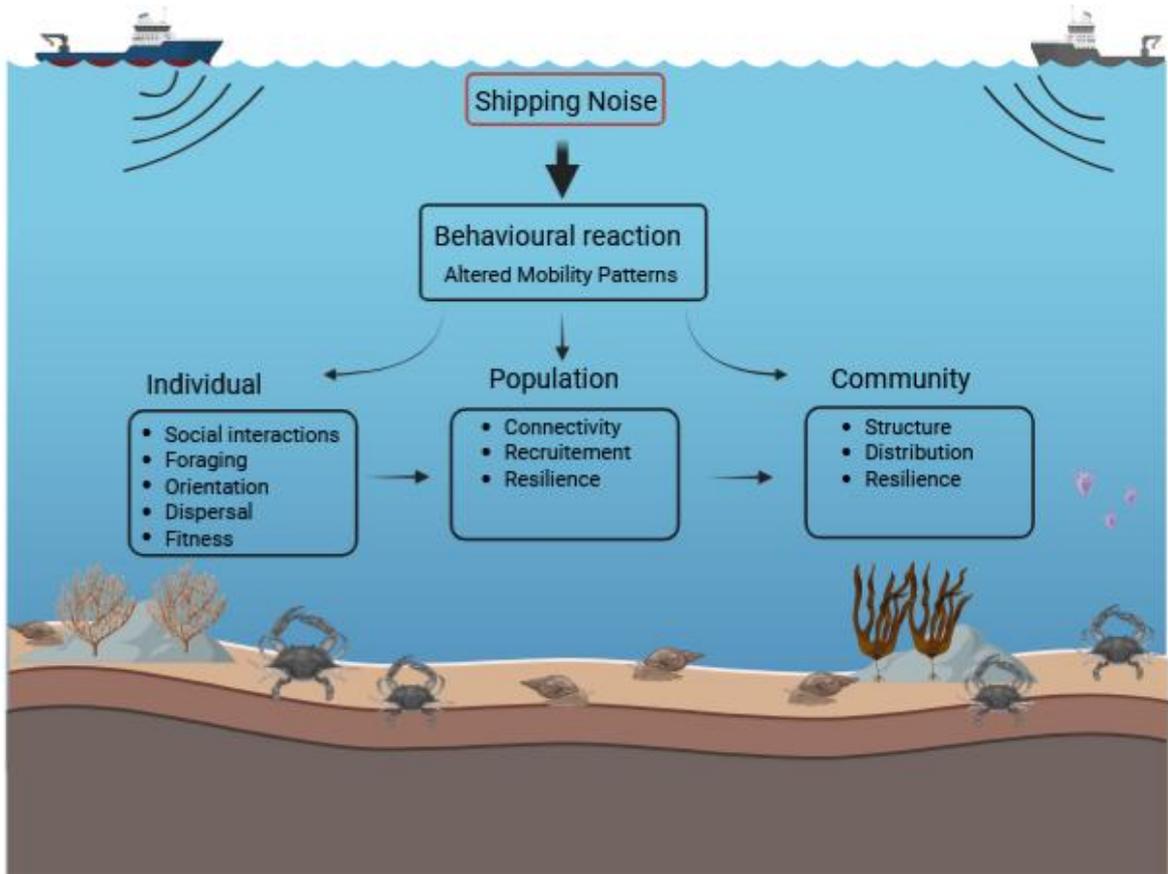
Figure 32: By altering the behavioural specificity and mobility patterns of several benthic-pelagic marine invertebrate species, shipping noise represents a significant stressor that can impair the fitness of individual organisms, potentially driving broader critical changes in animal population dynamics and ultimately affecting the structure of local communities. (Created in Biorender.com)

III. Prospectives: emerging Arctic trading routes and marine communities vulnerability

Based on results about the impact of anthropophony on various animal species (i.e., marine mammals, fish and marine invertebrates; Erbe et al., 2019; Ivanova et al., 2020; Solé et al., 2023), growing concern is now warranted regarding the potential ecological impact of opening new commercial shipping routes along strategical regions.

Indeed, large commercial ships' passages (beside to port development, cruising, echo-sounders, seismic exploration and resources extraction) will considerably alter the natural soundscape of the surrounding underwater environments, resulting in a sustained disturbance factor for locally exposed species dwelling along the coast (Halliday et al., 2020; Ivanova et al., 2020; Jones et al., 2023). This may be particularly true in the Great North regions, where new trade routes are being planned in near-to-pristine coastal areas supporting a biotope poorly adapted to anthropogenic noises (Halliday et al., 2020). The Statement on Canada's Arctic Foreign Policy indicates that *Arctic shipping is another key area of focus* in order to promote social and economic development

in northern areas. Indeed, ice clearance for extended periods during the summer will allow more commercial vessels to transit key naval corridors, such as the Canadian North-West Passage and the North-eastern Passage (also known as the Northern Sea Route NSR). In the last few years, traffic on the NSR rose from just over 30 transits in the whole 2011 to 153 transits in the sole June 2021 (Miller and Ruiz, 2014; Northen Seaway Information Office), indicating its rapidly growing importance between the world majors economies. The transit time between China and Europe via the NSR (18-20 days) is approximately half that of the Suez Canal route, providing considerable financial benefits to transport companies. In the Canadian Arctic, the commercial shipping passage is also very likely to increase in the next decades along the North West passage, deeply modifying the local underwater soundscape (Aulanier et al., 2017). Furthermore, the Arctic coastal regions present several islands and narrow channels that may create wide vessels concentrations, leading to shipping noise hotspots along the new commercial trading routes. Therefore, shipping passage along strategic lanes, commercial ports, sea channels and bays could considerably modify the natural soundscape over large areas and for extended period of time (beside other critical shipping related pollutants; Ng and Song, 2010; Aulanier et al., 2017; Jones et al., 2023), leading to considerable implications for the local biotic communities (Halliday et al., 2020; Ivanova et al., 2020; Lancaster et al., 2021).

Intense SPL_{rms} are frequently recorded in regularly used shipping lanes (McKenna et al. 2013) and in the proximity of commercial ports (Breeze et al. 2021; Ivanova et al., 2020). In the Saint Pierre et Miquelon archipelago, our recordings of a passing cargo ship revealed a SPL_{rms} of approximately 174 dB re 1 μPa at a distance of 350 meters. In an Arctic bay, a vessel passage was recorded to increase the ambient SPL_{rms} from 74 to 131 dB re 1 μPa [0.7-64 KHz], influencing the soundscape of the entire bay with maximum SPL_{rms} of 147 dB re 1 μPa (Ivanova et al., 2020). The study of Jones et al. (2023) observed that vessel passages, particularly from icebreakers and cargo ships, elevated the broadband SPL_{rms} from ambient levels of approximately 103 dB re 1 μPa to peaks of 129 dB re 1 μPa [0.02-10 KHz]. By an innovative modelling of shipping passage, Gervaise et al., (2015) also demonstrated that a substantial portion of the St. Lawrence estuary is exposed to sound exposure levels (SEL_{30min}) exceeding 149 dB re 1 μPa^2 s [63 Hz one-third-octave band] over 75% of time. Similar SPL_{rms}, already considered ecologically significant, could plausibly be reached in other strategic maritime corridors if shipping activity continues to increase. Concerning the Canadian Arctic, in 2013 shipping noise was absent from the studied regions about 68 to 90% of the time and loud shipping noise levels could be heard only 5 to 13% during the summer. However, considering a likely tenfold traffic increase scenario, the proportion of absent shipping noise periods

would dramatically decrease by 56 to 66%, with major consequences for the regional soundscape (Aulanier et al., 2017). Indeed, the spatial impact of vessel passage on the local soundscape can be considerable, resulting in increases in SPL_{rms} by 15 to >30 dB when ships are within 10 km and measurable shipping noise below 200 Hz at distances of >50 km (Jones et al., 2023).

As largely reported, a growing number of marine animals species are now observed to behaviourally react to similar SPL_{rms}, from marine mammals to fishes and invertebrates (Erbe et al., 2019; Ivanova et al., 2020; Solé et al., 2023; Chapter 2 and 3; Fig. 33). Rising ambient noise levels by anthropophony can trigger noise avoidance behaviours in some cetaceans (Johnston and Painter, 2024), species that are acustically more responsive to predator predicted to be more disturbance sensitive (Miller et al., 2022). The presence of large vessels also considerably affect fish mobility and habitat use in nearshore Arctic environments, with crucial implications for local management and conservation (Ivanova et al., 2018 and 2020; Fig. 33). Although there remains no clear consensus in the literature regarding the exact noisy threshold affecting different classes of marine invertebrates, number of studies document behavioural reactions occurring at SPL_{rms} comparable to those commonly recorded along commercial shipping routes (both in terms of larval and adult forms; Byrro-Gauthier et al., in press; Filiciotto et al., 2014; Di Franco et al., 2020; Solé et al., 2023; Fig. 33). Consistent with these findings, our results on *B. undatum* and *C. irroratus* demonstrate altered mobility patterns when exposed to shipping noise at SPL_{rms} levels typical of regular vessel passage (i.e., 122, 145, 174 dB re 1 μPa; see Chapters 2 and 3).

Overall, these reports indicate that many marine animal classes living in coastal communities near shipping noise hotsposts—particularly in newly exploited regions such as the Arctic—will be routinely exposed to SPL_{rms} levels high enough to impair individual fitness by disrupting essential behaviours, movement patterns and spatial distributions, potentially triggering broader cascading effects on the local community (Fig. 33).

To validate such hypothesis, long-term monitoring programs should be implemented in communities located in areas predicted to experience substantial increases in shipping traffic, in order to detect potential shifts in community composition and distribution. At the same time, there also remains significant potential to improve experimental approaches in order to more effectively capture the behavioural responses of a wide range of marine invertebrate classes exposed to anthropogenic noise. In particular, key questions persist regarding the effects of long-term noise exposure, including the potential for acclimation and the need for experimental designs that better replicate ecologically realistic environments.
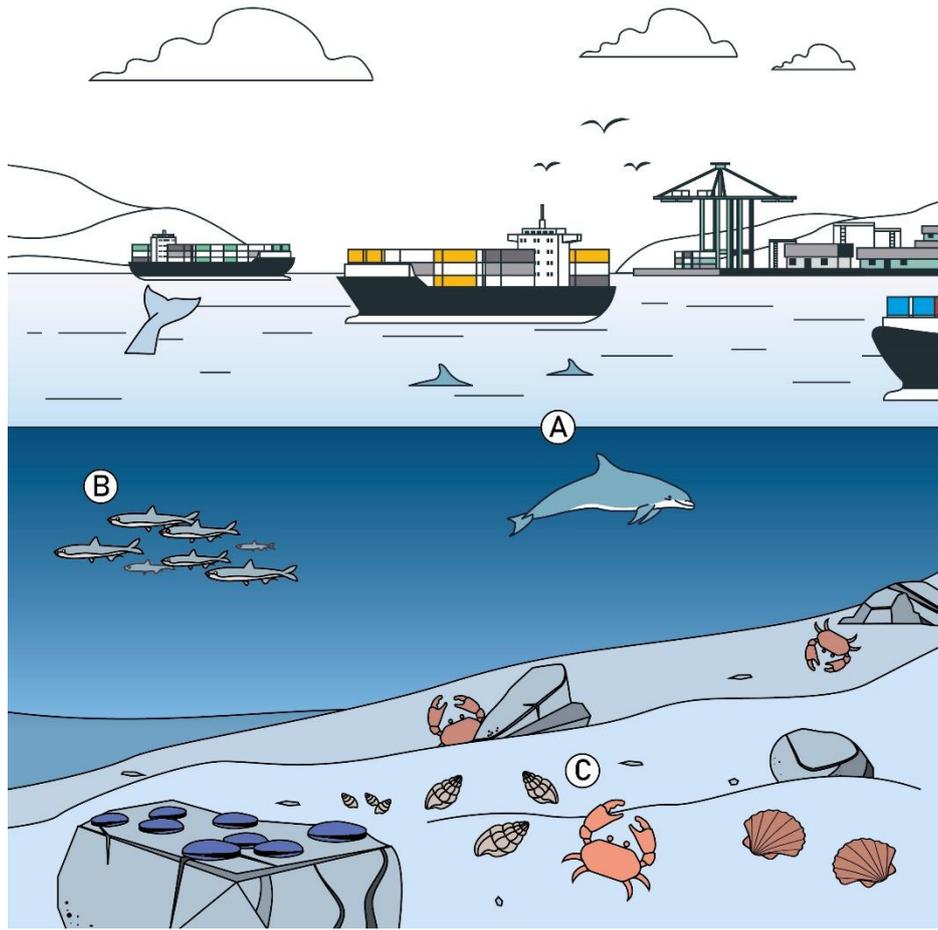
Figure 33: The increasing importance of Arctic regions for commercial exanges across countries will create some shipping noise hotspots along the most attended strategic lanes, commercial ports, sea channels and bays. By considerably increasing the ambient SPL_{rms}, shipping noise could considerably alter the distributional pattens—as well as many other essential behaviours—of a number of marine animal classes (from (A marine mammals, B) fish and C) marine invertebrates) ultimately triggering potential broader cascading effects on the local community. (Figure created by Sébastien Hervé - LEMAR)

IV. Enhancements for future research

Considering acclimation to anthropophony over the long term exposure

One of the key factors in considering the ecological consequences of anthropophony is the potential of acclimation of species to noise exposure. To date, noise acclimation remains an underreported phenomenon in behavioural studies related to acoustic pollution, with most of the reported researches assessing the impact of anthropogenic noises over short periods of time. This phenomenon, however, may deeply change the existing relationship between anthropophony and the behavioural responses of animals, influencing the resulting long-term consequences on ecological dynamics. According to Wilson et al. (2020), indeed, animal and ecological responses to human activities can vary in different ways depending on the exposure time and the intensity of the

environmental change (see Fig. 2 in Introduction 1.2). Whilst a short-term approach only allows punctual observations, longer exposures may reveal crucial complex behavioural responses to noise, inducing potential nonlinear relationships between anthropophony and animal behaviour such as decelerating, dampening or threshold effects (Fig. 2).

Most studies available today only analyse the primary animal behavioural response, overlooking the long-term effects (see Solé et al., 2023). However, few studies have reported potential acclimation to anthropogenic noises in bivalves and cephalopods (Samson et al., 2014; Jézéquel et al. 2023a and 2023b). For example, no evidence of behavioural responses was observed in thorny oysters *Spondylus americanus* exposed to daytime boat sound along the coral reef, possibly explained by an acclimation to a noisy environment due to the pervasiveness of boat sound pollution in the area (Jézéquel et al., 2023a). Considering punctual pile driving noises, Jézéquel et al. (2023b) also found surprisingly rapid acclimation of longfin squids' (*Doryteuthis pealeii*) alarm responses after an increasing number of strikes over following days.

Due to the critical importance of acclimation, further research is essential to better understand its behavioural implications. To this end, future studies should incorporate longer exposure periods to adequately capture potential acclimation to anthropogenic noise. In communities located along major trading routes, animals are regularly exposed to shipping noise. Only studies that consider the potential for acclimation over recurrent exposures will be able to accurately predict the long-term effects of noise exposure on ecological dynamics.

Adapt behavioural experimental settings to specie-specific behavioural aspects

Behavioural ecology is one of the most valuable tools to understand ecological changes driven by human activities (Wilson et al., 2020; Rahman and Candolin, 2022). However, interpreting the effects of noise pollution on animal behaviour requires a thorough understanding of species-specific behavioural aspects, using appropriately tailored experimental designs. In particular, our findings add to the growing number of observations documenting highly specialised behaviours in marine invertebrates, depending on the biological cycle and the life strategies adopted by the respective species.

In Chapter 2 and 3, both considered species showed altered mobility patterns following exposure to shipping noise, although behavioural changes were detected only after a latency period. The noise related effects were particularly evident during late spring and summer - *B. undatum* during breeding, and *C. irroratus* during the pre-breeding period with no significant effect in autumn (Chapter 2 and 3). Furthermore, crabs responded to noise primarily during night hours, with

negligible behavioural changes during daylight periods. These findings underscore the importance of accounting for acclimation time, exposure duration, and daily and seasonal biological rhythms of considered species when assessing behavioural responses to anthropogenic noise.

Previous studies have often underestimated the behavioural complexity of marine invertebrates, overlooking the potential effects of handling, time of day, and seasonality (see Chapter 3). Thus, some of the observed noise-induced responses may reflect artefactual effects rather than ecologically meaningful behaviours. In order to have a clear consensus about the effect of anthropophony on animal behaviour, future researches need to adapt over the behavioural specificity of marine invertebrates, envisioning adapted experimental settings according to the considered species.

Using field and controlled experimental designs in assessing the impact of anthropophony

Field based approaches offer a great capacity of observe the natural behavioural specificity of species within their living environment (Morse et al., 2018; Stieglitz and Dujon, 2017; Schlaff et al., 2020). In particular, acoustic telemetry is now providing unprecedented ecological insights by connecting animal movements with measures of their habitat (Hussey et al., 2015; but see also Chapter 1).

In Chapter 2, acoustic telemetry was used for the first time to study the impact of anthropogenic noise on invertebrates, revealing of an excellent effectiveness in study the behavioural reaction of *B. undatum* to noise and allowing evaluations over several experimental days directly in the sea. In this sense, acoustic telemetry would allow a continuous monitoring of tagged animals occupying a certain portion of habitat (e.g., a bay or fjord) over circadian and, even, seasonal cycles, making possible to assess the effect of noise along long-term exposures. Based on our results, however, a number of precautionary measures must be taken to obtain reliable data on the behaviour of the species examined. First, an appropriate species-specific acclimatisation time must be applied so that the animals can recover from tagging and show normal behaviour. Second, acoustic telemetry designs should also take into great account the mobility potential of considered species, adapting their extent to the mobility of the species. Some marine invertebrate species (i.e., crabs), indeed, show great potential for displacements, possibly exceeding the area exposed to noise and, eventually, the study site. By first exploring the species natural potential of dispersion within the study site, biotelemetry arrays' extent should be locally adapted to allow a continuous behavioural monitoring of noise-exposed individuals.

Where possible, acoustic telemetry studies should be complemented by tank-based experiments to validate field observations and investigate finer-scale behavioural responses. Indeed, behavioural laboratory studies offer valuable opportunities to examine the relationship between animal behaviour and specific SPL_{rms} of anthropogenic noise. Within appropriate tanks, it is possible to isolate specific noise sources and establish precise sound pressure levels triggering the most behavioural responses. However, as previously mentioned in Chapter 3, laboratory experiments suffer from several biases due to the removal of animals from their natural environments. Therefore, careful considerations must be taken to minimize these biases and reflect the natural specificity of animal behaviour. First, an appropriate acclimatisation time must be applied prior to exposure to the noise factor, so that the animal recovers its full faculties before the start of the experiment (Matveev and McGaw 2022; but also Chapter 3). Second, special attention must be paid to quantifying the sound pressure levels in the holding rooms that could lead to possible noise acclimatisation phenomena. Third, when evaluating behavioural aspects related to mobility, the size of the tanks should be adapted to the movement potential of the considered species, also adapting the bottom sediment type.

Together, our results highlight the importance of integrating behavioural specificities, life-history context, and species ecology into noise impact studies. Such integrative approaches are essential for drawing robust conclusions about the ecological effects of anthropogenic noise in marine ecosystems. Field and controlled experimental designs should be ideally combined to validate findings across different settings. While field-based experiments reveal potential noise-related impacts on animals' movement ecology within the living environment, laboratory studies allow for a more accurate characterization of the sound pressure levels that elicit the strongest behavioural responses. In this way, the scientific community will gain a deeper understanding of the behavioural ecology of noise-exposed species, supporting more effective management strategies and informed stakeholder actions regarding noise pollution. The study of the complex relationship between ambient soundscape and animal behaviour is now of a crucial importance in understanding the ecological impact of noise pollution in the ocean.

V. Underwater acoustics: a new sense for understanding the marine world

Until now, marine ecology has mainly described the underwater world from a biogeochemical point of view, neglecting its acoustic characteristics. Of the 2 000 000 species that inhabit the oceans, only a handful have been initially studied from an acoustic perspective, leaving all other species aside. In 1970, Roger Payne released his first album distributed to the general public, featuring the

songs of cetaceans in order to raise awareness about whaling. These songs had been widely known to sailors since time immemorial, who could hear them inside the hulls of their boats and mistook them for the songs of mermaids. The rest of marine biodiversity remained silent for centuries, and it is only recently that it has been given a voice thanks to growing interest in the underwater acoustic world.

To date, a great number of soniferous species have been identified in the marine habitat. Of the 33 462 considered species, Looby et al. (2023) identified 729 species and subspecies among marine mammals, other tetrapods, fish and invertebrates as producing active and/or passive sounds, and 21 911 other species considered likely to produce sounds based on assessed taxonomic relationships. In addition to recognising the growing importance of acoustic stimuli in intraspecific and/or interspecific relationships, geophonic sounds are increasingly recognised as important parameters in defining the relationship between organisms and their living environment (Farina et al., 2021). In this sense, acoustics can have a strong implication in defining the very basis of the marine ecology, potentially influencing every level of ocean ecosystems.

Just as sound influences the early larval stages of many marine invertebrates by affecting their overall fitness, sound may have an effect on the primary production of these environments ultimately affecting the entire ecological sphere of an ecosystem. In this regard, certain terrestrial plant species have been observed to have a close relationship with acoustics and sound, to such an extent that a new term has been proposed: *phytoacoustics* (Khait et al., 2019). As an example, the species *Oenothera drummondii* increases the sugar content of its nectar when it perceives vibrations produced by a nearby pollinating insect in order to increase its chances of pollination (Veits et al., 2018). *Pisum sativum* (the classic pea) has been observed to propel its roots towards a noisy source simulating a watercourse (Gagliano et al., 2017). To date, we still do not know the influence of the acoustic factor on primary aquatic production, but given the highly mechanical action of this stimulus (i.e., waterborn vibrations), it is possible to hypothesise a certain effect of sound waves on the unicellular structure of phytoplankton and, finally, to primary production.

Given the growing importance of acoustic parameters in the relationships between many biotic and abiotic components that make up the underwater and terrestrial environments, it is necessary for the natural sciences to rethink the way they observe (or listen to) their field of study. The ecology of a given ecosystem is possibly strongly linked to acoustic factors more than our auditory abilities have allowed us to realise since now, thus creating soniferous communities where the relationships between living and non-living entities are regulated, in great part, by sound.

Résumé de discussion en langue française

Cette thèse met en lumière plusieurs aspects comportementaux de deux espèces d'invertébrés marins — *Buccinum undatum* (un gastéropode) et *Cancer irroratus* (un crustacé malacostracé) — en explorant notamment leurs réponses face au bruit généré par le trafic maritime, à travers des approches expérimentales innovantes. De manière générale, les résultats soulignent le rôle critique des bruits anthropiques sous-marins dans l'altération de la mobilité des invertébrés benthiques vagiles, influençant ainsi leur comportement spatial et leur dispersion, avec de potentielles répercussions à l'échelle de l'environnement côtièr.

Bien qu'on ait largement étudié l'influence des facteurs abiotiques (lumière, température, salinité, oxygène) sur le comportement des invertébrés marins, l'importance du paysage sonore sous-marin reste encore sous-explorée. Or, des études récentes montrent que des signaux acoustiques peuvent induire des réponses comportementales cruciales, influençant la fitness individuelle.

Les deux espèces étudiées montrent des comportements spatiaux hautement spécialisés, adaptatifs, qui varient selon les saisons, et pour les crabes, même selon les moments de la journée (Chapitres 1 et 3). Ces stratégies de mobilité sont essentielles pour la recherche de nourriture, la reproduction, l'évitement des prédateurs et l'adaptation à l'hétérogénéité environnementale. Toutefois, le bruit anthropique — notamment le bruit chronique des navires — perturbe ces schémas naturels, réduisant la capacité de dispersion des individus et compromettant ainsi des fonctions biologiques et écologiques fondamentales liées au movement (Chapitres 2 et 3).

Implications potentielles sur la dynamique écologique

La dispersion, tant larvaire qu'adulte, est un trait biologique majeur façonnant la structure des populations d'invertébrés marins. Elle favorise le flux génétique, la connectivité et la colonisation d'habitats, contribuant ainsi à la résilience des écosystèmes côtiers. Toutefois, le bruit des navires peut affecter la morphologie, la physiologie et les stratégies comportementales des invertébrés à différents stades ontogéniques, ce qui risque de modifier la dynamique des populations locales et la structure des communautés et la résilience des écosystèmes.

Divers travaux montrent que certaines intensités de bruit anthropique (par exemple >140-150 dB re 1 µPa) peuvent retarder la métamorphose, augmenter les dépenses métaboliques et réduire la survie larvaire, entraînant des fixations précipitées, parfois dans des habitats défavorables, et affectant la biodiversité locale. Par exemple, des études dans l'archipel de Saint-Pierre-et-Miquelon ont révélé une baisse de la diversité et de l'équité spécifique des communautés larvaires exposées au bruit.

Chez les formes adultes, la mobilité est également un trait écologique fondamental, crucial pour la connectivité démographique et le maintien des populations. De nombreux exemples montrent comment les comportements de déplacement influencent la structuration des populations benthiques. S'ajoutant aux études déjà présentes en litterature, les données sur *B. undatum* et *C. irroratus* confirment que l'exposition au bruit perturbe la mobilité des formes adultes, réduisant leur dispersion et compromettant ainsi leur fitness individuelle. À long terme, cela peut nuire à la connectivité entre populations et à la structure des communautés locales.

En conclusion, ces travaux démontrent que les perturbations acoustiques d'origine anthropique, tant au stade larvaire qu'adulte, peuvent altérer profondément l'écologie du mouvement des invertébrés marins, compromettant la persistance, la stabilité et la résilience des populations et des communautés benthiques dans les zones côtières soumises à un trafic maritime intense.

Le cas des nouvelles routes commerciales arctiques

Dans un contexte écologique, l'ouverture de nouvelles voies commerciales dans l'Arctique suscite une inquiétude croissante. La fonte saisonnière de la glace permet désormais à davantage de navires de transiter par le passage du Nord-Ouest canadien et la Route maritime du Nord (NSR) en Russie. Le trafic sur la NSR est passé d'environ 30 transits en 2011 à 153 en juin 2021, ce qui transforme profondément le paysage sonore marin de ces zones jadis quasi intactes.

Des études montrent que les passages de navires, notamment des brise-glaces et cargos, augmentent les niveaux SPLrms de 15 à 30 dB jusqu'à plus de 50 km, créant des « hotspots sonores » susceptibles de perturber durablement la faune locale. Dans l'archipel Saint-Pierre-et-Miquelon, un cargo a généré 174 dB re 1 μPa à 350 m. Dans l'Arctique, le bruit d'un navire a fait passer le SPLrms de 74 à 131 dB dans une baie entière. Si le trafic augmente, les périodes sans bruit de navire pourraient chuter de 68-90 % à seulement 56-66 % du temps, altérant radicalement l'environnement acoustique.

Ces niveaux sonores sont comparables à ceux qui déclenchent des réactions comportementales documentées chez les mammifères marins, poissons et invertébrés, pouvant réduire leur aptitude individuelle et engendrer des effets en cascade sur l'écosystème locales. Pour confirmer ces hypothèses, des programmes de surveillance à long terme des communautés benthiques sont nécessaires, ainsi que des études expérimentales mieux adaptées pour explorer les effets du bruit à long terme et la possibilité d'acclimatation.

Amméliorations pour les recherches futures

Considérer l'acclimatation à l'anthropophonie sur le long terme

L'un des principaux défis pour évaluer les conséquences écologiques de l'anthropophonie est la possibilité d'une acclimatation des animaux au bruit. À ce jour, ce phénomène reste peu étudié, la plupart des recherches portant sur des expositions de courte durée. Pourtant, l'acclimatation pourrait modifier profondément la relation entre bruit et comportement animal, influençant ainsi les dynamiques écologiques à long terme. Wilson et al. (2020) ont montré que les réponses animales varient selon la durée et l'intensité du changement environnemental. Il est donc essentiel de mener des recherches sur des périodes plus longues pour comprendre ces effets.

Adapter les protocoles expérimentaux aux comportements spécifiques des espèces

Dans l'écologie comportementale, il est nécessaire de concevoir des expériences tenant compte des particularités comportementales, des cycles biologiques et des rythmes quotidiens et saisonniers des espèces. Dans les chapitres 2 et 3, les espèces étudiées ont montré des changements de mobilité sous bruit, souvent après un délai, avec des effets marqués en fin de printemps et en été, liés à leurs périodes reproductives. Beaucoup d'études négligent ces complexités, risquant d'interpréter des artefacts comme des réponses comportamentales. Les futures recherches doivent donc adapter leurs protocoles aux spécificités des espèces.

Combiner études en milieu naturel et en laboratoire

Les études de terrain permettent d'observer les comportements dans leur contexte naturel. La télémétrie acoustique, utilisée ici pour la première fois sur des invertébrés (Chapitre 2), a montré son efficacité pour suivre les réactions comportementales au bruit sur plusieurs jours. Pour être fiables, ces études nécessitent un temps d'acclimatation post-marquage et des dispositifs adaptés à la mobilité des espèces étudiées. Parallèlement, les expériences en laboratoire permettent de tester les réponses à des niveaux sonores précis, même si elles comportent des biais liés au retrait du milieu naturel. Il est donc essentiel d'assurer un temps d'acclimatation suffisant, de contrôler les niveaux sonores ambiants et d'adapter la taille des bacs et le substrat aux espèces. L'intégration des spécificités comportementales, du contexte biologique et des approches expérimentales variées est indispensable pour tirer des conclusions solides sur les effets écologiques du bruit. Quand possible, les études sur le terrain et en laboratoire devraient être combinées pour valider les résultats. Une telle démarche permettra de mieux comprendre l'écologie comportementale des espèces exposées au bruit et d'orienter les stratégies de gestion face à la pollution sonore des océans.

L'acoustique sous-marine : un nouveau sens pour explorer le monde marin

Jusqu'à présent, l'écologie marine a principalement abordé le monde sous-marin sous un angle biogéochimique, négligeant largement sa dimension acoustique. Sur les 2 millions d'espèces marines estimées, seule une minorité a été étudiée du point de vue sonore. Pourtant, depuis les années 1970, grâce notamment aux travaux de Roger Payne sur les chants de cétacés, l'intérêt pour les paysages sonores marins ne cesse de croître. Aujourd'hui, un nombre croissant d'espèces sonifères sont reconnues : selon Looby et al. (2023), 729 espèces produisent des sons de façon active ou passive, et plus de 21 000 autres sont susceptibles d'en produire.

Au-delà de la communication inter- ou intraspécifique, les sons naturels de l'environnement (géophonie) jouent un rôle essentiel dans la relation des organismes à leur habitat. L'acoustique pourrait ainsi contribuer à redéfinir les bases mêmes de l'écologie des écosystèmes marins.

Par ailleurs, des recherches en milieu terrestre ont révélé que certaines plantes répondent aux stimuli sonores, donnant naissance au concept de *phytoacoustique*. On a notamment observé qu'Oenothera drummondii augmente la teneur en sucre de son nectar en réponse aux vibrations d'un insecte pollinisateur, et que Pisum sativum dirige ses racines vers une source simulant un cours d'eau. Bien que les effets du son sur la production primaire marine restent encore méconnus, son action mécanique sur le phytoplancton pourrait en faire un facteur clé dans la dynamique des écosystèmes aquatiques.

Face à ces constats, il devient nécessaire que les sciences naturelles reconsidèrent leur manière d'étudier les écosystèmes, en intégrant pleinement la dimension acoustique. L'écologie des communautés biotiques pourrait en effet être bien plus liée aux paramètres sonores que ce que nos sens humains nous ont jusqu'à présent permis de percevoir.

Annexes

Fig. S1: Tracking locations of tag n° 72 before filtration (blue), after filtration according to HPE values (orange) and after filtration with behavioural filter (green).

Fig S2: Distribution of marginal residuals to verify that the assumptions of normality of the model related to the standardized speed [1] are met. Of note, the assumption of normality of the present model are respected.

Fig S3: Distribution of marginal residuals to verify that the assumptions of normality of the model related to the HUP [2] are met. Of note, the assumption of normality of the present model are respected. HUP was log-transformed to approximate normality of residuals.

Fig. S4: Pairs plot to look at covariation between the variables. As the coefficient of covariation never exceeded a value of 0.6, all fixed factors were retained in the models.
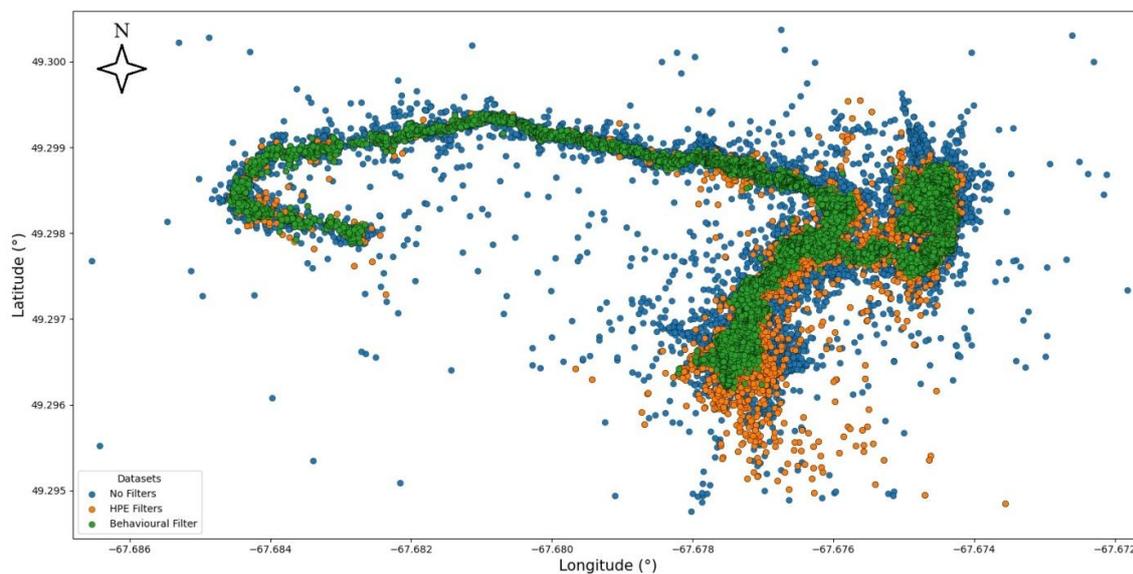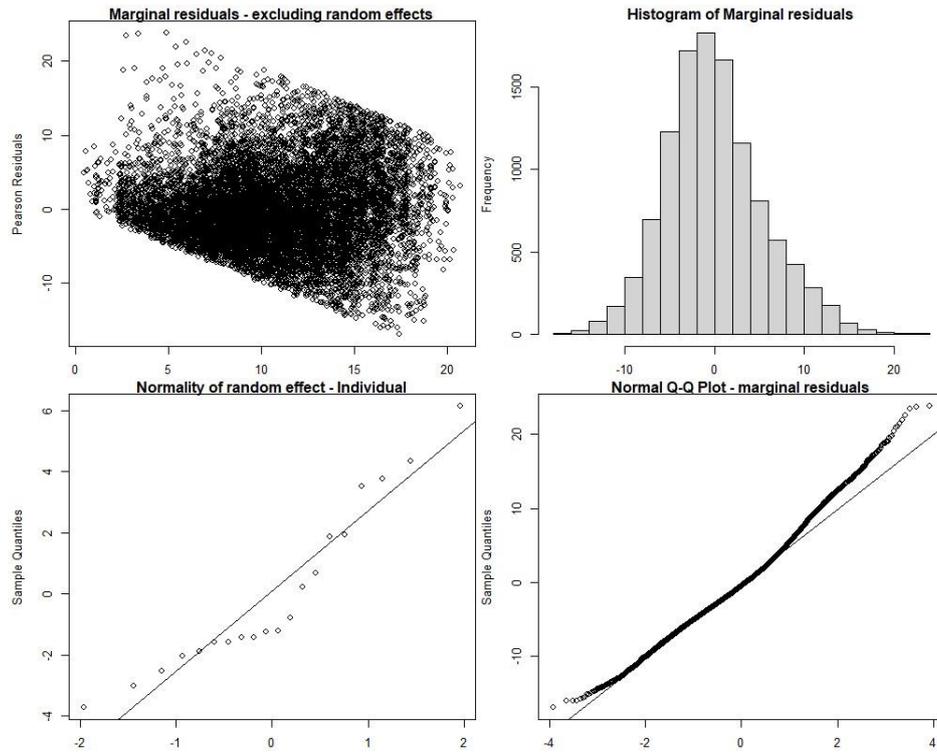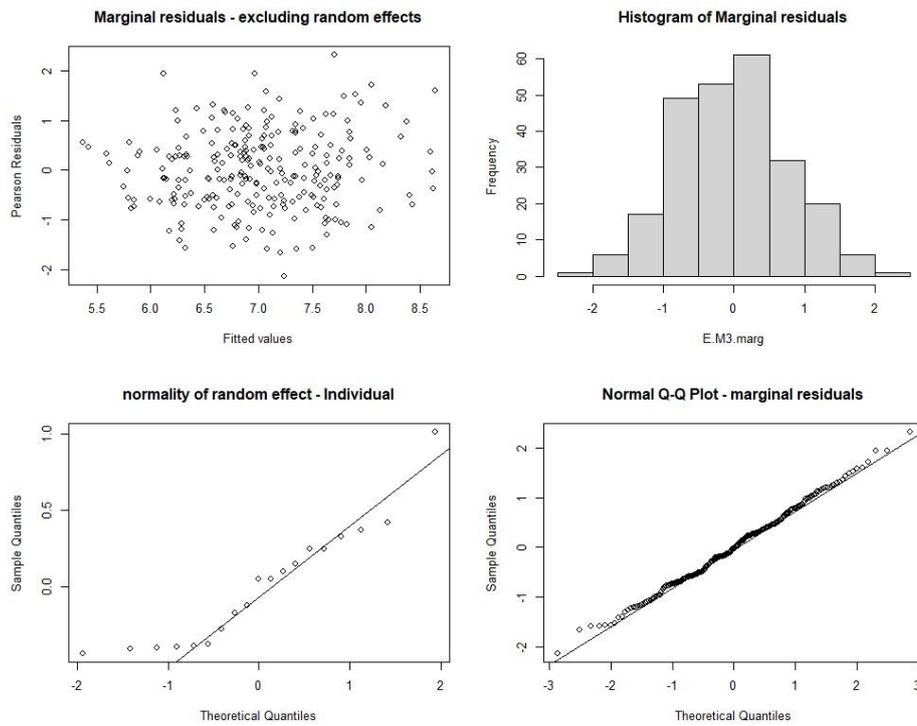

Figure S1
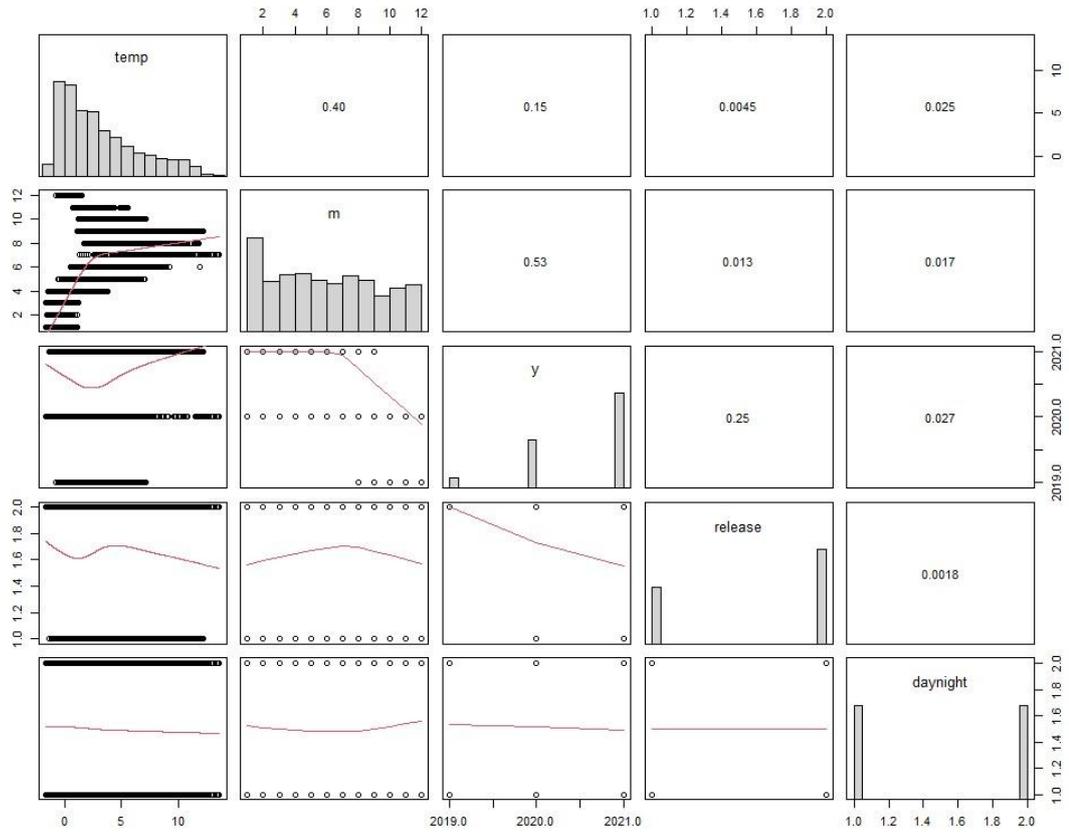
Figure S2

Figure S3

Figure S4

Chapter 2

Assessment of the impact of acoustic telemetry tags on waved whelks' behaviour

Because equipping individuals with acoustic telemetry tags could generate a potential bias on the whelk behaviour, we performed one experiment to assess the potential influence of such V9-x VEMCO. Individuals used in this experience were from the same batch as those used in the main laboratory experiment of the referred study. Selected whelks were subsequently separated into three distinct groups according to specific tagging conditions: I) with V9-x VEMCO tag attached to the shell, II) with false tag attached to the shell and III) without any tag. The false tags were made of plastic with the same size and density as the original V9-x tags in order to assess a possible effect caused by acoustic pulse (the "pings") typical of acoustic telemetry tags. Tags were attached to individuals using the same procedure described in the main text during the field experiment.

The experiment consisted of deploying 5 individuals of each group in front to a GoPro into a small basin (100x65x40 cm) with circulating water. Individuals were let 30 min to acclimatise to the new basin. Subsequently, whelks were manually overturned and the time necessary to return right on their foot was calculated. The experiment duration was of 1h after manual overturning for each trial. Individuals which were not able to return to their foot during the experiment were not retained for the time analysis, but still retained in the count of individuals not able to overturn.

There was no variation between the three different tagging conditions (PERMANOVA, pseudo-F = 0.568, p = 0.676; Fig. S4). All whelks employed a mean of 25.9 ± 8.3 s to return right on their foot after handling. Among all tested whelks, 3 individuals without tag remained overturned during the whole 1h experimental time, while 2 individuals with false tags and 2 individuals with V9-x tags did not return right on their foot.

Fig. S4: time employed by whelks to return right on their foot after manual overturning according to three different tagging conditions.

Fig. S5: Acoustic spectra (0–2000 Hz) of the ambient noise level (blue) and the shipping noise level (red) recorded at Site A. The x-axis is in logarithmic scale. PSD: power spectral density.

Fig. S6: Receivers were positioned 1.5 m above the seabed by a 50 kg mooring connected with a surface buoy over the sea surface

Fig. S7: Innovasea tagged whelk before release at the Miquelon Bay during the fieldwork. Tags employed in the supplementary materials were attached in the same way.

Fig. S8: accelerometer tagged whelk before release in the pool during the laboratory experiment. Lego® were used to quickly fix the accelerometers to the shell before each trial.

Fig. S9: Acoustic spectra (0–10 000 Hz) of the ambient noise level (8 min each) recorded in control conditions (blue) and the emitted shipping noise levels recorded in low (green), medium (black) and high (red) noisy conditions. The x-axis is in logarithmic scale. PSD: power spectral density.

Fig. S10: acoustic map of the experimental tank showing the relative sound pressure levels at different distances from the speaker (white box) during A) high, B) medium and C) low shipping noise level. Although noise emissions were not at the same level of the main experiment due to change in the amplifier, note that the propagation of noise is homogenous throughout the whole tank with a transmission loss of approximately 10 dB re 1 µPa between the emission zone and the release area at 210 cm from of the speaker.

Fig. S11: Distribution of marginal residuals to verify that the assumption of normality of the linearized mixed model related to the daily total covered distance [1] were met.

Fig. S12: Distribution of marginal residuals to verify that the assumption of normality of the linearized mixed model related to the daily speed [2] were met.

Fig. S13: Distribution of marginal residuals to verify that the assumption of normality of the linearized mixed model related to the daily net covered distance [3] were met.

Fig. S14: Distribution of marginal residuals to verify that the assumption of normality of the linearized mixed model related to the daily step length [4] were met.

Fig. S15: Distribution of marginal residuals to verify that the assumption of normality of the linearized mixed model related to the daily habitat usage potential (HUP) [5] were met.

Figure S16: Predicted values of A) daily covered distance, B) speed, C) daily net covered distance, D) daily HUP and E) step lengths according to the applied model over the whole 10 days study period. Handling effects on tagged animals were suspected during the first 3 days of experimentation. We choose to perform statistical comparison over the lasts 7 days, because clear mobility trends only appeared after day 3 at both sites. Thus, statistical comparison between sites was performed only from day 4 (but see Tab. S1).
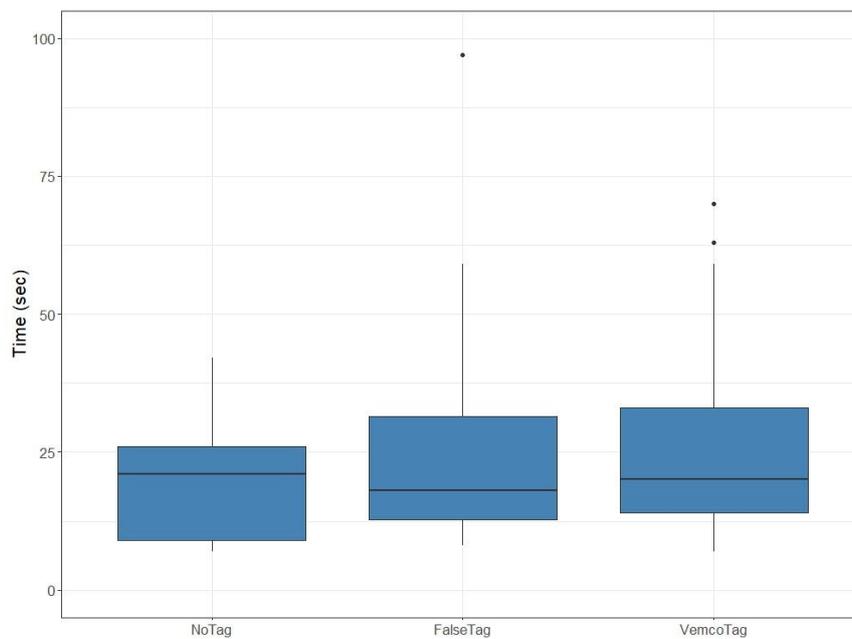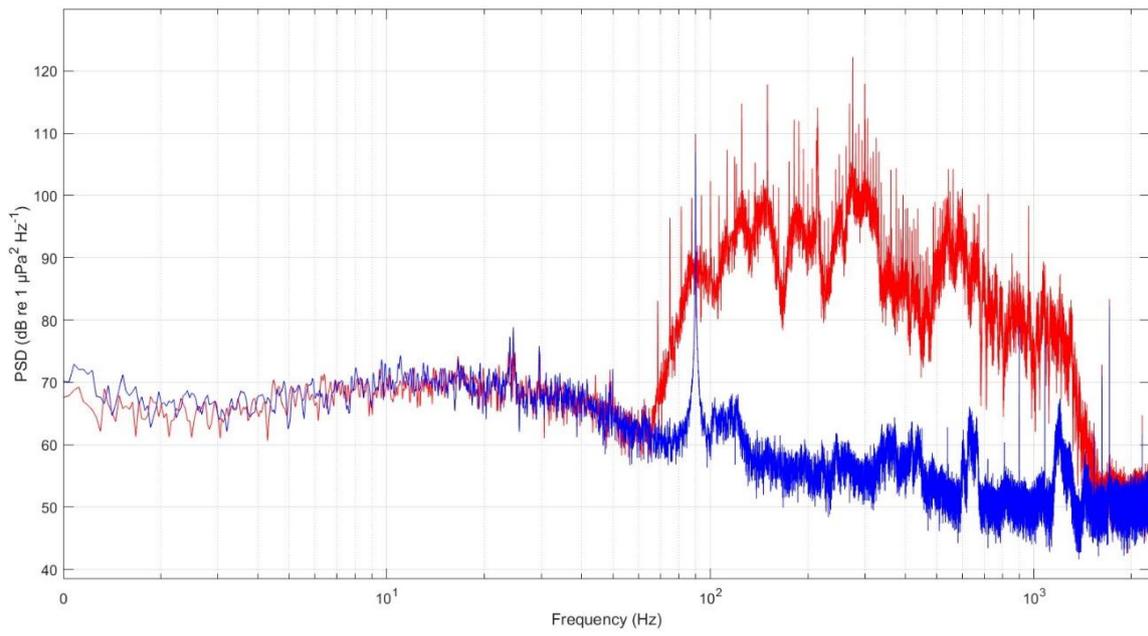

Figure S4

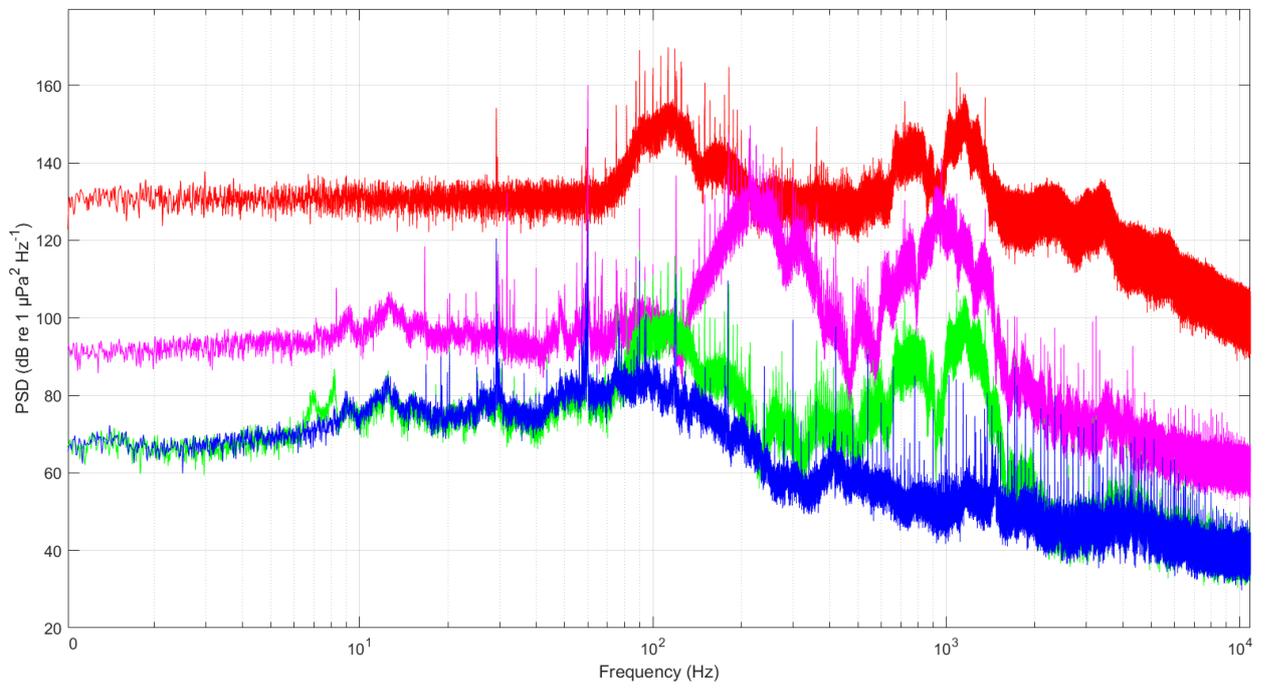Figure S5

Figure S6

Figure S7

Figure S8

Figure S9
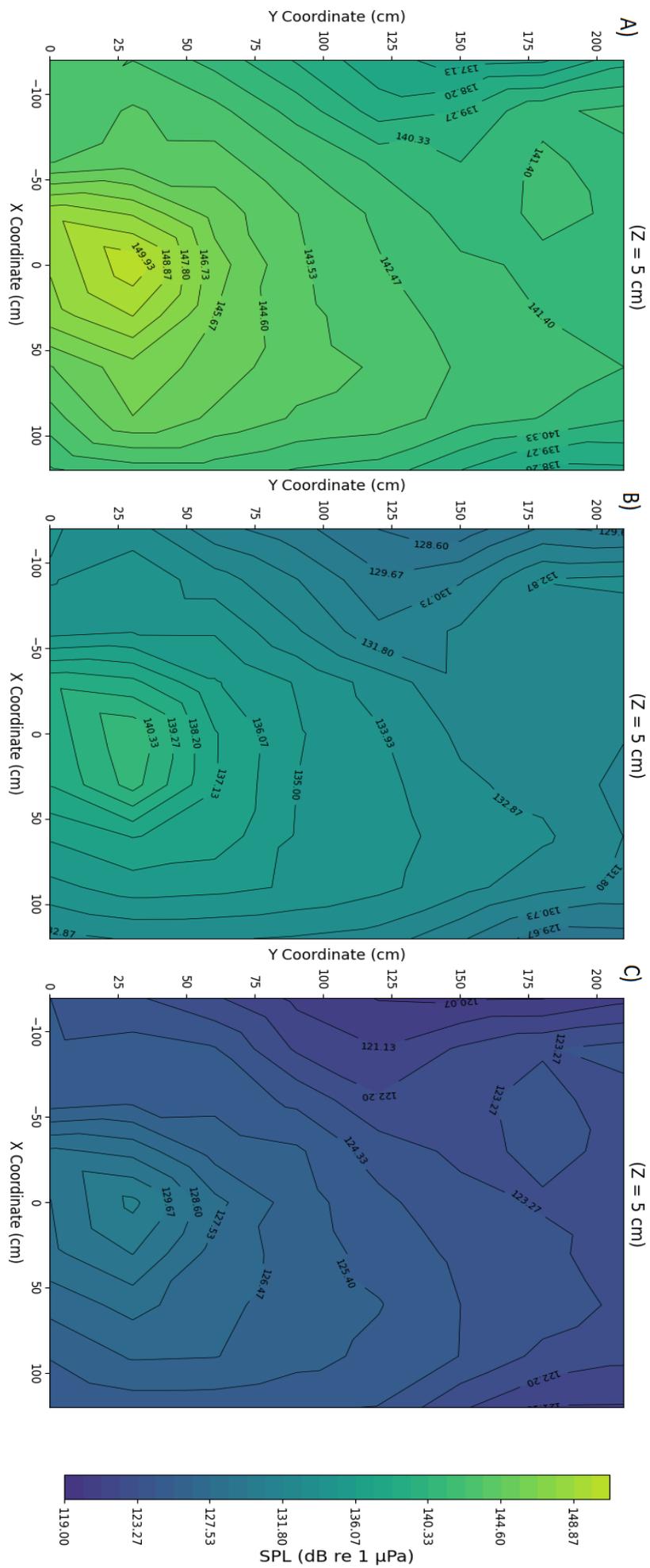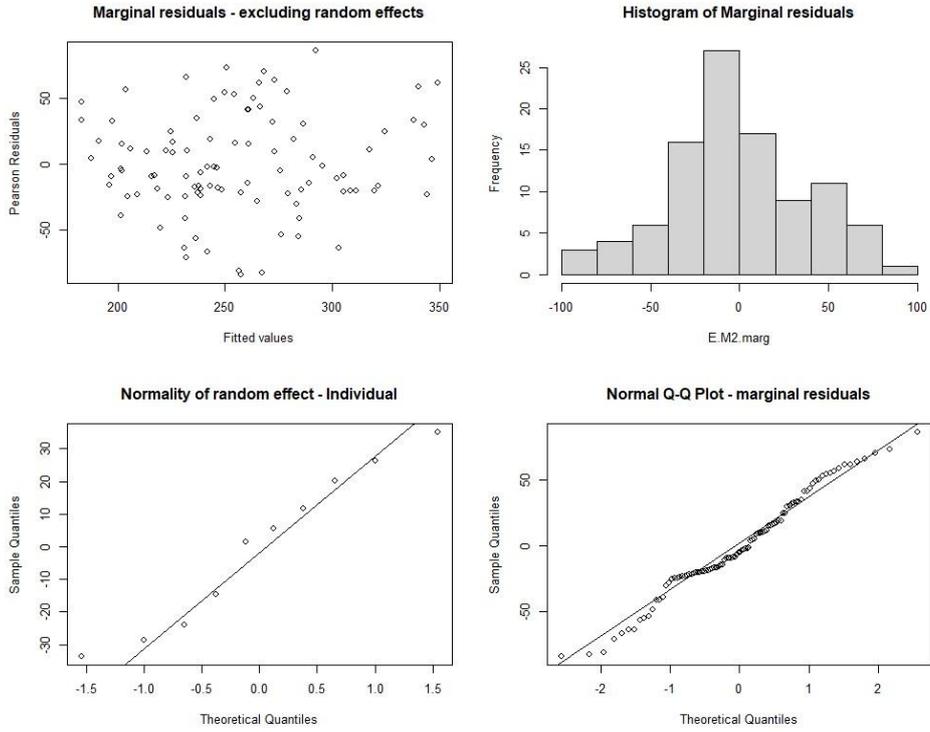
Figure S10

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Figure S11

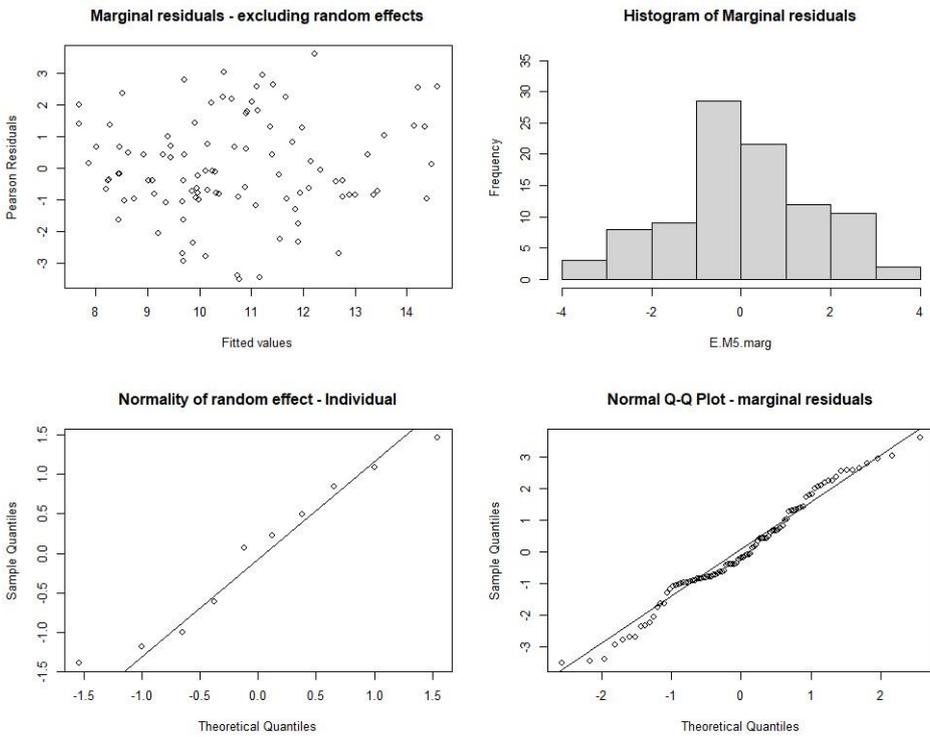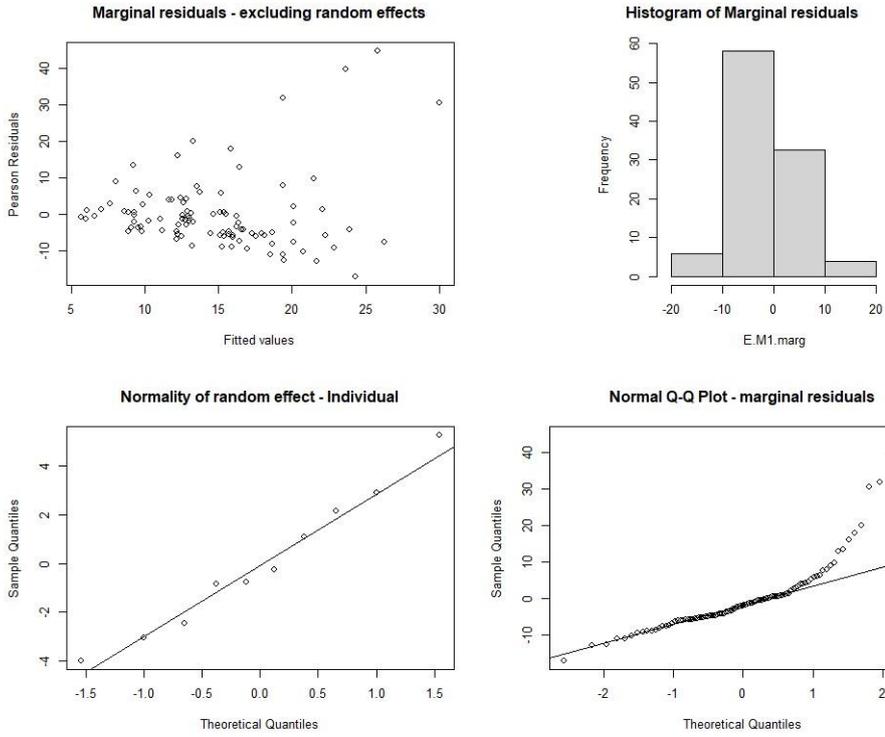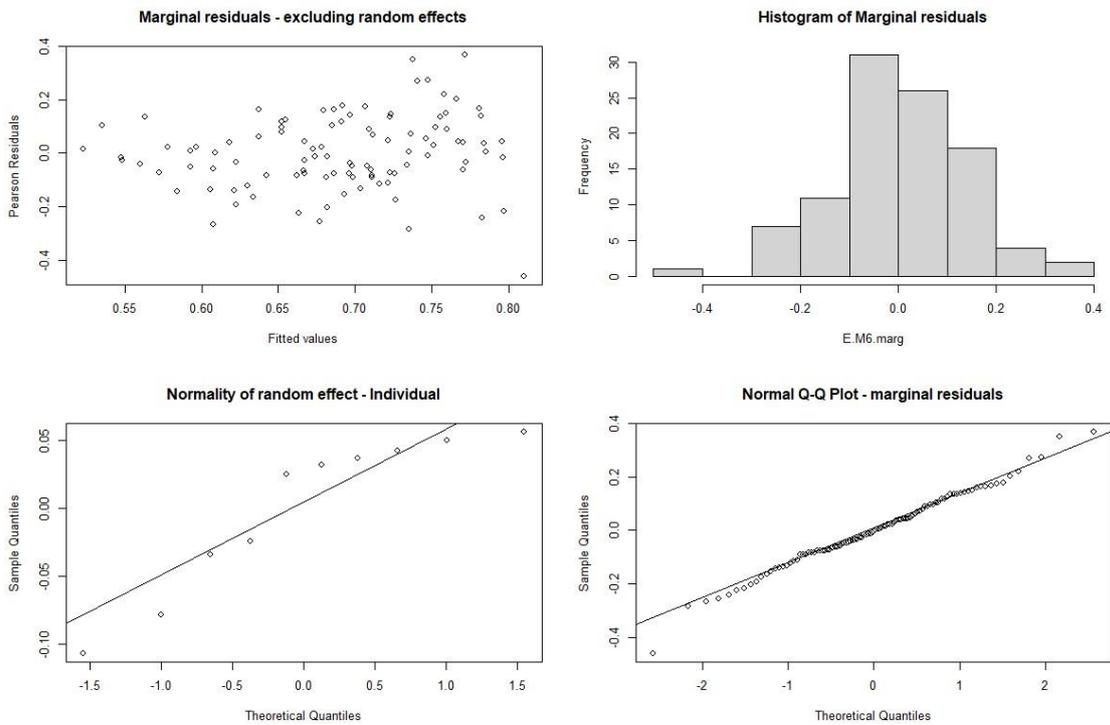

Figrue S12

Figure S13

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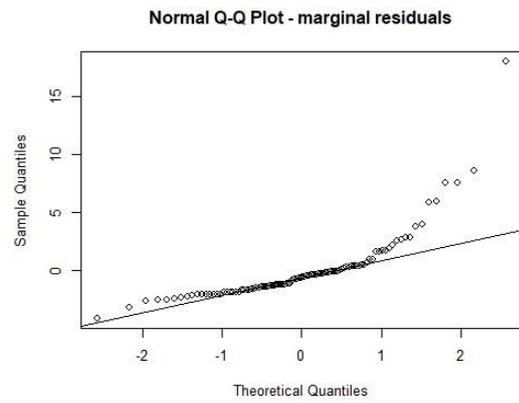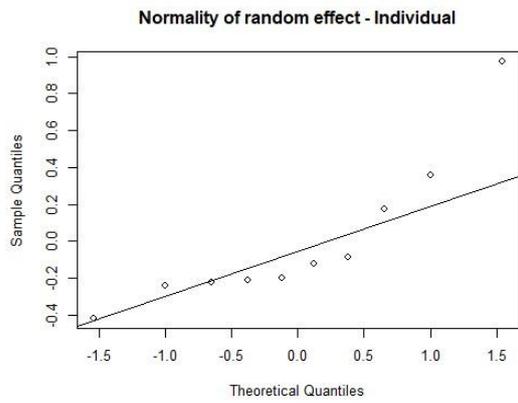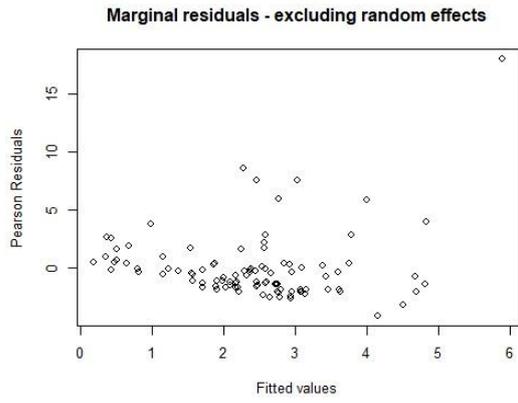
Figure S15

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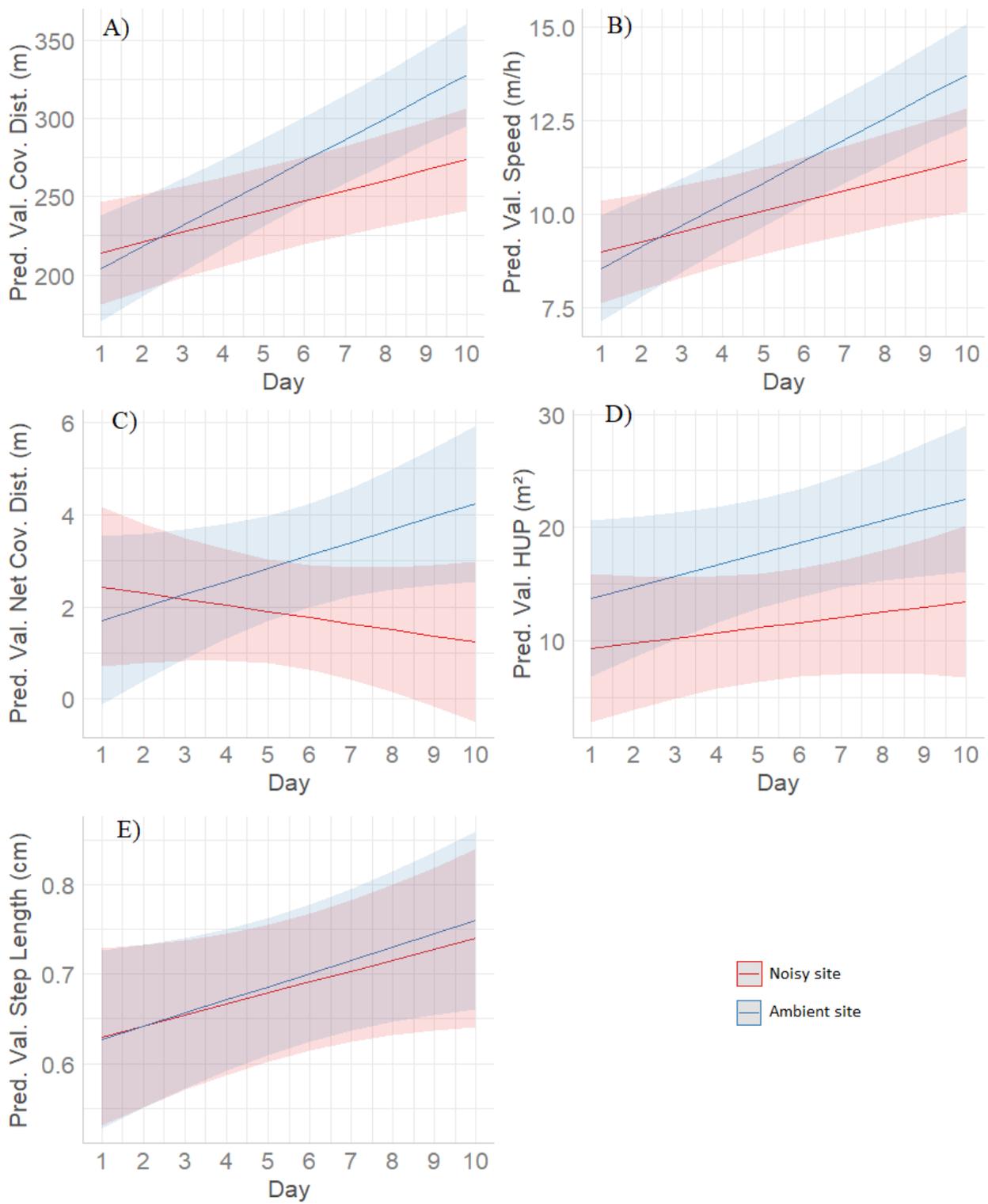
Figure S16

Table S1: Outputs from linear mixed models considering the influence of different fixed factors on the considered behavioural parameters over the whole 10 days study period. Significant effect (P-value < 0.05) are indicated in bold. Of interest, the significant effect of the interaction between Site and Day for several behavioural parameters, highlighting considerable differences between sites on mobility trends over following days. This fact was then confirmed by the significant effect of Site over the last 7 monitoring days (see Tab. 3 in the main text).

Daily Cov. Distance [1]	β	*SE*	χ^2	*Df*	*P-value*
Site	12.14	18.18	1.4	1	0.115
Day	10.17	1.42	50.55	1	**< 0.001**
Site : Day	5.05	1.98	6.49	1	**0.014**
Speed [2]	β	*SE*	χ^2	*Df*	*P-value*
Site	0.52	0.76	1.38	1	0.118
Day	0.42	0.06	49.81	1	**< 0.001**
Site : Day	0.21	0.08	6.55	1	**0.018**
Daily Net Cov. Distance [3]	β	*SE*	χ^2	*Df*	*P-value*
Site	0.81	1.04	2.16	1	0.141
Day	0.07	0.11	0.41	1	0.52
Site : Day	0.29	0.15	3.84	1	**0.041**
Step Length [4]	β	*SE*	χ^2	*Df*	*P-value*
Site	0.02	0.06	0.02	1	0.87
Day	0.01	0.01	7.11	1	**0.007**
Site : Day	0.02	0.01	0.06	1	0.8
HUP [5]	β	*SE*	χ^2	*Df*	*P-value*
Site	2.75	3.87	3.84	1	**0.046**
Day	0.72	0.37	3.7	1	0.052
Site : Day	0.37	0.52	0.51	1	0.475

Fig. S17: video recording related data showing the total covered distance (bars) and mean speed (lines) over different period of the day, seasons and audio conditions from Day1 to Day2. Night periods were not analyzed by video recordings. Errors bars indicate the standard error of measure.

Fig. S18: accelerometry related data showing the overall dynamic body acceleration (ODBA; bars) and moving time (lines) over different period of the day, seasons and audio conditions from Day1 to Day2. Asterisk shows statistically significant difference between Noise conditions. Darker backgrounds identify night periods. Errors bars indicate the standard error of measure.
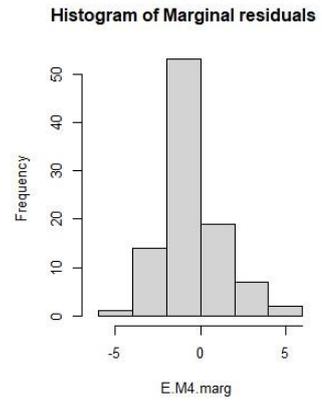

Figure S17

Figure S18

Tab. S2: Mean water chemical and physical parameters recorded at Day 1 (start) and Day 2 (end) within the experimental tank to assess eventual environmental changes during each trial. In Autumn, only water temperature and salinity were recorded.

Season	Day	Alk (mg/L)	pH	Phos (mg/L)	Ca (mg/L)	Mg (mg/L)	Ammo (mg/L)	Nitrite (mg/L)	Nitrate (mg/L)	O2 % Saturation	T °C	Sal. psu
Spring	Day1	106.75	7.72	0.325	354.37	966.75	0.1	0	1.87	88.83	11.4	26.18
	Day2	104.87	7.78	0.3	358.25	972.87	0.08	0	1.89	87.85	11.5	26.02
Autumn	Day1	-	-	-	-	-	-	-	-	-	10.2	27.56
	Day2	-	-	-	-	-	-	-	-	-	10.4	27.62

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Titre: Impacts acoustiques du trafic maritime sur les invertébrés marins benthiques vagiles des zones côtières subarctiques

Mots clés: bruit maritime, comportement, *Buccinum undatum*, *Cancer irroratus,* biotelemetrie

L'anthropophonie s'impose comme un facteur majeur de modification comportementale chez la faune marine, y compris les invertébrés. Parmi d'autres, le trafic naval intense altère profondément le comportement de nombreuses espèces, menaçant leurs rôles écologiques. Ce projet doctoral vise à évaluer l'effet du bruit maritime via trois volets portant sur deux invertébrés benthiques vagiles : *Buccinum undatum* et *Cancer irroratus*, étudiés in situ et en laboratoire sous des expositions prolongées. Ce travail doctoral a permis de mettre en évidence l'importance des cycles saisonniers dans le comportement spatial de *B. undatum*, grâce à un suivi pluriannuel par télémétrie acoustique qui a révélé une mobilité restreinte limitant la dispersion et la connectivité entre populations, augmentant ainsi la vulnérabilité à la surpêche locale. En s'appuyant sur ces observations, nous avons démontré que le bruit des navires réduit significativement la capacité locomotrice et le potentiel de dispersion de cette espèce, à la fois par des expérimentations in situ dans la Baie de Miquelon et en conditions contrôlées en laboratoire. Concernant *C. irroratus*, nous avons montré, grâce à un protocole intégrant ses rythmes circadiens et saisonniers, que l'activité des crabes est également affectée par le bruit maritime, mais de façon saisonnièrement modulée, avec un impact significatif uniquement la nuit au printemps. Ces travaux démontrent que l'exposition chronique au bruit maritime perturbe les comportements locomoteurs de ces invertébrés, compromettant leur dispersion, réduisant la connectivité des populations et potentiellement pouvant altérer la structure des communautés à long terme.

Title: Acoustic impacts of maritime traffic on mobile benthic vagile marine invertebrates in subarctic coastal areas

Keywords: Shipping noise, behaviour, *Buccinum undatum*, *Cancer irroratus,* biotelemetry

Anthropophony is emerging as a major factor in behavioral change among marine fauna, including invertebrates. Among other factors, heavy shipping traffic profoundly alters the behavior of many species, threatening their ecological roles. This doctoral project aims to assess the effect of marine noise through three components focusing on two benthic invertebrates: Buccinum undatum and Cancer irroratus, studied in situ and in the laboratory under prolonged exposure. This doctoral work has highlighted the importance of seasonal cycles in the spatial behavior of B. undatum, thanks to multi-year monitoring using acoustic telemetry, which revealed restricted mobility limiting dispersion and connectivity between populations, thereby increasing vulnerability to local overfishing. Based on these observations, we demonstrated that ship noise significantly reduces the locomotor capacity and dispersal potential of this species, both through in situ experiments in Miquelon Bay and under controlled laboratory conditions. With regard to C. irroratus, we showed, using a protocol that integrated its circadian and seasonal rhythms, that crab activity is also affected by marine noise, but in a seasonally modulated way, with a significant impact only at night in the spring. This work demonstrates that chronic exposure to marine noise disrupts the locomotor behavior of these invertebrates, compromising their dispersal, reducing population connectivity, and potentially altering community structure over the long term.