Université du Québec à Rimouski

L'impact du bruit du trafic maritime sur la dynamique et le recrutement précoce des invertébrés benthiques dans un environnement côtier de haute latitude

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AVANT-PROPOS

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ABSTRACT

Anthropogenic sounds, such as vessel noise, are increasingly common in coastal environments, and are recognized as an emerging marine stressor. Vessels generate noise through their propellers, motors and generators. The movement of propellers creates bubbles that burst, producing loud sounds. Inside the motor, fuel combustion causes small explosions in the cylinders generating steady noise, while additional noises arise from turning gears and other mechanical parts that transfer power. Although the effects of such noise on the behaviour and fitness of benthic invertebrates have been demonstrated in controlled settings, their ecological impacts in the field remain underexplored. Key processes like settlement and metamorphosis, which drive population dynamics and support biodiversity, may be disrupted by noise exposure as these organisms use sounds to detect a substrate. Moreover, vessel noise can propagate over long distances and overlaps with the hearing ranges of many taxa, including mollusks.

This thesis investigated the ecological effects of vessel noise on early life stages and population dynamics of benthic invertebrates, with a focus on settlement, metamorphosis and community structure. This thesis is composed of three research papers, corresponding to two *in situ* experiments: a short-term study (Chapter I) and a long-term study (Chapter II and III). The studied area included two subarctic sites, Saint-Pierre and Miquelon, characterized by distinct levels of maritime traffic. In the first study, trial was conducted in Miquelon, a pristine site with very limited maritime traffic. Artificial collectors were deployed at a noisy site, where they exposed to two vessel noise intensities: high and moderate (128 dB and at 116 dB at 25m and 175m). A control site with ambient noise (106 dB) was also included. Deployment followed a 3-day cycle, repeated over 3 weeks. Environmental conditions and acoustic characterization were monitored daily or weekly. Subsequently, a four-month field study (studies 2 and 3) was conducted at both Miquelon and Saint-Pierre, the latter being considered an anthropic site situated near an industrial harbor. Collectors were deployed along a vessel noise gradient (SPLs): high (137dB at 25m), moderate (120 dB at 175m), and ambient noise (106 dB at 890m). Environmental variables and acoustic conditions were monitored daily or monthly.

An integrative experimental approach combined with traditional and cutting-edge methodologies: the manipulation of vessel noise using an underwater speaker, taxonomic identification and diversity indices to evaluate species abundance, composition, diversity and evenness, shell morphometry to measure veliger and metamorphosis sizes as indicators of growth and developmental delays, and total length to detect drifters from secondary migrations and analyse population distribution, biochemical techniques, such fatty acid profiling via gas chromatography, and cell size-class abundance through flow cytometry, to characterize the trophic environment, and deployment of environmental sensors such as temperature, current and tides.

The first study (Chapter I) evaluated how vessel noise at high-moderate intensities influences settlement and metamorphosis of *Mytilus edulis* in the short term. We proposed that collectors nearer the playback source (high intensity) would exhibit high settlement rates, consistent with earlier patterns under laboratory conditions. However, no significant differences in settlement rates were found between control and noisy sites, likely due to a poor recruitment season. Nevertheless, post-larval abundance and successful metamorphosis were significantly reduced in the noisy site, supporting the view that anthropogenic noise disrupts establishment during critical early life stages. Despite observing an increase in post-settlers at both sites, we determined that a higher increase of drifters in the presence of vessel noise.

In the second study (Chapter II), we assessed the effects of vessel noise playback on *Mytilus* spp. larval development (size at metamorphosis, total length) and cohorts' structure along a gradient for 4 months. We tested two hypotheses: (1) that larval size-class distribution and cohort structure differ across noise intensities (SPLs, high 137 dB, moderate 120 dB and ambient noise 106 dB); and (2) that larvae exposed to high-moderate SPLs delay metamorphosis, resulting in increased prodissoconch II length. Mussel larvae from the second *in situ* trial were analyzed using shell morphometrics (size at metamorphosis, total length and cohort composition), Gaussian Mixture Model and Earth Mover Distance (EMD) to evaluate influence of sound exposure on larval size and cohort distribution. Results showed that while primary attachment and metamorphosis were unaffected across SPLs (106 – 153 dB), secondary attachment - a proxy for post-metamorphic drift - increased under moderate noise. Recruits > 2mm were more prevalent under these moderate vessel and ambient noise, whereas high noise in both pristine and anthropized sites reduced cohort numbers and recruit establishment.

Finally, in the third study (Chapter III), we examined the effects of vessel noise gradients on community structure and early recruitment in five dominant biological models, including gastropods and bivalves over 4 months. We hypothesized that invertebrate diversity and early recruitment decline with proximity of settlement collectors close to the noise source. While physical-trophic variables remained homogeneous across sites, sound profiles differed substantially: the pristine site experienced only vessel noise (SPLs < 140 dB re 1 μ Pa, SELs < 140 dB re 1 μ Pa^2.s), while the anthropized was exposed to both vessel and pile driving noise (SPLs > 140 dB re 1 μ Pa and SELs > 140 dB re 1 μ Pa^2.s). As hypothesized, the pristine site and anthropized sites showed variation on species diversity and evenness across distances and months, with a clear negative effect at stations near the noise. Species-specific early recruitment patterns demonstrated that sound levels (< and > 140 dB) altered population metrics and shifted species compositions, implying that this acoustic disturbance can lead to ecological restructuring.

Collectively, these studies offer field-based evidence that anthropogenic noise alters benthic invertebrate communities by disrupting early recruitment processes and modifying cohort structure. These findings underscore the ecological risks of noise pollution in subarctic coastal habitats and highlight the vulnerability of marine invertebrates to noise-induced stress. Observed changes in species composition, larval development, and secondary settlement behaviour call for urgent attention to noise regulation. Despite being a first study *in situ* with limited replication, we recommend that sound exposure thresholds not exceed 140 dB re 1 Pa^2.s to protect bentho-pelagic coupling and preserve diversity of bentho-pelagic communities.

This threshold should be considered preliminary, providing a start point for future experimental trials. Further work should aim to validate these levels under controlled conditions and across different species and life stages. Parallel studies could examine the effects of noise on secondary migrations and if noise might trigger a metabolic stress as in post-larvae. It would be interesting to couple multiple environmental stressors to contextualize what organisms experience *in situ*.

Keywords: anthropogenic noise, marine invertebrates, early recruitment, blue mussel, settlement behaviour, vessel noise, ecological impacts, larval drift.

RÉSUMÉ

Les sons d’origine anthropique, tels que le bruit généré par navires, sont de plus en plus fréquents dans les milieux côtiers et sont désormais reconnus comme un facteur de stress émergent pour les écosystèmes marins. Les navires produisent du bruit principalement par leurs hélices, leurs moteurs et leurs génératrices. Le mouvement des hélices entraîne la formation des bulles qui éclatent et génèrent des sons intenses. A l’intérieur du moteur, la combustion du carburant provoque de petites explosions dans les cylindres, produisant un bruit continu, tandis que d’autres composantes mécaniques qui transmettent la puissance.

Bien que les effets de ces bruits sur le comportement et la condition physiologique des invertébrés benthiques aient été démontrés en conditions contrôlées, leurs répercussions écologiques *in situ* demeurent peu documentées. Des processus clés, tels que la colonisation et la métamorphose - qui déterminent la dynamique des populations et contribuent au maintien de la biodiversité - peuvent être perturbés par l'exposition au bruit, puisque ces organismes utilisent les signaux acoustiques pour repérer un substrat approprié. De plus, le bruit des navires peut se propager sur de longues distances et chevaucher les plages auditives de nombreux taxons, y compris les mollusques.

Cette thèse a étudié les effets écologiques du bruit des navires sur les premiers stades de vie et la dynamique des populations d'invertébrés benthiques, en mettant l'accent sur la colonisation, la métamorphose et la structure des communautés. Cette thèse est composée de trois articles de recherche, correspondant à deux expériences *in situ* : une étude à court terme (chapitre I) et une étude à long terme (chapitres II et III). La zone étudiée comprenait deux sites subarctiques, Saint-Pierre et Miquelon, caractérisés par des niveaux de trafic maritime distincts. Dans la première étude, l'essai a été mené à Miquelon, un site vierge où le trafic maritime est très limité. Des collecteurs artificiels ont été déployés sur un site bruyant, où ils ont été exposés à deux intensités de bruit des navires : élevée et modérée (128 dB et 116 dB à 25 m et 175 m). Un site témoin avec un bruit ambiant (106 dB) a également été inclus. Le déploiement a suivi un cycle de trois jours, répété pendant trois semaines. Les conditions environnementales et la caractérisation acoustique ont été surveillées quotidiennement ou hebdomadairement. Par la suite, une étude de terrain de quatre mois (chapitres II et III) a été menée à la fois à Miquelon et à Saint-Pierre, cette dernière étant considérée comme un site anthropique situé près d'un port industriel. Des collecteurs ont été déployés le long d'un gradient de bruit des navires (SPL) : élevé (137 dB à 25 m), modéré (120 dB à 175 m) et bruit ambiant (106 dB à 890 m). Les variables environnementales et les conditions acoustiques ont été surveillées quotidiennement ou mensuellement.

Une approche expérimentale intégrative a été mise en œuvre, combinant des méthodologies traditionnelles et de pointe : la manipulation du bruit des navires à l'aide d'un haut-parleur sous-marin, l’identification taxonomique et indices de diversité pour évaluer l'abondance, la composition, la diversité et l'uniformité des espèces, la morphométrie des coquilles afin de mesurer la taille des pediveligères et des métamorphes comme indicateurs

de croissance et de retards de développement, et la mesure de la longueur totale pour détecter les dériveurs issus de migrations secondaires et analyser la répartition des populations, des techniques biochimiques, telles que le profilage des acides gras par chromatographie en phase gazeuse, et l'abondance des classes de taille cellulaire par cytométrie en flux, pour caractériser l'environnement trophique, et le déploiement de capteurs environnementaux tels que la température, les courants et les marées.

La première étude (chapitre I) a évalué dans quelle mesure le bruit des navires, à des intensités allant de modérées à élevées, influence la colonisation et la métamorphose de *Mytilus edulis* à court terme. Nous avons émis l'hypothèse que les collecteurs situés plus près de la source de lecture (intensité élevée) présenteraient des taux de colonisation élevés, conformément aux modèles antérieurs obtenus en laboratoire. Cependant, aucune différence significative n'a été observée entre les sites témoins et les sites bruyants en termes de taux de colonisation, probablement en raison d'une mauvaise saison de recrutement. Néanmoins, l'abondance post-larvaire et le succès de la métamorphose ont été considérablement réduits sur le site bruyant, ce qui confirme l'hypothèse selon laquelle le bruit anthropique perturbe l'établissement des organismes au cours des premiers stades critiques de leur vie. Bien que nous ayons observé une augmentation du nombre de post-colonisateurs sur les deux sites, l’augmentation du nombre de individus dérivants était plus marquée en présence de bruit des navires.

Dans la deuxième étude (chapitre II), nous avons évalué les effets de la diffusion de bruit de navire sur le développement larvaire (taille à la métamorphose, longueur totale) et la structure des cohortes de *Mytilus* spp. le long d'un gradient pendant 4 mois. Nous avons testé deux hypothèses : (1) que la distribution des classes de taille des larves et la structure des cohortes diffèrent selon l'intensité du bruit (SPL, élevé 137 dB, modéré 120 dB et bruit ambiant 106 dB) ; et (2) que les larves exposées à des SPL élevés à modérés retardent leur métamorphose, ce qui entraîne une augmentation de la longueur de la prodissoconche II. Les larves de moules issues du deuxième essai *in situ* ont été analysées à l'aide de la morphométrie des coquilles (taille à la métamorphose, longueur totale et composition des cohortes), du modèle de mélange gaussien et de la distance Earth Mover (EMD) afin d'évaluer l'influence de l'exposition sonore sur la taille des larves et la distribution des cohortes. Les résultats ont montré que, si la fixation primaire et la métamorphose n'étaient pas affectées par les niveaux sonores (106 à 153 dB), la fixation secondaire, qui est un indicateur de la dérive post-métamorphique, augmentait en présence d'un bruit modéré. Les recrues de plus de 2 mm étaient plus fréquentes en présence d'un bruit modéré provenant des navires et de l'environnement, tandis qu'un bruit élevé, tant sur les sites vierges que sur les sites anthropisés, réduisait le nombre de cohortes et l'établissement des recrues.

Enfin, dans la troisième étude (chapitre III), nous avons examiné les effets des gradients de bruit des navires sur la structure des communautés et le recrutement précoce dans cinq modèles biologiques dominants, notamment les gastéropodes et les bivalves, sur une période de quatre mois. Nous avons émis l'hypothèse que la diversité des invertébrés et le recrutement précoce diminuent à mesure que les collecteurs de peuplement se rapprochent de la source

de bruit. Alors que les variables physiques et trophiques sont restées homogènes d'un site à l'autre, les profils sonores ont considérablement varié : le site vierge n'était exposé qu'au bruit des navires (SPL < 140 dB re 1 μ Pa, SEL < 140 dB re 1 μ Pa^{2}.s), tandis que le site anthropisé était exposé à la fois au bruit des navires et au bruit des battages de pieux (SPL > 140 dB re 1 μ Pa et SEL > 140 dB re 1 μ Pa^{2}.s). Comme prévu, le site vierge et les sites anthropisés ont montré des variations dans la diversité et l'uniformité des espèces selon les distances et les mois, avec un effet négatif clair aux stations proches du bruit. Les modèles de recrutement précoce spécifiques à chaque espèce ont démontré que les niveaux sonores (< et > 140 dB) modifiaient les paramètres démographiques et changeaient la composition des espèces, ce qui implique que cette perturbation acoustique peut entraîner une restructuration écologique.

Collectivement, ces études fournissent des preuves sur le terrain que le bruit anthropique modifie les communautés d'invertébrés benthiques en perturbant les processus de recrutement précoce et en modifiant la structure des cohortes. Ces résultats soulignent les risques écologiques de la pollution sonore dans les habitats côtiers subarctiques et mettent en évidence la vulnérabilité des invertébrés marins au stress induit par le bruit. Les changements observés dans la composition des espèces, le développement larvaire et le comportement de colonisation secondaire exigent une attention urgente en matière de réglementation du bruit. Bien qu'il s'agisse d'une première étude *in situ* avec une réplication limitée, nous recommandons que les seuils d'exposition sonore ne dépassent pas 140 dB re 1 Pa^{2}.s afin de protéger le couplage bentho-pélagique et de préserver la diversité des communautés bentho-pélagiques.

Ce seuil doit être considéré comme préliminaire et servir de point de départ pour de futurs essais expérimentaux. Des travaux supplémentaires devraient viser à valider ces niveaux dans des conditions contrôlées et pour différentes espèces et différents stades de vie. Des études parallèles pourraient examiner les effets du bruit sur les migrations secondaires et déterminer si le bruit peut déclencher un stress métabolique comme chez les post-larves. Il serait intéressant de coupler plusieurs facteurs de stress environnementaux afin de contextualiser ce que les organismes subissent *in situ*.

Mots clés : bruit anthropique, invertébrés marins, recrutement précoce, moule bleue, comportement d'établissement, bruit des navires, impacts écologiques, dérive larvaire.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF SUPPLEMENTARY TABLES

LIST OF FIGURES

LIST OF SUPPLEMENTARY FIGURES

LIST OF ABBREVIATIONS AND ACRONYMS

ADCP	Acoustic Doppler Current Profiler
ANOVA	Analysis of variance
AS	Anthropized or anthropic site
ATP	Adenosine triphosphate
BrFA	Branched Fatty Acids
DHA	Docosahexaenoic acid (22:6w3)
EFA	Essential Fatty Acid
EMD	Earth's Mover Distance
EPA	Eicosapentaenoic acid (20:5w3)
FA	Fatty Acid
GC-MS	Gas Chromatography – Mass Spectrometry
GMM	Gaussian Mixture Model
GSL	Gulf of Saint-Lawrence
MTFA	Mass of Total Fatty Acids
MUFA	Monounsaturated fatty acids
PERMANOVA	Permutational Multivariate Analysis of Variance
PI	Prodissoconch I
PII	Prodissoconch II
POM	Particulate organic matter

POM	Particulate Organic Matter
PS	Pristine Site
PUFA	Polyunsaturated Fatty Acid
sBIC	Singular Bayesian Information Criteria
SD	Standard Deviation
SE	Standard Error
SEL	Sound exposure level
SFA	Saturated Fatty Acid
SIMPER	Similarity Percentage Analysis
Sp.	Species (singular)
SPL	Sound pressure level
SPM	Saint-Pierre and Miquelon
Spp.	Species (plural)
TAG	Triacylglycerol
TL	Total length
TPM	Total Particulate Matter

LIST OF SYMBOLS

<	Less than
>	Greater than
°	Degree
°C	Degree Celsius
cells.ml^{-1}	Cells per milliliter
dB	Decibels
Hz	Hertz
h	Hour
log	Logarithm
m	Meter
µg.mg	Microgram per milligram
µm	Micrometer
µPa	Micropascal
µPa^2.s	Micropascal per second
mg.L^{-1}	Milligram per litre
mm	Millimeter
min	Minutes
rms	Root mean square
pk	Peak

s	Seconds

GENERAL INTRODUCTION

COASTAL HABITATS IN A CHANGING OCEAN

Within marine environments, coastal regions worldwide are experiencing the fastest increase in cumulative anthropogenic pressures (Figure 1; Halpern et al. 2019). According to the same authors, subarctic coasts situated in the Americas (Figure 1), including the Canadian Eastern Seaboard and the Saint-Pierre and Miquelon archipelago (SPM) near the Gulf of Saint-Lawrence (GSL), are among the affected areas. These subarctic systems are of particular interest due to their marked seasonality and the presence of relatively pristine habitats (Dunbar, 1954; Thorson, 1950). The GSL is heavily used by human activities such as commercial shipping (Beauchesne et al., 2025; Drejou et al., 2020), and ongoing research has investigated how climate change and human pressures influence its benthic community using proxies ranging from exposure indices to network-scale assessments (Beauchesne et al., 2025; Drejou et al., 2023). Canadian harbors are economically important and highly subjected by several human activities, making them as a priority for management and conservation (Drejou et al., 2023). However, smaller harbors such as the one in SPM – unlike major ports such as Sept-Iles - remain understudied. Moreover, ecological and biodiversity data are limited for the SPM archipelago.

In subarctic systems, timing is crucial, as recruitment and population dynamics are regulated by seasonal phytoplankton blooms, temperature and light conditions (DFO, 2020; Dunbar, 1954; Miller and Wheeler, 2012). Among organisms inhabiting coastal zones, marine invertebrates are particularly susceptible to these environmental variations and remain underrepresented in the International Union for Conservation of Nature (IUCN), as highlighted by Chen et al. (2021). Benthic invertebrates - such as annelids, crustaceans and molluscs - are major components of high-latitude ecosystems, supporting associated fauna, participating in ecological interactions, and serving as sentinel species for environmental change (Chen et al., 2021; Lewis and Santos, 2016; Seed, 2000). Several species also have commercial value, with juveniles (seeds or spats) harvested directly from the wild for aquaculture activities (Cyr et al., 2007; DFO, 2022; FAO, 2024; South, 2021).

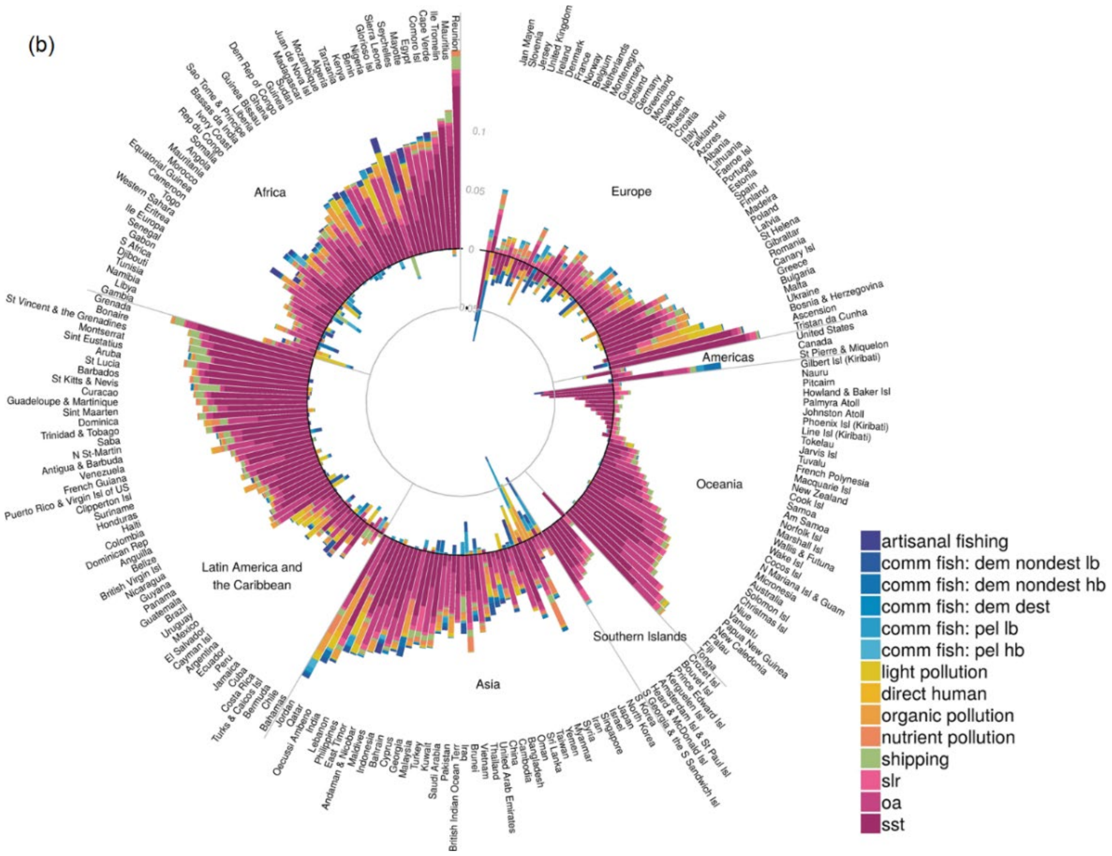


Figure 1: Cumulative human impacts within coastal regions of each country with outer bars greater than zero demonstrating increasing impacts (Source: Halpern et al., 2019). In Figure 1, legends refer to stressors from 4 primary categories: a) fishing, including artisanal fishing, commercial fishing demersal destructive (comm fish: dem dest), commercial demersal non-destructive low bycatch (comm fish: dem nondest lb) and high bycatch (comm fish: dem nondest hb), and commercial fishing pelagic low bycatch (comm fish: pel lb) and high bycatch (comm fish: pel hb); b) land-based, composed of light, direct human, organic chemical pollution, and nutrient pollution; c) ocean with shipping; and d) climate change, consisting of sea level rise (slr), ocean acidification (oa), and sea surface temperature (sst).

Despite their ecological and economic value, benthic communities face mounting pressures from ocean warming, acidification, pollution and anthropogenic noise (Aulanier et al., 2017; Benedetti, et al., 2021; Halpern et al., 2019; Jalkanen et al., 2022; O'Hara et al., 2021; Svavassorn et al., 2021). For instance, rising seawater temperatures may disrupt the synchronization of food and organism life cycles, as described by the match-mismatch hypothesis (Cushing, 1990), reshape phytoplankton communities (Baustian et al., 2014), and shorten planktonic phase of invertebrates (Bashevkin et al., 2020). Acidification further threatens calcifying organisms and impairs larval sensory abilities (Bashevkin et al., 2020; Bylenga et al., 2017; Leung and McAfee, 2020), while multiple stressors may shift planktonic diversity, and key ecosystem functions such as secondary production and organic matter cycling (Benedetti, et al., 2021; Strong et al., 2015). Moreover, shipping noise is expected to change from being occasional to dominant, particularly in Canadian Arctic and subarctic waters, reducing pristine soundscapes and increasing risks of behavioural disruption in marine life (Aulanier et al., 2017).

Understanding how human activities affect benthic communities requires local biodiversity assessments that integrate taxonomic, phylogenetic and functional dimensions of diversity (Bagousse-Piguet et al., 2019; Champagne et al., 2023; Tilmann, 2014). Taxonomic diversity, measured through species richness and evenness, is commonly used to detect community shifts caused by environmental stressors (Diaz, 1992; Perkins, 1983; Tilmann, 2014). The Shannon-Weiner index (H') quantifies community diversity by computing species distribution and abundance, while Pielou's evenness assesses the equity of species distribution - often detecting revealing anthropogenic impacts even when species richness remains unchanged (Perkins, 1983). These indicators are widely adopted in assessments of temperature to Arctic benthic communities (Aswathy et al., 2023; Drejou et al., 2020; Witman et al., 2008).

Although studies have examined benthic community structure in disturbed and undisturbed subarctic habitats (Drejou et al., 2020; Drejou et al., 2023; Witman et al., 2008), significant gaps remain - particularly regarding the ecological impacts of emerging stressors such as anthropogenic noise at both community and population scales (Kunc et al., 2016; Solé et al., 2023; Sordello et al., 2020). As coastal systems experience increasing pressures, recruitment has become a central concern since it is one of the crucial processes maintaining diversity and community stability (Austen et al., 2002).

RECRUITMENT OF BENTHIC INVERTEBRATES

Recruitment, the addition of new individuals to a population via settlement of pelagic larvae, plays a fundamental role in species distribution, population dynamics and community structure (Calley et al., 1996; Olafsson et al., 1994; Petraitis et al., 2020). Recruitment in several invertebrates varies spatially and temporally, influencing adult populations (Gosling, 2021; Le Corre al., 2013; Martel et al., 1991; Martel et al., 2014). This variability between adults and larvae has been debated since the 1920s and has given rise to several theories attempting to explain whether recruitment is controlled by planktonic or benthic processes (Calley et al; 1996; Hunt and Scheibling, 1997; Lewin, 1986; references within Lewin, 2006 and Pineda et al., 2010; Olafsson et al., 1994; Thorson, 1950).

One of the earliest theories proposed, by Thorson (1950), suggested that variability in adult populations is primarily dictated by adult reproduction and larval dispersal (high losses during egg and larval stages). He argued that factors such as fertilization, predation, unfavorable environmental conditions, and larval transport to unsuitable habitats were collectively driving these losses. In the 1980s, the '*supply-side*' ecology concept emerged, emphasizing that pre-settlement processes, such as larval dispersal and mortality, are major determinants of population dynamics. This became a central focus in ecological studies for several years. However, ecologists later debated that while larval supply is an important contributor, it is not the sole factor ruling recruitment (see Levin, 2006; Lewin 1986). Since the late 1990s, research expanded on these ideas, suggesting that temporal and spatial variability in recruitment arises from pre-settlement, settlement, and post-settlement processes (Figure 2; Fraschetti et al., 2003; Olafsson et al., 1994; Olivier and Retière, 1998; Pineda et al., 2009, 2010). These include settlement behaviour and cues (Kingsford et al., 2002; Pawlik, 1992), delayed metamorphosis (Bishop et al., 2006; Pechenik, 1990, 2006), migrations triggered by disturbances or physical-trophic factors (Günther 1992; Olivier et al., 1998), the physiological state of larvae (Pernet et al., 2003; Phillips, 2002; Tremblay et al., 2007), and post-settlement mortality, mainly due to predation (Gosselin and Quian, 1997; O'Connor et al., 2008). Moreover, the recruitment success varies within individuals and cohorts (Gosselin and Quian, 1997; Le Corre et al., 2013)

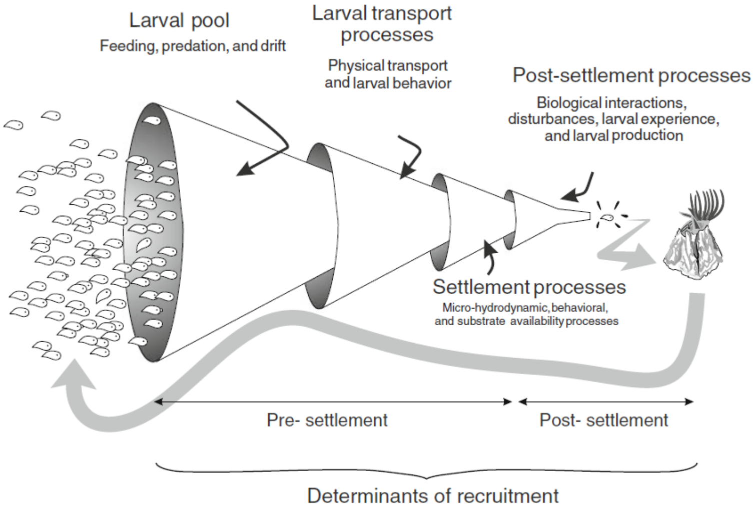


Figure 2: Diagram showing all processes and phases that influence recruitment in benthic invertebrates (Source: Pineda et al., 2009).

Because the determinants of recruitment consist of larval supply, settlement behaviour of larvae, many interactions between adult and settled individuals (predation, intra-and interspecific competition for space) during the post-settlement, and larval physiological state (Fraschetti et al., 2003; Keough and Downes, 1982; Pineda et al., 2009), it is necessary to delve into the biphasic lifecycle to define and understand how each process or mechanism might influence population dynamics in this Anthropocene Era.

FROM PLANKTONIC TO BENTHIC LIFE

Bentho-planktonic species play an essential role in coastal ecosystems, linking pelagic and benthic habitats through migration and recruitment (Austen et al., 2002; Baustian et al., 2014; Morgan, 2022). Their larval development plays a crucial role in this connections, varying widely in duration, nutritional mode and developmental type as shown in Figure 3 (see reviews Pechenik, 2006; Thorson, 1950). Some species hatch as miniature adults (direct development) while others go through various larval stages (indrect development), adopting either lecithrotrophic or planktotrophic strategies (Bishop et al., 2006). Lecithotrophic larvae rely on maternal reserves, whereas planktotrophic larvae, with minimal yolk reserves, must feed on particulate organic matter, and phytoplankton, extending their planktonic duration (Pechenik, 1990; Thorson, 1950).

Larval development is strongly influenced by environmental factors, primarily temperature, and food availability (Gosling, 2015; Pechenik, 1990; Thorson, 1950), which influence survival, growth, and settlement (Hadfield and Paul, 2001; Hunt and Scheibling, 1997). Laboratory studies have identified optimal conditions for aquaculture species (Gosling et al., 2015; Rayssac et al., 2010), but wild larvae experience far more variable conditions, that alter metabolic and developmental rates (South, 2021). Temperature regulates metabolic activity with species- and stage-specific thermal thresholds and early larval stages are typically the most sensitive (Gosling, 2015, 2021; Przeslawski et al., 2015; Zippay and Helmuth, 2012). This dependence on external conditions is particularly critical for planktotrophic larvae, whose energy demands increase as they begin feeding shortly after developing a shell and velum (Bishop et al., 2006).

In marine invertebrate larvae, lipids are the main energy source driving development (Fraser, 1989; Lucas et al. 1970). Lipids are broadly divided into polar lipids (e.g., phospholipids, etc.), which maintain cell structure and function, and neutral lipids (e.g., triglycerides commonly called TAG) that serve as energy reserves (Budge et al., 2006). During early development, larvae depend on stored TAGs until exogenous feeding begins

(Figure 3a-b). Bivalves metabolize energy-rich molecules such as glycogen/glucose, proteins/free amino fatty acids and lipids through anaerobic or aerobic pathways to generate adenosine triphosphate (ATPs), which supports basal maintenance (e.g. protein turnover, ion balance) and production (e.g. growth, reproduction, and storage) (Sokolova et al., 2012, Figure 4a). Surplus energy is stored as TAGs when food is abundant, while limited food conditions trigger rapid turnover of TAGs (Fraser, 1989). As TAGs provide a short-term energy source via the β-oxidation process (Budge et al., 2006), mainly utilizing saturated fatty acids (SFA), which release energy more efficiently than monounsaturated (MUFA) or polyunsaturated fatty acids (PUFA) (Langdon and Waldock, 1981). Among PUFAs, certain essential fatty acids (EFA), from ω3 and ω6 families play crucial roles in physiological and biochemical processes, including endocrine regulation, membrane fluidity and immune function (Glencross, 2009). Under environmental stress, ATP production becomes constrained, shifting metabolism from efficient aerobic to less efficient anaerobic pathways, with energy increasingly allocated to survival than growth, as shown in Figure 4b (Sokolova et al., 2012).

The synthesis of EFAs is absent or insufficient to meet nutritional needs in marine invertebrates, thus EFAs must be obtained through diet (see review by Knauer and Southgate, 1999), particularly marine microalgae that accumulate eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Gosling, 2015; Radakovits et al., 2010). Some bivalve larvae can convert precursors into arachidonic acid (ARA) and EPAs when nutritional resources are limited, but not DHA (Da Costa et al., 2015), with deficiencies in DHA may impact settlement and metamorphosis in subarctic scallops and subtropical mussels (Pernet and Tremblay, 2004; Leal et al., 2022). Beyond their metabolic roles, fatty acids (FAs) in particulate organic matter (POM) serve as a trophic fingerprint, tracing the flow of energy from bacteria, phytoplankton, and zooplankton to larvae (Budge et al., 2006; Chynel et al., 2022; Meziane et al., 2007).

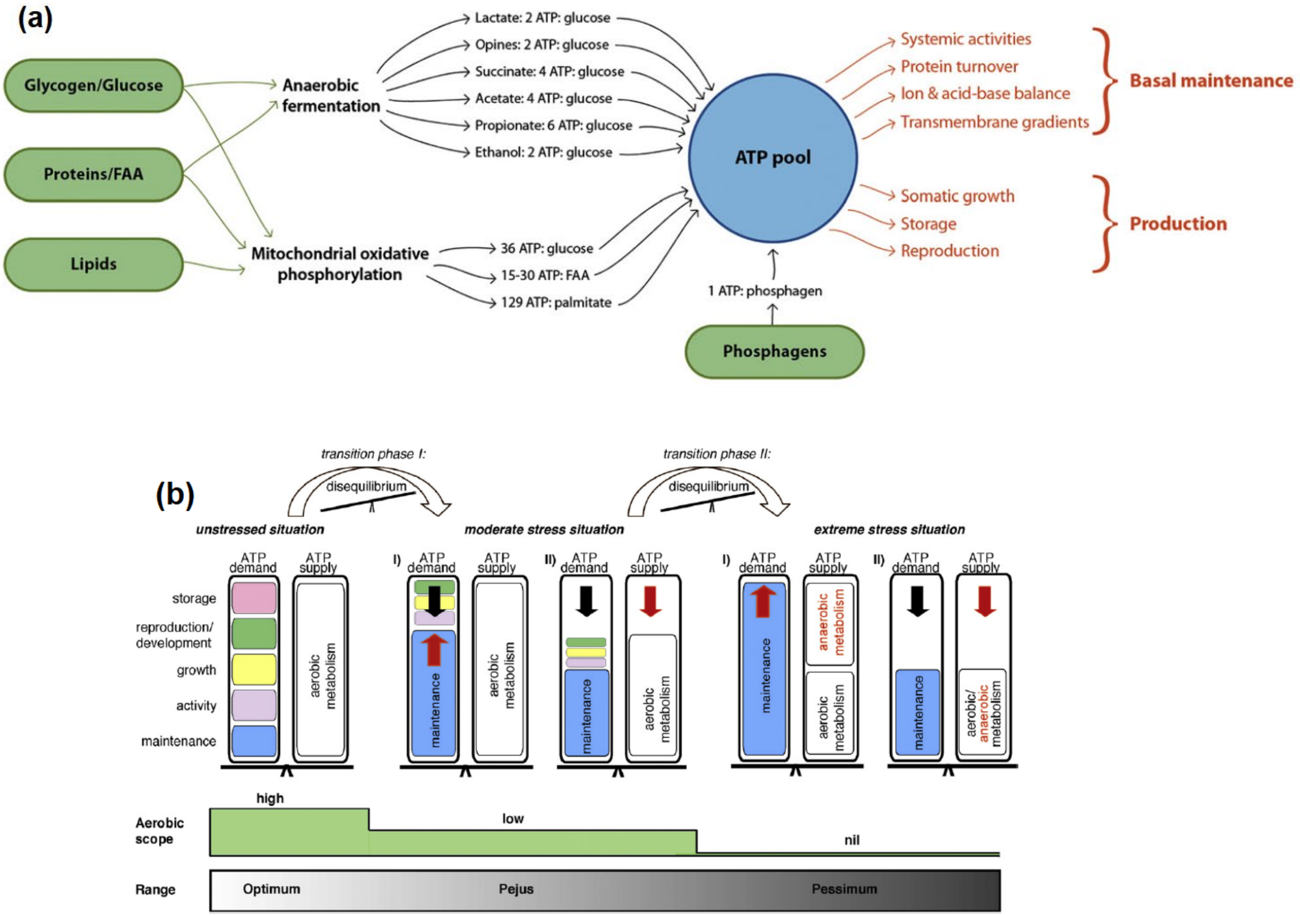


Figure 3 : Flowchart of energy production (ATP) and usage in marine invertebrates (**a**) and diagram showing how these organisms manage this energy demand under three different stress situations (**b**) (Source: Sokolova et al., 2012)

COMPETENCE, SETTLEMENT AND METAMORPHOSIS

The transition from planktonic to benthic stage marks one of the most critical phases in the lifecycle of marine invertebrates, encompassing competence, settlement, metamorphosis, and early post-settlement survival (Figure 4a-b). Attaining competence - a stage characterized by shell size and/or position (e.g., bivalves = 250-300 µm, veliger rotation in gastropods) and morphological traits such as development of a foot and eye spots – enables larvae to detect and respond to wide range of cues for settlement (Figure 4a-b; Gosling, 2021;

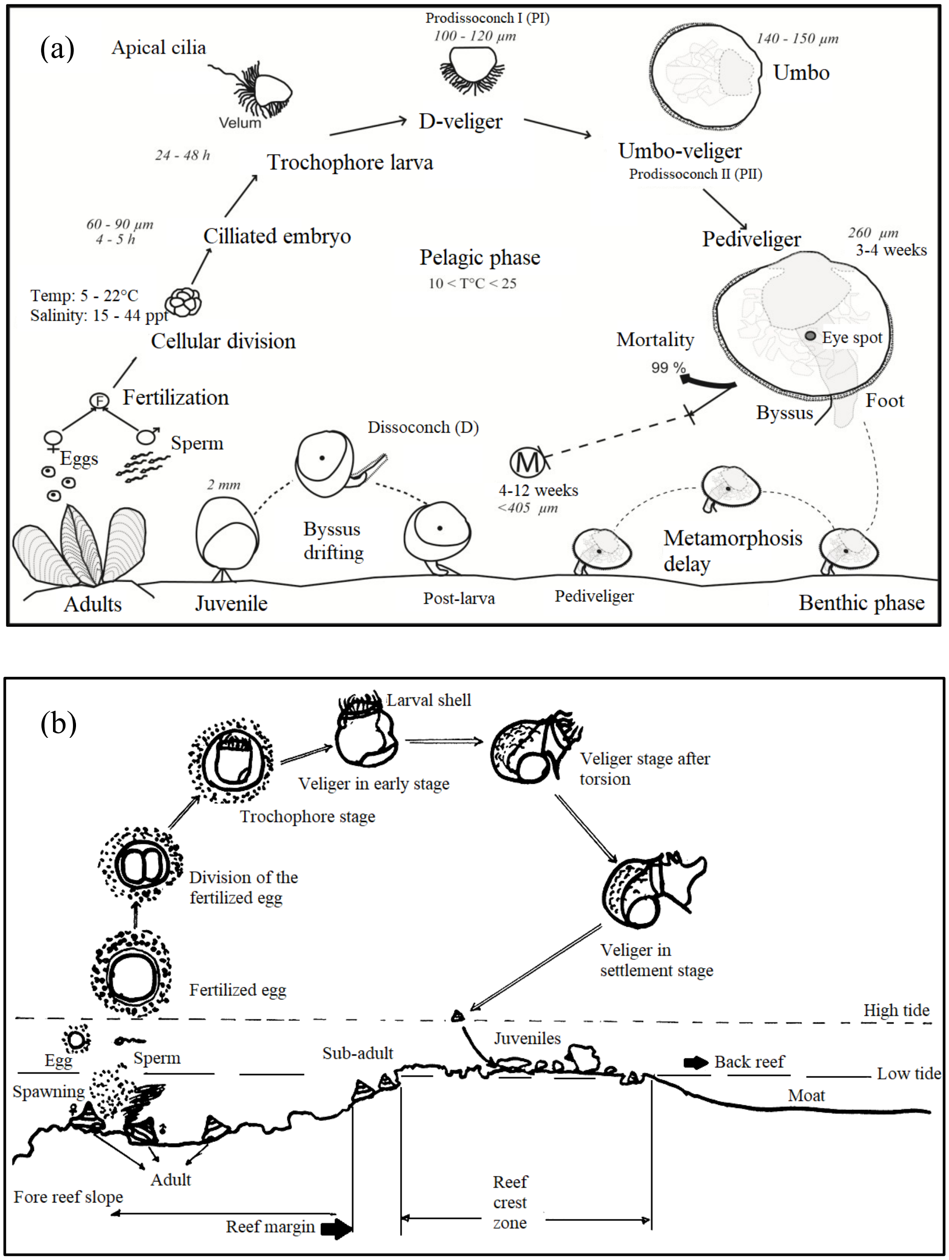


Figure 4: Schemes of life histories in marine invertebrates, including a bivalve and gastropod: **a**) *Mytilus edulis* life cycle translated from French (Source: Toupoint et al., 2012) and **b**) *Turbo mamoratus* lifecycle (Source: FAO website, n.d.).

Martel et al., 2014). These signals can be grouped into four groups: (1) chemical cues, such as dissolved compounds in water or adsorbed in biofilms, substrates, and associated with conspecifics or predators); (2) physical cues, including current speed, turbulence, and substrate textures; (3) trophic cues, like the pulse of phytoplankton rich in EFA; or (4) acoustic cues, which originate from natural and anthropogenic sources, and will be discussed later (Butman, 1997; Hadfield and Paul, 2001; Hadfield, 2011; Jolivet et al., 2016; Lillis et al., 2015; Martel et al., 2014; Pawlik, 1992; Pernet et al., 2003; Toupoint et al., 2012a, b).

Chemical and physical triggers are the most studied. For example, the composition and age of marine biofilms can either promote or inhibit larval settlement (Dobretsov and Rittschof, 2020; Hadfield and Paul, 2001; Toupoint et al., 2012b; Tremblay et al., 2007). Organic compounds from macroalgae also influence settlement choices in bivalve and gastropods (Martel and Chia, 1991; Hadfield and Paul, 2001), while turbulence and substrate type shape microhabitat selection (Frandsen and Dolmer, 2002; Pernet et al., 2003; Garcia et al., 2003; Brenner and Buck, 2010; Tremblay et al., 2020). Trophic conditions may also play a critical role in larval development: *the match-mismatch hypothesis* in fish (Cushing, 1990), and subsequent work on the *trophic settlement trigger* in bivalves (TST, Toupoint et al., 2012a) demonstrate that larval peaks might overlap phytoplankton blooms. Upon encountering favorable cues, competent larva retracts its velum, explores the surface with their foot, followed by attachment and metamorphosis (Gosling, 2021).

Metamorphosis is a high energy-intensive process involving loss of larval features and the development of juvenile structure, such as gills and labial palps (Pechenik, 2006; Thorson, 1950). In mussels, this transformation starts within 24-72h of secretion of byssus in which velum disintegrates and labial palps form, with adult gills/palps feeding becoming functional within 48h but mature in several days, and both foot and gills adjust their positions to improve filter feeding efficiency (Figure 4a, Cannuel et al., 2009; Gosling, 2021; Smolovitz, 2021). During this non-feeding phase, larvae rely on stored energy reserves, mainly TAGs, to fuel this process (Lucas et al., 1979; Pernet et al., 2003; Tremblay et al., 2007). When settlement conditions are unsuitable, some species can "*delay metamorphosis*" or "*retain the competent stage*" for days or weeks until finding a favorable site to settle (Figure 4a, Bishop et al., 2006; Pechenik et al., 2006). For example, delays ranging from 2 days to 6-7 weeks have been observed in *M. edulis* (Bayne, 1965) due to temperature, with *in situ* delays of 1-2 weeks due to absence of trophic cues (Martel et al., 2014). Prolonged delays may deplete energy reserves, reduce juvenile growth (Pechenik, 2006), and lead to "*desperate settlement*" in suboptimal habitats (Knight-Jones, 1953, Bishop et al., 2006).

POST-SETTLEMENT SURVIVAL AND POPULATION DYNAMICS

Following settlement, early benthic life is characterized by high mortality and strong selective pressures. Predation is a major source of mortality (Beal et al., 2020; Keough and Downes, 1982; O'Connor et al., 2008), with rates sensitive to body size (Duffy, 2021; Gooding and Harley, 2015) and prey abundance (Beal et al., 2020). Physiological stress, food limitation, competition and physical disturbance also contribute to losses (Jenewein and Gosselin, 2013; Calley et al., 1996; Hunt and Scheibling, 1997). For instance, newly settled *Mytilus trossulus* are vulnerable to lethal temperatures ≥ 33ºC and desiccation (Jenewin and Gosselin, 2013*).* Nutritional quality during larval stages further affects juvenile performance (Phillips, 2002; 2004), with poor larval feeding conditions leading up to 99% mortality post-settlement. Competition among bivalves is also significant (Calley et al., 1996; Cyr et al., 2007; Khalaman, 2005), with *Hiatella arctica* and *M. edulis* competing strongly against *Placopecten magellanicus* (Cyr et al., 2007) and even each other (Garcia et al., 2003; Khalaman, 2005). Some species may relocate through secondary dispersal via byssal-drifting or mucus-assisted crawling to escape unfavorable conditions (Bayne 1964; Forêt et al., 2018a; Martel and Chia, 1991; Olivier and Retière, 2006). This post-settlement mobility changes primary settlement patterns, enhances habitat connectivity, and recruitment success, often reflecting larval dispersal scales but with greater competency (Le Corre et al., 2013; Olivier and Retière, 1998; Pilditch et al., 2015).

In bivalves, early shell morphology provides insights into population dynamics especially as some invertebrate species are in decline (Baden et al., 2021; Butler et al., 2019; Petraitis and Dudgeon 2020). Prodissoconch I (PI) and II (PII) shells serve as archives of larval development before metamorphosis (Figure 5a, Martel et al., 2014; Leal et al., 2022), while the dissoconch (D) shell forms after metamorphosis (Martel et al., 2014; Gosling 2015). Shell growth and quality reflect temperature, food availability, and exposure to stressors such as acidification and pollutants (Bylenga, et al., 2017; Lasota et al., 2018; Leal et al., 2022; Lutz et al., 1978; Martel et al., 2014). Cohort and size-frequency analyses further offer valuable insights on temporal and spatial population dynamics (Figure 5b, Le Corre et al., 2013; Toupoint et al., 2012a), helping unveil recruitment variability (Duffy, 2021; Gosling, 2015; Valiela, 2015). Although metamorphosis was once considered a reset point, increasing evidence shows that pre-settlement conditions may exert carryover effects on post-settlement survival and growth (Pechenik, 2006). These effects – persistent, amplified or compensatory – demonstrate how early stress can shape later life history outcomes (Podolsky and Moran, 2006; Gigot et al., 2024). Among these stressors, the effect of anthropogenic noise in populations is still poorly understood, despite evidence that acoustic signals play a crucial role in guiding larvae toward favorable habitat.

OCEAN SOUNDSCAPE AND DETECTION OF SOUND BY BENTHIC INVERTEBRATES

The ocean is far from silent; its soundscape comprises biological (biophonies) and non-biological sounds (geophonies and anthrophonies) (Erbe, 2020; Farina, 2014). Biophonies consist of signals marine organisms use for mating, prey detection and predator avoidance, habitat selection and larval settlement (Figure 6a, de Soto and Knight, 2016). Geophonies originate arise natural phenomena such as waves, wind, rain, and volcanic activity, while anthropophonies – hereafter referred to as anthropogenic sounds – stem from human activities, including shipping, pile driving, sonar, and seismic surveys (Figure 6a-c). In shallow waters, these sounds often overlap (de Soto and Kight, 2016; Farina, 2014; Hildebrand, 2009), influencing the ecology of marine organisms (Kingsford et al., 2002).

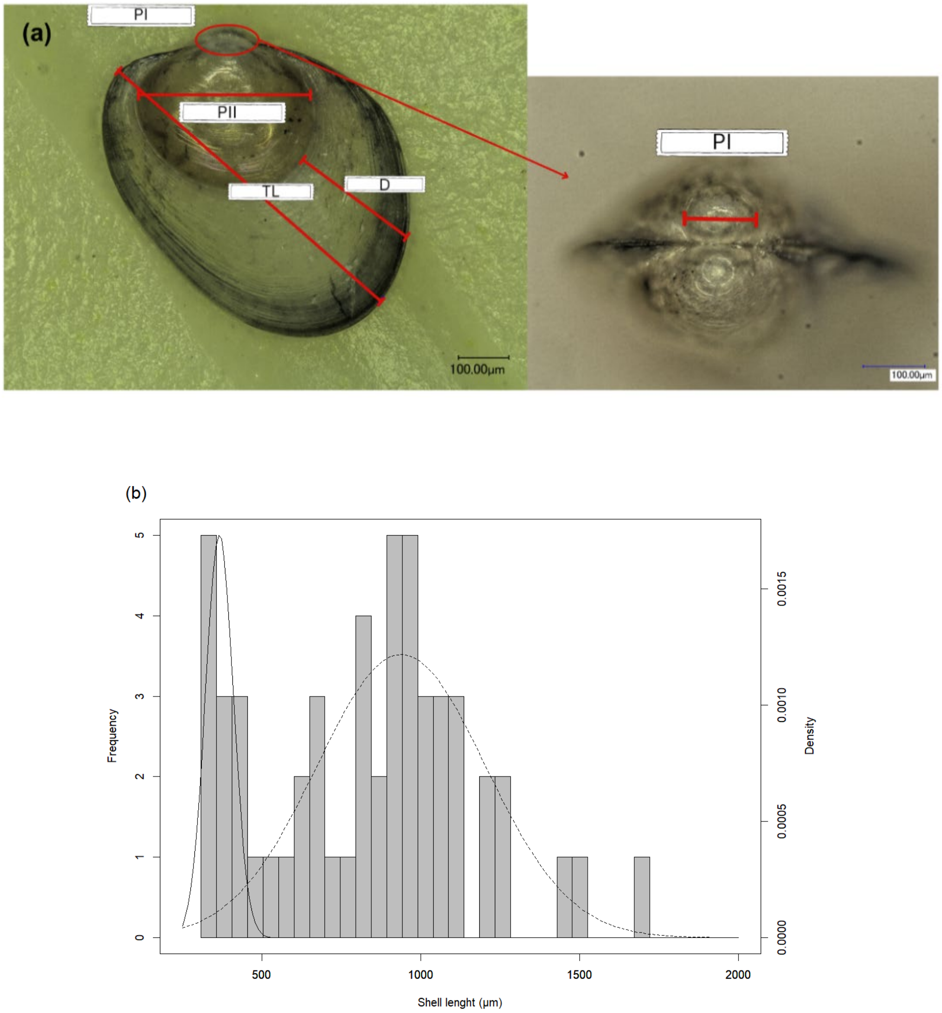


Figure 5 Diagrams showing mussel shell dimensions and cohort distribution: (**a**) prodissoconch I and II – PI and PII, and total length – TL, and (**b**) plots featuring the age structure of a mussel population showing two cohorts and size-class distribution composed of recruits (pediveligers, post-larvae and juveniles). Figures (a) and (b) were created by this author.

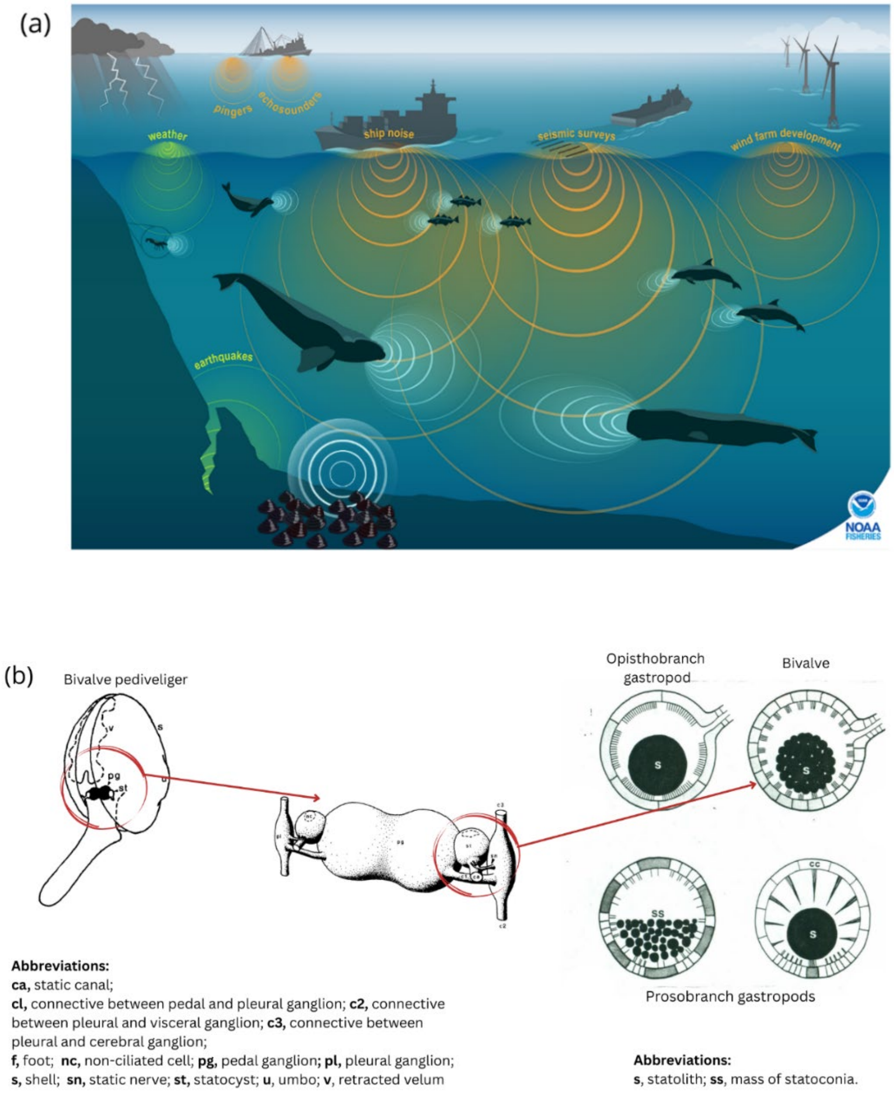
Underwater soundwaves have two components: sound pressure and particle motion. Marine mammals primarily detect sound pressure, while fish and invertebrates mainly perceive particle motion (Coates, 1990; Nedelec et al., 2016; Nedelec et al., 2021; Urick, 1975). Because mammals possess specialized hearing organs, most research has focused on pinnipeds and cetaceans (NMFS, 2018; NRC, 2003; Solé et al., 2023). However, attention is shifting to fish (Cox et al., 2018; Faria et al., 2021; Hawkins et al., 2020; Pieniazek et al.,

2023) and invertebrates (see table in Solé et al., 2023; Davies et al., 2024), as many benthic species rely on acoustic cues for orientation (Kingsford et al., 2002; Lillis et al., 2013, 2015). For instance, oyster larvae settle more readily when exposed to reef sound playback at different distances from the source (Lillis et al., 2015; Williams et al., 2022, 2024).

Sound perception in invertebrates is enabled by sensory structures such as statocysts, abdominal sensory organs, and cilia around the foot, which can detect acoustic signals across different life stages (Figure 6b; Buldemann, 1992; Cragg and Nott, 1977; Zhadan, 2005; Nikishchenko et al., 2023; Yurchenko et al., 2019). Yet, the mechanisms of sound detection remains poorly understood (Chauvaud et al., 2018; Cones et al., 2023). Hearing range and sound production frequencies vary across taxa (see Figure 6c-e). Bivalves generally detect sounds between 0.01 kHz to 1 kHz and produce sounds within 10 kHz to 100 kHz (Chauvaud et al., 2018; Duarte et al., 2021; Melo Junior et al., 2020). Species such as *Pecten maximus*, and *Perna perna,* exhibit acoustic activities concentrated in frequency bands of 4-9 kHz and 33-49 kHz (Coquereau et al., 2016; Melo Junior et al., 2020). Despite some advances, knowledge gaps remain across life stages and frequency ranges (Cones et al., 2023; Zhadan, 2005). While marine organisms have evolved to detect and respond to natural soundscapes, the increasing presence of anthropogenic sounds raises concerns about the potential disruptions to these processes.

NAVIGATION IN NOISY ENVIRONMENTS: ACOUSTIC CUES THREATENED BY THE INCREASE OF ANTHROPHONY

Anthropogenic sounds are classified as impulsive or continuous (Erbe, 2020; Rako-Gospie and Picciulin, 2018). Impulsive sounds (e.g., pile driving, seismic airguns) have short duration and variable frequency (see tables in Hildebrand, 2009 and Rako-Gospie and Picciulin, 2018, and Figure 6e), whereas continuous sound, such as from shipping, persists for long periods, reach great distances and often dominate low-frequency ranges (Stanley and Jeffs, 2016; Erbe, 2020). Pile driving, a growing concern due to wind farm expansion, produces intense low-frequency noise (192 to 270 dB re 1 μPa at 1m, 100-1,000 Hz) (Bonnel et al., 2022; Erbe, 2020; Gigot et al., 2023a,b; 2024). Vessel noise is the main contributor to background ocean noise, with large ships (> 100m) generating high-intensity of low-frequency sounds (SPL_{rms}, 160-220 dB re 1 μPa at 1m, 5-1,000Hz) due to propeller cavitation and machinery (Hildebrand, 2009; Rako-Gospie and Picciulin, 2018).



Abbreviations:
ca, static canal;
cl, connective between pedal and pleural ganglion; **c2,** connective between pleural and visceral ganglion; **c3,** connective between pleural and cerebral ganglion;
f, foot; **nc,** non-ciliated cell; **pg,** pedal ganglion; **pl,** pleural ganglion;
s, shell; **sn,** static nerve; **st,** statocyst; **u,** umbo; **v,** retracted velum

Abbreviations:
s, statolith; **ss,** mass of statoconia.

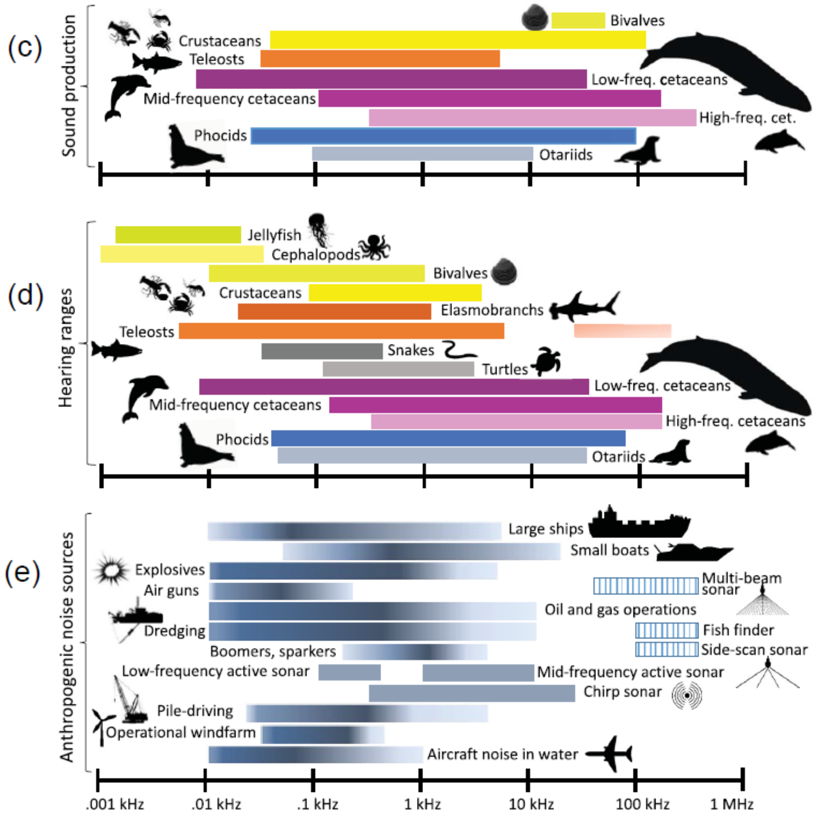


Figure 6: Sound sources present in the marine environment including biophonies, geophonies and anthropophonies (**a**, modified from National Oceanic and Atmospheric Association, n.d.), a diagram showing a crawling bivalve pediveliger and nervous system of statocyst from a bivalve, and the morphological diversity of statocysts in invertebrates (**b**, modified from Cragg and Notton, 1977, and Buldemann, 1992), and three graphs showing sound ranges (kHz) produced by each taxon, hearing ranges of marine taxa and frequency ranges of selected anthropogenic sound sources (**c**, **d**, **e**, Source: Duarte et al. 2021).

Increasing levels of anthropogenic noise (vessel and pile driving noises), especially in coastal environments, may reduce biophonies and disrupt biological processes such as settlement and recruitment (Sole et al., 2023; Thomsen and Popper, 2024). Under controlled conditions, the effects of anthropogenic noise vary with species life stage and noise source (Cervello et al., 2023; Davies et al., 2024; Gigot et al., 2023a,b; 2024; Jolivet et al., 2016; McDonald et al., 2014). Vessel noise can alter settlement, antipredator, and valve behaviours (Jolivet et. al, 2016; Hubert et al., 2022; McDonald et al., 2014; Tidau and Briffa, 2019; Wale et al., 2019; Wilkens et al., 2012), while pile driving noise can impair juvenile and adult behaviours (Jézéquel et al., 2022; Ledoux et al., 2023), and even enhance recruitment in certain species (Cervello et al., 2023). Physiological and transgenerational effects have been also reported (Gigot et al., 2023a, 2023b; Gigot et al., 2024). Despite growing awareness, substantial gaps remain in understanding how vessel noise affects biodiversity and population dynamics in natural settings (Kunc et al., 2016; Sordello et al., 2020).

Recognizing these risks, international organizations such as the United Nations (UN, 2018), the European Union (European Commission, 2017), the Arctic Council (PAME, 2019) have launched regulatory efforts (see overview in Breeze et al., 2022; and Merchant et al., 2022). These initiatives rely on standardized acoustic metrics – such as sound pressure levels (SPL, dB re 1 µPa) and sound exposure level (SEL, dB re 1 $\mu Pa^2.s$) – based on species- or group-specific hearing sensitivities (Bonnel et al., 2022; NMFS, 2018; Rako-Gospic and Picculin, 2018). However, progress is limited by scarce *in situ* data, particularly in defining safe exposure thresholds for invertebrates (Sole et al., 2023), which remain to be established as they have been more developed for marine mammals and fish (see for overview: Bonnel et al., 2022; Breeze et al., 2022; Merchant et al., 2022; Roberts et al., 2015).

OBJECTIVES AND HYPOTHESES

The main objective of this thesis was to assess, for the first time, the effect of vessel noise on the dynamics of marine benthic invertebrates in the field. Laboratory experiments suggest that vessel noise can impact settlement behaviour and affect the fitness of invertebrates, with potential consequences for the recruitment and community structure of coastal habitats. We specifically examined whether processes such as settlement, metamorphosis, and secondary migrations are affected by vessel noise, thereby impacting the input of new individuals into populations and community diversity. A comparative study was conducted at two distinct sites, one in Miquelon (a pristine site) and the other in Saint-Pierre (an anthropic/anthropized site) using artificial collectors deployed along a transect representing a gradient of sound exposure from vessel noise (from high intensity to low - similar to ambient noise) in Figure 7.

This research focused on three interconnected specific objectives (Figure 8), each corresponding to a thesis chapter:

i. compare the effects of ambient noise and vessel noise at two intensities (high-moderate) on the settlement of *M. edulis* in the pristine site (Chapter I);

ii. examine the impact of vessel noise intensities (high, moderate and low) on population metrics (size at metamorphosis, total length and cohort distribution) along a noise gradient from two contrasting sites *in situ* (Chapter II); and

iii. assess the effect of vessel noise intensity on community structure (species diversity and evenness) and early recruitment of multiple species across a gradient of noise (varying distances from the emission source) in two distinct sites *in situ* (Chapter III).

Chapter I: Where to settle? In situ Mytilus edulis *settlement in changing soundscapes*

This chapter builds on the vessel noise-trigger proposed by Wilkens et al. (2012) and validated in controlled conditions by Jolivet et al. (2016), which suggests that moderate-intensity vessel noise (126-128dB) can act as a settlement cue for *M. edulis,* especially when combined with a picoplankton signal under controlled conditions. To test whether this response occurs in natural settings, we used *M. edulis* as a biological model to examine the effects of vessel noise playback at high and moderate-intensities on larval settlement *in situ*. We hypothesized that collectors located closer to vessel noise playback (exposed to high intensity) would experience higher settlement rates compared to those exposed to ambient noise. Furthermore, we predicted that mussel size at metamorphosis would vary with both larval cohort and intensity of vessel noise, as Jolivet et al. (2016) observed that larvae settled rapidly and were smaller in moderate-intensity vessel noise. This chapter forms the basis of the article "*Where to settle? In situ Mytilus edulis settlement in changing soundscapes*", to be submitted to the scientific journal *Marine Ecology Progress Series.*

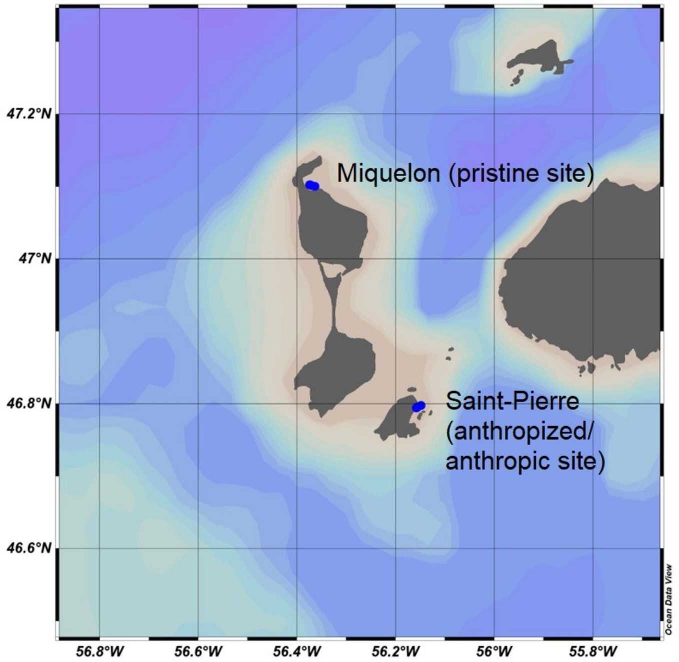


Figure 7: Map of the archipelago Saint-Pierre and Miquelon, France

Chapter II: Size at metamorphosis and recruit cohort dynamics of blue mussels exposed to anthropogenic noise in situ

This chapter builds upon the findings presented in Chapter I, where mussel pediveligers were found in low abundance, with a significant proportion of larger individuals observed over a 3-day sampling period. These patterns may indicate an influx of juveniles performing secondary migrations, as identified in several studies without exposure to anthropogenic noise (Le Corre et al., 2013; Foret et al., 2018). We conducted a second study focusing on demographic parameters and larval developmental traits. Therefore, we tested two hypotheses: (1) larval cohort composition and size-class distribution will differ between high/moderate noise intensities (SPLs) and low SPLs (ambient noise conditions); (2) larvae exposed to high and moderate SPLs would delay metamorphosis, resulting in larger prodissoconch II lengths compared to those under low SPLs. This chapter is ready for submission to the journal *Marine Ecology Progress Series* under the title "*Size at metamorphosis and recruit cohort dynamics of blue mussels exposed to anthropogenic noise in situ*".

Chapter III: "Should I stay, or should I go": anthropogenic noises disrupt early recruitment of subarctic invertebrates

This final chapter builds on the findings presented in chapters I and II. While previous studies have mainly focused on single species responses to vessel noise under controlled settings, here we expanded the scope to examine five ecologically and economically important taxa - two gastropods (*Lacuna* sp. and *Skenea* sp.) and three bivalves (*Hiatella arctica*, *Mytilus edulis* and *Placopecten magellanicus*) - along a gradient of vessel noise in both pristine and anthropized sites. Through this approach, we aimed to evaluate whether increasing vessel noise intensity alters community composition and recruitment of species, as previous studies reported an increase of settlement (Jolivet et al., 2016; Stanley et al., 2012; Wilkens et al., 2012). We hypothesized higher vessel noise levels would lead to reduced species diversity and lower early recruitment of invertebrates on collectors. This chapter is the subject of the article entitled "*Should I stay, or should I go": anthropogenic noises disrupt early recruitment of subarctic invertebrates*", accepted in the scientific journal *Ecological Applications* on July 22, 2025.

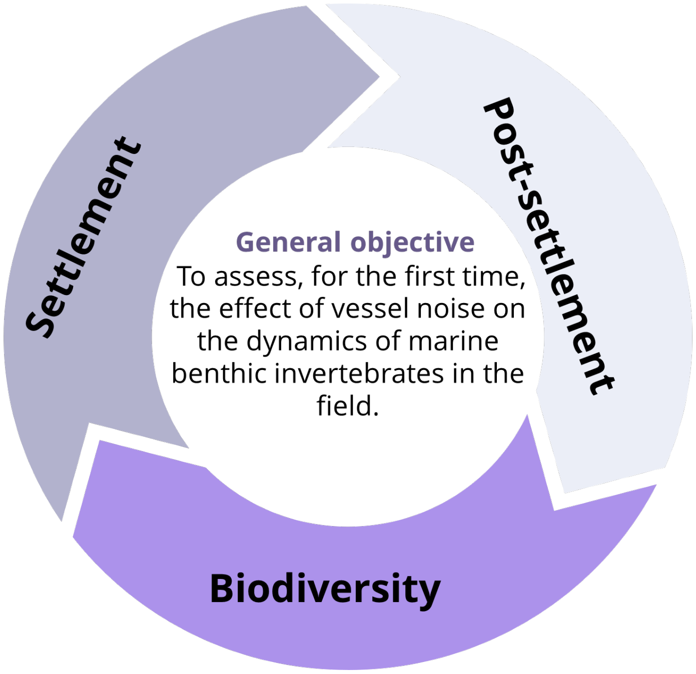


Figure 8 : Conceptual model of the thesis structure, illustrating the main objective and key mechanisms addressed in this thesis.

CHAPITRE 1/ CHAPTER I
WHERE TO SETTLE? *IN SITU* MYTILUS EDULIS SETTLEMENT IN CHANGING SOUNDSCAPES

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In preparation for submission in the Marine Progress Ecology Series (MEPS)

Où s'installer ? L'établissement *in situ* de *Mytilus edulis* dans des paysages sonores changeants.

1.1 Résume

Le bruit anthropogénique des cargos peut affecter le comportement et la distribution des bivalves tels que la moule bleue (*Mytilus edulis*). Cependant, l'impact de ce bruit sur la colonisation des moules reste peu étudié, particulièrement sur le terrain. Afin d'améliorer notre compréhension de l'impact du bruit anthropique sur la phase d'établissement et métamorphose, nous avons suivi la dynamique d'établissement des moules ainsi que la morphométrie de leur coquille dans une zone subarctique, tous les trois jours, du 2 au 21 juillet. Les collecteurs ont été déployés dans deux stations situé sur deux sites caractérisés par des paysages sonores distincts : un site de contrôle- témoin soumis au bruit ambiant et un site bruyant équipé d'un haut-parleur reproduisant le bruit d'un cargo. Les conditions trophiques ont été évaluées chaque semaine et la température a été mesurée quotidiennement. Les conditions environnementales étaient spatialement homogènes. Nos résultats montrent que les taux d'établissement benthique ne variaient pas selon les paysages sonores (site témoin vs. site bruyant) ni selon la distance à la source sonore, probablement en raison d'une faible saison de recrutement (< 200 ind. collecteur^{-1}). En revanche, les taux de métamorphose étaint réduits sur le site bruyant par rapport au site témoin. Notre étude souligne l'importance de comprendre l'impact de l'anthropophonie liée aux passages des navires sur l'établissement et la métamorphose d'espèces côtières clés, illustrant le rôle que peuvent jouer la fréquence et la distance du bruit des cargos dans ces processus écologiques.

Mots clés : anthropogénie, peuplement, bivalves, moule bleue, pollution sonore.

1.2 Abstract

Anthropogenic noise from cargo vessels may affect the behaviour and distribution of bivalves such as the blue mussel (*Mytilus edulis*). However, the impact of this noise on mussel settlement remains unclear due to the scarcity of field data. To enhance our understanding of the effects of anthropogenic noise on the settlement/metamorphosis phases, we monitored mussel settlement dynamics and shell morphometrics in a subarctic area every three days from July 2nd to 21st. Collectors were deployed at two stations within each of two sites characterized by different soundscapes: a control site with ambient noise and a noisy site equipped with a speaker mimicking vessel noise. Trophic conditions were assessed weekly, and the temperature was monitored daily. Environmental conditions were spatially homogeneous. Our results demonstrated that settlement rates did not vary between soundscapes (control vs. noisy site) or with distance from sound source, likely due to a low recruitment season (< 200 ind. collector-1). In contrast, metamorphosis rates were reduced at the noisy compared to the control. Our study highlights the importance of understanding the impact of vessel-related anthropophony on the settlement and metamorphosis of key coastal species, illustrating that both frequency and distance should be considered when assessing noise impacts on ecological processes.

Keywords: anthropogeny, settlements, bivalves, blue mussels, noise pollution.

1.3 Introduction

Mytilus edulis (Linnaeus, 1758), commonly known as the blue mussel, is a bentho-planktonic species that is a valuable biological model in coastal marine research due to its ecological and economic significance (Baden et al., 2021; Le Corre et al., 2013; Seed, et al., 2000). This bivalve produces free-swimming pelagic larvae that feed, grow, and disperse via currents until they become competent to choose a suitable substratum for settlement and metamorphosis (Bayne, 1965; Cannuel et al., 2009; Martel et al., 2014). Specific morphological traits such as eye spots and foot evolve during this competency stage to explore settlement surface. Mussel larvae exhibit active behaviours and can detect a broad range of cues, like the substratum surface, biofilms, pelagic trophic environment, and even underwater sound (Brenner and Buck, 2010; Frandsen and Dolmer, 2002; Hadfield, 2011; Jolivet et al., 2016; Toupoint et al., 2012a; Toupoint et al., 2012b). Invertebrates remain understudied, despite emerging evidences that noise promotes behavioral and fitness effects (Gigot et al., 2024; Jolivet et al., 2016; Olivier et al., 2023; Stocks et al., 2012; Veillard et al., 2025; Wilkens et al., 2012).

The development of blue mussels is strongly influenced by temperature, food availability and quality (Bayne, 1965; Martel et al., 2014; Rayssac et al., 2010; Toupoint et al., 2012a). If environmental conditions are suboptimal, blue mussel larvae may delay metamorphosis and stay in the water column (Martel et al., 2014) or young recruits may undertake secondary dispersal after the primary settlement (Bayne, 1965; Forêt et al., 2018a; Le Corre et al., 2013). Metamorphosis delay impacts the competent size range of *M. edulis,* which typically falls between 240-260 µm but can extend over 400 µm (Martel et al., 2014). Recent studies have underlined the importance of the trophic cues in the settlement of *M. edulis* and the secondary migration of Mytilidae (Forêt et al., 2018a; Toupoint et al., 2012a). Thus, this species responds to a combination of cues (Jolivet et al., 2016; Morello and Yund, 2016) and may distinguish between positive and negative signals when settling onto the seabed (Morello and Yund, 2016). Some underwater sounds have been recognized as cues by bivalve larvae, aiding in orientation and habitat detection during settlement (Lillis et al., 2013, 2015; Williams et al., 2022). For example, reef sound playbacks may attract oyster larvae, increasing the settlement rates at 500 m from the source of the sound emission (Lillis et al., 2015). More recently, research indicated that sound playbacks from healthy hard bottom habitats (complex soundscapes containing large numbers of snapping shrimp snaps) can influence larval settlement response of bivalves at distances of 10 to 100 m (E. R. Anderson et al., 2021). Despite the evidence of auditory response to sounds (Lillis et al., 2015), the mechanism behind their perception remains unclear (Chauvaud et al., 2018; Solé et al., 2023). Sound propagation in water requires that the sensory system of larvae, including *M. edulis,* be adjusted to this denser medium (Stanley and Jeffs, 2016). To adjust to this media, some pediveligers possess mechanoreceptors such as statocysts, which are fully formed before the larvae begin to crawl (Budelmann, 1992; Cragg and Nott, 1977; Smolowitz, 2021). In adult bivalves, such as the congener *Mytilus galloprovincialis*, a well-developed abdominal sense organ (ASO) is also present (Gosling, 2015; Haszprunar, 1985; Zhadan, 2005).

Non-biological sources of sound, such as anthropogenic sounds (e.g., vessel noise, pile driving, among others), have been increasingly introduced into the ocean soundscape, both intentionally and as a by-product of human activities over the last decades (Duarte et al., 2021; NRC, 2003). Shipping noise, hereafter referred to as vessel noise, is a major contributor to the acoustic background noise in various habitats (Halliday et al., 2021; Hildebrand, 2009; McKenna et al., 2024; NRC, 2023). Moreover, vessel noise has doubled over the past 11.5 years, and projections indicate that this energy emission will double within a similar time frame (Jalkanen et al., 2022). Such noise has a low-frequency range (5-500 Hz up to 10,000Hz), which is detectable by bivalves, and can persist in the water, propagating over long distances (Duarte et al., 2021; Hildebrand, 2009; NRC, 2003; Roberts et al., 2015). In fact, the noise emitted by cargo/container ships dominates the list of the 100 loudest vessels, occupying the top 50 positions regarding source energy input (Jalkanen et al., 2022). In addition to disrupting and masking biophonies, vessel noise has been reported to impact fitness and behaviour of several bivalves and could stimulate the settlement and metamorphosis of biofouling species in laboratory settings (Cervello et al., 2023; McDonald et al., 2014; see table in Solé et al., 2023; Wilkens et al., 2012) and recruitment success in field condition (Gauthier et al., in press). An increased settlement of blue mussels was also observed when vessel noise was combined with a trophic cue, highlighting the need to investigate coastal areas where multiple interacting factors influence species dynamics (Jolivet et al., 2016).

To date, studies investigating the effects of anthropogenic noise on key life stages critical for population replenishment remain sparse (Solé et al., 2023). This gap raises important concerns about how larval settlement and subsequent recruitment may be impacted when pelagic larvae are exposed to noise in combination with multiple stressors. To address this, we carried out *in situ* experiments using artificial collectors deployed in two soundscape environments: ambient sound (control site) and site exposed to vessel noise playback (noisy site). The main objective of this study was to assess and compare the effect of ambient and vessel sounds at two intensities (different distances from the emission source) on the settlement of *M. edulis* during the spawning season in a subarctic area. We hypothesized that collectors positioned closer to vessel noise playback would experience higher settlement rates than those with ambient sound, as seen by Jolivet et al. (2016) under controlled conditions. Our second hypothesis was that the size at metamorphosis for *M. edulis* settlers is impacted and would vary among larval cohorts depending on their proximity to the noise emission.

1.4 Materials and Methods

1.4.1 Study site and experimental design

Newly settled *M. edulis* (pediveligers and post-metamorphosed larvae) were sampled in Miquelon Bay (47°09'73.30" N, -56°38'41.04"W), from Saint-Pierre and Miquelon (SPM) archipelago. SPM is marked by strong and seasonal thermal conditions with an oligotrophic environment (Bridier et al., 2021; Lazure et al., 2018). Miquelon has a sparse population and is only minimally affected by human activities (IEDOM, 2022). Miquelon Bay is considered a near-pristine spot, where only a small ferry navigates in these waters on a regular basis, with a few boats potentially lacking automatic identification system (AIS) during the day, as demonstrated by Gauthier et al. (in press). In addition, a few small recreational boats lacking AIS may be present during the day. The shallow portion of the Miquelon Bay experiences fewer thermal fluctuations and maintains stable trophic conditions (Bridier et al., 2021; Gauthier et al., in review; Lazure et al., 2018). These features and the almost flat bathymetry present in SPM make it an ideal hotspot for conducting sound emission experiments as described in Bonnel et al. (2022). Two sampling sites separated by over 1 km were monitored in Miquelon Bay for the experiments (Figure 9), one with an emission speaker of vessel noise (noisy site) and another without emission, representing ambient conditions (control site). In each site, mussel settlement and environmental conditions were monitored in two stations separated by 150 m (D1 and D2) to assess the influence of vessel noise emission (D1 and D2 at 25 or 175m from the speaker) as well as of the local natural settlement heterogeneity (control site).

1.4.2 **Acoustic characteristics**

To create the experimental vessel soundtrack, we recorded the noisiest vessel in the SPM archipelago, the ‘Nolhan Ava’ (a 120 m cargo ship), standardizing the anthropogenic noise source while varying only the noise level emitted at each distance. This approach was better suited for estimating biological responses across settlers and metamorphosed post-larvae which were sampled every three days. The 1h20min vessel soundtrack was constructed using segments from the Nolhan Ava featuring the arrival and departure (11 min and 8.5 min) at Saint-Pierre harbour separated by silent periods (39 min and 21.5 min), as in our previous study (Gauthier et al., in press).

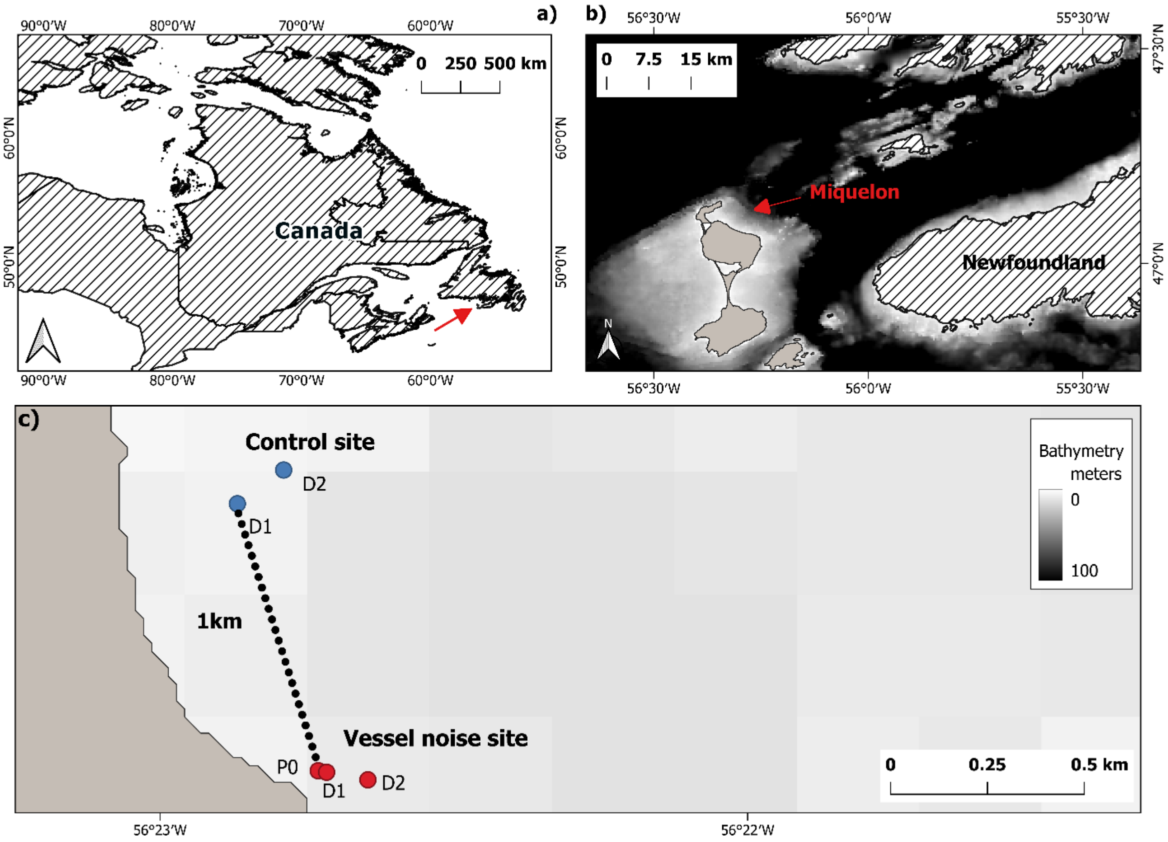


Figure 9: Set of maps describing the study site: (a, b, c). Location of the French Saint-Pierre and Miquelon archipelago in the North Atlantic, Canada. Bathymetric map containing stations (D1, D2) from each sampling site, one site without anthropic noise emission (blue) and a site with vessel noise source (red) positioned close to the pier (P0). Bathymetry data was retrieved from General Bathymetric Chart of the Oceans (GEBCO). Bathymetric maps are composed using grayscale where white represents 0-1 m, 2-30m light to dark gray, and values > 100m are black.

This soundtrack was played in a continuous loop during the experimental period through underwater speakers (Lubell Labs ®VC2C, Columbus, Ohio, USA, 1500 Hz), that were suspended at an 8m depth (P0) and oriented offshore (Fig. 18). The acoustic characterization of ambient and vessel noise was conducted at both sites. In the control site, underwater acoustic recorders (RTSYS-RESEA 320, Caudan, France; Hydrophone Colmar GP1516M, Sensitivity -172 dB re 1V/ µPa @ 5kHz) were deployed for two days in the first sampling week (Table 1).

As a sound wave travels from a source to a receiver in the water, it dissipates energy due to a sum of transmission losses by geometric spreading (spherical, cylindrical or mixed) and attenuation of signals (Urick, 1975). To estimate the transmission loss (TL) at the noisy site, we adopted a mixed spreading loss equation (1) using the geometric spherical spreading loss near the source and the cylindrical spreading loss within the shallow environment (Erbe, 2020; Urick, 1975) to estimate sound levels received at each distance along this site (Table 8) following the equation below:

$$\mathrm{TL} = \frac{20\ log_{10}(\mathrm{D})] + 10\ log_{10}(\mathrm{D})]}{2} = 15\ log_{10}\ (\mathrm{D}) \qquad (1)$$

where TL is the transmission loss in dB, and D is the distance in meters as described in (Coates, 1990, p.19). We opted to estimate TL using a mixed spreading loss because our distance of propagation was five times greater than the water depth (8m) (Bonnel et al., 2022; Erbe, 2020). Based on these calculations, the speaker emitted 144 dB re 1µPa at 0 m from the source, and root mean square of sound pressure level ($\mathrm{SPL_{rms}}$) received at D1-D2 were 128 and 116 dB re 1µPa, where the last station in the noisy site has a similar $\mathrm{SPL_{rms}}$ to ambient sound in the control site (Table 8). Regarding the ambient sound in the control transect, recorders were deployed at 0, 25 and 175m from D1 and D2 stations, respectively for two days on the first week, but also in the second or third sampling week to measure potential heterogeneity of ambient sound. Sound levels within stations were of 116 dB at D1 and 106 dB re 1µPa at D2 in the control site.

Both vessel soundtrack playback and *in situ* recordings from ambient and vessel noise emitted were visually inspected using the spectrogram function of Audacity 3.0.4 (Audacity Team, 2021) to detect the frequency and amplitude of the vessel and ambient sound (0 – 8 kHz). Posteriorly, each 14-min audio was cut into 8 min, and sound pressure level ($\mathrm{SPL_{rms}}$) and power spectral density (PSD) of these recordings were analyzed using the software MATLAB R2021a, as described in Gauthier et al. (in press).

Table 1: Location and sampling points, distances (m) from the ambient conditions (control site) or speaker playing vessel noise (noisy site), point coordinates (º,",'), depth (m), and levels of sound received (dB re 1µPa) at each distance (D1, D2) sampled in control and noisy site in Miquelon, France

Sites and sampling distances	Distances sampled at control and vessel noise sites (m)	Received level of sound (dB)	Depth (m)	Coordinates	
Control				Latitude	Longitude
D1	25	116	8	47° 41' 09" N	56° 13' 24" W
D2	175	106	8	47° 41' 47" N	56° 13' 12" W
Noisy					
P0	0	144	8	46° 47' 39" N	56° 09' 29.5" W
D1	25	128	8	46° 47' 38.5" N	56° 09' 28.4" W
D2	175	116	8	46° 47' 41.3" N	56° 09' 23.6" W

We characterized sound levels received in each site and station using the SPL_{rms} (0 – 10 kHz), and sound exposure level (SEL_min, 0 – 10 kHz). For this characterization, we chose to present the sound levels recorded from 10 pm to 3 am to minimize potential daily interferences by fishing and recreational boats. For the PSD, we detailed how the sound energy or intensity is distributed within a large band [0- 10,000 Hz] as well as in a low frequency band [0 - 2,000Hz], as it is a sensitive hearing range for mussels (Roberts et al., 2015).

1.4.3 Environmental conditions

Temperature was monitored at both sites in the bay during the experimental period. Due to a parallel trial on the bay using a similar design of noisy and control sites, we assessed temperature using VR2Tx receivers (Innovasea, Halifax, Canada) anchored by a 50kg mooring system and positioned at 1.5 m from the seafloor at the noisy site (60m from the speaker, n = 3) and the control site (n = 3) as described in Uboldi et al., (submitted). Trophic characterization was realized by sampling water weekly in the middle of D1 and D2 stations in each site and was conducted to assess the food available for *M. edulis* settlers and post-larvae. This design was established given the previous year's findings of homogeneity in seston quantity (mg.L^{-1} dry weight) and quality (mass of total fatty acids, fatty acid profile, fatty acids trophic markers) along a transect near 1 km (Gauthier et al., in press). Seawater samples (n=3.5 L each) were collected at 6 m depth using Niskin bottles and stored in opaque bottles to be transported to the coast for filtration on pre-combusted and pre-weighed 47mm GF/F filters, stored at -40ºC for a month, and subsequently transferred to -80ºC. The planktonic composition of the seston was assessed on three samples (4.5 ml of pre-filtered seawater) filtered through a 40µm sieve, fixed with glutaraldehyde (0.1 % final v/v) and stored at -40ºC for a month before their transfer to -80ºC for further analysis. To quantify bacteria, cyanobacteria and eukaryotes according to pico- (0.2 – 2µ), and nanoplankton size classes (< 20µ) in both transects, samples were identified and quantified using an Epics Altra flow cytometer (Beckman Coulter Inc., Fullerton, CA, USA) following the methods outlined by Belzile et al. (2008) and Tremblay et al. (2009). Unfortunately, five samples from the noisy site could not be analyzed due to sample loss during transport.

1.4.4 Mussel settler's monitoring

We conducted the study from July 2nd to 21st, 2022 with sample collection every three days (six sampling periods). At each station, a set of five collectors (replicates) consisting of 2-mm mesh bags, containing four inverted Netron® sections (40 x 80 cm, mesh size 5 mm, area 0.320 m²) was moored close to the bottom and kept in place by subsurface buoys, as detailed in Gauthier et al. (in press) and in Fig. S4. At each sampling date, the five collectors were individually cleaned over a 100µm plankton net and replaced with new ones. The accumulated material of each collector was transferred to labelled plastic bags, preserved on ice, identified (Aucoin et al., 2004) and quantified under a stereomicroscope. Settled pediveligers (settlers) were distinguished by the presence of a mobile foot, eye spot, and prodissoconch II shell, while metamorphosed post-larvae were identified by the presence of gills and a dissoconch shell (Toupoint et al., 2012a). Settlement and metamorphosis rates were assessed by counting the number of settlers and post-larvae every three days at each station. Both settlement and metamorphosis rates were expressed as the number of individuals per collector (ind.collector^{-1}). Individual post-larvae were preserved at -40ºC for further morphometric analyses. Once in the laboratory, we assessed the total shell length (TL), prodissoconch I (PI), prodissoconch II (PII) and dissoconch lengths (µm), as described by Martel et al. (2014) using a Keyence VHX-2000 Series digital microscope with VH-Z100UR objectives (Osaka, Japan, 1µm and HDR resolution, 300x and 500x). The morphometric analyses of ~ 6 randomly selected individuals per collector (~30 individuals per station and sampling period) were performed on a total of 740 post-larvae.

1.4.5 Fatty acid composition of seston

Filters containing seston were freeze-dried for 24 h using a Labconco freeze-dry system (Kansas City, MO, USA) prior to the lipid extraction procedure. Lipids were extracted following a Folch et al. (1957) procedure adopted by Parrish (1999). Fatty acid methyl esters (FAME) were prepared according to the method describes in Lepage and Roy (1984) and were analyzed by a GC-MS (Thermo Fisher Scientific Inc., GC model Trace Ultra and MS model ITQ900) equipped with a Supelco Omegawax 250 capillary column (30 m x 250 µm x 0.25 µm film thickness). Initial oven temperature was 100ºC for 2 min, then 140ºC for 1 min and was increased at a rate of 10ºC min^{-1} until it reached 270ºC for 15 min. Injector temperature was 90ºC, with a constant helium flow of 1.0 mL min^{-1}. A 1 µL sample was injected. Fatty acids (FA) were identified and quantified by comparing retention times and mass spectrum with known standards calibration curve with concentration ranging from 0.5 to 20 µg/ml (Supelco 37 Component FAME Mix Supelco Inc., Belfonte, PA, USA) with the use of Xcalibur v.2.1 software (Thermo Scientific, Mississauga, ON, CA). The list and relative contributions (%) (i.e. FA profile) of all FA contained in samples were further detailed in Table S13. FA profile was also discriminated into trophic markers such as bacteria (∑ai15:0, iso15:0, 18:1ω7), degraded organic matter (∑ 14:0, 16:0, 18:0), diatoms (∑16:1ω7, 20:5ω3), dinoflagellates (∑22:6ω3), green (∑18:2ω6, 18:3ω6, 18:4ω3) and brown macroalgae (∑ 18:1ω9) following references cited in Table S14.

1.4.6 **Statistical analyses**

Differences in temperature at control (n = 3) and noisy sites (n = 3) were evaluated using a two-way permutational multivariate analysis of variance (PERMANOVA) to detect if there were any differences in temperature within date (14 levels, July 8^{th} to July 21^{st}), and sites (2, levels). Temperature data was converted into a matrix through Euclidean distance. Due to our previous work showing that seston quantity (TPM) and quality (MTFA, FA profile, trophic markers, food sources) were homogenous in Miquelon Bay (Gauthier et al., in review), we opted for globally characterizing these parameters using descriptive statistics. A three-way PERMANOVA was conducted to analyze settlement (pediveliger) and metamorphosis rates (post-larvae) of *M. edulis*, with factors including two levels of distance from the source (D1, D2), two types of sound (ambient and vessel noise) and six dates (5, 8, 11, 14, 17 and 20 July 2022). Each development stage data was converted into a matrix using Euclidean distance. Similarly, post-larvae shell morphometrics (PI, PII, TL, and larval growth rates) were tested using the same three-way PERMANOVA model and factors. Each morphometric parameter was converted into a matrix using Euclidean distance. For all statistical analyses, results were reported using the language of evidence rather than significance, adopting the ranges suggested by Muff et al. (2022): little or no evidence ($0.1 < p < 1.0$), weak evidence ($0.05 < p < 0.1$), moderate evidence ($0.01 < p < 0.05$), strong evidence ($0.0001 < p < 0.01$), and very strong evidence ($0.0001< p < 0.001$). All PERMANOVA analyses were performed using PRIMER 7.0. Graphs for settlement, and shell morphometrics were plotted using GraphPad Prism 8.0.

1.5 Results

1.5.1 Environmental conditions and acoustic characterization

Statistical analyses confirmed an interaction effect between date and site on temperature (Table 2). Daily mean temperature (SE) ranged from 7.3 ± 0.1 to 9.8 ± 0.1 °C in the control site, while values fluctuated from 8.0 ± 0.1 to 10.5 ± 0.1 °C in the noisy site, with pairwise tests showing strong evidence of variations on almost all dates within sites and between sites (Table S1).

Table 2: Results of two-way permutational multivariate analyses (PERMANOVA) testing the effect of date (Da, 14 levels), and site (Si, 2 levels) on the daily temperatures recorded at sites with distinct soundscapes (ambient sound – Control vs speaker emitting vessel noise - Noisy) during July 8th to 21st 2022 in Miquelon, France. Significant values ($p<0.05$) are indicated in bold.

		Temperature (°C)		
Control vs. Noisy	*df*	*Pseudo-F*	*p-perm*	*perms*
Date	13	91.8	**0.0001**	9934
Site	1	311.8	**0.0001**	9830
Da x Si	13	2.7	**0.0007**	9923
Res	1894			
Total	1921			

Seston concentration (TPM dry mass mg.L^{-1}) varied between 2.3 and 3.5 mg.L^{-1}, with a mean concentration (SE) of 2.7 ± 0.3 mg.L^{-1}. Food sources included a high dominance of total bacteria concentrations of 0.8 ± 0.03 x 10^{6} cells.ml^{-1}, an abundance of pico-cyanobacteria and pico-eukaryotes (12.8 ± 0.7 x 10^{3} cells.ml^{-1}, 10.9 ± 0.6 x 10^{3} cells.ml^{-1}) greater than that of nano-cyanobacteria (0.21 ± 0.03 x 10^{3} cells.ml^{-1}) and nano-eukaryotes (2.9 ± 0.2 x 10^{3} cells.ml^{-1}). The mass of total fatty acids (MTFA) ranged from 4.3 to 6.8 µg.mg^{-1}, mean concentration (SE) of 5.7 ± 0.6 µg.mg^{-1} (Fig. 10b-f) The fatty acid composition was dominated by saturated fatty acids (52-55%), followed by monounsaturated (22-24%) and polyunsaturated fatty acids (22-25%, Table S2-S3). Trophic markers indicated a predominance of degraded organic matter (50.3%) in seston, along with contributions from diatoms (12.7%), dinoflagellates (9.6%), brown (15.1%), and green macroalgae (4.4%, Table S3). Bacteria markers (∑iso15:0) were found to be less than 0.4%, and certain markers such as ai15:0 and 18:1w7 were not detected in the samples.

For the acoustic characterization, theoretical calculations and sound pressure levels recorded *in situ* were overall similar. The mean SPL (SE) recorded at the control site was 103.0 ± 0.1 dB 1 re µPa, whereas the vessel noise emission at source (P0) in the noisy site had a mean SPL (SE) of 128.9 ± 0.1 dB re 1 µPa (Table 2, Figure 11a-b), indicating a Δ25 dB of SPL between both sites. The power spectral density analysis (PSD, Figure 11c-d) illustrated a clear distinction in the maximum power levels between ambient sound and vessel noise. The PSD graph revealed that the noisy site consistently had higher PSD levels than the control site, indicating that the sound energy produced by vessel noise contributed significantly across nearly all frequencies. A notable difference between the vessel noise emission and the surrounding ambient sound was observed below 2,000 Hz, with vessel noise being significantly louder than ambient sound (Figure 11c). Noise emission from the vessel reached a maximum of 110 dB re 1 µPa. Hz^{-1} at 100 Hz, while the control site peaked at 80 dB 1 re µPa. Hz^{-1}. The PSD decrease was also distinct in both sites, with vessel noise maintaining higher energy levels compared to the control site (Figure 11d). Mean sound exposure levels at the control site were 121.4 ± 0.1 dB 1 re μPa^2.s, compared to 146.7 ± 0.2 dB re 1 μPa^2.s at P0, 126.6 ± 0.2 at D1, and 127.1 ± 0.1 D1 at D2, in the noisy site. In the low-frequency range perceived by bivalves (0-2,000 Hz, Roberts et al., 2015, Duarte et al., 2021), the mean SPL was 129.5 ± 0.7 dB 1 re µPa at the noisy site and 101.9 ± 0.2 dB 1 re µPa at the control site.

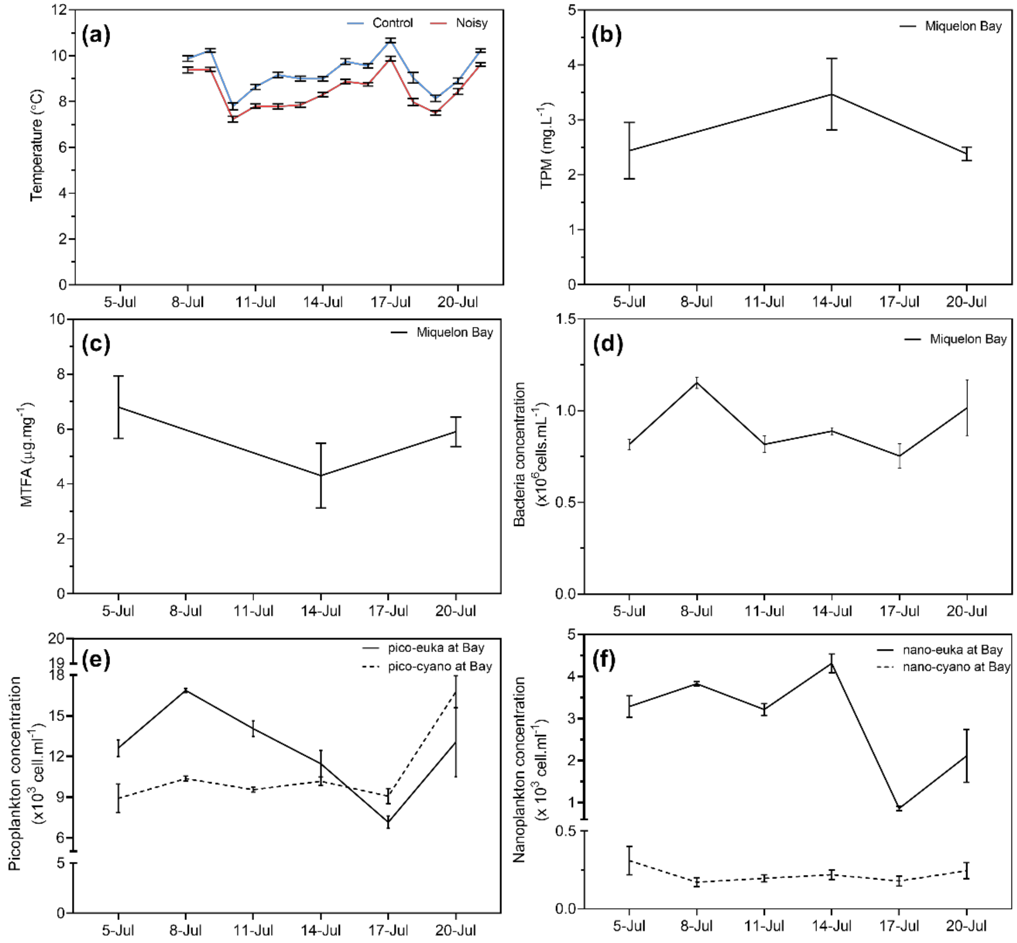
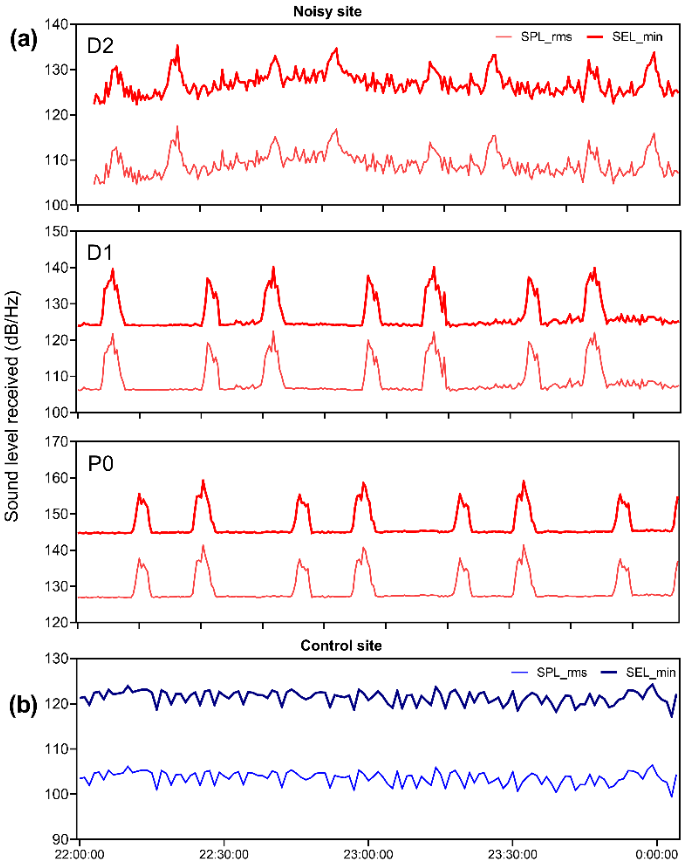
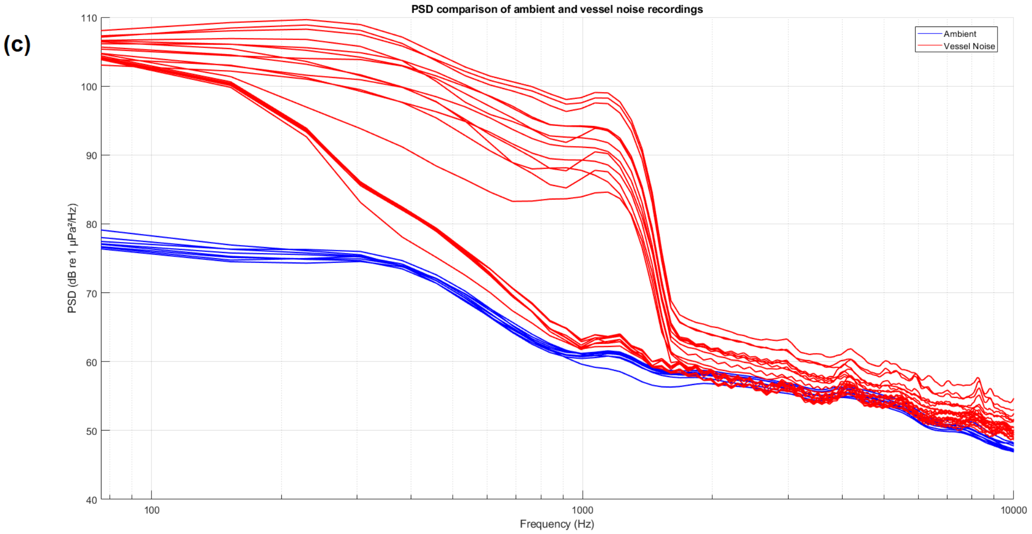


Figure 10: Mean (±SEM) of temperature (n = 3, a) at each site, seston quantity (TPM, n = 6, b) and quality (MTFA, c, n = 6, along with food sources – bacteria, picoplankton and nanoplankton, d, e, f, n = 6) at Miquelon Bay, encompassing both control and vessel noise sites, during the sampling period from July 3 to 21st, 2022. Due to consistent patterns across distances in 2021 (Gauthier et al., in press), and the similarity of physical-trophic conditions between the two years (2021 and this study), we present mean levels for both sites combined. Y-axis on figures 2e and 2f were divided into two or three segments to visualize both size classes (nano and pico) of nanoplankton and picoplankton.


Noisy site
(a)
D2
SPL_rms
SEL_min
140
130
120
110
100
D1
150
140
130
120
110
100
P0
170
160
150
140
130
120
Sound level received (dB/Hz)
Control site
(b)
SPL_rms
SEL_min
130
120
110
100
90
22:00:00
22:30:00
23:00:00
23:30:00
0:00:00


(c)
PSD comparison of ambient and vessel noise recordings
Ambient
Vessel Noise
110
100
90
80
70
60
50
40
PSD (dB re 1 μPa²/Hz)
100
1000
10000
Frequency (Hz)

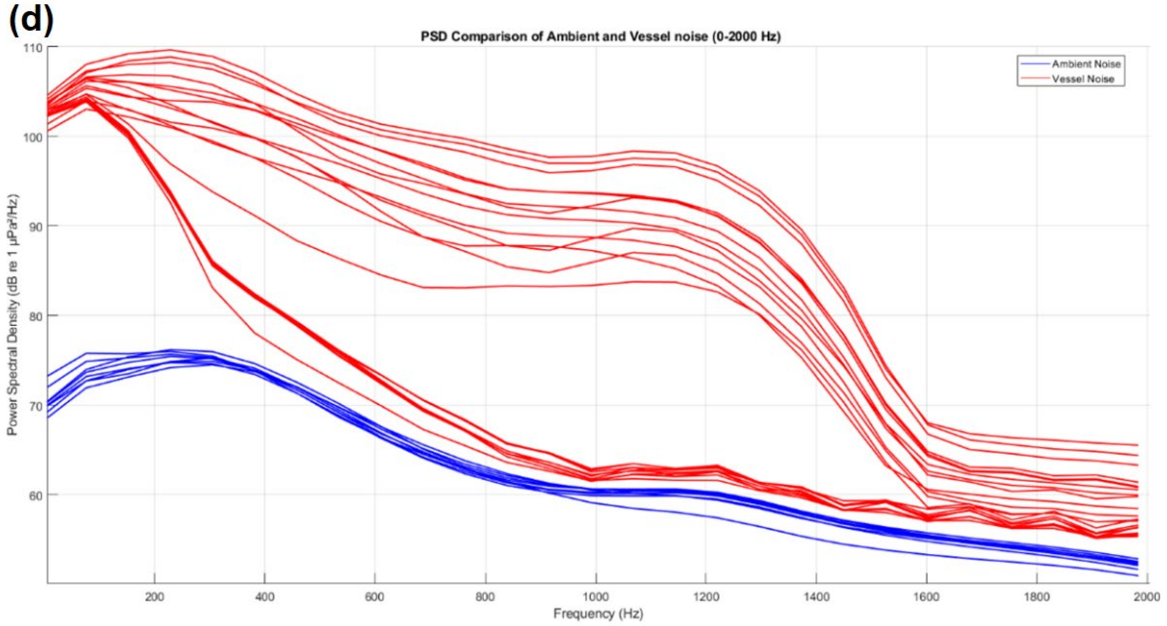


Figure 11: Acoustic characterization of the two sites with soundscapes composed of ambient sound (control) or vessel noise soundtrack emitted *in situ* (noisy site). Root-mean-squares of sound pressure level (SPLrms, 0 - 10,000 Hz), and sound exposure level per minute (Le, 0 – 10,000 Hz) recorded at noisy site (vessel noise, a) and control site (ambient noise, b). Power spectral density comparison (PSD, c and d) between ambient and vessel noise respectively recorded at control and noisy sites. Plot A and B have an x-axis of sampling period from 10pm to 3am, and y-axis corresponding to SPLrms or SEL_min in decibels re 1µPa. Due to some recording issues, we are only able to plot SPL and SEL_min in the control site from 10 pm to 00am. Plot C and D have an x-axis of frequency in hertz (b, 0 – 10,000 Hz; c, 0 – 2,000 Hz), and y-axis of PSD in decibels/Hz.

1.5.2 **Settlement of *Mytilus edulis* in different site soundscapes**

The settlement rate of *M. edulis* exhibited similar patterns at both sites, showing a very strong temporal decline over the sampling period (Table 3, Figure 12a). There was little to no evidence that the interaction of the three factors – date, distance and sound (Da x Di x So, Table S4) – or any of the two-factor interactions (Da x Di, Da x So or Di x So) influenced the settlement success. Pairwise analyses revealed that settlement success was higher for the first sampling dates (Figure 12a) with the highest abundance recorded on July 5th and 8th with means of 14 ± 5, and 9 ± 4 ind.collector $^{-1}$, respectively, then decreasing sharply to fewer than 4 ind.collector $^{-1}$.

Table 3: Results of three-way permutational multivariate analyses (PERMANOVA) testing the effect of date (Da, 6 levels), distance (Di, 2 levels), and sound type (2, levels) on settlement and metamorphosis rates of Mytilus edulis retrieved on sites exposed to ambient (Control) or a speaker emitting vessel noise (Noisy) in Miquelon, France. Significant values ($p<0.05$) are indicated in bold.

	Settlement (ind.collector^{-1})				**Post-larvae abundance (ind.collector^{-1})**			
Control vs. Noisy	*df*	*Pseudo-F*	*p-perm*	*perms*	*df*	*Pseudo-F*	*p-perm*	*perms*
Da	**5**	**3.08**	**0.01**	**9923**	**5**	**9.51**	**0.0001**	**9948**
Di	1	0.48	0.51	9756	1	0.30	0.60	9852
So	1	0.45	0.52	9787	**1**	**8.86**	**0.002**	**9830**
Da x Di	5	0.22	0.94	9953	5	0.71	0.64	9934
Da x So	5	1.10	0.38	9938	**5**	**3.54**	**0.004**	**9940**
Di x So	1	0.23	0.62	9796	1	1.26	0.28	9848
Da x Di x So	5	0.64	0.73	9936	5	0.21	0.96	9942
Res	92				93			
Total	115				116			

Post-larvae abundance was a magnitude higher than that of settlers, peaking at 119 ind.collector^{-1}, without interaction among the three factors (Da x Di x So, p = 0.94). However, there was strong evidence that post-larvae abundance varied between date and sound type interaction (Table 3). Pairwise tests indicated that the metamorphosis rates at the control site were at least three times more important during half of sampling periods compared to the noisy site (Figure 12b, and Table S5). Post-larvae abundance peaked at both sites on July 5th, followed by a subsequent decline that was more pronounced at the noisy site.

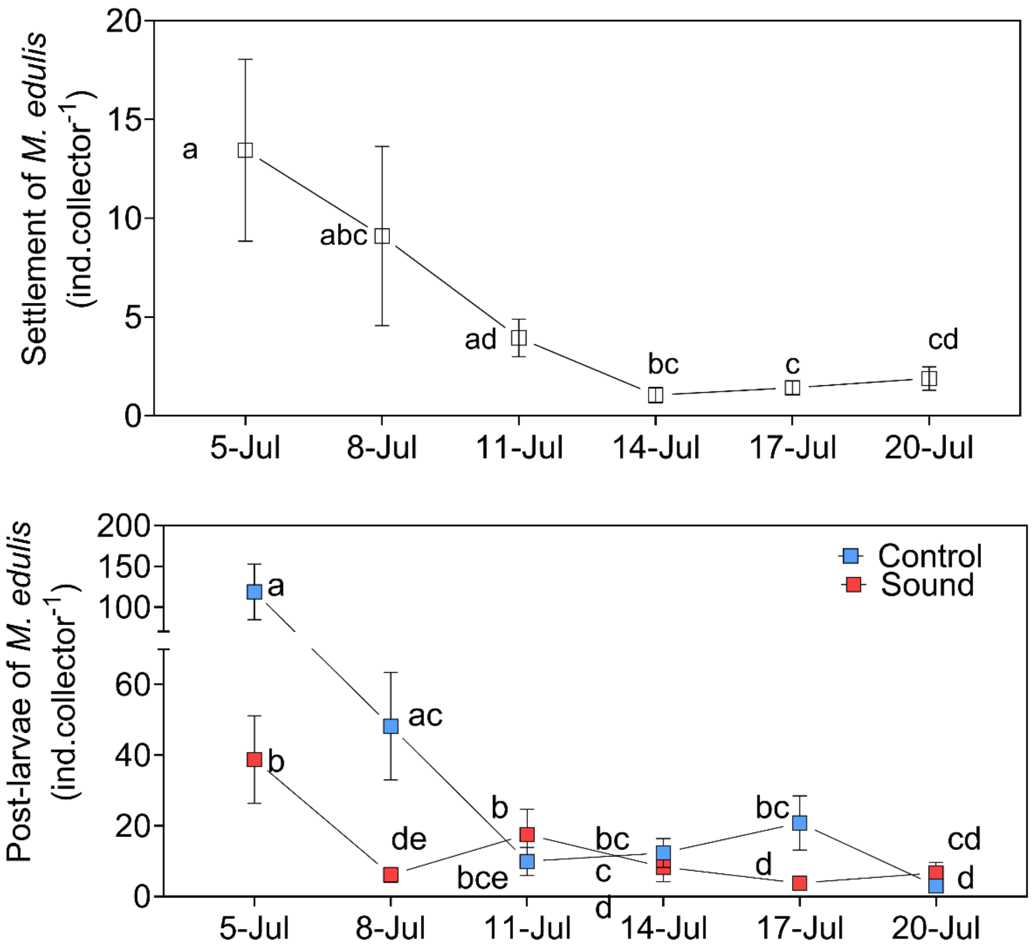


Figure 12: *Mytilus edulis* settlers (**a**) and metamorphosed post-larvae (**b**) abundance per date (5, 8, 11, 14, 17 and 20 July) in collectors moored from the ambient sound (blue, control) or vessel noise (red, noisy) sites over 3-weeks in July 2022. Squares represent the means at each date with standard error bars. Settlement is compared over dates, as no significant effect of distance or the interaction among distance, date or sound was revealed ($p > 0.05$). Post-larvae abundance showed strong evidence of an interaction between date and sound type ($p < 0.05$). Dissimilar letters indicate moderate to strong evidence of differences in post hoc analysis.

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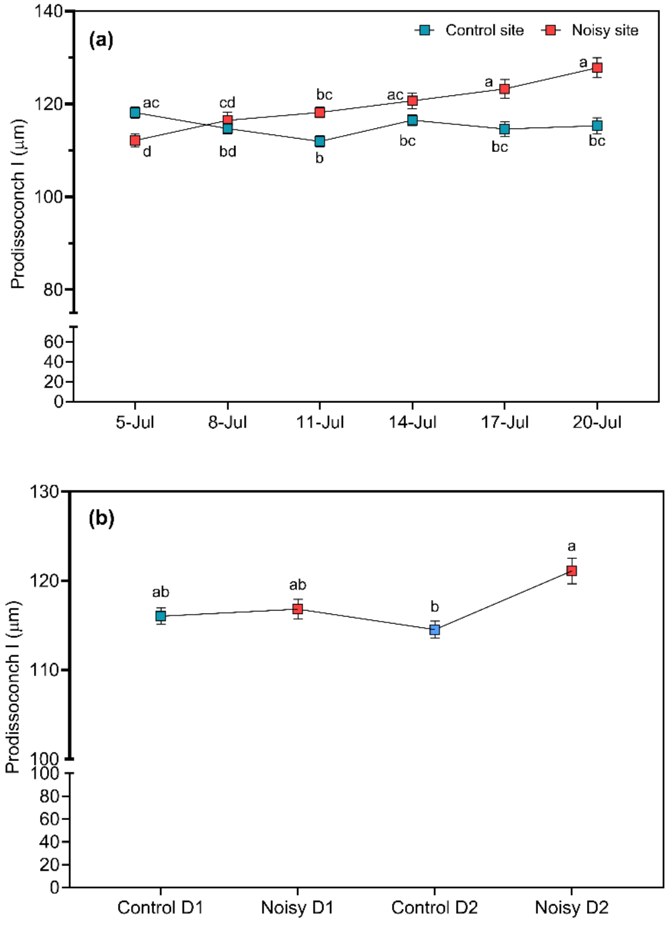
1.5.3 Shells morphometrics in the presence of different sounds

PI size was not affected by the three-factor interaction, but there was moderate and strong evidence for a two-factor interaction between distance and sound, and between dates and sound treatments (Table 4). Regarding distance and sound, a 5% difference in PI size was observed at D2 between the noisy site and the control site, while no size differences were detected within distances at either the control or noisy sites (Figure 13a-b).

Table 4 : Results of three-way permutational multivariate analyses (PERMANOVA) testing the effect of date (Da, 6 levels), distance (Di, 2 levels), and sound type (2, levels) on shell morphometrics composed by prodissoconch I, prodissoconch II and total lengths of *Mytilus edulis* retrieved on sites exposed to ambient (Control site) and vessel noise playback (Noisy site) in Miquelon, France. Significant values ($p<0.05$) are indicated in bold.

Sites	**Prodissoconch I (µm)**				**Prodissoconch II (µm)**			
Control vs. Noisy	*df*	*Pseudo-F*	*p-perm*	*perms*	*df*	*Pseudo-F*	*p-perm*	*perms*
Da	5	2.89	**0.014**	9939	5	1.31	0.26	9939
Di	1	1.22	0.27	9826	1	0.74	0.39	9919
So	1	10.77	**0.0011**	9827	1	1.27	0.27	9923
Da x Di	5	1.06	0.38	9945	5	0.80	0.56	9957
Da x So	5	6.02	**0.0003**	9950	5	0.50	0.78	9944
Di x So	1	4.04	**0.04**	9808	1	0.35	0.55	9936
Da x Di x So	5	1.69	0.13	9936	5	1.25	0.28	9945
Res	481				510			
Total	504				533			
	Larval growth (µm.d^{-1})				**Total length (µm)**			
Control vs. Noisy	*df*	*Pseudo-F*	*p-perm*	*perms*	*df*	*Pseudo-F*	*p-perm*	*perms*
Da	5	2.61	**0.026**	9953	5	4.23	**0.001**	9948
Di	1	2.15	0.15	9829	1	0.66	0.43	9938
So	1	7.88	**0.0051**	9849	1	0.89	0.34	9943
Da x Di	5	0.26	0.93	9948	5	2.44	**0.03**	9940
Da x So	5	1.21	0.30	9946	5	2.11	0.06	9948
Di x So	1	0.92	0.34	9960	1	2.24	0.13	9942
Da x Di x So	5	1.12	0.35	9938	5	3.22	**0.006**	9944
Res	484				510			
Total	507				533			

Variations in PI sizes according to sound treatments and date were observed at the first and the last two samplings, showing inverse trends: PI size was 5% larger under ambient sound conditions on July 5th, but 10% smaller on the 17th and 20th ($t = 2.18 – 2.48$, $p < 0.01$, Table S6). Larger PI sizes were recorded on July 20th at the noisy site's most distant station from the speaker, with a mean of 127.8 ± 2.1µm, representing a 12% increase in PI compared to July 5th (Figure 13a-b, Table S6). No interaction or factor effects were observed for prodissoconch II (PII) size, with a mean length of 331.6 ± 1.3µm (Table 4, Figure 13c), and a maximum value of 413.3 µm, exceeding the theoretical competent size of 250 - 260 µm.



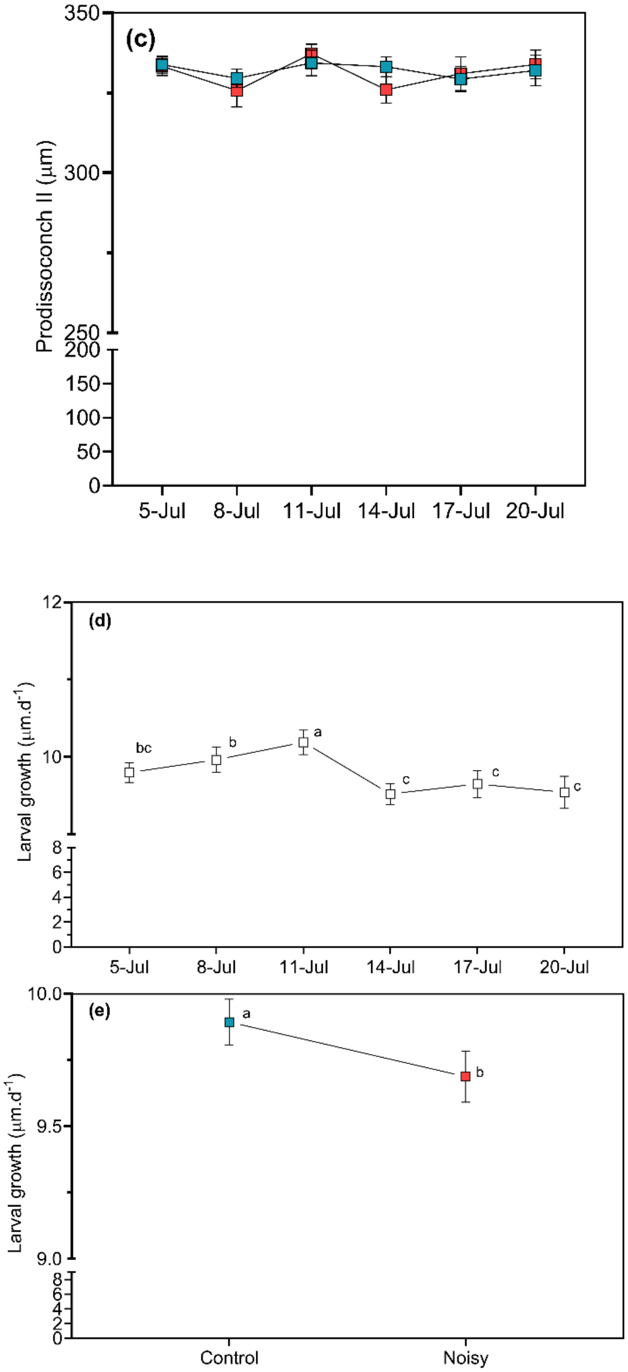


Figure 13: Mytilus edulis prodissoconch I length (a, b), prodissoconch II length (c), and daily larval growth (µm. d-1) (d, e) in the presence of ambient sound (Control site) and vessel noise (Noisy site) from two intensities (D1, 25m/128 dB; and D2, 175m/116 dB).

We estimated the larval growth rate (from veliger to competent pediveliger stage) by calculating the difference between PII and PI size, divided by 22 days of larval growth period identified by Rayssac et al. (2010) for *M. edulis* at 10°C, which was the maximum temperature recorded during this study. There was strong evidence that only date and sound individually affected mussel larval growth (Table 4). In the control site, mean larval growth was 3% higher than in the noisy site, with the highest growth observed on July 11th (10.2 ± 0.2 $\mu m.d^{-1}$) (Figure 13e, Table 4, Table S7). Only total length (TL) of post-larvae was strongly affected by the interaction of the three factors (Table 4, with no evident trend to explain the observed variations in TL, which ranged from 500 to 700 µm (Figure 14a-b).

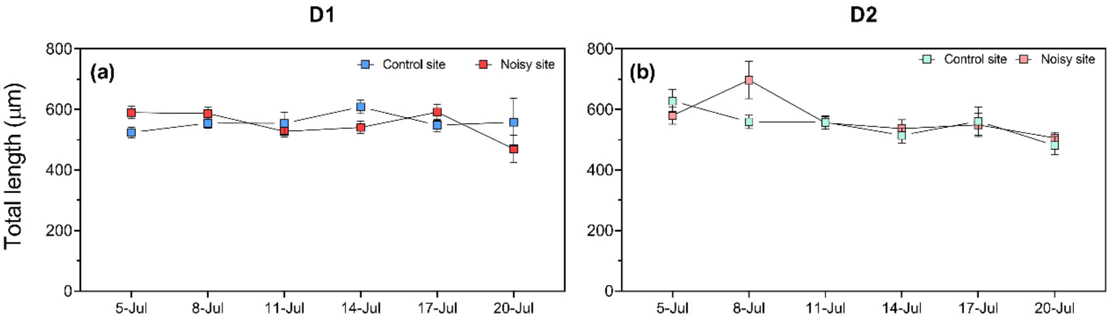


Figure 14 : Mean total length of *Mytilus edulis* retrieved from two distances (D1, 25m; and D2, 175m) from ambient sound (Control, blue and light blue) and vessel noise sites (Noisy site, red and light coral) over July 2022 in Miquelon, France. Due to a three-factor interaction and no clear pattern, graphs are only showing total length at sites and distances. Coloured squares represent the mean; error bars indicate the standard error.

1.6 Discussion

Underwater soundscapes have been generally recognized as crucial cues for bivalve settlement (Anderson et al., 2021; Lillis et al., 2013, 2015; Stocks et al., 2012). The effectiveness of these cues relies on the type of sound and the distance over which it is detected (Anderson et al., 2021; Radford et al., 2010; Williams et al., 2022). Some experimental studies indicate that vessel noise may intensify (Jolivet et al., 2016 ; Veillard et al., 2025) or not (Cervello et al. 2023) the settlement and metamorphosis success of blue mussels. A field study based on monthly sampling showed that recruitment success may be stimulated by vessel noise, depending on noise intensity (Gauthier et al., in review), with stimulation observed at threshold levels below 135 dB re 1 μPa^2.s, while inhibition occurred at levels above 140 dB 1 re μPa^2s. However, in this field study, based on an experimental design involving a three-day sampling interval, we did not validate the hypothesis of settlement stimulation by vessel noise. Nonetheless, metamorphosis rates of post-larvae – the most abundant stage in the artificial collectors in this experiment– were modulated by the sound environment, with vessel noise impairing the first larval cohort. The presence of post-larvae up to 700 µm total length within the collectors immersed for three days suggests that their occurrence seem likely due to secondary migration process, a behaviour largely documented in *M. edulis* (Bayne, 1965; Forêt et al., 2018a; Forêt et al., 2018b; Lane, Beaumont and Hunter., 1985; Le Corre et al., 2013). By visually inspecting the temperature data, slight variations occurred within dates in each (0.7 –2.5 °C) and between sites (0.6 – 1.4 °C). These variations should be considered non-stressful for mussels, as previous studies have shown that mussel metabolism is thermosensitive to a broader temperature range (5-20°C) than those recorded in this study (Tremblay et al., 1998). This absence of temporal and spatial variations in environmental and trophic conditions in Miquelon Bay during the July sampling period indicates that the settlement and secondary migration peaks observed in early July were not driven by these external factors. The oligotrophic conditions of Miquelon Bay are highlighted by the prevalence of degraded organic matter markers (> 50%), and notable dominance of total bacteria (0.8 to 1.2 x 106 cells.ml-1), as already demonstrated by

Bridier et al. (2021) and Gauthier et al. (in press, Chapter III). Such organic matter, rich in saturated fatty acids (SFA), could serve as a potential energetic food source for bivalve larvae and post-larvae (Leal et al., 2022), creating a favorable benthic environment in this typically nutrient-depleted region (Flores et al., 2015; Leal et al., 2018). However, the low level of essential fatty acids (below 18%), particularly in 20:5ω3 and 22:6ω3 could affect settlement success (here < 20 settlers. collector-1), as demonstrated by Toupoint et al. (2012a) who observed similar results in *M. edulis* when the content of the same fatty acids was below 20% in POM and higher settlements for values over 25%.

1.6.1 **Soundscapes and settlement**

Soundscapes differed between ambient (SPL_{rms} = 103.7 dB re 1µPa) and vessel noise sites (SPL_{rms} = 128.9 dB re 1µPa), exposing mussels to distinct sound pressure and sound exposure levels (P0 at each transect, $SEL_{min\ ambient}$ vs. $SEL_{min\ vessels}$ = 121.4 vs 146.7 dB re 1 μPa^2.s i.e. ~ 25 dB re 1 μPa^2.s of difference). These sound levels in the control site are consistent with a previous study in the western Canadian Arctic, where ambient sound levels (bands 50-1,000Hz) may range from 90 dB to 110 dB re 1µPa depending on the wind speed (Halliday et al., 2021). According to the literature, the impact of anthropogenic noise on bivalves can vary depending on factors such as duration of exposure, the species affected, and the distance from the noise source (Hawkins and Popper, 2017). Recent findings by Gauthier et al. (in press, Chapter III) reveal that early recruitment of Mytilidae was 4-5 times higher at a close distance (25m, 137 dB re 1 µPa) compared to farther distances (890m, 106 dB re 1µPa) when exposed to vessel noise, suggesting a threshold of noise exposure level (SEL < 140 dB re 1μPa^2.s) to prevent shifts in recruitment. Contrary to this previous work where collectors were removed and replaced each month, representing cumulative temporal recruitment, the pattern of sampling here was only three days and focus on the early settlement process. With similar $Spe_{rm's}$ and SEL_{min} (< 140 dB 1 re μPa^2.s), the increase in settlement relative to distance was not observed. The results are not in accordance with laboratory experiments on the same species, where settlement of mussels was increased by vessel noise emission with or without the presence of trophic settlement trigger (Jolivet et al. 2016). However, these authors use larvae produced in hatchery feed with a constant feeding regime (mix of *Pavlova lutherie*, *T-isochrysis lutea* and *Chaetoceros muelleri*), demonstrated to be rich in essential fatty acids (EFA) with the sum of 20:5ω3 and 22:6ω3 over 35% (Bassim *et al*. 2015). Thus, in the absence of particulate organic matter rich in EFA, vessel noise was not efficient in triggering the settlement. Sensitivity to noise can vary in the ambient soundscape (Radford et al., 2010), with some sounds potentially serving as cues for larval settlement (Anderson et al., 2021; Kingsford et al., 2002; Lillis et al., 2013, 2015). In our previous work conducted in 2021, we explored whether anthropogenic noises (vessel noise and mix of vessel noise + pile driving) could disrupt early recruitment of bivalves in Saint-Pierre and Miquelon archipelago. Our findings revealed shifts in early recruitment of bivalves including mytilids were related to anthropogenic noises with different sound exposure levels (vessel noise = 132-135 dB vs. mixture > 140 dB re 1µPa^2.s). Interested in unveiling if vessel noise could stimulate the settlement at a finer temporal scale, we focused this sampling effort on July when the major peak of abundance of *M. edulis* recruits was observed in collectors (Gauthier et al., in review). In the present study, the vessel noise exposure level was within the range of 126-127 re 1 µPa^2.s (D1-D2), a 6-8 dB reduction compared to 2021. Despite this reduction in the exposure level, the comparison of data from 2021 and 2022 at a similar distance (2021: 1,815 and 913 ind. collector, 2022: 3 and 6 ind.collector^{-1}) and similar sampling dates (end of July) suggests a poor annual recruitment or an early or late recruitment season in 2022. The high variability in *M. edulis* settlement and recruitment has been widely documented across some regions of the GSL, with strong fluctuations depending on the environmental conditions (Cyr et al., 2007; Guillou et al., 2020; Le Corre et al., 2013; Martel et al., 2014; Toupoint et al., 2012a). Thus, the poor settlement success observed in this study could be related to the limited sampling period of three weeks or to a low larval production season. This low abundance of settlers during the experiment could limit the observation of a noise effect. Anderson et al. (2021) similarly reported a low larval response when broadcasting oyster reef sounds from a healthy and degraded habitats at various distances, suggesting that the probability of a few larvae to encounter sounds over distances was minimal. Given the complexity and presence of multiple of cues, the timing of the larval settlement, larval quality and environmental variations, more fieldwork is necessary to validate if settlement is triggered by vessel noise at a finer scale and if the response could be modulated by larval abundance.

1.6.2 **Soundscapes and metamorphosis**

Settlement of mussel larvae is followed by their metamorphosis into post-larvae, where individuals develop their gills increasing their feeding capacity and growth rate (Cannuel et al., 2009; Riisgård et al., 1980). This process is highly energetic (Pechenik, 2006), where larvae do not feed up to three days before this process and relies only in the energy reserves accumulated, followed by significant mortality (Gagné et al., 2010). Studying this process is crucial but challenging because it involves monitoring small individuals over short sampling intervals in environments where factors vary across spatial-temporal scales (Butman, 1987; Hunt and Scheibling, 1997). This variability in spatial and temporal patterns may be attributed to a mosaic of factors before, during and after the settlement (Pawlik, 1992), thereby modulating the metamorphosis process. In this study, we observed substantial reductions (3 to 8-fold) in post-larvae abundance for the first larval cohort exposed to vessel noise compared to control conditions (but see Figure 25). This *in situ* reduction (67-87%) contrasts with the findings of Veillard et al. (2025), where mussel larvae had higher metamorphosis success (~50 %) when exposed to high intensity of vessel noise (151 dB re 1µPa) compared to control conditions (20%, 116 dB re 1µPa) in a controlled *Larvosonic* system. Our observed decline in metamorphosis aligns more closely with the results of Gigot et al. (2023), who reported a 43% reduction in scallop metamorphosis success when larvae were exposed to continuous drilling noise emitted at two levels (SPL_{rms} = 126.8 and 175.4 re 1 µPa) compared to control, also using the *Larvosonic* system. It is important to note that this present study was carried out in the field, where the ecological realism is higher, but the controllability of environmental factors is null compared to laboratory studies (Spicer, 2014). Furthermore, these two previous studies have the potential to standardize the parameters as much as possible, varying only the sound emission through the *Larvosonic* system.

Although contrasting results are found here when compared to those of Veillard et al. (2025), the possibility of metabolic stress remains a plausible outcome *in situ*, as these authors demonstrated that metabolic stress increased in mussel post-larvae exposed to a SPL_{rms} > 137 re 1µPa. These authors reported that noise exposure triggered metabolic adjustments including enhanced gluconeogenesis, amino acid turnover, lipid oxidation, and disrupted neurotransmission, reflecting adaptive stress responses that may affect growth and fitness. Here, although post-larval physiological parameters were not monitored, the observed sharp reductions in metamorphosis success to vessel noise could reflect a high metabolic stress but also several other processes impacting post-settlement survival (e.g., competition, predation, etc.). *M. edulis* settle around 260µm in optimal feeding condition when reared at 20ºC (Bassim et al. 2015). The mean of 320µm observed in this study could be at least partially explained by the cold temperature around 10ºC observed during all the experiments, as the size at the end of the larval stage is inversely related to temperature (Lutz and Jablonski, 1978). Another possible explanation could be a postponement in metamorphosis related to the absence of a settlement trigger, supporting the potential feeding quality deficiency hypothesis. Temperature and food are the most crucial factors regulating the growth and larval duration of *M. edulis* (Bayne, 1965; Pechenik et al., 1990; Rayssac et al., 2010). Larval daily growth may vary from 1.2 to 8.1 $\mu m.d^{-1}$, depending on temperature (10°C - 18°C), food quality, and concentration (uni-, bi- or multiple species of microalgae; 1,000 to 30,000 cells.ml) as shown in several laboratory studies (Bassim et al., 2015; Bayne, 1965; Pechenik et al., 1990; Rayssac et al., 2010). According to Bayne (1965), growth rates are very stable between 10-13°C than between 13-16°C. In the present study, growth rates were relatively similar between the site (~10 $\mu m.d^{-1}$) and show important values. Thus, the particulate organic matter rich in saturated fatty acids seems adequate to support larval growth, suggesting that the low level of 20:5ω3 and 22:6ω3 could be mostly related to a trigger to stimulate the settlement. Absence of important differences in larval growth under vessel noise exposure agree with Aspirault et al. (2023) data, demonstrating the absence of the impact of noise exposure on mussel clearance rate larvae from different ontogenic stages.

1.6.3 **Soundscapes and drifters**

The larger size of post-larvae (up to 700µm) suggests that recruitment dynamics in Miquelon Bay could be influenced by secondary migrations (Forêt et al., 2018b; Olivier and Retière, 1998) since > 40% of drifters (TL > 360µm with presence of dissoconch shell) were collected over a course of three days. This result aligns with Gauthier et al. (in press, chapter III) who reported that vessel noise might trigger secondary migrations, due to a high occurrence of larger post-larvae (> 500 µm) and juveniles (> 1.7mm) in collectors. Mussels have different attachment preferences when settling onto hard-bottom or soft-bottom habitats (Baden et al., 2021; Frandsen and Dolmer, 2002). They anchor their byssus threads on several surfaces, such as hard substrates, on top of other mussels, on biofilms, on filamentous algae, and a variety of artificial substrates as the one adopted in this study (Brenner and Buck, 2010; Cyr et al., 2007; Frandsen and Dolmer, 2002; Hadfield, 2011; Toupoint et al., 2012b). The process of byssal detachment and subsequent migration of post-larvae may come at an energetic cost, as suggested by Forêt et al. (2018a, 2020) for several bivalve species including mussels. In the present study, although we did not analyze mussel energetic reserves, we suggest that this migratory process and production of byssus threads may be energetically costly for post-larvae. Previous studies have shown that the energy reserves of settlers such as mussel and scallop pediveligers are not directly impacted by vessel and pile driving noises (Cervello et al., 2023; Gigot et al., 2023a), but post-larval performance might be disrupted (Veillard et al., 2025) and this remains an open question.

1.7 Conclusion

This study did not show a strong impact of adding vessel noise to the ambient conditions on the settlement success of mussels, likely due to a poor recruitment season, the limited three-week sampling, the of trophic settlement triggers and larval quality. However, we demonstrate *in situ* that vessel noise disrupted metamorphosis rates of *M. edulis* by substantially reducing post-larvae abundance compared to control sites. The reduced metamorphosis abundance observed at the noisy site may lead to potential cascade scenarios on mussel post-larvae and future population. Larval delays of metamorphosis extend planktonic life with high metabolic stress due to noise, pushing the energy reserves to a critical level. Larvae are then less discriminatory because they find themselves in a 'desperate larval state' (Knight-Jones, 1953; Tremblay et al., 2007), and are forced to settle in a noisy environment. Once they have settled, the larvae that primarily settled and metamorphosed in the noisy environment actively undergo a secondary migration to seek a more suitable habitat. The post-settlement dispersal of mussels, which can be triggered by several environmental factors (Forêt et al., 2018a,b), is an important migration process contributing to the recovery of disturbances, connectivity and diversity in different habitats (Günther 1992; Pilditch et al., 2015), but also often resulting in a high presence of drifters in collectors (Forêt et al., 2018a; Le Corre et al., 2013). Given the presence of vessel noise causing changes in the ambient soundscape (Halliday et al., 2021; McKenna et al., 2024), the shifts on the behaviour of larvae when exposed to noise (Solé et al., 2023), and the high occurrence of drifters in the noisy site, we propose that vessel noise might be a new trigger for secondary dispersal of mussels. However, this relocation could also lead drifters to choose inappropriate habitats for population renewal. For example, if this noise is being propagated from a vessel, drifters could be attracted to propeller blades, generators and other surfaces that will theoretically be a "suitable" substrate for mussels.

1.8 Acknowledgements

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1.10 Supplementary materials

Table S1: Pair-wise test results from a two-way PERMANOVA analyzing the interaction between dates and sites, showing temperature differences among dates (from 8 to 21 july), and between two sites (control and noisy) in Miquelon Bay, France. Significant values (p<0.05) are indicated in bold.

		Factor Sites	
	Pair-wise tests	t-test	P(MC)
08 jul.	control,noisy	3.74	**0.001**
09 jul.	control,noisy	7.05	**0.0001**
10 jul.	control,noisy	1.95	0.06
11 jul.	control,noisy	5.67	**0.0001**
12 jul.	control,noisy	9.04	**0.0001**
13 jul.	control,noisy	8.59	**0.0001**
14 jul.	control,noisy	4.53	**0.0001**
15 jul.	control,noisy	5.91	**0.0001**
16 jul.	control,noisy	6.50	**0.0001**
17 jul.	control,noisy	4.90	**0.0001**
18 jul.	control,noisy	4.03	**0.0001**
19 jul.	control,noisy	4.05	**0.0001**
20 jul.	control,noisy	4.46	**0.0001**
21 jul.	control,noisy	5.05	**0.0001**

		Factor Dates		
Pair-wise tests	t-test	P(MC)	t-test	P(MC)
	Control		*Noisy*	
08 jul., 09 jul.	1.45	0.15	3.33	**0.001**
08 jul., 10 jul.	6.28	**0.0001**	6.29	**0.0001**
08 jul., 11 jul.	9.51	**0.0001**	6.80	**0.0001**
08 jul., 12 jul.	8.37	**0.0001**	2.93	**0.006**
08 jul., 13 jul.	8.88	**0.0001**	4.13	**0.0002**
08 jul., 14 jul.	4.74	**0.0002**	3.90	**0.0002**
08 jul., 15 jul.	2.25	**0.02**	0.38	0.7
08 jul., 16 jul.	2.6	**0.011**	0.92	0.35
08 jul., 17 jul.	3.02	**0.003**	4.06	**0.0001**
08 jul, 18 jul	3.53	**0.001**	0.98	0.33
08 jul, 19 jul	10.9	**0.0001**	8.06	**0.0001**
08 jul, 20 jul	13.97	**0.0001**	4.35	**0.0001**
08 jul, 21 jul	12.78	**0.03**	2.76	**0.009**
09 jul., 10 jul.	10.5	**0.0001**	12.3	**0.0001**
09 jul., 11 jul.	13.97	**0.0001**	13.4	**0.0001**
09 jul., 12 jul.	12.78	**0.0001**	7.59	**0.0001**
09 jul., 13 jul.	13.17	**0.0001**	9.52	**0.0001**
09 jul., 14 jul.	7.95	**0.0001**	9.20	**0.0001**
09 jul., 15 jul.	4.68	**0.0001**	4.02	**0.0003**
09 jul., 16 jul.	5.09	**0.0001**	5.22	**0.0001**
09 jul., 17 jul.	2.48	**0.01**	2.14	**0.04**
09 jul, 18 jul	6.46	**0.0001**	3.51	**0.0009**
09 jul, 19 jul	16.03	**0.0001**	15.14	**0.0001**
09 jul, 20 jul	9.01	**0.0001**	9.75	**0.0001**
09 jul, 21 jul	1.63	0.11	0.75	0.46
10 jul., 11 jul.	0.54	0.59	2.32	**0.02**
10 jul., 12 jul	0.80	0.42	5.54	**0.0001**
10 jul., 13 jul.	1.09	0.28	4.91	**0.0001**
10 jul., 14 jul.	4.45	**0.0001**	5.22	**0.0001**
10 jul., 15 jul.	6.76	**0.0001**	8.41	**0.0001**
10 jul., 16 jul.	7.44	**0.0001**	8.46	**0.0001**
10 jul., 17 jul.	11.68	**0.0001**	12.82	**0.0001**
10 jul, 18 jul	3.32	**0.001**	4.91	**0.0001**
10 jul, 19 jul	1.41	0.16	0.19	0.85
10 jul, 20 jul	3.24	**0.002**	4.32	**0.0002**
10 jul, 21 jul	11.80	**0.0001**	11.69	**0.0001**
11 jul., 12 jul.	0.37	0.71	4.16	**0.0002**
11 jul., 13 jul.	0.77	0.43	3.33	**0.0009**
11 jul., 14 jul.	5.36	**0.0001**	3.73	**0.0004**
11 jul., 15 jul.	8.5	**0.0001**	7.81	**0.0001**

11 jul., 16 jul.	10.01	**0.0001**	8.00	**0.0001**
11 jul., 17 jul.	14.82	**0.0001**	13.59	**0.0001**
11 jul., 18 jul.	3.51	**0.001**	3.66	**0.0003**
11 jul., 19 jul.	2.65	**0.01**	2.95	**0.004**
11 jul., 20 jul.	3.65	**0.001**	2.60	**0.008**
11 jul., 21 jul.	16.43	**0.0001**	12.67	**0.0001**

		Factor Dates					*Factor Dates*		
Pair-wise tests	t-test	p (MC)	t-test	P(MC)	Pair-wise tests	t-test	p (MC)	t-test	P(MC)
	Control		*Noisy*			*Control*		*Noisy*	
12 jul.,13 jul.	0.35	0.72	1.03	0.30	16 jul.,17 jul.	7.03	**0.0001**	6.44	**0.0001**
12 jul.,14 jul.	4.72	**0.0001**	0.69	0.49	16 jul.,18 jul.	3.25	**0.001**	0.89	0.37
12 jul.,15 jul.	7.7	**0.0001**	3.27	**0.002**	16 jul.,19 jul.	12.37	**0.0001**	10.31	**0.0001**
12 jul.,16 jul.	8.95	**0.0001**	3.03	**0.004**	16 jul.,20 jul.	5.07	**0.0001**	4.89	**0.0001**
12 jul.,17 jul.	13.8	**0.0001**	8.50	**0.0001**	16 jul.,21 jul.	7.26	**0.0001**	4.52	**0.0001**
12 jul.,18 jul.	3.12	**0.003**	0.94	0.34					
12 jul.,19 jul.	2.87	**0.005**	6.62	**0.0001**	17 jul.,18 jul.	7.90	**0.0001**	4.45	**0.0001**
12 jul.,20 jul.	3.13	**0.0001**	1.57	0.12	17 jul.,19 jul.	16.7	**0.0001**	15.32	**0.0001**
12 jul.,21 jul.	14.94	**0.0001**	6.97	**0.0001**	17 jul.,20 jul.	10.41	**0.0001**	10.42	**0.0001**
					17 jul.,21 jul.	1.18	0.24	2.74	**0.008**
13 jul.,14 jul.	4.62	**0.0001**	0.37	0.72					
13 jul.,15 jul.	7.75	**0.0001**	4.55	**0.0001**	18 jul.,19 jul.	5.38	**0.0001**	5.42	**0.0001**
13 jul.,16 jul.	9.16	**0.0001**	4.43	**0.0001**	18 jul.,20 jul.	0.59	0.55	1.99	**0.05**
13 jul.,17 jul.	14.12	**0.0001**	10.2	**0.0001**	18 jul.,21 jul.	7.71	**0.0001**	3.13	**0.002**
13 jul.,18 jul.	2.95	**0.003**	1.63	0.11					
13 jul.,19 jul.	3.37	**0.0001**	5.98	**0.0001**	19 jul.,20 jul.	5.95	**0.0001**	5.24	**0.0001**
13 jul.,20 jul.	2.94	**0.002**	0.60	0.55	19 jul.,21 jul.	18.41	**0.0001**	14.5	**0.0001**
13 jul.,21 jul.	15.56	**0.0003**	8.84	**0.0001**	20 jul.,21 jul.	10.87	**0.0001**	9.09	**0.0001**
14 jul.,15 jul.	3.05	**0.002**	4.23	**0.0001**					
14 jul.,16 jul.	3.73	**0.0003**	4.08	**0.0002**					
14 jul.,17 jul.	9.48	**0.0001**	9.91	**0.0001**					
14 jul.,18 jul.	0.51	0.62	1.42	0.16					
14 jul.,19 jul.	7.70	**0.0001**	6.36	**0.0001**					
14 jul.,20 jul.	1.40	0.16	0.96	0.33					
14 jul.,21 jul.	9.91	**0.0001**	8.52	**0.0001**					
15 jul.,16 jul.	0.28	0.78	0.54	0.58					
15 jul.,17 jul.	6.54	**0.0001**	5.34	**0.0001**					
15 jul.,18 jul.	2.85	**0.006**	1.17	0.24					
15 jul.,19 jul.	10.69	**0.0001**	10.03	**0.0001**					
15 jul.,20 jul.	4.31	**0.0002**	4.98	**0.0001**					
15 jul.,21 jul.	6.44	**0.0001**	3.39	**0.001**					

Table S2: Fatty acid composition (FA%, mean ± SE, n=6) of bottom particulate organic matter (b-POM) retrieved from artificial collectors moored at distances D1 (25m), D2 (175m) from Miquelon Bay containing ambient site (control) and noisy site (underwater speaker emitting vessel noise) over 3-weeks in July 2022. Values are reported as traces (tr.) when percentages are inferior 0.1%. Abbreviations: branched fatty acids (brFA), saturated fatty acids (SFA), monosaturated fatty acids (MUFA) polyunsaturated fatty acids (PUFA), eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and essential fatty acids (EFA). BrFA is composed of 15:0iso, while EFA consists of AA, EPA and DHA. In 2022, some SFAs (13:0, 20:0, 22:0 and 26:0) and MUFAs (14:1ω3, 16:1ω5, 16:1ω9, and 18:1ω7) were not detected in 2022 as in 2021. Similarly, no PUFAs from family 16:0 or 18:0 were not detected in 2022, which might reflect on the calculated percentage of 2021.

	Miquelon Bay 2022			**Miquelon Bay 2021**
FA	**05 jul**	**14 jul**	**20 jul**	
12:0	1.3 ± 0.2	1.3 ± 0.1	1.5 ± 0.1	0.4 ± 0.1
14:0	10.3 ± 0.8	11.2 ± 0.2	10.2 ± 0.5	6.1 ± 0.4
15:0	0.7 ± 0.05	0.9 ± 0.1	1.0 ± 0.1	0.7 ± 0.05
16:0	29.9 ± 1.1	31.4 ± 0.9	28.8 ± 0.6	27.9 ± 1.6
17:0	0.2 ± 0.04	0.2 ± 0.02	0.3 ± 0.05	tr.
18:0	9.8 ± 0.9	10.9 ± 1.4	8.4 ± 0.5	14.5 ± 2.3
24:0	tr.	tr.	tr.	0.1 ± 0.01
Σ SFA	**52.2 ± 3.0**	**55.9 ± 2.7**	**50.3 ± 1.9**	**51.4 ± 3.4**
15:1ω7	tr.	tr.	tr.	n.d
16:1ω7	6.4 ± 0.3	7.5 ± 0.2	7.7 ± 0.2	6.4 ± 0.4
17:1ω7	0.2 ± 0.04	0.2 ± 0.02	0.3 ± 0.02	0.2 ± 0.03
18:1ω9	15.9 ± 0.8	13.7 ± 0.6	15.6 ± 0.4	7.9± 0.4
20:1ω9	0.2 ± 0.07	tr.	0.1 ± 0.02	n.d
22:1ω9	0.2 ± 0.02	tr.	0.1 ± 0.09	n.d.
Σ MUFA	**22.9 ±0.5**	**21.7 ± 1.1**	**24.1 ± 0.9**	**20.8 ± 1.2**
18:2ω6	5.3 ± 0.3	4.0 ± 0.4	3.6 ± 0.2	3.2 ± 0.2
18:3ω3	3.9 ± 0.1	3.5 ± 0.3	3.4 ± 0.2	3.1 ± 0.3
18:3ω6	tr.	tr.	tr.	tr.
20:2ω6	tr.	tr.	tr.	n.d.
20:3ω3	tr.	tr.	tr.	n.d.
20:4ω6 (AA)	0.7 ± 0.2	0.8 ± 0.2	0.9 ± 0.1	0.4 ± 0.04
20:5ω3 (EPA)	5.7 ± 0.9	4.5 ± 0.5	6.2 ± 0.4	5.3 ± 0.6
22:6ω3 (DHA)	8.3 ± 0.4	9.4 ± 0.2	11.0 ± 0.4	6.3 ± 0.8
Σ PUFA	**23.9 ± 1.9**	**23.1 ± 1.9**	**26.3 ± 1.4**	**25.3 ± 2.4**
ΣbrFA	0.3 ± 0.02	0.3 ± 0.01	0.4 ± 0.03	2.5 ± 0.2
PUFA/SFA	0.5 ± 0.05	0.4 ± 0.05	0.5 ± 0.04	0.5 ± 0.1
Σ EFA	14.8 ± 1.3	14.6 ± 0.8	18.1 ± 0.8	12.0 ± 1.4

16:1ω7/16:0	0.2 ± 0.02	0.2 ± 0.01	0.3 ± 0.01	0.2 ± 0.03
EPA/DHA	0.7 ± 0.1	0.5 ± 0.1	0.6 ± 0.03	0.9 ± 0.04

Table S3: List and respective composition (% mean, SE, n=6) of trophic markers adopted in the present study in total particulate matter retrieved from sites of shallow waters (8m) in Miquelon Bay over the 3-weeks (05 Jul., 14 Jul., and 20 Jul.) in 2022.

Fatty acid	Marker of	References	**Miquelon (2022)**			**Miquelon (2021)**
			05 Jul.	**14 Jul.**	**20 Jul.**	**July (3-week)**
∑ai15:0, iso15:0, 18:1ω7	Bacteria	(Meziane and Tsuchiya, 2000, 2002)	0.3 (0.02)	0.3 (0.02)	0.4 (0.03)	7.3 (0.4)
∑ 14:0, 16:0, 18:0	Degraded organic matter	(Bridier *et al.*, 2021; Canuel and Zimmerman, 1999; Connelly *et al.*, 2015)	49.9 (2.6)	53.5 (2.2)	47.4 (1.3)	48.5 (3.5)
∑16:1ω7, 20:5ω3	Diatoms	(Dalsgaard *et al.*, 2003; Kelly and Scheibling, 2012)	12.1 (1.3)	11.9 (0.7)	13.9 (0.6)	11.7 (0.9)
∑ 22:6ω3	Dinoflagellates	Kelly and Scheibling, (2012)	8.3 (0.4)	9.4 (0.2)	11.0 (0.4)	6.3 (0.8)
∑18:2ω6, 18:3ω6, 18:4ω3	Green macroalgae	(Bridier *et al.*, 2021; Graeve *et al.*, 2002; Kelly and Scheibling, 2012; Gaillard *et al.*, 2017)	5.4 (0.3)	4.1 (0.5)	3.7 (0.2)	7.8 (0.6)
∑ 18:1ω9	Brown macroalgae	Kelly and Scheibling (2012)	15.9 (0.8)	13.7 (0.6)	15.6 (0.4)	7.9 (0.4)

Table S4: Pair-wise test results on the factor dates (three-way PERMANOVA) showing differences among dates (5 jul., 8 jul., 11 jul., 14 jul., 17 jul. and 20 jul.) in the settlement rates of Mytilus edulis in Miquelon, France.

Factor Dates	Pair-wise tests	t-test	P(MC)
	05 jul, 08 jul	0.65	0.52
	05 jul, 11 jul	1.93	0.06
	05 jul, 14 jul	2.56	**0.01**
	05 jul , 17 jul	2.49	**0.02**
	05 jul, 20 jul	**2.31**	**0.03**
	08 jul, 11 jul	1.10	0.28
	08 jul, 14 jul	1.76	0.09
	08 jul,17 jul	1.68	0.10
	08 jul , 20 jul	1.53	0.13
	11 jul, 14 jul	**3.16**	**0.004**
	11 jul, 17 jul	2.85	**0.009**
	11 jul, 20 jul	2.02	**0.05**
	14 jul, 17 jul	0.73	0.47
	14 jul, 20 jul	1.15	0.26
	17 jul, 20 jul	0.68	0.51

Table S5: Pair-wise test results on the interaction of dates and sounds (three-way PERMANOVA) showing differences in the metamorphosis rate of *Mytilus edulis* among dates (5 jul., 8 jul., 11 jul., 14 jul., 17 jul. and 20 jul.), and sounds (ambient noise, and vessel noise playback) on two sites (control and noisy) located in Miquelon Bay, France. Significant values (p<0.05) are indicated in bold.

Factor Sounds	Pair-wise tests	t-test	P(MC)	*Factor Dates*	Pair-wise tests	t-test	P(MC)
05 jul.	control,noisy	2.09	**0.05**	*Control*	05 jul, 08 jul	1.80	0.09
					05 jul, 11 jul	3.02	**0.009**
08 jul.	control,noisy	2.66	**0.02**		05 jul, 14 jul	2.98	**0.008**
					05 jul , 17 jul	2.70	**0.02**
11 jul.	control,noisy	1.11	0.28		05 jul, 20 jul	3.23	**0.005**
					08 jul, 11 jul	2.38	**0.03**
14 jul.	control,noisy	0.48	0.64		08 jul, 14 jul	2.28	**0.04**
					08 jul,17 jul	1.65	0.12
17 jul.	control,noisy	3.12	**0.008**		08 jul , 20 jul	2.88	**0.01**
					11 jul, 14 jul	0.23	0.82
20 jul.	control,noisy	1.59	0.13		11 jul, 17 jul	1.74	0.10
					11 jul, 20 jul	2.02	0.06
					14 jul, 17 jul	1.44	0.17
					14 jul, 20 jul	1.95	0.07
					17 jul, 20 jul	3.27	**0.005**
				Noisy	05 jul, 08 jul	2.47	**0.03**
					05 jul, 11 jul	1.47	0.16
					05 jul, 14 jul	2.21	**0.04**
					05 jul , 17 jul	2.64	**0.02**
					05 jul, 20 jul	2.22	**0.04**
					08 jul, 11 jul	1.83	0.09
					08 jul, 14 jul	0.50	0.62
					08 jul,17 jul	1.24	0.23
					08 jul , 20 jul	0.39	0.72
					11 jul, 14 jul	1.26	0.22
					11 jul, 17 jul	2.23	**0.04**
					11 jul, 20 jul	1.49	0.16
					14 jul, 17 jul	1.06	0.31
					14 jul, 20 jul	0.21	0.84
					17 jul, 20 jul	1.28	0.23

Table S6: Pair-wise test results of the interaction of dates and sounds (three-way PERMANOVA) showing differences in prodissoconch I (PI) of post larvae of *Mytilus edulis* among dates (5 jul., 8 jul., 11 jul., 14 jul., 17 jul. and 20 jul.), and sounds (ambient and vessel noise) on control and noisy sites located in Miquelon Bay, France. Significant values ($p<0.05$) are indicated in bold.

Factor Sounds	Pair-wise tests	t-test	P(MC)	*Factor Dates*	Pair-wise tests	t-test	P(MC)
05 jul.	control,noisy	2.77	**0.006**	*Control*	05 jul, 08 jul	2.49	**0.01**
					05 jul, 11 jul	2.18	**0.03**
08 jul.	control,noisy	0.57	0.57		05 jul, 14 jul	1.61	0.11
					05 jul , 17 jul	1.17	0.25
11 jul.	control,noisy	1.71	0.09		05 jul, 20 jul	1.22	0.23
					08 jul, 11 jul	0.32	0.75
14 jul.	control,noisy	1.92	0.06		08 jul, 14 jul	0.84	0.40
					08 jul,17 jul	0.87	0.39
17 jul.	control,noisy	2.81	**0.007**		08 jul , 20 jul	0.45	0.65
					11 jul, 14 jul	0.95	0.34
20 jul.	control,noisy	2.94	**0.005**		11 jul, 17 jul	0.95	0.33
					11 jul, 20 jul	0.62	0.53
					14 jul, 17 jul	0.16	0.87
					14 jul, 20 jul	0.13	0.90
					17 jul, 20 jul	0.23	0.82
				Noisy	05 jul, 08 jul	0.86	0.39
					05 jul, 11 jul	2.23	**0.03**
					05 jul, 14 jul	2.74	**0.008**
					05 jul , 17 jul	3.99	**0.0002**
					05 jul, 20 jul	4.46	**0.0002**
					08 jul, 11 jul	0.43	0.67
					08 jul, 14 jul	1.14	0.27
					08 jul,17 jul	2.11	**0.04**
					08 jul , 20 jul	2.26	**0.03**
					11 jul, 14 jul	1.12	0.26
					11 jul, 17 jul	2.71	**0.008**
					11 jul, 20 jul	3.11	**0.002**
					14 jul, 17 jul	1.44	0.15
					14 jul, 20 jul	1.72	0.09
					17 jul, 20 jul	0.27	0.78

Table S7: Pair-wise test results (three-way PERMANOVA) showing differences in larval growth (µm. d-1) of *Mytilus edulis* between sounds (ambient and vessel noise) and dates (5 jul., 8 jul., 11 jul., 14 jul., 17 jul. and 20 jul.) on two sites (control and noisy) situated in Miquelon Bay, France. Significant values (p<0.05) are indicated in bold.

Factor Sounds	Groups	t-test	P(MC)	perms	*Factor Dates*	Groups	t-test	P(MC)	perms
	control,noisy	2.81	**0.005**	9965		05 jul, 08 jul	0.66	0.51	9816
						05 jul, 11 jul	2.05	**0.04**	9847
						05 jul, 14 jul	1.72	0.09	9844
						05 jul , 17 jul	0.83	0.41	9852
						05 jul, 20 jul	0.78	0.43	9837
						08 jul, 11 jul	2.01	**0.04**	9827
						08 jul, 14 jul	0.58	0.55	9841
						08 jul,17 jul	0.02	0.98	9848
						08 jul , 20 jul	0.05	0.95	9825
						11 jul, 14 jul	3.32	**0.001**	9794
						11 jul, 17 jul	2.35	**0.02**	9824
						11 jul, 20 jul	2.16	**0.03**	9861
						14 jul, 17 jul	0.65	0.51	9830
						14 jul, 20 jul	0.54	0.59	9810
						17 jul, 20 jul	0.04	0.97	9815

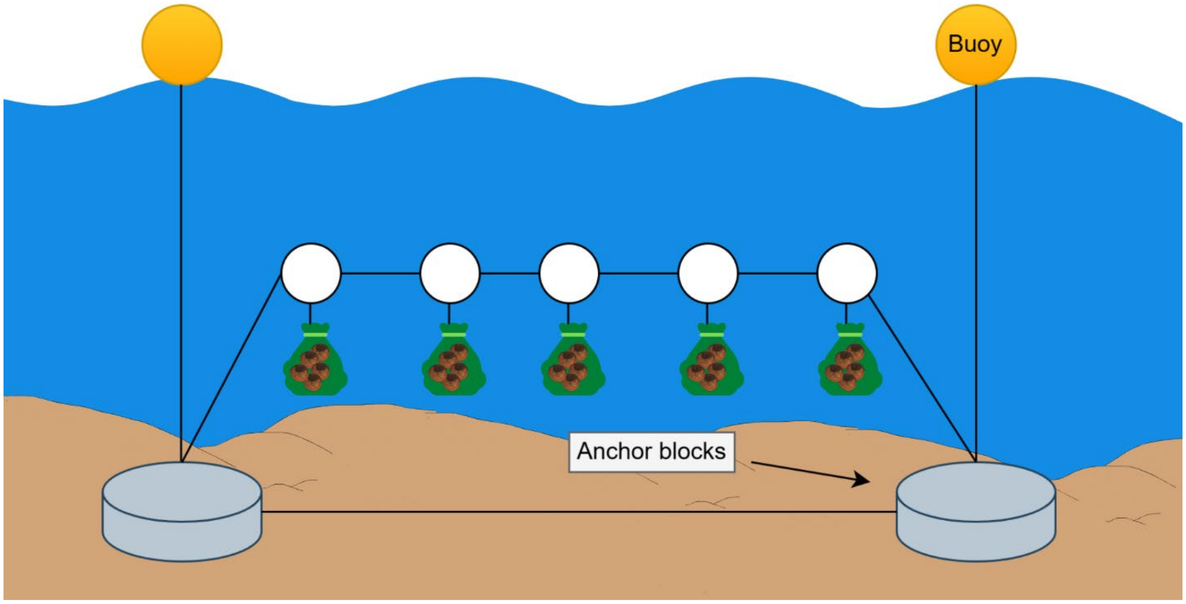
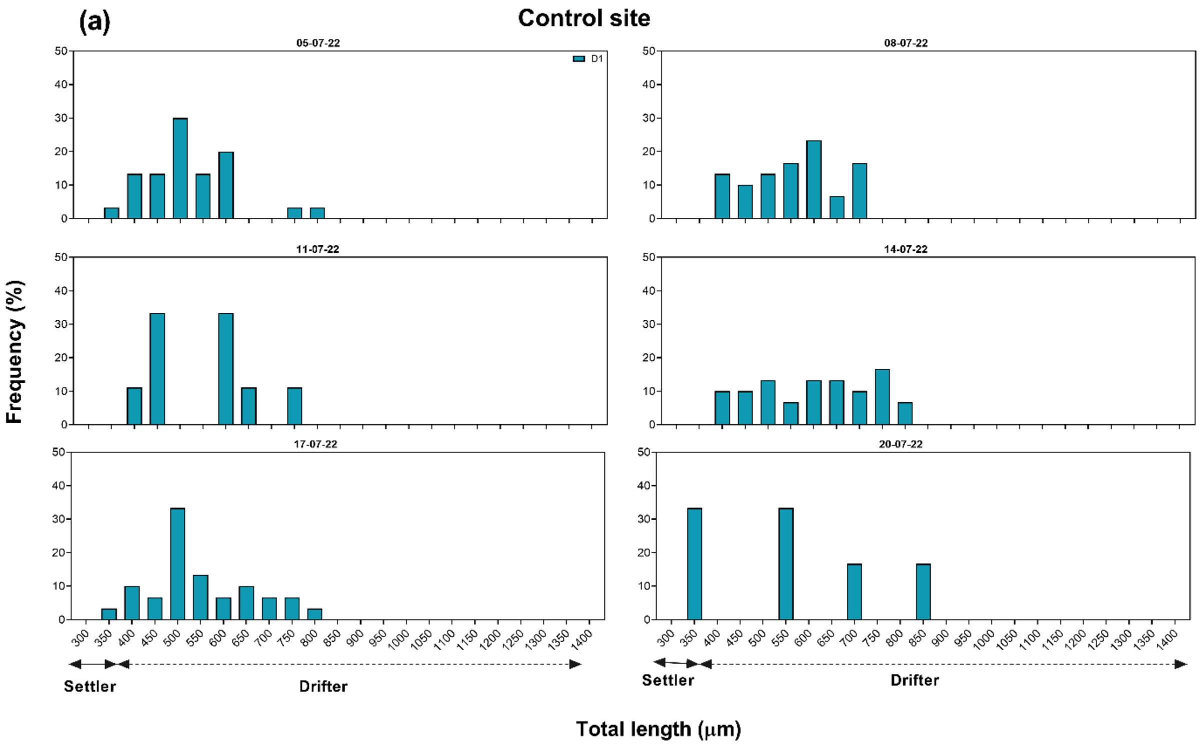
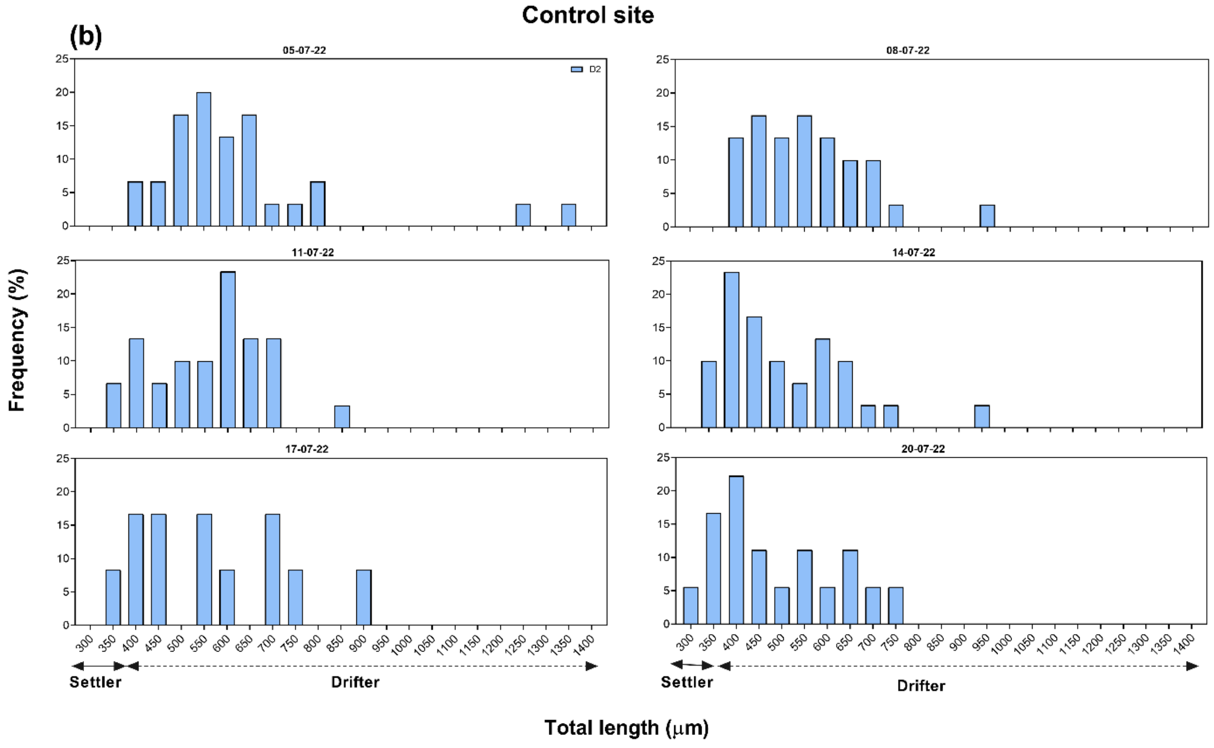


Figure S1: Design of submerged longline system for mussel spat collectors (based on Cyr et al., 2007; Gauthier et al., in press) installed at all stations (D1 and D2) in both control (ambient sound) and noisy (vessel noise) sites within the Miquelon Bay, France. Spat collectors were kept at 1 m above the seafloor, and concrete blocks anchored the whole system on the seabed. Photos of mussel settlers were retrieved from Jolivet et al. (2016).


(a)
Control site
05-07-22
08-07-22
11-07-22
14-07-22
17-07-22
20-07-22
D1
Frequency (%)
0
10
20
30
40
50
300 350 400 450 500 550 600 650 700 750 800 850 900 950 1000 1050 1100 1150 1200 1250 1300 1350 1400
Settler
Drifter
Total length (µm)


Control site
(b)
05-07-22
08-07-22
11-07-22
14-07-22
17-07-22
20-07-22
D2
Frequency (%)
0
5
10
15
20
25
300 350 400 450 500 550 600 650 700 750 800 850 900 950 1000 1050 1100 1150 1200 1250 1300 1350 1400
Settler
Drifter
Total length (µm)

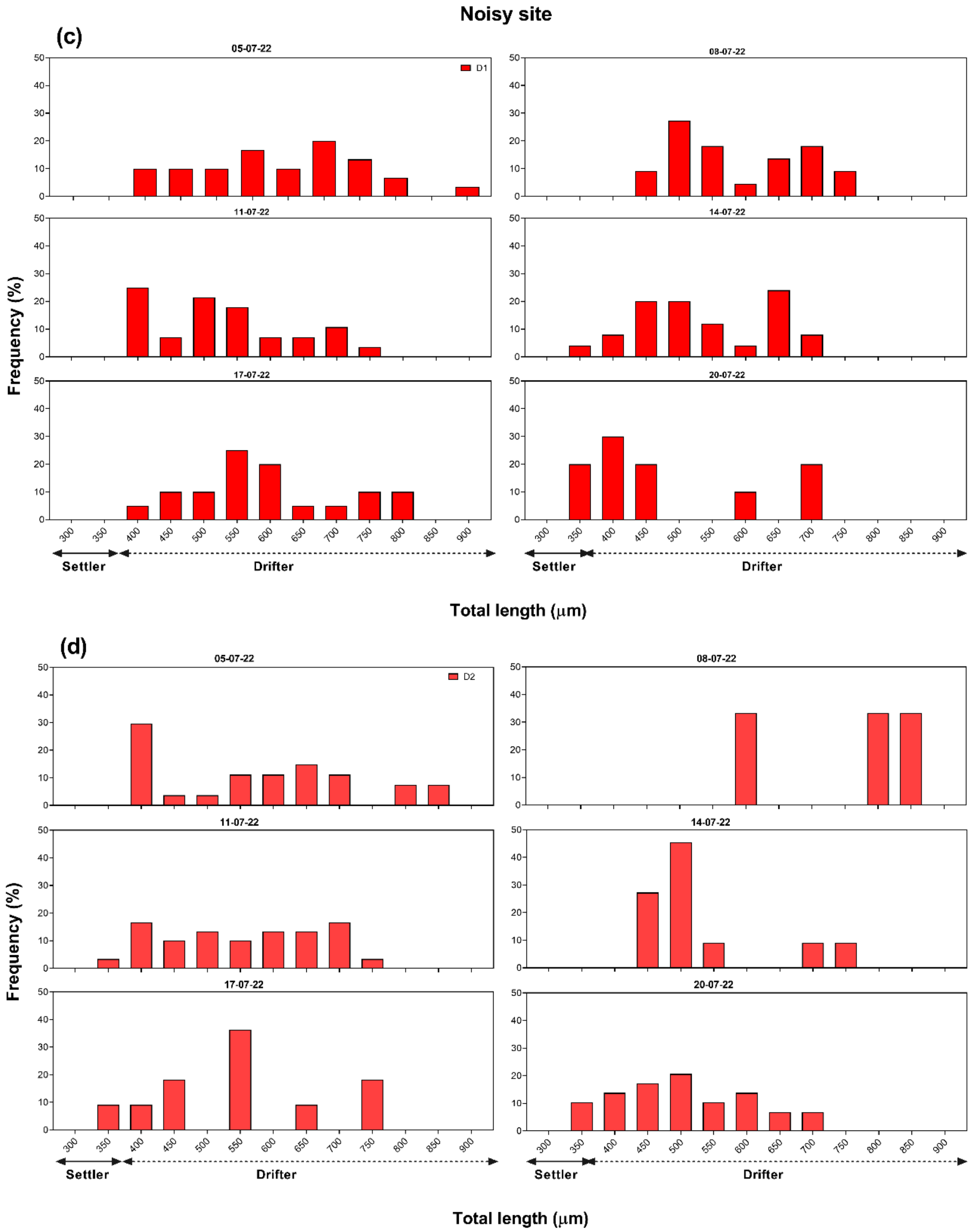


Figure S2: Size–frequency distributions of *Mytilus edulis* and total length of post larvae collected at two distances (D1 – 25m, D2 – 175m) from ambient (control site, a, b, blue gradient) or vessel noise playback (noisy site, c, d, red gradient) in Miquelon Bay from July 5th to 20th, 2022. Settlers are individuals with a total length inferior 360 µm and drifters are mussels with a total length superior 360 µm.

CHAPITRE 2/CHAPTER II

SIZE AT METAMORPHOSIS AND RECRUIT COHORT DYNAMIC OF BLUE MUSSELS EXPOSED TO ANTHROPOGENIC NOISES *IN SITU*

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Taille à la métamorphose et dynamique des cohortes de recrues des moules bleues exposées à des bruits anthropogéniques *in situ*

2.1 Résume

La moule bleue (*Mytilus edulis*) est confrontée à des risques croissants liés à la pollution sonore d'origine anthropique, qui peut perturber la dynamique de recrutement précoce des Mytilidae *in situ*, en fonction du type et de l'intensité du signal sonore. Les bruits perturbateurs peuvent influencer les comportements d'attachement primaires et secondaires, cruciaux pour le renouvellement des populations. Afin d'améliorer notre compréhension de l'effet du bruit anthropique sur les processus de recrutement, nous avons suivi les recrues de moules *in situ* en déterminant le nombre de cohortes et en analysant la morphométrie des coquilles (taille à la métamorphose et longueur totale) sous différentes intensités sonores. Les niveaux de pression acoustique étaient la seule variable environnementale ayant varié entre les sites et les stations expérimentaux, allant de 106 à 153 dB re 1 µPa. L'attachement primaire et le succès de la métamorphose n'ont pas été affectés par ces bruits. Des fixations secondaires (> 500 µm), indiquant une dérive post-métamorphique, ont été observée dans tous les échantillons, la taille des recrues variant en fonction de l'intensité du bruit. Des niveaux de pression modérés (120 dB re 1 µPa) ont favorisé la présence de juvénile plus grands (> 2 mm), tandis que des niveaux de pression plus élevés (> 140 dB re 1 µPa) ont inhibé leur occurrence. Grace à l'analyse de la distance de Wasserstein (EMD) pour caractériser la structure des cohortes, nous avons mis en évidence des différences dans la distribution des tailles en fonction de l'intensité du bruit, avec une variabilité plus faible observée sur le site le plus exposé. Nos résultats montrent, pour la première fois, que la fixation primaire mesuré sur le terrain n'est pas altérée par les émissions sonores contrôlée de bruit *in situ*, mais qu'un bruit modéré des navires peut induire un afflux de juvéniles. En revanche, le bruit des navires enregistré en fin de saison a limité l'établissement des recrues de plus grande taille, en particulier à proximité de la source acoustique, soulignant que les stades juvéniles (> 2mm) pourraient être plus vulnérables aux perturbations acoustiques que les stades post-larvaires.

Mots clés : anthropogénie, peuplement, bivalves, moule bleue, pollution sonore.

2.2 Abstract

The blue mussel (*Mytilus edulis*) faces increasing risks from marine noise pollution, which can either perturb the early recruitment dynamic of Mytilidae, depending on the sound type and pressure. Disruptive noise may interfere with both primary and secondary attachment behaviours, which are crucial for population renewal. To enhance our understanding of how anthropogenic noise influences mussel populations, we monitored *in situ* mussel recruits by determining the number of cohorts and evaluating shell morphometrics (size at metamorphosis and total length) across varying noise intensities. Sound pressure levels were the only environmental condition that varied among experimental sites and stations, ranging from 106 to 153 dB re 1 µPa. Primary attachment and metamorphosis success remained unaffected by these noises. However, secondary settlement (> 500 µm), indicating of post-metamorphic drifting, was observed in all samples, with recruit size varying due to the noise level. Moderate sound pressure levels (120 dB re 1 µPa) promoted the presence of larger drifters (> 2mm), whereas higher pressure levels (> 140 dB re 1 µPa) inhibited their occurrence. Analysis using Earth Mover's Distance to define cohort structure confirmed distinct differences in the mussel length distributions across noise intensities, with lower variability observed at the more exposed site. Our findings provide the first field-based evidence that primary attachment was not altered by controlled noise emission *in situ*, while moderate vessel noise can induce an influx of secondary drifters. Toward the end of the season, vessel noise also restricted the establishment of larger recruits (> 2 mm), particularly near the vessel noise source, suggesting that juvenile stages may be more vulnerable to acoustic disturbances than post-larval stages.

Keywords: anthropogeny, settlement, bivalves, blue mussel, noise pollution.

2.3 Introduction

Oceans are filled with meaningful sounds from biological sources, including those produced to find a mate or detect a predator, and those created by natural forces like from rain and wind (Erbe et al., 2022). However, increasing background noise from human activities pose a growing threat to these essential acoustic signals, affecting the behaviour of organisms (Halliday et al., 2021; Hildebrand, 2009; McKenna et al., 2024). Anthropogenic activities, such as maritime traffic, pile driving, seismic air guns, and fishing boats, are some of the activities that contribute to rising ambient noise levels, thereby transforming the underwater soundscape of marine environments (Duarte et al., 2021; NRC, 2003). Among these, cargo vessels are the dominant source of noise in the ocean, and the global shipping fleet is projected to nearly double (from 20 to 48%) by 2030 due to the transport of goods (Kaplan and Solomon 2016) and as the opening of new routes in the North due to ocean warming (Aulanier et al., 2017; Bashkevin et al., 2020), increasing noise energy from maritime traffic two-fold (Jalkanen et al., 2022). This growing anthropic stressor not only affects the auditory health of marine life but can also disrupt fundamental biological processes (see Davies et al., 2024; Duarte et al., 2021; Solé et al., 2023).

In this context, an emerging research area is devoted to investigating the effects of anthropogenic noise on the early life stages of bivalves (Cervello et al., 2023; Gigot et al., 2023; Jolivet et al., 2016). Mussels (*Mytilus* spp.) are widely studied in this field (see table in Solé et al., 2023) due to their ecological and aquaculture importance and their role as bioindicators of environmental changes (Baden et al., 2021; Seed et al., 2000; South et al., 2022). While mussel populations are widespread, some studies have reported a reduction in mussel populations in some areas of the North Atlantic due to ocean warming (Baden et al., 2021). Other stressors have been impacting mussel populations (Petraitis and Dudgeon, 2020; Seed et al., 2000), including anthropogenic noises (Gauthier et al., in review). Studies suggest that some bivalves use natural soundscapes to orient themselves and select suitable settlement habitats (Lillis et al., 2013; Williams et al., 2022). Additionally, previous laboratory studies have revealed that broadcasting anthropogenic noises can influence *M.*

edulis settlement metamorphosis (Cervello et al., 2023; Jolivet et al., 2016), with some noises disrupting early recruitment and metamorphosis in the field (Gauthier et al., in review; in prep.). The effects of vessel noise on coastal mussel populations (Jolivet et al., 2016) are gaining attention, as recruitment depends on larval supply, settlement behaviour, physiological state, and survival and migration dynamics, all shaped by complex biotic and abiotic factors (Butman, 1987; Fôret et al. 2018a,b; Günther, 1992; Hunt and Scheibling, 1997; Leal et al., 2022; Lewin, 1986) .

Although the mechanism of hearing in bivalves is not fully understood (Solé et al., 2023), research has revealed that sound-detecting organs develop at different life stages - pediveligers and adults – while data for juveniles remain limited (Cragg and Nott, 1977; Zhadan, 2005). Earlier research also shows that the hearing frequency of bivalves overlaps with various anthropogenic noises, including cargo vessels and pile driving (Duarte et al., 2021; Roberts et al., 2015; Zhadan, 2005). Rapid shifts in environmental conditions– through such as ocean warming, acidification, chemical pollution, and growing noise pollution –are prompting investigations into their effects on mussel populations, particularly through cohort distribution and shell morphology (Butler et al., 2019; Halpern et al., 2019, Jalkanen et al., 2022; Slabbekoorn et al., 2010). Analyzing life-stage abundances and shell traits (total length and prodissoconch II) provide insights into population dynamics. Size-frequency distributions reveal how mussels are structured over spatial-temporal scales (Bayne, 1964, Butler et al., 2019; Le Corre et al., 2013; Lutz and Jablonski, 1978; Martel et al., 2014; Toupoint et al., 2012a). In this context, the Earth mover's distance (EMD), or Wasserstein distance, stands out as an innovative and robust method for comparing morphometric histograms across noise exposure gradients. The EMD quantifies the effort required to transform one distribution into another, with the results expressed in EMD units (Rubner et al., 2000; Kranstauber et al., 2017). Originally developed for shape comparison in image analysis (Rubner et al., 2000, Su et al., 2015; Weller and Westneat, 2019), and later applied in social sciences and in ecology to study voter distributions, spatial distribution patterns and movement behaviour (Bonnet-Lebrun et al., 2021;s; Kranstauber et al., 2017; Potts et al., 2014). Applied to mussels, EMD can provide new insights into how noise affects recruitment and attachment across a noise gradient.

Despite numerous recommendations, field investigations focusing on the gradient of noise exposure remain scarce (Kunc et al., 2016; Popper et al., 2020; Solé et al., 2023). Most research has been carried out in laboratory settings (see gaps and perspectives in Hawkins and Popper, 2017 and tables in Solé et al., 2023), with limited studies estimating how far larvae are and their response to noise over distance (Gigot et al., 2023; Olivier et al., 2023; Veillard et al., 2025). Recent fieldwork by Gauthier et al. (in prep., Chapter I) detected that settlement of mussels were not impacted by vessel noise at sound pressure levels (SPL) below 140 dB re 1 μPa. However, the impacts of such noise on recruit length distributions were not assessed. Within this context, we aim to assess the cohort characteristics, total length distribution, and prodissoconch II shell lengths of blue mussel recruits exposed to noise gradient intensity. Based on the high proportion of drifters also observed in the field by Gauthier et al. (in prep., Chapter I), we hypothesize that: i) larval cohorts exposed to high vessel noise intensities will have a significantly narrower size distribution compared to lower intensities, and ii) larvae exposed to high and moderate vessel noise intensities will delay their metamorphosis, resulting in a wider prodissoconch II lengths than larvae exposed to low intensities.

2.4 Materials and Methods

2.4.1 Experimental design

Recruits of Mytilidae, consisting of pediveligers, post-larvae and young juveniles, were collected at Saint-Pierre and Miquelon (SPM), a French archipelago situated at 25 km south of Newfoundland and Labrador, Canada. Samples were collected during the spring of 2021. Given the urgent need to evaluate population-level changes under anthropophony exposure in the field (Hawkins and Popper, 2017; Popper et al., 2020), we analyzed mussel samples from the *in situ* experiment of Gauthier et al. (in press, Chapter III). Briefly, recruits were monitored monthly in two sites (Pristine and Anthropic Sites, PS and AS, Fig. 15) by a set of artificial collectors made of 2 mm mesh bags, filled with four inverted Netron® sections (40 x 80 cm with a mesh size of 5 mm). In each site, 3 stations (4 collectors by station) were defined on a transect related to an increasing gradient of vessel noise emitted by an underwater speaker (Table 5, Fig. S2a-b). Collectors were moored for one month in each of July, August, September, or October 2021, retrieved by divers and transported to the shore in individual bags to avoid spat losses. Each collector (n = 4) was placed in a 100 µm plankton net and cleaned using a low-pressure seawater jet. The material accumulated in the plankton net cup was transferred to labelled Ziplock bags and frozen at -40ºC for further analysis. Temperature and trophic conditions were homogenous across stations at each site. The PS site stood out with slightly elevated fatty acid markers from diatoms in the seston compared to AS (Gauthier et al., in press).

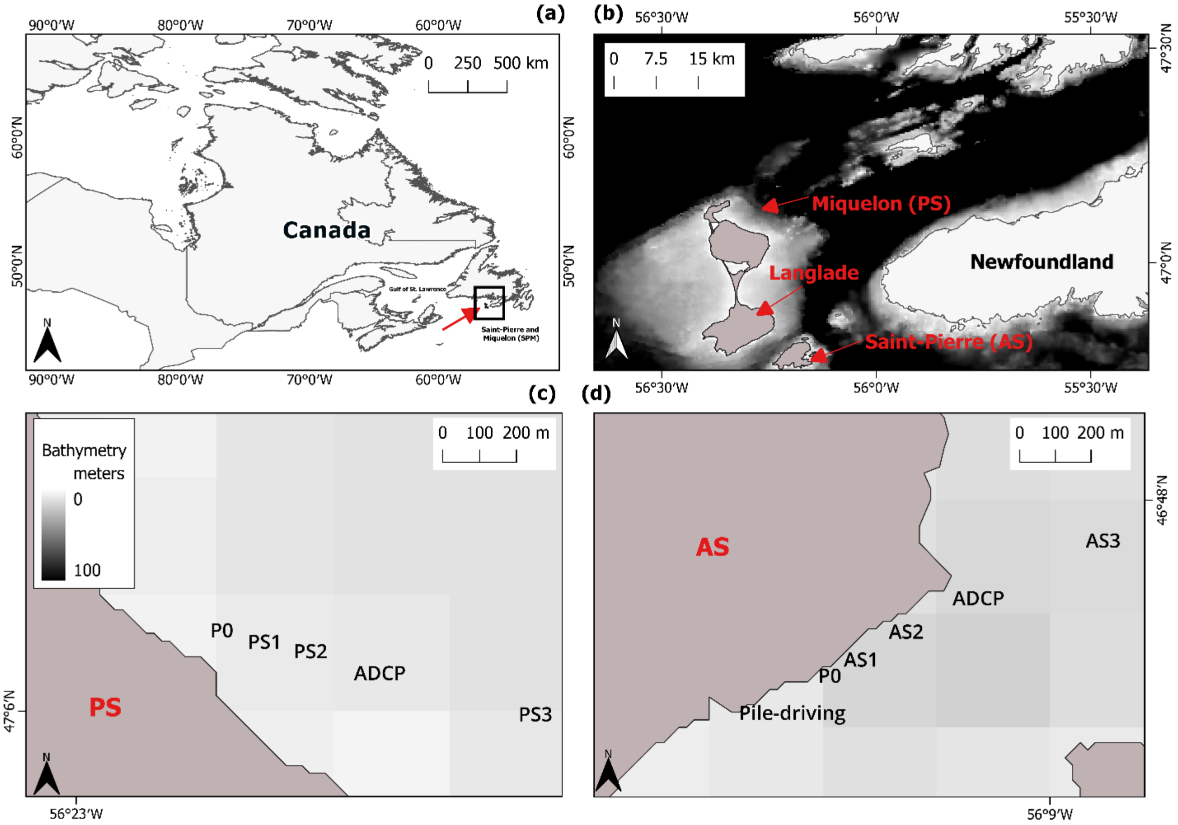

Figure 15: Set of maps describing the study sites. (a, b) Location of Sant-Pierre and Miquelon's archipelago (SPM), where each site is referred to as Pristine (PS) or Anthropic (AS) due to the level of anthropogenic noise at the islands of Miquelon and Saint-Pierre, respectively (modified from Gauthier et al., in review). Bathymetric maps containing sites and stations from the sound (PS1-PS3 and AS1-AS3) on transects exposed to an anthropogenic noise source (P0) at the Pristine site (PS, c) and the Anthropic site (AS, d), which had pile driving operations occurring at the same time of sampling. Bathymetry data was retrieved from the General Bathymetric Chart of the Oceans (GEBCO). Bathymetric maps are composed using grayscale where white represents 0-1 m, 2-30m light to dark gray, and values > 100m are black.

Table 5: Sampling locations and distances (25–890 m) from the speaker, with coordinates (°, ", '), depth (m), and received sound levels (dB re 1µPa) at each point in Pristine (PS, Miquelon) and Anthropic (AS, Saint-Pierre) sites. Distance categories were renamed as PS1-PS3 and AS1-AS3 to reflect site-specific noise characteristics.

Site and station name	**Distance from noise source (m)**	**Received level of sound (SPLrms or SPLpk)**	**Depth (m)**	**Coordinates**	
PS				Latitude	Longitude
P0	0	167	8	47° 06' 08.39" N	56° 22' 28.62" W
PS1	25	137	8	47° 06' 08.22" N	56° 22' 27.59" W
PS2	175	120	8	47° 06' 06.66" N	56° 22' 20.70" W
PS3	890	106	8	47° 05' 59.88" N	56° 21' 48.53" W
ADCP				47° 06' 04.38" N	56° 22' 12.54" W
AS					
P0	0	154	15	46° 47' 39.00" N	56° 09' 29.58" W
AS1	30	153	20	46° 47' 38.46" N	56° 09' 28.44" W
AS2	144	150	20	46° 47' 41.28" N	56° 09' 23.64" W
AS3	848	143	20	46° 47' 52.73" N	56° 08' 54.96" W
ADCP				46° 47' 45.06" N	56° 09' 16.02" W

2.4.2 Vessel noise emission and acoustic analyses

We employed a vessel traffic sound sequence featuring the departure and arrival of one of the noisiest 120m cargo ships of SPM (but see Veillard et al., 2025). Briefly, the 1h20min vessel soundtrack consisted of a continuous sound with a frequency range from 5 to 10,000

Hz, and most energy concentrated in low-frequency bands of 5 to 500 Hz (Duarte et al., 2021; Hildebrand, 2009). This recording was played for 4 months at each site through underwater speakers (Lubell VC2C, Columbus, Ohio, USA, 50-1500Hz) suspended at 8m below the surface (Fig. S2b-c). *In situ* acoustic characterization was performed in both sites, classifying Miquelon as pristine site and St-Pierre as anthropic site (detailed in Gauthier et al. in review). Sound pressure levels (SPL_{rms} in dB re 1 µPa) reaching the collectors were estimated using a spherical model of transmission loss (TL = $20\ \log_{10} R$, where R is the range in meters, Table 5). At the most distant collector from the speaker, SPL_{rms} was 106 dB re 1 µPa in the pristine site (PS) comparable to ambient sound levels (SPL_{rms} = 90-110 dB re 1 µPa) measured for shallow temperate and subarctic environments. This baseline, however, is likely influenced by wind speed and ice concentration as both can modulate underwater SPLs (Halliday et al., 2021; Mathias et al., 2016). However, an unexpected overlap of pile driving from the construction of a platform coincided with vessel noise emission at the anthropic site (AS), exposing mussels to SPL_{rms} > 140 dB re 1 µPa.

2.4.3 **Identification of Mytilus spp. Recruits and morphometric analyses**

In the laboratory, recruits were sorted, identified (according to Aucoin et al. 2004), and counted in a Dollfus counting chamber under a stereomicroscope (Leica®, Wetzlar, Germany). Fifteen random individuals from each station (PS1-PS3 and AS1-S3) were stored in labelled microtube (1.5ml) per replicate (n = 4). Before taking measurements, shells were treated with a low sodium hypochlorite solution (1-2%) to remove salt incrustations and any remaining tissue. To prevent shell weakening, samples were immersed in this solution for a maximum of 3 minutes, then rinsed with distilled water, and mounted on slides containing a 1mm layer of polymer clay (FIMO, Germany). A total of 720 individuals were measured at each site (60 ind. x 3 stations x 4 months). Morphometric analyses were carried out in one valve (left valve, anterior-posterior, see Supplementary materials: Fig. S2b) by measuring the total (TL) and prodissoconch II (PII) lengths as described by Martel et al. (2014).

Measurements were taken using Keyence VHX-2000 Series digital microscope with VH-Z100UR objectives (Osaka, Japan, 1 µm and HDR resolution, Fig. S3d in the Supplementary materials).

2.4.4 **Statistical analyses**

To investigate cohort composition and age structure within distances from anthropogenic noises, we performed a length-frequency analysis and estimated the proportion of individuals in each cohort per distance and per month, adapting the model from Veillard et al. (2023). We analyzed cohort composition using a finite probabilistic Gaussian mixture model (GMM), which assumes that the data follow a mixture of several normal distributions (Bouveyron and Brunet-Saumard, 2014). To determine the optimal number of components in the finite mixture model, we applied the Singular Bayesian Information Criterion (sBIC), which is a useful criterion and remains robust in cases where Gaussian mixture models exhibit irregularities (Weihs and Plummer, 2022). The package 'sBIC' in R uses the Expectation-Maximization (EM) algorithm to provide maximum likelihood estimates for the model parameters (Bouveyron and Brunet-Saumard, 2014). Within this framework, we incorporated Bayes' theta (θ), the set of parameters governing model probability in a Bayesian inference. Model probability is derived by integrating over all possible values of θ, weighted by their prior and likelihood, allowing for a more robust estimation of the number of mixture components while accounting for uncertainty (Bouveyron and Brunet-Saumard, 2014; Doll and Jacquemin, 2019). Here, θ represents the estimated proportion of individuals within each Gaussian component, capturing different cohort structure in the population. We examined a maximum of 10 components for the mixture model and used the sBIC to compare models, selecting the one that best represent the data generating process. After determining the number of components, the R package 'mclust' was utilized to generate a density estimate for each data point and compute the mean and standard deviation for each Gaussian component (Scrucca et al., 2016).

Histogram distributions were compared among distances within each month using the “emdist” package in R (Urbanek and Rubner, 2023), which quantifies the dissimilarity between distributions as the effort required to transform one into another. Using counts, we defined a fixed bin width (200 µm) and set bin edges to cover the entire range across all distances for each month. Although mussel population studies typically adopt smaller bin widths (25-100 µm) to plot distribution frequency (Bayne, 1964; Le Corre et al., 2013), a wider bin was chosen here to facilitate comparisons among treatments. Afterwards, we extracted the counts per bin from each histogram and transformed them into a two-column matrix (bins, counts) for EMD calculations. Matrices were created using Euclidean distance, and analyses were performed employing the function emd (A, B, dist="Euclidean", ...). The EMD is a measure that can take any non-negative value (Urbanek and Rubner, 2023). We reported EMD values using closer ranges adopted by Bergmann et al. (2024): low ($0 \leq x < 0.3$), moderate ($0.3 \leq x < 0.6$) and high ($x \geq 0.6$) levels of dissimilarity. Both cohort analysis and histogram comparisons were performed in R software (R Core Team, 2021, version 4.1.2) using a customized script.

Shell measurements (TL and PL) were individually compared in each site (AS and PS) using a two-way PERMANOVA with distances (stations PS1/AS1, PS2/AS2 and PS3/AS3 corresponding to distances from the speaker of 25 m, 175 m and 890 m, respectively) and months (July, August, September, and October) as factors using PRIMER 7.0. Resemblance matrices were created using the Euclidean distance. We also performed Spearman rank correlations between mean monthly temperature and PII size for both sites using GraphPad Prism 8.0. For these statistical tests, α level was set to 0.05, and we adopted a language of evidence to report our results following the framework proposed by Muff et al. (2022). This approach recommends using evidence-based terminology instead of a binary approach ($p<0.05$ or $p>0.05$) in ecological and evolutionary research. The language of evidence proposed by Muff et al. (2022) categorizes statistical support into levels of evidence: little or no evidence ($0.1 < p < 1.0$), weak evidence ($0.05 < p < 0.1$), moderate evidence ($0.01 < p < 0.05$), strong evidence ($0.0001 < p < 0.01$), and very strong evidence ($0.0001< p < 0.001$).

2.5 Results

2.5.1 Size-class distribution

In the PS, the overall length of recruits in the monthly moored collector spanned from 293 µm to 15 mm. In July and October, the number of cohorts showed slight spatial variability among stations characterized by high values (6 to 9). In contrast, in August and September, the pattern shifted significantly, revealing a detrimental impact of noise exposure, as the number of cohorts decreased to 2 in PS1, while cohort values were >7 in PS3 (Table 6, Figure S3a-d).

In the AS, shell lengths of recruits exhibited less variation, with values ranging from 307 µm to 2.5 mm. Comparable negative impacts of noise were observed; nonetheless, for three months (July, August, and September), only 2-3 cohorts were present in AS1, whereas 5-10 cohorts were found in AS2 and AS3 (Table 6, Figure 16b, check Figure S3 for more details). An exception was observed, with one cohort measured in collectors from the AS3 station in August. Moreover, the cohort number in October was high and similar between AS1 (8) and AS3 (10).

Table 6: Size class distribution, number of cohorts and number of post-larvae of Mytilidae retrieved at specific distances from vessel noise emission (PS1: 137 dB at 25m; PS2: 120 dB at 175m, and PS3: 106 dB re 1 µPa at 890m) and mixture of vessel noise emission and pile driving operations (AS1: 153 dB at 30m, AS2: 150 dB at 144m, and AS3: 143 dB re 1 µPa at 848m) over 4 months at pristine (PS, Miquelon) and anthropic (AS, Saint-Pierre) sites in France, respectively. Due to distinct noise levels and noise types received at the pristine and anthropic sites, we opted to call stations from sound emission using PS1-PS3 and AS1-AS3 to avoid confusion since noise levels were distinct at each site. Cohort structure was determined using mixture distribution models fitted by maximum likelihood, the selected model showed the highest posterior probability and the lowest log-likelihood.

Distance	Size class (n. cohort, interval of means of each size classes in µm)		Model probability	Log (likelihood)	df	n
Pristine site (vessel noise, 106 dB to 137dB re 1 µPa)						
July						
PS1	9	326 – 1230	0.46	- 389.77	26	60
PS2	8	313 – 1860	0.34	- 373. 53	23	60
PS3	8	313 – 1189	0.25	- 379.44	23	60
August						
PS1	2	932 – 1650	0.39	- 409.33	5	60
PS2	6	399 – 2172	0.25	- 425.18	17	60
PS3	7	387 – 1267	0.51	- 402.92	20	60
September						
PS1	2	603 – 1142	0.50	- 426.70	5	60
PS2	2	698 – 2029	1.0	- 438.40	5	60
PS3	10	337 – 2292	0.40	- 416.86	29	60
October						
PS1	8	409 – 2351	0.78	- 403.07	23	60
PS2	5	673 – 9393	0.31	- 469.97	14	60
PS3	6	709 – 7426	0.25	- 451.69	17	60
Anthropic site (vessel and pile driving noises, 143 dB to 153 dB re 1 µPa)						
July						
AS1	2	367 – 939	0.54	- 374.36	5	53
AS2	5	424 – 1137	0.79	- 408.14	14	60

AS3	8	329 – 1960	0.40	- 354.84	23	54
			August			
AS1	3	376 – 1198	0.51	- 420.18	8	59
AS2	6	349 – 1403	0.45	- 406.12	17	60
AS3	1	697	0.50	- 390.86	2	60
			September			
AS1	2	545 – 836	0.48	- 403.22	5	60
AS2	10	440 – 1149	0.60	- 357.99	29	60
AS3	6	419 - 1006	0.36	- 383.04	17	60
			October			
AS1	8	425 – 1261	0.86	- 381.83	23	60
AS2	1	738	0.41	- 395.03	2	58
AS3	10	428 – 1294	0.57	- 388.03	29	60

When considering the length of individuals in the PS, recruits collected in July and August were 18-22% longer in PS1 than those in PS3, with total length ranging from 665 to 968 µm compared to 561 to 789 µm, respectively. An inverse trend was observed in October (Table 6-7, Table S8, S9), revealing that recruits were smaller in PS1 than in the other stations ($t_{PS1-PS2} = 3.10$, $p < 0.001$; $t_{PS1-PS3} = 2.70$, $p < 0.001$). Finally, a third pattern was observed in September, with recruits displaying similar lengths across all stations (PS1-PS3: 795 to 844 µm). Mean size increased over the duration of the experiment, with larger recruits in October (Figure 16a-c).

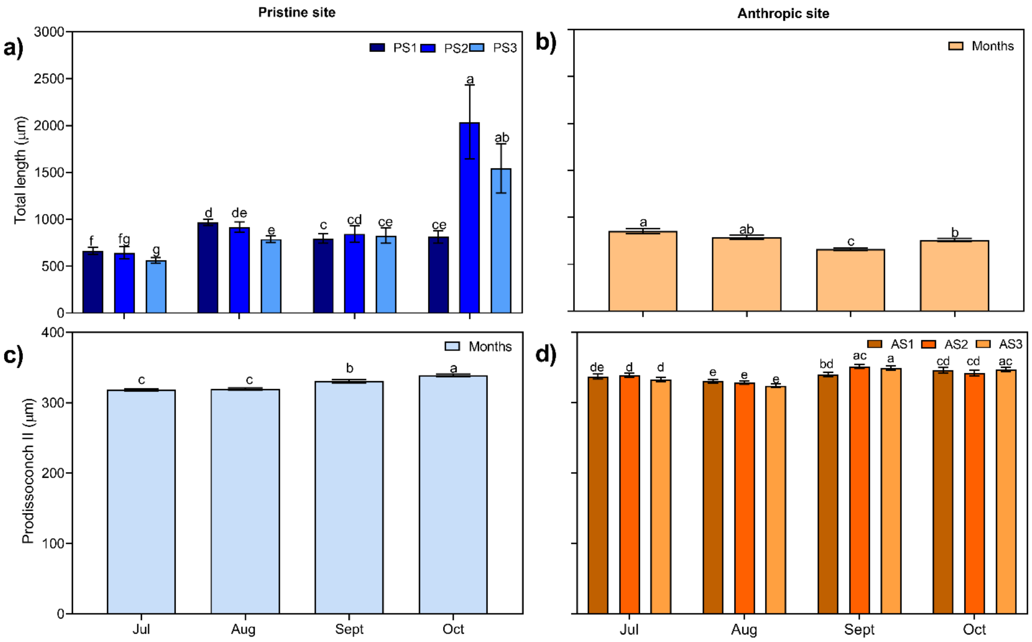

Figure 16: Mean and standard error of total lengths and prodissoconch II of Mytilidae recruits retrieved at three stations (PS1 = 137 dB at 25m or AS1 = 153 dB at 30m, PS2 = 120 dB at 175m or AS2 = 150 dB at 144m, PS3 = 106dB at 890m or AS3 = 143 dB at 848m) distinct anthropogenic noises over 4 months in the pristine (PS, Miquelon, vessel noise **a, c**) and anthropic sites (AS, Saint-Pierre, pile driving and vessel noise **b, d**). Groups with distinct letters indicate evidence of effect (p-perm < 0.05).

By setting a threshold of 500 µm to identify the primary settlement (Le Corre et al., 2013), we noted that a high proportion of the primary settlement (<500 µm) occurred in the early season (July), while secondary settlers were rare (≤ 10%) at all stations of the PS site. The proportion of secondary settlers substantially increased across PS1 to PS3 in August (55-63%) and remained significant (16-31%) during periods of high recruitment (September and October). Overall, four to six cohorts had a mean size > 500 µm in all stations, which was related to the occurrence of secondary settlers (Figure 16a-17a).

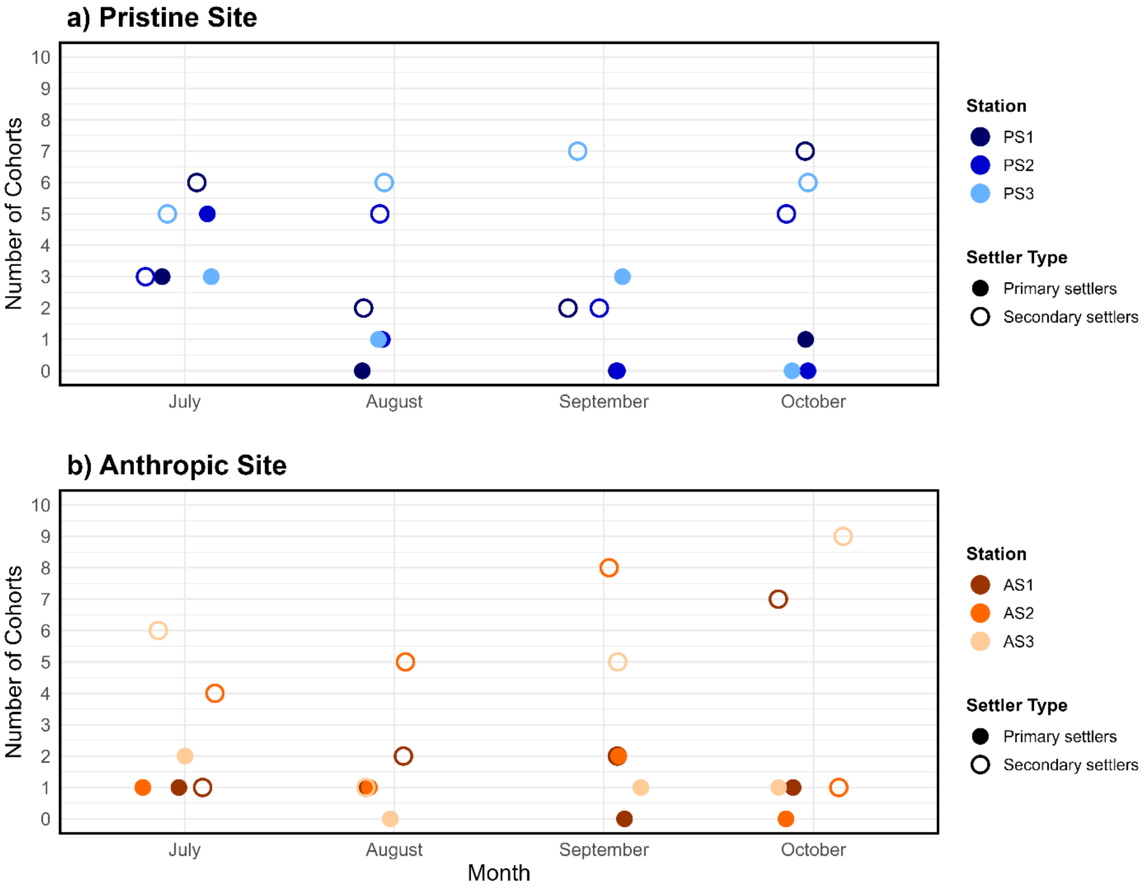

Figure 17: Number of cohorts and distribution of primary (< 500µm) and secondary settlers (> 500µm) found at stations (PS1-PS3 and AS1-AS3) characterized by distinct anthropogenic noises (vessel noise vs a mix of pile driving and vessel noises) at the Pristine (**a**) and Anthropic (**b**) sites. Cohorts were identified using the sBIC and mclust R packages (Scrucca et al. 2016, Drton and Plummer, 2017), and length distributions were compared using the Earth Mover's Distance analysis (Urbanek and Rubner 2023). Consult Table S7 and Figure S3 in supplementary materials for more details.

In the AS, there was minimal to no evidence that mussel total length was affected by the two-factor interaction (distance from noise emission × sampling months) and the distance factor alone (Table 7, S8, S9). There was, however, strong evidence that the total length of recruits was controlled exclusively by the month (Table 7). In all stations, mussels collected in July (853 ± 25 µm) were found to be 12 to 29% larger than those captured in September (660 ± 15 µm) and October (757 ± 18 µm). Differences among months were evident, except for the length comparison between July (853 µm) and August (786 µm) (Figure 16b, Table S9). Our analysis revealed that the month of July was characterized by a high prevalence of secondary settlers (53 to 76%) in all stations. In fact, this proportion of secondary settlers was at least 30% higher than primary settlers in all stations in the other months (August, September, and October). Overall, up to six cohorts were related to secondary settlers, independent of the station and sampling month (Figure 17b).

2.5.2 Prodissoconch analysis

In the PS, mean prodissoconch II size (PII) varied between 263 and 414 µm without an interaction effect between distance and month or only the distance from noise emission, as factors (Table 7). However, temporal variability was observed (Table 7), with PII sizes increase by 3-4% with time, resulting in smaller PII size in July (318µm) and August (320 µm) compared to September and October (mean greater than 331 µm; Figure 16c, Table S10). This PII size increase was not correlated with temperature (S = 6, rho = 0.40, p = 0.75).

In the AS, PII size had similar values, with mean values by station fluctuating from 276 to 430µm, alongside moderate evidence of a two-factor interaction between distance and month (Table 7, S11, Figure 16d). The only notable difference across distances from the noise source was that the PII size at the station near the emission source (AS1) was 3% lower than at the other stations (AS2 and AS3) in September (Figure 16d, Table S11). Similarly to the PS, the rise in mean PII size was not correlated with temperature (S = 4, rho = 0.60, p = 0.42).

Table 7: Results of two-way permutational multivariate analyses (PERMANOVA) testing the effect of noise intensity at specific distances (Di, 3 levels, D1: 25-30m, D2: 144-175m, D3: 848-890m), and months (Mo, 4 levels, July-October) on shell morphometrics composed by prodissoconch II and total lengths of Mytilidae retrieved on sites exposed to vessels (Pristine site - PS, PS1: 137 dB, PS2: 120 dB and PS3: 106 dB re 1µPa) and mix of pile driving and vessel noise (Anthropic site - AS, AS1: 153 dB, AS2: 150 dB and AS3: 143 dB re 1µPa) in the archipelago of Saint-Pierre and Miquelon, France. Significant values ($p < 0.05$) are indicated in bold.

	PS				**AS**			
	Total length (µm)				**Total length (µm)**			
	df	*Pseudo-F*	*p-perm*	*perms*	*df*	*Pseudo-F*	*p-perm*	*perms*
Di	2	4.27	**0.015**	9954	2	1.10	0.34	9940
Mo	3	18.24	**0.0001**	9965	3	14.64	**0.0001**	9954
Di x Mo	6	4.66	**0.0003**	9955	6	1.59	0.09	9942
Res	708				691			
Total	719				701			
	Prodissoconch II (µm)				**Prodissoconch II (µm)**			
	df	*Pseudo-F*	*p-perm*	*perms*	*df*	*Pseudo-F*	*p-perm*	*perms*
Di	2	0.76	0.46	9955	2	0.42	0.65	9956
Mo	3	28.61	**0.0001**	9958	3	24.61	**0.0001**	9936
Di x Mo	6	0.25	0.96	9942	6	2.37	**0.03**	9939
Res	708				708			
Total	719				719			

2.5.3 Similarity among population distributions

Distinct EMD values were observed for each site. In the PS, we observed a substantial monthly decrease (3 to 10x) from moderate-high to low dissimilarity level (0.7 to 2.1) in all stations, with lowest values in September (0.1 – 0.3) and October (0.1, Table 7). In the AS, dissimilarity varied among stations in July, August, and September (0.9 to 2.8). These levels decreased to a moderate level in October, particularly between AS1-AS2 (0.5), as shown in Table 8. PS and AS sites also displayed inverse trends in September and October.

Table 8: Results of Earth mover's distance comparison on a pool of recruits retrieved at stations located at a different distance from noise emission (PS1-AS1:25-30m, PS2-AS2:144-175m and PS3-AS3:848-890m) and characterized by two distinct sources of anthropogenic noise in the pristine (PS, vessel noise, PS1: 137 dB, PS2: 120 dB and PS3: 106 dB re 1µPa) and anthropic (AS, pile driving and vessel noises, AS1: 153 dB, AS2: 150 dB and AS3: 143 dB re 1µPa) sites over a 4-month monitoring in Saint-Pierre and Miquelon archipelago, France. Due to different levels of noises present in each site, we will refer to stations PS1-PS3 and AS1-AS3 to highlight these differences between sites.

	PS			**AS**		
EMD values	*PS1 vs PS2*	*PS1 vs PS3*	*PS2 vs PS3*	*AS1 vs AS2*	*AS1 vs AS3*	*AS2 vs AS3*
July	2.0	0.7	2.1	1.4	0.8	1.2
August	1.7	1.6	1.9	1.1	1.9	0.9
September	0.2	0.3	0.1	2.4	2.8	1.5
October	0.1	0.1	0.1	0.5	1.0	0.8

2.6 Discussion

2.6.1 Early recruitment patterns and size-class distribution in different soundscapes

In a companion paper (Gauthier et al., in press, thesis chapter 3), we reported that patterns of early mytilid recruitment were controlled by the anthropogenic soundscape, with shifts corresponding to SPL_{rms} and SEL thresholds of ~ 140 dB re 1 µPa and ~ 140 dB re 1 µPa².s, respectively. Below these values, at a pristine site, recruits' abundances increased with less intense peaks occurring in July-September compared to October. By contrast, recruitment was inhibited above such threshold values at anthropic site, with low abundance peaks in July, and a gradual increase observed from August to October. In this study, we focus on the impacts of anthropogenic noises on the population structure by performing a cohort and length distribution analysis and thereby assessing the influence of these noises on early recruitment (settlement, secondary migrations). We validate the hypothesis that larval cohorts and size-class distribution varied depending on the noise type and the sound pressure level threshold. We also confirmed that the size-class distribution varied spatially due to noise intensity and temporally in both sites. At both sites, we observed that model probability varied across most stations every month (0.40-1.0). At the pristine site, cohort numbers were initially consistent (8-9 cohorts), mainly driven by secondary settlers, but fluctuated significantly when the pressure threshold fell below 140 dB re 1 µPa and over the months, especially at 137 and 120 dB re 1 µPa (PS1 and PS2). In contrast, our findings indicated that cohort numbers at the anthropic site, largely driven by secondary settlers, started off unevenly and remained consistent at 153 dB re 1 µPa (AS1) for three months, with sharper variations noted at 150 (AS2) and 143 dB re 1 µPa (AS3) over the first months. Single cohorts were observed when the sound pressure threshold was above 140 dB re 1 µPa (AS2, AS3) in August and October. Overall, these patterns suggest that increasing noise intensity alters recruitment and natural variability of cohort structures. The fact that cohort numbers were constant at the highest noise level in the anthropic site is not a positive outcome, because this means vessel and pile driving noises repeatedly inhibited cohort establishment. Recruitment of primary settlers, mostly related to spawning events, is generally in accordance with literature in the St. Lawrence system with the presence of 1 to 3 events from mid-July to mid-September (Le Corre et al., 2013; Martel et al. 2014). The high mobility of mussels after settlement and during adulthood (Forêt et al., 2018b; Petrović and Guichard, 2008; Pilditch et al.; 2015) further illustrate the dynamism of mussel populations, especially when exposed to different type and levels of noise.

2.6.2 Secondary migrations as a key element in the early recruitment

Secondary migrations can occur after the settlement, from post-larvae and juveniles throughout adulthood (Bayne, 1964; Forêt et al., 2018a,b; Günther, 1992; Pilditch et al., 2015). These migrations have been identified in bivalves and gastropods from distinct coastal habitats, changing the spatial distribution of organisms (Bayne, 1964; Forêt, et al. 2018a,b;

Günther, 1992; Martel and Chia, 1991; Olivier and Retière, 1998). These movements result from passive or active processes in which passive resuspension is often coupled to physical disturbances like hydrodynamics, whereas active migration is an organism's response to different triggers such as temperature, trophic factors, predators, salinity, and tides (Forêt et al., 2018a; Günther, 1992; Hunt et al., 2007; Olivier and Retière, 1998). Such active secondary migration is referred to as a secondary settlement, which for mussels consists of an active detachment of a post-metamorphic stage from the substrate, allowing them to drift or crawl, reattaching to a new substrate and changing the primary settlement pattern (Bayne 1964, 1965; Forêt et al. 2018b; Le Corre et al., 2013). The monthly sampling prevented us from accurately assessing the threshold size for secondary settlement ("drifters") using the mussel's competent size of approximately 250 µm plus a daily growth rate less than 10 µm day^{-1} in the St. Lawrence system, as recommended by Martel et al. (2014). This limitation led us to choose a greater threshold size (>500 µm) showing an increase in secondary settlers over time. This trend agrees with Le Corre et al. (2013) observation in the St. Lawrence estuary, but we obtain unexpected results, as drifters represented up to 100% of the recruits in some collectors. In all stations, the cohorts present in collectors were most likely related to secondary settlement. Forêt et al. (2018b) showed in laboratory studies that blue mussels (*Mytilus edulis*) could resuspend within 52-155 days following the first settlement, depending on the growth rate until the size of 1.9mm. In the present *in situ* study, we detected juvenile drifters up to a length of 13mm at the pristine site, confirming the importance of validating laboratory experiments in field studies.

2.6.3 Secondary migrations are inhibited by high sound pressure level noise

Cohorts with size over 3mm were present only in September/October at the pristine site and on collectors from stations with low noise exposure levels (moderate SPL_{rms} = 120 re 1 µPa and close to the ambient noise levels SPL_{rms} = 106 re 1 µPa). All recruits collected at the station with high intensities of vessel noise (SPL_{rms} = 137 dB re 1 µPa) belonged to cohorts smaller than 3mm. That was not the case at the anthropic site, where we observed no recruits over 3mm (maximum size < 2mm) colonizing collectors moored at the highest intensities of the mix of anthropogenic noises (153 dB re 1 µPa). We suggest that high noise levels of vessel noise (137 dB re 1 µPa) and a mix of pile driving, and vessel noises (153 dB re 1 µPa) regulated the size class of recruits, creating unfavourable conditions for the establishment of larger drifters.

As mussels develop from larvae (trochophore, veliger and pediveliger) to a juvenile, and later to an adult, their sensory organs become more complex (Cragg and Nott, 1977; Smolowitz, 2021; Zhadan, 2005). In the initial stages, mussels depend on the apical organ, which contains tufts of cilia positioned to sense and respond to environmental signals (Bayne, 1965; Yurchenko et al., 2019). This organ may still be present in the pediveliger stages of some species (Nikishchenko et al., 2023). Later, pediveliger rely on statocysts situated on their ciliated foot (Cragg and Nott, 1977), while adults develop an additional sense organ, the abdominal sense organ (ASO) (Zhadan, 2005). Within these stages, other organs develop like gills, the mantle and siphons with their sensory tentacles/palps (Smolowitz, 2021), becoming more complex in their organization (Cannuel et al., 2009).

These organs may play an important role in detecting the surrounding movement of water particles, as highlighted by Peng et al. (2016) for adults of *Sinonovacula constricta*. This could be the reason why mussels are more sensitive to some acoustic stimuli in some post-metamorphic stages. Laboratory studies showed that mussel pediveliger's stage is not as sensitive to vessel noise as post-metamorphosed larvae (Cervello et al., 2023; Veillard et al., 2025). This higher sensitivity after metamorphosis aligns with our results, where the lack of larger drifters suggests that these recruits avoided >150 dB re 1 µPa impulsive/continuous noisy conditions, and as well as the range of 120 to 137 dB re 1 µPa for the continuous vessel noise playback. We suggest that such inhibition patterns, close to the sound emission area in both sites, could be explained when considering available findings on the opening/closure valve behaviour already seen in several bivalve species, including adult mussels, juvenile and adult scallops, and adult oyster (Jézéquel et al., 2022; Ledoux et al. 2023; Roberts et al., 2015, Wale et al., 2019). All these studies reveal that those disruptions in valve closures occur in the presence of different sound environments. Most importantly, Jézéquel et al. (2022) demonstrated that juvenile scallops were much more affected than adults and subadults in the near site, displaying more valve closures synchronized to hammer strikes of pile driving. This increased sensitivity in juvenile stages may also affect mussels. For instance, it could reduce mussel feeding as demonstrated by Wale et al. (2019), and increase metabolic stress, such as higher production of gluconeogenesis and higher energy demand but which will deplete quickly, as highlighted by Veillard et al. (2025) for mussel post-larvae exposed to vessel noise intensity above SPL_{rms} 137dB re 1 μPa. We hypothesize that anthropogenic noises with SPLs >137 dB re 1 μPa (either continuous or a mixture of impulsive/continuous sounds) may disrupt mussel valve activity, compromising mussel size due to feeding struggles and stress, which could have repercussions for population dynamics (Gauthier et al., in press) and mussel farming (Petraitis and Dudgeon 2020, Baden et al. 2021, South et al. 2022).

2.6.4 Delay on metamorphosis and environmental conditions

The hypothesis that anthropogenic noise emitted *in situ* could trigger mussels in postponing metamorphosis was not confirmed, as a minor reduction (1-3μm) of PII size was observed between stations. Mussel growth rates and larval duration have often been regulated by environmental factors such as water temperature and food availability (Bayne, 1965; Pechenik et al., 1990; Rayssac et al., 2010). Additionally, the size at metamorphosis provides crucial information, functioning as a valuable tool for assessing changes in prodissoconch II length in response to environmental variations (Lutz and Jablonski, 1978; Martel et al., 2014; Seed et al., 2000). An increase in PII can originate from cold temperatures (9-14°C), which are known to extend larval duration, as reported by Bayne (1965) and Lutz and Jablonski (1978). Here, we did not find any significant correlation between temperature and the prodissoconch II length, as already seen by Le Corre et al. (2013) and Martel et al. (2014) in other areas of the St. Lawrence system. In agreement with these studies, we observed mussels displaying larger PII sizes in both sites (~340-350 µm) in late-summer as well as in early fall. These authors proposed that this larger PII size reveals a delay of metamorphosis which could be due to the absence of a trophic cue. Here, we are unable to validate the *trophic settlement trigger* hypothesis of Toupoint et al. (2012) since mussels and seston samples were collected every 30 days. Recent work from Gauthier et al. (unpublished data) demonstrated that the low percentage of essential fatty acids in POM might be the main reason why the settlement success of mussels in Miquelon Bay was low in July.

2.6.5 Comparison of distributions within distances of different soundscapes using the EMD

Mussels exhibit spatial-temporal variations in population distribution driven by environmental factors (Martel et al., 2014; Seed et al., 2000; Toupoint et al., 2012) and anthropogenic stressors (Baden et al., 2021; Petraitis and Dudgeon, 2020). Understanding the spatial distribution of this bivalve is essential to comprehend their behaviours and forecast recruitment changes, as well as identify stressors which may weaken the stock (Baden et al., 2021; Jolivet et al., 2016). Length-frequency distributions, in the form of histograms, are helpful tools to visualize the size classes of mussels and their proportion at stations characterized by different levels and types of anthropogenic noise. One way to compare frequency distributions of bivalve lengths, including mussels, is by adopting statistical tests like Kolmogorov-Smirnov (Diez et al., 2023; Le Corre et al., 2013), which is a one-dimension method sensitive near the center of the distribution but not at the right tail of distribution (Rubner et al., 2000). In this context, the EMD histogram analysis emerges as a powerful tool for quantifying the dissimilarity between recruit distributions at stations located at specific distances from simulated vessel passages or a mix of anthropogenic noises. The integration of EMD into ecological research is still a work in progress (Kranstauber et al., 2017), but our analysis reveals it can provide richer information if population distributions are dissimilar at specific distances from a noise disturbance, unlike the Kolmogorov-Smirnov test, which is less effective test into account location and shape of distributions (see details in Filion, 2015). Here, dissimilarities between distributions at each site largely varied in relation to noise type and level. In July-August, population distributions displayed higher levels of dissimilarity between noise intensities (106 to 137 dB re 1 μPa) in the pristine site, then became more uniform over time despite the rising mean size class due to four and ten larger recruits settling in a less noisy environment (106 and 120 dB re 1 μPa). When natural soundscapes were more impacted by shipping and pile driving noise (>140 dB re 1 μPa), dissimilarities between the size frequencies of early recruits were more pronounced and persistent at both spatial and temporal scales. We hypothesize that such differences originate from the anthropophony influence (SPL and SEL) with potential negative impacts on mussel recruitment dynamics, especially when both continuous and impulsive noises occur at high levels. By contrast, one vessel noise source <140 dB re 1 μPa can stimulate mussel recruitment nonetheless on suitable natural habitats but also on unsuitable ones as selectivity could be impaired. Thus, all these noise disturbances involving maritime traffic and harbour building operations can disturb population dynamics and modify recolonization patterns in coastal areas, which constitutes a current concern since invertebrates might face multiple anthropogenic noise pressures (Thomsen and Popper, 2024). Moreover, human-noise exposure of post-larval stages can generate latent effects on future stages in the lifecycle (Pechenik, 2006; Podolsky and Moran, 2006). One possible scenario is that inhabiting noisy environments, like the anthropic site of St-Pierre harbour, may also trigger generational effects in the maternal and larval level, as Gigot et al. (2024) demonstrated with adults and larvae of *Pecten maximus* exposed to pile driving emissions under controlled conditions. Establishing a noise threshold is crucial to prevent harm to the organism, population or community level (Hawkins and Popper, 2017; Solé et al., 2023). For bivalves, Gauthier et al. (in review, chapter III) suggested that sound exposure level (SEL_{1min}) below 140 dB re 1 μPa^2.s may result in less deleterious effects on Mytilidae's recruitment. The present data, based on shell length distributions and EMD approach, further reinforce that noise threshold for mussels should remain 140 dB re 1 μPa^2.s. Finally, this work underlines that mixture of several anthropogenic noises, combining continuous and impulsive signals, seems to have a stronger effect on recruitment, including secondary drifters, thereby emphasizing the need for more research focused on multiple anthropogenic pressures, as already suggested by Thomsen and Popper (2024).

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2.9 Supplementary materials

Table S8: Number of components and model posterior probability estimated using sBIC package for mussel recruits retrieved from collectors moored at specific stations (intensities at distances) from anthropogenic emissions of vessel noise (PS1/PS3) and a mix of vessel and pile driving noises (AS1/AS3) at pristine and anthropic sites, respectively. Stations at the pristine site (PS) were exposed to intensities 137 dB re 1 μPa (PS1), 120 dB re 1 μPa (PS2) and 106 dB re 1 μPa (PS3). At the same time, stations at the anthropic site (AS) experienced higher noise intensities of 153 dB re 1 μPa (AS1), 150 dB re 1 μPa (AS2) and 143 dB re 1 μPa (AS3). Probabilities inferior to 1 x 10-5 are noted as < 0.00001. Traces (--) indicate that we could not run the model to estimate 10 components in a station.

	Pristine site (PS)									
	Number of components and model probability by sBIC									
	1	2	3	4	5	6	7	8	9	10
	July									
PS1	0.0002	0.03	0.04	0.004	0.38	0.06	0.007	0.001	0.46	0.02
PS2	< 0.00001	< 0.00001	0.01	0.04	0.07	0.17	0.24	0.34	0.08	0.04
PS3	< 0.00001	< 0.00001	0.17	0.19	0.05	0.07	0.22	0.26	0.03	0.004
	August									
PS1	0.06	0.39	0.10	0.05	0.03	0.10	0.02	0.20	0.02	0.004
PS2	0.002	0.12	0.05	0.16	0.15	0.24	0.13	0.08	0.04	0.02
PS3	0.01	0.02	0.009	0.01	0.002	0.38	0.51	0.005	0.04	0.0001
	September									
PS1	< 0.00001	0.49	0.14	0.32	0.04	--	--	--	--	--
PS2	< 0.00001	1.0	--	--	--	--	--	--	--	--
PS3	< 0.00001	0.004	0.04	0.18	0.07	0.10	0.08	0.002	0.12	0.40
	October									
PS1	< 0.00001	0.03	0.009	0.001	0.0002	0.07	0.12	0.77	0.002	0.0007
PS2	< 0.00001	0.004	0.11	0.24	0.18	0.31	0.09	0.04	0.008	0.0009
PS3	< 0.00001	0.0001	0.005	0.02	0.25	0.34	0.26	0.10	0.02	0.003
	Anthropic site (PS)									
	Number of components and model probability by sBIC									
	1	2	3	4	5	6	7	8	9	10
	July									
AS1	0.02	0.54	0.18	0.13	0.02	0.05	0.04	0.01	0.008	0.004
AS2	0.04	0.01	0.03	0.01	0.79	0.09	0.02	0.03	0.01	0.002

AS3	< 0.00001	< 0.00001	0.18	0.04	0.02	0.17	0.15	0.40	0.04	0.003
August										
AS1	0.003	0.04	0.51	0.44	--	--	--	--	--	--
AS2	< 0.00001	0.002	0.04	0.14	0.09	0.40	0.09	0.01	0.02	0.03
AS3	0.50	0.06	0.01	0.01	0.01	0.21	0.14	0.03	0.002	0.001
September										
AS1	0.07	0.48	0.08	0.17	0.02	0.09	0.06	0.01	0.01	0.001
AS2	< 0.00001	0.003	0.002	0.002	0.008	0.002	0.003	0.04	0.33	0.60
AS3	0.0003	0.13	0.03	0.07	0.04	0.36	0.09	0.07	0.04	0.17
October										
AS1	0.002	0.002	0.001	0.0002	0.0007	0.04	0.09	0.86	0.0002	0.006
AS2	0.41	0.17	0.06	0.09	0.05	0.04	0.005	0.03	0.11	0.03
AS3	< 0.00001	0.30	0.09	0.03	0.02	0.003	0.004	0.004	0.0006	0.57

Table S9 : Pair-wise test results on the interaction of distance × month (two-way PERMANOVA) showing differences in the total length of Mytilidae recruits among distances (PS1= 137 dB re 1 µPa at 25m , PS2 = 120 dB re 1 µPa at 175m and PS3 = 106dB re 1 µPa at 890m) and months (July, August, September, and October) from vessel noise emission on the pristine site located in Miquelon Bay, France. Significant values ($p<0.05$) are indicated in bold.

Factor Distance	Pair-wise tests	t-test	P(MC)	*Factor* Month	Pair-wise tests	t-test	P(MC)
Jul	PS1, PS2	0.28	0.78	*PS1*	Jul, Aug	6.23	**0.0001**
	PS1, PS3	2.17	**0.03**		Jul, Sept	2.07	**0.043**
	PS2, PS3	1.12	0.26		Jul, Oct	1.91	0.06
					Aug Sept	2.85	**0.005**
Aug	PS1, PS2	0.77	0.44		Aug, Oct	2.06	**0.04**
	PS1, PS3	3.68	**0.0003**		Sept, Oct	0.20	0.84
	PS2, PS3	1.94	**0.05**				
				PS2	Jul, Aug	3.15	**0.002**
Sept	PS1, PS2	0.48	0.63		Jul, Sept	1.83	**0.07**
	PS1, PS3	0.32	0.75		Jul, Oct	3.49	**0.0011**
	PS2, PS3	0.15	0.88		Aug Sept	0.72	0.47
					Aug, Oct	2.81	**0.006**
Oct	PS1, PS2	3.06	**0.002**		Sept, Oct	2.96	**0.0041**
	PS1, PS3	2.70	**0.008**				
	PS2, PS3	1.04	0.30		Jul, Aug	4.76	**0.0001**
				PS3	Jul, Sept	3.02	**0.003**
					Jul, Oct	3.73	**0.0005**
					Aug Sept	0.42	0.67
					Aug, Oct	2.85	**0.004**
					Sept, Oct	2.61	**0.010**

Table S10: Pair-wise test results on the month factor (two-way PERMANOVA) showing differences among months (July, August, September and October) in the total length of Mytilidae in the anthropic site at Saint-Pierre, France.

Factor Months	Pair-wise tests	t-test	p-value (MC)
	Jul, Aug	1.93	0.06
	Jul, Sept	6.61	**0.0001**
	Jul, Oct	3.06	**0.003**
	Aug Sept	4.62	**0.0001**
	Aug, Oct	0.98	0.33
	Sept, Oct	4.20	**0.0001**

Table S11: Pair-wise test results on the month factor (two-way PERMANOVA) showing differences among months (July, August, September and October) in the prodissoconch II length of Mytilidae in the pristine site at Miquelon, France. Significant values ($p < 0.05$) are indicated in bold.

Factor Months	Pair-wise tests	t-test	P(MC)
	Jul, Aug	0.56	0.58
	Jul, Sept	4.50	**0.0001**
	Jul, Oct	8.35	**0.0001**
	Aug Sept	4.10	**0.0003**
	Aug, Oct	7.89	**0.0001**
	Sept, Oct	2.86	**0.004**

Table S12: Pair-wise test results of the interaction of distance and month (two-way PERMANOVA) showing differences in prodissoconch II (PII) of recruits of Mytilidae among distances from a mixture of pile driving and vessel noises (AS1 = 153 dB re 1 µPa at 30m, AS2 = 150 dB re 1 µPa at 144m, and AS3 = 143 dB re 1 µPa at 848m), and months (July, August, September, October) collected from an anthropic site in Saint-Pierre Bay, France. Significant values ($p < 0.05$) are indicated in bold.

Factor Distance	Pair-wise tests	t-test	P(MC)	*Factor* Month	Pair-wise tests	t-test	P(MC)
Jul	AS1, AS2	0.92	0.38	*D1*	Jul, Aug	1.94	0.06
	AS1, AS3	1.02	0.33		Jul, Sept	0.65	0.53
	AS2, AS3	1.49	0.15		Jul, Oct	1.26	0.21
					Aug Sept	2.27	**0.03**
Aug	AS1, AS2	0.73	0.48		Aug, Oct	3.30	**0.002**
	AS1, AS3	1.79	0.07		Sept, Oct	1.28	0.20
	AS2, AS3	1.28	0.20				
				D2	Jul, Aug	2.91	**0.004**
Sept	AS1, AS2	2.79	**0.006**		Jul, Sept	3.13	**0.002**
	AS1, AS3	2.10	**0.04**		Jul, Oct	0.89	0.38
	AS2, AS3	0.53	0.59		Aug Sept	6.34	**0.0001**
					Aug, Oct	3.04	**0.002**
Oct	AS1, AS2	0.73	0.47		Sept, Oct	1.95	0.06
	AS1, AS3	0.26	0.78				
	AS2, AS3	1.14	0.26		Jul, Aug	2.29	**0.03**
				D3	Jul, Sept	3.59	**0.001**
					Jul, Oct	3.37	**0.001**
					Aug Sept	6.00	**0.0001**
					Aug, Oct	5.80	**0.0001**
					Sept, Oct	0.42	0.68

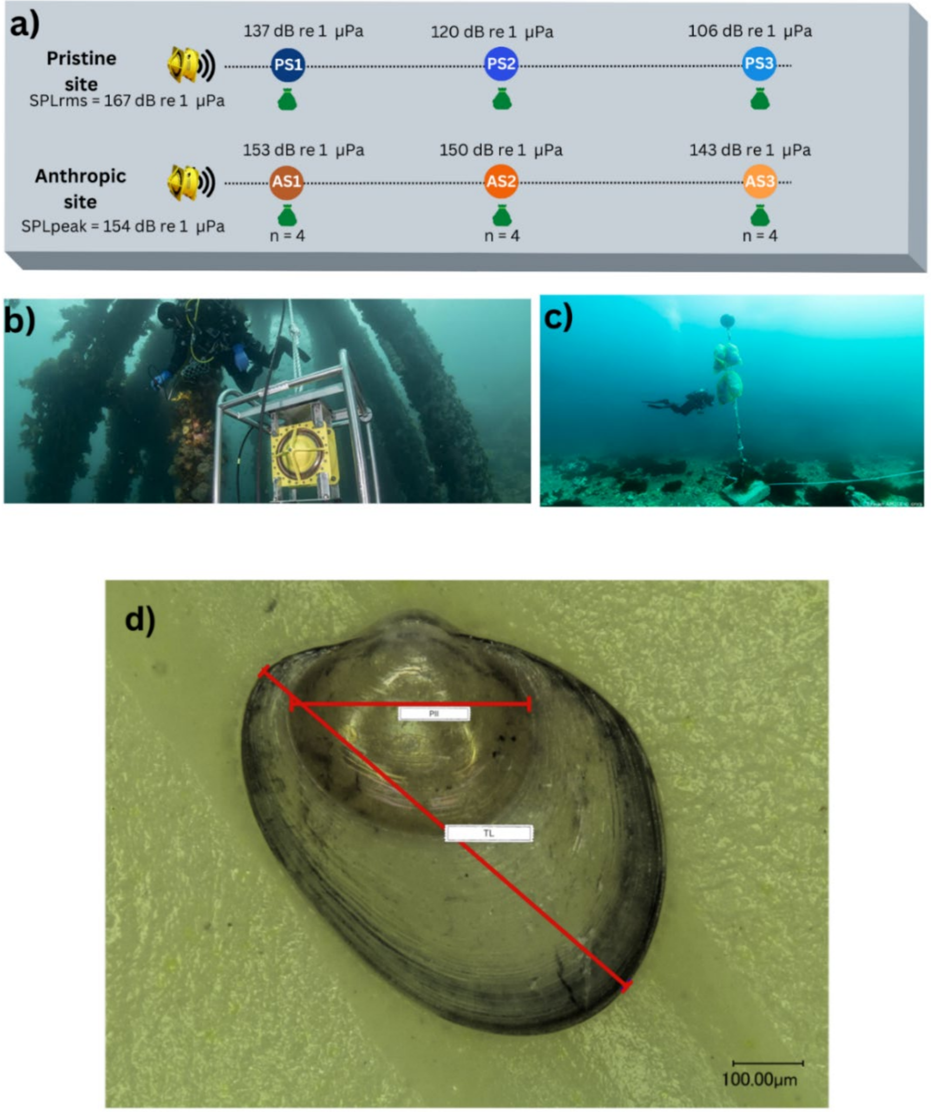
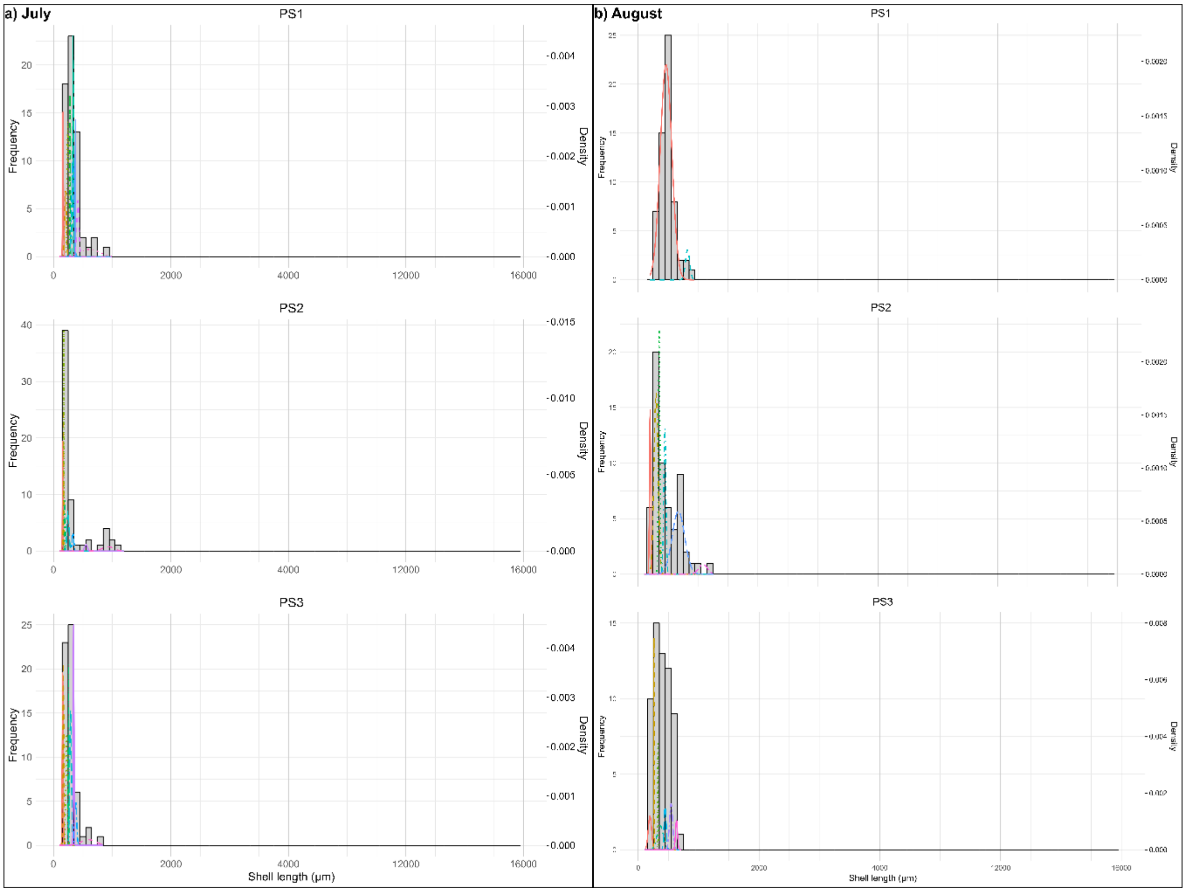
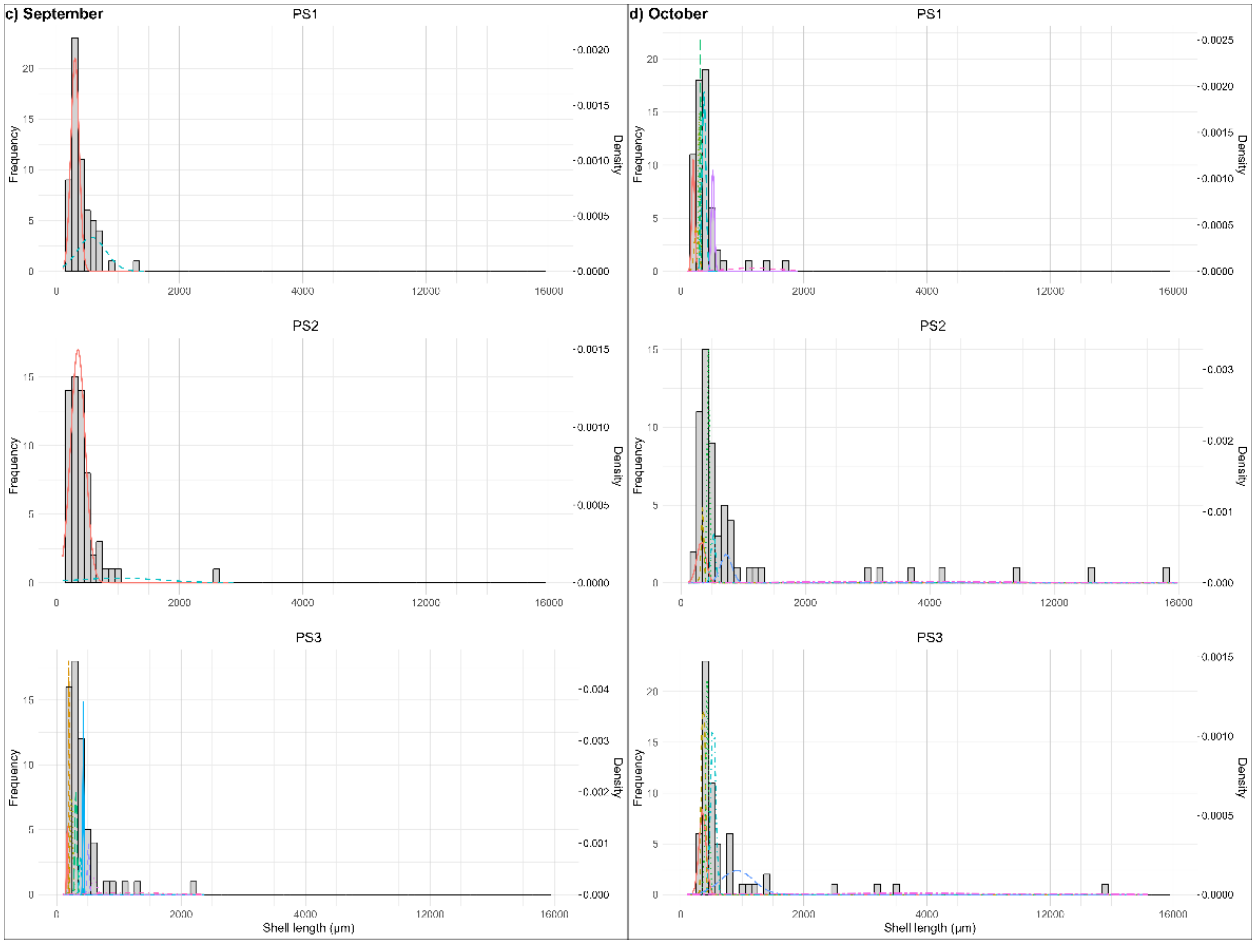
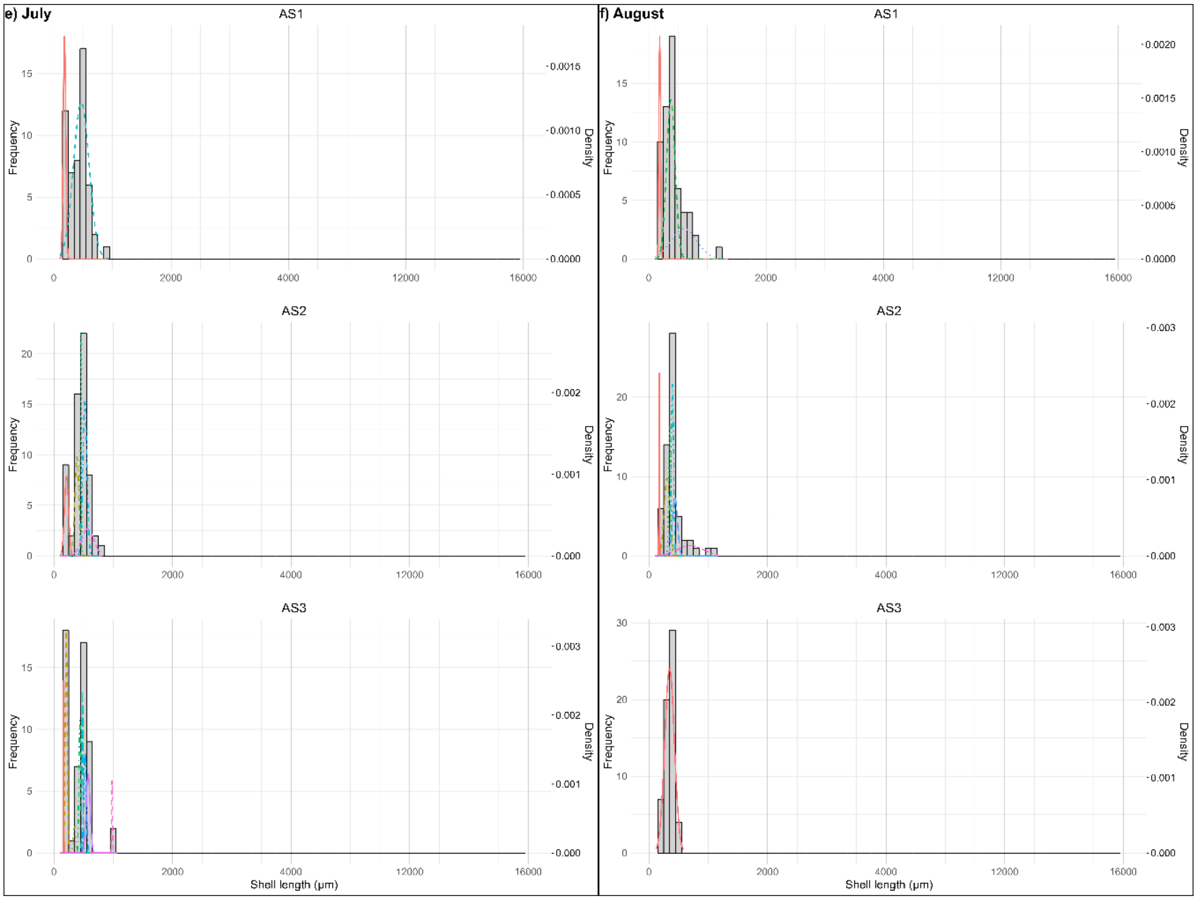


Figure S3: Graphic and photos describing the *in situ* experimental design and shell morphometric analyses. (a) Schematic representation of *in situ* experimental design where recruits were exposed to increasing levels of vessel noise (PS1 = 137 dB re 1 µPa at 25m, PS2 = 120 dB re 1 µPa at 175m, and PS3 = 106 dB re 1 µPa at 890m) or a mix of vessel and pile driving noises (AS1 = 153 dB re 1 µPa at 30m, AS2 = 150dB re 1 µPa at 144m, and AS3 = 143 dB re 1 µPa at 848m) along transects at the pristine (PS) and anthropic (AS) sites, respectively. (b) Underwater photo showing the deployment of the underwater speaker used in each site. (c) Underwater photo of artificial collectors (n = 4) used to retrieve recruits at each station. (d) Shell measurements performed at each individual to estimate prodissoconch II (PII) and total lengths (TL).


a) July
PS1
Frequency
Density
0
5
10
15
20
0.000
0.001
0.002
0.003
0.004
0
2000
4000
12000
16000
PS2
0
10
20
30
40
0.000
0.005
0.010
0.015
PS3
0
5
10
15
20
25
0.000
0.001
0.002
0.003
0.004
Shell length (µm)
b) August
PS1
25
20
15
10
5
0
0.0020
0.0015
0.0010
0.0005
0.0000
PS2
20
15
10
5
0
0.0020
0.0015
0.0010
0.0005
0.0000
PS3
15
10
5
0
0.008
0.006
0.004
0.002
0.000
0
2000
4000
12000
16000
Shell length (µm)


c) September
d) October
PS1
PS2
PS3
Frequency
Density
Shell length (µm)
0
2000
4000
12000
16000


e) July
f) August
AS1
AS2
AS3
Frequency
Density
Shell length (µm)
0
2000
4000
12000
16000

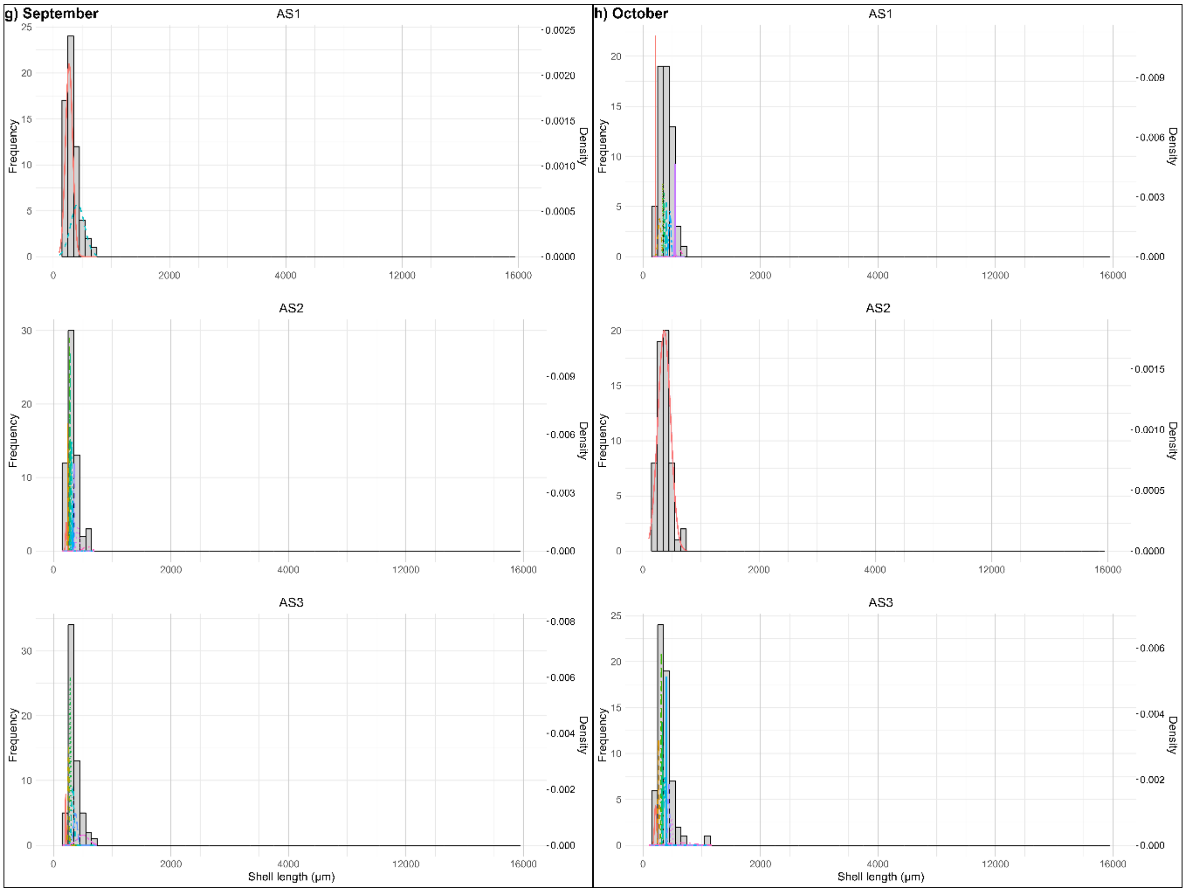


Figure S4: Size-class of recruits of Mytilidae collected from distinct intensities from vessel noise emission (a, b, c, d, pristine with PS1 = 137 dB re 1 µPa at 25m, PS2 = 120 dB re 1 µPa at 175m, PS3 = 106 dB re 1 µPa at 890m) and mix of pile driving and vessel noise (e, f, g, h, anthropic with AS1 = 153 dB re 1 µPa at 30m, AS2 = 150 dB re 1 µPa at 144m, and AS3 = 143 dB re 1 µPa at 848m) over 4-months at either: a) pristine site in Miquelon (PS), France, and b) anthropic site (AS) in Saint-Pierre, France. Lines represent the estimated Gaussian densities (probability density) corresponding to the different cohorts (Gaussian finite mixture model), one-line type by cohort. To standardize size classes over stations and months, we chose x-axis ranging from 200 to 16000, with a bin width of 200 µm.

CHAPITRE 3/CHAPTER III

SHOULD I STAY OR SHOULD I GO: ANTHROPOGENIC NOISE DISRUPT EARLY RECRUITMENT OF SUBARCTIC INVERTEBRATES

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Les bruits anthropiques perturbent le recrutement précoce des invertébrés subarctiques

3.1 Résume

Les systèmes côtiers subarctiques sont habités par des bivalves et des gastéropodes qui, en raison de leur cycle de vie et de leur longévité, sont des indicateurs fiables des altérations écologiques de l'environnement. De récentes études en laboratoire ont montré que les jeunes stades de vie des invertébrés perçoivent les sons naturels, et que leur sélection d'habitat, leur comportement et leur morphologie pourraient être altérés par le bruit anthropogénique. Dans le cadre d'une étude de terrain menée sur deux sites différant par leur niveau de pollution sonore (Pristine PS ou Anthropisé AS), nous avons testé si les distances (de 25 à 890 m) des bruits anthropiques pouvaient affecter la diversité et le recrutement précoce de plusieurs espèces dans des sites vierges et anthropisés en utilisant des collecteurs artificiels amarrés sur des transects. Dans l'ensemble, les conditions environnementales (à l'exception des niveaux sonores) étaient homogènes sur les transects. Le scénario acoustique différait entre les sites PS (bruit de navire, 132-138 dB 1μ Pa^2.s) et AS (mélange de bruit de battage de pieux et de bruit de navire, > 140 dB 1μ Pa^2.s), le site AS subissant un niveau d'exposition sonore plus élevé que le site PS. La richesse des espèces a fluctué en fonction de la distance par rapport au bruit, mais uniquement dans le site anthropisé. En ce qui concerne la diversité et la régularité des espèces, elles varient en fonction de la distance et du mois sur les deux sites, ce qui montre un effet négatif évident des bruits anthropogéniques et une modification de la composition des espèces. Des réactions différentes de recrutement précoce ont été observées pour chaque espèce soumises aux bruits anthropiques, mais avec un schéma différent pour chaque site en raison des variations de la pression acoustique et des niveaux d'exposition. Les résultats de notre étude sur le terrain montrent, pour la première fois, que les émissions sonores anthropiques contrôlées entraînent des changements écologiques dans la structure des communautés et les paramètres des populations d'espèces d'invertébrés marins benthopélagiques. Pour éviter les perturbations de la structure des communautés et du recrutement, nous recommandons que le niveau de bruit seuil pour les invertébrés soit inférieur à 140 dB re 1 μPa^2.s.

Mots clés : anthropophonie, bivalves, gastéropodes, pollution sonore marine, effets du bruit, dynamique des populations.

3.2 Abstract

Coastal subarctic systems are inhabited by bivalve and gastropods, which due to their lifecycle and longevity are reliable indicators of ecological alterations in the environment. Recent laboratory studies have shown that young life stages of invertebrates perceive natural sounds, and their settlement, behaviour, and fitness could be altered by anthropogenic noise. Through a field study conducted on two sites differing by their noise pollution level (Pristine PS or Anthropized AS), we tested whether the distances (from 25 to 890 m) of anthropogenic noises might affect the diversity and early recruitment of multiple species in pristine and anthropized sites using artificial collectors moored on transects. Overall, environmental conditions (except sound levels) were homogeneous through the transects. The acoustic scenario differed between the PS (vessel noise, 132-138 dB re 1 $\mu Pa^2.s$) and AS (mix of pile-driving and vessel noise, > 140 dB re 1 $\mu Pa^2.s$) sites, with the AS site experiencing a higher level of sound exposure than the PS site. Species richness fluctuated with distance from the noise, but only in the anthropized site. Regarding species diversity and evenness, they varied with distance and month at both sites, displaying a clear negative effect of anthropogenic noises and shifting species composition. Specific early recruitment responses were observed for each species to anthropogenic noise, but with different pattern for each site due to variations in sound pressure and exposure levels. The findings of our field study document, for the first time, that controlled anthropogenic noise emission leads to ecological shifts in community structure and population metrics of benthopelagic marine invertebrate species. To avoid disruptions in community structure and recruitment, we recommend that a noise threshold level for invertebrates should be below 140 dB re 1 $\mu Pa^2.s$.

Keywords: anthropophony, bivalves, gastropods, marine noise pollution, noise effects, population dynamics.

3.3 Introduction

Subarctic ecosystems are dynamic and fragile environments characterized by a remarkable diversity of marine organisms, including the ubiquitous marine invertebrates (Dunbar, 1954). These organisms are essential components of coastal ecosystems as well as reliable indicators of environmental disturbances (Baden et al., 2021; Seed et al., 2000). Over the years, the subarctic region is increasingly enduring multiple anthropogenic stressors. These include ocean warming and acidification, chemical pollution (see details on Halpern et al., 2019; Svavarsson et al., 2021), and anthropogenic noise - recently recognized as a distinct and pervasive form of pollution (Duarte et al., 2021; Merchant et al., 2022; Slabbekoorn et al., 2010). Collectively, these pressures jeopardize the health and stability of the ecosystem at risk (Halpern et al., 2019). Therefore, monitoring subarctic communities through metrics such as species richness, diversity, and evenness became vital and response to anthropogenic stressors became vital. These ecological indicators offer insights into recruitment patterns, help to predict responses to anthropogenic disturbance, and support the development of sustainable mitigation and management strategies (Austen et al., 2002; Campagne et al., 2023; Dreujou et al., 2020). Among emerging stressors, anthropogenic noise (such as vessel noise, pile driving, drilling, and related activities) has gained increasing attention. Some countries have incorporated such noises (such as vessel noise, pile driving, drilling, etc.) into marine directives or are working toward guidelines to address its ecological implications to prevent harmful effects (Breeze et al., 2022; Merchant et al., 2022). The frequency, intensity, and temporal characteristics of anthropogenic noises turn them into pervasive pollutants, capable to generate ecological effects across both terrestrial and marine ecosystems (Jerem and Matthews, 2020; Kunc et al., 2016; Sordello et al., 2020). Despite growing research into its effects on wildlife, birds and marine mammals remain the most intensively studied groups, with invertebrates and reptiles receiving the least attention (Jerem and Matthews, 2020; Sordello et al., 2020). Noise has been shown to alter bird diversity (Perillo et al., 2017; Proppe et al., 2013) and amphibian species composition (Trowbridge and Litzgus, 2022). However, the ecological effects of anthropogenic noise on benthic invertebrates remain understudied, despite emerging evidences that noise promotes behavioral and fitness effects (Gigot et al., 2024; Jolivet et al., 2016; Olivier et al., 2023; Stocks et al., 2012; Veillard et al., 2015; Wilkens et al., 2012).

One particularly sensitive phase in the life cycle of benthic invertebrates, like bivalves and gastropods, is the transition from planktonic larvae to benthic sessile or slow-moving juvenile. These stages are connected by a milestone event filled with exploratory behaviour and cue detection, known as settlement (Hadfield and Paul, 2001; Thorson, 1950). Numerous studies have demonstrated that larvae evaluate a range of cues when selecting or rejecting settlement sites, including hydrodynamics (Butman, 1987; Fuchs et al., 2018; Pernet et al., 2003), substrate characteristics (Bayne, 1965; Fraschetti et al., 2003), biofilm composition (Hadfield and Paul, 2001; Toupoint et al., 2012a), the presence of conspecifics or predators (Beal et al., 2020; Hadfield and Paul, 2001; Morello and Yund, 2016), trophic signals (Androuin et al., 2022; Toupoint et al., 2012b), and, more recently, underwater soundscapes (Lillis et al., 2013, 2015; Williams et al., 2022). Some of these acoustic cues are anthropogenic in origin (i.e., maritime traffic, pile driving or drilling operations) and recent research suggests that larvae can perceive and respond to them. Laboratory studies have shown that larvae may respond or not to the combination of trophic cue with anthropogenic noise (Gigot et al., 2023a,b; Jolivet et al., 2016). If a suitable substrate and environmental conditions are found, larvae settle and metamorphose, transforming into a benthic form (Hunt and Scheibling, 1997). However, in the absence of suitable cues, settlement-metamorphosis of species may be delayed. This delay provides larvae with another opportunity to locate a suitable settlement site but also increase their vulnerability to environmental stressors (Bayne, 1965; Lagarde et al., 2018; Martel et al., 2014; Pechenik, 1990). Post-metamorphic stages are also vulnerable, but in this case, substantial mortality is often driven by predation (reviewed by Beal et al., 2020; Gosselin and Qian, 1997; O'Connor et al., 2008). In some species, this first attachment is not permanent, and post-metamorphic stages may passively resuspend or actively respond to environmental stimuli (i.e. hydrodynamics, trophic environment, pollution, etc.), resulting in secondary migration and new spatial distribution (Forêt et al., 2018a,b; Günther, 1992; Martel and Chia, 1991). Consequently, recruitment is governed not only by larval availability (supply-side theory), but also by larval behaviour during settlement, physiological state, and post-settlement survival and migration, all modulated by a complex interplay of biotic and abiotic factors (Hunt and Scheibling, 1997; Keough and Downes, 1982; Leal et al., 2022; Martel and Chia 1991).

Shipping noise is increasingly recognized as a disruptor of natural soundscapes (Duarte et al., 2021) with potential consequences for populational processes and community structure (Kunc et al., 2016; Solé et al., 2023). To progress in this context, field experiments are required, as they offer ecologically insights by incorporating seasonal variation, species interactions and simultaneous environmental stressors (Spicer, 2014). This limitation is compounded by the lack of *in situ* data on the distances from the source at which noise begins to impair invertebrate functions, making it difficult to define biologically relevant thresholds (Hawkins and Popper, 2017). In contrast, regulatory thresholds for sound pressure and exposure levels have been more thoroughly established for marine mammals, and to a lesser extent, to fish. Similarly, regulatory efforts across other taxa and countries remain uneven compared to marine mammals (see Bonnel et al., 2022; Breeze et al., 2022; Merchant et al., 2022; NFMS, 2018; Popper et al., 2014).

Understanding how vessel noise affects organisms at specific distances from its source is especially important for invertebrate communities and foundation species inhabiting both nearly pristine and more anthropized environments, where differing acoustic soundscapes may lead to distinct impacts (Halliday et al., 2021; NRC, 2003). To address this, we selected experimental sites with contrasting acoustic profiles to assess whether a gradient of vessel noise produces different ecological responses at each site. We deployed artificial collectors at three distances (D1, D2 and D3) from a commercial vessel noise source along transects at two sites with different levels of maritime traffic: Miquelon (pristine) and Saint-Pierre (anthropized). This setup exposed collectors to a gradient of vessel noise intensities: 137 dB at D1, 120 dB at D2 and 106 dB re 1 μPa at D3. Therefore, the main objective of this study was to assess the effect of distances from such anthropogenic noise – measured as sound intensity - on the diversity and early recruitment of multiple benthic species in a field setting.

We hypothesized that as the distance between the re-emitted vessel noise and collectors decreases, the diversity and early recruitment of subarctic invertebrates would also decline. To test this hypothesis, we first estimated the number of taxa, diversity and evenness in the collectors, using indices such as Richness (S), Shannon-Wiener (H'), and Pielou's Evenness (J'). We then examined the abundance (potential settlers, post-larvae, juveniles) from different invertebrate taxa on collectors placed at increasing distances from vessel noise sources over four months in the field.

3.4 Material and methods

3.4.1 Study sites

The study was carried out in Saint-Pierre and Miquelon archipelago (SPM), a French archipelago in the Northwest Atlantic Ocean, which is surrounded by the Grand Banks, the Gulf of Saint-Lawrence, and the Scotian Shelf (Dubois, 2010; IEDOM, 2022, p.20, Figure 18). SPM lies at the convergence of the warm Gulf Strean and the cold Labrador Current creating a subarctic environment with a strong seasonal thermocline. These currents are generally weak during spring, but they intensify during fall and winter. SPM experiences large near-bottom diurnal temperature amplitude (at depths > 30m), with low and high stratification periods in early July and late August, respectively. Tides are mostly semi-diurnal of relatively low range (~1.3 m) (Lazure et al., 2018). The trophic environment is mostly oligotrophic, with spring and occasional microalgal blooms (April, September/October). Seston quality, assessed by fatty acid methods, is influenced by stratification conditions, which might potentially impact nutrient exchange between surface and sub-surface waters (Bridier et al., 2021), however, this thermal-trophic variability is lower in shallow waters (<20 m).

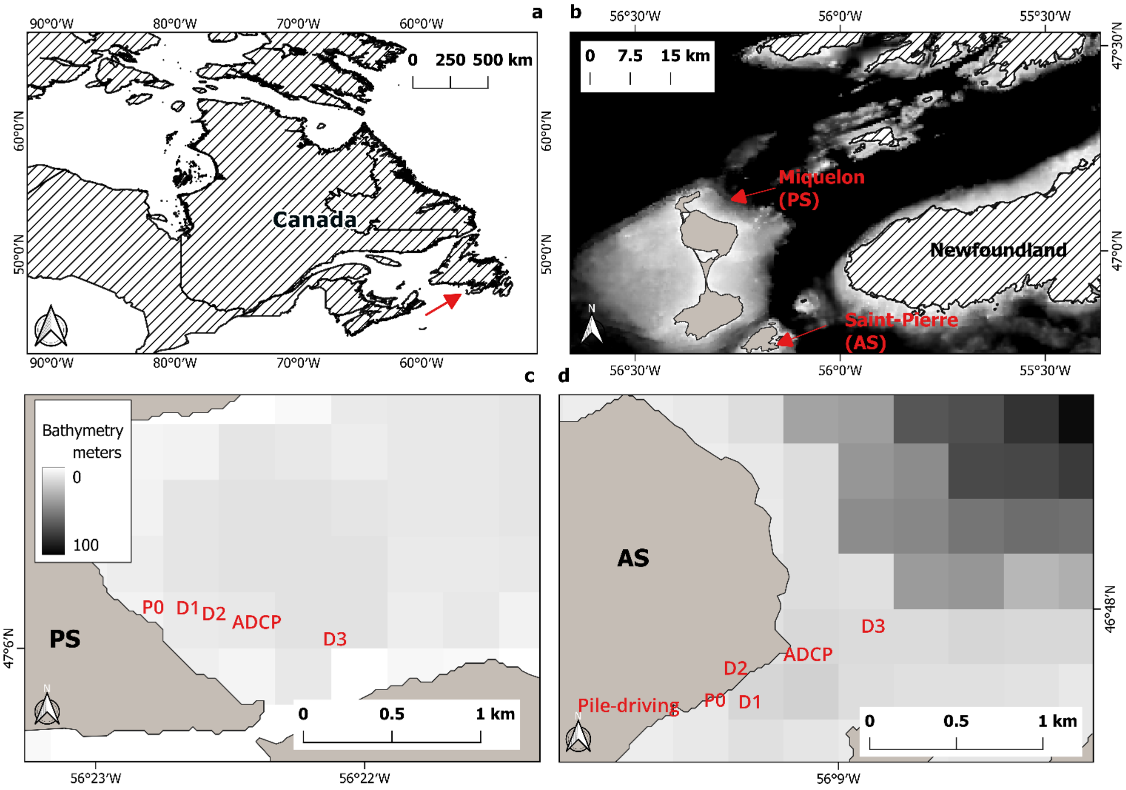


Figure 18: Set of maps of our study area : (a, b) Location of Sant-Pierre and Miquelon's archipelago, where each site is referred as Pristine (PS) or Anthropized (AS) due to the level of anthropogenic noise at the islands of Miquelon and Saint-Pierre, respectively. Bathymetric maps containing sites, and stations from the sound (D1, D2 and D3) on transects exposed to an anthropogenic noise source (P0) at pristine site (PS, **c**) and anthropized site (AS, **d**), which had pile driving operations occurring at the same time of sampling. Bathymetry data was retrieved from General Bathymetric Chart of the Oceans (GEBCO). Bathymetric maps are composed using grayscale where white represents 0-1 m, 2-30m light to dark gray, and values > 100m are black.

Additionally, the relatively flat shallow seafloor (Lazure et al. 2018) makes SPM ideal for *in situ* acoustic playback experiments (Bonnel et al. 2022), as sound propagation in shallow waters depends heavily on depth and physical properties of the seafloor (NRC, 2003). Together, these features make SPM a suitable site to conduct *in situ* experiments that assess the impact of noise on marine organisms. To minimize variability in the physical and trophic conditions - to avoid confounding effects from sound propagation, we selected two sites: a pristine site (Miquelon, Pristine, PS) with no industrial marine traffic, and an anthropized site (Saint-Pierre, Anthropized, AS) near an industrial harbor. For both sites, vessel activity was obtained using the Automatic Identification System (AIS) from MarineTraffic Professional Plus software (www.marinetraffic.com). At the PS site, only a small ferry and a few recreational boats were detected, whereas 103 vessel trajectories were recorded at the AS between May 12 to 29, 2021.

3.4.2 Vessel noise recordings and soundtrack compilation

Acoustic recordings were collected from the AS site (46°46'44.90" N, -56°10'38.28"W) from November 2020 to April 2021 using calibrated hydrophone moored close to the seabed at the Saint-Pierre harbour (Aural-M2, Multi-Électronique, Rimouski, Canada). Recordings made at the AS site contain noise from the '*Nolhan Ava*', a 120-m commercial ship that provides cargo services to SPM. The spectral composition and source sound level were also determined using the software MATLAB (2021a). From these recordings, a 1-hour and 20 minutes maritime traffic soundtrack was created, alternating between vessel noise (11 min, then 8.5 min) and silent segments (39 min, then 21.5 min), as in Veillard et al. (2025). This vessel noise soundtrack was played and looped during the experimental period from July to October 2021 at each site (PS and AS) using underwater speakers (Lubell Labs ®VC2C, Columbus, Ohio, USA), which emitted approximately a root mean square sound pressure level (SPL_{rms}) of 167 dB re 1 µPa of vessel noise at 0 m (Table 9).

3.4.3 Transmission loss calculations and acoustic features of pristine and anthropized sites

Transmission loss calculations using the formula TL = 20logR (where R is the range in meters) were made to estimate sound intensities received at each distance on each transect (Table 9). Based on the transmission loss calculation, these distances received different levels of SPL_{rms} ranging from 106 to 137dB re 1 µPa in both sites (Table 9). The characterization of ambient noise was conducted for the two sites (Figure 19). Due to the low levels of anthropogenic activity in the PS site, underwater acoustic recorders (RTSYS-RESEA 320, Caudan, France; Hydrophone Colmar GP1516M, Sensitivity -172 dB re 1V/ µPa @ 5kHz) were deployed two days in August, two days in September and one day in October. An AURAL hydrophone was deployed continuously a month before starting the trial (June) and during the entire experimental period (July-October 2021) in the AS site. The sound exposure level per minute (SEL_{1min}, dB re 1 $\mu Pa^2 s$) was also calculated and acoustic metrics were analyzed according to Bonnel et al. (2022). Therefore, we characterized sound levels at each site using SPL_{rms} and SEL_{1min}.

Table 9: Location and sampling points, distances from the speaker (m), point coordinates (º,",'), depth (m), and levels of sound received (dB re 1 µPa) at each distance sampled in Pristine (PS, Miquelon) and Anthropized (AS, Saint-Pierre).

Sites and sampling distances	Distance from speaker (m)	Received level of sound (dB)	Depth (m)	Coordinates	
PS				Latitude	Longitude
P0	0	167		47° 06' 08.39" N	56° 22' 28.62" W
D1	25	137	8	47° 06' 08.22" N	56° 22' 27.59" W
D2	175	120	8	47° 06' 06.66" N	56° 22' 20.70" W
D3	890	106	8	47° 05' 59.88" N	56° 21' 48.53" W
ADCP				47° 06' 04.38" N	56° 22' 12.54" W
AS					
P0	0	154		46° 47' 39.00" N	56° 09' 29.58" W
D1	30	153	15	46° 47' 38.46" N	56° 09' 28.44" W
D2	144	150	20	46° 47' 41.28" N	56° 09' 23.64" W
D3	848	143	20	46° 47' 52.73" N	56° 08' 54.96" W
ADCP				46° 47' 45.06" N	56° 09' 16.02" W

3.4.4 In situ **experimental design**

This study was carried out from the end of June to mid-October 2021 in SPM. Underwater speakers protected by a metal frame were suspended to a depth of 8m at both sites oriented offshore. Both transects were exposed to a replayed soundtrack of vessel sound.

A set of collectors made of 2-mm mesh bags, each filled with four inverted Netron sections (40 x 80 cm with a mesh size of 5 mm, area of 0.320 m^2), were moored at three stations from the sound emission: D1 (close, 137dB re 1 µPa at 25-30m), D2 (intermediate, 120 dB re 1 µPa at 144-175m), and D3 (far, 106 dB re 1 µPa at 848-890m) (Figure 19a-b).

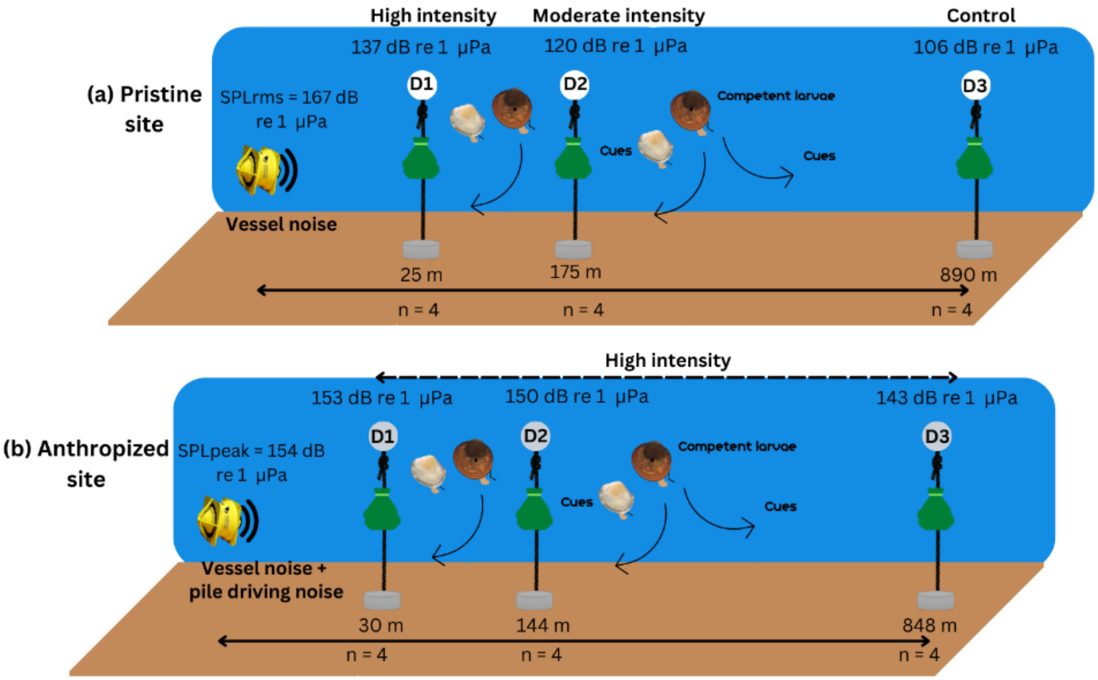


Figure 19: Graphical representation of the experimental design carried out at the pristine (**a**) and anthropized sites (**b**). Recruits (pediveligers, post-larvae and juveniles) of benthic invertebrates were exposed to a gradient of vessel noise (D1 = 137 dB at 25m, D2 = 120 dB at 175m and D3= 106 dB re 1 µPa at 890m) or a mix of vessel noise and pile driving noises (D1 = 153 dB, D2 = 150 dB and D3 = 143 dB re 1 µPa) along transects, where artificial collectors were placed at each station (n = 4).

On each mooring, four artificial collectors were installed close to the bottom and were kept in place by subsurface buoys, as detailed in Cyr et al. (2007). A total of 96 collectors were assessed during the experimental period (4 replicates x 3 distances along the transect x 4 months - July, August, September, October x 2 sites – PS and AS). The sanitary restrictions related the COVID-19 downscaled our original design since it was unfeasible to have control transects at each site without having enough personnel to carry out the manipulation. For these reasons, the collectors at station D3 (far distance) in the PS site were considered as control since the sound reaching these collectors had similar levels of ambient sound (SPL_{rms} = 106 dB re 1µPa) than levels documented in literature (Halliday et al., 2021; Mathias et al., 2016).

3.4.5 Monitoring environmental conditions of an *in-situ* recruitment

Temperature and currents were monitored throughout the entire experimental period at each site. Temperature was measured by probes (HOBO Pendant® Temperature/Light 64 K, contained within waterproof casings), while current velocity was determined using two acoustic doppler current profilers (ADCP Teledyne RD Instruments 600 and 1200 kHz models, refer to the Table 9 for position on the transect at each site). To monitor the distribution pattern of total particulate matter (TPM, hereafter referred to as seston), seawater samples (n=2, 5 L each) were collected monthly at each distance (D1-D3) of both transects at each site at the mooring depths using Niskin bottles and stored in opaque vials. Two bottles per sampling were used as replicates for determining seston quantity (TPM $mg.L^{-1}$ dry weight) and quality as mass of total fatty acids (MTFA, fatty acids composition). After being collected, samples were filtered on pre-weighed and pre-combusted 47mm GF/F filters and stored at -40ºC for a maximum of 4 months, then transferred to -80ºC until further analysis as described in Toupoint et al. (2012a). Additionally, at each sampling event, another 3 x 4.5 ml of pre-filtered seawater (over a 40µm - mesh) were fixed with 20µl glutaraldehyde (0.1 % final v/v) and kept at -40°C for determination of bacteria, pico- and nanoplankton using flow cytometry. Samples were stored at -40ºC up to 4 months then transferred to -80ºC until analyses.

3.4.6 Response to anthropogenic noise: community dynamics and early recruitment

During this experiment, the first collectors were moored at the end of June and retrieved by divers at the end of July 2021 and transported to the shore in individual bags to avoid spat losses. To retrieve all organisms inside, each collector (replicate) was placed in a 100µm plankton net and cleaned using a low-pressure seawater jet. The material accumulated in the net cup was filtered on a 100µm mesh and transferred to labeled Ziplock bags and stored at -40ºC for further analysis. In the laboratory, all species were sorted, counted, and identified to family, genus, or species level, when possible, under a stereomicroscope. The identification of species and families were made using the following taxonomic keys: Aucoin et al. (2004), Hayward and Ryland (2017), and Lutz et al. (2018).

3.4.7 Laboratory procedures

a) *CHARACTERIZATION OF TROPHIC ENVIRONMENT*

Fatty acid extraction and trophic markers

Several sources of organic matter contribute to feeding benthic species (diatoms, dinoflagellates, bacteria, macroalgae, etc.). Fatty acids (FA) are useful trophic markers to monitor the seston quality being delivered to recruits in the benthic realm (Bridier et al., 2021; Kelly and Scheibling, 2012; Meziane et al., 2007). Given the role of seston, particularly its quality of polyunsaturated fatty acids (PUFA) and essential fatty acids (EFA), in mussel settlement (Toupoint et al., 2012a; Martel et al., 2014), we analyzed the FA profile of seston samples collected at the two study sites. To process seston filters collected over the sampling period, we adopted biochemical techniques such as fatty acid extraction and quantification. Detailed information on the methodology for extracting fatty acids, FA composition and trophic markers is available in the Supplementary materials (Supplementary materials S1: Material and Methods).

Flow cytometry analyses to determine food sources

Various food sources (e.g., picoplankton, nanoplankton, bacterial concentration) have been identified as mediators of bivalve settlement and early recruitment (Androuin et al., 2022; Lagarde et al., 2018; Toupoint et al., 2012b; Veillard et al., 2023). In conditions where planktonic sources are limited, biofilm cues (its composition) may play an important role triggering settlement (Toupoint et al., 2012a). To characterize concentration of food sources available our study sites, seston samples were analyzed using an Epics Altra flow cytometer (Beckman Coulter Inc., Fullerton, CA, USA). Fluorescently labeled cells were identified and quantified into different categories, including pico (0.2–2µm) and nano (2–20µm) eukaryotes, cyanobacteria, as well as heterotrophic bacteria, following the methods outlined by Belzile et al. (2008), and Tremblay et al. (2009), as detailed in Toupoint et al. (2012a).

b) *IDENTIFICATION AND ABUNDANCE OF BENTHIC INVERTEBRATES*

Samples were sieved over decreasing mesh sizes (1.7mm, 500 and 150 µm) using seawater to distinguish primary settlers (>150 µm), from secondary settlers (>500 µm) and from larger juveniles (>1.7 mm). Fractions were sorted in a basin (>1.7 mm), and in a Dollfus counting chamber (>500 and >150 µm) under a Leica microscope (M125, Germany). Due to the high abundance of individuals, only a quarter of the samples from September and October were analyzed, and splits were prepared by using a Folsom splitter. Sub-sampling adjustments were made for high abundance species such as *Hiatella arctica* and *Mytilidae* (25 squares spread out in eight square intervals). For low abundant species, individuals were counted in all 200 squares in the chamber. Even though individuals from *Mytilus* spp. and *Modiolus* spp. were identified to species level in larger fractions, the smallest fraction (>150 µm) was considered as Mytilidae. Since only a few taxa could not be identified to the species or family level, they were named after the group followed by a species number (i.e., Bivalve sp.1, Gastropod sp.1 etc.).

c) *COMMUNITY AND SPECIES SELECTION*

The community composition was described using percentages of abundance. The community diversity was evaluated using different indices such as species number (Richness, S), the diversity (Shannon-Wiener Index, H'), and equitability (Pielou's evenness index, J') of assemblages retrieved at different distances at the PS and AS sites. These indices were estimated without *H. arctica* because this species was the overwhelmingly dominant in our collectors at both sites. To compare the effect of sound level exposure on species recruits, we chose five taxa based on the following conditions: (1) species or family that have been used as suitable environmental indicators for decades such as *H. arctica*, Mytilidae species, and *Placopecten magellanicus* (Cyr et al., 2007; Garcia et al., 2003; Foret et al., 2018; ; Veillard et al., 2023); (2) foundation species such as *Modiolus* sp. and *Mytilus* spp. (= Mytilidae) (Baden et al., 2021; Seed et al., 2000) ; (3) important commercial and ecological bivalve and gastropod species such as *P. magellanicus* (Aucoin et al., 2004; Cyr et al., 2007; Tremblay et al., 2020) and *Lacuna* spp. (Martel and Chia 1991; Martel and Diefenbach, 1993); and (4) taxa such as *Skenea* sp. that were present (>40 individuals/month) at both sites.

3.4.8 **Data analysis**

At the PS site, due to data loss, temperature differences were only assessed between D1 and D2 using the non-parametric Mann-Whitney test. At the AS site, variations in temperature were assessed between stations (D1, D2, D3). Data was transformed using the square root function, and residuals were tested for normality and homogeneity with the Shapiro-Wilk and Levene tests before conducting one-way analysis of variance (ANOVA).

Achieving a normal distribution of biological and trophic data is challenging when there is a wide variation in replicates and missing data at some sampling points (Anderson, 2001). Because of this, permutational multivariate analysis of variance (PERMANOVA) was used with PRIMER-E 7.0 (9,999 permutations) to detect differences in trophic and biological data among distances at each site. Seston quantity (TPM) and quality (MTFA, fatty acid composition, and trophic markers, n = 6 or 8 depending on site) as well as food sources (heterotrophic bacteria, pico- and nanocyanobacteria and pico- and nanoeukaryotes, n = 3 or 4 depending on site) were compared between stations at each site (3 levels – D1, D2 and D3) using one-way PERMANOVA. TPM and MTFA matrices were individually constructed using the Euclidean distance while food sources data was ranked, due to different concentration levels, and then converted together into Euclidean distance matrix. A Bray Curtis dissimilarity matrix was calculated based on trophic marker data comprising bacteria (∑ai15:0, iso15:0, 18:1ω7), degraded organic matter (∑ 14:0, 16:0, 18:0), diatoms (∑16:1ω7, 20:5ω3), dinoflagellates (∑ 22:6ω3), green (∑18:2ω6, 18:3ω6) and brown macroalgae (∑ 18:1ω9). Significant PERMANOVA results ($p<0.05$) were followed by pair-wises tests, and similarity percentage analyses (SIMPER) were conducted on untransformed data to identify dissimilarities in all metrics within each distance from the underwater speaker (D1, D2 and D3). We estimated species abundances (ind. collector^{-1}) from our biological data and then expressed each species/taxa in a Bray-Curtis similarity matrix. Diversity indices were calculated from this biological dataset using the function DIVERSE on PRIMER 7.0 and each calculated index was converted into an Euclidean distance matrix. These distance matrices were analyzed each using a two-factor PERMANOVA, to examine the effect of distance from the noise (Di, 3 levels – D1, D2 and D3), month (Mo, 4 levels – July, August, September and October), and their interaction (Di x Mo) on the early recruitment, richness, diversity, and evenness at each site. If results were significant ($p<0.05$), pairwise comparisons were performed coupled to a Monte Carlo simulation test to validate the probability of our results when a limited number of permutations were executed. We also conducted SIMPER analyses to identify the species that most contributed (%) to dissimilarities between collector assemblages at each distance and month. All statistical tests used a 0.05 significance level, performed with PRIMER 7.0 and GraphPad Prism 10.5. Plots were generated using GraphPad Prism 10.5 and MATLAB2021a.

3.5 Results

3.5.1 Physical environment

Temperatures (mean ± SD) in PS were uniform across distances (13.1 ± 0.5°C, U = 6934, p = 0.93), with seasonal fluctuations ranging from 8.5 to 17.0ºC (Fig. 20a). A 5°C drop and a 3ºC rise in mid- and late September (Fig. 20a,b, Brown, 2021), likely due to Hurricane Larry, resulted from a vertical mixing of the water column and heat loss from strong winds. In October, temperatures dropped from 15 to 11.5ºC. At the AS site, temperatures were comparable along the transect (12.1 ± 1.5°C, ANOVA, df = 3, F = 0.41, p = 0.74), fluctuating seasonally fluctuations between 5.5ºC (early July) and 16-17ºC (mid-August). Greater semi-diurnal and diurnal oscillations (7 to 10ºC) from mid-August to mid-September (Fig. 20c) were driven by internal waves caused by barotropic tides, facilitated by stronger stratification at AS. The barotropic tide generates internal waves that cause the cold-water masses on the bottom to oscillate in the cross-shore direction at the tidal frequency (Lazure et al., 2018). These oscillations weakened after September 11 storm due to increased vertical mixing. The seasonal temperature gradient in the PS site (2 - 4°C) was over two times lower than in the AS site (7-10°C), and possibly due to an intense effect of internal waves in the AS site (Lazure et al., 2018). Currents at PS ranged from 0 and 0.4 $m.s^{-1}$, with greater variability at the beginning of October (Fig. 20b). Bottom and surface currents were weak and predominantly north-south and north-west, respectively. Residual currents followed the bottom current pattern and moved towards north. Tides were semi-diurnal to mixed semi-diurnal ranging from 1.3 to 2.0 m (Appendix I: Fig. S5a-b). Bottom pressure sensors recorded a tidal cycle on September 11, whose range rose from 1.7 m for the preceding and following tides to 2.5 m, likely caused by the passage of a storm-triggered continental shelf wave over Newfoundland, as described by Brown (2021). At the AS site, current speed ranged from 0 to 0.3 $m.s^{-1}$ from July to early September (Fig. 20c), rising to 0.5-0.7 $m.s^{-1}$, mixing the water column and shifting the prior temperature amplitude. Bottom and surface currents were predominantly east-northeast, with residual currents strengthening slightly in autumn and moving northward. Tidal patterns were similar to those at PS, varying from 1.3 to 2.0m (Fig. S5c-d).

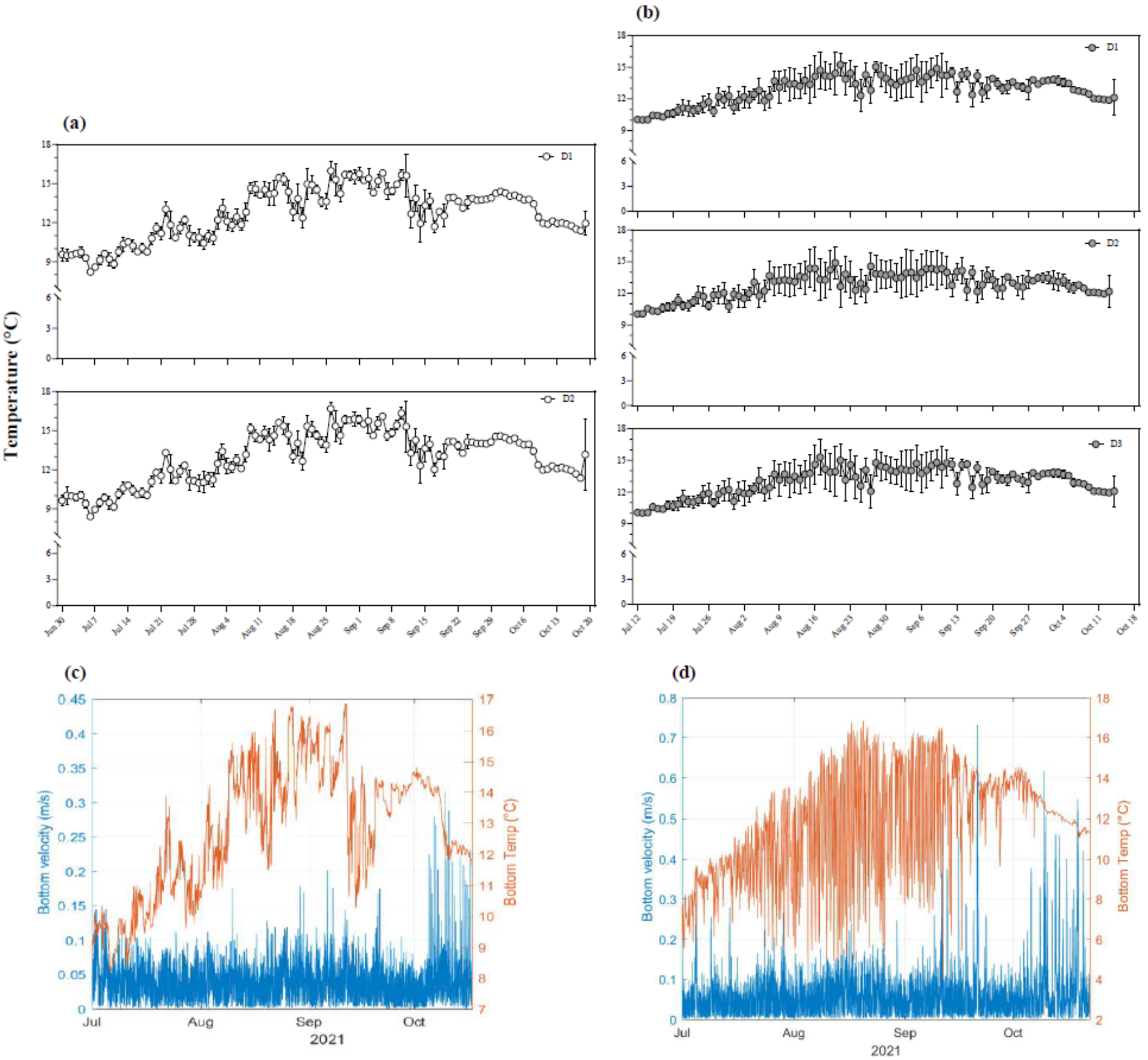


Figure 20: Temperature (ºC) and current profiles (velocity m.s^{-1}) on each transect in Pristine (PS, **a**, **b**) and Anthropized (AS, **c**, **d**) sites during the sampling period from July to October 2021.

3.5.2 Trophic environment

Seston quantity (TPM) and quality (MTFA, fatty acid composition, food sources, trophic markers) (mean ± SE) available for recruits were homogeneous along both transects, as shown in, as shown in Table 10 and Table S13 (Supplementary materials: Table S13). Seston concentration (mg.L^{-}1) and the mass of total fatty acids (µg.mg -1) had mean values (± SE) of 4.1 ± 0.4 and 5.7 ± 0.2 at PS, and 4.9 ± 0.5 and 4.8 ± 0.1 at AS. Total bacteria consisted of high nucleic acid bacteria (HNA, 73 and 56%) and low nucleic acid bacteria (LNA, 27 and 44%) at PS-AS, respectively. Picocyanobacteria (52 ± 0.3 and 34 ± 0.5 x103 cell.ml-1) and picoeukaryotes (19 ± 2.5 and 17 ± 4.4 x103 cell.ml-1) were the first and second predominant food sources in seston at both sites; however, concentrations of other food sources differed between them. Fatty acid composition (FA %) was dominated by saturated fatty acids (SFA, 38-56%), monosaturated (MUFA, 18-31%) and polyunsaturated fatty acids (PUFA, 18-30%) (detailed information on FA% of seston over the months in the supporting information (Supplementary materials: Table S13).

Trophic markers such as bacteria and degraded organic matter comprised more than 40% of seston available at PS and AS sites across stations (Table 10) and throughout the months (Supplementary materials: Table S14). Diatoms and dinoflagellates represented nearly 18-26% in the PS, and 15-18% in the AS, suggesting that microalgae rich in eicosapentaenoic acid (EPA, 20:5ω3), and docosahexaenoic acid (DHA, 22:6ω3) were available for recruits at both sites. Green and brown macroalgae together accounted for 15-19% in the PS and 17-19% in the AS, indicating an important contribution to the organic matter source at both sites.

Table 10: Mean (±SEM) of food quantity (TPM, n = 8) and quality (MTFA – n = 6 or 8, food sources – n = 3 or 4, trophic markers) at stations D1, D2 and D3 in the Pristine (PS) and Anthropized (AS) sites during our sampling period from July to October 2021.

	PS	**AS**
TPM (mg.L^{-1})	4.1 ± 0.4	4.9 ± 0.5
MTFA (µg.mg $^{-1}$)	5.7 ± 0.2	4.8 ± 0.1
Food sources		
Total bacteria (x10^{6} cell.ml^{-1})	2.5 ± 0.2	1.0 ± 0.1
Pico cyanobacteria (x10^{3} cell.ml^{-1})	5.2 ± 0.3	3.4 ± 0.5
Nano cyanobacteria (x10^{3} cell.ml^{-1})	0.1 ± 0.0	0.04 ± 0.0
Pico eukaryotes (x10^{3} cell.ml^{-1})	19.4 ± 2.5	17.1 ± 4.4
Nano eukaryotes (x10^{3} cell.ml^{-1})	3.5 ± 0.2	3.7 ± 0.3
Trophic markers (%)		
Bacteria	9.9 ± 0.1	9.8 ± 0.1
Degraded organic matter	37.2 ± 1.2	46.1 ± 0.9
Diatoms	16.5 ± 0.4	10.4 ± 0.4
Dinoflagellates	5.4 ± 0.3	6.4 ± 0.5
Green macroalgae	3.3 ± 0.1	4.4 ± 0.2
Brown macroalgae	10.2 ± 0.4	9.1 ± 0.6

3.5.3 Acoustic characterization of pristine and anthropized sites

Overall, theoretical calculations (SPL_{rms}, 106-137dB dB re 1 µPa) and mean SEL_{1min} levels (±SE, 132 ± 0.2 to 138 ± 0.3 dB re 1 µPa^{2}s) at the PS site were similar throughout the months (Table 9, Figure 21). In contrast, the acoustic scenario at the AS site changed completely due to pile driving operations during the same period, making it impossible to distinguish the vessel noise being emitted, resulting in a mixture of both. Noise levels at the AS site ranged from 143 to 154 dB re 1µPa (SPL_{rms}, Table 9), with monthly SEL_{1min} levels (mean ± SE) received by the hydrophone superior to 144 ± 0.3 dB re 1 µPa^{2}s, and maximum levels reaching 165 dB µPa^{2}s (Figure 21). SEL differences between the PS and AS sites were of a minimum of 9 dB re 1 µPa^{2}s in August, September and October (Figure 21).

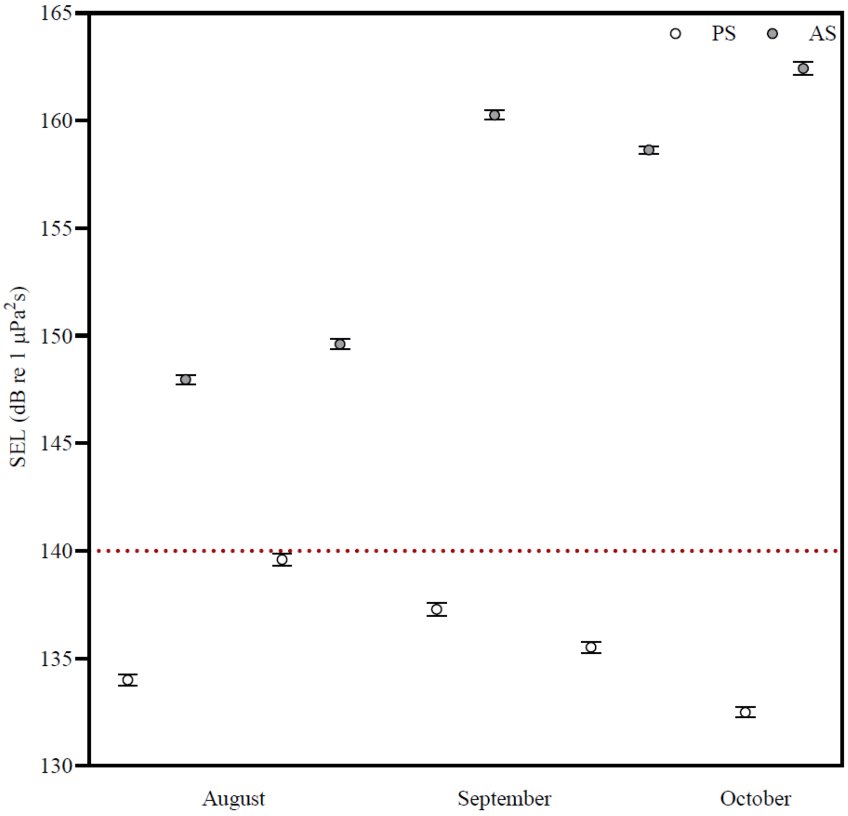


Figure 21: Acoustic characterization at Pristine (PS) and Anthropized (AS) sites with daily mean (±SE) of sound exposure level (SEL_{1min}, dB re 1 µPa^2s), and comparison between pristine and anthropized sites during August, September and October.

3.5.4 Community diversity and structure in response to anthropogenic noise

We identified a total of 373,099 and 486,134 individuals over a 4-months monitoring period in both sites. Thirty-two taxa were identified across all combined stations (D1 to D3) from the noise source in both sites, with bivalves and gastropods comprising the majority of the catch (Figure 22a-b).

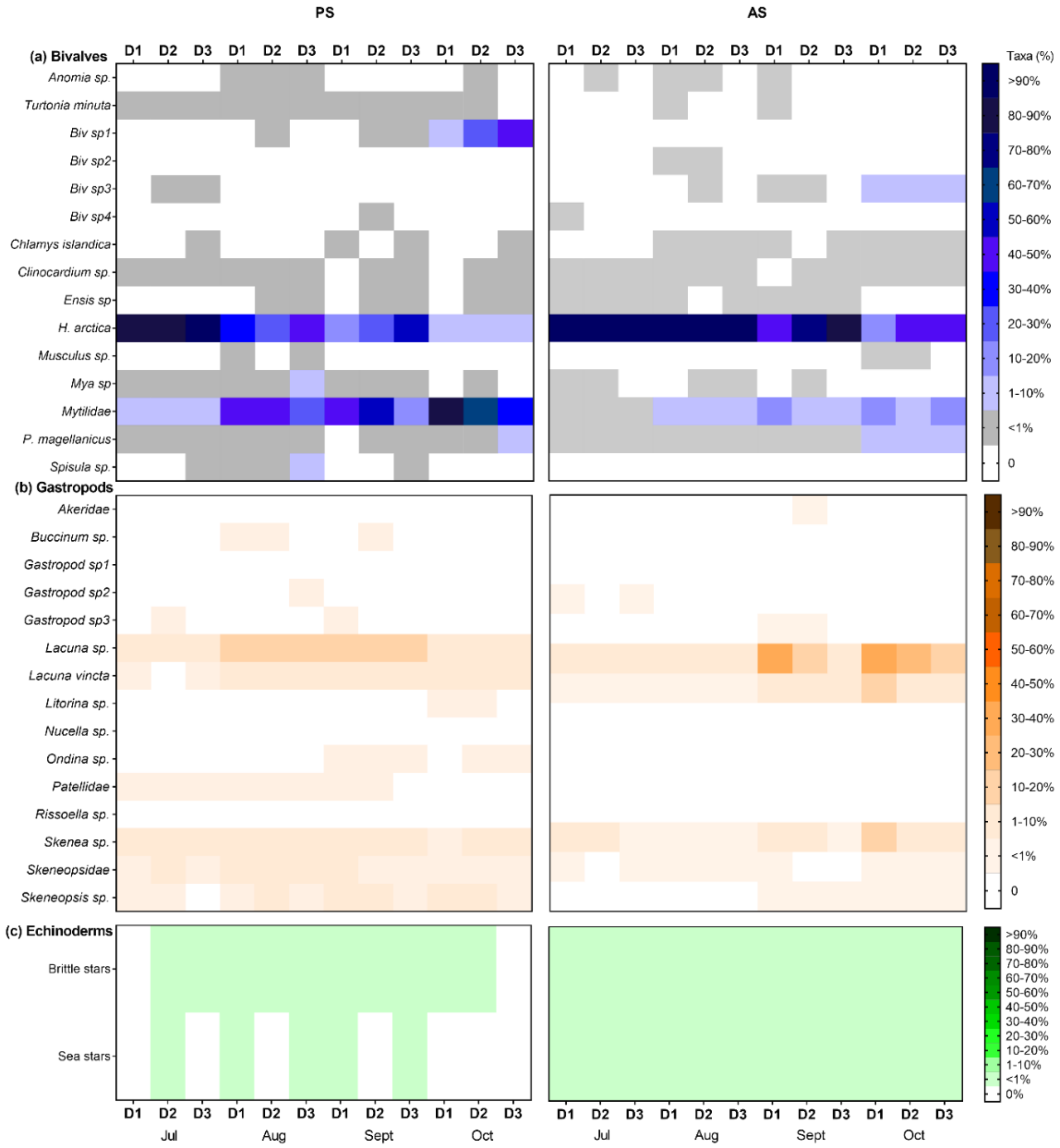


Figure 22: Heatmap of bivalves (blue gradient, **a**), gastropods (orange-brown gradient, **b**), and echinoderms (green gradient, **c**) taxa found in artificial collectors at D1 (25-30m), D2 (144-175m), and D3 (848-890m) distances from anthropogenic sounds in both experimental sites Pristine (PS) and Anthropized (AS) from July to October 2021.

Diversity indices (S, H' and J') displayed distinct patterns at each site (Table 11). In the PS site, richness significantly decreased over time without no distance or interaction effects (Table 11, Figure 23a, c). Fewer taxa were recorded in September compared to July

($t = 3.28$, $p=0.004$, perms = 6641), and August ($t=2.60$, $p=0.02$, perms=9755). Diversity and evenness both increased with distance from the source but declined over time, with no significant interaction of factors (Table 11, Figure 23c, e). The lowest values for both diversity and evenness were observed at the highest noise level (137 dB re 1 μPa at 25m, H'=0.95, J=0.39) compared to moderate and control levels (120 vs 106 dB re 1 μPa, H'=1.18, J'= 0.47, H'=1.28, J'=0.54). The highest level of taxa diversity was found in July (H'= 1.42), while evenness peaked in July and September (J'= 0.55 and 0.50).

At the AS site, richness slightly varied only by distance from the noise source, with lowest levels at highest intensity noise (D1, 153 dB re 1 μPa at 30m) compared to other high intensities (D2, 150 dB re 1 μPa at 144m; D3, 143 dB re 1 μPa at 848m; S = 12 and 11, Figure 23b, Table 12). Diversity and evenness showed a significant interaction between distance and month, with the lowest values at D3 in July and August ($H' \leq 1.28$; J'= 0.44-0.54). In September, both metrics declined across all distances ($H' < 1.24$; $J' < 0.48$), followed by a stabilization in evenness across distances (J'= 0.70), and slightly increase in diversity across intensities (Figure 23d-f).

The community composition varied in interaction with distance and month in both PS (df=6, pseudo-$F_{DixMo} = 5.82$, $p<0.001$, perms = 9910) and AS sites (df = 6, pseudo-$F_{DixMo} = 16.70$, $p<0.001$, perms = 9928). In the PS, community composition at high-intensity noise (D1) differed from moderate-low intensities (D2-D3), especially between D1 and D3 (SIMPER, up to 62% dissimilarity) in almost all periods. At AS, community also varied near high intensity pile driving (D1) from other higher intensities (D2-D3) (Supplementary materials: Table S16), with also a pronounced distance effect between D1 and D3 and dissimilarity (SIMPER, up to 74%). SIMPER analysis showed that these differences were driven by *H. arctica* and/or Mytilidae, which were dominant taxa across months in both sites and contributed to 60-80% to dissimilarities. Assemblages varied significantly across months at all distances in the PS and AS, though some similar compositions occurred in the AS, especially at D1 between July-August and D2-D3 between August-September. (Supplementary materials: Table S16).

Table 11: Results of two-way permutational multivariate analyses (PERMANOVA) testing the effect of station distances (Di, 3 levels), month (Mo, 4 levels) and their interaction (Di × Mo) on species richness (S), Shannon-Weiner diversity (H') and Pielou's evenness (J') on the assemblages of bivalves, gastropods and echinoderms retrieved from collectors moored at different distances on transects at Pristine site (PS) and at Anthropized site (AS).

Species richness (S)

	Pristine site (PS)				*Anthropized site (AS)*			
	df	Pseudo-F	p (MC)	Perm	df	Pseudo-F	p (MC)	Perm
Di	2	1.08	0.35	9952	2	7.50	**0.002**	9963
Mo	3	4.19	**0.01**	9953	3	1.68	0.19	9935
Di x Mo	6	0.87	0.53	9944	6	0.38	0.97	9941

Shannon-Wiener diversity (H')

	Pristine site (PS)				*Anthropized site (AS)*			
	df	Pseudo-F	p (MC)	Perm	df	Pseudo-F	p (MC)	Perm
Di	2	16.01	**0.0002**	9961	2	25.56	**0.0001**	9965
Mo	3	19.19	**0.0001**	9961	3	55.63	**0.0001**	9954
Di x Mo	6	2.08	0.08	9955	6	6.13	**0.0008**	9957

Pielou's evenness (J')

	Pristine site (PS)				*Anthropized site (AS)*			
	df	Pseudo-F	p (MC)	Perm	df	Pseudo-F	p (MC)	Perm
Di	2	21.80	**0.0001**	9956	2	22.16	0.0001	9953
Mo	3	21.29	**0.0001**	9947	3	57.10	0.0001	9963
Di x Mo	6	2.27	0.06	9936	6	4.37	0.0013	9942

Notes: Significant values ($p<0.05$) are indicated in bold. Abbreviations: Permutational multivariate analyses (PERMANOVA), Distance (Di), Month (Mo), Species richness (S), Shannon-Weiner diversity (H'), Pielou's evenness (J'), Pristine (PS) and Anthropized (AS).

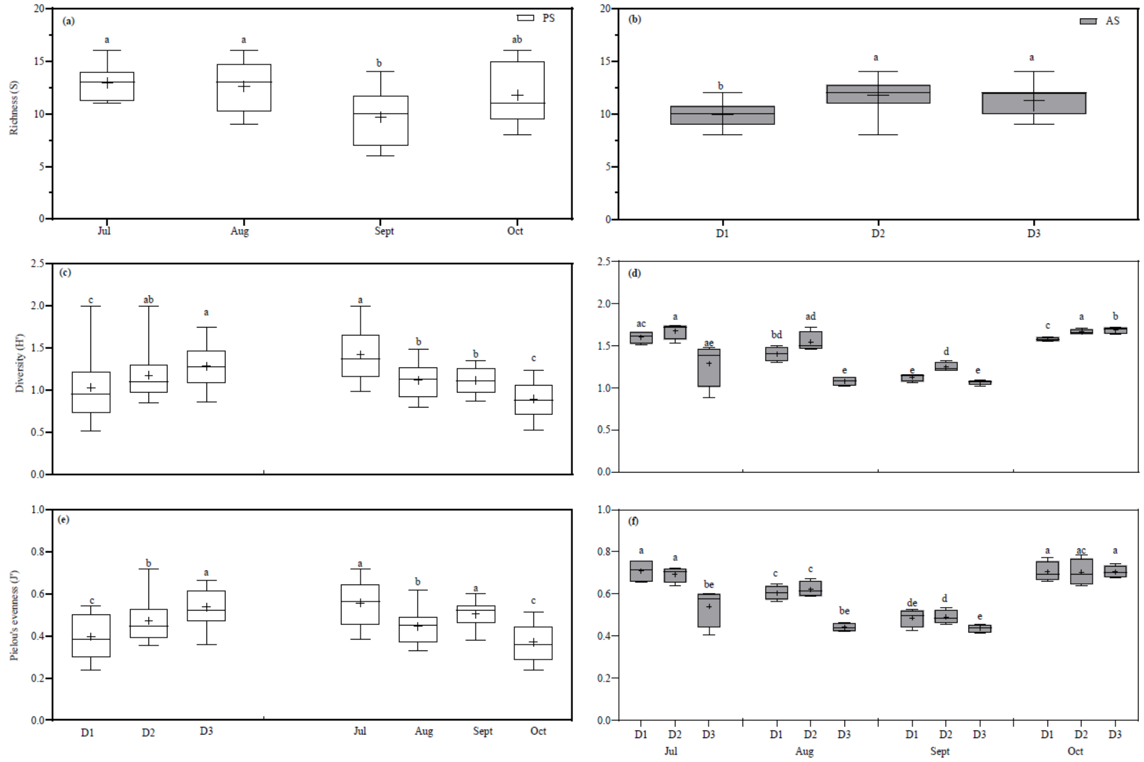


Figure 23: Box plot of Species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') of assemblages obtained from collectors placed at different stations : D1 (25-30m), D2 (144-175m), and D3 (848-890m) near anthropogenic noise sources in the Pristine (PS,8a, 8c, 8e) or Anthropic (AS, 8b,8d,8f) sites across 4-months – July, August, September and October 2021.Boxes represent 25th and 75th quartiles. Whiskers show minimum and maximum values. Solid line is median, symbol plus "+" is the mean. Dissimilar letters indicate significant difference in post hoc analysis.

3.5.5 Species response to noise in both sites

3.5.5.1 *Hiatella arctica*

In the PS site, *H. arctica* abundance varied significantly, displaying a notable interaction between distance from noise source and month (PERMANOVA, df = 6, pseudo-$F_{Di \times Mo}$= 2.90, p = 0.004, Figure 24a). temporal trend: recruitment peaked in July, reaching up to

19,260 ± 1,748 individuals per collector in D1 (SPL_{rms}, 137 dB re 1 µPa, Figure 24a). In subsequent months, abundances dropped sharply (<2,000 $ind.collector^{-1}$) and showed no significant variation across distances (Supplementary materials: Table S17).

In the AS site, both distance from the noise and month interactively inhibited *H. arctica* recruitment ($pseudo\text{-}F_{Di \times Mo}=21.68$, $p<0.001$, Figure 24b). Abundances (Supplementary materials: Table S4) increased with distance from the noise, and they were 2 to 12 times higher in D3 (SPL_{pk}, 143 dB re 1 µPa, 1,370 – 31,899 ind.) compared to D1 across all months (153 dB re 1 µPa, 165 – 7,347 ind.; Figure 24b). As in the PS site, recruitment peaked in July for all distances from the source, followed by a sharp reduction from August to October (Figure 24b).

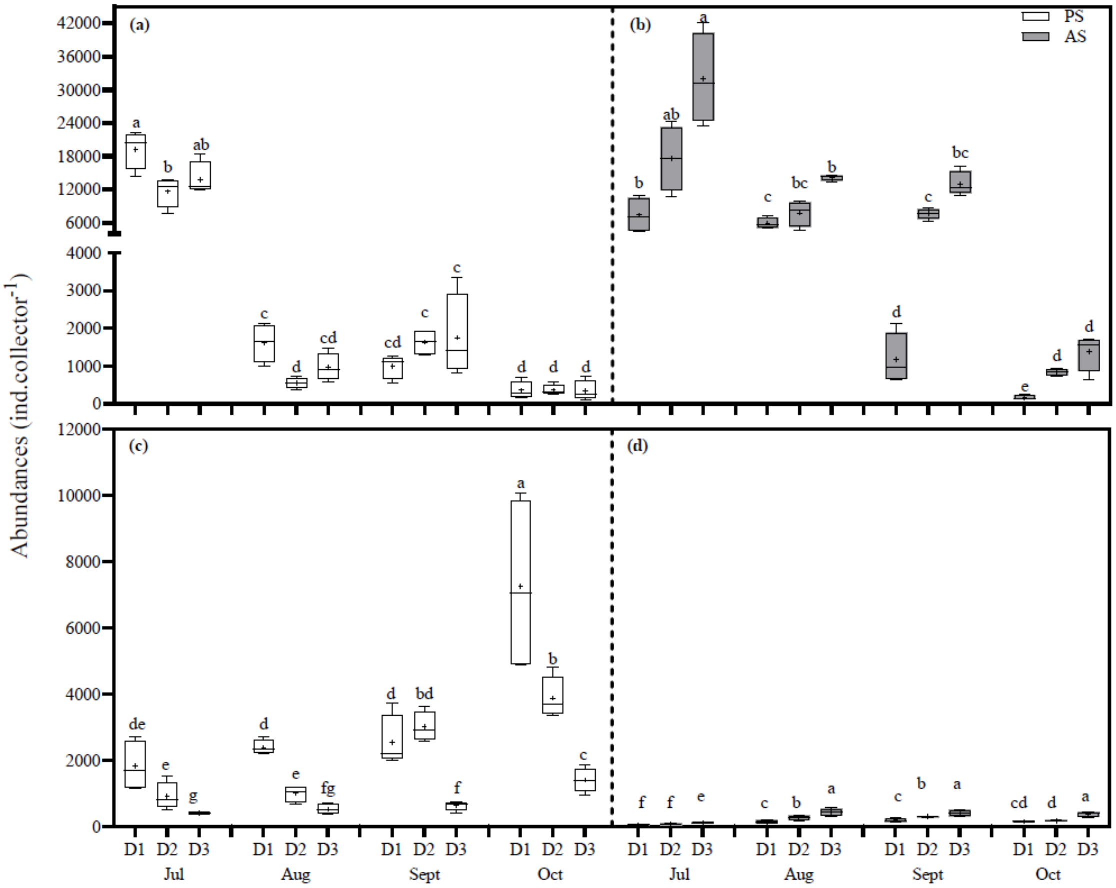


Figure 24: Box plots of abundances of the two most dominant bivalves *Hiatella arctica* (a, b) and Mytilidae (c, d) at different distances (D1, 25-30m; D2, 144-175m; and D3, 848-890m) from anthropogenic sounds during our experimental period from July to October in the Pristine (PS, **a, c**) and in Anthropized sites (AS, **b,d**). Boxes represent 25th and 75th quartiles. Whiskers show minimum and maximums values Solid line is median, symbol plus "+" is mean. Dissimilar letters indicate significant difference in post hoc analysis.

3.5.5.2 Mytilidae

In contrast to *H. arctica*, patterns of early recruitment were much clearer according to distance but also opposite between sites. In both sites, the abundance of recruits of Mytilidae was influenced by the distance from source and month (PS, PERMANOVA, df = 6, pseudo-$F_{Di \times Mo}$ = 9.76, p<0.001, and AS, df = 6, pseudo-$F_{Di \times Mo}$ = 7.17, p<0.001). In the PS, recruits were notably less abundant in the collectors moored at D3 (SPL_{rms}, 106 dB re 1 μPa, 398 - 1,396 individuals, Figure 24c) in comparison to D1 and D2 (137 *vs* 120 dB re 1 μPa, 1,814 – 7,253 ind. vs 913 – 3,873 ind., please refer to Supplementary materials: Table S17). The most pronounced decrease occurred between D1 and D3 in October, coinciding with the peak abundance of Mytilidae (7,253 vs 1,396, Figure 24c). Throughout the early recruitment season, Mytilidae abundances gradually increased overtime so that they were 4.5 to 5.0-fold higher (> 400%) at D1 when compared to D3 (Figure 24c). Over the monitoring period, recruit abundances showed a 4-5-fold increase among intensities in the AS site (SPL_{pk}, 153 dB re 1 μPa, 46 – 186 ind.; 150 dB re 1 μPa: 61 – 288 ind.; 143 dB re 1 μPa: 112 – 433 ind.), suggesting a clear avoidance to noisy conditions. In general, abundances were much lower in July (46 – 186 ind., Figure 24d, Supplementary materials: Table S17) than the other months.

3.5.5.3 *Placopecten magellanicus*

P. magellanicus recruits were only collected in October in both sites, and their abundance were similar between distance in the PS (SPL_{rms} 106-137 dB, 23 to 43 ind., pseudo-F_{Di} = 2.79, p=0.11, perms=2214, Figure 25a) whereas they increased with distance (pseudo-F_{Di} = 13.72, p=0.001, perms=4756) from D1 to D3 in the AS site (SPL_{pk} from153 reducing to 143 dB; 32, 48, 77 ind., t_{D1-D3} = 5.14, p = 0.001; t_{D2-D3} = 2.391, p = 0.048; Figure 25b).

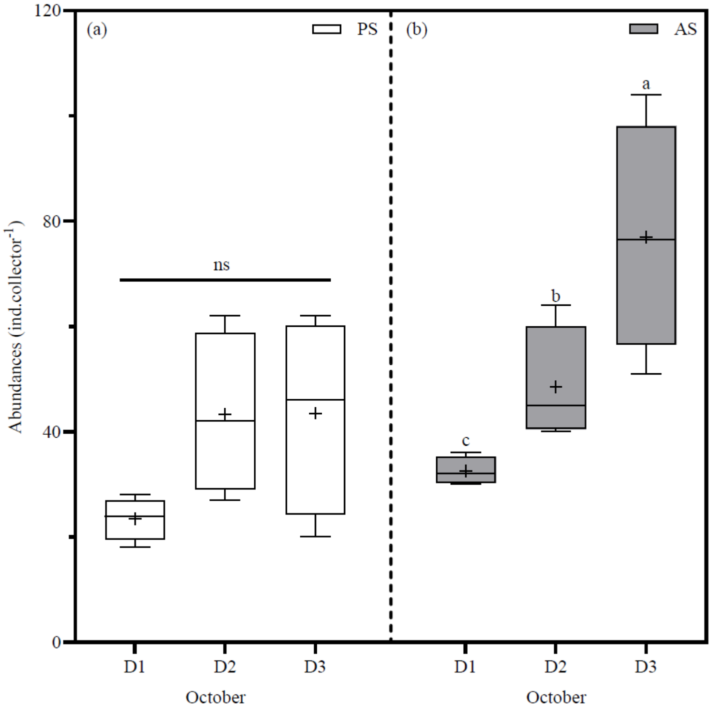


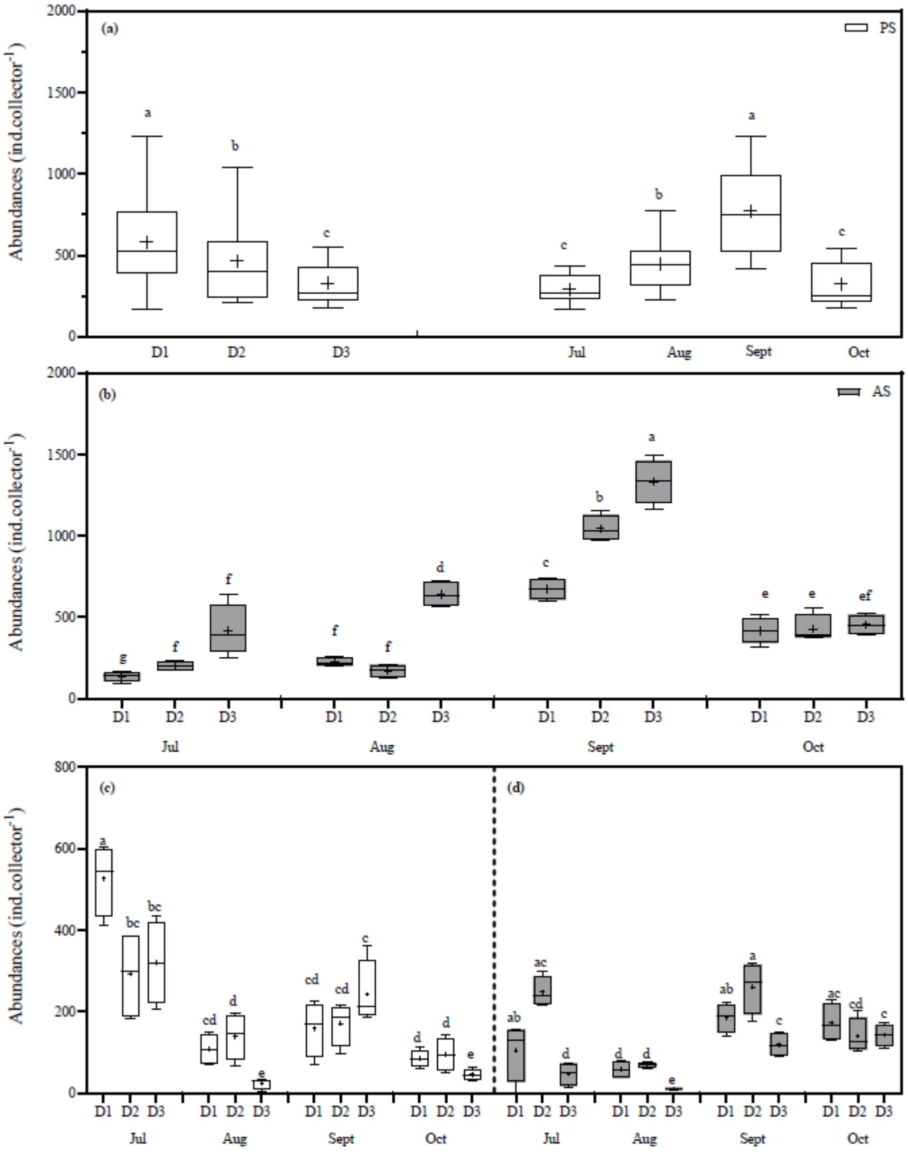
Figure 25: Box plots of *Placopecten magellanicus* abundances in Pristine (**a**) and Anthropic (**b**) sites per distances from the sound (D1, 25-30m; D2, 144-175m; and D3, 848-890m) over October. Boxes represent lower (25%) and upper (75%) quartiles. Whiskers show minimum and maximum values. Solid line is median, and the mean is represented by the symbol plus "+". Dissimilar letters indicate significant difference in post hoc analysis.

3.5.5.4 *Lacuna* sp.

In PS, *Lacuna* sp. recruitment was influenced by both distance from source (pseudo-F_{Di} = 11.47, p = 0.001) and month (pseudo- F_{Mo} = 24.37, p = 0.001) without interaction of factors (Figure 26a). Recruit abundance decreased from 580 to 329 ind. collector across D1 to D3 ($\mathrm{SPL}_{\mathrm{rms}}$, 137 dB – 106 dB re 1 μPa, $t_{\mathrm{D1\text{-}D2}} = 2.02$, p = 0.04; $t_{\mathrm{D1\text{-}D3}} = 5.12$, p<0.001; $t_{\mathrm{D2\text{-}D3}} = 2.68$, p = 0.01, Figure 26a) peaking in September (771 ind., $t_{\mathrm{Jul\text{-}Sept}} = 7.76$, p<0.001; $t_{\mathrm{Aug\text{-}Sept}} = 5.121$, p<0.001; $t_{\mathrm{Sept\text{-}Oct}} = 7.583$, p<0.001). In the AS site, the pattern was inverse, and there was a significant interaction between both factors for *Lacuna* sp. abundances (pseudo-$F_{\mathrm{Di\ x\ Mo}}$= 15.325, p<0.001, perms = 9942). In this site, recruit abundance was ~3-fold higher at D3 than at D1 across months ($\mathrm{SPL}_{\mathrm{pk}}$ 140 vs 153 dB re 1 μPa; 136 *vs* 417, 225 *vs* 641, 673 *vs* 1,331 ind.), except in October when abundances were similar among distances. The highest peak of early recruitment was observed in September (Figure 26b, Supplementary materials: Table S17).

3.5.5.5 *Skenea* sp.

Skenea sp. abundances varied significantly with distance and month at both sites (details in Supplementary materials: Table S5) (PS: pseudo- $F_{\mathrm{Di\ x\ Mo}} = 3.97$, p = 0.001, perms = 9940; AS: pseudo- $F_{\mathrm{Di\ x\ Mo}} = 16.57$, p<0.001, perms = 9932, Figure 26c-d). In the PS, abundances decreased with distance from noise (526 vs 319, 107 vs 23 ind.) and over time. Overall, higher abundances were firstly observed in D1, and later D1-D2 ($\mathrm{SPL}_{\mathrm{rms}}$, 137-120 dB re 1 μPa, Figure 26c). In the AS, D1 and D2 consistently showed 2-3-fold higher abundances compared to D3 ($\mathrm{SPL}_{\mathrm{pk}}$, 153-150 vs 143 dB re 1 μPa, 104 and 247 *vs* 46 ind., 184 and 259 *vs* 118 ind., Figure 26d), a possible stimulation effect on D1-D2 *vs* D3 over three months. Temporal patterns showed that *Skenea* sp. recruitment peaked at different times across noise intensities: D1-D2 had similar high abundances in July and September (184 vs 172, 247 vs 259, D1-D2), while D3 peaked later, between September-October (118-142 ind., Figure 26d).


(a)
PS
Abundances (ind.collector^{-1})
2000
1500
1000
500
0
a
b
c
c
b
a
c
D1
D2
D3
Jul
Aug
Sept
Oct
(b)
AS
Abundances (ind.collector^{-1})
2000
1500
1000
500
0
g
f
f
f
f
d
c
b
a
e
e
ef
D1 D2 D3
Jul
D1 D2 D3
Aug
D1 D2 D3
Sept
D1 D2 D3
Oct
(c)
(d)
Abundances (ind.collector^{-1})
800
600
400
200
0
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D1 D2 D3
Oct

Figure 26 : Box plots of (a, b) *Lacuna* sp. and (c, d) *Skenea* sp. abundances per station from the sound (D1, 25-30m; D2, 144-175m; and D3, 848-890m) during our experimental period from July to October 2021 in the Pristine site and Anthropic site. Boxes show 25th and 75th quartiles, while whiskers show minimum and maximum values. Solid line is median, symbol “+” denotes the mean. Dissimilar letters indicate significant difference in post hoc analysis.

3.6 Discussion

To our knowledge, the present study provides the first field evidence of ecological shifts at the community and species level during early recruitment in response to anthropogenic noise.

3.6.1 Pristine and Anthropized sites differ in environmental conditions and soundscapes

The SPM archipelago experiences extreme thermal oscillations, with temperatures shifting by up to 11ºC in 90 minutes during September, driven by non-linear internal waves amplified by diurnal tides (Lazure et al., 2018). These fluctuations are more pronounced at 30-60m depths than in shallower waters (< 20m). Temperature conditions were homogeneous across stations within each site and seasonal shifts were evident, aligning with previous studies (Bridier et al., 2021; Lazure et al., 2018; Poitevin et al., 2020). Given that temperature is a key factor regulating the physiology and behaviour of bivalves and gastropods (Bayne 1965; Pechenik 1990; Tremblay et al., 1998), short and intense thermal events caused by internal waves may impose significant stress on (Garwood et al., 2020; Woodson, 2018), likely in the AS. These site-specific dynamics highlight the complex relationship between temperature and bivalve development in SPM (Poitevin et al. 2020).

Hydrodynamic conditions, including turbulence, and current flow, influence larval behaviour and distribution, and ultimately settlement, with bivalve and gastropods showing preferences to water motion and turbulence depending on their habitat (Fuchs et al., 2018; Pernet et al., 2003; Tremblay et al., 2020). In addition, to expose larvae to temporary thermal stress, internal waves can affect larval transport, potentially facilitating larvae final delivery to settlement sites (see references and discussion in Garwood et al., 2020; Woodson, 2018).

In this study, weak bottom and residual currents likely promoted recruit retention during early months along both transects. After mid-September, bottom current intensities peaked up at the AS site, coinciding with a stronger thermal gradient (7-10°C), possibly linked to internal wave activity in August-September. These changes may have disrupted larval delivery, with less larvae reaching stations across the transect on the AS site. Furthermore, inshore current patterns did not favour recruit accumulation near collectors close to the noise source, as depicted by ADCP figures (D1, refer to Supplementary materials: Fig. S5b-d).

The trophic environment plays a key role in supporting larval development and recruitment by supplying nutritional resources and acting as a cue, synchronizing settlement-recruitment events, as observed in *M. edulis*, Mytilidae, and *Crassostrea gigas* in temperate habitats (Androuin et al., 2022; Lagarde et al., 2018; Toupoint et al., 2012a). Consistent with Bridier et al. (2021) and Toupoint et al. (2012a), the pelagic trophic environment of the SPM, including both sites, is oligotrophic. This was supported by the high proportions of bacterial and degraded organic matter markers (> 40%, Table 10) and elevated concentrations in the potential food source (1.0 to 2.5 x 10^6 cells.mL^{-1}, Table 10). Flow cytometry data indicated a dominance of picoplankton (picocyanobacteria and picoeukaryotes, Table 10, and Table S13-14) over nanoplankton in both sites, likely contributing to the diet of filter-feeders in SPM. Food quantity (TPM) and quality available (MFTA, trophic markers, food sources) were consistent across distances at each site. However, the PS site showed a greater food availability and quality than the AS site, including higher proportions of diatom markers and evidence of diatom blooms in September and October, confirming secondary autumnal blooms in SPM (Bridier et al., 2021). Importantly, similar trophic conditions across distances ruled out trophic variation as a confounding factor when assessing the effects of noise in our trials.

Soundscapes differed markedly between the PS site (vessel noise, SPL_{rms} = 106-137 dB re 1 μPa) and AS site (mix of pile driving and vessel noise, SPL_{pk} >140 dB re 1 μPa), where a combination of pile driving and vessel noise produced higher sound levels. Correspondingly, organisms were exposed to different sound exposure levels (PS: 132-138 dB re 1 μPa^2.s vs AS: > 140 dB re 1 μPa^2.s). Recent research shows that impulsive and continuous noises differ acoustically and can reduce habitat sensitivity, causing varied behavioral and physiological effects depending on sound pressure, frequency and distance from source (for review see Bonnel et al., 2022 and in Solé et al., 2023). Given that both physical and trophic conditions were overall consistent across sampling distances within each site, the observed patterns (species distribution, settlement, and early recruitment) are more likely attributed to the noise gradient rather than environmental variability.

3.6.2 Impact of noise on biodiversity features of recruit assemblages

In the last years, researchers have increasingly underlined the need for field-based assessments of anthropogenic impacts on marine ecosystems. Yet, significant gaps remain in understanding how anthropogenic noise affects biodiversity and population dynamics (Kunc et al., 2016; Solé et al., 2023; Sordello et al., 2020). This study provides the first field evidence of invertebrate community shifts due to anthropogenic noise exposure. Recruit diversity and evenness shifts aligned with the nature and intensity of the noise source: introducing vessel noise at the PS site (137 dB re 1 μPa, SEL < 132-138 dB 1 μPa^2.s) led to lower diversity and evenness (H' and J') near the source favoring stress-tolerant species, while higher intensity mixed noises at AS site (SPL_{pk} > 143 dB re 1 μPa, SEL > 140 dB re 1 μPa^2.s) was associated with differences in H' and J' indices, greater species turnover and higher diversity at moderate intensity (D2) due to rare species in August and October. Such diversity increase at D2 could be in line with the intermediate disturbance hypothesis (IDH) proposed by Connell (1978) where diversity is highest on intermediate levels of disturbance due to the trade-off in the presence of common and rare species. We suggest that a threshold below < 140 dB re 1 μPa^2.s is required to avoid changes in community structure. While terrestrial studies report declines in bird species richness under anthropogenic traffic noise

(Perillo et al., 2017; Proppe et al., 2013), and unchanged biodiversity of amphibians under turbine audio recordings at 500m (Trowbridge and Litzgus, 2022), such comparisons are limited given the propagation of sound in water (Bonnel et al., 2022; Farina, 2014; NRC, 2003). Despite the growing interest and urgent need of developing threshold criteria based on sound pressure level and sound exposure thresholds (SPL – dB re 1 µPa and SEL, dB re 1 μPa^2.s) to prevent several biological effects in marine fauna, framework connecting noise disturbances and impulsive and continuous noises have been mostly developed for marine mammals, and to an extent to fish (see Bonnel et al., 2022 for a detailed reviewed; NRC, 2003' NFMS, 2018; Popper et al., 2014). In general, behaviour modifications are seen in different groups of marine mammals when SPL and SEL of impulsive sounds are above 224 dB re 1 µPa and 173 dB re 1 μPa^2.s (references in Bonnel et al., 2022, p. 84). Auditory effects such as temporary threshold shift (TTS) in different hearing groups may occur if continuous sounds are above 153 dB re 1 μPa^2.s (SEL_{cum}), with higher SPL and SEL threshold for impulsive noises like pile driving (196 dB re 1 µPa and 140 dB re 1 μPa^2.s). (references cited within Bonnel et al. 2022, p. 86; NMFS 2018). Fish injury thresholds, depending on hearing group, are set at 183-187dB re 1 μPa^2.s (SEL_{cum}) and 206 dB re 1 µPa (SPL_{pk}), while TTS are above 186 dB re 1 μPa^2.s (SEL) for pile driving. For fish behavioral effects under ship or pile driving exposure, threshold is set at 150 dB re 1 µPa, uncertain if it is SPL_{pk} or SPL_{rms}) (Popper et al. 2014, p. 35).

Community diversity and stability depend on recruitment processes such as predation and competition (Austen et al., 2002; Butman, 1987; Fraschetti et al., 2003), and secondary migrations – key mechanism in the movement of *M. edulis, H. arctica*, and *Lacuna vincta* (Forêt et al., 2018; Le Corre et al., 2013; Martel and Chia 1991; Veillard et al., 2023). In this 4-month study, we accounted for these post-settlement processes (Hunt and Scheibling, 1997). Predation, a major source of settler mortality (Beal et al., 2020; Gosselin and Qian, 1997; O' Connor et al., 2008), was likely minimal here due to the scarcity (< 10%) or absence of sea stars and crabs. Interspecific competition, often affecting growth and survival in aquaculture collectors (Cyr et al., 2007; Garcia et al., 2003; Khalaman, 2005), likely had little effect due to the short deployment (1-month). Although noise may disrupt both predation and competition (Chan et al., 2010; Roberts et al., 2015), its role remains unclear *in situ.* However, we noticed a high proportion of larger recruits (10-80%, > 500 µm) of Mytilidae and *Lacuna* sp. were concentrated near the noise source (137 dB re 1 µPa) in the PS site, suggesting vessel noise may trigger secondary migrations. Conversely, in the AS site, larger recruits of *H. arctica*, Mytilidae, *P. magellanicus* were more abundant farther from the pile driving source (143 dB re 1 µPa, 40 to 90%, species-dependent), supporting that mixed noises may differently influence post-settlement movement. Further research is needed to understand how anthropogenic noise shapes post-settlement dispersal.

Given the species-specific responses noticed in this study, we present site-specific findings to showcase contrasting patterns and propose potential sound pressure and noise exposure thresholds that may elicit invertebrate behavioral responses.

3.6.3 Should I stay or should I go? Toward identifying a noise threshold for recruitment

Early studies with oysters suggest that the exposure to acoustic cues may alter developmental trajectories or trigger physiological responses that interact with other settlement cues. A recent study has demonstrated that this orientation in oyster larvae may go beyond vertical orientation, as larvae exhibited horizontal movements along a reef sound gradient, in field and lab studies (Williams et al., 2022). Research also suggest that larvae may prioritize certain cues – pulse of phytoplankton *vs* biofilm (Toupoint et al., 2012a,b) – or interpret them as positive or negative, as with algae *versus* predator (Morello and Yund, 2016). Because vessel noise and pile driving fall within invertebrate hearing ranges (Chauvaud et al., 2018; Duarte et al., 2021), they can mask critical ambient cues and interfere larval behaviours during habitat selection and settlement (Kingsford et al., 2002; Lillis et al., 2013, 2015; Fuchs et al., 2018).

3.6.3.1 *Pristine site vs Anthropized site*

In this study, early recruitment patterns were strongly influenced by the anthropogenic soundscape, with site-specific shifts corresponding to SPL and SEL thresholds. At the pristine site (PS), vessel SPLs decreased from high-moderate intensities (137-120 dB re 1 µPa) to control (106 dB re 1 µPa), and SELs remained below 138 dB re 1 µPa².s. Under these high-moderate conditions, recruitment of Mytilidae, *H. arctica*, *Lacuna* sp. *and Skenea* sp. was 3 to 5-fold enhanced, while trends of *P. magellanicus* were inconclusive due to limited sampling. The similar responses among most taxa here suggest that a threshold of 132-138 dB re 1 µPa².s may elicit behavioral change, increasing early recruitment near vessel noise source. In contrast, the anthropized site (AS) experienced cumulative noise from pile driving and vessel noise, with SPLs exceeding 140 dB re 1 µPa and SELs above 140 dB re 1 µPa².s. In these circumstances, recruitment of most taxa declined 2-3-fold, except *Skenea* sp., which increased by a similar magnitude.

While studies on bivalve or gastropod settlement under noise exposure remain scarce *in situ*, insights can be drawn from laboratory-based trials about the behaviour under certain vessel noise or pile driving exposure (SPL_{rms}, SPL_{pk}). The stimulation pattern seen in bivalve and gastropods align with the following studies. Veillard et al. (2025) observed a 2-fold increase in mussel settlement and metamorphosis under higher vessel noise compared to control levels in the (SPL_{rms}, 151 vs. 116 dB re 1 µPa) using the *Larvosonic* system, which simulates a sound gradient from the sound source (see Olivier et al., 2023 for details). This suggests that a similar behavioral shift as in the PS. In contrast, Jolivet et al. (2016) revealed a 27% increase after 67h of noise exposure (127 dB re 1 µPa, 100-1,000 Hz), while Cervello et al. (2023) found no differences between control and boat noise treatments (128 and 139 dB re 1 µPa). However, differences in these two studies may stem from that the first experiments were conduct in tanks where several acoustical biases can occur such as resonance and reverberations, whereas the absence of water motion as in the natural environment was one of the main issues in Cervello et al. (2023). The slight stimulation of *H.arctica* abundances towards vessel noise at the PS is a new result since there is no research using this species as a biological model for noise impact. Given the habitat overlap of mytilids and *Hiatella* (Garcia et al., 2003), we suggest that similar behavioral effects may occur to noise threshold at the PS.

For gastropods, few studies exist - Stocks et al. (2012) reported increases in swimming activity despite not describing sound levels, while Solé et al. (2021) documented statocyst damage at waves sweep of 157 dB 1 µPa (50-400 Hz). As *Lacuna* sp. recruitment increased near high-moderate (120-137 dB re 1 µPa, D1-D2) at PS, we hypothesize that their presence near the source may reflect a behavioural threshold near 132-135 dB re 1 µPa².s in the PS.

For pile driving sources in the anthropized site (AS), Cervello et al. (2023) noticed a downward trend in mussel settlement under pile driving and control treatments in *Larvosonic* trials (166.4 vs 128 dB re 1 µPa), though their results were not statistically significant. Scallop recruitment also declined near pile-driving sources (> 150 dB re 1 µPa), contrasting with controlled studies using a pectinid, *Pecten maximus,* which showed no survival or metamorphosis declines at even higher pile driving sounds (*Larvosonic*, SPL_{pp} 148 to 188 re 1 µPa, Gigot et al., 2023a; Olivier et al., 2023). Nonetheless, stress responses have been recorded in *P. magellanicus* juveniles *in situ* at lower SEL (SEL_{ss} < 94.39 dB re 1µm.s^{-2} at 8m), suggesting that our higher exposures (SEL > 140 dB re 1 µPa².s) may have triggered similar responses that potentially interfered with settlement or feeding (Robson et al. 2012). Likewise, *Lacuna* sp. abundances declined at under higher intensities (150-153 dB re 1 µPa), we propose that abundance decreases at D1-D2 may result from auditory damage at higher exposure (above 140 dB re 1 µPa².s), consistent with auditory damage observed by Solé et al (2021).

Though the mechanism of hearing in invertebrates remains poorly understood (Chauvaud et al., 2018), evidence suggests that they detect particle motion via statocysts, allowing perception and orientation toward sound sources (Hawkins and Popper, 2017). This sensory system becomes more complex after metamorphosis and involving different structures at specific life stages (references in Solé et al., 2023; Zhadan, 2005). In addition to statocysts in the ciliated foot, superficial mechanoreceptors on the epiderma work as accelerometers (Budelmann, 1992; Cragg and Nott, 1977; Roberts et al., 2015).

Several potential mechanisms may underlie the observed responses to vessel noise and mixed noises. Beyond sound intensity, frequency is critical, as many invertebrates produce and perceive a range of sounds that overlap natural and anthropogenic sources (Chauvaud et al., 2018; Roberts et al., 2015; Zhadan, 2005). In this study, the low-frequency vessel sound may have mimicked some natural cues from rocky shores/waves, attracting larvae, as initially proposed by Jolivet et al. (2016). Additionally, in the absence of physical, chemical or natural acoustic cues, anthropogenic sounds (e.g. vessel) may fill-in as substitute signal with similar acoustic signature, modifying larval behaviour and accelerating this transition. However, when vessel and pile driving noises were combined, the resulting higher intensity and threshold may have indicated suboptimal conditions for most of taxa, as strong substrate-borne vibrations and particle motion near the source could interfere valve closure or foot extension, as suggested by Robert et al. (2015) and Jézéquel et al (2022).

Considering our findings, we suggest a sound exposure threshold not exceeding 140 dB re 1 μPa^2.s as a potential upper limit for maintaining normal recruitment patterns of key invertebrate species. Below this level (132-135dB re 1 μPa^2.s), early recruitment of several species was enhanced or unaffected, which need to be interpreted with caution here as this could impair selectivity and increase metabolic stress metabolic in post-metamorphic stages (Veillard et al., 2025). While these thresholds are broadly consistent with preliminary criteria for marine mammals and fishes (Bonnel et al., 2022; NMFS, 2018; Popper et al., 2014), more studies should be carried out obtain complete dose-response curves and validate these proposed levels.

3.7 Futures perspectives

This study demonstrates that anthropogenic noise alters marine community diversity and evenness, affecting recruitment of stress-tolerant species *in situ* depending on noise nature and thresholds. This is the first field study to examine the effect of noise on marine community traits and propose a preliminary threshold for invertebrates (< 140 dB re 1 $\mu Pa^2.s$). While several gaps remain unaddressed in noise impact studies (Duarte et al., 2021; Hawkins and Popper, 2017; Solé et al., 2023), we highlight three areas requiring further attention:

i) Environmental stressors - such as anthropogenic soundscapes, temperature shifts, and food availability - may cause latent effects in young juveniles that persist, amplify or compensate over time (Lagarde et al., 2018; Martel et al., 2014; Podolsky and Moran, 2006). For example, delayed metamorphosis, triggered by low temperature or insufficient trophic conditions, have been referred as amplification effects, which might result in a decrease in larval energetic reserves available to metamorphose, reduced ability to identify specific cues to settle and in the end, reduced fitness, survival, and growth in juveniles and adults (Hunt and Scheibling, 1997; Pechenik, 2006; Podolsky and Moran, 2006). Noise exposure categorized these effects in three scenarios: *persistence*, where effects occur prior and continue in later stages; *amplification*, where effects not only persist but enhance in later stages; and *compensation*, where effects counterbalance and decrease in later stages. A great example of amplifying effect is the study developed by Gigot et al. (2024), found that scallops (*P. maximus*) exposed to moderate pile-driving noise produced fewer eggs than control condition (SPL_{pp} 148 vs 100 dB re 1 µPa), but their larvae exhibited enhanced growth – a cross-generational response likely amplify the survival of offspring. Although we did not measure size at metamorphosis, previous studies on oysters suggest that larvae settling earlier (at smaller sizes) achieved higher recruitment success (Lagarde et al., 2018). These findings highlight the need to better understand how interacting stressors may produce latent effects that compromise recruitment in the Anthropocene era.

ii) *In situ* experiments offer greater ecological realism than laboratory studies, despite reduced experimental control (Spicer, 2014). Despite some design constraints, this study successfully accounted for major confounding factors (temperature, trophic conditions, currents) and proposes a realistic baseline threshold (> 140 dB re 1 μPa^2.s) for inhibited recruitment across taxa. This threshold may offer guidance for conservation policy. Future research should validate these levels by examining long-term physiological response, trophic quality available *in situ*, temperature and ecological interactions under single and multiple noise exposures.

iii) The post-settlement phase of bivalve and gastropods – often downplayed due to high mortality, plays a critical role in population dynamics. These relocations are prompted by environmental conditions but also the active behaviour of post-larvae (Fôret et al., 2018a; Leal et al., 2022; Le Corre et al., 2013; Martel and Diefenbach, 1993). Noise may disrupt these secondary migrations, influencing substrate choice and habitat selection. A shift to a less suitable habitat could undermine population replenishment, particularly in disturbed intertidal zones. More research is needed to understand how noise affects this phase of the benthic life cycle.

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Supplementary materials

Table S13: Fatty acid composition (FA%, mean ± SE, n=6) of bottom particulate organic matter (b-POM) retrieved from artificial collectors moored at distances D1 (25-30m), D2 (144-175m) and D3 (848-890m) from an underwater speaker sound on a transect in the pristine (PS) and anthropized (AS) site between July, August, September, and October 2021, respectively. Values are reported as traces (tr.) when percentages are inferior 0.1%. Abbreviations: branched fatty acids (brFA), saturated fatty acids (SFA), monosaturated fatty acids (MUFA) polyunsaturated fatty acids (PUFA), eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and essential fatty acids (EFA). BrFA are composed of 13:0iso, 14:0iso, 15:0anteiso, 15:0iso and 16:0iso.

	PS				**AS**		
FA	*July*	*August*	*September*	*October*	*August*	*September*	*October*
12:0	0.45 ± 0.06	0.4 ± 0.05	0.36 ± 0.05	0.39 ± 0.09	0.44 ± 0.09	0.37 ± 0.04	0.54 ± 0.09
13:0	0.11 ± 0.01	0.13 ± 0.01	0.16 ± 0.01	0.19 ± 0.01	0.1 ± 0.02	0.1 ± 0.01	0.12 ± 0.02
14:0	6.11 ± 0.41	6.55 ± 0.31	8.62 ± 0.28	8.31 ± 0.41	10.16 ± 0.26	10.07 ± 0.21	9.04 ± 0.44
15:0	0.74 ± 0.05	1.02 ± 0.06	0.94 ± 0.02	1.34 ± 0.02	0.89 ± 0.03	0.93 ± 0.04	1.28 ± 0.03
16:0	27.92 ± 1.56	22.12 ± 0.98	19.14 ±0.21	19.79 ± 0.2	27.87 ± 1.57	26.74 ± 0.36	26.6 ± 0.93
17:0	tr.	0.12 ± 0.02	0.93 ± 0.03	0.7 ± 0.08	tr.	0.42 ± 0.01	0.08 ± 0.01
18:0	14.47 ± 2.3	7.19 ± 0.96	4.12 ± 0.07	5.21 ± 0.1	11.93 ± 1.65	6.85 ± 0.39	8.97 ± 0.49
20:0	1.25 ± 0.36	1.45 ± 0.24	3.09 ± 0.16	0.98 ± 0.14	3.62 ± 0.32	4.19 ± 0.11	3.11 ± 0.29
22:0	0.1 ± 0.02	0.19 ± 0.01	0.21 ± 0.01	0.38 ± 0.02	0.18 ± 0.02	0.15 ± 0.01	0.2 ± 0.03
24:0	0.1 ± 0.01	0.17 ± 0.03	0.18 ± 0.03	0.26 ± 0.08	0.07 ± 0.04	tr.	tr.
26:0	tr.	0.15 ± 0.08	tr.	0.27 ± 0.09	0.41 ± 0.13	tr.	tr.
Σ SFA	**51.38 ± 3.38**	**39.5 ± 1.94**	**37.8 ± 0.61**	**37.81 ±0.53**	**55.72 ± 2.79**	**49.93 ± 0.57**	**50.07 ± 0.51**
14:1ω3	0.16 ± 0.01	0.23 ± 0.01	0.29 ± 0.03	0.35 ± 0.04	0.19 ± 0.01	tr.	0.21 ± 0.02
16:1ω5	0.58 ± 0.04	0.36 ± 0.01	0.48 ± 0.02	0.59 ± 0.02	0.45 ± 0.02	0.57 ± 0.01	0.45 ± 0.02
16:1ω7	6.44 ± 0.41	9.95 ± 0.34	12.64 ±0.17	16.1 ± 0.59	5.21 ± 0.13	6.95 ± 0.12	8.09 ± 0.35
16:1ω9	tr.	tr.	tr.	0.1 ± 0.02	tr.	tr.	0.39 ± 0.35
17:1ω7	0.23 ± 0.03	0.22 ± 0.02	0.43 ± 0.02	0.08 ± 0.02	0.29 ± 0.05	0.37 ± 0.01	0.32 ± 0.05
18:1ω7	5.5 ± 0.31	8.53 ± 0.51	6.32 ± 0.41	10.02 ±0.32	3 ± 0.08	3.51 ± 0.13	4.11 ± 0.24
18:1ω9	7.87 ± 0.43	11.66 ± 0.32	9.05 ± 0.37	12.28 ±1.35	8.83 ± 0.83	8.4 ± 0.2	10.16 ± 0.56
Σ MUFA	**20.83 ± 1.19**	**31.04 ± 0.83**	**29.27 ±0.67**	**39.52 ± 0.9**	**18 ± 0.88**	**19.93 ± 0.3**	**23.74 ± 0.84**
16:2ω4	0.16 ± 0.03	0.22 ± 0	1.1 ± 0.02	0.79 ± 0.09	0.4 ± 0.01	0.61 ± 0.01	0.32 ± 0.02
16:3ω3	0.15 ± 0.03	0.39 ± 0.06	0.11 ± 0.01	0.24 ± 0.02	0.37 ± 0.01	0.18 ± 0.02	0.47 ± 0.07
16:3ω4	0.23 ± 0.04	0.43 ± 0.02	0.41 ± 0.01	0.73 ± 0.03	0.22 ± 0.06	0.31 ± 0.02	0.83 ± 0.12
16:4ω1	tr.	0.11 ± 0.01	1.13 ± 0.04	0.7 ± 0.09	tr.	tr.	0.1 ± 0.01
16:4ω3	0.96 ± 0.08	0.9 ± 0.05	1.45 ± 0.06	0.9 ± 0.03	0.82 ± 0.05	1.19 ± 0.01	1.47 ± 0.09
18:2ω6	3.24 ± 0.22	3.37 ± 0.15	2.84 ± 0.09	3.05 ± 0.2	3.76 ± 0.22	4.05 ± 0.17	4.72 ± 0.39
18:2ω9	0.8 ± 0.06	1.05 ± 0.17	0.58 ± 0.06	1.02 ± 0.06	0.12 ± 0.01	0.15 ± 0.01	0.21 ± 0.01
18:3ω3	3.06 ± 0.29	3.64 ± 0.34	3.09 ± 0.12	1.95 ± 0.04	3.43 ± 0.15	3.94 ± 0.07	2.92 ± 0.1
18:3ω6	0.12 ± 0.02	0.2 ± 0.01	0.27 ± 0.01	0.22 ± 0.03	0.17 ± 0.01	0.2 ± 0.01	0.18 ± 0.02

18:4ω3	4.47 ± 0.41	4.13 ± 0.16	4.79 ± 0.1	2.43 ± 0.06	4.7 ± 0.29	5.5 ± 0.07	3.88 ± 0.24
20:4ω6	0.42 ± 0.04	0.5 ± 0.05	0.65 ± 0.01	0.71 ± 0.06	0.36 ± 0.05	0.32 ± 0.01	0.21 ± 0.01
20:5ω3	5.29 ± 0.58	5.34 ± 0.36	6.78 ± 0.13	3.17 ± 0.24	3.05 ± 0.37	4.46 ± 0.07	3.55 ± 0.37
22:6ω3	6.32 ± 0.81	5.76 ± 0.55	6.6 ± 0.3	2.28 ± 0.11	7.22 ± 1.07	6.84 ± 0.27	4.98 ± 0.64
Σ PUFA	**25.28 ± 2.39**	**26.06 ± 1.17**	**29.79 ± 0.27**	**18.2 ± 0.46**	**24.7 ± 2.03**	**28.25 ± 0.41**	**23.85 ± 1.27**
ΣbrFA	2.52 ± 0.15	3.4 ± 0.46	3.14 ± 0.12	4.47 ± 0.15	1.58 ± 0.07	1.9 ± 0.09	2.35 ± 0.1
PUFA/SFA	0.52 ± 0.07	0.67 ± 0.06	0.79 ± 0.01	0.48 ± 0.01	0.46 ± 0.06	0.57 ± 0.01	0.48 ± 0.03
Σ EFA	12.03 ± 1.42	11.61 ± 0.87	14.03 ±0.36	6.16 ± 0.32	10.63 ± 1.47	11.62 ± 0.33	8.74 ± 1
16:1ω7/16:0	0.24 ± 0.03	0.46 ± 0.03	0.66 ± 0.01	0.81 ± 0.04	0.19 ± 0.01	0.26 ± 0.01	0.3 ± 0.01
EPA/DHA	0.86 ± 0.04	0.95 ± 0.06	1.04 ± 0.05	1.41 ± 0.13	0.43 ± 0.01	0.66 ± 0.02	0.73 ± 0.03

Table S14: Results of one-way permutational multivariate analyses (PERMANOVA) testing the effect of distance (Di, 3 levels) on total particulate matter (TPM, mg.L-1, n=6 or 8), fatty acid composition (%), total mass of fatty acid (MTFA, µg.mg -1 , n=6 or 8), trophic markers (%) and food sources (total bacteria, pico- and nano cyanobacteria, pico- and nano eukaryotes) available for recruits collected on transects at pristine (PS) and anthropized (AS) sites. Significant values (Monte-Carlo p<0.05) are indicated in bold.

	TPM (mg.L^{-1})				**FA composition (%)**				**MTFA (µg.mg $^{-1}$)**			
	df	*Pseudo-F*	*p*	*Perm*	*df*	*Pseudo-F*	*p*	*Perm*	*df*	*Pseudo-F*	*p*	*Perm*
PS												
Di	2	0.22	0.80	9947	2	0.65	0.64	9942	2	0.42	0.74	9953
Res	21				21				21			
Total	23				23				23			
AS												
Di	2	0.12	0.63	9895	2	1.43	0.22	9932	2	0.36	0.78	9930
Res	15				14				14			
Total	17				16				16			

	Trophic markers				**Food sources**			
	df	*Pseudo-F*	*p*	*Perm*	*df*	*Pseudo-F*	*p*	*Perm*
PS								
Di	2	0.73	0.58	9941	2	1.00	0.44	1622
Res	21				9			
Total	23				11			
AS								
Di	2	1.08	0.38	9928	2	0.73	0.60	226
Res	15				6			
Total	17				8			

Table S15: List and respective composition (% mean, SE, n=6) of trophic markers adopted in the present study in total particulate matter retrieved from shallow waters (8-20m) in the Pristine (PS) and the Anthropized sites (AS) over the 4 months (July, August, September and October).

Fatty acid	Marker of	References	**PS**				**AS**		
			Jul	**Aug**	**Sept**	**Oct**	**Aug**	**Sept**	**Oct**
∑ai15:0, iso15:0, 18:1ω7	Bacteria	Meziane and Tsuchiya (2000; 2002)	7.31 (0.4)	11.02 (0.83)	8.49 (0.46)	13.00 (0.32)	4.16 (0.13)	5.75 (0.23)	4.83 (0.2)
∑14:0, 16:0, 18:0	Degraded organic matter	Bridier et al. (2021), Canuel and Zimmerman (1999), Connelly et al. (2015).	48.49 (3.51)	35.87 (2.1)	31.88 (0.48)	33.32 (0.41)	50.58 (2.87)	44.62 (0.82)	43.66 (0.50)
∑16:1ω7, 20:5ω3	Diatoms	Dalsgaard et al. (2003), Kelly and Scheibling (2012)	11.73 (0.86)	15.29 (0.6)	19.41 (0.17)	19.28 (0.79)	8.14 (0.30)	11.64 (0.32)	11.42 (0.07)
∑ 22:6ω3	Dinoflagellates	Kelly and Scheibling, (2012)	6.32 (0.81)	5.76 (0.55)	6.6 (0.3)	2.28 (0.11)	6.97 (1.03)	4.98 (0.64)	6.84 (0.27)
∑18:2ω6, 18:3ω6, 18:4ω3	Green macroalgae	Bridier et al. (2021), Gaillard et al. (2017), Kelly and Scheibling, (2012)	7.83 (0.61)	7.7 (0.25)	7.9 (0.09)	5.7 (0.17)	8.42 (0.39)	8.78 (0.3)	9.74 (0.17)
∑ 18:1ω9	Brown macroalgae	Kelly and Scheibling (2012)	7.87 (0.43)	11.66 (0.32)	9.05 (0.37)	12.28 (1.35)	8.85 (0.84)	10.16 (0.56)	8.4 (0.2)

Table S16: Pairwise test results (two-way PERMANOVA) showing differences on species richness (S), Shannon-Weiner diversity (H') and Pielou's evenness (J') among distances (D1, D2, D3), and months (July, August, September, and October) in the pristine (PS) and anthropized (AS) sites. Significant values (p<0.05) are indicated in bold.

			Richness (S)				
		PS			*AS*		
Month	t-test	P(MC)	perms	t-test	P(MC)	perms	Distance
Jul, Aug	0.37	0.72	9392	3.84	**0.0008**	9738	D1, D2
Jul, Sept	3.28	**0.004**	6441	2.63	**0.014**	9729	D1, D3
Jul, Oct	1.32	0.20	9700	1.04	0.307	6768	D2, D3
Aug, Sept	2.60	**0.017**	9755				
Aug, Oct	0.81	0.43	9731				
Sept, Oct	1.87	0.08	9725				
			Diversity (H')				
		PS			*AS*		
	t-test	P(MC)	perms	t-test	P(MC)	perms	Pair-wise
Month							*D1*
Jul, Aug	3.54	**0.002**	9855	3.50	**0.011**	22	Jul, Aug
Jul, Sept	3.77	**0.009**	9853	10.69	**0.0001**	25	Jul, Sept
Jul, Oct	6.30	**0.0001**	9840	0.61	0.56	25	Jul, Oct
Aug, Sept	0.08	0.93	9838	5.76	**0.001**	35	Aug, Sept
Aug, Oct	3.99	**0.0009**	9845	3.95	**0.0061**	35	Aug, Oct
Sept, Oct	4.43	**0.0005**	9825	16.92	**0.0001**	35	Sept, Oct
Distance							*D2*
D1, D2	3.36	**0.003**	9834	1.67	0.143	35	Jul, Aug
D1, D3	7.71	**0.0001**	9842	7.75	**0.0001**	32	Jul, Sept
D2, D3	1.61	0.12	9819	0.24	0.8135	31	Jul, Oct
				4.53	**0.0048**	32	Aug, Sept
		Evenness (J')		1.91	0.11	34	Aug, Oct
		PS		13.18	**0.0001**	35	Sept, Oct
	t-test	P(MC)	perms				
Month							*D3*
Jul, Aug	4.02	**0.0007**	9817	1.50	0.18	32	Jul, Aug
Jul, Sept	1.85	0.08	9814	1.62	0.16	35	Jul, Sept
Jul, Oct	6.92	**0.0001**	9824	2.92	**0.027**	35	Jul, Oct
Aug, Sept	2.63	**0.015**	9831	0.43	0.68	34	Aug, Sept
Aug, Oct	3.90	**0.002**	9844	18.73	**0.0001**	35	Aug, Oct
				25.65	**0.0001**	34	Sept, Oct
Distance							
D1, D2	3.42	**0.0028**	9827				*Jul*
D1, D3	7.99	**0.0001**	9799	1.19	0.27	24	D1, D2
D2, D3	2.73	**0.0114**	9833	2.26	0.06	22	D1, D3
				2.71	**0.03**	35	D2, D3
							Aug
				1.91	0.10	35	D1, D2
				6.54	**0.0011**	35	D1, D3

7.10	**0.0005**	32	D2, D3

Table S16 continued

Evenness (J')				**Diversity (H')**			
AS				*AS*			
t-test	P(MC)	perms	Pair-wise	t-test	P(MC)	perms	Pair-wise
			D1				*Sept*
3.23	**0.015**	35	Jul, Aug	**3.30**	**0.018**	35	D1, D2
6.39	**0.0006**	35	Jul, Sept	2.10	0.08	32	D1, D3
0.12	0.92	34	Jul, Oct	5.72	**0.002**	35	D2, D3
4.30	**0.005**	35	Aug,Sept				
3.38	**0.016**	35	Aug, Oct				*Oct*
6.74	**0.001**	35	Sept, Oct	4.23	**0.007**	34	D1, D2
				4.64	**0.0024**	30	D1, D3
			D2	0.85	0.43	33	D2, D3
2.69	**0.04**	35	Jul, Aug				
8.36	**0.0003**	35	Jul, Sept				
0.28	0.79	35	Jul, Oct				
5.32	**0.002**	35	Aug,Sept				
2.19	0.07	34	Aug, Oct				
5.99	**0.0007**	35	Sept, Oct				
			D3				
2.07	0.08	32	Jul, Aug				
2.17	0.07	35	Jul, Sept				
3.36	**0.012**	34	Jul, Oct				
0.31	0.76	35	Aug,Sept				
14.74	**0.0002**	35	Aug, Oct				
15.23	**0.0001**	34	Sept, Oct				
			Jul				
0.52	0.62	35	D1, D2				
3.13	**0.02**	35	D1, D3				
3.04	**0.025**	35	D2, D3				
			Aug				
0.65	0.53	35	D1, D2				
8.20	**0.0004**	35	D1, D3				
8.37	**0.0001**	35	D2, D3				
			Sept				
0.14	0.94	35	D1, D2				
2.06	0.08	35	D1, D3				
2.85	**0.03**	35	D2, D3				
			Oct				
0.07	0.95	35	D1, D2				
0.03	0.98	35	D1, D3				
0.05	0.96	35	D2, D3				

Table S17: Pair-wise test results of the interaction of distance and month (two-way PERMANOVA) showing differences in the early recruitment of bivalves (*Hiatella arctica*, Mytilidade) and gastropods (*Lacuna* sp., and *Skenea* sp.) among distances (D1, D2, D3), and months (July, August, September, and October) in the pristine (PS) and anthropized (AS) sites. Significant values ($p<0.05$) are indicated in bold.

			H. arctica		Mytilidae		*Lacuna* sp.*	*Skenea* sp.	
PS	*Factor Distance*	Pair-wise tests	t-test	P(MC)	t-test	P(MC)		t-test	P(MC)
	Jul	D1, D2	2.96	**0.02**	2.00	0.08		2.77	**0.03**
		D1, D3	2.33	**0.05**	5.19	**0.001**		2.69	**0.03**
		D2, D3	1.00	0.35	2.94	**0.02**		0.40	0.73
	Aug	D1, D2	4.38	**0.002**	5.77	**<0.001**		0.76	0.49
		D1, D3	1.90	0.10	7.70	**<0.001**		2.60	**0.01**
		D2, D3	2.23	0.05	2.96	**0.02**		2.75	**0.008**
	Sept	D1, D2	2.22	0.03	1.23	0.26		0.38	0.76
		D1, D3	1.16	0.25	6.06	**<0.001**		1.42	0.18
		D2, D3	0.53	0.68	8.69	**<0.001**		1.40	0.20
	Oct	D1, D2	0.47	0.73	2.64	**0.03**		0.37	0.79
		D1, D3	0.28	0.89	5.50	**<0.001**		2.90	**0.02**
		D2, D3	0.74	0.55	5.97	**<0.001**		2.32	**0.04**
	Factor Month	Pair-wise tests	t-test	P(MC)	t-test	P(MC)			
	D1	Jul, Aug	8.54	**<0.001**	1.54	0.17		6.24	**<0.001**
		Jul, Sept	8.40	**<0.001**	1.36	0.22		3.98	**0.001**
		Jul, Oct	6.09	**<0.001**	3.95	**0.002**		9.32	**<0.001**
		Aug, Sept	1.70	0.12	0.32	0.78		1.06	0.329
		Aug, Oct	3.59	**0.003**	4.78	**0.002**		0.87	0.42
		Sept, Oct	2.64	**0.023**	3.79	**0.005**		1.87	0.10
	D2	Jul, Aug	9.65	**<0.001**	0.60	0.61		2.19	**0.04**
		Jul, Sept	8.76	**<0.001**	4.72	**<0.001**		1.78	0.10
		Jul, Oct	8.45	**<0.001**	5.38	**<0.001**		3.23	**0.01**
		Aug, Sept	5.92	**<0.001**	6.52	**<0.001**		0.76	0.49
		Aug, Oct	1.93	0.1	7.51	**<0.001**		1.07	0.32
		Sept, Oct	6.23	**<0.001**	2.32	0.06		1.96	0.08
	D3	Jul, Aug	8.11	**<0.001**	1.23	0.27		3.78	**0.001**
		Jul, Sept	5.14	**<0.001**	2.73	**0.03**		1.18	0.29
		Jul, Oct	5.01	**<0.001**	6.63	**<0.001**		6.27	**<0.001**
		Aug, Sept	1.28	0.23	1.02	0.35		3.66	**0.001**

		Aug, Oct	2.35	**0.03**	4.24	**0.002**			1.38	0.2
		Sept, Oct	2.60	**0.02**	3.84	**0.005**			6.03	**<0.001**

			H.arctica		Mytilidae		*Lacuna* sp.		*Skenea* sp.	
AS	*Factor Distance*	Pair-wise tests	t-test	P(MC)	t-test	P(MC)	t-test	P(MC)	t-test	P(MC)
	Jul	D1, D2	2.81	**0.02**	1.22	0.27	2.828	**0.02**	3.096	**0.01**
		D1, D3	4.87	**<0.001**	8.77	**0.001**	4.28	**0.002**	0.847	0.45
		D2, D3	2.64	**0.03**	3.67	**0.010**	3.202	**0.01**	2.054	0.06
	Aug	D1, D2	1.29	0.25	2.46	**0.035**	2.14	0.08	1.720	0.08
		D1, D3	9.68	**<0.001**	4.34	**0.002**	11.99	**<0.001**	0.429	0.83
		D2, D3	3.61	**0.006**	2.68	**0.028**	8.67	**<0.001**	1.26	0.23
	Sept	D1, D2	5.57	**<0.001**	3.22	**0.016**	7.03	**<0.001**	1.119	0.31
		D1, D3	6.20	**<0.001**	3.87	**0.006**	9.27	**<0.001**	1.311	0.19
		D2, D3	4.88	**0.002**	2.29	0.059	3.73	**0.008**	0.761	0.59
	Oct	D1, D2	7.83	**<0.001**	2.02	0.086	0.19	0.90	0.96	0.41
		D1, D3	5.48	**<0.001**	6.88	**<0.001**	0.79	0.46	1.67	0.07
		D2, D3	1.92	0.09	5.59	**0.002**	0.59	0.58	3.62	**0.002**
	Factor Month	Pair-wise tests	t-test	P(MC)	t-test	P(MC)	t-test	P(MC)	t-test	P(MC)
	D1	Jul, Aug	0.75	0.488	4.13	**0.003**	3.71	**0.008**	3.20	**0.003**
		Jul, Sept	4.09	**0.015**	7.24	**<0.001**	10.12	**<0.001**	3.60	**0.001**
		Jul, Oct	6.95	**<0.001**		**<0.001**	6.39	**<0.001**	3.11	**0.003**
		Aug, Sept	5.00	**<0.001**	1.38	0.206	13.69	**<0.001**	0.74	0.62
		Aug, Oct	10.32	**<0.001**	0.80	0.464	5.22	**0.002**	0.87	0.51
		Sept, Oct	4.58	**<0.001**	1.47	0.192	4.35	**0.003**	0.58	0.74
	D2	Jul, Aug	3.02	**0.01**	5.47	**0.001**	1.29	0.243	5.36	**<0.001**
		Jul, Sept	3.99	**0.004**	7.71	**<0.001**	17.36	**<0.001**	3.54	**0.001**
		Jul, Oct	9.93	**<0.001**	5.44	**<0.001**	6.13	**<0.001**	8.12	**<0.001**
		Aug, Sept	0.28	0.83	1.11	0.30	11.45	**<0.001**	0.92	0.44
		Aug, Oct	9.03	**<0.001**	2.35	**0.05**	5.589	**<0.001**	2.77	**0.01**
		Sept, Oct	18.79	**<0.001**	7.46	**<0.001**	8.416	**<0.001**	1.87	0.07
	D3	Jul, Aug	5.74	**<0.001**	8.63	**<0.001**	2.36	**0.048**	1.94	**0.03**
		Jul, Sept	5.37	**0.001**	8.67	**<0.001**	5.51	**<0.001**	2.57	**0.01**
		Jul, Oct	7.14	**<0.001**	8.70	**<0.001**	0.73	0.512	3.21	**0.003**
		Aug, Sept	1.14	0.29	0.49	0.66	8.98	**<0.001**	1.00	0.39
		Aug, Oct	7.46	**<0.001**	0.74	0.50	3.88	**0.007**	1.14	0.30
		Sept, Oct	6.83	**<0.001**	0.25	0.84	11.79	**<0.001**	0.48	0.82

* Due to the lack of interaction between distance and month factors on *Lacuna* sp. abundances at the PS site, the pairwise tests were not included in this table but are presented in the results section in the main document.

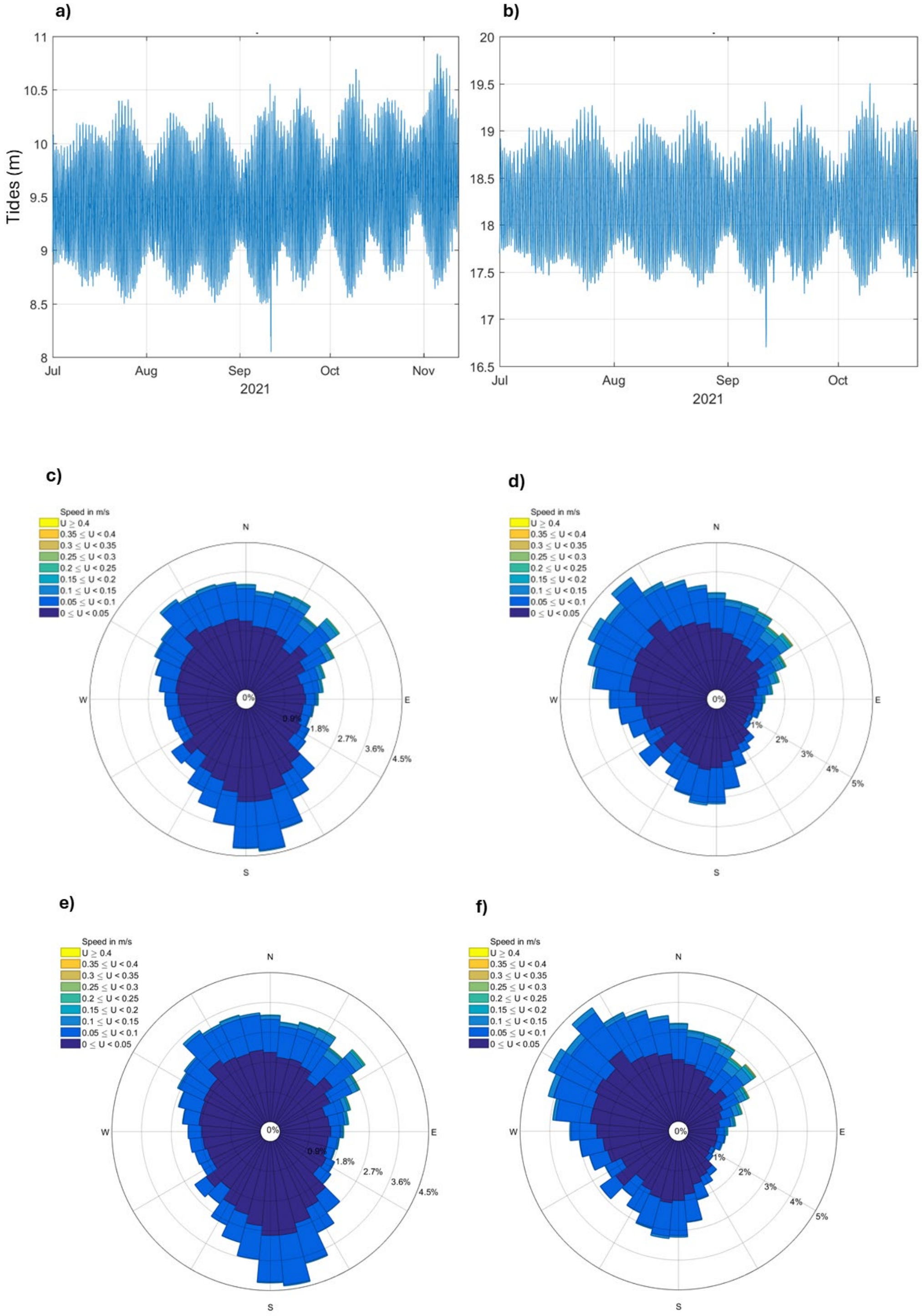

Figure S 5: Characterization of tides and currents at 8m and 1m above the bottom in both Pristine (PS, a, c, e) and the Anthropized (AS, b, d, f) experimental sites during the sampling months of July, August, September, and October.

GENERAL CONCLUSION

In this thesis, we investigated how vessel noise affects critical processes mediating the pelagic-benthic transition – settlement, metamorphosis – that shape population structure and dynamics of benthic invertebrates. This research integrates population dynamics and behavioural approaches to address three main objectives:

1) comparing the effects of ambient noise and vessel noise at two intensities (distances from the source) on the settlement of *M. edulis in situ* (Chapter I);
2) assessing the impact of vessel noise playback on *M. edulis* population metrics (size at metamorphosis, total length and cohort distribution) along a noise gradient *in situ* (Chapter II); and
3) evaluating the impact of vessel noise intensity on community structure (species diversity and evenness) and early recruitment of multiple species across a gradient of noise (varying distances from the emission source) in two distinct sites *in situ* (Chapter III).

Through a combination of noise manipulation, environmental monitoring, and species-specific analyses over temporal and spatial gradients of sounds, this thesis provides novel insights into *in situ* ecological consequences of anthropogenic noise. The results demonstrate that anthropogenic noise can alter species composition, impact metamorphosis and influences post-settlement migration depending on noise type and sound exposure levels. This research benefited from interdisciplinary collaborations and sets the stage for future studies on the ecological impacts of anthropogenic noise. By demonstrating the role of anthropogenic sounds in shaping population processes, this work addresses an emerging concern in marine ecology (Solé et al., 2023). Because each article has a dedicated section for discussion, this general conclusion is structured into three main sections: (1) contributions of this research, (2) study limitations, and (3) future perspectives, highlighting both the broader implications of these findings and potential directions for further investigation.

RESEARCH CONTRIBUTIONS

Towards establishing sound exposure criteria for invertebrates

Over the past two decades, significant progress has been made in defining sound exposure thresholds for marine mammals, leading to regulatory frameworks for continuous and impulsive noise. These frameworks typically rely on sound pressure level (SPL_{pk} or SPL_{rms}) and sound exposure level (SEL), which are guided by species- or group-specific hearing sensitivities (Bonnell et al., 2022; NMFS, 2018; Rako-Gospić and Picculin, 2018). Similarly, initial threshold criteria have been developed for fish, based on their hearing characteristics and fish-group response to sound types (see details in Popper et al., 2014). However, substantial gaps remain, particularly regarding how fish respond to sound gradients and how individual-level effects observed in controlled and field studies translate to populational-level outcomes (Hawkins et al., 2020; Pieniazek et al., 2023).

In contrast, research on invertebrates (bivalve and gastropods) has begun to integrate SEL into experimental designs. Early studies primarily relied solely on SPL_{pk} or SPL_{rms}, but recent laboratory research with bivalve post-larvae has included and tested SEL >150 dB re 1 $\mu Pa^2.s$ under pile driving and drilling conditions (e.g. Olivier et al., 2023). To date, similar SEL-inclusions or investigations for gastropods are lacking. Although invertebrates detect the acceleration of particles rather than pressure per se (Nedelec et al., 2016), recent work have emphasized that frequency is also a critical factor in how sound is propagated and perceived (Coquereau et al., 2016; Duarte et al., 2021; Melo Junior et al., 2020). For example, Olivier et al. (2023) reported that the highest daily growth rates did not correspond to the highest noise levels. Other studies have demonstrated that invertebrates tend to concentrate their activities within low and high frequency bands (Coquereau et al., 2016). Thus, frequency emerges as a key factor in invertebrate response to anthropogenic noise.

Despite efforts to standardize metrics and advancements in detecting particle acceleration in lab- and ongoing for field trials, a key gap remains linking individual-level effects to population and community impacts. This highlights the urgent need for *in situ* research to define the sound exposure threshold that can prevent physiological and behavioural adverse effects (Hawkins and Popper , 2017; Solé et al., 2023). In this thesis, we tackled this challenge by employing a combined approach using both SPL_{rms} and $SEL_{1\text{-min}}$ thresholds to characterize acoustic exposure (chapter I-III). While we observed distinct responses in bivalve and gastropods responses to varying SPLs across noise types, our discussion centers on the use of a preliminary SEL threshold (< 140 dB re 1 $\mu Pa^2.s$) to synthesize our contributions. To our knowledge, this thesis is the first to propose a preliminary SEL threshold for multiple species of bivalve and gastropods, based on *in situ* exposure to vessel noise and mixed-noise, aiming to mitigate negative impacts on community structure and recruitment. However, this is a starting point for further research as there are many practical considerations to address, feasibility for industry, and implementation.

Across all trials (Chapter I-III), distinct biological responses were observed when sound thresholds exceeded or stayed below 140 dB re 1 $\mu Pa^2.s$. These effects will be discussed in the following sections. Additionally, this thesis suggests an initial threshold for one of the most studied species, *M. edulis*, in the context of key population-level processes. Although the absence of detailed dose-response curves and audiograms defining species-specific frequency sensitivity limits the precision of these proposed thresholds (Cones et al., 2023), our findings represent an important first step toward developing ecologically relevant exposure criteria. Moving forward, refining these thresholds will require controlled laboratory trials to confirm the observed effects (which will be covered in **Future perspectives**).

Mussel settlement and metamorphosis exposed to noise thresholds

At the end of the veliger stage, mussel pediveliger become competent to settle, transitioning from a pelagic to benthic lifestyle. For blue mussels, competency is defined by a size range (250-260µm) and the appearance of morphological traits. Settlement can be triggered by physical, chemical, and more recently acoustic cues. During a three-day exposure, vessel noise at a threshold of < 140 dB re 1 µPa^2.s had no measurable effect on settlement (Chapter I). However, due to the low number of settlers in this trial, we could not conclusively determine whether vessel noise acts as a settlement cue *in situ*. Likewise, over four-month period, no significant impact of vessel noise or mixed noises was observed on primary settlement (Chapter II). However, our final study (Chapter III) suggested that cumulative settlement was stimulated at the sound threshold < 140 dB re 1 µPa^2.s and inhibited above that threshold (Figure 28).

Once larvae have settled, they undergo metamorphosis in which mussels rely on internal energy reserves to fuel this demanding transformation. Metamorphosis may be delayed as a survival strategy under suboptimal environmental conditions (e.g., temperature, food quality or chemical signals), allowing larvae to remain in the water column for weeks and grow over 400 µm (Bayne, 1965; Hadfield and Paul, 2001; Leal et al., 2018; Lutz and Jablonski, 1978; Toupoint et al., 2012a). In the first and second trials (Chapters I and II), we observed that mussels had a mean PII size of 331 µm, with shell size increasing from 318 to 345 µm over time, suggesting a delay in this transition. Similar delay suggestions have been reported by Guillou et al. (2023) and Martel et al. (2014) in the GSL. While we initially hypothesize that vessel noise would delay metamorphosis, results from first and second trials did not support this, as no direct relationship between sound exposure and the observed delay in SPM was found. Additionally, no link between temperature and metamorphic delay was found either (Chapters II-III). Although vessel noise did not seem to directly impact settlement or delay metamorphosis, contrasting with some lab-based studies using single vessel noise exposures that reported stimulation (Veillard et al., 2025), our results align with those of Cervello et al. (2023). Nevertheless, we observed a significant reduction in post-larval abundance, suggesting that vessel noise may still influence overall metamorphosis success. Some studies have reported mixed results, with studies showing a better post-larval growth under different sources of anthropogenic noises (Gigot et al., 2023a; Olivier et al., 2023), while others, including our second trial, found declines in metamorphosis. This decrease in success may be linked to increased metabolic stress from vessel noise exposure, as previously reported by Veillard et al. (2025). Even though we did not measure mussel energy reserves, we hypothesize that mussels exposed to noise within the proposed threshold might expend more energy coping with a noisy environment, thereby reducing survival and successful transition.

Insights from mussel cohorts exposed to distinct noise thresholds

The life cycle of bivalves, including mussels, begins with the release of gametes into the water, leading to fertilized embryos. This then progresses through several pelagic larval stages before becoming a benthic juvenile and eventually recruiting into the adult population (Bayne, 1965; Gosling 2021). This lifecycle is influenced by environmental factors and stressors, and there is growing concerns over the potential effect of anthropogenic noise at the population level. Using *M. edulis* as a model species and its morphometric data, we validate the hypothesis that larval cohorts and size-class distribution vary depending on the sound type and pressure level thresholds (Chapter II).

Mussel cohort structure differed between thresholds, with variations in cohort numbers and individual size distribution observed between the pristine site (Miquelon) and the anthropic site (Saint-Pierre). To characterize this cohort, we coupled Gaussian Mixture Model (GMM), and the singular Bayesian Information Criteria (sBIC) with Earth Mover's Distance (EMD). This analytical approach confirmed that differences in cohort structure (primary vs secondary settlers) were associated to noise type and threshold. A notable influx of secondary settlers (2-7 cohorts) was observed at the pristine site, whereas fewer and more variable cohorts (1-9 cohorts) were found at the anthropic site. A likely explanation for these variations is the dynamic nature of coastal habitats, where mussel beds are interconnected and secondary migrations might occur due to specific triggers (Forêt et al., 2018a; Gunther et al., 1992). We hypothesized that vessel noise may act as a trigger for secondary migration, as initially proposed in first trial (Chapter I). In our experiments (Chapter II), we initially observed a stimulation of smaller drifting mussels (< 3mm) under vessel noise exposure, followed by an inhibition of larger drifters (> 3mm). We propose that this inhibition could be due to the evolution of juveniles' sensory organs and receptors, as described in Cannuel et al. (2009), who reported that gills filaments in late pediveliger (390 μm) and post-larvae (1 mm) were substantially different. Pediveligers have a gill basket shape, but as post-larvae develop inner and outer demibranchs, their gills take on a V-shape, eventually forming a W-shape, as they transition to adult stage (Cannuel et al., 2009). Moreover, post-larval sizes in the second trial were consistently above 0.7mm (Chapter III). Under mixed noise conditions, sound exposure threshold > 140 dB re 1μPa^2.s inhibited larger drifters (> 2mm) from colonizing collectors. Migration events of mussel juveniles (2-32mm) have been documented in no anthropogenic noise habitats in the GSL (Le Corre et al., 2013; Petrović and Guichard 2008). Based on the size range of drifters observed at the pristine site, we propose that vessel noise may represent a novel trigger for secondary dispersal of mussels. However, this response may be size limited to early juvenile stages and could potentially result in a secondary settlement in suboptimal habitats for population renewal.

Anthropogenic noise as a driver modifying community, and recruitment processes in multiple species

Anthropogenic noises, particularly from vessels, can modulate the behaviour and fitness of benthic invertebrates (e.g., Davies et al., 2024). However, research into how vessel noise affects critical ecological processes that support community diversity and population structure has been largely restricted to laboratory settings (Cervello et al., 2023; Jolivet et al., 2016; Stocks et al., 2012; Wilkens et al., 2012), and has been scarce in field settings, a gap addressed by this thesis. In this thesis, we showed that community and early recruitment are influenced by anthropogenic noises. Figure 27 summarizes these effects and variations observed across experiments (Chapter I-III), depending on whether the sound exposure was above or below a threshold of 140 dB re 1 μPa^2.s. Recruit diversity and evenness shifted, suggesting species-specific sensitivities to noise type and SEL < 140 dB or > 140 dB re 1 μPa^2.s in the first experiment (Chapter III).

When analyzing responses across species (*M. edulis*, *H. arctica*, *P. magellanicus*, *Lacuna* sp.), consistent patterns emerged. Vessel noise below 140 dB re 1 μPa^2.s stimulated early recruitment of species, with increased abundance of medium-sized individuals (>500μm, drifters). This suggests that such sound levels may be a *trigger for secondary migration* in multiple species (*M. edulis*, *H. arctica*, and *Lacuna* sp.). In contrast, combined noise from pile driving and vessels exceeding this threshold (> 140 dB re 1 μPa^2.s) inhibited recruitment across nearly all species and restricted the presence of medium-sized individuals (>500μm, drifters). Given their ecological and economic importance, and species-specific responses to sound thresholds, mussels offer a valuable model for assessing how anthropogenic sounds disrupt key population processes, such as cohort dynamics and settlement-metamorphosis.

A trophic trigger modulating mussel settlement in SPM

Marine invertebrates must obtain high lipid-quality food (EFAs – EPA, DHA) from the environment, as they are unable to synthesize these compounds or produce them in sufficient quantities to meet their nutritional needs (da Costa et al., 2015; Knauer and Southgate, 1999). While these organisms can synthesize de novo SFA and MUFAs (Glencross, 2009), EFAs are supplied by marine microalgae (Radakovits et al., 2010). In addition to their role as a source of EFAs, microalgal-derived FAs serve as trophic markers in ecological studies, facilitating the assessment of nutritional quality of waters and elucidating links between diet and consumer profiles (Dalsgaard et al., 2003; Kelly and Scheibling, 2012; Leal et al. 2019).

The impact of vessel noise on benthic invertebrates

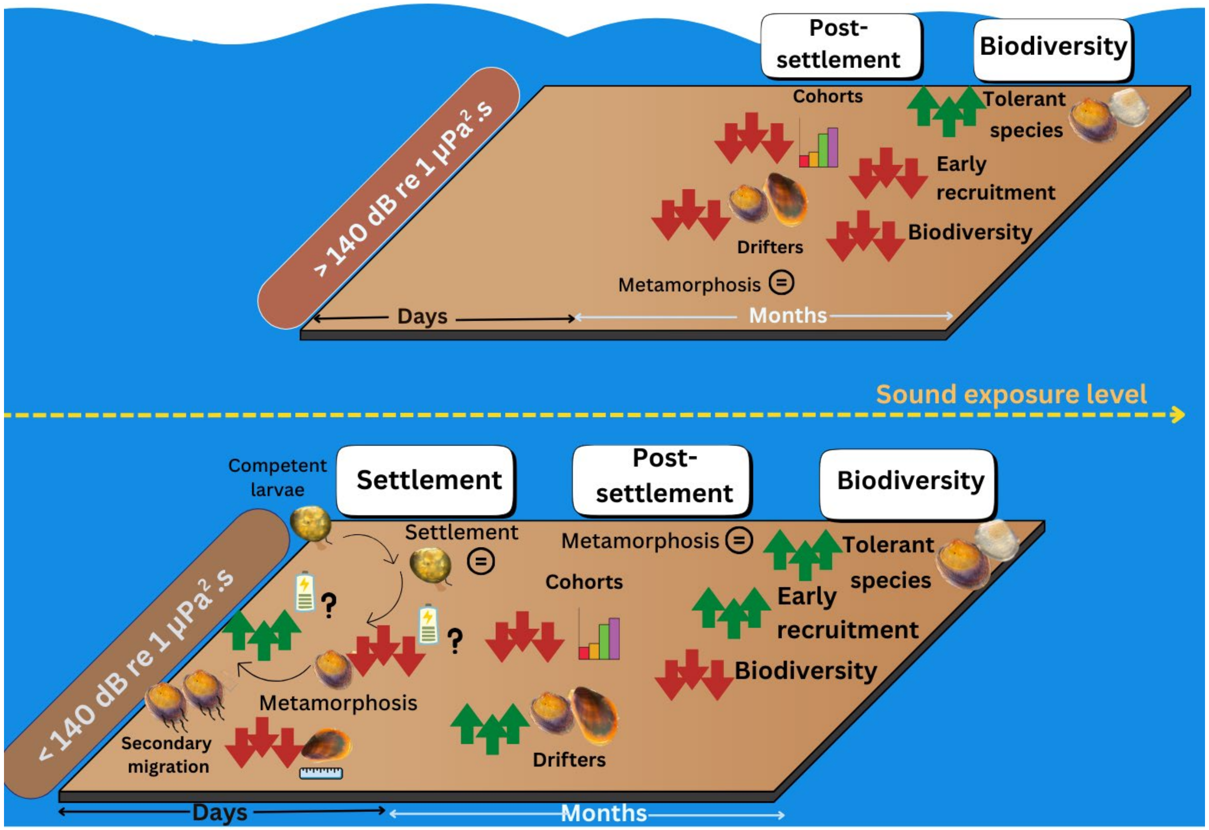

Figure 27: Conceptual figure showing changes in the community and recruitment processes of recruits of invertebrates exposed to anthropogenic noises above and below a critical sound threshold of 140 dB re 1 μPa^2.s based on *in situ* experiments at SPM.

Lipids are essential for larval development, with TAGs providing energy, and EFAs supporting vital physiological functions. Thus, trophic quality in POM is critical for growth and survival (Fraser et al., 1989) and the presence of stressful conditions organisms my shift into a basic maintenance for survival instead of growing, storing energy and breeding (Sokolova et al., 2012).

Our findings in first and second trials characterize the waters around SPM as an oligotrophic (TPM < 4.9 $mg.L^{-1}$; MTFA < 5.7 $\mu g.mg^{-1}$, Chapter I and III), consistent with earlier observations by Bridier et al. (2021). FA profiles were relatively uniform across sampling stations (SFAs > 40%, MUFA > 20%, PUFAs > 19%), with only minor differences between Saint-Pierre and Miquelon observed in the first study (Chapter I).

The trophic environment plays a crucial role in larval development and recruitment by providing essential nutritional resources and serving as cue that synchronizes settlement and recruitment peaks (Androuin et al., 2022; Lagarde et al., 2018; Toupoint et al., 2012a). The quality of trophic resource should ensure an adequate supply of EPA and DHA, as bivalves have limited or lost capacity to synthetize these EFAs (Da Costa et al., 2015; Pernet et al., 2004; Toupoint et al., 2012a). Additionality, although EPA + DHA were present in our samples, they were relatively low (< 20%) across all trials (Chapter I, II and III). While SFAs could serve as an important energy source for mussel larvae and post-larvae (Leal et al., 2022), low EFA availability may limit successful larval settlement (Pernet et al., 2004; Tremblay et al., 2020). The low settlement rates and delayed metamorphosis observed in first and second studies may reflect the absence of trophic cues, lending support to the *Trophic Settlement Trigger* (TST) hypothesis (Toupoint et al., 2012a). Indeed, Toupoint *et al.* (2012a) also found increased settlement of mussels when EFA levels in POM exceeded 25%. Other recent field studies have linked trophic cues - picoplankton, nanoplankton, SFAs, bacterial concentration – as mediators of the settlement, early recruitment and secondary migration of bivalves across various latitudinal gradients (Androuin et al., 2022; Forêt et al., 2018a; Lagarde et al., 2018; Leal et al., 2022; Veillard et al., 2023). We propose that trophic cue (EFA quality in POM) may play a key role in influencing *M. edulis* settlement in oligotrophic subarctic environments like SPM. Finally, although previous work demonstrated that vessel noise combined with a trophic cue can enhance settlement in controlled conditions (Jolivet et al., 2016), this effect was not observed *in situ* in our first experiment (Chapter I), likely due to low EFA content in POM. This potential interaction warrants further investigation.

STUDY LIMITATIONS

Sampling in situ*: constraints and design*

Field studies often encounter logistical constraints, and our trials were no exception. The design of the first experiment (Chapter I), based on a biweekly sampling, was limited in space and time, which may have resulted in missing the initial settlement peak in 2022. Such interannual variability in mussel stocks is well documented in the Gulf of Saint-Lawrence (Guillou et al., 2020; Le Corre et al., 2013; Martel et al., 2014;). Ultimately, low settlement abundances limited our ability to assess the combined effects of vessel noise and trophic cue in field condition. Future research should aim to explore how trophic quality and anthropogenic interact to shape mussel settlement in subarctic coastal habitats.

The second experiments (chapter II-III) employed a cumulative sampling method, making it difficult to distinguish between settlement and post-settlement processes - a critical limitation given the high post-settlement mortality (Hunt and Scheibling, 1997). As a result, we were unable to determine whether competition and predation influenced recruitment outcomes under vessel noise exposure. For example, the absence of vessel noise effects on scallop abundances in the pristine may have reflect limited sampling or competition from dominant species (*H. arctica* and *Mytilus* spp.), which may restrict *P. magellanicus* settlement even in habitats with no anthropogenic noise (Cyr et al., 2007). Depth may also have constrained scallops' presence in Miquelon, as they prefer to settle at depths > 8m. Predation pressure seemed minimal, as collectors were suspended 40 cm above the seabed, and predator abundance (sea stars and brittle stars) remained < 10% in the second trial

(Chapter II). Although we could not test the effects of vessel noise on mussel anti-predator behaviour in the field, we hypothesize that *in situ* responses may mirror laboratory observations (Hubert et al., 2022), where simultaneous exposure to multiple cues (predators + vessel cues) makes it difficult for mussels - especially in earlier life stages – to process them.

A third limitation was the absence of a control transect during the second experiment (Chapters II and II). Despite this constraint, using a distance gradient from vessel noise emissions in experiments helped mitigate the issue, as the furthest collectors in the pristine site received similar ambient noise levels comparable to those recorded in Arctic and temperate regions (Halliday et al., 2021; Mathias et al., 2016). Moreover, unexpected noise overlaps at the anthropized site hindered clear comparisons of vessel noise effects between sites with distinct levels of pollution. Even though this overlapping of sound was not planned, we noted that the combined noise levels surpassed proposed thresholds. Migrations and early recruitment of invertebrates appeared more impacted, suggesting that organism response to single vs multiple noises *in situ* vary drastically. Recent reviews have emphasized the importance of combining anthropogenic noise with other pressures in future studies (Thomsen and Popper, 2024).

While we propose sound exposure thresholds in this thesis, several challenges arise in defining them. One major limitation is the absence of complete dose-response curves, which was beyond the scope of this project and would require more stations along the transect. Few studies have examined the behavioural response curves of adult mussels and scallops to different frequencies, but these represent sound sensitivity rather than minimum hearing threshold for each species (details in Cones et al., 2023; Roberts et al., 2015). Moreover, our interpretations are based on relatively short temporal window (4 months in 2021 and 21 days in 2022) and spatial close sites. Another current limitation in this study is the difficulty on conducting experiments under naturally variable environmental conditions while maintaining sufficient replication (Filazzola and Cahill Jr., 2021). Although we increased sample replication (n = 4 or 5) and repeated our experiments biweekly over 3 weeks or within

30 days for 4 months, we cannot fully exclude the limited replication on our results. Despite these constraints, this study had an overall success in controlling confounding factors *in situ* (temperature, trophic conditions, currents), and the proposed initial thresholds provide a foundation for future, more replicated research.

FUTURE PERSPECTIVES

First proposition of a threshold for invertebrates related to vessel traffic

Vessel noise may act as an initial trigger for secondary migrations, with sensitivity potentially increasing in post-metamorphic stages (< 2mm). Juveniles larger than 2 mm appear more likely to avoid vessel noise or respond differently to mixed noise sources. By identifying these preliminary noise exposure thresholds, this thesis may help inform future management tools and policy development aimed at reducing the impacts of the vessel and mixed noise sources on benthic invertebrates. These early thresholds could also suggest areas that may warrant consideration for protective measures such as adjusting shipping lanes, or reducing vessel speed, until further research provides greater certainty. In Canada, the Ocean Soundscape Atlas, has begun mapping and contextualizing ship noise patterns and identifying overlaps with key habitats or species of interest, with ongoing efforts to expand data coverage. Additionally, this former project is in the process of integrating these acoustic datasets into dynamic energy budget models (DEB) across different life stages of invertebrates (*perso. comm.*, Pierre Potvin and F. Aulanier). DEB models describe energy flow through individual organisms - from assimilation of food to its use for maintenance, growth, development and reproduction (Van der Veer et al., 2006) - and can provide insights on how vessel noise impacts energy allocation and physiological processes at various life stages of mussels. The sound exposure threshold and sound pressure levels tested may, in the future, be considered for inclusion in mapping tools such as the one developed by Meridian team at UQAR (the Ocean Soundscape Atlas, 2013-current) or as provisional reference point in assessments like the Good Environmental Status (GES) (Merchant et al., 2022).

Furthermore, threshold proposed in this thesis opens the door to future studies to validate these initial levels through laboratory, assessing finer responses of bivalves, such as behavioural responses to these exposure levels, which could eventually be incorporated into DEB models.

Multiple stressors and latent effects in this Anthropocene era

Ocean warming and acidification are critical stressors threatening marine invertebrates, as particularly during early life stages (embryo, larvae and juveniles) (Pandori and Sorte, 2018; Przeslawski, et al., 2015). These environmental changes affect key physiological processes: elevated temperature increase metabolism, while acidification decrease pH and carbonate ion availability essential for shell formation (Bylenga et al., 2017; Lasota et al., 2018; Przeslawski et al., 2015). Importantly, these stressors often act synergistically, compounding their impacts on marine organisms (Przeslawski et al., 2015). In addition to physiological effects, climate-driven changes also alter the acoustic environment (Kunc et al., 2016). Warmer temperatures might reduce sound speed, while acidification diminishes absorption of low-frequency sounds, potentially intensifying anthropogenic noise and reducing biological sounds (Hester et al., 2008; Ilyina, Zeebe and Brewer, 2010; Rossi et al., 2016).

Exposure to multiple, and co-occurring stressors (i.e., anthropogenic noise, temperature and food shifts, and acidification) during early stages can lead to latent effects that emerge later in life (Leung and McAfee, 2020; Pechenik, 1990). Despite the significant of these effects, research in bivalves and gastropods remains limited, especially concerning the impact of anthropogenic noise. Recent findings in *Pecten maximus* exposed to pile driving noise revealed complex responses, including accelerated early development and lack of parental effects on post-larvae (Gigot et al., 2024), highlighting amplification and compensation latent effects. This raises a compelling question: could vessel noise trigger similar latent effects in mussels and other coastal invertebrates in the field? This concern is heightened by the ongoing increase in vessel traffic in coastal areas (Campagne et al., 2023;

Halpern et al., 2019), alongside laboratory findings of tolerance to vessel noise in the laboratory (Cervello et al., 2023), suggesting that these organisms may misinterpret anthropogenic sounds as ecologically relevant cues. Mussels inhabit intertidal and subtidal zones where a diverse variety of underwater sounds are present (Jolivet et al., 2016), including wave crashing on frequencies from 30 to 500 Hz (Carey and Fitzgerald, 1993). These frequencies overlap with the low-frequency band of vessel noise adopted in this thesis and in previous lab studies (100-1,000Hz) (Aspirault et al., 2023; Cervello et al., 2023). This spectral overlap raises further questions: Is the frequency of sound more relevant than the sound intensity on early stages? As adults concentrate their activities within one or two frequency ranges (Coquereau et al., 2016; Melo and Junior. 2020), does that mean the frequency sensitivity increases with age and varies during the development of an individual? Does repeated exposure lead to the development of maladaptive behavioural phenotypes, with larvae misinterpreting the frequencies of vessel noise as a cue? These questions open a new avenue for research into investigating latent effects and adaptive responses.

In future scenarios with increased maritime traffic, vessel noise could accelerate the settlement, potentially reduce the larval selectivity window and increase the likelihood of mussels settling in suboptimal habitats. Once settled, increased metabolic stress could occur, reducing the success of metamorphosis. If energy permits, juveniles might subsequently migrate to more favorable substrates if they are still available. However, if mussels stay in these noisy environments, energy may be diverted to stress mitigation and potential consequences for fitness. As illustrated in Figure 3b from the General Introduction, increasing stress reduces aerobic scope, forcing reallocation of ATP from production (growth, migration activity) to basal maintenance, which may compromise fitness (Sokolova et al., 2012).

Mussel aquaculture and sustainable management of fisheries

Mussels *(Mytilus spp.)* are economically important for aquaculture in Canada and Europe, through farming techniques varying among countries (DFO, 2022; FAO, 2024). One common feature among these countries is the reliance on wild seed collection to sustain mussel production (Baden et al., 2021; Gosling, 2021; South et al., 2021). Seed capture is highly variable, influenced by a combination of pre- and post-seeding factors (South et al., 2021). Food quality, seed condition, pollution, thermal stress, migratory behaviour, predation, and competition all affect nursey success and contribute to post-settlement losses. Among these, migratory behaviour is particularly difficult to manage as it can drive seeds away from collectors. Yet, small-scale migration is necessary, especially when seeds relocate from a settlement substrate to grow out areas (Le Corre et al., 2013; South et al., 2021). Anthropogenic noise adds further complexity, as it may stimulate or inhibit mussel cohorts depending on noise type and intensity – particularly when secondary drifters are involved – and may also reduce the successful establishment of post-larvae. Consequently, vessel traffic and combined noises present a potential risk to sustainable aquaculture not only by influencing habitat selection but also potentially compromising juvenile survival. While efforts are underway to enhance acoustic environments using reef sounds in degraded areas to boost invertebrate recruitment (Lillis et al., 2015; Williams et al., 2022), near by vessel or boating noise has been shown to hinder the progress of these restoration initiatives (Sussan and Charpentier, 2024; Williams et al., 2024).

Parallel field and laboratory work to investigate secondary migrations

Secondary migrations play a crucial role in the movement of many bivalves and gastropods, redirecting juveniles to either favourable or unfavourable habitats. In particular, secondary settlement appears to be a major driver for recruitment dynamics in some areas of the GSL (Le Corre et al., 2013), including SPM, as demonstrated in this thesis. The observed stimulation and inhibition of drifting juveniles of various sizes in response to different types of anthropogenic noise is both concerning and compelling. In particular, it would be interesting to explore more deeply the mechanisms and physiological consequences of vessel noise on mussel secondary migration. Although a study has shown that the key energy components (neutral and polar lipids) of pediveligers remain unaffected by vessel noise emissions under laboratory conditions (Cervello et al., 2023), more recent work shows a different pattern. Adopting similar noise intensities as the ones as in this thesis, post-larvae showed increased glucogenesis and energy production under vessel noise exposure (Veillard et al., 2025). This suggests that examining energy dynamics in mussel juveniles during secondary migration could be valuable, especially since previous research has shown that energy reserves influence dispersal patterns (Forêt et al., 2018b; 2020a). To further investigate these mechanisms, we propose modifying the *Larvosonic* system (see Olivier et al., 2023 for details) by replacing the original 6-acrylic cylinders with 4 to 5-miniature flume mesocosms, each equipped with a water flow meter. To track post-larvae and juvenile movement in the water column, we would mark individuals using calcein marking technique (Moran and Marko, 2005; Spires and North, 2022). Sampling marked larvae at set time intervals would allow us to assess changes in behaviour patterns and energetic condition in response to the varying noise intensities and threshold levels tested in this research.

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