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Diversity in Benthic Foraminifera: From pattern to function

Vincent M.P. Bouchet

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Vincent M.P. Bouchet. Diversity in Benthic Foraminifera: From pattern to function. Biodiversity and Ecology. Université de Lille, 2022. tel-04365494

HAL Id: tel-04365494

<https://hal.science/tel-04365494>

Submitted on 28 Dec 2023

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Synthèse des travaux en vue de l'obtention de

L'Habilitation à Diriger des Recherches

Présentée par

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**Diversity in Benthic Foraminifera:
From pattern to function**

La diversité chez les foraminifères benthiques :
Des patrons de distribution à leur rôle

Le 08 09 2022

Devant le jury composé de :

Pr. Sigal Abramovich, Ben-Gurion University of the Negev, Israël	Rapporteur
Pr. Emmanuelle Geslin, Université d'Angers	Rapporteur
Dr. Florian Mermillod-Blondin HDR, DR CNRS, UMR5023 LEHNA	Rapporteur
Pr. Antoine Grémare, Université de Bordeaux	Examineur
Pr. Edouard Metzger, Université d'Angers	Examineur, Président
Dr. Laurent Seuront HDR, DR CNRS, UMR8187 LOG	Garant

« Dans ce jeu qu'est le rugby, tout le monde a toujours raison. Heureusement, pour progresser, qu'un autre jour, tout le monde a tort. »

Jacques Fouroux (1947-2005), dit le petit caporal

(capitaine du quinze de France victorieux du grand chelem dans le tournoi des V nations 1977 et entraîneur du quinze de France finaliste de la première coupe du monde de rugby en 1987 en Nouvelle-Zélande)

« J'éprouvais toujours une soif ardente de découvertes et de recherches, chaque fois que je voyais un nouveau pays, et la première nuit, mon émotion était telle, que je ne dormais pas. »

Alcide d'Orbigny (1802-1857), rochelais d'adoption et père de la micropaléontologie

Alcide Charles Victor Marie Dessalines d'Orbigny est né à Couëron (près de Nantes), le 6 septembre 1802. Il était issu d'une famille de voyageurs et de naturalistes, et son père Charles-Marie, médecin dans la marine lui transmit son enthousiasme pour les sciences naturelles. Le rayonnement culturel de la ville de La Rochelle, ouverte sur la mer et le voyage, où sa famille s'installa en 1820, fut de nature à éveiller, ou tout au moins à entretenir chez le jeune Alcide, des rêves de découvertes et d'exploration.

C'est sur le littoral rochelais qu'il se passionna très jeune pour l'étude d'un groupe d'animaux microscopiques qu'il nomma " Foraminifères ". Il lui consacra son premier travail scientifique, posant ainsi les fondements d'une science nouvelle, la micropaléontologie. Ce travail qu'Alcide d'Orbigny publia à l'âge de 23 ans sur les foraminifères impressionna beaucoup Georges Cuvier et les scientifiques de l'époque.

En 1853, quatre ans avant sa mort, un décret du chef de l'Etat crée au Muséum la première chaire de paléontologie destinée à Alcide d'Orbigny, officialisant par là, non seulement une nouvelle discipline mais encore désignant Alcide d'Orbigny comme l'un des pères de la micropaléontologie. (source : <http://www.mnhn.fr/expo/orbigny/index/index1.htm>)

« Il est juste qu'on se préoccupe des pluies acides ou des diverses pollutions, mais je ne veux pas cacher mon opinion : l'enjeu de notre futur concerne davantage d'autres aspects de l'écologie, parmi lesquels la mobilisation et le contrôle par l'homme de fractions croissantes d'énergie qui ont des influences sur l'organisation de l'espace et, ce qui est plus préoccupant, sur l'organisation des rapports entre les êtres humains. »

Ramon Margalef (1919-2004), un des pères fondateurs de l'écologie moderne

Parmi ses plus grandes contributions scientifiques, on note l'application de la théorie de l'information à l'écologie. Dans *On certain unifying principles in ecology*, publié en 1963, Margalef met en commun plusieurs théories utilisées en écologie pour définir la structure d'un écosystème comme l'ensemble des éléments de celui-ci (la matière) et des interactions entre ces éléments de l'écosystème (l'énergie). Il introduit par la suite la notion de maturité d'un écosystème. Avec le temps, la maturité d'un écosystème croît, dans un milieu sans perturbations. Un écosystème à maturité a une structure complexe (grande diversité, riche en information) et une grande efficacité d'un point de vue énergétique (peu de perte d'énergie). D'autre part, selon Ramon Margalef, la succession écologique consiste en une maturation de l'écosystème (augmentation de la complexité de la structure et diminution du flux d'énergie). Enfin, de son point de vue, la succession est empreinte d'incertitudes et est assujettie aux perturbations.

Ramon Margalef est un scientifique dont le travail s'est inscrit dans le contexte social et politique de son époque. Il a porté une attention particulière à la place de l'homme et de la femme dans la biosphère. Déjà, dans *On certain unifying principles in ecology*, il conclut sur la maturité et la succession des organisations humaines, en lien avec la complexité de leurs structures et leurs flux d'énergie. (source : wikipedia)

SOMMAIRE

AVANT-PROPOS	3
CURRICULUM VITAE	7
FORMATION	9
EXPERIENCES PROFESSIONNELLES	9
ENCADREMENT	10
PROJETS DE RECHERCHE	12
EXPERTISES	13
FORMATION CONTINUE : TAXONOMIE MACROFAUNE	13
FINANCEMENT ET PRIX INDIVIDUELS	13
INDICATEURS DU RAYONNEMENT SCIENTIFIQUE	13
EXPERTISE (ORGANISMES NATIONAUX OU INTERNATIONAUX)	13
ACTIVITES EDITORIALES (EXPERTISES, RESPONSABILITES DE COLLECTIONS...)	14
PARTICIPATION JURYS DE THESE ET DE HDR (HORS ETABLISSEMENT)	14
ORGANISATION COLLOQUES, CONFERENCES, JOURNEES D'ETUDE	15
PARTICIPATION A UN RESEAU DE RECHERCHE, INVITATIONS DANS DES UNIVERSITES ETRANGERES	15
RESPONSABILITES COLLECTIVES ET ADMINISTRATIVES	16
PRESENTATION SYNTHETIQUE DES RESPONSABILITES	16
RESPONSABILITES ADMINISTRATIVES	17
RESPONSABILITES ET MANDATS LOCAUX OU REGIONAUX	17
Participation aux conseils de composantes, de laboratoires	17
Autres	17
ACTIVITES D'ENSEIGNEMENT	17
PUBLICATIONS	18
PUBLICATIONS DE RANG A	18
PUBLICATIONS DE RANG B	23
CHAPITRE D'OUVRAGE	23
RAPPORTS ET MEMOIRES	24
COMMUNICATIONS INVITEES	25
COMMUNICATIONS	26
EXPERIENCES EXTRA-PROFESSIONNELLES	31
AFFILIATIONS SCIENTIFIQUES	31
LANGUES	31
SYNTHESE DES TRAVAUX DE RECHERCHE	33
RESEARCH SUMMARY	33
CHAPTER 1. INTRODUCTION	33
1.1 TRANSITIONAL WATERS ARE UNDER THREATS	33
1.2 THE ERA OF ENVIRONMENTAL BIOMONITORING	36
1.3 BIODIVERSITY TO MONITOR THE HEALTH OF TRANSITIONAL WATERS	38
1.4 BENTHIC FORAMINIFERA ARE PART OF THE SOLUTION	41
1.4.1 Foraminifera as indicator of pollution	41
1.4.1.1 At community level	41
1.4.1.2 At individual level	43

1.4.2 Role of benthic foraminifera in the benthic ecosystem functioning	44
1.4.2.1 A major trophic link?	44
1.4.2.2 A key element in fluxes at the sediment-water interface?	45
1.5 OUTLINE OF THE PRESENT THESIS	47
CHAPTER 2. WHAT CAN WE LEARN FROM ALPHA AND BETA DIVERSITY IN BENTHIC FORAMINIFERAL COMMUNITIES?	49
2.1 NATURAL FEATURES OF TRANSITIONAL WATERS CONSTRAIN BENTHIC FORAMINIFERAL COMMUNITIES	49
2.2 HUMAN ACTIVITIES ALTERED BENTHIC FORAMINIFERAL COMMUNITIES	54
2.3 THE USE OF FORAMINIFERAL ALPHA DIVERSITY IN ENVIRONMENTAL MONITORING	59
2.3.1 Ecological quality status assessment with benthic foraminifera	59
2.3.2 Comparison with benthic macrofauna	63
2.3.3 Reconstructing past-EcoQS with benthic foraminifera	64
CHAPTER 3. TOWARDS A BIOTIC INDEX BASED ON FORAMINIFERAL SPECIFIC RESPONSE TO POLLUTION	69
3.1 INDICATIVE VALUE OF BENTHIC FORAMINIFERAL SPECIES AS PROXY OF THE ENVIRONMENTAL CONDITIONS	70
3.2 DEVELOPING A SENSITIVE-BASED INDEX BASED ON BENTHIC FORAMINIFERA: FORAM-AMBI	77
CHAPTER 4. THE FUTURE OF FORAMINIFERAL RESEARCH: TACKLING DIVERSITY AT INDIVIDUAL LEVEL	85
4.1 TACKLING DIVERSITY AT CELLULAR LEVEL	85
4.2 TACKLING DIVERSITY THROUGH BEHAVIOR ASSESSMENT	89
4.2.1 High Inter-individual variability in motion-behavior	89
4.2.2 Motion-behavior is species-specific	91
4.2.3 Foraminifera showed typical behavior of stressed/unstressed organisms	92
4.3 TACKLING FUNCTIONAL DIVERSITY IN BENTHIC FORAMINIFERA	93
4.3 BENTHIC FORAMINIFERA: A PROMISING BIOASSAY?	98
4.3.1 Response to temperature	99
4.3.2 Response to plastic leachates	101
CHAPTER 5. ON WHAT I WOULD LIKE TO FOCUS ON OVER THE NEXT YEARS	103
5.1 TOWARDS IMPROVED BIOMONITORING WITH BENTHIC FORAMINIFERA	103
5.1.1 Getting foraminifera in observation networks	103
5.1.2 Foraminifera as a biological quality element	105
5.1.3 On the use of metabarcoding in biomonitoring	107
5.2 TOWARDS IMPROVED UNDERSTANDING OF BENTHIC FORAMINIFERAL FUNCTIONAL ROLE	109
5.2.1 Bioturbation	109
5.3 TOWARDS IMPROVED UNDERSTANDING OF THE EFFECT OF NEW GLOBAL STRESSORS (EXTREME EVENTS AND PLASTICS)	112
5.3.1 Plastic leachates	112
REFERENCES	117
RESUME	132
ABSTRACT	132

Avant-propos

J'ai réalisé ma thèse de doctorat en majorité au CREMA à L'Houmeau ainsi qu'en partie au LPG à Angers sous la direction de Pierre-Guy Sauriau et Jean-Pierre Debenay d'octobre 2003 à juin 2007. J'ai ensuite obtenu un post-doctorat au Département de Géosciences de l'Université d'Oslo (Norvège) pour travailler avec Elisabeth Alve de août 2008 à juillet 2012. Recruté en septembre 2012 au département Station Marine de l'Université de Lille, j'effectue mes activités de recherche au sein du Laboratoire d'Océanologie et de Géosciences à Wimereux (Pas-de-Calais). Hormis mon escapade norvégienne, j'ai pu effectuer mes recherches en France depuis des bâtiments en prise direct avec mes terrains de jeu i.e. l'ancien séminaire à L'Houmeau puis la station marine à Wimereux ; et surtout hors du tumulte des campus universitaires. C'est une vraie chance, et j'espère que cela pourra perdurer dans un contexte où l'avenir des stations marines dans le paysage de la recherche française est parfois menacé.

Mes thématiques de recherche ont évolué au gré des rencontres avec les chercheurs avec qui j'ai pu travailler. Pendant ma thèse de doctorat, Pierre-Guy et Jean-Pierre m'ont initié à l'écologie des communautés benthiques de macro-invertébrés et de foraminifères dans le contexte de l'ostréiculture en Charente-Maritime (un sujet qui me tenait particulièrement à cœur avec un papi ostréiculteur). Mon post-doctorat en Norvège m'a permis de me spécialiser sur les foraminifères benthiques, et j'ai pu élargir mes questionnements aux faunes fossiles, et ainsi de comprendre comment « getting back to the past » est important pour étudier les phénomènes actuels. Enfin, ma rencontre avec Laurent Seuront lors de mon arrivée au LOG a été déterminante pour faire évoluer mes questionnements de l'échelle de la communauté à l'échelle de l'individu. Il serait facile de dire aujourd'hui que je leurs dois tout. Je crois plutôt que j'ai eu la chance de rencontrer sur mon chemin des grands chercheurs derrière lesquels

se cachent des personnes aux qualités humaines indéniables. Pierre-Guy, Jean-Pierre et Elisabeth ont su m'accompagner au mieux, me donner les coups de pied aux fesses nécessaires, et surtout me mettre toutes les cartes en mains pour grandir à leur côté. Nous nous revoyons toujours avec plaisir, ce qui montre qu'au-delà de la science des liens ont pu se créer, et c'est la chose la plus importante à mes yeux. Finalement, je crois que ce processus de maturation est dépendant des 2 parties, certes il faut les bonnes personnes pour vous accompagner, mais il faut aussi à un moment donné tracer son sillon, se prendre en main et se donner les moyens d'atteindre ses objectifs. Qu'ils soient tous les 3 très sincèrement remerciés pour leur patience et leur investissement pour toutes ces années passées auprès d'eux. Enfin, Laurent Seuront est aujourd'hui un camarade de jeu privilégié doublé d'un ami, ce qui est un élément essentiel pour le plaisir de faire de la recherche ensemble. Ironiquement, notre histoire a commencé de manière assez originale, Laurent déclarant au cours d'une réunion à mon arrivée à Wimereux « Vincent, je ne te connais pas, mais peut être que tu es une raclure qui va coloniser l'espace recherche sans t'inquiéter de tes collègues », le ton était donné. Finalement, notre passion du ballon ovale et une certaine idée de comment faire de la science nous ont très vite rapproché. Peut-être le fait que je réponde à la plupart de ses questions sur les foraminifères par « on ne sait pas » a aussi contribué à éveiller sa curiosité pour ces petites bêtes. Son enthousiasme, son exigence et sa curiosité scientifique sont vraiment entraînant, encore merci pour notre première collaboration « Seuront & Bouchet 2015 », ce travail a été un vrai déclic pour lancer mon travail au LOG. Merci, surtout, de m'avoir initié à « *Good science is fun science* ». Je te remercie d'avoir accepté d'être le garant de ce travail.

Je souhaite aussi remercier le jury qui a accepté d'évaluer ce mémoire, Emmanuelle, Edouard, Sigal, Florian et Antoine. Il a été facile de constituer ce jury, entre collaborateurs

ponctuels et regards neufs, je sais que la discussion que nous aurons autour des orientations prises pendant mon parcours et mes idées pour le futur sera enrichissante.

La rédaction de ce manuscrit d'HDR permet aussi de regarder en arrière, et de repenser aux collègues qui ont jalonné ma carrière jusqu'à aujourd'hui. Je pense en particulier à Fabrizio Frontalini qui au fil des années est devenu un ami avec qui la collaboration est très suivie, toujours enrichissante, et surtout très libre dans notre fonctionnement. Mon voisin d'étage Nicolas Spilmont, même si nous collaborons peu, joue un rôle important dans mon quotidien au laboratoire, il sait comment désamorcer la bombe ambulante que je suis, et aussi me sensibiliser avec franchise quand je dépasse les limites, c'est important de pouvoir compter sur lui dans mes moments éruptifs (et dans les autres aussi bien sur). Je profite aussi de l'occasion pour remercier Florian Mermillod-Blondin, Christine Barras, Frans Jorissen, Bruce Hayward, Martin Langer, Olivier Maire, Eric Armynot du Châtelet, Eric Goberville, tous les étudiants avec qui j'ai pu travailler, mes collègues du SNO BenthOBS et tous les personnels techniques d'hier et d'aujourd'hui qui facilitent notre travail au jour le jour.

Je souhaite remercier les différents directeurs du LOG (François Schmitt puis Hubert Loisel) et de la station marine (Sébastien Lefebvre puis Lionel Denis). Comme tout enseignant-chercheur, la moitié de mon temps est dévoué à l'enseignement. Notre fonctionnement au département est très collectif, et je remercie les collègues de toujours jouer le jeu pour nous faciliter la vie à tous. Je remercie particulièrement Valérie Gentilhomme qui assume une grande partie des tâches administratives liées à l'enseignement, notre quotidien serait beaucoup plus compliqué si tu ne le faisais pas.

Enfin, les remerciements les plus importants. Merci à Clelia d'être Clelia, de nous donner chaque jour de la force, de nous montrer la voie, tu es une petite fille formidable, Papa et Maman ont de la chance de t'avoir. Merci à Federica d'être toujours à mes côtés, de subir

mes obsessions permanentes pour la recherche (week-end et jours fériés inclus), nous avons traversé quelques tempêtes, mais nous arrivons à garder le cap, à nous relever. Que cette force nous habite pour toujours, et je ne sais comment te dire à quel point je serai heureux que tu deviennes ma femme le 10 juin 2023. Ti amo tanto.

Je finirai cet avant-propos en dédiant ce travail à mes grands-parents (Jeannine, Marcel, Jacqueline et Pierre) et à Paolo qui nous a quitté bien trop tôt. Vous me manquez tous tellement.

Curriculum Vitae

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- 2003 **DEA Exploitation Durable des Ecosystèmes Littoraux** mention Bien, Université de La Rochelle
- 2002 **Maitrise de Biologie des Populations et des Ecosystèmes** mention Environnement, Université de La Rochelle
- 2001 **Licence de Biologie Marine**, Université de La Rochelle
- 1999 **DEUG Sciences de la Vie**, Université de La Rochelle
- 1997 **Baccalaureat Scientifique** (spécialité Mathématiques)

Expériences professionnelles

- Depuis Mai 2022** **Responsable de l'équipe INTEREST au LOG**
- Depuis Juin 2019** **Co-coordonateur du Service National d'Observation de la Macrofaune Benthique SNO BenthOBS** (*en incubation*), CNRS-Ifremer-Universités-MNHN
- Depuis Septembre 2012** **Maître de Conférences**, Université de Lille rattaché à l'UMR8187 CNRS-U. Lille-IRD-ULCO Laboratoire d'Océanologie et de Géosciences
- Août 2008-Janvier 2012** **Post-doctorat**, responsable : Pr. Elisabeth Alve, Department of Geosciences, University of Oslo, Norway
- Juillet 2007- Juin 2008** **Charge d'Etude CNRS**, ELA (CNRS, IFREMER), France
- Décembre 2003 – Juin 2007** **Thèse de doctorat**, Université d'Angers, co-direction : Dr Pierre-Guy Sauriau (CNRS) et Pr Jean-Pierre Debenay (Uni. Angers/IRD), CRELA (CNRS, IFREMER, Université de La Rochelle, France) : Dynamique et réponse fonctionnelle des foraminifères vivants et de la macrofaune benthique en zone ostréicole dans les pertuis charentais

Encadrement

Post-doctorant

- 2022 Dr Julien Richirt (avec Dr Laurent Seuront), Effet combiné de la température et des exudats de plastiques sur les foraminifères benthiques
- 2019-2020 Dr Dewi Langlet (avec Dr Laurent Seuront et Dr Lionel Denis), Rôle des foraminifères benthiques sur les flux dissous à l'interface eau-sédiment, Projet COFFEE STARS Région Hauts de France/FEDER

Doctorant

- 2020 – 2023 Camille Delaeter (avec Dr Laurent Seuront et Dr Nicolas Spilmont), Effect des exsudats de plastiques sur la faune intertidale : approche multi-organismes, Université de Lille, allocation Région Hauts-de-France-ULille
- 2019 - 2022 Jean-Charles Pavard (avec Dr Laurent Seuront), Développement d'un indice utilisant les foraminifères dans les milieu de transitions et les ports des Hauts de France et de Normandie, Université de Lille, allocation Agence de l'Eau Artois-Picardie-UL
- 2017 - 2020 Noémie Deldicq (avec Dr Grégory Beaugrand), Rôle fonctionnel des foraminifères benthiques : Approche par la bioturbation, Université de Lille, allocation UL1-Fonds propres
- 2013 - 2017 Fabio Francescangeli (avec Pr Alain Trenteseaux et Dr Eric Armynot du Châtelet), L'impact des changements globaux sur la biodiversité des environnements littoraux du Nord-Pas-de-Calais : approche par les foraminifères, Université Lille 1, allocation UL1-Région Nord-Pas-de-Calais

Master 2

- Février – Juillet 2020 Antoine Dubois, Impact des fermes d'élevage de poissons en Corse, Master 2 FOGEM, Université Lille
- Février – Juillet 2019 Jean-Charles Pavard, Communautés de foraminifères benthiques dans l'estuaire de la Gironde, Master 2 FOGEM, Université Lille
- Février – Juin 2019 Riccardo Riso, Les communautés de foraminifères benthiques des écosystèmes profonds de l'Aleutian Magic, Master 2 FOGEM, Université Lille
- Janvier-Juin 2017 Noémie Deldicq, "Historique de l'introduction de 2 espèces de foraminifères benthiques dans 2 écosystèmes différents : *Nonionella stella* dans le fjord d'Oslo (Norvège) et *Quinqueloculina carinatastriata* dans les pertuis charentais (France), Master 2 FOGEM, Université Lille1

Janvier-Juin 2013 Julien Richirt, "Les foraminifères benthiques : un nouvel outil pour déterminer les conditions de références", Master 2 FOGEM, Université Lille 1

Master 1

Avril-Juin 2022 Caroline Diotel (avec L. Seuront et N. Spilmont), Effet de la température sur le comportement cirral des balanes, Université de Lille

Avril-Mai 2022 Bastien Carnec (avec L. Seuront) , Effet des leachates de masques chirurgicaux sur le foraminifère *Haynesina germanica*, Université de Lille

Avril-Mai 2018 Margot Grimmelpont, Effet intra-cellulaire des nanoparticules sur le foraminifère benthique *Ammonia parkinsoniana*, Université de Lille

Avril-Mai 2018 Cassandre Depardé, Distribution vertical dans la colonne sédimentaire des foraminifères de la Baie d'Authie, Université de Lille

Avril-Mai 2018 Melvin Béatrix, Impact des fermes d'élevage de poissons en Corse, Université de Lille

Avril-Mai 2016 Noémie Deldicq, "Effets de la salmoniculture sur les peuplements de foraminifères benthiques dans la rade de Cherbourg (Cotentin, France)", Université Lille 1

Avril-Mai 2014 José Paulo DANTAS AZEVEDO, "Reconstruction des paléo-statuts écologiques des écosystèmes côtiers de la Côte d'Opale : exemple du port de Boulogne et de la Baie de Canche", Master 1, Université Lille 1

Avril-Juin 2006 Edith Bordage, "Influence des cultures de l'huître *Crassostrea gigas* sur la macrofaune benthique intertidale de Marennes-Oléron", Master 1 Systèmes écologiques, Université de Bordeaux I

Avril-Juin 2005 Julien Bernard, "Réponse structurelle des peuplements de la macrofaune benthique en présence des cultures ostréicoles", Master 1 Biologie des populations et des écosystèmes, Université de La Rochelle

Licence

Mai-Juin 2022 Louis Lanoy (avec L. Seuront), Effet des leachates de masques chirurgicaux sur le foraminifère introduit *Trochammina hadai*, Université de Paris-Saclay

Mai-Juin 2022 Alice Deiss, Effet d'un stress thermique sur le déploiement des pseudopodes chez le foraminifère *Haynesina germanica*, Université de Lille

Mai-Juin 2022 Louis Tailliez, Effet des leachates de billes plastiques sur le déploiement des pseudopodes chez le foraminifère *Haynesina germanica*, Université de Lille

Mai-Juin 2017 Margot Grimmelpont, Dynamique de population des foraminifères benthiques en Baie d'Authie, Université de Lille

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Licence Pro

Août 2021-Août 2022	Apolyne Courleux, Alternance, Soutien technique dans le cadre du projet Foram-INDIC, ULCO
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Projets de Recherche

2021-2022	Pollution by microplastics: spatial distribution and effects of leachates on the motion-behaviour of intertidal foraminifera, PHC Sakura (co-porteur), 12k€
2020-2022	HABISS : Habitats Intertidaux Benthiques Sensibles (participant), Office Français pour la Biodiversité, 400k€
2020	Les stress émergents chez les organismes intertidaux : approche par la protéomique, SFR Campus de la Mer (co-porteur), 2,5k€
2019-2022	Projet Foram-INDIC, Agence de l'eau Artois-Picardie et Agence de l'eau Seine-Normandie (porteur), 130 k€
2019-2020	Projet STARS Jeunes chercheurs d'Avenir, Région hauts de France (porteur) : COFFEE, 96k€
2015-2020	CPER CLIMIBIO (partenaire) : Changement Climatique, dynamique de l'atmosphère, impacts sur la biodiversité et la santé humaine
2015-2017	Projet IMPECAPE (partenaire) financé par l'Agence des Aires Marines Protégées : Evaluations des impacts écologiques engendrés par pressions physiques sur les habitats benthiques : cas de la pêche et de l'extraction
2015-2016	Projet EC2CO DRIL (partenaire) : AMTEP – Invasion récente d'un phylotype exotique du complexe d'espèces cryptiques <i>Ammonia tepida</i> (foraminifère benthique)
2014-2016	Projet ANR Blanc Benthival (partenaire) : Valorisation de la base de données Macrofaune benthique du RESOMAR : évaluation la dynamique spatio-temporelle des communautés benthique côtières et de l'État Écologique des habitats dans le cadre de la DCSMM et de la DCE
2013	Projet émergent IRePSE Université Lille 1 REFORAM (porteur) : Utilisation des foraminifères benthiques pour définir l'état de référence et le bon état écologique des habitats marins dans le cadre de la DCE et de la DCSMM

Expertises

Utilisation de la macrofaune benthique pour l'évaluation de la qualité des milieux marins côtiers et de l'impact des activités humaines.

2015 : La vulnérabilité aux pollutions marines des communautés de la macrofaune benthique dans la zone intertidale du Nord-Pas-de-Calais

2013 : Suivi des travaux d'implantation du terminal méthanier du Port de Dunkerque : caractérisation de l'état de santé des communautés de la macrofaune benthique du port de Dunkerque ouest

2012-2018 : Acquisition des données biologiques (invertébrés des sédiments meubles) dans le cadre du réseau de surveillance Reben-DCE Manche, en application de la D.C.E.

Formation continue : Taxonomie Macrofaune

- | | |
|-----------|--------------------------------------------------------------------------------------------------------------------------------|
| Juin 2017 | Atelier RESOMAR |
| Juin 2014 | Atelier RESOMAR : Annélides polychètes de la famille des Spionidae à la station Marine de Roscoff, expert : Vasily Radashevsky |
| Juin 2013 | Atelier RESOMAR : Annélides polychètes à élytres à l'Université de La Rochelle, expert : Ruth Barnish |
| Juin 2012 | Atelier RESOMAR : Micro-mollusques bivalves et gastéropodes à la station Marine de Wimereux, expert : Serge Gofas |

Financement et Prix Individuels

- | | |
|------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 2008 | Financement Post-doctoral (2008-2012) du Norwegian Research Council |
| 2006 | 1 ^{er} prix (1000 US \$) de la Cushman Foundation for Foraminiferal Research (Smithsonian Institution) pour le congrès FORAMS2006, septembre 2006, Natal, Brésil |
| 2003 | Bourse doctorale (2003-2006) de ANGERS Loire métropole |

Indicateurs du Rayonnement Scientifique

Données bibliographiques (Web of Science au 1 juillet 2022)

39 articles, 910 citations, h-index = 14

Expertise (organismes nationaux ou internationaux)

Je fais partie de différents groupes de travail au titre de mon expertise en écologie benthique, et je suis régulièrement sollicité pour évaluer des projets de recherche :

- Membre de l'atelier « Espèces Non Indigènes » de la **DCSMM** (Directive Cadre Stratégie pour le Milieu Marin)
- Membre du groupe de travail sur le milieu marin du **SDAGE Artois-Picardie** (DREAL-Agence de l'Eau Artois Picardie-Ifremer-DDTM-Parc naturel marin)
- Membre du **comité de Pilotage du Projet FORESTAT** (PI : F. Jorissen, U. Angers) financé par l'Agence Française pour la Biodiversité (2019-2022)
- Expert pour Austrian Science Fund, King Fahd University of Petroleum and Minerals, Icelandic Research Fund et pour la Région Bretagne appel à projet BIENVENÛE Call 2021 (H2020-MSCA-COFUND-2019)
- Expertise pour les demandes nationales de campagne en mer pour la Flotte Océanographique Française

Activités éditoriales (expertises, responsabilités de collections...)

J'ai **co-édité** avec la Dr Daniela Zeppili (Ifremer Brest) et le Dr Fabrizio Frontalini (Universita d'Urbino, Italie) **un numéro spécial de la revue Water** (Facteur d'impact : 3.10) intitulé « Ecological Quality Status Assessment of Aquatic Ecosystems: New Methods and Perspectives for the Future ».

Je suis relecteur **d'environ 40 articles pour des revues internationales** à comité de lecture :

Hydrobiologia, Marine Pollution Bulletin, Journal of Foraminiferal Research, Estuaries and Coasts, Marine Micropaleontology, Marine Ecology Progress Series, Aquaculture, Science of the Total Environment, Marine Environmental Research, Ecological Indicators, PlosOne, Estuarine, Coastal and Shelf Science, Limnology and Oceanography, Scientific Reports, Water, Frontiers in Marine Science.

Participation jurys de thèse et de HDR (hors établissement)

Hors établissement, j'ai participé à **deux jurys de thèse** (examineur) :

- Membre (examineur) du jury de thèse de J. Richirt, Université d'Angers. Le genre *Ammonia* (Foraminifères) dans les écosystèmes côtiers de la façade atlantique, soutenue le 2 septembre 2020

- Membre (examinateur) du jury de thèse de C. Choquel, Université d'Angers. Ecologie des foraminifères benthiques, interactions biologiques et géochimiques: approche pluridisciplinaire à différentes échelles, soutenue le 9 juillet 2021.

Organisation colloques, conférences, journées d'étude

- J'ai **co-organisé deux workshops internationaux** :

"Third Foraminiferal Biomonitoring Working group workshop" (1 semaine en Juillet 2013, Wimereux, France) avec Dr Eric Armynot du Châtelet (LOG)

"A new threat for marine environments and foraminifera: micro- and nano- plastics" (1 journée en Juillet 2019, Université de Fribourg, Suisse) avec Dr Hidetaka Nomaki (JAMSTEC, Japon), Dr *Masashi Tsuchiya* (JAMSTEC, Japon) et Dr Dewi Langlet (LOG)

- J'ai **organisé une session dans un congrès international** :

Co-animateur de la session « Milieux littoraux Holocènes : quels outils pour affiner les reconstitutions paléoenvironnementales et les chronologies très haute résolution ? », colloque internationale Q11, 13-15 février 2018, Orléans, France

- J'ai participé à l'organisation d'un colloque national :

Membre de l'organisation du colloque national RESOMAR au LOG à Wimereux (21-23 novembre 2016)

- J'ai organisé une session dans un congrès national :

Organisateur et Modérateur de la session « Ecologie benthique » lors du colloque RESOMAR au LOG à Wimereux (23 novembre 2016)

Participation à un réseau de recherche, invitations dans des universités étrangères

Depuis le début de ma carrière, j'ai pu donner **8 conférences invitées** (voir liste en annexe).

Depuis ma prise de fonction à l'Université de Lille, je participe activement aux travaux du groupe des benthologues des laboratoires et stations marines françaises, d'abord au sein du **RESOMAR** puis maintenant au sein d'**ILICO**. Cela m'amène à **co-porter depuis 2019 la création d'un service national d'observation de la macrofaune benthique** dont je suis *de facto* le co-coordonateur. D'autre part, j'ai participé à 2 projets (ANR et OFB, valorisé dans 11) dans la cadre de ce réseau ainsi qu'au dépôt de projets de recherche (EC2CO, PPR Océan et Climat).

Au niveau international, depuis 2018, je suis membre du bureau du **groupe de travail « FOBIMO-Foraminiferal Bio-Monitoring »** avec mes collègues Dr M. Martinez-Colon (U. Floride, USA), Dr I. Polovodova-Asteman (U. Göteborg, Suède), Dr S. Hess (U. Oslo, Norvège) and Dr O. Hyams-Kaphzan (Geological Survey Of Israël, Israël). Cela m'a amené à co-porter une demande COST (non financée) avec mes collègues Dr. Polovodova-Asteman et Dr Hyams-Kaphzan. Ce travail a donné lieu à 2 publications (29, 31).

Enfin, j'ai été invité à donner des **séminaires dans des universités étrangères** (Université de Genève, Suisse-février 2020, Université de Göteborg, Suède-reporté à juin 2022 à cause du Covid). D'autre part, j'ai été **invité au colloque BIOFOM** qui a eu lieu à l'Université de **Sao Paulo, Brésil** du 13 au 15 mai 2019 (i) en tant qu'expert pour accompagner les collègues brésiliens sur l'utilisation des foraminifères pour les études d'impact et (ii) pour donner une keynote. Ce travail se poursuit avec l'organisation d'une semaine de travail (financement interne LOG dotation IRD) organisée à Wimereux en décembre 2021 avec Dr S. Sousa (U. Sao Paulo, Brésil), Dr V. Martins (U. Rio de Janeiro, Brésil), Dr F. Francescangeli (U. Fribourg, Suisse), Dr F. Frontalini (U. Urbino, Italie), J.-C. Pavard (LOG, thésard) et Dr E. Armynot du Châtelet (LOG). Ces échanges avec les collègues brésiliens ont donné lieu à 6 publications (21, 27, 29, 31, 38 et 1 en révision).

Responsabilités Collectives et Administratives

Présentation synthétique des responsabilités

Depuis mon recrutement, je me suis présenté comme candidat à différents mandats électifs au conseil de composante et de laboratoire. J'ai été enfin élu en 2018 au conseil de département de la Station Marine de Wimereux (réélu en 2022). J'ai auparavant été nommé suite à ma candidature au comité local d'évaluation du navire de station SEPIA II (depuis 2016). Ces différentes activités me permettent de mieux comprendre le fonctionnement des institutions ainsi que les contraintes des collègues lors de leurs embarquements. J'ai aussi été pendant 3 ans (2019-2021) le responsable des séminaires de LOG avec pas moins de 75 séminaires organisés pendant cette période. Cet investissement local m'a poussé à prendre des responsabilités au niveau national en tant que co-coordonateur du service national d'observation de la macrofaune benthique BenthOBS (en incubation) au sein de l'IR ILICO. J'occupe cette fonction depuis juin 2019 ce qui m'amène à faire partie du bureau fédéral de l'IR ILICO.

Responsabilités administratives

Je suis depuis juin 2019 le **co-coordonateur national du SNO BenthOBS**, je réalise cette mission avec N. Desroy (Ifremer, Dinard). Il regroupe 10 laboratoires métropolitaines et 1 laboratoire ultra-marin sur l'île de La Réunion. Le réseau est constitué d'environ 50-60 personnels des différents corps des laboratoires de recherche. C'est un vrai challenge qui nous est offert que d'obtenir la labélisation de ce réseau par le CNRS-INSU ; cela demande un effort d'homogénéisation de nos pratiques et de rigueur dans nos suivis pour assurer la pérennité de ce réseau d'observation du compartiment benthique à ce jour manquant dans le paysage de l'IR ILICO.

Je suis aussi depuis mai 2022 le **responsable de l'équipe INTEREST au LOG**.

Responsabilités et mandats locaux ou régionaux

Participation aux conseils de composantes, de laboratoires

- Depuis 2018 : Membre élu pour le collège « Maître de Conférence et assimilés » au Conseil de département Station Marine de Wimereux de l'Université de Lille
- Depuis 2018 : Représentant pour le collège « Maître de Conférence et assimilés » du département Station Marine de Wimereux de l'Université de Lille à la commission mixte formation/recherche avec le laboratoire LOG

Autres

- Depuis 2016 : Membre nommé au comité local d'évaluation du navire de station SEPIA II
- 2019-2021 : Responsable des séminaires au LOG

Activités d'Enseignement

Le tableau ci-après correspond aux enseignements qui auraient dû être faits en 2020-2021 sans Covid (les volumes horaires peuvent varier à la marge en fonction des effectifs). Comme l'ensemble de mes collègues du Département Station Marine de Wimereux je dispose d'une décharge horaire d'environ 15h pour compenser le temps passé dans les allers-retours entre Wimereux et Lille (300 kms AR).

Diplôme	Année	UE	Type de formation	Effectif approximatif	CM/TD	TD	TP	Jury de stage
Licence SV	L2	Biostatistiques 1	Initiale, présentielle	70	0	24	14	
Licence SV	L2	Biostatistiques 2	Initiale, présentielle	70	0	15	8	
Licence BOP	L3	Faune et Flore Marine 1	Initiale, présentielle	130	0	10	80	
Licence BOP	L3	Faune et Flore Marine 2	Initiale, présentielle	130	0	0	35	
Licence BOP	L3	Insertion professionnelle	Initiale, présentielle	30	0	0	0	12
Master BEE	M1	Ecosystèmes Marins	Initiale, présentielle	50	0	0	10	
Master BEE	M1	Stage de recherche	Initiale, présentielle	10	0	0	0	8.5
Master BEE	M2 FOGEM	Atelier Indicateur	Initiale, présentielle	15	0	4	0	
Master BEE	M2 FOGEM	Atelier Mesures des processus e	Initiale, présentielle	5	0	2	3	
Master BEE	M2 FOGEM	Impact Anthropiques	Initiale, présentielle	10	2	1	0	
Master BEE	M2 FOGEM	Interactions et Processus	Initiale, présentielle	7	2	1	0	
DEUST GNM	DEUST	Biologie et Ecologie	Initiale, présentielle	15	2	0	0	
Total					6	57	150	20.5

Je suis responsable de l'EC Atelier Indicateurs du M2 FOGEM (dans l'UE Ateliers dont je suis aussi responsable) qui est suivie par environ une quinzaine d'étudiant chaque année.

Publications

En révision

- i. Ash-Mor A., Almogi-Labin A., **Bouchet V.M.P.**, Seuront L., Guy-Haim T., Ben-Avraham Z., Bookman R. Reply to a comment by John J.G. Reijmer (*Sedimentology*, 69, 1231-1251) on the paper 'Going with the flow: Experimental simulation of sediment transport from a foraminifera perspective' by Ash-Mor et al. (2022). *Submitted to Sedimentology*
- ii. Deldicq N., Mermillod-Blondin F., **Bouchet V.M.P.** Sediment mixing of intertidal sediments by the benthic foraminifera *Haynesina germanica*. The importance of motion behaviour and densities. *Submitted to Proceedings of the Royal Society B*
- iii. **Bouchet V.M.P.**, Seuront L., Tsujimoto A., Delaeter C., Spilmont N., Richirt J., Frontalini F., Tsuchiya M., Matsuba M., Nomaki H. Benthic foraminifera as the missing link to understand the effect of plastic pollution on blue carbon ecosystems. *Submitted to Environmental Science and Technology*
- iv. Nunes M., Alves Martins M.V., Frontalini F., **Bouchet V.M.P.**, Francescangeli F., Hohenegger J., Figueira R., Senez-Mello T.M., Fernanda W, Castelo L., Damasceno F.L., Laut L., Duleba W., Sousa S.H.d.M., Antonioli L., Geraldés M.C. Inferring the ecological quality status (EcoQS) based on benthic foraminiferal indices in the marginal areas of the Guanabara Bay (SE Brazil). *Submitted to Environmental Pollution*

Publications de Rang A

(Le nom des étudiants et post-doctorants est souligné)

- [43] Seuront L., **Bouchet V.M.P.**, Delaeter C., Henry S., Nicastro K., Spilmont N., Uguen M., Zardi G., 2022. A whale of a plastic tale: a plea for interdisciplinary studies to tackle micro- and nano-plastics pollution in the marine realm. *Science of the Total Environment*. (F.I. 7.96)
- [42] da Silva L.C., Alves Martin V.M., Figueira R., Frontalini F., Pereira E., Senez-Mello T.M., Castelo W.F.L., Saibro M.B., Francescangeli F., Sousa S.H.M., Bergamaschi S., Antonioli L., **Bouchet V.M.P.**, Terroso D., Rocha F., 2022. Unraveling the Anthropocene paleoenvironmental conditions combining sediment and foraminiferal data: proof-of-

- concept in the Sepetiba Bay (SE, Brazil). *Frontiers in Ecology and Evolution*, 10:852439. (F.I. 4.17)
- [41] Delaeter C., Spilmont N., **Bouchet V.M.P.**, Seuront L., 2022. Plastic leachates: bridging the gap between a conspicuous pollution and its pernicious effects on marine life. *Science of the Total Environment*, 826:154091. (F.I. 7.96)
- [40] Dauvin J.-C., Gofas S., Raoux A., **Bouchet V.M.P.**, Pavard J.-C., Pezy J.-P., 2022. The American protobranch bivalve *Yoldia limatula* (Say, 1831) in European waters. *BiolInvasions Records*, 11:473-481. (F.I. 1.61)
- [39] Ash-Mor A., Almogi-Labin A., **Bouchet V.M.P.**, Seuront L., Guy-Haim T., Ben-Avraham Z., Bookman R., 2022. Going with the flow: Experimental simulation of sediment transport from a foraminifera perspective. *Sedimentology*, 69:1231-1251. (F.I. 4.15)
- [38] Castelo W.F.L., Martins M.V.A., Martinez-Colon M., Nascimento I.C.d., Silva L.C.d., Menezes C., Oliveira T., Sousa S.H.M., Aguilera O., Laut V., Laut L., Duleba W., Frontalini F., **Bouchet V.M.P.**, Armynot du Châtelet E., Francescangeli F., Geraldés M.C., Reis A.T.d., Bergamashi S., 2022. Bioaccumulation of potentially toxic elements in *Ammonia tepida* (foraminifera) from a polluted coastal area. *Journal of South American Earth Sciences*, 115:103741. (F.I. 2.09)
- [37] Pavard J.-C., Richirt J., Courcot L., Bouchet P., Seuront L., **Bouchet V.M.P.**, 2021. Fast and reliable identification of *Ammonia* phylotypes T1, T2 and T6 using a stereomicroscope: implication for large-scale ecological surveys and monitoring programs. *Water*, 13:3563. (F.I. 3.10)
- [36] Dubois A., Barras C., Pavard J.-C., Donnay A., Beatrix M., **Bouchet V.M.P.**, 2021. Distribution patterns of benthic foraminifera in fish farming areas (Corsica, France): implications for the implementation of biotic indices in biomonitoring studies. *Water*, 13:2821. (F.I. 3.10)
- [35] O'Brien P., Polovodova Asteman I., **Bouchet V.M.P.**, 2021. Benthic foraminiferal indices and environmental quality assessment of transitional waters: a review of current challenges and future research perspectives. *Water*, 13:1898. (F.I. 3.10)
- [34] Deldicq N., Seuront L., **Bouchet V.M.P.**, 2021. Inter-specific and inter-individual trait variability drive the contribution of intertidal benthic foraminifera to surface sediment reworking. *Marine Biology*, 168: 101. (F.I. 2.57)
- [33] Cavaliere M., Barrenechea I., Montresor M., Bucci C., Brociani L., Balassi E., Margiotta F., Francescangeli F., **Bouchet V.M.P.**, Pawlowski J., Frontalini F., 2021. Assessing the Ecological Quality Status in the highly polluted Bagnoli area (Tyrrhenian Sea, Italy) using foraminiferal eDNA metabarcoding. *Science of The Total Environment*, 790: 147871. (F.I. 7.96)

- [32] Richirt J., Schweizer M., Mouret A., Quinchard S., Saad S.A., **Bouchet V.M.P.**, Wade C.M., Jorissen F.J, 2021. Biogeographic distribution of three phylotypes (T1, T2 and T6) of *Ammonia* (Foraminifera, Rhizaria) around Great Britain: new insights using a combination of molecular and morphological recognition. *Journal of Micropaleontology*, 40:61-74. (F.I. 1.67)
- [31] **Bouchet V.M.P.**, Frontalini F., Francescangeli F., Sauriau P.-G., Geslin E., Martins M.V.A., Almogi-Labin A., Avnaim-Katav S., Di Bella L., Cearreta A., Coccioni R., Costelloe A., Dimiza M.D., Ferraro L., Haynaert K., Martinez-Colon M., Melis R., Schweizer M., Triantaphyllou M., Tsujimoto A., Wilson B., Armynot du Châtelet E, 2021. Relative abundances of benthic foraminifera in response to total organic carbon in sediments: Data from European intertidal areas and transitional waters. *Data-In-Brief*, 35:106920.
- [30] Deldicq N., Langlet D., Delaeter C., Beaugrand G., Seuront L., **Bouchet V.M.P.**, 2021. Effects of temperature on the behaviour and metabolism of an intertidal foraminifera and consequences for benthic ecosystem functioning. *Scientific Reports*, 11:4013. (F.I. 4.38)
- [29] **Bouchet V.M.P.**, Frontalini F., Francescangeli F., Sauriau P.-G., Geslin E., Martins M.V.A., Almogi-Labin A., Avnaim-Katav S., Di Bella L., Cearreta A., Coccioni R., Costelloe A., Dimiza M.D., Ferraro L., Haynert K., Martinez-Colon M., Melis R., Schweizer M., Triantaphyllou M., Tsujimoto A., Wilson B., Armynot du Châtelet E., 2021. Indicative value of benthic foraminifera for biomonitoring: assignment to ecological groups of sensibility to total organic carbon of species from European intertidal areas and transitional waters. *Marine Pollution Bulletin*, 164:112071. (F.I. 5.55)
- [28] Langlet D., **Bouchet V.M.P.**, Riso R., Matsui Y., Suga H., Fujiwara Y, Nomaki H, 2020. Foraminiferal ecology and role in nitrogen benthic cycle in the hypoxic southeastern Bering Sea. *Frontiers in Marine Science*, 7:582818. (F.I. 4.91)
- [27] Jesus S.d.S.M., Frontalini F., **Bouchet V.M.P.**, Yamashita C., Sartoretto J.R., Figueira R.C.L., Sousa S.H.D.M, 2020. Reconstruction of paleo-ecological quality statuses in an anthropogenised estuary using benthic foraminifera: the Santos estuary (Sao Paulo State, SE Brazil). *Marine Environmental Research*, 162:105121. (F.I. 3.13)
- [26] **Bouchet V.M.P.**, Deldicq N., Baux N., Dauvin J.-C., Pezy J.-P., Seuront L. and Méar Y, 2020. Benthic foraminifera to assess ecological quality statuses: the case of salmon fish farming. *Ecological Indicators*, Special Issue SeventyIMCO, the 17th International Meiofauna Conference: Meiofauna in a changing world, 117:106607. (F.I. 4.96)
- [25] Francescangeli F., Quijada M., Armynot du Châtelet E., Frontalini F., Trentesaux A., Billon G., **Bouchet V.M.P.**, 2020. Multidisciplinary study to monitor consequences of pollution on intertidal benthic ecosystems (Hauts de France, English Channel, France): comparison with natural areas. *Marine Environmental Research*, 160:105034. (F.I. 3.13)

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- [20] C. Ciacci, M.V. Grimmelont , I. Corsi , E. Bergami , D. Curzi , D. Burini , **V.M.P. Bouchet** , P. Ambrogini , P. Gobbi , Y. Ujjié , Y. Ishitani , R. Coccioni , J.M. Bernhard and F. Frontalini, 2019. Nanoparticle-Biological Interactions in a Marine Microbial Eukaryote. *Scientific Reports*, 9:19441. (F.I. 4.38)
- [19] Deldicq N., Alve E., Schweizer M., Polovodova-Asteman I., Hess S., Darling K. and **Bouchet V.M.P.**, 2019. History of the introduction of a species resembling *Nonionella stella* in the Oslofjord (Norway): morphological, molecular and paleo-ecological evidences. *Aquatic Invasions*, 14:182-205. (F.I. 2.17)
- [18] Melis R., Celio M., **Bouchet V.M.P.**, Varagona G., Bazzaro M., Crosera M. and Pugliese N., 2019. Response of benthic foraminifera to anthropogenic pressure in the Gulf of Trieste (northern Adriatic Sea): the marine protected area of Miramare versus the Servola water sewage outfall. *Mediterranean Marine Science*, 20:120-141. (F.I. 2.31)
- [17] Richirt J., Schweizer M., **Bouchet V.M.P.**, Mouret A., Quinchard S. and Jorissen F., 2019. Morphological distinction of three *Ammonia* phylotypes occurring along the European coasts. *Journal of Foraminiferal Research*, 49:77-94. (F.I. 1.15)
- [16] Alve E., Hess S., **Bouchet V.M.P.**, Dolven J. and Rygg B., 2019. Intercalibrating biotic indices based on benthic foraminifera and macro-invertebrates: an example from the Norwegian Skagerrak coast (NE North Sea). *Ecological Indicators*, 96:107-115. (F.I. 4.96)
- [15] Francescangeli F., Portela M., Armynot du Châtelet E., Billon G., Andersen T.J., **Bouchet V.M.P.** and Trentesaux A., 2018. Infilling of the Canche estuary (Eastern English

- Channel, France): insight from benthic foraminifera and historical pictures. *Marine Micropaleontology*, 142:1-12. (F.I. 2.41)
- [14] **Bouchet V.M.P.**, Telford R.J., Rygg B., Oug E. and Alve E. 2018. Can benthic foraminifera serve as proxies for changes in benthic macrofaunal community structure? Implications for the definition of reference conditions. *Marine Environmental Research*, 137:24-36. (F.I. 3.13)
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Expériences Extra-Professionnelles

- | | |
|-----------|--------------------------------------------------------------------------------------------------------------------|
| 2012 | Formateur d'arbitre de rugby (cours théoriques et pratiques) pour la Fédération Européenne de Rugby (Rugby Europe) |
| 2007 | Arbitre Fédéral de Rugby classé en 2ème Division Fédérale |
| 1986-1995 | Joueur de Rugby à l'US Saujon Rugby |

Affiliations Scientifiques

- | | |
|-------------|-------------------------------------------------------------|
| Depuis 2013 | Membre du Benthic Ecology Working Group de l'ICES |
| Depuis 2004 | Membre de the Cushman Foundation for Foraminiferal Research |

Langues

- | | |
|-----------|---------------------------|
| Français | Langue maternelle |
| Anglais | Bilingue (parlé et écrit) |
| Italien | Courant |
| Norvégien | Notions |
| Espagnol | Notions |

Synthèse des travaux de recherche

Research summary

Chapter 1. Introduction

1.1 Transitional waters are under threats

Intertidal and transitional waters (hereafter TWs; see definition in McLusky and Elliott 2007), situated at the interface between marine and terrestrial ecosystems, are under the influence of both marine and fresh water inputs. These ecotones at the land-sea transition are some of the most productive ecosystems globally (Camacho-Valdez et al. 2013). Representing at least 13% of the world's coastline (Nixon 1982), they provide human societies with a range of ecosystem goods and services. Noticeably, coastal areas exhibit high capacity to capture and store high amounts of carbon in their sediments over long time periods (Duarte et al. 2013; Fig. 1). In this context, European tidal marshes are identified as major blue carbon hotspots (Sousa et al. 2017, Sousa et al. 2019). They have an important ecological value; providing habitat and food resources for migratory birds (Degré et al. 2006) and nursery habitats for juvenile specimens of fish species of high commercial value (e.g., eels, flatfishes; Beck et al. 2001, Couturier et al. 2007).

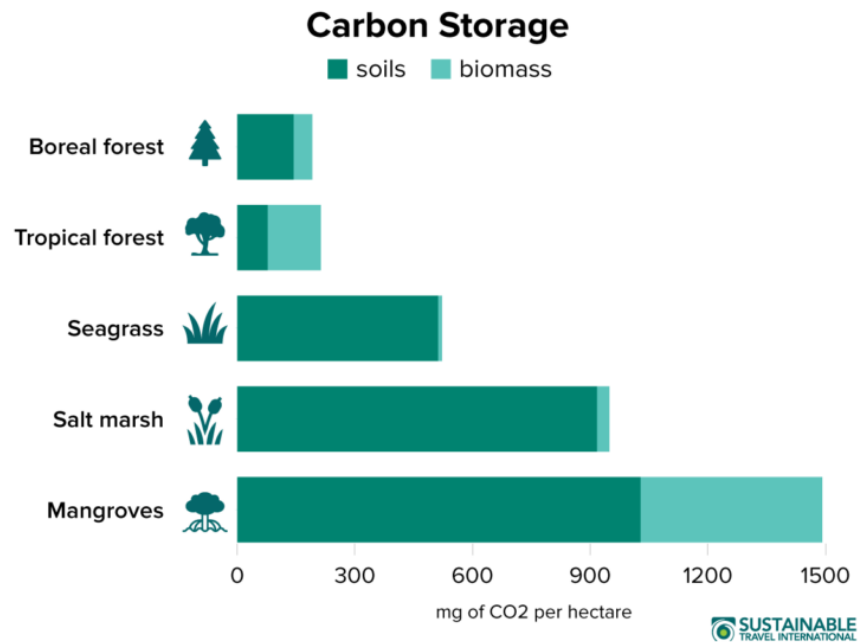


Figure 1. Blue carbon storage (mg of CO₂ per hectare) in continental and coastal ecosystems (source: <https://sustainabletravel.org/what-is-blue-carbon/>)

Noticeably, transitional waters, particularly tidal marsh sediments, commonly exhibit very high total organic carbon (TOC) values, due to the halophile vegetation, responsible for the presence of large quantities of poorly reactive organic matter (Middelburg et al. 1997, Arminot du Châtelet et al. 2009, Leorri et al. 2018). The sediment is composed of a mixture of refractory and labile organic matter (Pusceddu et al. 2009). The labile (food) directly stimulates growth and reproduction, while the refractory (terrestrial origin) TOC is not directly bioavailable (Pusceddu et al. 2009). Furthermore, benthic organisms are more likely to be exposed to extreme temperature events due to the succession of emersion/immersion period depending on the tide. Noticeably, in temperate ecosystems, surface intertidal soft-sediment temperature can frequently reach up to 30°C (Harley et al. 2006) and sometimes even 40°C during summer at low tide (Garrabou et al. 2009, Caputi et al. 2016, Caputi et al. 2019) during spring and summer. Consequently, intertidal species are adapted to a broader thermal range than their subtidal counterparts (Murphy and Reidenbach 2016, Seuront et al. 2019).

However, these organisms often live close to the upper limit of their thermal tolerance window, which make them particularly sensitive to thermal stress (Li et al. 2019). A major factor of the variability of these processes is the amplitude of the tide. In hyper tidal estuaries, tidal range leads marshes to be extremely dynamic and instable areas. In north European estuaries, salt marshes are not covered by the tide every day, but only periodically during spring high tides. Hence, environmental conditions encountered at low tide (*e.g.*, aerial exposure, low salinity, thermal stress) (Alve and Murray 1999), as well as seasonal changes (*e.g.*, desiccation or increased salinity during the dry season), further constrain benthic species (De Rijk and Troelstra 1997, Alve and Murray 1999, Reiss and Kröncke 2005, Zettler et al. 2007, Zettler et al. 2013). Hence, the succession of emersion and immersion in intertidal areas naturally generate quite a number of stressors (Dauvin 2007, Elliott and Quintino 2007) which effects on the living fauna became exacerbated over the last decades due to global changes.

Transitional waters are also exposed to high levels of anthropogenic stresses such as aquaculture, habitat destruction (*e.g.*, agricultural occupation, coastal reinforcements), urban sewage and industrial discharges (Armynot du Châtelet et al. 2004, Morvan et al. 2004). Despite the crucial ecological role of these habitats, anthropogenic pressure has drastically increased in those blue carbon ecosystems. This jeopardizes their health and stability through pollution and eutrophication, which provoke drastic spreading of dead zones and massive loss of species affecting ecosystem functioning (Solan et al. 2004). Benthic species distribution in these environments are the results of the interplay between natural and human-induced stressors. In the context of global changes due to natural changes, pollution and global warming, transitional waters are of particular interest, specifically intertidal areas.

1.2 The era of environmental biomonitoring

To protect and restore these fragile ecosystems, many nations have enacted legislations such as, for instance, the Clean Water Act (CWA) or Oceans Act in the USA, Australia or Canada, the Water Framework Directive (WFD, 2000/60/EC) and the Marine Strategic Framework Directive (MSFD, 2008/56/EC) in Europe. In fact, the term “transitional waters” first came to prominence in 2000 with the publication of the Water Framework Directive of the European Communities (WFD, 2000/60/EC) with the aim to cover the continuum from fresh-, brackish to coastal sea-waters. In the WFD, TWs are defined as « *bodies of surface water in the vicinity of river mouths which are partially saline in character as a result of their proximity to coastal waters but which are substantially influenced by freshwater flows* » (European Communities 2000, p.6). In the Mediterranean Sea, TWs also include mesohaline, poly-euhaline and hyperhaline lagoons (Reizopoulou et al. 2018). The term “transitional waters” is thus intended as a simple term that can encompass all these habitats, most commonly tidal estuaries and non-tidal brackish/marine lagoons, and might be easily understood by legislators in all countries.

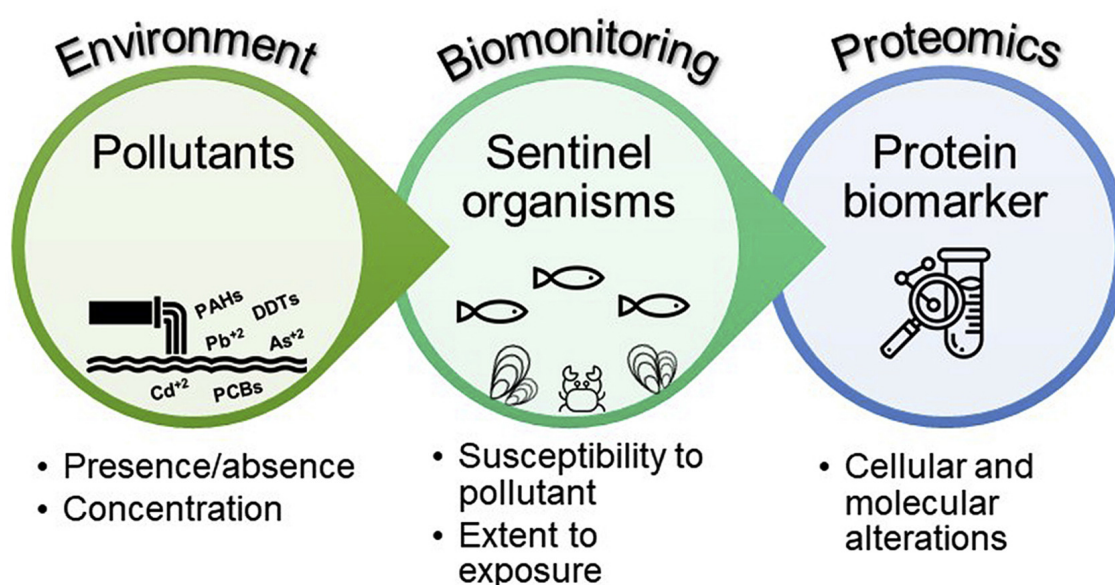


Figure 2. Possible workflow process in biomonitoring studies (adapted from Lopez-Pedrouso et al., 2020)

The implementation of these marine legislations worldwide is generating a fruitful debate amongst marine scientists about how to define and implement efficient and reliable bio-assessment tools (Fig. 2). A plethora of methodologies and tools, based on benthic macrofauna (Borja et al. 2000), seagrasses (Krause-Jensen et al. 2005), fishes (Coates et al. 2007) and, more recently, on benthic foraminifera (Alve et al. 2009), have been suggested in this sense. Noticeably, benthic macrofauna is the most widely biological element used to assess Ecological Quality Status (EcoQS) in marine environments (Dauvin et al. 2012). However, in a review paper, Spilmont (2013) noticed that the endless development of new biotic indices based on different biological groups « *contribute to the current indicator inundation that sometimes leads to awkward situations when the index values are much more difficult to determine than the environmental factor it is supposed to be representative of* ». Although raising interesting questions to be tackled, this somehow provocative statement is rather a shortcut. Noticeably, what is meant to be important should be the indicative value of the chosen biological group or species and not the ease or the complexity that leads to the index value. It would be true to say that direct indicators like measuring concentrations of trace metals in sediments is quicker and easier to implement than assessing the state of the associated benthic macro-invertebrates or meiöfaunal community *i.e.* indirect indicators. In fact, we end up with two different and complementary informations. Specifically, measuring concentrations informs about the presence/absence of a pollutant, and contribute to further assess the level of the pollution. However, this direct indicator does not provide any evidence on the potential threat for living organisms. Conversely, indirect indicators like biotic indices give an assessment of the health of the community, hence on the possible harmful effects of the pollution; and it further monitor the ecological quality status defined as the biological

quality of surface waters in the WFD. It nevertheless does not give any indication on the source of the pressure. Direct indicators and indirect indicators like biotic indices are hence relevant and complementary tools to meet the objectives of current marine legislations in the applied science realm. In fact, the main weaknesses of biotic indices are not necessarily that they may be more difficult to calculate than a simple concentration of a contaminant, but it is that *“the current indicator inundation”* leads to significant redundancy between indices; feeding the need for recognition of their authors.

1.3 Biodiversity to monitor the health of transitional waters

Following marine legislations, biodiversity is one of the parameters meant to be monitored in order to characterize the ecological status. Unfortunately, most methods used to assess the health of benthic ecosystems in the context of the WFD and MSFD are solely based on species richness of a site or an ecosystem; which is a highly simplified view of biodiversity. In fact, biological diversity means *“the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems”* (Rio convention on biodiversity, article 2, 1992). Hooper et al. (2005) further stated *“The term biodiversity encompasses a broad spectrum of biotic scales, from genetic variation within species to biome distribution on the planet... Biodiversity can be described in terms of numbers of entities (how many genotypes, species, or ecosystems), the evenness of their distribution, the differences in their functional traits, and their interactions”*. In this context, the conclusion of Spilmont (2013) in his review on current biotic indices perfectly makes sense when he claimed that *“new benthic indicators are needed and should*

be developed based on the functioning of the ecosystem rather than on community composition". Behavior, metabolism and isotopic composition are also relevant proxies of environmental conditions and can serve to detect any changes in the environment, either of natural or of anthropogenic origin. To summarise, there are endless ways to monitor biodiversity; offering new potential indicators to be tested and implemented to assess the health of benthic ecosystems.

In order to correctly assess biodiversity, it is then crucial to estimate (i) how much diversity an ecosystem can host, and (ii) how the natural features of a habitat constrain diversity. Characterizing and understanding the natural framework in which an ecosystem and the associated biodiversity was established and structured is a mandatory step in order to evaluate the potential of human induced changes. In short, it is important to determine how much diversity can be expected under pristine conditions in this habitat. In the context of environmental monitoring, the state of an ecosystem, called the ecological quality status, is something relative to reference conditions *i.e.* pristine conditions.

This is a crucial point in the European Water Framework Directive, reference conditions (*i.e.* a pristine, unpolluted, or anthropogenically undisturbed state; Hughes 1995, Davies and Jackson 2006) are mandatory to assess the EcoQS, and the Marine Strategic Framework Directive asking to set ecological targets in order to reach the good ecological status (GES). According to the WFD, the reference conditions (also called "high" status) are defined as *"for any surface water body type reference conditions or high ecological status is a state in the present or in the past where there are no, or only very minor, changes to the values of the hydromorphological, physico-chemical, and biological quality elements which would be found in the absence of anthropogenic disturbance"* (Common implementation strategy for the Water Framework Directive (2000/60/EC), Guidance Document No.5, transitional and

coastal waters typology, reference conditions and classification systems p. 106). Assessment of environmental quality is based on the extent of deviation from these reference conditions, following the definitions in the WFD (www.ec.europa.eu/environment/water/marine.htm). Most of the coastal areas are being modified or have been modified by human activities (Diaz and Rosenberg 2008). Hence, EcoQS assessment within the WFD is facing issues to determine true reference condition (Nielsen et al. 2003, Elliott and Quintino 2007). The WFD and the MSFD identify four options to define reference conditions or to set targets: (i) a comparison with a pristine/undisturbed area, (ii) using historical data, (iii) performing modelling approaches or (iv) using expert judgment (Muxika et al. 2007). The assessment of the EcoQS or the GES of a site is based on the comparison between a value, calculated from any index, and a given reference which corresponds to the value of the index in the absence of any pollution: the closer to the reference, the better the EcoQS or the ES. Setting “true” or “reliable” reference conditions/targets is therefore crucial (Borja et al. 2012), although each option has its own strengths and weaknesses (Borja et al. 2012). Although the use of pristine or minimally impacted area is often recommended to define reference conditions (Borja et al. 2012), it is a conundrum to characterize pristine areas in coastal systems as most of these regions are already under the influence of human activities (Diaz and Rosenberg 2008). An alternative is to estimate an acceptable level of disturbance to represent an achievable reference condition, *e.g.* set in relation to what is considered to be unimpacted or minimally impacted condition within sites or similar ecosystems where human pressures are negligible. Such reference would not equally mirror the pristine conditions; in fact, they considered a level of human-induced disturbances which do not affect the health of benthic ecosystems. In order to be implemented, such approach needs inputs from best expert knowledge in defining acceptable levels of human pressures (Borja et al. 2012). In turn, hindcasting *i.e.* the use of

historical information, is often considered the least adequate method to define reference conditions (Borja et al. 2012). This is because, for most areas, there are no long-term survey data available from pre-impact times to use as reference conditions, and with which to compare the current EcoQS. However, biological groups with fairly good fossilisable capacities (e.g., foraminifera, diatoms), could be used in hindcasting. Several authors indeed showed that the fossil record has great potential to reconstruct palaeoecological quality status (PalaeoEcoQS) and thereby establish *in situ* historical reference conditions from pre-impact times (Alve 1991b, Nielsen et al. 2003, Andersen et al. 2004, Dolven et al. 2013). The approach has considerable potential to decipher the effects of pollution from the natural environmental features shaping benthic communities, and should be, when possible, more often used to establish reference conditions. It has the advantage to be completely objective compare to the best expert judgment which leads sometimes to different evaluations amongst experts (Spilmont 2013).

1.4 Benthic foraminifera are part of the solution

1.4.1 Foraminifera as indicator of pollution

1.4.1.1 At community level

Considering their short generation time, foraminifera have the potential to respond faster than macrofauna to changes in environmental conditions. Benthic foraminifera are therefore acknowledged as accurate indicators of human-induced stresses (e.g., Alve 1995, Mojtahid et al. 2006, Denoyelle et al. 2010, Polovodova Asteman et al. 2015), such as oil spills (Morvan et al. 2004), heavy metals (Armynot du Châtelet et al. 2004), and aquaculture (Damak et al. 2020). Specifically, fish farms induce clear shifts in the community structure of benthic foraminifera (Pochon et al. 2015) and promote tolerant species (Angel et al. 2000). The ability

of benthic foraminifera to respond to pollution led to the development of biotic indices to evaluate the EcoQS. Foraminiferal indices based either on diversity (Alve et al., 2009) and on the sensitivity of species to organic pollution (Barras et al. 2014, Alve et al. 2016, Dimiza et al. 2016, Jorissen et al. 2018) have been designed and successfully applied to assess EcoQS of benthic habitats (Dolven et al. 2013, Dijkstra et al. 2017, Damak et al. 2020, El Kateb et al. 2020, Fossile et al. 2021, Parent et al. 2021). Benthic foraminifera also leave an easily accessible and abundant fossil record, which allows reconstruction of the characteristics and timing of historical environmental variations (e.g., Alve 1991a, b, Hayward et al. 2004, Debenay and Fernandez 2009). Consequently, it is possible to trace the record of human-induced disturbances over decades or centuries and reconstruct palaeo-EcoQS (Fig. 3).

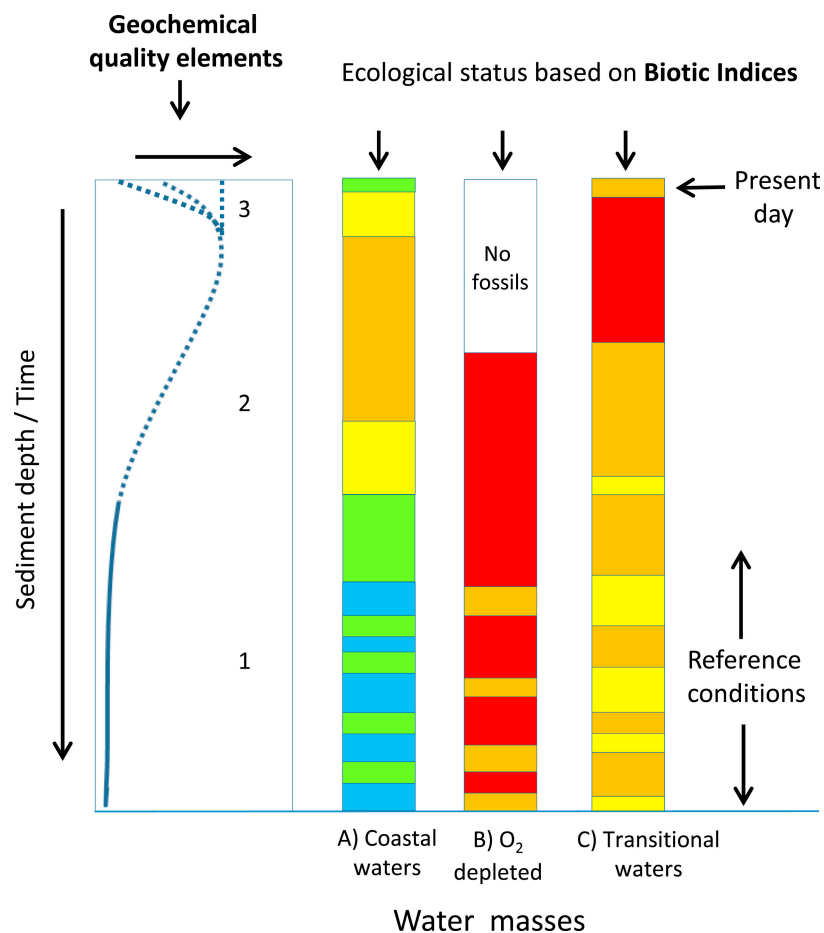


Figure 3. Conceptual model of the reconstruction of palaeo-EcoQS with recent fossil foraminifera (adapted from Hess et al. 2020).

1.4.1.2 At individual level

Metal pollution can provoke physiological and ultrastructural damages involving thickening of organic lining, mitochondrial degeneration, proliferation of degradation vacuoles, lysosomes, residual bodies and the increased production of neutral lipids and of reactive oxygen species (Frontalini et al. 2018, Frontalini et al. 2019). Thermal stress also induces a number of cellular processes in benthic foraminifera. For instance, in *Amphistegina gibbosa*, up-regulation of chaperones protein and elevated proteosynthesis and proteolysis allowed individuals to maintain homeostasis; they further switched from mixotrophy to heterotrophy (Fig. 4). Microplastics were also shown to alter the heterotrophic behavior in the coral-reef foraminifera *Amphistegina gibbosa* (Joppien et al. 2022). Foraminiferal behaviour may also serve as an indicator of environmental conditions (Jauffrais et al. 2016). For instance, the species *Ammonia tepida* is able to adapt its foraging strategy to satisfy its carbon/nitrogen requirements. Deep-sea foraminifera may also adapt their behavior to temperature, oxygen and food availability (Gross 2000).

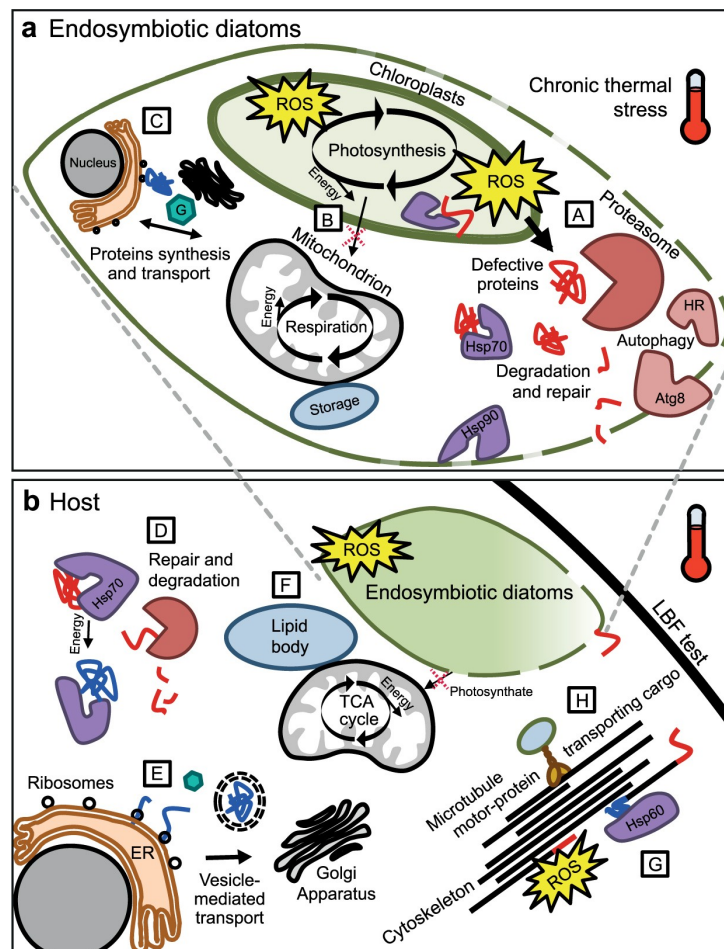


Figure 4. Cellular processes involved in *Amphitesgina g44ibbosa*'s response to thermal (adapted from Stuhr et al. 2018).

1.4.2 Role of benthic foraminifera in the benthic ecosystem functioning

1.4.2.1 A major trophic link?

Benthic foraminifera may represent up to 50% of the eukaryotic biomass (Murray 2006). They play a key role in the global carbonate production (Langer 2008). Like most heterotrophic protists, they constitute a major link from bacteria and algae to higher trophic level (Nomaki et al. 2008, Dupuy et al. 2010, Jauffrais et al. 2016a, Chronopoulou et al. 2019); further contributing to nitrogen and carbon cycle (Moodley et al. 2000, Risgaard-Petersen et al. 2006). Experimental studies observed that intertidal foraminifera exhibit clear varied and species-specific trophic behaviors and were shown to feed on different food sources (Jauffrais et al. 2016 and reference therein). Specifically, the highly abundant intertidal species

Ammonia tepida may prefer to consume algae, but is also able to feed on bacteria (Pascal et al. 2008). Furthermore, species like *Haynesina germanica* and *Criboelphidium williamsoni* are able to sequester chloroplast from benthic diatoms, *i.e.* to perform kleptoplasty (Cesbron et al. 2017); hence most likely behaving as a mixotroph (Tsuchiya et al. 2020). However, an *in situ* study showed that the feeding behavior of intertidal benthic foraminifera is more specific than what has been observed experimentally (Chronopoulou et al. 2019). In fact, *Ammonia* sp. showed a tendency toward being a secondary consumer and possibly preying actively on small eukaryote classes, such as Acoela, Nematoda, and Maxillopoda. In turn, Elphidiids and nonioniids (*Elphidium* sp., *Haynesina* sp.) showed a more herbivorous tendency with a clear preference for phototrophs, which could be related to kleptoplasty (Chronopoulou et al. 2019). Despite all these findings, the trophic role of benthic foraminifera is still largely overlooked.

1.4.2.2 A key element in fluxes at the sediment-water interface?

Benthic foraminifera may also play a significant role in fluxes at the sediment-water interface (Fig. 5). A few typical features of the ecology of benthic foraminifera such as cyst building (Heinz et al. 2005) and locomotion (Jaufrais et al. 2016) are, however, likely leading to displace sediment particles. Specifically, foraminiferal movements typically lead to the creation of intense networks of surface trails (Severin and Erskian 1981, Severin et al. 1982, Severin 1987). Benthic foraminifera are able to migrate down through the sediment, up to a depth of 4 cm for *Quinqueloculina impressa* (Severin and Erskian 1981, Severin et al. 1982). This process leads to the construction of biogenic structures, such as networks of galleries for *Q. impressa* (Severin and Erskian 1981, Severin et al. 1982) and cavities for *Elphidium*

excavatum clavatum (Wetmore 1988, Linke and Lutze 1993). These biogenic structures contribute to a better oxygenation of the surface layer (Hemleben and Kitazato 1995) and ultimately participate in fluxes of both particulate and dissolved materials at the sediment-water interface. However, to the best of our knowledge only one deep-sea study estimated the bioturbation rate of a population of benthic foraminifera as $0.2 \text{ cm}^2 \text{ year}^{-1}$ (Gross 2002). This rate is noticeably comparable to the rates reported for a population of benthic macrofauna in a coastal lagoon, *i.e.* $0.5 \text{ cm}^2 \text{ year}^{-1}$ (Duport et al. 2007). Despite all these evidences, the role of benthic foraminifera in bioturbation processes still remain a largely overlooked open question (see review in Schratzberger and Ingels 2018).

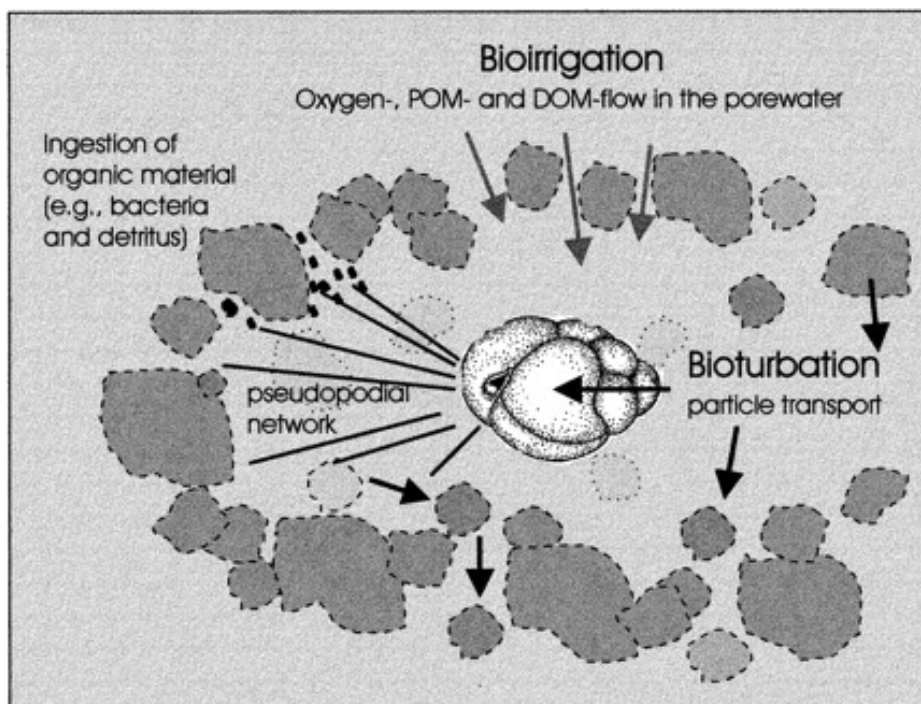


Figure 5. Schematic role of benthic foraminifer in sediment mixing and bio-irrigation in bottom sediments (adapted from Gross 2002)

The diversity in response in benthic foraminifera and the diversity of potential approaches/levels suggest that they could contribute to tackle key questions in ecology *i.e.* what are the effect of new stressors like extreme events or plastic pollution? Or what is the role of meiofauna in the benthic-ecosystem functioning? However, ecological studies on living

foraminifera are still a minor topic compared to fossil foraminifera-related ones over the last 30 years (Fig. 6). Focusing on living foraminifera, hence, offer a yet poorly explored playground for any ecologist or biologist.

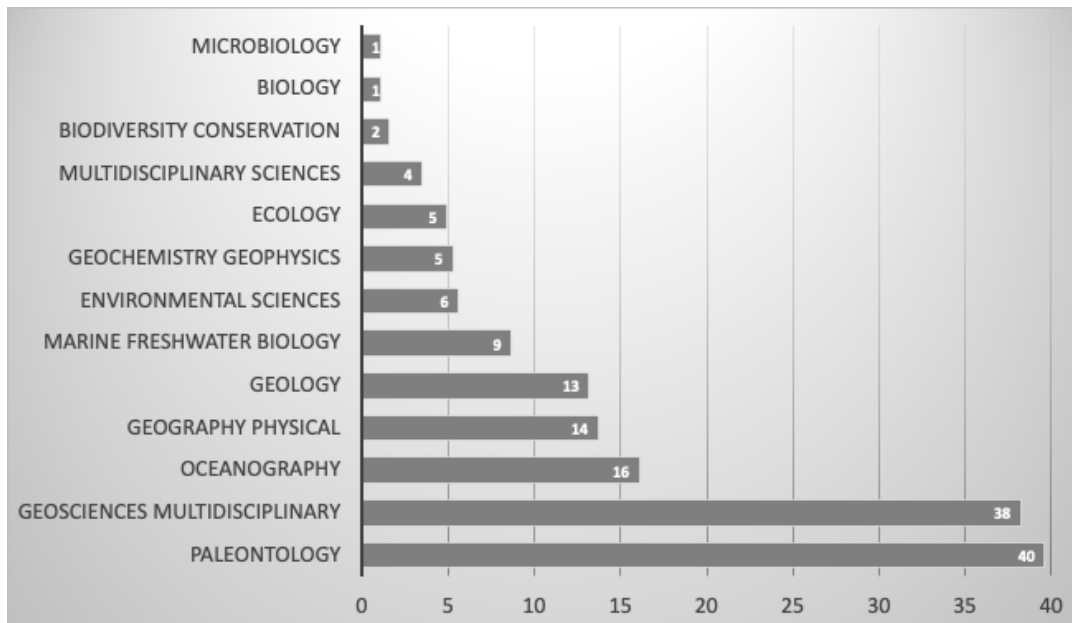


Figure 6. Percentage of publications grouped by research topic indexed in the Web of Science (accessed 20 June 2022) related to benthic foraminifera from 1991 to 2022.

1.5 Outline of the present thesis

In this context, the research projects I am involved in aimed at answering the following questions:

- What are the drivers of foraminiferal communities in naturally variable ecosystems and under anthropogenic pressures in transitional waters like estuaries and intertidal mudflats?
- How can the knowledge gain on the living fauna be transferred and apply to recent (last century) fossil fauna in order to reconstruct past environments? This aspect has strong implications in terms of defining accurate reference conditions from pre-impacted times.

- Can benthic foraminifera be reliable indicators in the context of the implementation of marine legislations, *i.e.* European Water Framework Directive and Marine Strategic Framework Directive? This includes the development of indices based on benthic foraminifera and direct comparison with benthic macrofauna to evaluate ecological quality status (EcoQS) and palaeocological-EcoQS.
- What are the ecological functions of foraminifera and the faunal/biogeochemical processes they contribute to? Specifically, how are they involved in bioturbation and bio-irrigation of intertidal sediments?

In the view of the above questions, this HDR manuscript is organized as it follows. The second chapter focuses on the response of benthic foraminifera to natural and anthropogenic pressures at community level considering alpha and beta diversity. In the third chapter, the use of foraminiferal species as bioindicators of the environmental conditions is detailed. In both the second and third chapter, it is discussed how the implementation of biotic indices based on benthic foraminifera frame the future of studies aiming to assess the health of benthic habitats. The fourth chapter describes the role of benthic foraminifera in sediment mixing and highlights their potential as bioassays. Finally, the last chapter introduces some perspectives for the future next years.

In the following chapters, it is referred to my publications as they are numbered in the publication list.

Chapter 2. What can we learn from alpha and beta diversity in benthic foraminiferal communities?

In a context of strong anthropogenic pressures on blue carbon coastal ecosystems, marine legislations were enforced to define strategies to protect and restore these habitats. In order to do so, an accurate assessment of the ecological quality is needed. This requires a deep knowledge of the response of living organisms to such pressure. As stated in Chapter 1, I used benthic foraminiferal communities to characterize the effect of natural changes and human activities on benthic habitats. Due to their short life cycles, benthic foraminifera respond quickly to both environmental variability (see review in [6]) and changes in population dynamics and species composition are indicative of changes in environmental conditions (see review in [35]). In this context, we mostly focused on transitional waters, particularly intertidal areas and fjords.

2.1 Natural features of transitional waters constrain benthic foraminiferal communities

Tidal range is a primary factor constraining benthic communities in intertidal marshes. In a study in the pristine Baie of Canche, we studied foraminiferal communities along different transects of decreasing elevation. We showed that alpha diversity measured with $\exp(H'_{bc})$ decreased with elevation (Fig.7, [10]). In turn, abundances were higher at the most elevated stations.

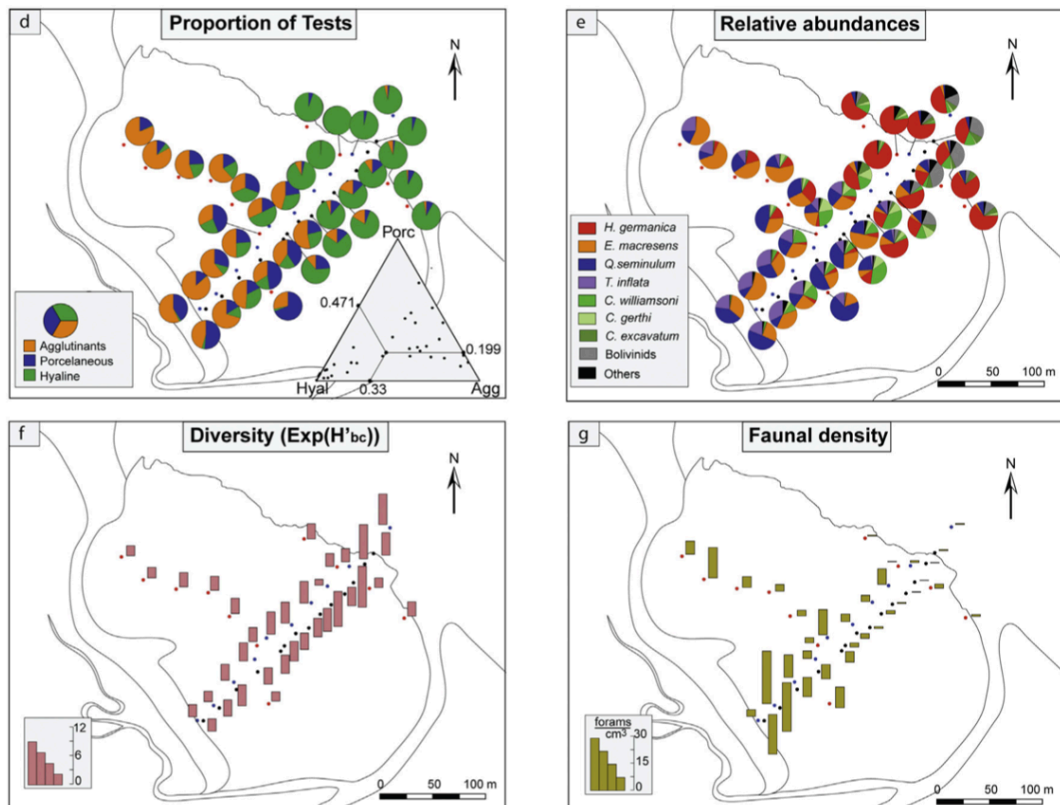


Figure 7. Diversity parameters of foraminiferal communities along an elevation gradient in the tidal marsh of the Baie de Canche, adapted from [10].

A switch in beta-diversity, *i.e.* species composition from agglutinated-dominated communities to hyaline dominated ones, along the decreasing elevation gradient was also observed (Fig. 8). This work illustrated the key role played by the subaerial exposure in shaping foraminiferal communities. Other measured parameters *i.e.* TOC, sulphur contents and grain-size, did not primarily influence the benthic foraminiferal distribution. This suggests, that foraminiferal alpha and beta diversity is mostly linked to elevation (see review in Berkeley et al., 2007) in absence of any pollution in tidal marshes.

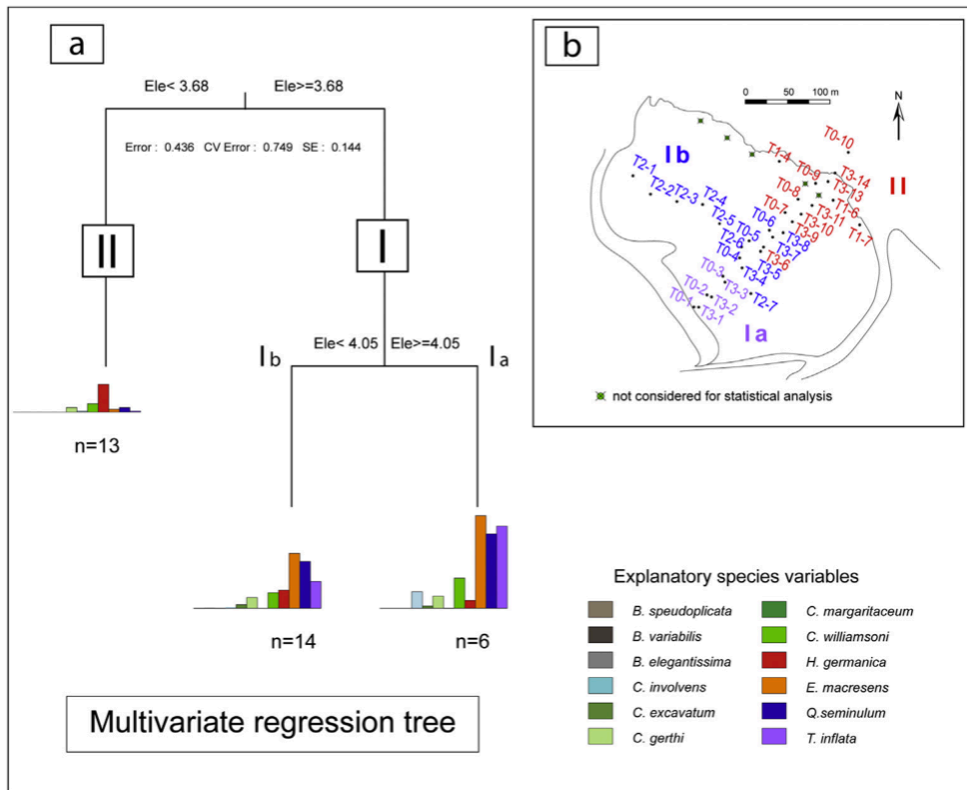


Figure 8. a) Multivariate regression tree. At each node threshold values are indicated. The bar plots represent the species abundance at each leaf (cluster). b) In top-right sampling station positions within the study area colored according to cluster reference, adapted from [10].

In contrast, in fjords, the oxygen content is the main limiting factor; which is largely dependent on the basin natural features like water renewal frequency, which in turn depends on fjord topography (sill-depth, the cross-sectional area at the sill, and the basin depth below the sill). Hence, in these ecosystems, bottom-water oxygen concentrations strongly constrain benthic communities. This was investigated in eleven fjords from southeastern Norway [5][14]. Specifically, in this work, alpha diversity i.e. ($\exp'H'_{bc}$) significantly increased with oxygen [5]; the most oxygenated sites exhibiting a 5 times higher diversity (Fig. 9).

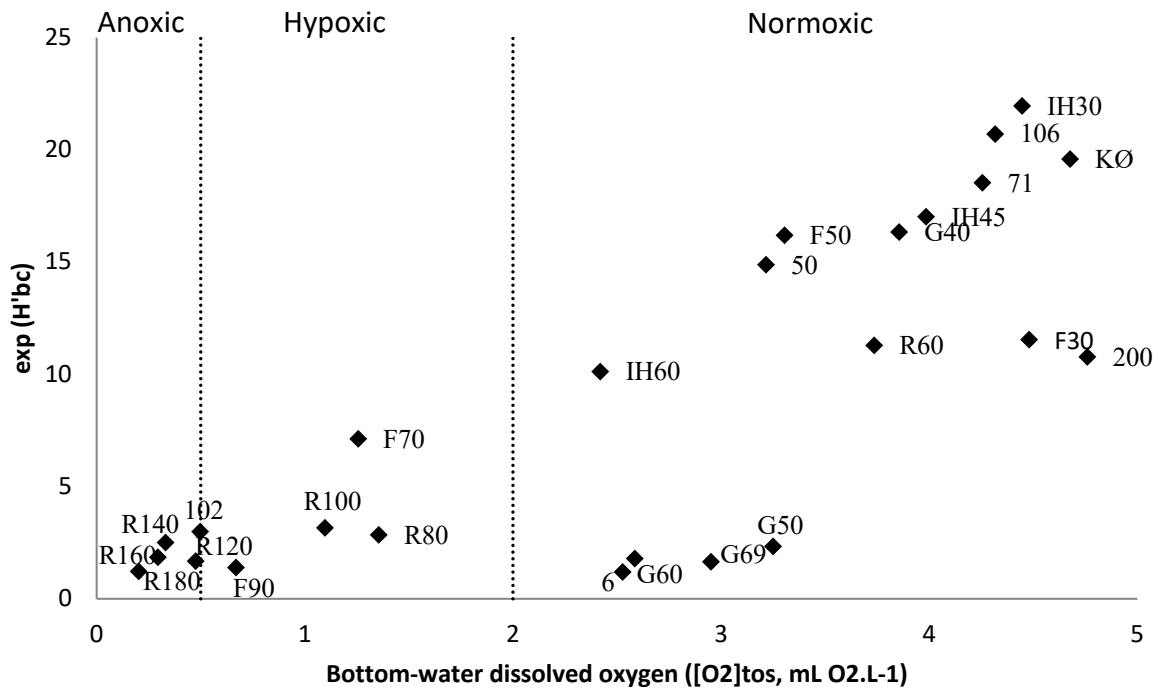


Figure 9. Exp(H'_{bc}), of complete living (stained) assemblage (0-2 cm, >63 µm) against bottom-water dissolved oxygen concentration. Threshold between anoxic, hypoxic and normoxic bottom-water conditions are from Diaz and Rosenberg (2008), adapted from [5].

Changes in beta diversity was further highlighted in a redundancy analysis (Fig. 10). The depth below threshold (DBT) and TOC together explained 43% of the variation for foraminiferal communities. The DBT *i.e.* the difference between the water depth at a station and the sill depth of the fjord, has been characterized for each station. It is not a factor *sensu stricto*, but a measure that reflects the degree or duration of water stagnation in the deep areas of the fjord. Deep-water renewal and oxygenation in a fjord depend on DBT as well as on the supply of organic matter (*i.e.* impacts oxygen consumption). DBT will, however, also represent the influence of other variables, *e.g.* pigments, different organic components and temperature, that increase or decrease due to the gradually changing conditions with depth. Hence, DBT *sensu stricto* can be seen as a proxy of the oxygen conditions occurring in a fjord. This work further confirmed that oxygen is one of the main environmental parameters shaping foraminiferal communities in fjordic systems (Alve 1990, Gustafsson and Nordberg 2000).

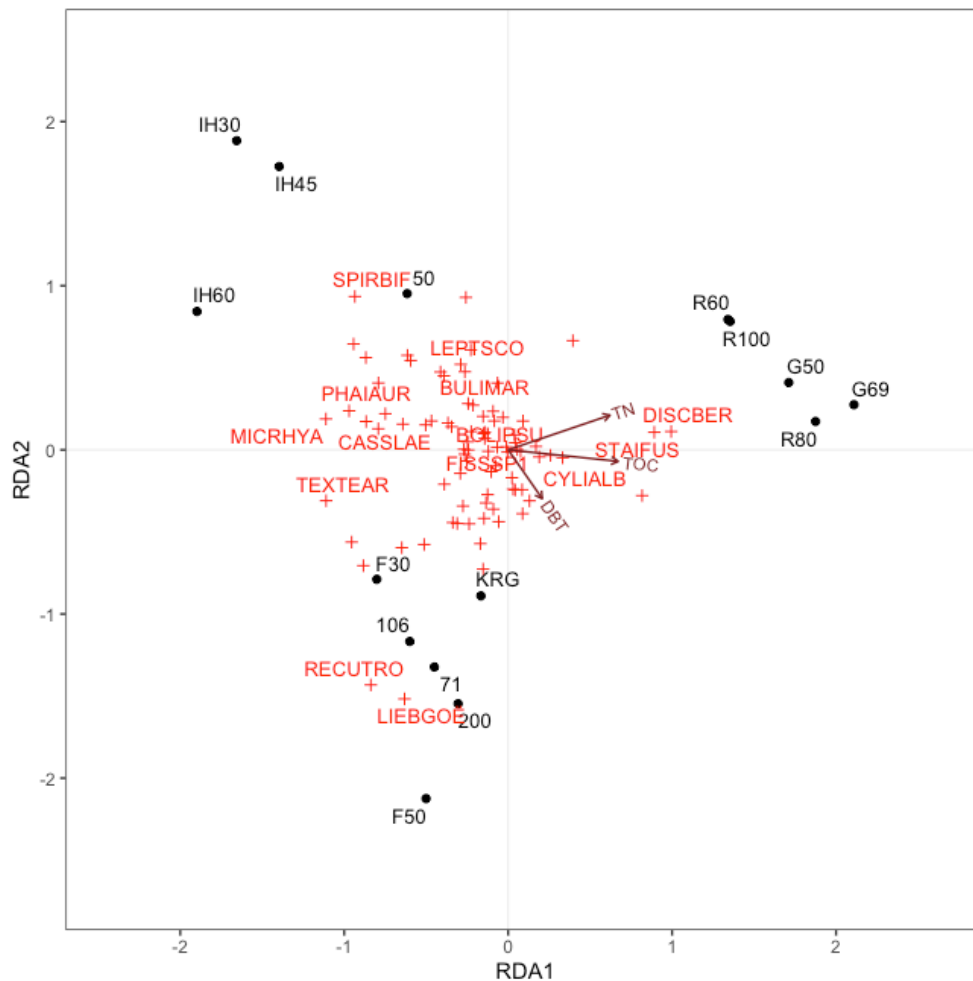


Figure 10. Redundancy analysis (RDA) of foraminiferal species assemblages: triplot of species (crosses), stations (dots) and significant environmental variables (vectors). Most dominant species are indicated by abbreviated names, adapted from [14].

These examples illustrate the strong natural pressure on benthic foraminifera in TWs. In the absence of any pollution, community structure and species composition are largely driven by the natural features; limiting alpha diversity and leading to the rearrangement of communities. Unfortunately, TWs are exposed to high levels of anthropogenic stresses such as aquaculture, habitat destruction, urban sewage and industrial activities which further constrain foraminiferal communities [9][12][18][26].

2.2 Human activities altered benthic foraminiferal communities

Alpha diversity can be assessed using rank-frequency distributions (Frontier 1976, Legendre and Legendre 1984, Frontier and Etienne 1990). This method was applied on foraminiferal data collected from April to August 2004 on tidal mudflats of the macrotidal Marennes-Oléron Bay (SW France), famous for the cultivation of Pacific oysters (*Crassostrea gigas*) [2]. The response of living (stained) benthic foraminifera to short-term biogeochemical disturbances in the sediment and overlying water was monitored. Short-term hypoxia occurred in early June, in conjunction with a sudden rise in temperature. In mid-June, the ammonia content of sediment porewater increased, leading to potentially maximal flux towards overlying waters. Based on RFDs, it appeared that foraminiferal assemblages in the topmost sediments were more affected than those in the deepest which were equally dominated by two species for the entire survey period (Fig. 11 and [2]). Changes in RFDs are sensitive to events that affects dynamics of foraminiferal populations like recruitment and mortality. Large recruitment of a dominant species increases both its abundance and rank and lead to a shift in RFDs from intermediate or mature stages (curves 2 and 3, Fig. 11b) to pioneer stage (curve 1, Fig. 11b). In the uppermost slice, the living foraminiferal assemblage was at a mature stage on 22 April. This assemblage was subsequently altered by 9 June and species dominances were similar to those of deeper layers. From late June, a recovery in environmental conditions allowed regeneration and reorganisation of the living foraminiferal assemblages dominated by large recruitments of juvenile *Ammonia tepida*. Contrary to the topmost layers, benthic foraminiferal assemblages in the 5-8 cm slice were not modified during the hypoxic crisis recorded in surface sediment.

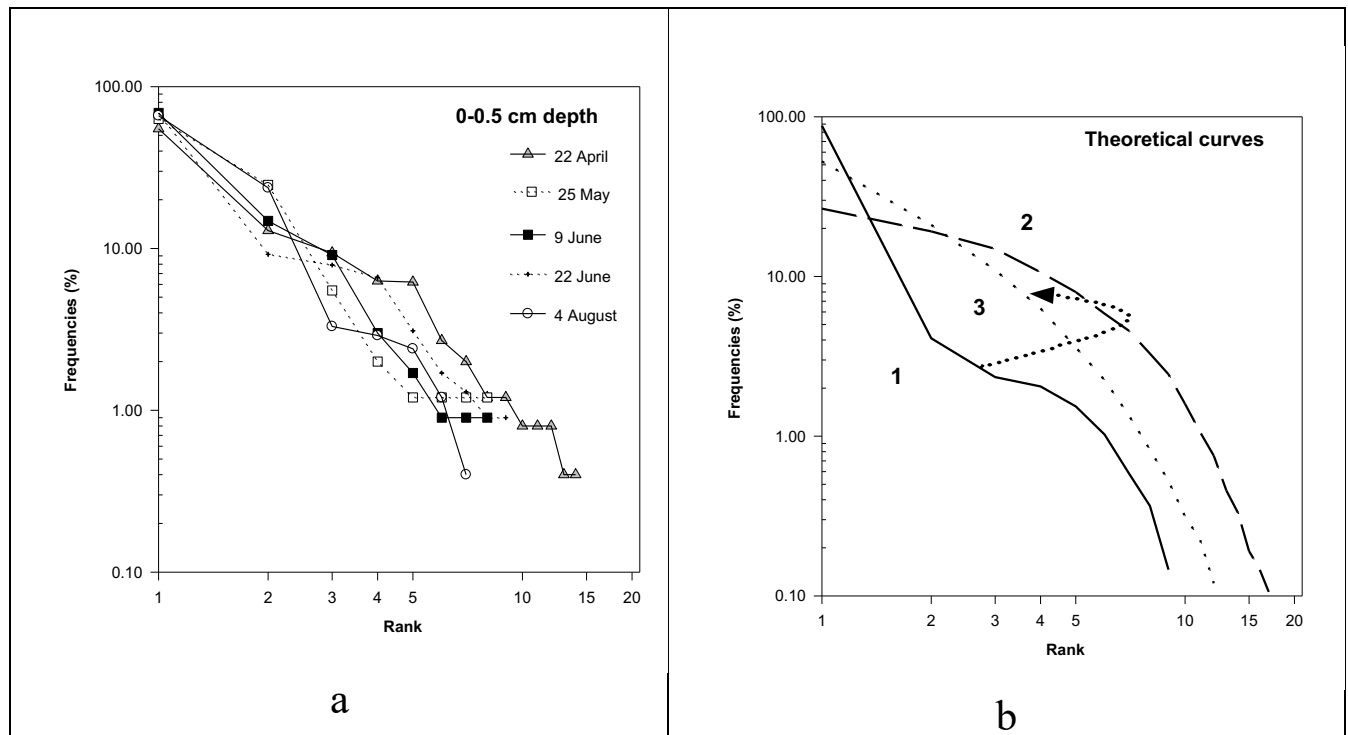


Figure 11. Benthic foraminifera rank-frequency diagrams (0-0.5cm topmost sediment layer) sampled at Ronce-Perquis (South-Western France) from 22 April to 4 August and theoretical RFD curve shapes (d, 1: linear-concave = pioneer assemblage, 2: convex = intermediate assemblage and 3: straight-line = mature assemblage, dotted arrow = example of ecological succession: recovery in the assemblage). Adapted from [2]

In the context of water sewage pollution in the Gulf of Trieste in Italy [18], benthic foraminiferal assemblages reached different degrees of maturity throughout the year at both stations. Based on RFDs, at the impacted station (Ser), foraminiferal assemblages showed an ecological succession from a mature assemblage in winter to an unbalance done in spring, reaching an intermediate assemblage in summer and autumn (Fig. 12a). At the unimpacted station in the nearby marine protected area of Miramare (Res), RFDs highlighted an annual ecological succession from a mature assemblage in winter, to an unbalanced one in spring, an intermediate assemblage in summer, ending up with a mature assemblage in autumn (Fig. 12b). Foraminiferal assemblages were found to be quite resilient over the annual cycle under consideration, as they recovered from an unbalanced to a mature state, depending on the season. Seasonal variations in RFDs at both stations are due to changes in diversity and in dominant species. Stressful conditions at the impacted Ser station, mainly due to TOC

accumulation and high Zn concentration, produced a more unbalanced foraminiferal assemblage in comparison with the unimpacted Res station. Furthermore, the mature assemblage observed at Res station suggests that the marine protected area of Miramare is efficient in preserving good environmental conditions in the Gulf of Trieste.

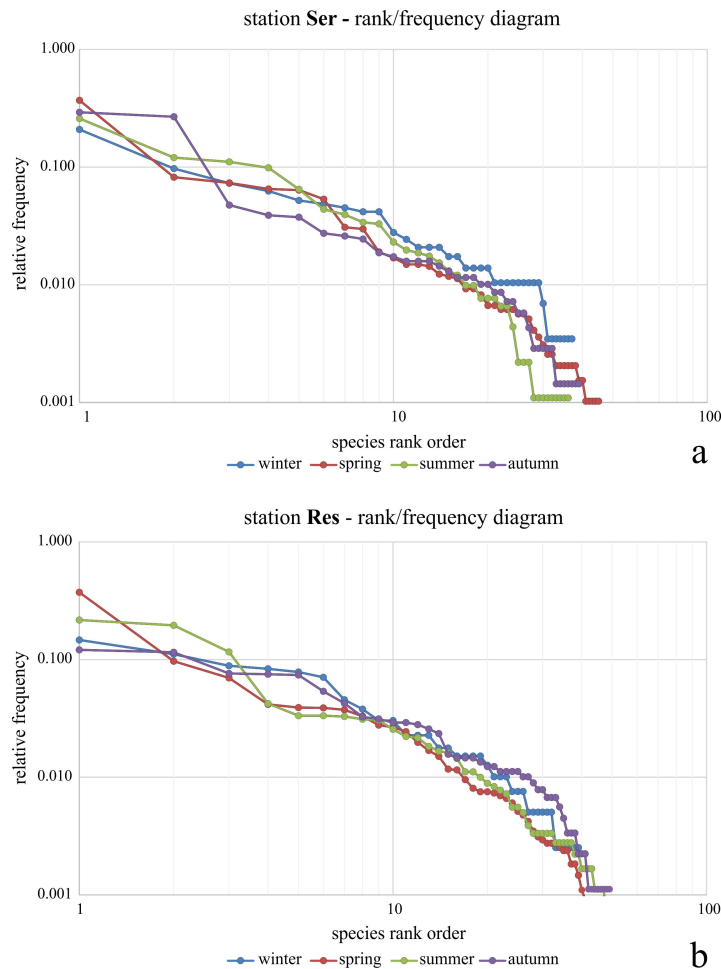


Figure 12. Rank-frequency diagram for the Ser and Res stations. Adapted from [18]

The study in the Rade of Cherbourg which hosts the only marine salmon fish farm along the French coasts, further highlighted the potential of RFDs [26]. The parameters α and ϕ allowed for a synthetically analysis of the RFDs to highlight the effect of the salmon farm (see below the box 1 for more details on the method). Noticeably, the parameter ϕ was significantly different outside and within the salmon farm (t-test, $p < 0.05$), for both macrofaunal and foraminiferal assemblages (Fig. 13). In the Rade of Cherbourg, RFDs

appeared well adapted to identify differences in benthic foraminiferal and macrofaunal communities between the area impacted by the salmon farm and the non-impacted stations. Specifically, outside the farm, the parameters α and ϕ were highly significantly linearly correlated for foraminifera, *i.e.* $\phi = 7.21$ and $\alpha = 10.6$, while no significant correlation was found for macrofaunal assemblages. In the salmon farm, the parameters α and ϕ were significantly linearly correlated for foraminifera ($\phi = 1.96$ and $\alpha = 2.48$) and macrofauna ($\phi = 1.99$ and $\alpha = 3.07$). Following the theoretical work of Frontier (1976, 1985), RFDs shape allowed us to assign benthic communities to stage 2 corresponding to a mature stage outside the salmon farm, hence equivalent to a good or high EcoQS. In turn, under the salmon farm, benthic communities were at stage 1 highlighting that they were under pressure, hence an EcoQS between moderate and bad.

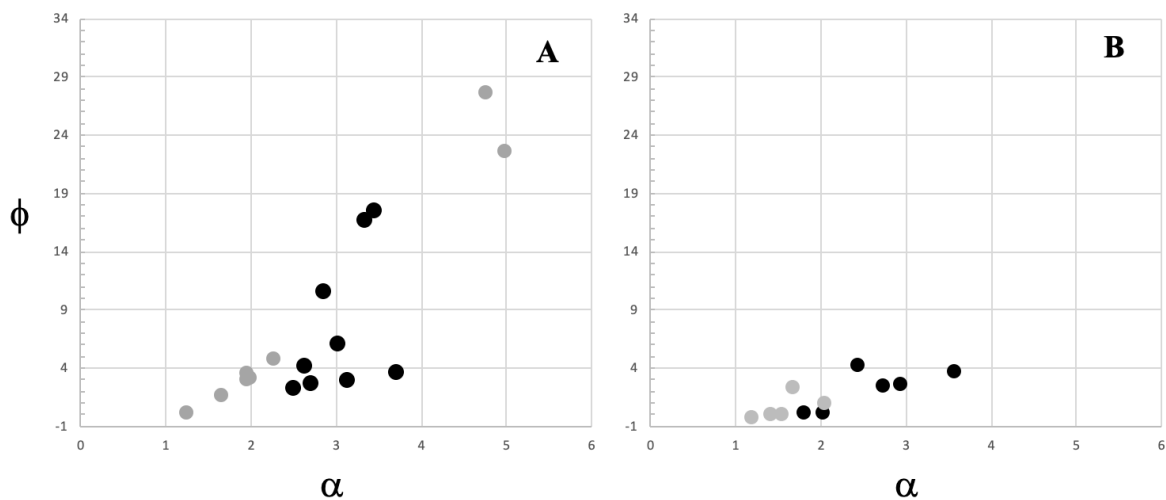


Figure 12. Values of the parameters α and ϕ characterizing the rank-frequency diagrams of macrofaunal (black dots) and foraminiferal (grey dots) assemblages in the Rade of Cherbourg outside the farm (A) and in the salmon farm (B). Adapted from [26]

These three examples illustrated the potential of RFDs to monitor the health of benthic habitats. Although effective to monitor the state of diversity, rank-frequency diagrams have been so far quite unfriendly to describe by scientists to stakeholders from governmental agencies. The use of the simplified canonical law to describe the distribution of data in RFD

would be a simple mean to assess the diversity [26], hence the ecological status. It would be possible to objectively measure the deviation of a study site conditions from the reference conditions. calculated for both groups. They further suggest that this method may be included in the general reflexion on the evaluation of the good environmental status within the European marine strategic framework directive. Conversely to the water framework directive, which enforced to follow a chart of five EcoQS, the MSFD aims at achieving good ecological status, *i.e.* to differentiate between undisturbed and disturbed areas.

Box 1: Rank-frequency distributions to describe alpha-diversity

The structure of benthic foraminiferal communities has been assessed using the rank-frequency relationship

$$f_s = f(r + \phi)^{-\alpha} \quad (1)$$

*where f_s is the frequency (*i.e.* relative abundance) of a species of rank r (the most abundant species has a rank $r=1$, the second more abundant a rank $r=2$, and so on, and the less abundant species has a rank $r=N$, where N is the number of species found in a sample), f is a pre-factor based on the overall abundance of a community, and α and ϕ fitting parameter describing the diversity and evenness of a given community. Rank-frequency diagrams consist of frequencies of species plotted against their respective ranks organized in decreasing order, and with both axes in logarithmic scale.*

*Specifically, when $\phi=0$ (*i.e.* Eq. (1) writes as $f_s = fr^{-\alpha}$) a low value of α means a slow decrease in species abundance (that is, a more even distribution of individuals among species), and a high value of α means a rapid decrease of species abundance (that is, a more heterogeneous distribution). The former and the latter give less and more vertical rank-frequency distributions (RFDs), hence respectively high diversity/evenness and low diversity/evenness. On the other hand, $\phi \neq 0$ describes the diversity and evenness of the most abundant species. Specifically, a positive value of ϕ results in a greater evenness among the most frequent species, hence a higher diversity. Alternatively, a negative ϕ describes a community marked by the dominance of a few (even one) species and provides a low diversity index and a low evenness. The parameters α and ϕ were estimated for each sample using a nonlinear least-squares Levenberg–Marquardt algorithm, and were chosen as the values that respectively maximized and minimized the coefficient of determination r^2 and the sum of the squared residuals between empirical data and Eq. (1) (Seuront 2013).*

The effects of pollution was further investigated on alpha and beta diversity by mean of diversity index i.e. $\exp(H'_{bc})$ [9][12][16][18][25][26][27][33][36][42], heatmap describing assemblages composition [36] and multivariate analyses i.e. principal components analysis, redundancy analysis, constrained hierarchical analysis, detrended correspondence analysis, correspondence canonical analysis [9][25][27][28][33][42]. These works clearly confirmed the hypothesis of benthic foraminifera being accurate indicators of the environmental conditions. This allowed us to move forward toward the definition of biotic indices based on foraminiferal alpha diversity to be implemented in the context of the WFD and MSFD.

2.3 The use of foraminiferal alpha diversity in environmental monitoring

2.3.1 Ecological quality status assessment with benthic foraminifera

Following the work from Alve et al. (2009), we adjusted the methodology to assess EcoQS with the Shannon index, and used Hill's number (N_1) $\exp(H'_{bc})$ (1973). The development of a foraminiferal biotic indices clearly benefited from what is shortly presented above in section 2.1 and 2.2. We further developed novel quantitative threshold values for the EcoQS categories. This was the first study defining criteria to determine EcoQS using living benthic foraminifera for environmental monitoring [5][7]. At our study sites, bottom-water oxygen concentration reflects a disturbance gradient. Living benthic foraminiferal assemblages diversity ($\exp(H'_{bc})$, the effective number of species of complete living assemblages) is significantly correlated with oxygen. Improved EcoQS as reflected by foraminiferal diversity is observed along with increasing oxygen concentrations. Disturbed stations, *i.e.* here exposed to anoxic conditions, were classified as reflecting “bad” EcoQS based on foraminiferal diversity (Fig. 14). On the other hand, well-oxygenated stations were ranked from “moderate” to “high”

EcoQS using the diversity index $\exp(H'_{bc})$. We obtained a clear pattern from bad to high EcoQS using living benthic foraminifera, and this is in accordance with the bottom-water oxygen gradient. Indeed, different studies reported drops in benthic foraminiferal diversity in response to a gradient of disturbance (Mojtahid et al. 2008, Alve et al. 2009, Elshanawany et al. 2011). Consequently, diversity-based indices derived from benthic living foraminifera seem to be an adequate method to highlight a gradient of disturbances, and to determine EcoQS.

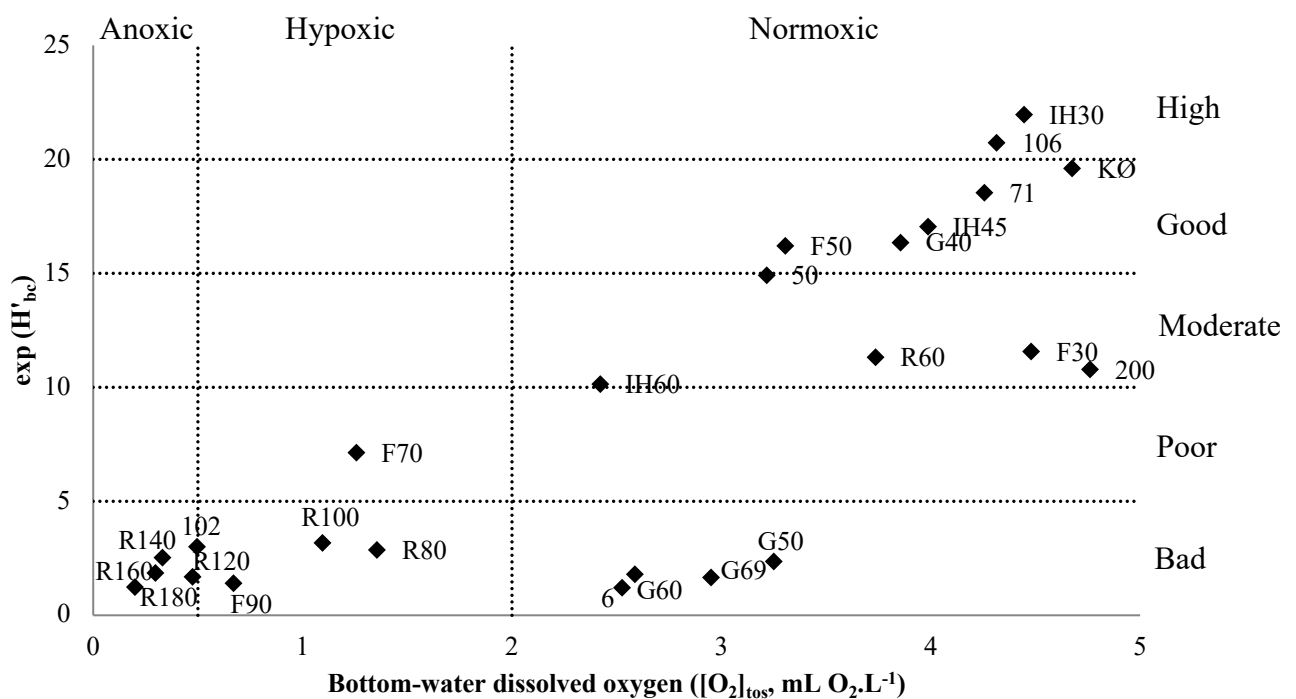


Figure 14. Ecological quality statuses in southeastern Norwegian fjords based on $\exp(H'_{bc})$ of complete living (stained) assemblage (0-2 cm, $>63 \mu m$). Threshold between anoxic, hypoxic and normoxic bottom-water conditions are from Diaz and Rosenberg (2008). Adapted from [5]

The foraminifera-based $\exp(H'_{bc})$ method has, since then, been successfully tested in a variety of transitional waters (see review in [35]), *i.e.* Norwegian fjords [16], Italian coastal lagoons and lakes [12], French and Brazilian harbors [9][27][33], Italian, French and Brazilian bays [18][26][42], and French estuaries [25], in both subtidal and intertidal conditions. All these studies have demonstrated several advantages of using benthic foraminifera-based

diversity indices. The index $\exp(H'_{bc})$ was reported to be significantly correlated with environmental parameters, such as organic matter enrichment in the context of aquaculture [12][26] (Fig. 15), sewage outfall [18], or metal pollutants such as copper (Cu), zinc (Zn), and lead (Pb) [9][27][33][42]. It is, however, important to note that recording such correlations does not necessitate a causal link without considering other key parameters and synergistic effects known to influence benthic foraminifera (e.g., organic carbon flux, salinity, sediment pore-water hypoxia/anoxia), which usually require lab culturing and controlled experimentation (Alve et al. 2009). Studies using the $\exp(H'_{bc})$ index, however, showed that this index is applicable to different stressors and in disparate biogeographic regions, presenting the potential for wider application. Studies have also found some shortfalls, as the accuracy of the results is dependent on the sampling effort (number of replicates), high seasonal variability may affect EcoQS assessment, and that the method needs to be better adjusted to the naturally low baseline diversity in transitional waters [5][14]. For the instance, the criteria to define EcoQS were adapted to the naturally low diversity occurring in Italian transitional waters [12]. Furthermore, the first application of this method on eDNA data *i.e.* $\exp(H'_{bc})$ led to reliably identify poor-to-bad EcoQS in the polluted area in front of the former industrial plant of the Bagnoli area in the Naples harbor [33].

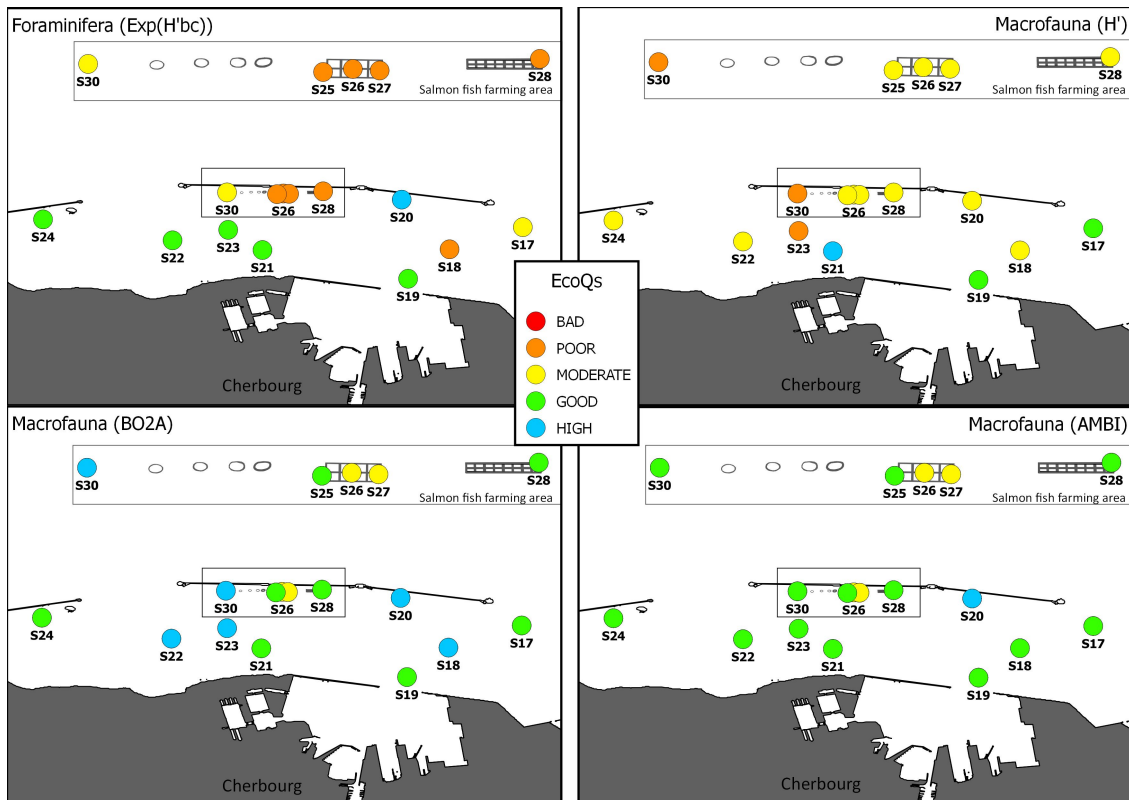


Figure 15. Ecological quality status in the Rade of Cherbourg in the context of Salmon fish farming according to A- Foraminifera – Exp(H'_{bc}), B- Macrofauna – H' , C- Macrofauna – BO2A and D- Macrofauna – AMBI. Adapted from [26]

In conclusion, these examples further stressed the fact that foraminifera can be considered as a reliable biological quality element to assess EcoQS in transitional and marine systems. Specifically, the use of the diversity index $\exp(H'_{bc})$ based on benthic foraminifera showed good performance in detecting the impact of pollution in different contexts. This method was originally tested along a decreasing gradient of bottom-water oxygen concentration in SE Norwegian fjords [5] and we showed it may work against most pollution sources [9][12][18][26][27][33][42]. Note that in oligotrophic open-marine habitats from the Mediterranean Sea, in the first stage of organic matter enrichment, an increase in diversity index is observed (Parent et al. 2021; Barras et al. 2014)[36]. This succession follows the model of Pearson & Rosenberg (1978), the often named “the hypertrophic zone theory” in other studies (Schafer et al. 1995, Angel et al. 2000). Oligotrophic characteristics of the Mediterranean Sea habitats further enhance this phenomenon (Hyams-Kazphan et al. 2009);

the EcoQS assessment being biased towards better EcoQS with impacted stations exhibiting higher values of $\exp(H'_{bc})$ compared to unimpacted ones [36]. Diversity indices must therefore be used with cautious in oligotrophic ecosystems.

2.3.2 Comparison with benthic macrofauna

In the literature, the main biological group considered in biomonitoring studies is benthic macrofauna. In this context, it appeared relevant to further compare the outcomes of benthic foraminifera in terms of EcoQS assessment to the ones of macrofauna. It would strengthen the conclusions showing the accuracy of foraminiferal biotic indices. Such comparisons were done in Italian lagoons and lakes [12], Norwegian fjords [14][16] and in the Rade of Cherbourg (France) [26].

We showed that Foraminiferal and macrofaunal community data were significantly correlated (Procrustes analysis $m^2=0.66$, $p=0.001$, Fig. 16). Hence, benthic foraminiferal distribution patterns mirror those of benthic macrofauna [14]. In all studies [12][14][16][26], the characterisation of EcoQS using diversity indices led to similar conclusions between benthic foraminifera and macrofauna (see Fig. 15 for an example). This was also reported in the Firth of Clyde where similar diversity (H') patterns were reported for both groups (Mojtahid et al. 2008). In details, in the Rade of Cherbourg, foraminifera and macrofauna showed similar trends *i.e.* a spatially limited and moderated degradation of EcoQS under the salmon cages [26]. In our studies in Italy and France [12][26], benthic foraminifera-based EcoQS classification were also more severe than macrofauna to the presence of a perturbation, suggesting that may be more sensitive (efficient?) to detect the deleterious effects of pollution; like previously observed in a study on the impact of oil-drill mud disposal (Denoyelle et al. 2010).

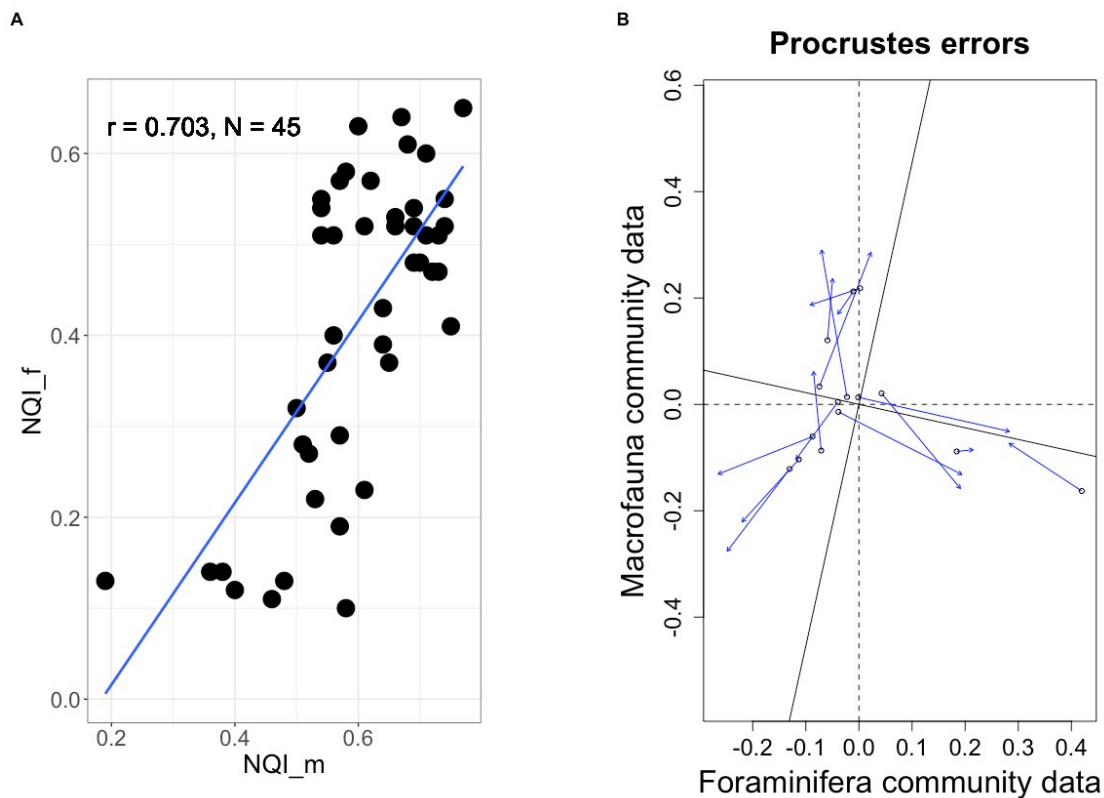


Figure 16. (A) Significant correlation ($R = 0.70$, $p < 0.0001$) between foraminiferal and macrofaunal NQI indices in Norwegian fjords [16] (B) Significant correlation (procrustes errors analysis $m2 = 0.66$, $p = 0.001$) between foraminiferal and macrofaunal communities in Norwegian fjords, adapted from [14].

These few examples suggest that benthic foraminiferal indices correlate significantly with their macrofaunal counterparts, demonstrating that benthic foraminifera-derived diversity indices can be used to complement the results of other biological quality elements like macrofauna and can be applied where macrofauna are absent or difficult to sample.

2.3.3 Reconstructing past-EcoQS with benthic foraminifera

In contrast to most benthic macrofauna (Poirier et al. 2009), the preservation of benthic foraminiferal tests provides information about long-term environmental and biological changes [9][15][19][27][42]. In environmental monitoring, hindcasting (*i.e.* the use of historical information) is one of the methods recommended by marine legislations to determine reference conditions. It implies the existence of long-term monitoring or fossil records of taxa used to characterize the EcoQS. In different studies, we illustrated how fossil

benthic foraminifera can enable the reconstruction of *in situ* local reference conditions in transitional environments with long-term pollution history to determine either contemporary EcoQS or its evolution over time and may contribute to deciphering between natural and anthropogenic stresses. For instance, we obtained a robust assessment of palaeo-EcoQS for transitional waters with benthic foraminifera using site-specific local reference conditions in the Boulogne sur Mer harbor, France (Fig. 17)[9], in the Santos estuary, Brazil (Fig. 18)[27] and in the Sepetiba bay, Brazil [42]. Furthermore, geochemical analyses of dated sediment cores can be used in combination with benthic foraminifera to determine ecological reference conditions in transitional waters (Hess et al. 2020).

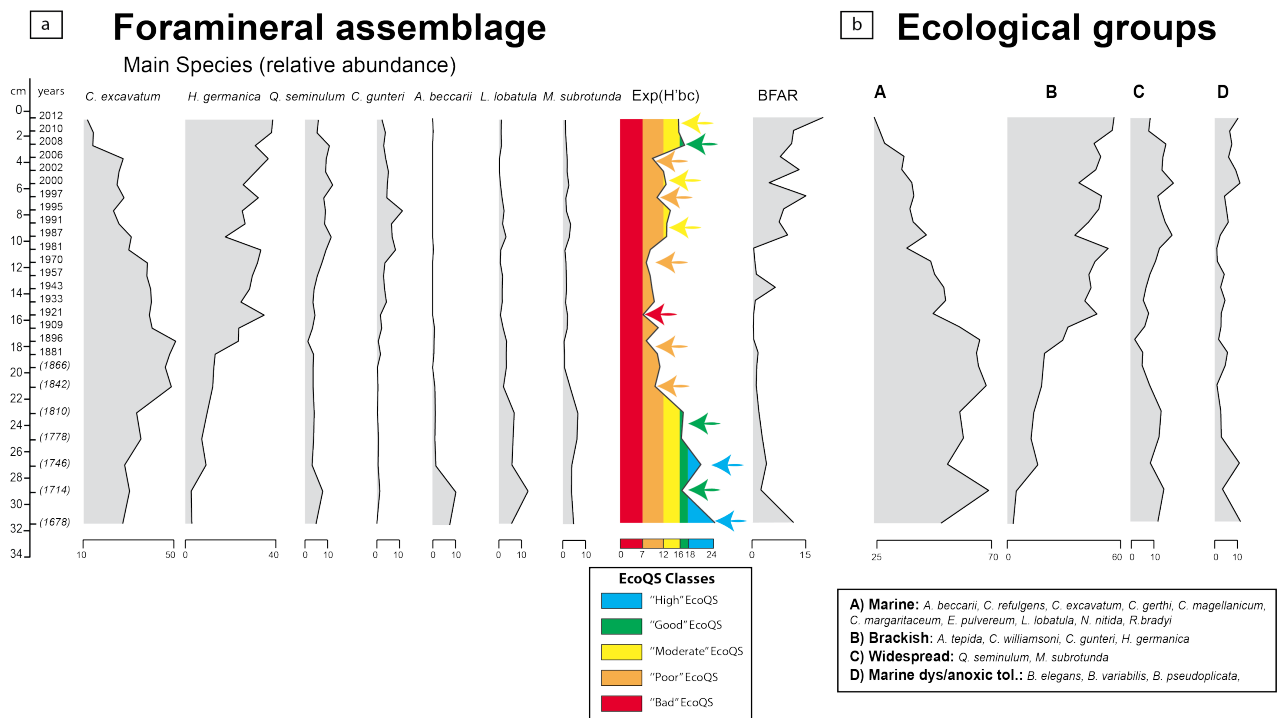


Figure 17. a) Trends of relative abundance of the main species: *Criboelphidium excavatum*, *Haynesina germanica*, *Quinqueloculina seminulum*, *C. gunteri*, *Ammonia beccarii*, *Lobatula lobatula*, *Miliolinella subrotunda*. Trend of diversity ($Exp(H'_{bc})$) and related ecological quality status (EcoQS): $Exp(H'_{bc}) < 7$ "Bad", 7-12 "Poor", 12-16 "Moderate", 16-18 "Good" and > 18 "High" status. Trend of benthic foraminiferal accumulation rate (BFAR: tests/cm²/year). b) Trends of 4 ecological groups. Each group represents the percentage of specimens with the same ecological affinity. Adapted from [9]

The use of fossil benthic foraminifera led to an accurate implementation of the ecological quality ratio (EQR) as required by marine legislations. The EQR is the ratio between

the value of the observed biological parameter for a given water body and the expected value under reference conditions (Andersen et al. 2004). The ratio ranges as a numerical value between 0 and 1, with high ecological status represented by values close to one and bad ecological status by values close to zero. The EQR boundaries to define Palaeo-EcoQS were determined using the “Reference Conditions Working Group” recommendations (REFCOND 2003). Type-specific reference conditions (including hydromorphological and physicochemical conditions unique to each water body) are the anchor point of EQR based classifications. Hence, the EQR approach can also be used to resolve issues related to the definition of threshold values. Using the foraminiferal fossil record, it is possible to determine *in situ* local reference conditions. For example, in the Santos estuary (Brazil) [27], the highest value of diversity was defined in the year 1902, *i.e.* $\exp(H'_{bc})$ of 11.66. It corresponds to the pre-impacted period and was defined as the reference value. The EQR was calculated accordingly: $EQR = \exp(H'_{bc})_{\text{observed value}} / \exp(H'_{bc})_{\text{reference value}}$ (Fig. 18). In that study, the foraminiferal fossil record allowed evaluation of Palaeo-EcoQS based on *in situ* local reference conditions reflecting the environmental history of the region.

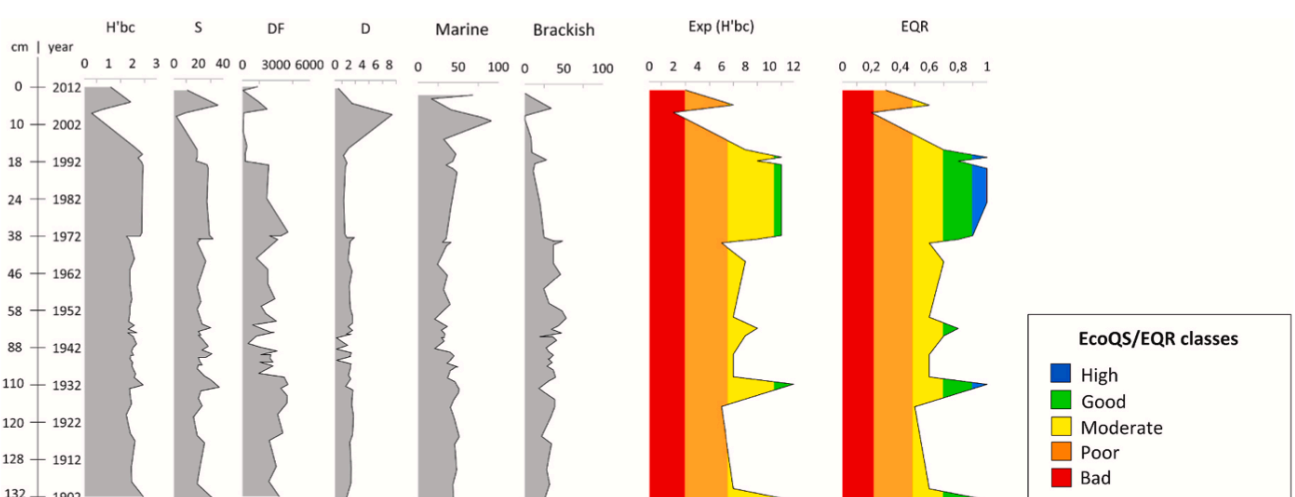


Figure 18. Variations of the main benthic foraminiferal assemblages' parameters: diversity (H'_{bc}), richness (S), density of foraminifera (DF), dominance (D), Palaeo-Ecological Quality Status assessed by the $\exp(H'_{bc})$ and Ecological Quality Ratio as well as marine and brackish groups. Adapted from [27]

In conclusion, living benthic foraminiferal species being good indicators of environmental modifications, fossilised organisms might therefore be considered as appropriate candidates to define local and/or regional reference conditions. This approach, more objective than methods such as “best professional judgment”, will allow to better monitor the EcoQS of water bodies and to accurately reconstruct palaeo-EcoQS [9][27][42] with the aim to improve management and conservation plans.

Chapter 3. Towards a biotic index based on foraminiferal specific response to pollution

As exemplified in Chapter 2., at the community level, benthic foraminifera can be used in different ways (Fig. 19) to characterize the environmental conditions, such as changes in population density and species abundance [28], community compositional shifts (pre-impact sensitive species vs. post-impact opportunists [27] or calcareous vs. agglutinated species [14]), as well as increase or decrease in diversity indices [5]. In fjords [14], lagoons [12], estuaries [25], and harbours [33] alike, the presence/absence of a foraminiferal species have been shown to reflect environmental conditions. For instance, certain opportunistic species such as *Stainforthia fusiformis* [13], *Bolivina* spp. [18], *Quinqueloculina stelligera* [26], *Quinqueloculina stalkerii* [36], and *Ammonia tepida* [2] have all been linked to adverse environmental conditions caused by OM enrichment and severely hypoxic bottom waters. The understanding of foraminiferal species response to environmental changes led to the definition of indicator species. These species are meant to provide information about environmental conditions. The knowledge of the environmental requirements of a species can be used to detect changes in abiotic conditions or to assess the environmental health of the study area.

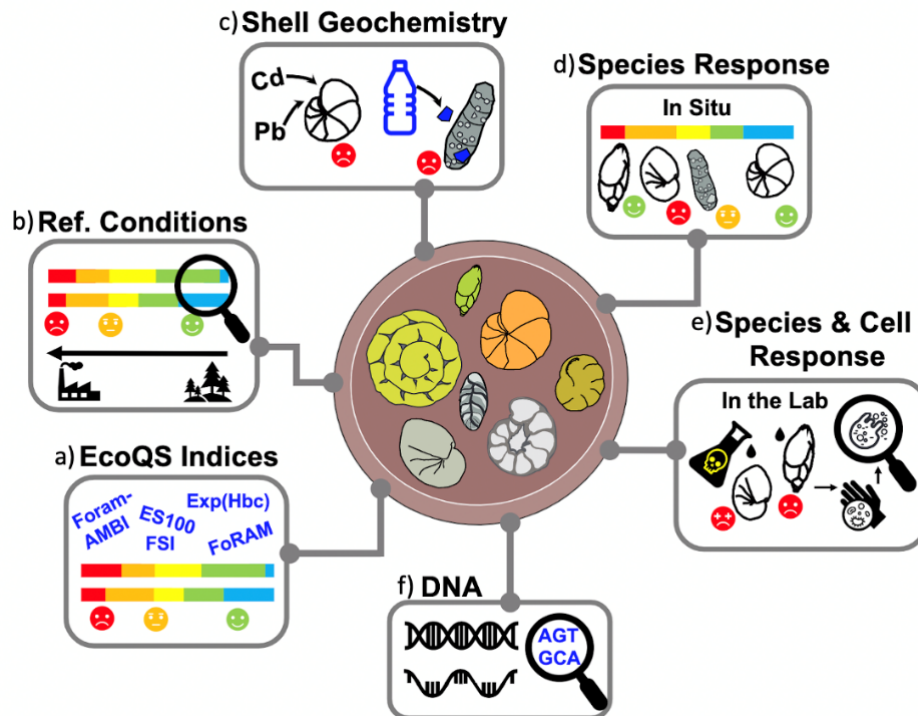


Figure 19. Overview of foraminiferal applications within biomonitoring studies, including (a) EcoQS indices based on species diversity and sensitivity; (b) reconstruction of preindustrial baseline (reference conditions); (c) accumulation of pollutants (e.g., heavy metals and present in situ (e.g., field studies) and (e) simulated in the lab (e.g., culturing experiments); and (f) genomic methods, such as eDNA and sedaDNA. Adapted from [35]

3.1 Indicative value of benthic foraminiferal species as proxy of the environmental conditions

In the Marennes-Oléron Bay, changes in living (stained) benthic foraminiferal assemblages were analysed and compared with temporal changes in the properties of intertidal sediments influenced by Pacific oyster cultivation during a critical period in spring/summer oyster mortality [2]. From the end of May to mid-June 2004, the geochemical characteristics at the water–sediment interface and within the sedimentary column underwent marked changes. Both organic enrichment by oyster cultures and seasonal warming induced an alteration of the biogeochemical cycles in the sedimentary column (Fig. 20).

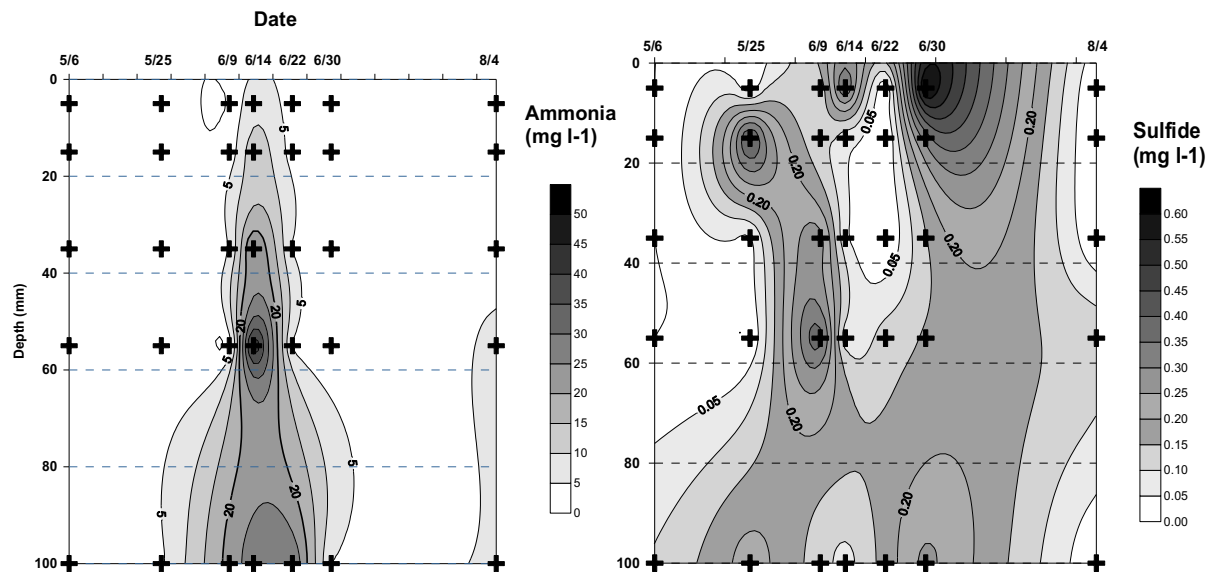


Figure 20. Temporal changes in depth profiles of porewater ammonia and sulfide contents (mg L^{-1}) within sediment cores sampled at Ronce-Perquis from 22 April to 4 August. Adapted from [2]

This acute environmental stress largely constrained foraminiferal species (Fig. 21). *Ammonia tepida* dominated the stained assemblage during the whole sampling period with an average occurrence of 80%. Conversely, the abundances of *Haynesina germanica* and *Brizalina striatula*, decreased significantly and rapidly during the hypoxic event. Last, *Criboelphidium gunteri* abundances drastically increased when the environmental conditions became more favorable. These results are in accordance with the known ecology of these species. Specifically, *A. tepida* is a known highly tolerant species (Armynot du Châtelet et al. 2004, Bergin et al. 2006). *Haynesina germanica* may tolerate the first stage of stress (Samir and El-Din 2001, Romano et al. 2008, Armynot du Chatelet et al. 2011) but abundances would drop at the maximum of a perturbation like observed in the Pertuis Charentais [9]. Conversely, *C. gunteri* is a pioneer species (Debenay et al. 2003) even exhibiting an opportunistic behavior [9]. In the Pertuis Charentais, it clearly benefited from the huge drop in abundances of the other species.

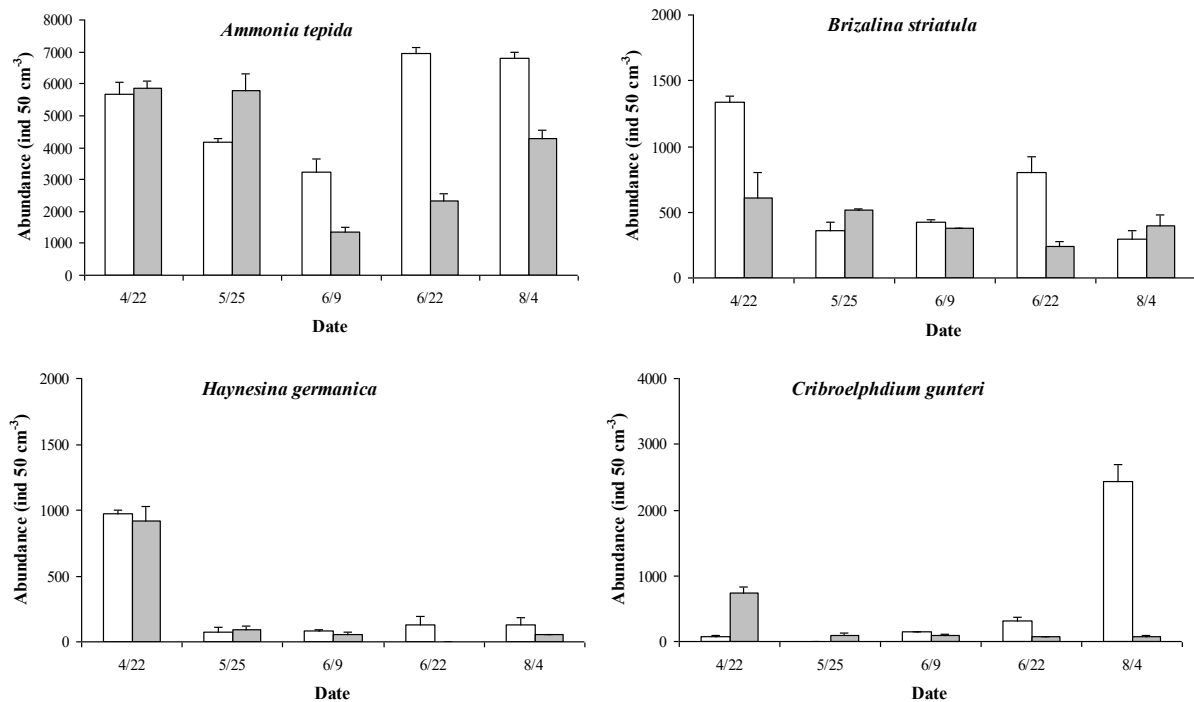


Figure 21. Abundances of *Ammonia tepida* (a), *Brizalina striatula* (b), *Cribroelphidium gunteri* (c) and *Haynesina germanica* (d) at 0-0.5 (white) and 0.5-1 cm depth (grey) of sediment cores sampled at Ronce-Perquis from 22 April to 4 August. Modified from [2]

In studies in the Rade of Cherbourg and Corsica (France), we clearly identified indicator species of the presence of fish farming. The abundances of tolerant and sensitive species were clearly constrained by the presence of fish cages. Tolerant species were more abundant in the assemblages impacted by the farms while sensitive species were more abundant outside the fish farms. This is mostly due to the accumulation of organic matter that leads to anoxia in sediments under fish farm cages (Porrello et al. 2005, Yokoyama et al. 2006). In the Rade of Cherbourg, sensitive species like *Discorbis vilardeboanus*, *Cribroelphidium magellanicum* (Armynot du Châtelet et al. 2004) and *Bolivina pseudoplicata* (Alves Martins et al. 2009) mostly occurred outside the farm, while their relative abundances dropped under the cages. Under the Salmon cages in the Rade of Cherbourg, only the tolerant species *Bolivina variabilis* (Debenay et al. 2001, Armynot du Châtelet et al. 2009) and *Quinqueloculina stelligera* (Armynot du Chatelet 2003, Bergamin et al. 2003, Jorissen et al. 2018) remained highly

abundant. Likewise, in Corsica, *Rosalina bradyi*, *Quinqueloculina stelligera*, *Eggerelloides scaber* and *Textularia agglutinans* appeared to tolerate the first stage of the TOC enrichment but were replaced by opportunistic species under the cages. Noticeably, *Bulimina aculeata*, *Bolivina dilatata* and *Quinqueloculina stalkerii* exhibited a clear trend of increasing relative densities towards the fish farming cage (Fig. 22). Like other bolivinids, this species is able to flourish under harmful conditions (Martins et al. 2015) and is often considered a stress-tolerant or opportunistic species (Barras et al. 2014; Dimiza et al. 2016, [29]); able to positively respond to labile OM (Mojtahid et al. 2009) and to increasing TOC content (Donnici and Barbero 2002). The species *R. bradyi* is often considered a sensitive species, hence it was surprising to observe a tolerant behavior toward TOC enrichment. However, high abundances for *R. bradyi* were also reported in fish farms in Tunisia (Damak et al. 2020) and in abalone farms in Korea (Choi et al. 2019). Furthermore, *Rosalina* spp. are often abundant in organic-rich habitats (El Kateb et al. 2018), being influenced by the quality of the OM (Buosi et al. 2012). Our observations of *R. bradyi* in the fish farms of Corsica further confirm that it may benefit from the organic matter released by aquaculture.

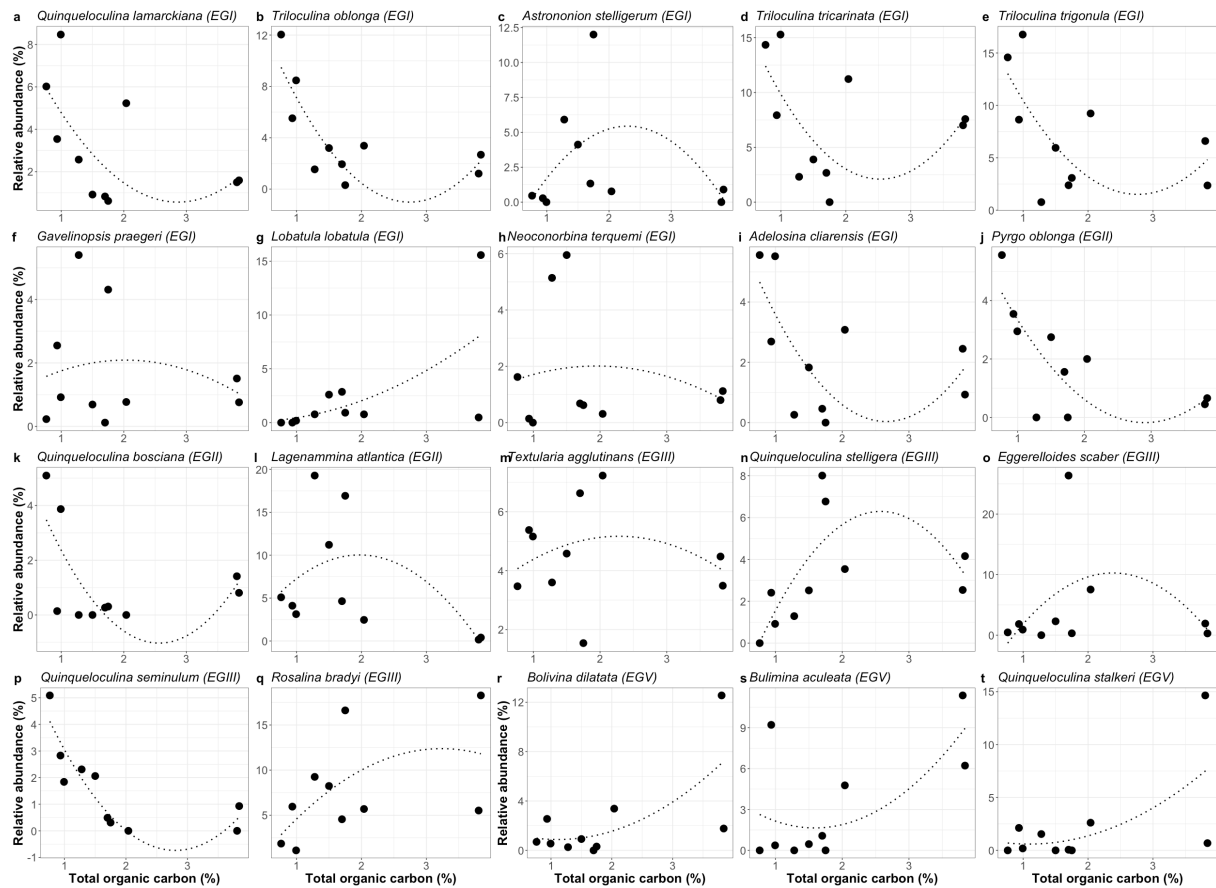


Figure 22. Distribution patterns of the relative abundances (filled black circles) against TOC at sampling sites (black dotted-line: second-order polynomial regression) of the main foraminiferal species in Corsican fish farming areas. Modified from [36]

The outcomes of such studies aiming at understanding the indicative values of foraminiferal species led to the definition of key species typical of different habitats. The presence of these species would give key information on the environmental features prevailing at study sites.

For example, along the intertidal areas of the Hauts-de-France we documented the occurrence of three main type of foraminiferal assemblages reflecting contrasting ecological conditions at regional scale (Fig. 23): 1) estuarine macro-tidal assemblages (*Haynesina germanica* associated to Elphidiidae) in minimally impacted estuaries; 2) industrial-perturbed assemblages (*H. germanica* and *Criboelphidium excavatum*) in harbor areas; and 3) infaunal-

dominant assemblages (*Bolivina variabilis* and *Brizalina pseudoplicata*) in embankment areas [25].

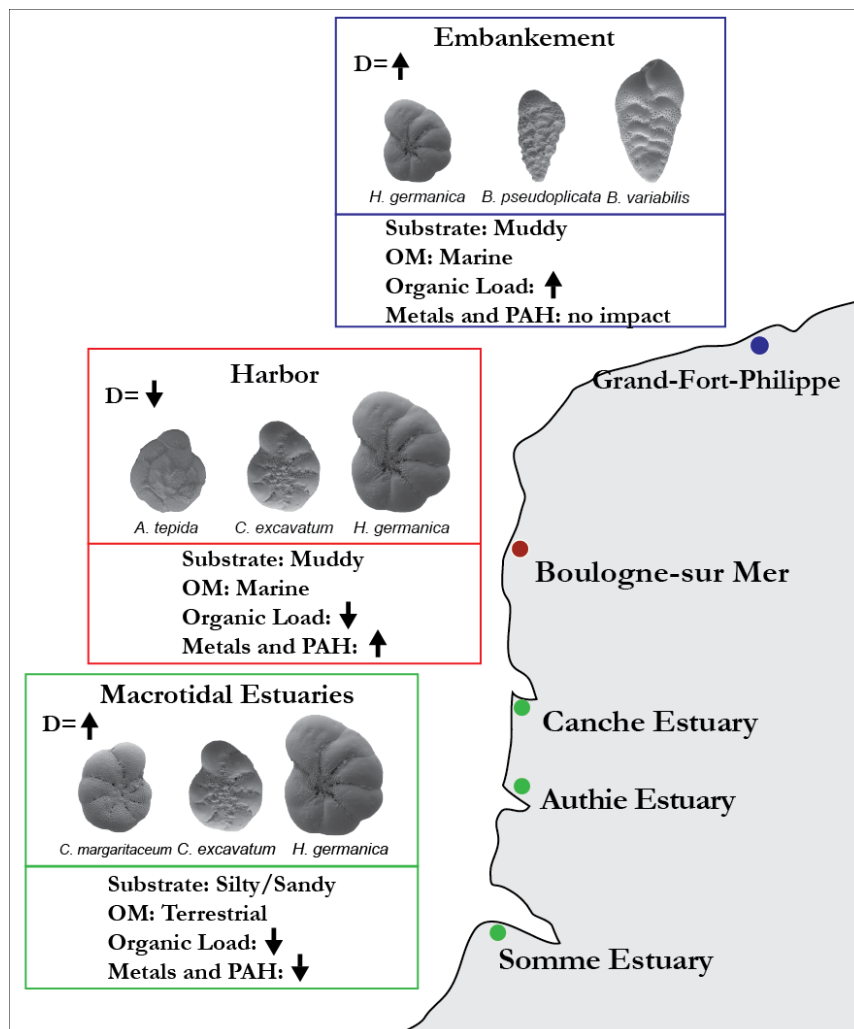


Figure 23. Synthetic scheme of the foraminiferal communities in relation to the different ecological characteristics in the Hauts-de-France. (D=Diversity, OM=Organic Matter, PAH=Polycyclic aromatic hydrocarbons). Adapted from [25]

The presence/absence of species can be also used to identify species association typical of natural benthic habitats at biogeographical scale. Specifically, we performed a thorough review of the literature to synthesize foraminiferal data and biodiversity in transitional waters in the southern North Sea and the eastern English Channel [13]. This work allowed us to associate foraminiferal species to specific environmental units found in TWs (Fig. 24). In order to so, we selected relevant datasets have been strictly selected based on: *i*) living foraminifera (rose Bengal stained), *ii*) availability of raw data, *iii*) georeferenced samples, at

least by means of an explicit map, and, if available, iv) a description of the environmental parameters including sediment grain size, elevation, and TOC content. On the basis of the available databases including 700 sampling stations from subtidal to salt marsh areas, we synthesised the regional distribution of living benthic foraminifera in transitional environments along the English Channel and southern North Sea. Indicator species analyses assign 37 foraminiferal taxa to high salt marsh, middle salt marsh, low salt marsh, tidal flat, tidal channel, and subtidal environmental units. Species are indicator of a single unit (e.g., *Criboelphidium gunteri* for tidal flat) up to four units (e.g., *Haynesina germanica* from tidal flat to middle marsh).

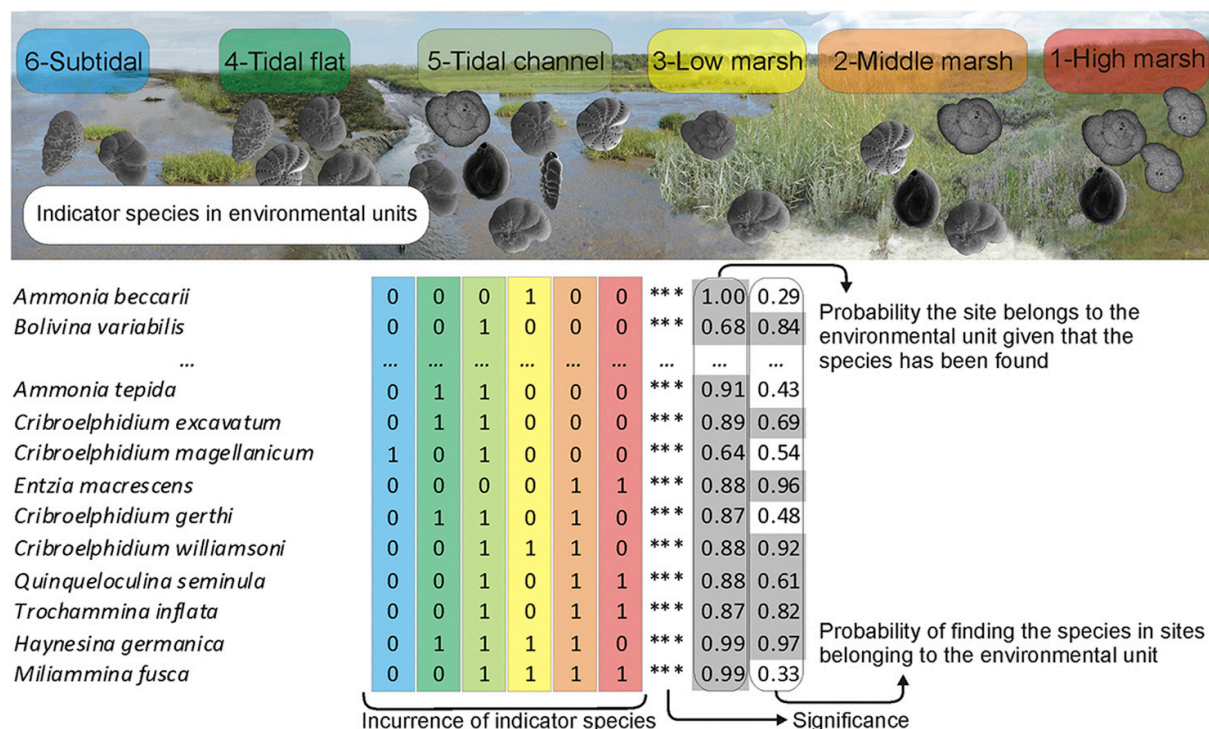


Figure 24. Scheme presenting examples of distribution of indicator species whose abundance is greater than 5%, along the transitional environment gradient of the English Channel and the North Sea. Units provided show where the species are calculated as indicator species. Index is the number of samples where the species is found with the environmental unit or the combination of units. The degree of significance is provided: ***: 0.001, **: 0.01, *: 0.05. Component 'A' is the probability that the surveyed site belongs to the target site group given that the species has been found. This conditional probability is called the specificity of the species as an indicator of the site group (De Cáceres et al., 2010). Component 'B' is the probability of finding the species in sites belonging to the site group. This second conditional probability is called the fidelity of the species as an indicator of the target site group (De Cáceres et al., 2010). For A and B, probability values greater than 0.6 are underlined. The association statistic (De Cáceres and Legendre, 2009) is provided. [13]

These examples illustrate the accuracy of benthic foraminiferal species to inform about environmental conditions in natural and human-modified habitats. Amongst others, these quantitative studies constitute a baseline for the planning of future foraminiferal-based biomonitoring programs. It further contributes to the international effort of getting a better understanding of benthic foraminiferal response along organic and chemical gradient of pollution in order to implement a foraminiferal sensitivity-based biotic index in intertidal and transitional waters.

3.2 Developing a sensitive-based index based on benthic foraminifera: Foram-AMBI

In 2011, the informal FOraminiferal Bio-Monitoring (FOBIMO) international working group (WG) was established with the aims (i) to standardize methods for the use of benthic foraminifera in environmental biomonitoring [6] and (ii) to unify the effort of “foraminiferologists” to establish a common biotic index to assess the EcoQS (Alve et al. 2016, Jorissen et al. 2018). The first aim of the FOBIMO WG was to agree to focus on and design an index based on the ecological response of benthic foraminiferal species to total organic carbon (TOC). Specifically, this implied assessing the level of sensitivity/tolerance of foraminiferal taxa to TOC by assigning them to ecological groups (EGs). In the pioneer work of Alve et al. (2016), the authors proposed to assign benthic foraminifera to five EGs following the terminology and definitions used in the macrofauna-based AZTI Marine Biotic Index (AMBI) (Borja et al. 2000) *i.e.*, sensitive (EGI), indifferent (EGII), tolerant (EGIII), second-order opportunistic (EGIV) and first-order (most) opportunistic (EGV) (Fig. 25). Recently, Jorissen et al. (2018) suggested using a more explicit terminology and definitions for benthic foraminifera; describing species belonging to EGIII as “third-order opportunists”.

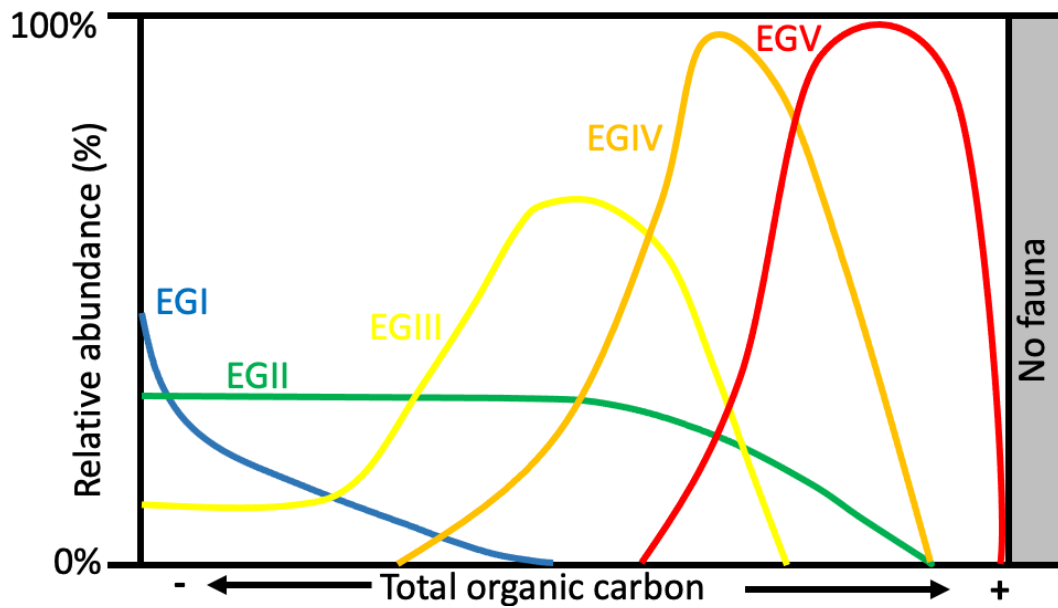


Figure 25. Theoretical graph providing the succession of benthic foraminifera belonging to the five EGs according to their response to organic carbon enrichment. Adapted from [36]

In the FOBIMO sub-working group on intertidal and transitional waters, we aimed at (i) developing an objective protocol for the species' assignment to EGs, (ii) investigating if it is possible to assign benthic foraminiferal species from intertidal areas and TWs from the considered geographical zones to the five EGs described in Alve et al. (2016) according to species responses to sediment TOC content, (iii) if applicable, validating the established lists by testing them using a sensitivity-based index on separate and independent datasets from the same geographic regions, and (iv) testing the hypothesis that species ecological requirements may vary between habitats/ecosystems and along latitudinal gradients by comparing species assignment lists [29][31]. One of the main issues to overcome was that intertidal areas and TWs are naturally stressed environments characterized by strong environmental gradients (*e.g.* salinity, temperature, grain-size, dissolved oxygen and organic matter) but they also commonly experience high levels of anthropogenic stresses. Species distribution in these environments is the result of the complex interplay between natural and human-induced stressors. Therefore, it was challenging to achieve a reliable assignment of

benthic foraminiferal species from these environments to EGs according to species response by considering only TOC (see Box 2 for details on the method).

Box 2: Methodology to assign species to ecological groups

For the purpose of the sub-WG work, we seek for an approach to avoid any use of the « best expert judgment ». A method based on a modification of the log-normal distribution of individuals among species was proposed by Gray and Pearson (1982), and successfully tested to identify potential indicator species (Pearson et al. 1983). In an early attempt to classify intertidal benthic foraminiferal species into AMBI EGs during my PhD work, we used canonical correspondence analysis to look for similarity in the response of benthic macrofauna and foraminifera to environmental conditions. The resulting classification was meaningful, but similarities between macrofauna and foraminifera were not quantitatively assessed, making this approach not robust enough. Finally, we decided to use the weighted-averaging (WA) optimum and tolerance approach (Ter Braak 1987, Birks et al. 1990). The idea behind WA is that in a coastal lagoon with a certain TOC range, benthic foraminifera with their TOC optimum close to the coastal lagoon's TOC concentrations will most likely be the most abundant species. A simple and ecologically reasonable estimate of a benthic foraminiferal species' optimum is the average of all TOC values for intertidal areas and TWs in which the species occurs, weighted by the species relative abundance (WA regression). The estimated optimum allows to give an objective assessment of the species environmental requirements. To summarize, the WA optimum method is rapid, easy to implement, theoretically sound, robust (Birks et al. 1990) and led to an objective assessment of species-specific indicative values (Fig. 26A and 26B). [29][31]

Our work focused on the European coasts. Because of the particular characteristics of foraminiferal habitats and communities, we decided to present the foraminiferal species assignments split in two lists: one for the European Atlantic (Fig. 26A) and one for the Mediterranean region (Fig. 26B) [29]. A literature review allowed us to select 42 studies that met the retained criteria: 21 studies from the English Channel/European Atlantic intertidal and TWs and 21 from the Mediterranean Sea (data available in [31]).

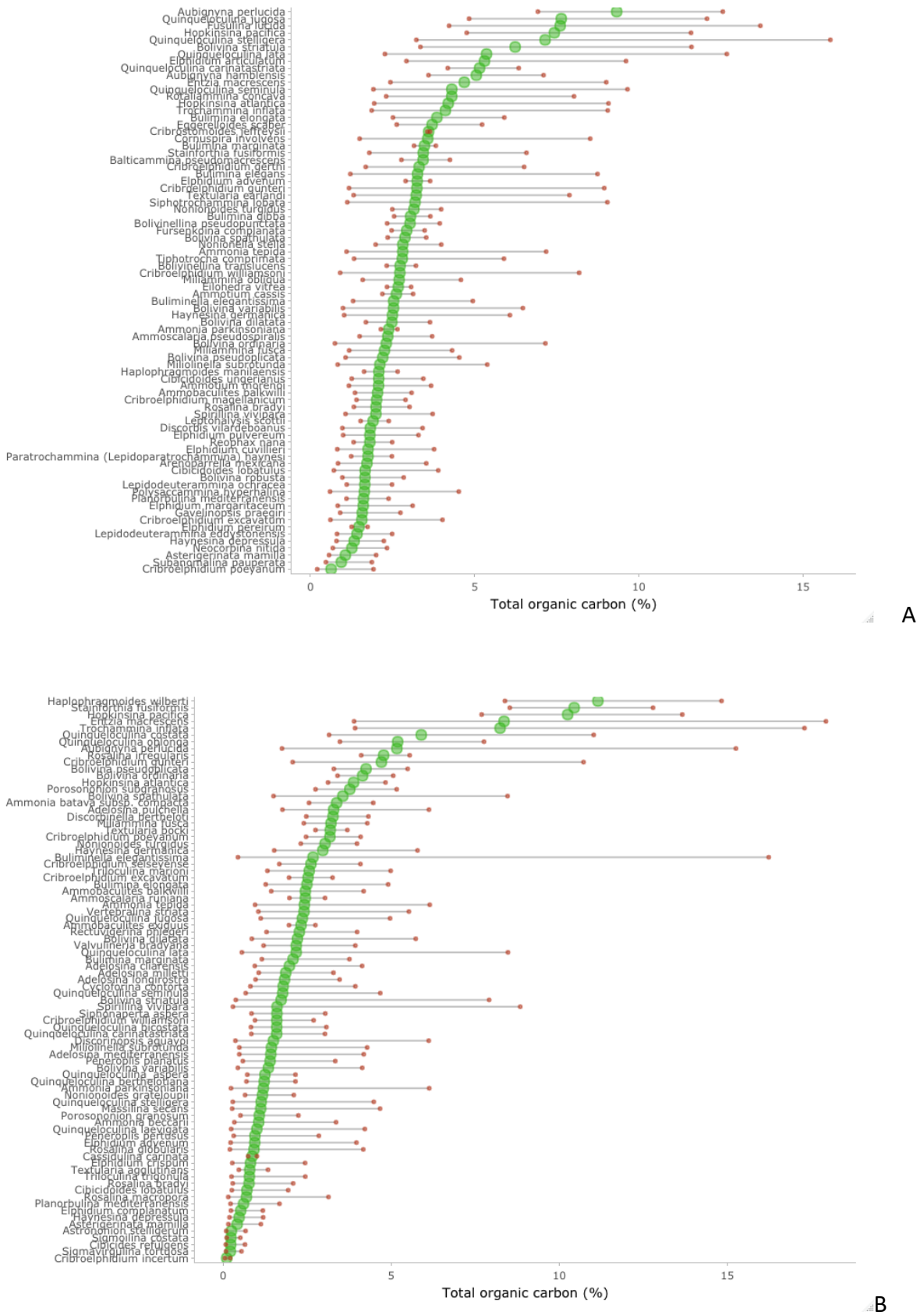


Figure 26. Caterpillar plot showing the optimum (green dots) and tolerance range (bars) to TOC of benthic foraminiferal species (A) in the English Channel/European Atlantic and (B) in the Mediterranean Sea intertidal areas and transitional waters. Adapted from [31]

The recently developed Foram-AMBI (Alve et al. 2016), adapted from AMBI for benthic foraminifera, was used to test the reliability of the species lists [29] on two independent datasets from the Pertuis Charentais [M8] and the Harbord of Cagliari (Schintu et al. 2016).

In both validation datasets, Foram-AMBI yielded a positive significant correlation with organic matter content; reflecting changes in the EcoQS (Fig. 27). The results of the tests showed that the classification, obtained with the calculation of the WA “optimum” values for each species, probably adequately reflects differences in species tolerance of organic load-related stress. The outcome was a reliable assessment of EcoQS in the Pertuis Charentais and in the Harbor of Cagliari.

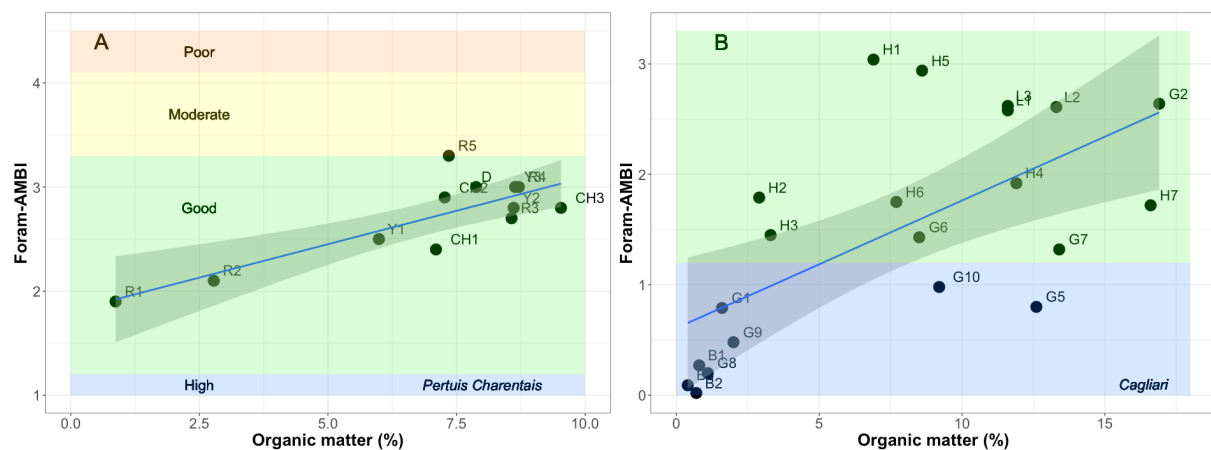


Figure 27. Relationship between indices and OM in the Pertuis Charentais (A) and in the harbor of Cagliari (B). Linear regression models are in blue, grey shaded areas being the 95% confidence interval. In both panels, EcoQS are reported. Modified from [29]

However, in studies in Norway [14] and Corsica [36], we stressed that species lists from Alve et al. (2016) and Jorissen et al. (2018) must be updated. Specifically, according to their distribution patterns along the TOC gradient in two Fish farms in Corsica (Fig. 22), we proposed to re-assign some species from the original list (Jorissen et al. 2018): *Triloculina oblonga* and *Quinqueloculina lamarckiana* to Ecological Group (EG) I, *Rosalina bradyi* to EGIII, *Bolivina dilatata*, *Bulimina aculeata* and *Quinqueloculina stalkerii* to EGIV. It led to a more accurate assessment of the health of the ecosystem below the fish cages (Fig. 28). The index Foram-AMBI based on Dubois et al.’s updated list [36] significantly correlated with TOC, while Foram-

AMBI computed with Jorissen et al.'s original list (Jorissen et al. 2018) did not. These results emphasize the need to conduct more quantitative studies to improve the knowledge of benthic foraminiferal response to TOC in order to improve the species' assignment to EG, and further facilitate the implementation of Foram-AMBI.

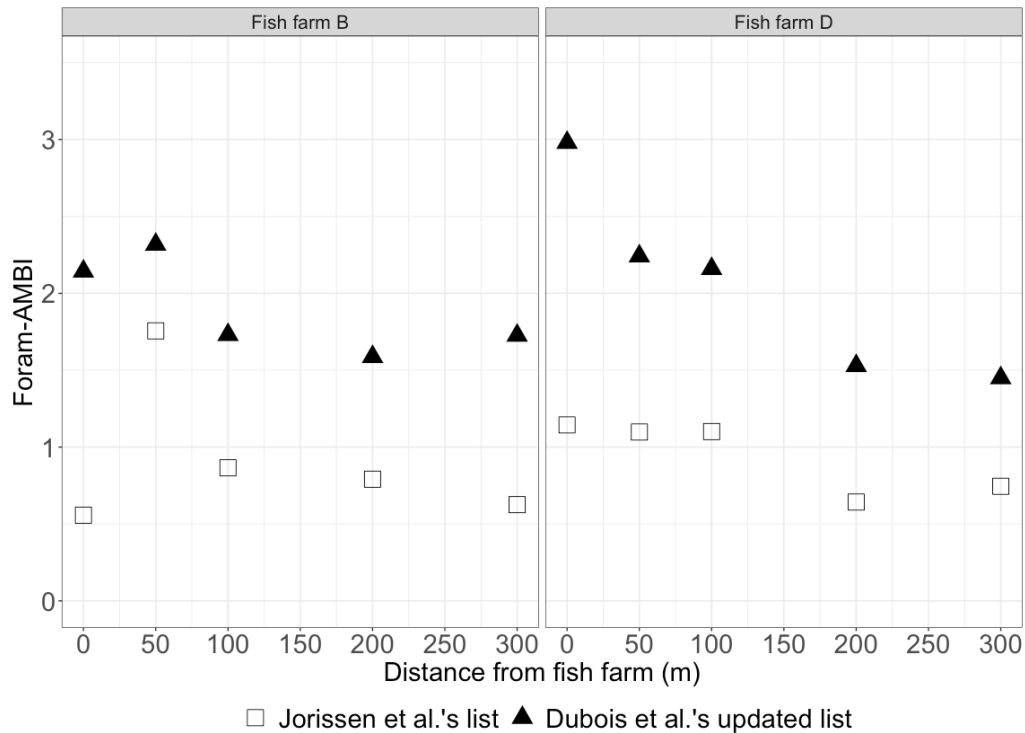


Figure 28. Comparison of Foram-AMBI values according to Jorissen et al.'s species list and the Dubois et al.'s updated list. Adapted from [36]

We also evaluated the accuracy of Foram-AMBI and define the EcoQS in the Bagnoli area (Tyrrhenian Sea, Italy) based on a traditional morphology-based approach and eDNA metabarcoding. [33]. To summarize, significant differences (*i.e.* diversity and assemblage composition) in both morphological and molecular datasets were found between the relatively low- to unpolluted and the most polluted areas. Similarly, the selected ecological indices of both morphological and molecular datasets strikingly and congruently resulted in a clear separation following the environmental stress gradient (Fig. 29). The molecular indices (*i.e.* $g\text{-exp}(H'_{bc})$, $g\text{-Foram AMBI}$, and $g\text{-Foram AMBI-MOTUs}$) reliably identified poor-to-bad EcoQS in the polluted area in front of the former industrial plant.

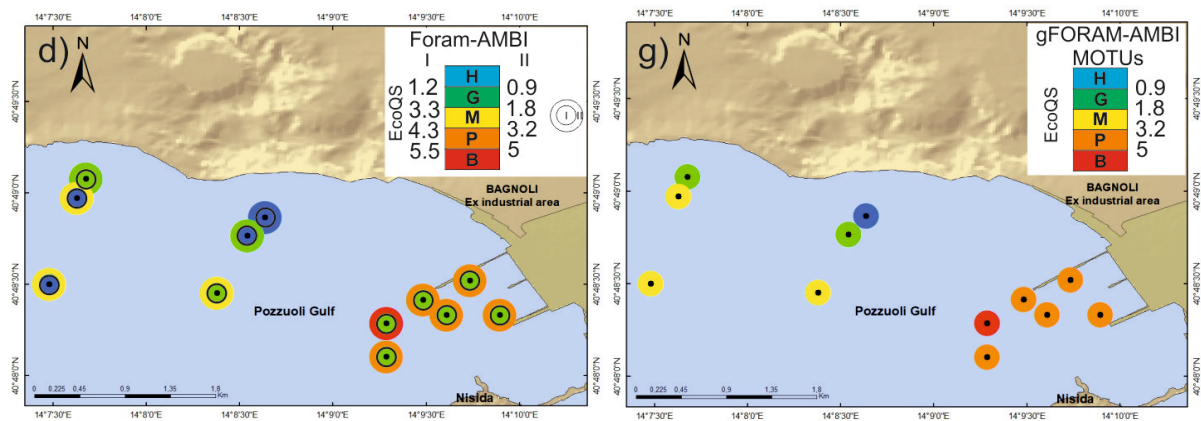


Figure 29. Spatial plots of a) Foram-AMBI and b) g-Foram-AMBI MOTUs. Adapted from [33]

In conclusion, our effort to assign foraminiferal species to ecological groups of sensitivity to total organic carbon showed that the classification reflects differences in species tolerance of organic load-related stress. The tests of the species' lists on the different datasets can be considered a promising start which is worthy to pursue using other data sets. In transitional waters, the assignment of typical salt marsh species was, however, not possible, since their classification in the opportunist EGs was not reflecting their natural ecological requirements. Furthermore, the few promising results from studies testing Foram-AMBI does not ensure that this index and comparable methods will perform in all waters. There is hence an urgent need to apply and test sensitivity-based foraminiferal indices in different ecosystems and against different pollution sources. In addition, the congruent and complementary trends between morphological and molecular biotic indices reported in the port of Bagnoli further support the need for more studies considering and testing the application of foraminiferal metabarcoding in routine biomonitoring to assess the environmental impacts of heavily polluted marine areas.

Chapter 4. The future of foraminiferal research: tackling diversity at individual level

The latest technological advances offer new perspective in terms of research on benthic foraminifera. Fluorescence-based methods allow visual and (semi)quantitative studies of the ultrastructural organization and processes of the cell under natural as well as manipulated conditions. They were used to study esterase activity, cell viability, calcium signaling, pH variation, reactive oxygen species, neutral and polar lipids, lipid droplets, cytoskeleton structures, Golgi complex, acidic vesicles, nuclei, and mitochondria in different foraminiferal species (see review in Frontalini et al. 2019). In this context, the study of kelpoplasty in benthic foraminifera draws much attention, and largely beneficiates from the latest progress in microscopy imaging (Jauffrais et al. 2016b, Frontalini et al. 2018, LeKieffre et al. 2018, Jauffrais et al. 2019, Jesus et al. 2022). Furthermore, following the seminal work from Arnold (1953) and many studies since then (until 2000), they have been more interest over the last years on the behavior of benthic foraminifera (Jauffrais et al. 2016a, Maire et al. 2016). The development of such methods allows the understanding of processes at the scale of an individual; hence providing mechanistic explanations of processes observed at the scale of a population or community.

4.1 Tackling diversity at cellular level

The adverse effects of engineered nanomaterials (ENM) in marine environments have recently attracted great attention although their effects on marine benthic organisms such as foraminifera are still largely overlooked. In a study, we documented the effects of three negatively charged ENM, different in size and composition, titanium dioxide (TiO₂), polystyrene (PS) and silicon dioxide (SiO₂), on the benthic foraminifera *Ammonia*

parkinsoniana) using multiple approaches *i.e.* transmission electron (TEM), environmental scanning electron (ESEM), coupled with energy dispersive X-ray spectrometry (EDS), and confocal laser scanning (CLSM) microscopies, to highlight the cellular response to such nanoparticles stressors [20]. This research clearly shows the presence, within the foraminiferal cytoplasm, of metallic (Ti) and organic (PS) ENM (Fig. 29) that promote physiological stress as already documented for pelagic species (*e.g.* fish, shrimp) (Baker et al. 2014, da Costa et al. 2016). Given their smaller size and large surface area per unit mass, ENM have greater potential of being accumulated, possibly causing deleterious effects in the host (Bochicchio et al. 2017).

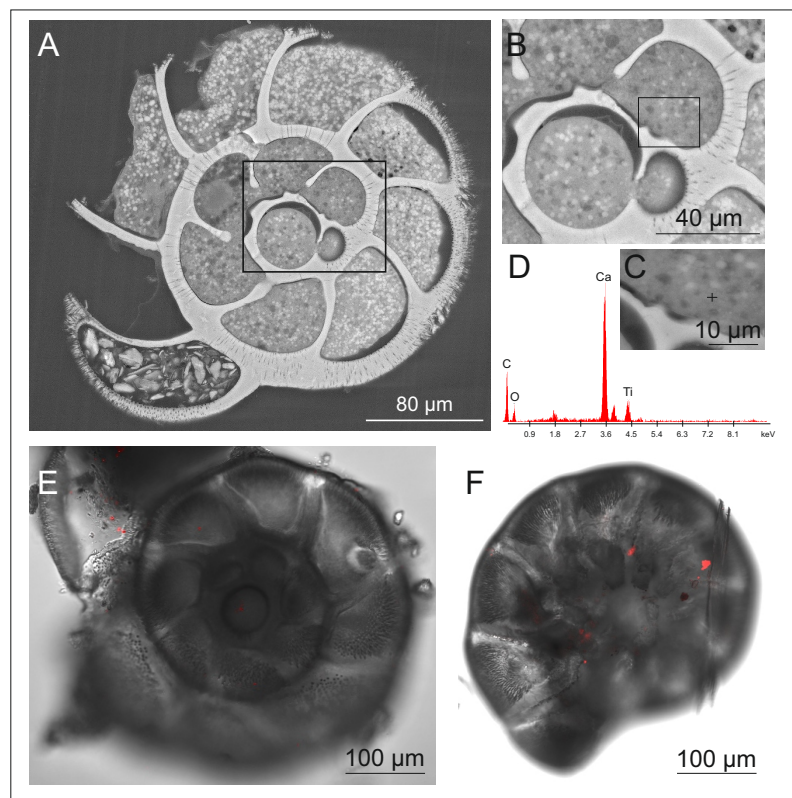


Figure 30. ESEM micrographs (A–C) showing the presence of Ti nanoparticles in the treated *Ammonia parkinsoniana* specimens. (A) Overview of specimen section where the chamber containing Ti nanoparticles, as dark spots, has been highlighted (black rectangle). (B) High magnification of the three last chambers. (C) High magnification of the ante-penultimate chamber with the arrow marking the occurrence of Ti nanoparticles. (D) EDS spectrum of the agglomerate shown in C. Fluorescent confocal image and bright field overlay micrographs of single optical sections (E–H) showing the localization of Flash Red conjugated-PS in *A. parkinsoniana*. Adapted from [20]

Specifically, marked increases in the accumulation of neutral lipids (Fig. 31) and enhanced reactive oxygen species production (Fig. 32) occurred in ENM-exposed specimens regardless of ENM type. Proliferation of neutral lipid droplets (e.g., esterified cholesterol, triglycerides) was also reported in benthic foraminifera exposed to heavy metals (Le Cadre and Debenay 2006). Production of reactive oxygen species is also known in the symbiont-bearing foraminifera *Amphistegina lessonii* and *A. gibbosa* as a response to Zn exposure or light stress, respectively (Williams and Hallock 2004, de Freitas Prazeres et al. 2011). In foraminifera, oxidative stress may induce cellular damage and death as a possible response to different environmental stressors, though they may use oxygen derived from the breakdown of environmentally and metabolically produced H_2O_2 (Bernhard and Bowser 2008).

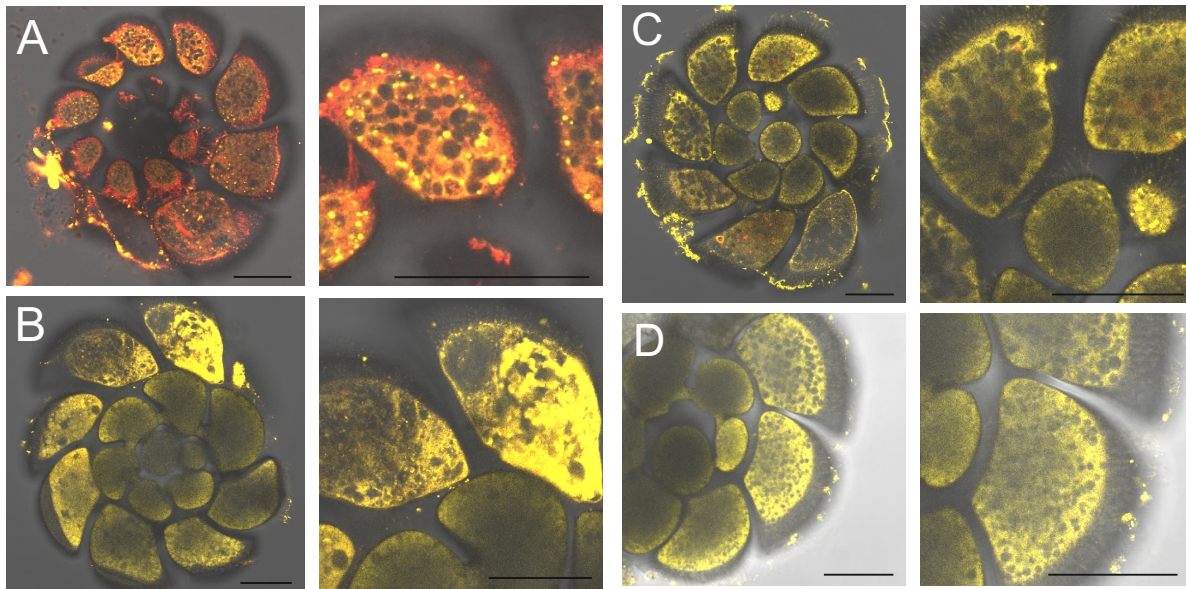


Figure 31. CLSM images showing the effect of NP exposure on lipid distribution of *Ammonia parkinsoniana* labeled with Nile Red. CLSM micrographs of single optical sections showing overlay of NR yellow (neutral lipids) and red (polar lipids) fluorescence for control (A) and treated TiO₂ (B), SiO₂ (C), PS (D) specimens. Scale bar: 50 μ m. Adapted from [20]

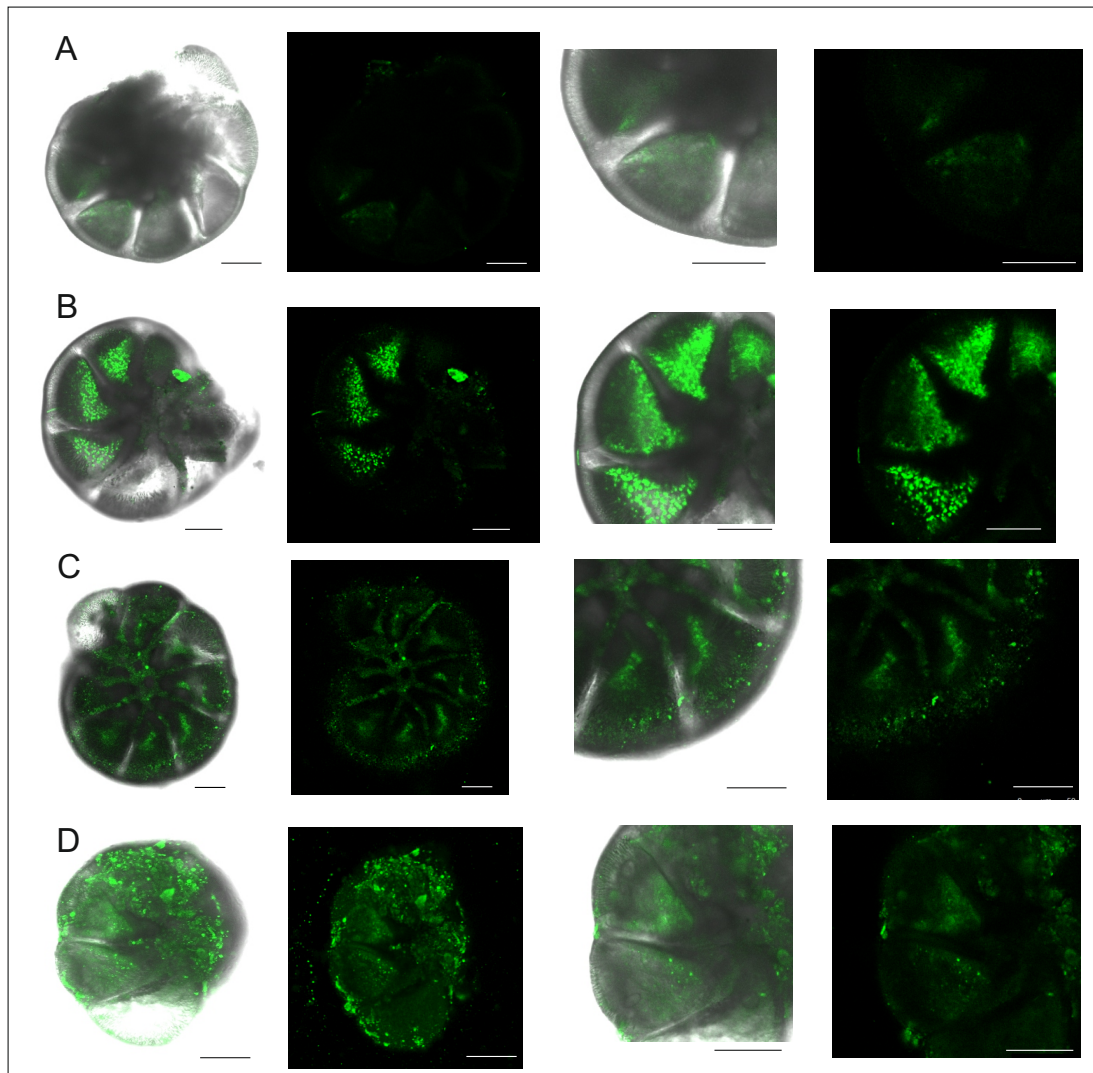


Figure 32. CLSM images showing the effect of NP exposure on ROS production of *Ammonia parkinsoniana* labeled with CellROX® Green. CLSM micrographs of single optical sections showing overlay of green fluorescence-bright field image and fluorescence for control (A) and treated TiO₂ (B), SiO₂ (C), PS (D) specimens. Scale bar: 50 µm. Adapted from [20]

This study showed that ENM represent ecotoxicological risks for benthic foraminifera. Our study also confirmed the potential of microscopy and fluorescent and fluorogenic probes to study foraminiferal ultrastructures. The application of these methods in foraminiferal biology represents a complementary technique to understand the effects of natural and anthropogenic stressors at individual scale.

4.2 Tackling diversity through behavior assessment

In a study on three key foraminiferal species from temperate intertidal mudflats *i.e.*, *Ammonia tepida*, *Haynesina germanica* and *Criboelphidium excavatum*, we developed experimental protocols to specifically focus on the detailed nature of their motility, in terms of geometric and stochastic complexity of their motion behavior, species-specific variability and specimen-specific variability (Fig. 33) [8]. This approach is critical to understanding the ecology of motile organisms, as the adaptive value of individual variability in motion behavior is increasingly acknowledged as a competitive advantage in temporally and spatially complex landscapes (see, e.g., Chapperon and Seuront 2011 for a discussion on this topic). We further assessed their geotactic behavior in order to evaluate their behavioral response to gravity.

4.2.1 High Inter-individual variability in motion-behavior

The motion behavior of the three species of foraminifera was consistently characterised in both control and geotaxis experiments by a strong inter-individual variability in the complexity of the trajectories followed by distinct individuals, and strong fluctuations in the temporal dynamics of their successive movements along the aforementioned trajectories (Fig. 33). Specifically, *Ammonia tepida*, *Haynesina germanica* and *Criboelphidium excavatum* exhibited trajectories with highly variable levels of geometric complexity in both control and geotaxis experiments (Fig. 33A, E). Likewise, the velocity v_t of specimens along their trajectories are consistently characterised by a very high variability, independent of both the complexity of the trajectory and the treatment considered (Fig. 33B–D, F–H). Inter-individual variability was also observed in our study considering the potential of benthic

foraminiferal species (*Ammonia tepida*, *Haynesina germanica*, *Quinqueloculina seminulum*, *Miliammina fusca* and *Criboelphidium williamsoni*) to rework surface sediments [34].

Note that the differences identified in [8] and [34] cannot be related to environmental factors or size, since our experiments were performed on similar-sized individuals under controlled conditions in the absence of any cues. The above mentioned inter-individual variability is then more likely to be an intrinsic property of the species considered here. Behavioral plasticity has previously been reported in foraminifera (Hallock and Hansen 1979, Prazeres et al. 2017), but also in pelagic copepods (e.g., Seuront et al. 2004) and intertidal gastropods (e.g., Chapperon and Seuront 2011) with individuals from the same species showing both a large repertoire of behavioral traits (e.g. feeding activity, trajectory complexity, intensity of displacement) and a large variability in the values of each trait.

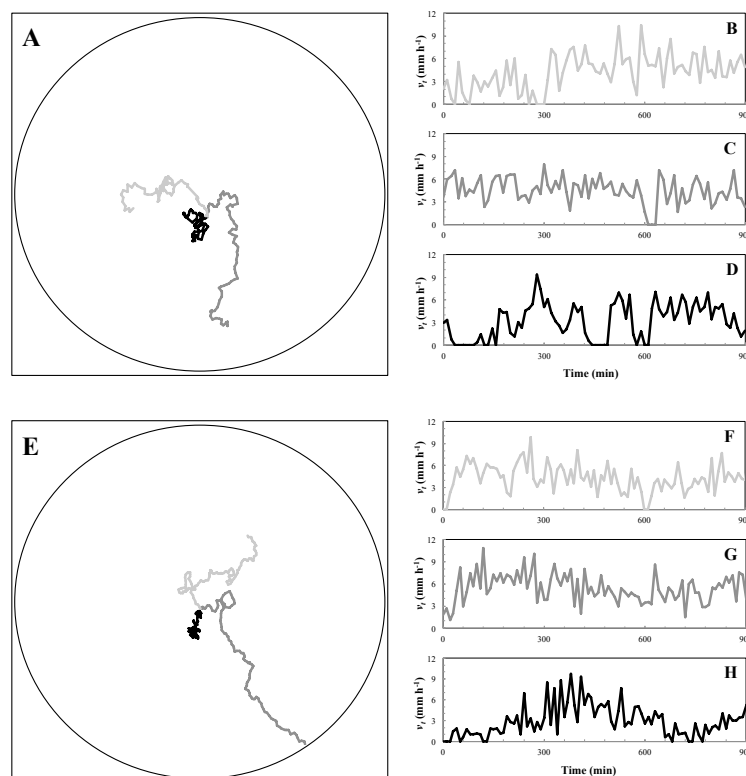


Figure 33. Illustration of the archetypical geometric (A, E) and stochastic (B–D, F–H) behavioral properties of three foraminiferal specimens (here *Ammonia tepida*) observed in control (A–D) and geotaxis (F–H) experiment, conducted in circular experimental arenas 7.5 cm in diameter. Distinct individuals were used in control and geotaxis experiments. Each colour code corresponds to the same *A. tepida* specimen in both (A) and (E), and the colour codes used for the three trajectories shown in (A, E) matches those used in (B–D) and (F–H). Adapted from [8]

4.2.2 Motion-behavior is species-specific

We observed differences in the motion behavior of *Ammonia tepida*, *Haynesina germanica* and *Criboelphidium excavatum*. It indicates that each species may have its own behavioral repertoire, which here specifically relates to the range of behavioral levels of activity, movement speed and trajectory complexity (Fig. 34). The lower speed and higher NGDRs of *Ammonia tepida* and *Haynesina germanica*, for example, imply they explore their environment slowly and extensively with straighter trajectories. In contrast, *C. excavatum* individuals explore the environment more rapidly and intensively with more convoluted trajectories. These behavioral strategies are consistent with an optimal foraging strategy: an intensive (area restricted) search strategy (Pyke 1984) and extensive search strategy (or transecting; Bell 1991) are respectively optimal under conditions of high food concentration and spatially-localised food patches. Specifically, *Haynesina germanica* and *Ammonia tepida* are both able to feed on benthic diatoms (Ward et al. 2003, Pascal et al. 2008). Since microphytobenthos microscale (*i.e.* centimetre-scale) distribution is extremely patchy (Seuront and Spilmont 2002, Seuront and Leterme 2006, Seuront 2010, Spilmont et al. 2011), both species would benefit from the extensive search strategy to optimize their likelihood to locate food patches. In contrast, *Criboelphidium excavatum* feed both on benthic diatoms (Lopez 1979) and metazoans (Murray 2006). The lack of clear overlap in the microscale distribution of meiofauna and microphytobenthos (Blanchard 1990) suggests that omnivorous species such as *C. excavatum* may experience a more homogenous distribution of food items through a continuum of meiofaunal and microphytobenthos patches, which consumption would hence benefit from an intensive search strategy.

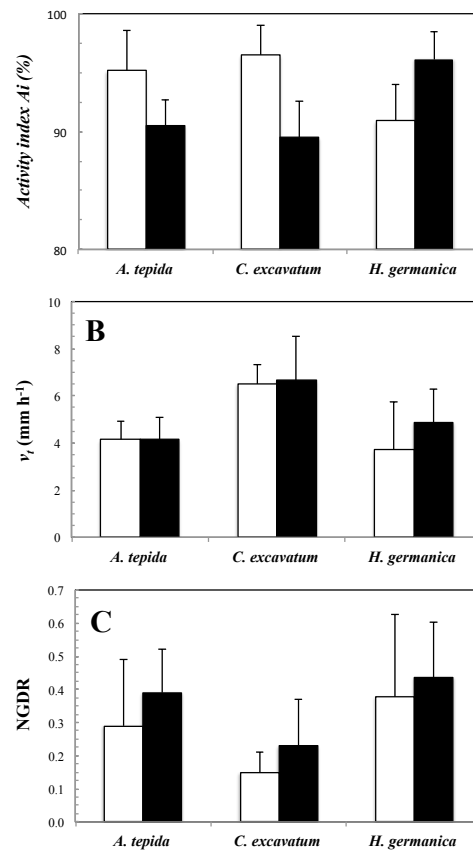


Figure 34. Behavioral properties (activity index, A_i , %, actual speed, v_t (mm h⁻¹) and NGDR of *Ammonia tepida*, *Criboelphidium excavatum* and *Haynesina germanica* estimated from 10-min resolution tracking of specimens in control (white bars) and geotaxis (black bars) experiments. The error bars are standard deviations. Adapted from [8]

4.2.3 Foraminifera showed typical behavior of stressed/unstressed organisms

As a response to gravity, both *C. excavatum* and *Ammonia tepida* exhibited higher NGDRs than during the control experiment, indicative of more extensive foraging behavior consistent with less complex trajectories typically found in stressed organisms; see Seuront (2011a, b) for a detailed discussion on this topic in the context of copepod behavioral ecology. In turn, the lack of changes in *Haynesina germanica* in the geometric complexity in the movement of *H. germanica* between control and geotaxis treatments (Fig. 34C) may indicate that the observed positive geotaxis is not stress related, hence a more natural behavior than the positive and negative geotaxis respectively observed in *C. excavatum* and *A. tepida*. We

see their responses as adaptive advantages in spatially and temporally complex environments prone to a range of both predictable and unpredictable rapid stressors.

In our experiments, conspecific individuals of *Ammonia tepida*, *Criboelphidium excavatum* and *Haynesina germanica* displayed a high variability in their travelled distance but also in their motion behavior, e.g. tortuosity, vertical position (see [22] for further details). Having a wide diversity in the behavioral repertoire between conspecific individuals may be a selective advantage for species facing long-term environmental fluctuations as previously suggested for intertidal gastropods (Chappon and Seuront 2011).

4.3 Tackling functional diversity in benthic foraminifera

The role of benthic foraminifera in the benthic-ecosystem functioning and the associated functional diversity is a fairly untapped question (Schratzberger and Ingels 2018). The movement ability of intertidal foraminifera suggest that they may have a role, yet to be quantified, in benthic–pelagic coupling through their movement on the sediment surface, at the sediment–water interface and within the sediment (Severin et al. 1982, Wetmore 1988, Gross 2002, Cedhagen et al. 2021).

The investigation of the behavioral traits of 5 benthic foraminiferal species typical of European temperate mudflats (*Ammonia tepida*, *Haynesina germanica*, *Quinqueloculina seminulum*, *Miliammina fusca* and *Criboelphidium williamsoni*) revealed an unexpected functional diversity in benthic foraminifera [22]. Specifically, *C. williamsoni* belongs to the epifaunal-biodiffusors, *A. tepida* and *H. germanica* belong to the surficial-biodiffusors, and *Q. seminulum* and *M. fusca* are considered gallery-biodiffusors (Fig. 35).

Species	Activity	Distance	Position
<i>Quinqueloculina seminula</i>	Intensive	High	Burrowed
<i>Criboelphidium williamsoni</i>		Medium	Surface
<i>Haynesina germanica</i>		Low	Surface → Burrowed
<i>Ammonia tepida</i>	Low	Low	Surface → Burrowed
<i>Milliammina fusca</i>			Burrowed

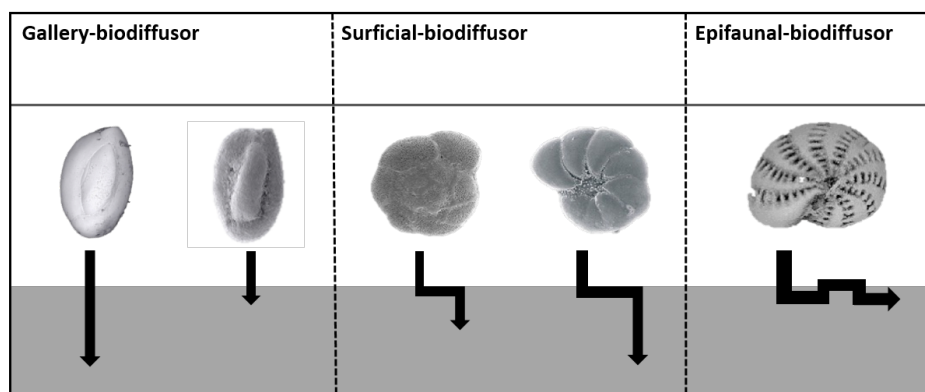


Figure 35. Conceptual schema summarizing the difference between studied species and their classification into functional groups with *Quinqueloculina seminulum* and *Miliammina fusca* in gallery-biodiffusor group, *Ammonia tepida* and *Haynesina germanica* in surficial-biodiffusor and *Criboelphidium williamsoni* in epifaunal-biodiffusors. Adapted from [22]

The classification of benthic foraminifera in these functional groups implies that they would contribute differently to benthic-ecosystem functioning [22][23]. For instance, although *Criboelphidium williamsoni* is larger than *Haynesina germanica* and that both species displayed similar travelled distance, the latest was more efficient to rework the surface sediment (Fig. 36)[34]. This is consistent with previous studies which showed that gallery-biodiffusor (*i.e.* burrowing organism) macro-invertebrates are more efficient bioturbators than epifaunal-biodiffusors as they displaced a larger amount of sediment particles through their burrowing activity (Mermillod-Blondin et al. 2004; Michaud et al. 2005). However, our work also showed that the most and the least efficient surface sediment reworkers *i.e.* *Quinqueloculina seminulum* and *Miliammina fusca* both belonged to the gallery-diffusor group (Fig. 36). As a consequence, the potential link between the intensity of surface sediment reworking and the functional groups of a species is not straightforward; suggesting

we are still at the very early beginning in our understanding of bioturbation processes in benthic foraminifera. Noticeably, we also observed features such as velocity, activity and tortuosity may mediate sediment-mixing intensity. *Qinqueloculina seminulum*, *H. germanica* and *C. williamsoni*, which are the most active species, have a larger effect on particle reworking rates than the less active *Ammonia tepida* and *M. fusca* [34]. Our results further suggested that higher was the surface area of the test, lower was the species-specific $SSRR_i$. To summarise, the travelled distance is likely the parameter that drives the intensity in the surface sediment reworking. This is consistent with previous work conducted on macro-invertebrate species, where large bivalves may have lowest sediment reworking rate than small polychaetes as the latter have more intensive displacements, *i.e.* different motion-behaviour traits (Mermillod-Blondin et al. 2004, Michaud et al. 2005, Gilbert et al. 2007).

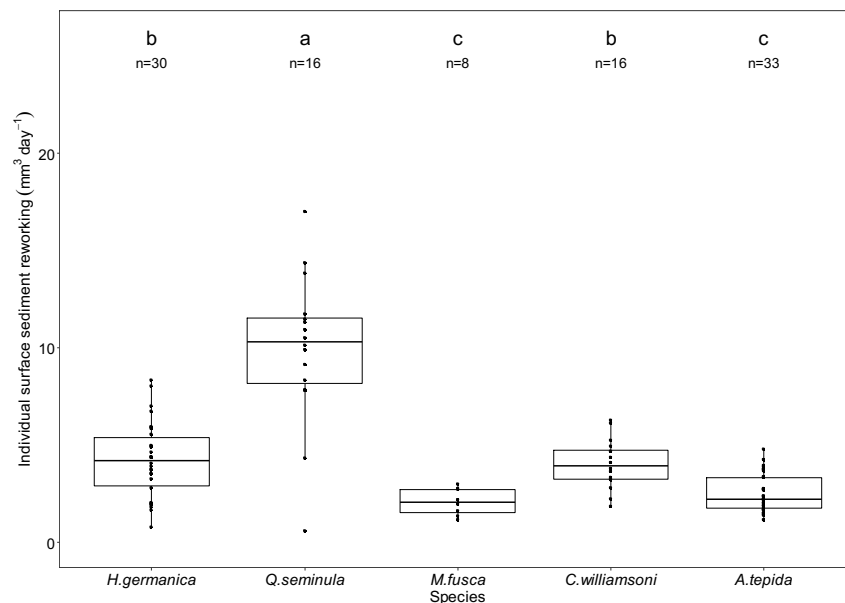


Figure 36. Value of the $SSRR_i$ for each experiment performed on the five tested species. The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range; Individual values are represented by black dots. n denotes the number of individuals used in the experiments. Letters on top ('a', 'b' and 'c') identify significantly different groups (Dunn test, $p < 0.05$) between species. Adapted from [34]

Taken together, our work suggests that despite their minute size benthic foraminifera may play a significant role, though still largely overlooked, in intertidal mudflats sediment

reworking. In details, bioturbation by benthic foraminifera is the result of the complex interplay between species-specific features such as motion behavior, phenotypic plasticity and functional classification, *i.e.* bioturbation mode. The five studied species showed non-negligible sediment mixing rates at the sediment water interface through their active displacements. It is further stressed that because the fluxes of dissolved elements at the sediment-water interface and bio-irrigation are known processes driven by meiofauna bioturbation (Aller and Aller 1992, Nascimento et al. 2012, Bonaglia et al. 2014), foraminifera may play an unsuspected role in the patterns and processes driving intertidal soft-sediment ecosystems. Further work is nevertheless needed to thoroughly assess *i)* the relative contribution of a community of foraminifera compared to the one of macro-invertebrates, *ii)* the sediment reworking related to foraminiferal vertical movements and *iii)* their ability to enhance dissolved fluxes at the sediment-water interface. For instance, further assessment of the vertical mixing generated by foraminiferal motion behavior should be an urgent question to tackle, since specimens were consistently shifting between “on the sediment surface” and “in sediment” positions our different studies. Furthermore, a deep understanding of the parameters driving the species-specific traits is also mandatory, since it controls their activity. These traits may depend on both allogenic (*e.g.* temperature, food availability) and autogenic (*e.g.* size, age) factors.

Box 3: Quantification of sediment mixing

For the first time, the surface sediment reworking (SSRR) of benthic foraminifera was estimated [23][30][34]. We had first to seek for the most accurate method considering the minute size of these organisms. Among the range of methods available to assess sediment reworking rates (see review in Maire et al. 2008), the surface image analysis method (Fig. 37) appeared to be the most appropriate one for benthic foraminifera at this stage since i) little was still known about reworking activities by

benthic foraminifera, ii) their contribution to bioturbation is likely to occur during locomotion, and iii) they are described as mostly living at the sediment-water interface.

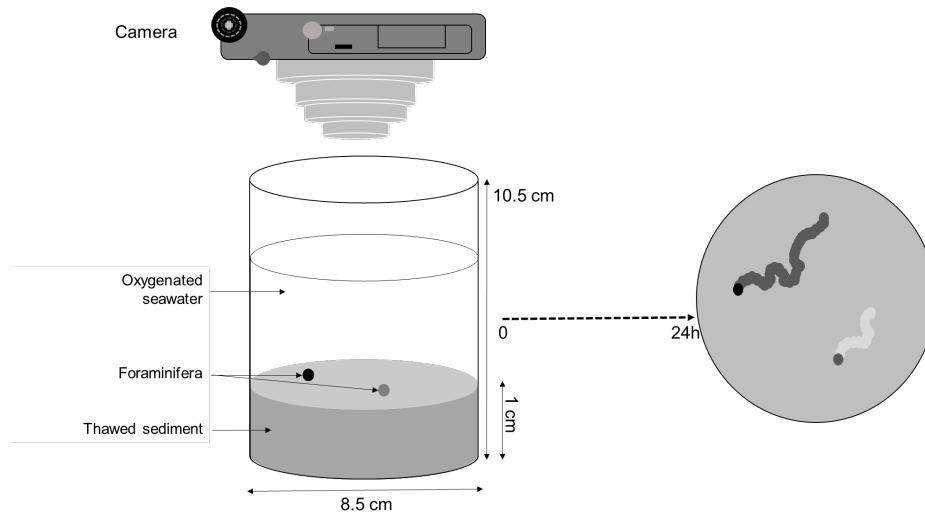


Figure 37. Experimental set-up for time-lapse the quantification of surface sediment reworking rates. Adapted from [34]

In our studies, the use of the surface area of the test instead of the maximum test length therefore appears to be the more ecologically relevant metric to be considered in the calculation of the surface sediment reworking rate (Fig. 38) [34]. Furthermore, intertidal foraminifera exhibited different test shape. Noticeably, the prolate ellipsoid-shaped test of *Quinqueloculina seminulum* and *Miliammina fusca* is asymmetrical with the length being much larger than the width. Similarly, within rotaliid species i.e. *Ammonia tepida*, *Haynesina germanica* and *Criboelphidium williamsoni* test length typically is about 1.2 times larger than test width. As a consequence, the approach followed in [23] most likely leads to a wrong estimation of the $SSRR_i$ values by considering only the length as representative of the test size.

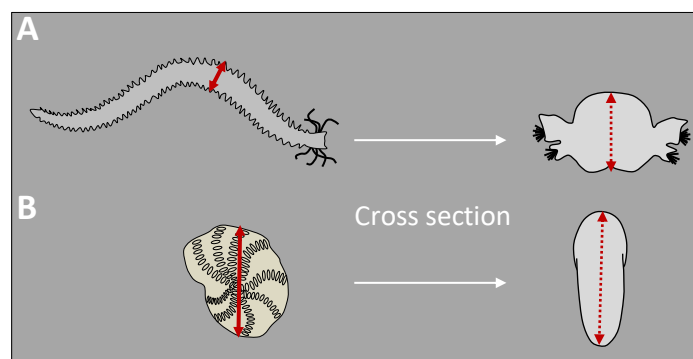


Figure 38. Illustration of the cross section of (A) polychaete and (B) benthic foraminifera that may be used for sediment reworking calculation. Adapted from [34]

It further appeared relevant to consider the temporal evolution in the vertical position of each individual in $SSRR_i$ calculation [34]. This method allows a more rigorous estimation of the surface

sediment reworking intensity of each species as it consider the real portion of the surface area of the test that is actually involve in the reworking of surface particles during individual displacement (Fig. 39).

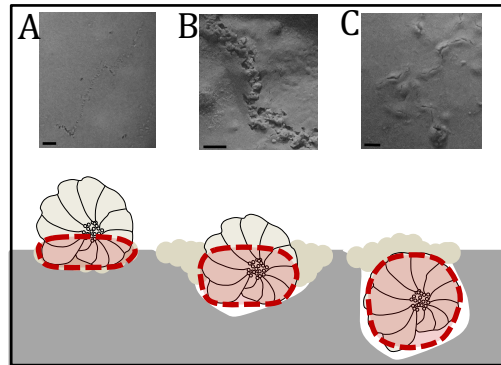


Figure 39. Discrimination between the vertical positions taken by benthic foraminifera in the sediment to estimate SSRR. Images were taken from experiments containing living individuals of *Haynesina germanica*. Adapted from [34]

4.3 Benthic foraminifera: a promising bioassay?

Our preliminary work on the geotactic behavior of intertidal foraminifera suggested that they are able to adapt their motion behavior to external stimuli. These findings are particularly timely in a context of transitional ecosystems being more and more affected by new threats like plastic pollution and extreme weather events due to global warming. Microplastics and nanoplastics pollutions have affected many marine environments from coastal to pelagic settings, shallow water to deep trenches, and tropic to polar regions. Micro- and nanoplastics have been also reported as serious threats for many marine organisms, though their effect is largely unknown. For instance, they can generate measurable stresses at the individual level either by ingestion or exposures to plastic leachates [41]. Lethal and sub-lethal effects of these small particles need, however, further experimental studies. Furthermore, extreme weather events like heatwaves, cold waves, storms have increased in intensity, duration and frequency over the last decades due to climate change (Oliver et al. 2019). Intertidal species, living in a highly variable environment, are likely to be exposed to such extreme events since they can be emerged for more than 6 h during a tidal cycle.

4.3.1 Response to temperature

We examined how temperature influences motion-behaviour and metabolic traits of the dominant temperate foraminifera *Haynesina germanica* by exposing individuals to usual (6, 12, 18, 24, 30 °C) and extreme (high; 32, 34, 36 °C) temperature regimes [30]. Our results show that individuals reduced their activity by up to 80% under high temperature regimes whereas they remained active under the temperatures they usually experience in the field (Fig. 40). In the range 12–30 °C, they exhibited a more intensive foraging behavior consistent with the more complex trajectories and more intensive foraging behavior exhibited by unstressed organisms (Seuront 2011a, 2015)[8]. Furthermore, the Q_{10} values reported in the range 6–24 °C for respiration ($Q_{10} = 1.75$) and photosynthesis ($Q_{10} = 1.22$) (Fig. 41) suggest (i) a maximum performance level and a relatively low thermal dependence of respiration and (ii) that photosynthesis is not affected by temperature inside this thermal range.

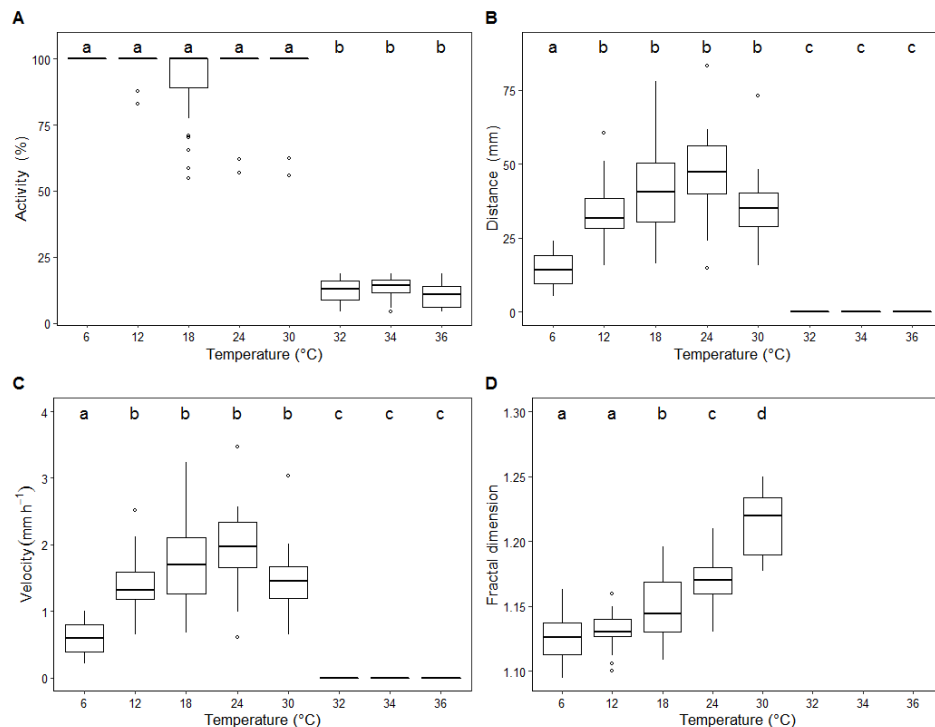


Figure 40. The influence of temperature on (A) the activity (B) the distance travelled (over 24h), (C) the velocity and (D) the fractal dimension of *H. germanica*. The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range; values outside this range are represented by open circles. Number of replicates are 30, 23, 30, 25, 15, 69, 28 and 26 for 6, 12, 18, 24, 30, 32, 34 and 36°C respectively. Due to the absence of motion it was impossible to estimate fractal dimension at 32, 34 and 36°C. Letters above the boxes ('a', 'b', 'c' and 'd') identify significant different groups (Dunn test, $p < 0.05$). [30]

When exposed to a hyper-thermic stress (*i.e.* 36 °C), all individuals remained burrowed and the photosynthetic activity of their sequestered chloroplasts is more affected than respiration (Fig. 41). The later has been also found in other symbiont-bearing benthic foraminifera (van Dam et al. 2012, Sinutok et al. 2014, Pinko et al. 2020). Recovery experiments subsequently revealed that individuals initially exposed to a high thermal regime partially recovered when the hyper-thermic stress ceased. *Haynesina germanica* contribution to surface sediment reworking substantially diminished from 10 mm³ indiv⁻¹ day⁻¹ (usual temperature) to 0 mm³ indiv⁻¹ day⁻¹ when individuals were exposed to high temperature regimes (*i.e.* above 32 °C). Given their role in sediment reworking and organic matter remineralisation, our results suggest that heatwaves may have profound long-lasting effects on the functioning of intertidal muddy ecosystems and some key biogeochemical cycles.

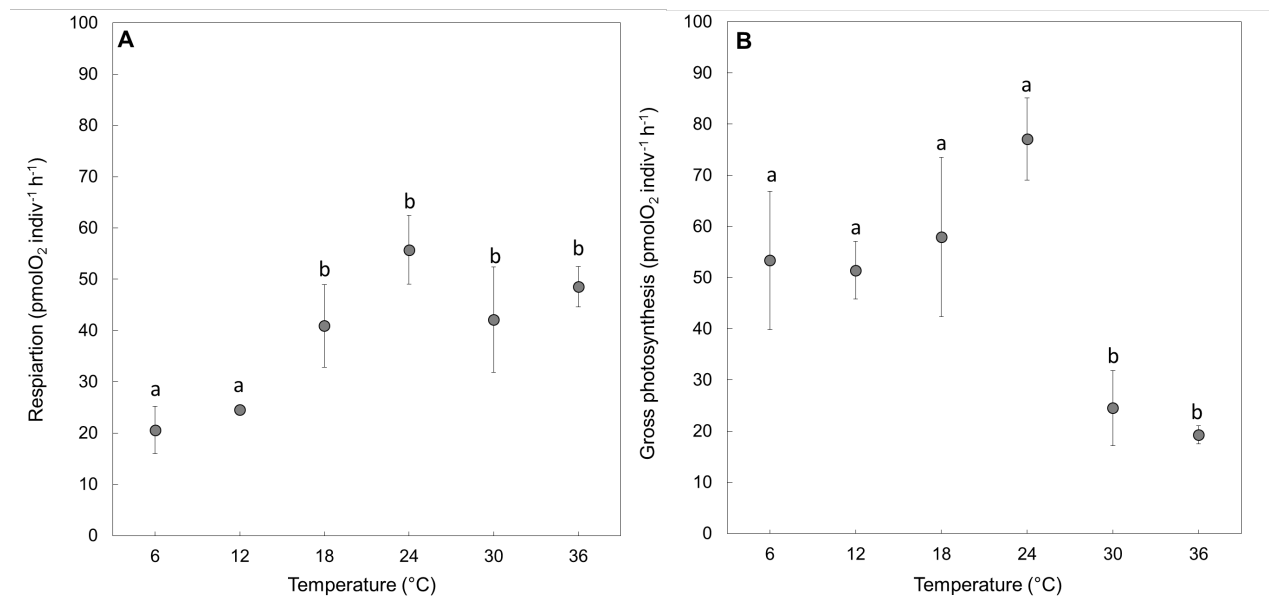


Figure 41. Mean values of (A) respiration and (B) gross photosynthesis (pmol.O₂ indiv⁻¹ h⁻¹) of *H. germanica* under different thermal regime in 3 replicate measurements. The error bars are the standard errors of the mean. Letters 'a' and 'b' identify significant different groups (Tukey test, $p < 0.05$). Adapted from [30]

4.3.2 Response to plastic leachates

We monitored the effect of polypropylene (PP) plastic bead leachates on the same behavioral features [24]. The toxicity of virgin microplastics leachates have been reported in various marine faunal taxa (see review in [41]). Noticeably, in plastic leachates-related studies, only 0.64% studies considered benthic foraminifera, while about 98% were on macro-invertebrates (see review in [41]). In the few publications considering the effect of plastics on benthic foraminifera, physiological stress [20], alteration of feeding behavior (Joppien et al. 2022) and accumulation of protein associated with oxidative stress cytotoxicity (Birarda et al. 2021) were reported.

Overall, both the behavioral and metabolic activity data gathered (Fig. 42) in this preliminary study [24] indicated that the benthic foraminifera *Haynesina germanica* do not respond to MP unlike some other unicellular and metazoan organisms. For instance, previous evidenced that PP-plasticizers reduce fish larvae velocity in the first days after hatching (Wang et al. 2013, Inagaki et al. 2016) and negatively impact adult-fish locomotion and re-productive behavior after at least 2 months of exposure (Gray et al. 1999, Xia et al. 2010). Though this is highly speculative, this observation may suggest that their resistance to leachates from virgin PP might induce a competitive advantage for benthic foraminifera. Such a competitive advantage for foraminifera has previously been observed in relation to some stressors such as organic-matter enrichment and anoxia (Langlet et al. 2013, Stachowitsch 2014).

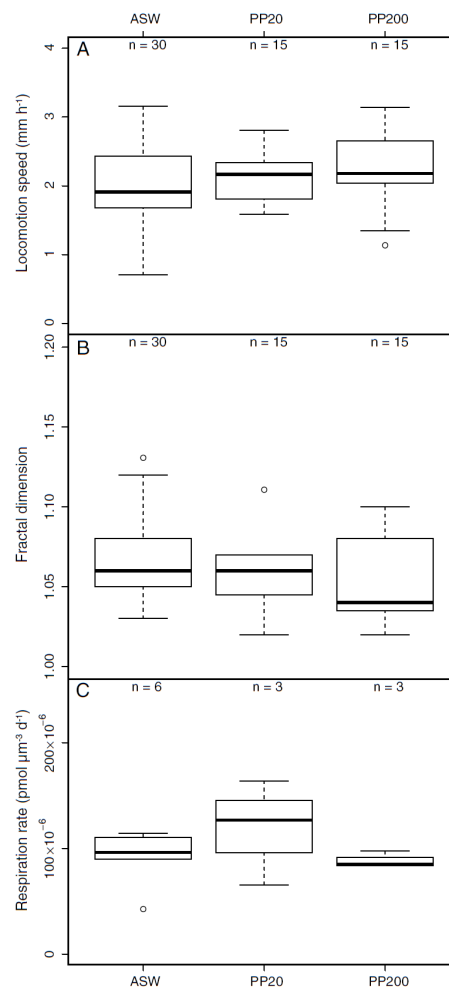


Figure 42. Locomotion speed (A), fractal dimension (B) and respiration rate (C) of *Haynesina germanica* under the three experimental conditions (ASW: artificial seawater, i.e. control conditions; PP20 and PP200: seawater prepared with 20 and 200 ml l⁻¹ polypropylene pellets, respectively). The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range. Values outside of this range are represented by open circles. Adapted from [24]

In conclusion, benthic foraminifera are clearly able to adapt their motion-behavior to changing experimental conditions [8][30], although we did not observe any effect of plastic leachates [24]. Likewise, *Ammonia tepida* can exhibit a motion behavior response to different type of organic and inorganic matter (Jauffrais et al. 2016). These findings open perspectives to develop the use of benthic foraminifera as bioassay. Specifically, their motion-behavior may be a relevant approach to understand pernicious non-lethal effects of contaminants. It would also strengthen our understanding of toxical effects very often observed at species or community levels.

Chapter 5. On what I would like to focus on over the next years

5.1 Towards improved biomonitoring with benthic foraminifera

5.1.1 Getting foraminifera in observation networks

Since the beginning of my research career, my curiosity has always been triggered by the study of introduced (NIS) and invasive species [1][17][19][32][37][40]. One may notice that this area of research is fairly untapped in foraminifera. Most records of NIS occurred by chance during field sampling. The latest surveys we conducted in the Gironde estuary and in the French side of the Eastern English Channel confirmed (Foram-INDIC project) that there are foraminiferal introduced species yet unrecorded (*Ammonia confertitesta* in the Gironde estuary and *Trochammina hadai* in Le Havre harbor).

Over the next years, I would like to conduct field surveys to document the presence of NIS, particularly in harbors which are one of the main gateways for the introduction of alien species. This will be done in the harbor of Boulogne sur Mer and Marseille in surveys funded by the Office Français pour la Biodiversité within the framework of the European Marine Strategy Framework Directive (Descriptor D2) which enforces the need to survey that non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystem.

The competition between native and NIS is still poorly explored in benthic foraminifera. The status of invasive species is solely based on the relative abundance, and little is known about the ecology of some famous invasive foraminifera i.e. *Trochammina hadai* in the Bay of San Francisco in the USA, the bay of Flamengo in Brazil and the Leschenault inlet in Australia (McGann et al. 2000, Eichler et al. 2018, Tremblin et al. 2021) or *Amphistegina* spp.

in the Mediterranean Sea (Yokes et al. 2007) (i) to explain why they are flourishing and taking over the natives and (ii) to understand what would be the consequence to the functioning of the ecosystem. Recently, it was shown that the invasive foraminifera *Nonionella* sp. T1 [19] could impact the nitrogen cycle under oxic conditions by increasing the sediment denitrification and could counterbalance potential eutrophication of the Gullmar Fjord (Choquel et al. 2021).

As a first step, it would be interesting to compare the ecological requirements, the trophic needs and the role in bioturbation processes between the 2 natives *Ammonia* species and the allochthonous one to further understand why the (probably) alien species *Ammonia confertitesta* is over-dominated in the Gironde estuary. Furthermore, getting back to the past with the study of the fossil fauna would allow us to accurately date the introduction period for *A. confertitesta* in the Gironde estuary and *T. Hadai* in Le Havre harbor, and to improve our hypotheses on the potential introduction pathways as we did for *Nonionella* sp. T1 [19].

In the French and European research landscape, the development of observation networks and infrastructure is blossoming since about a decade. In this context, I am co-leading the National Observation Network on macro-invertebrates (SNO BenthOBS). It involves 11 research institutes and consists of 20 stations sampled twice a year (early spring and end of summer) every year. In addition to document species distribution patterns, the acquisition of long-term time-series will allow us to consider temporal community trajectories; providing meaningful information to understand macro-invertebrates communities' changes in the context of global changes. The BenthOBS network still only considers macro-invertebrates. In the next few years, we would like to contribute to the integration of benthic foraminifera in this observation network (in collaboration with

colleagues from the LPG in Angers). As presented in this thesis, benthic foraminifera are accurate sentinel of the environmental conditions, and can be a good complement to macro-invertebrates.

The French research community working on foraminifera is now *(i)* mature enough in terms of the understanding of foraminiferal ecology, *(ii)* well advanced on the development of indicators based on foraminifera and *(iii)* (last but not the least) big enough in terms of manpower to handle a long-term survey at a national scale. The integration of benthic foraminifera in the BenthOBS observation network should be done simultaneously to the addition of biogeochemical measures, providing a more integrative picture of soft-bottom sediments. It will further allow the community of meio-, benthologists and biogeochemists to improve our understanding of the long-term evolution of the benthic habitat.

5.1.2 Foraminifera as a biological quality element

As introduced in Chapter 1, coastal and transitional waters result in a patchwork of highly heterogeneous conditions, which require easily implemented and robust biotic indices. The natural features of transitional waters make difficult to disentangle natural and human-induced drivers of foraminiferal community distribution patterns (see review in Jorissen et al. 2022). In particular, silt, clay, and organic matter (OM) sedimentary contents are naturally high in transitional waters, promoting tolerant and opportunistic species, while sensitive species naturally decline (Elliott and Quintino 2007, Munari and Mistri 2008). In addition, total organic carbon (TOC) in transitional waters is a mix of labile and refractory OM with important terrestrial inputs (Pusceddu et al. 2003). In transitional waters, benthic communities could therefore be naturally similar to those found in anthropogenically disturbed areas (Blanchet et al. 2008, Munari and Mistri 2008, Fouet et al. 2022). These ecosystems further naturally

exhibit low diversity (Elliott and Quintino 2007). Consequently, pristine, naturally disturbed intertidal areas and transitional waters could easily be misclassified in moderate to bad EcoQS (the estuarine quality paradox, Dauvin 2007, Elliott and Quintino 2007, Dauvin and Ruellet 2009), severely complicating the decision-making process (Salas et al. 2004, Muniz et al. 2005, Quintino et al. 2006, Blanchet et al. 2008). The work conducted in the FOBIMO sub-working group “Intertidal and transitional waters allowed us to define a classification of foraminiferal species in ecological group of sensitivity to total organic carbon [29][31]. Noticeably, there are currently only species list for European habitats (Alve et al. 2016, Jorissen et al. 2018)[29]; hence there is an urgent need to implement the same concept in other regions. For this purpose, a small workshop (granted by IRD local fundings) was organised in Wimereux in December with Dr V. Martins (U. Rio do Janeiro, Brazil), Dr. S. Sousa (U. Sao Paulo, Brazil), Dr F. Francescangeli (U. of Geneva, Switzerland), Dr. F. Frontalini (U. Urbino, Italy), Dr E. Armynot du Châtelet and J.-C. Pavard (LOG) with the aim (i) to gather and select relevant database containing TOC and living foraminiferal data from transitional environments from the Atlantic coasts of South America, (ii) to assign foraminiferal species to ecological groups following [29] and (iii) to test the species’ classification with Foram-AMBI on independent datasets. We achieved the first and second steps, we are currently in the process of finalising the species’ list and implementing Foram-AMBI on independent datasets.

The challenge of environmental monitoring in transitional waters is being explored in the Foram-INDIC project (funded by the Agences de l’Eau Artois-Picardie et Seine-Normandie, PI : V. Bouchet, in collaboration with Pr J.-C. Dauvin and Dr J.P. Pezy (U. Caen, benthic macrofauna), Dr M. Schweizer (U. Angers, metabarcoding), Dr F. Henry (ULCO, element trace metals), Dr. E. Goberville (Sorbonne University, numerical ecology), and Dr. E. Armynot du Châtelet and Dr L. Seuront (LOG). Benthic foraminifera (for morpho-taxonomy and

metabarcoding) and macro-invertebrates (only morphology) are sampled in pristine (Authie bay, Orne estuary and Bays of Veys) and in heavily modified environment with a special focus on harbors (Dunkerque, Calais, Le Havre and the Caen canal).

Coupled analysis of the data from environmental parameters, benthic foraminifera and macro-invertebrates will allow us to tackle the following questions in the Foram-AMBI project:

- What are the environmental drivers of benthic foraminifera distribution patterns in pristine transitional environments and in harbors?
- What is the beta diversity pattern of foraminiferal assemblages across the sampling site along the French coast of the English Channel?
- Are benthic foraminifera and macrofauna congruent in their response to environmental conditions?
- Are existing biotic indices i.e. $\exp(H'_{bc})$ and Foram-AMBI performing well in transitional waters?
- What is the benefit of metabarcoding compare to the traditional morpho-taxonomic method?

The Foram-INDIC project is also a unique opportunity to record the presence of alien foraminiferal species.

5.1.3 On the use of metabarcoding in biomonitoring

In the context of improved biomonitoring, environmental DNA (eDNA) metabarcoding appears to be a relevant, cost- and time-saving complement or alternative (in my opinion, the question still stands....) to the traditional morpho-taxonomic approach for benthic foraminiferal inventories. Noticeably, diversity and species composition of foraminiferal

assemblages inferred from eDNA metabarcoding data well respond to the impacts of fish and finfish farming (Pochon et al. 2015, He et al. 2019), industrial pollution [33] and offshore gas and oil platform activities (Cordier et al. 2019, Frontalini et al. 2020). Yet, little has been done to test the application of foraminiferal biotic indices using eDNA-metabarcoding data to monitor EcoQS [33]. Furthermore, there is not a consensus on sampling and analytical protocols (see review in Pawlowski et al. 2022), which may give different results, (i) hampering comparisons between studies and (ii) questioning the reliability of metabarcoding. This problematic would have been tested in the project eDNA-Foram-Survey in collaboration with Dr C. Barras and Dr M. Schweizer from the LPG-Angers (PI : V. Bouchet) submitted to the Office Français pour la Biodiversité; which turned to not be funded. At the moment, we are considering other calls to which submit this project.

The aims of the eDNA-Foram-Survey will be:

- conduct a state-of-the-art of current protocols in order to identify strengths/weaknesses and provide an optimized protocol to be tested,
- compare morpho-taxonomy and metabarcoding data outcomes to evaluate the pros and the cons of each method,
- evaluate the indicative value of OTUs and develop a method to evaluate the ecological quality status with foraminiferal eDNA data via the use of taxonomy-free approach (Apothéloz-Perret-Gentil et al. 2017) or *de novo* index (Mauffey et al. 2020).

The project will benefit from data from ongoing projects (Foram-INDIC, LOG, Wimereux, PI : V. Bouchet; IMPEC, LPG, Angers, PI : C. Barras). It will further involve sampling cruise in order to test new protocols. The project will largely benefit from the expertise of researchers from the Laboratoire d'Océanologie et de Géosciences in Wimereux and the

Laboratoire de Planétologie et de Géosciences in Angers. In the meantime, in collaboration with Dr F. Frontalini (University of Urbino, Italy), Pr J. Pawlowski (University of Geneva, Switzerland) and Dr E. Goberville (Sorbonne University), I am conducting preliminary studies to test (i) foraminiferal biotic indices and (ii) taxonomy-free methods on metabarcoding data from gas platforms in the Adriatic Sea (Bouchet et al., *in prep.*) and in the North Sea.

5.2 Towards improved understanding of benthic foraminiferal functional role

5.2.1 Bioturbation

As detailed in Chapter 4, the different studies we conducted over the last few years open new perspectives on the understanding of role of intertidal benthic foraminifera in bioturbation and bio-irrigation processes. In soft bottom habitats, motion behavior of intertidal foraminifera can generate horizontal displacement of sediment particles in soft-bottom habitats [22][23][30][34]. Some species may be further involved in the vertical transport of sediment as they moved below the sediment-water interface [22][30]. Yet, quite a number of questions still remains to be tackled (Fig. 43):

- Are foraminiferal movements affecting surface sediment cohesiveness?
- Are they contributing to sediment mixing?
- Are they playing a role in sediment bio-irrigation?
- Does foraminiferal bioturbation modify microbial communities?

Based on the literature, we may hypothesise that foraminiferal vertical movements may (i) have major impacts on the stability and erodibility of the surficial sediment layer (Nehring 1993, Coull 1999), (ii) produce a substantial downward transport of particles and (iii) enhance fluxes of dissolved oxygen and solutes at the sediment-water interface (Aller and Aller 1992, Schratzberger and Ingels 2018). To our knowledge, only one study estimated the sediment

reworking rates generated by a benthic foraminiferal community in deep-sea sediment (Gross 2002). Furthermore, the surface crawling activities of benthic foraminifera [22][23] resemble those of the gastropod *Peringia ulvae*, that involve both sediment reworking and the creation of a fluffy layer of sediment around the tracks (Orvain et al. 2004). Fluffy layers are disconnected from the surface matrix, decrease sediment cohesiveness; hence foraminifera may increase sediment erodibility (Cedhagen et al. 2021). Such a pelletised surface layer created by the activity of foraminifera can ease the resuspension of sediments by tidal currents as described for macro-invertebrates (Orvain et al. 2004, Davies and Blackwell 2007) and affect sediment bio-irrigation. These physical and chemical changes would impact microbial communities (Piot et al. 2013), organic matter mineralisation and nutrient cycles (Aller 2004, Gilbertson et al. 2012).

In this context, it appears critical to further describe the role of benthic foraminifera in sediment mixing and bio-irrigation processes and to quantify their contribution to solutes fluxes at the sediment-water interface (Fig. 43).

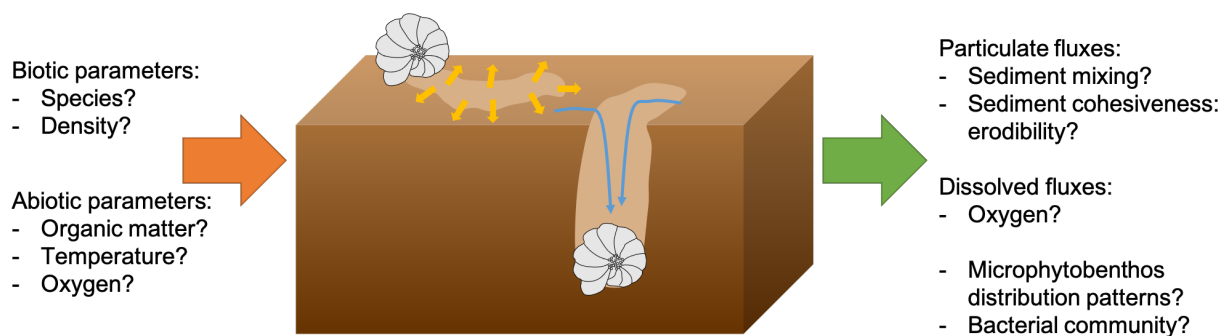


Figure 43. Schematic of the questions to be tackled to understand (i) how abiotic and biotic parameters may constrain bioturbation processes in benthic foraminifera and (ii) their potential role a) in sediment mixing, b) on dissolved fluxes at the sediment-water interface and c) in interspecific facilitation interactions.

This problematic will be tackled in a research project (EC2CO call, to be submitted in September 2022); the framework of this project being synthetized in Fig. 43. Specifically, the project will aim at:

- Understanding the driving forces of foraminiferal motion behavior, which has direct implication on sediment mixing and bio-irrigation
- Quantifying sediment mixing rates in intertidal species following our preliminary work (Deldicq et al., *in revision*)
- Monitoring changes in surface sediment micro-topography, which further affects sediment erodibility
- Quantifying dissolved fluxes at the sediment-water interface
- Describing to what extend intertidal foraminifera may constrain microphytobenthos distribution patterns on the sediment surface and bacterial communities within the sediment matrix.

The research project will be co-led by O. Maire (micro-topography of the sediment surface with a CD camera, dissolved fluxes) and V. Bouchet, and it will involve Dr L. Seuront (LOG CNRS, behavioral ecology), Dr. F. Mermillod-Blondin (LEHNA Lyon CNRS, archae and bacterial communities) and Pr. F. Orvain (U. Caen, micro-phytobenthos distribution patterns with a PAM system). This project should be a starting point to further initiate an international collaboration with Dr S. Bonaglia and Dr. Polovodva-Asteman (U. Göteborg) and Dr. F. Nascimento (U. Stockholm) who have a good experience on meiofaunal bioturbation processes (Nascimento et al. 2012, Bonaglia et al. 2014) and Pr. E. Metzger (U. Angers, biochemistry). It is planned that I will visit them and give a seminar in Göteborg between September and December 2022.

5.3 Towards improved understanding of the effect of new global stressors (extreme events and plastics)

5.3.1 Plastic leachates¹

Part of my ongoing research focuses on the effects of plastic leachates on foraminiferal species *i.e.* *Haynesina germanica*, *Trochammina hadai* and *Ammonia confertitesta* (phylotype T6). In order to deeply understand the harmful effect of plastics, we are using different approaches *i.e.* motion-behavior (with Dr Laurent Seuront), surface sediment micro-topography et quantification of dissolved fluxes at the sediment water-interface (with Dr Olivier Maire, EPOC-Bordeaux), foraminiferal ultrastructure modifications (with Dr Fabrizio Frontalini) and proteomics (with Dr Fabrice Bertille). This question is also being tackle in the PHC Sakura project “*Pollution by microplastics: spatial distribution and effects of leachates on the motion-behaviour of intertidal foraminifera*” (2021-2022) I am co-leading in collaboration with Dr Akira Tsujimoto (Shimane University) and Dr Hidetaka Nomaki (JAMSTEC).

Benthic foraminifera may not be only prime suspects but also guilty of sequestering both MPs and NPs in sediment through their bioturbation activity that would actively transfer plastic items from the water column to the sediment. Noticeably, they are able to burrow particles in the size range (10-125 μm) of MP (Gross 2002). The inclusion of plastic particles in the test of agglutinated benthic foraminifera (Tsuchiya and Nomaki 2019, Birarda et al. 2021) further contributes to the sequestration of MPs and NPs in the sediment. Preservation of plastic and benthic foraminifera in fossil sediments also provides an archive illustrating accumulation of MPs and NPs in blue carbon habitats, and are *in fine* likely to provide additional evidence of how plastic can be considered as a key geological indicator of

¹ This section is part of Bouchet et al., Benthic foraminifera as the missing link to understand plastic pollution in blue carbon ecosystems, *under revision in Environmental Science and Technology*

Anthropocene as a distinctive stratal component (Corcoran et al. 2015, Zalasiewicz et al. 2016, Dibley 2018). In this specific context, benthic foraminifera became their own victims as the burial of MPs and NPs is likely to expose them to ever increasing concentrations of the countless additives and chemicals carried by plastic items. We hence advocate for more comprehensive research programs *(i)* to understand the role of benthic foraminifera in plastic sequestration in sediments, and *(ii)* to improve our poor knowledge of the effect of plastic items and their leachates on benthic foraminifera.

The pernicious non-lethal effects of MPs and NPs to living organisms are a challenge to assess in the benthic marine realm, particularly in minute organism like benthic foraminifera that are an emerging model in blue carbon ecosystems. Despite their noticeable small number relative to the available literature (see Figure 1), the recent studies on the response of benthic foraminifera to various aspects of plastic exposure (Birarda et al. 2021, Joppien et al. 2022; [20][24]) have stressed how critical it is to understand why, how and under which environmental conditions MPs and NPs affect benthic foraminifera, and incentive that generates the following roadmap (Fig. 44):

(i) motion behavior is an acknowledged keystone process behind the success of foraging, mate-finding and habitat selection (Bowler and Benton, 2005). Motion behavior is still, however, the forgotten child of foraminiferal ecology, despite its increasingly recognized variability (Jauffrais et al. 2016; [8]) and role in bioturbation [22][23][34]. In this context, investigating the behavioral changes induced by MPs and NPs on foraminifera will contribute to improve our understanding of the effects of plastic pollution on blue carbon ecosystems functioning;

(ii) future research should also—and ideally concurrently—assess the biological and physiological processes involved in the response of benthic foraminifera to MPs and NPs

particles and leachates, which are now deeply accessible through the advance in transcriptomics (Titelboim et al. 2020), proteomics (Stuhr et al. 2018) and microscopy (Frontalini et al. 2019);

(iii) the still relatively untapped area of research related to the ecological role of symbiont-bearing and kleptoplastic foraminifera also holds the promises to decipher the role of benthic foraminifera in blue carbon production and storage;

(iv) finally, MPs and NPs may implicitly alter the quality of their habitat, hence undermine the survival of some species and ultimately constrain the composition of foraminiferal communities. Taking advantage of the recent development of the use of benthic foraminifera to assess ecological quality statuses (Alve et al. 2016, Jorissen et al. 2018; **[29]**), may provide an opportunity to develop an index of the degree of plastic pollution in blue carbon ecosystems sediment through the identification of indicator species of the presence/absence of MPs and NPs.

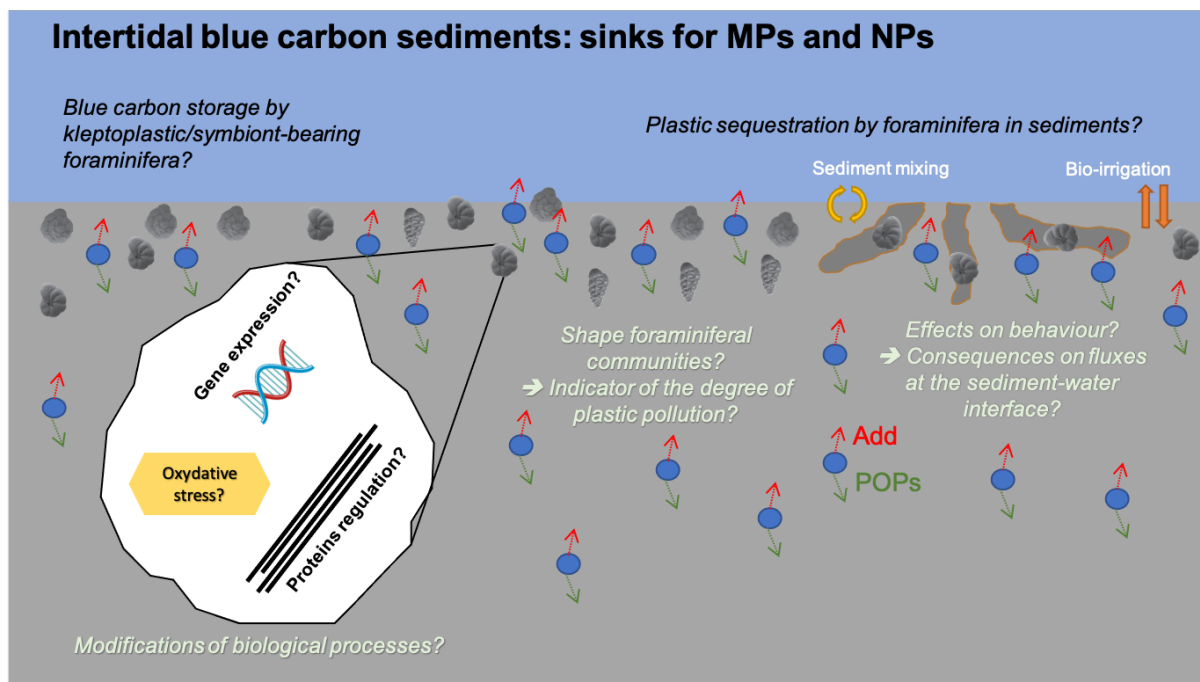


Figure 44. Schematic of the questions to be tackled to understand (i) to what extent foraminifera may contribute to the storage of MPs and NPs in blue carbon sediments and (ii) the potential harmful effect of plastic on (a) blue carbon sequestration by foraminifera, (b) physiological and biological processes, (c) behavior and the possible consequences on sediment mixing and bio-irrigation and (d) species composition of foraminiferal communities. This roadmap is intended to provide foraminiferal proxies for the characterization of plastic pollution in blue carbon ecosystems. (Filled blue circles: MPs/NPs particles, Add: additives, POPs: persistent organic pollutants)

In conclusion, we believe that benthic foraminifera offer a putatively endless sets of opportunities to tackle the question of the potential effects of new global stressors, from the physiological to the ecosystem level. We plea here to embrace the opportunity to see in these minute organisms a unique prospect to refine our understanding of the effects of the new environmental threats of the “Anthropocene” on the structure and functions at play behind the future of blue carbon ecosystems under climate change.

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Résumé

Les eaux de transition et les zones intertidales, situées à l'interface terre-mer, sont sous l'influence des eaux marines et des eaux douces. Ces écotones sont parmi les écosystèmes les plus productifs au monde. Ils représentent environ 13% des zones côtières, et offrent un grand nombre de services écosystémiques à la société. Pour protéger et restaurer ces habitats fragiles, les états ont promulgué un grand nombre de lois, directives et traités. La mise en œuvre de ces législations génère une grande réflexion scientifique pour définir et proposer des méthodes pour définir la qualité écologique de ces milieux. Un groupe de la méiofaune, les foraminifères benthiques (protistes), est de plus en plus utilisé comme un bio-indicateur pertinent dans les eaux de transition. Dans ce travail, je synthétise les différentes études que nous avons menées afin de (i) proposer des méthodes pour utiliser les foraminifères benthiques pour évaluer le statut écologique des masses d'eaux de transition, (ii) de caractériser le comportement de déplacement des foraminifères et son application possible en écotoxicologie, et (iii) de comprendre leur rôle dans les processus de bioturbation à l'interface eau-sédiment.

En détail, nos travaux ont confirmé que les foraminifères sont un bio-indicateur pertinent pour évaluer le statut écologique des eaux de transition et côtières. Pour cela, nous avons utilisé l'indice de diversité $\exp(H'_{bc})$ qui est performant pour détecter différentes sources de pollution. Cette méthode a été développée le long d'un gradient décroissant d'oxygène, et a ensuite été testée dans le cadre de différentes perturbations comme l'aquaculture, la construction de digues et les éléments traces métalliques. D'autre part, nous avons classé les espèces en groupes écologiques de polluo-sensibilité en réponse au carbone organique sédimentaire. Ce classement a permis de tester avec succès l'indice Foram-AMBI. De plus, nos expériences sur le comportement des foraminifères intertidaux ont montré qu'il existe une très forte variabilité inter-individuelle et inter-spécifique en termes de distance parcourue mais aussi de comportement *i.e.* tortuosité, position verticale. Ils montrent ainsi des réponses comportementales typiques d'organismes stressés. Enfin, malgré leur petite taille, les foraminifères jouent probablement un rôle non négligeable dans le remaniement sédimentaire des zones intertidales. Leur rôle va dépendre des caractéristiques de chaque espèce comme leur comportement de déplacement, leur plasticité phénotypique et leur mode de bioturbation.

Pour conclure, nous pensons que les foraminifères offrent un grand nombre d'opportunités pour répondre à des questions écologiques clés dans le cadre des changements globaux, depuis leur réponse physiologique jusqu'au niveau des communautés. Ces organismes peuvent être considérés comme un groupe d'intérêt pour préciser notre compréhension des effets des nouvelles menaces environnementales de la période de l'Anthropocène sur la structure et le fonctionnement des milieux de transitions et intertidaux.

Abstract

Intertidal and transitional waters, situated at the interface between marine and terrestrial ecosystems, are under the influence of both marine and fresh water inputs. These ecotones are some of the most productive ecosystems globally. Representing at least 13% of the world's coastline, they provide human societies with a range of ecosystem goods and services. To protect and restore these fragile ecosystems, many nations have enacted marine legislations. The implementation of these legislations worldwide is generating a fruitful debate amongst marine scientists about how to define and implement efficient and reliable bio-assessment tools. A component of the meiofauna, benthic foraminifera (protists), has been widely used as bio-indicators of several pollution sources in coastal and transitional waters. In this work, I will synthesize studies we conducted with the aim (i) to develop the use of benthic foraminifera as indicator of the health of benthic habitats, (ii) to characterize the motion-behavior of benthic foraminifera and possible application of this group as a bioassay and (iii) to understand the function of benthic foraminifera in bioturbation processes.

In details, our works confirmed that foraminifera can be considered as a reliable biological quality element to assess the ecological quality status in transitional and marine systems. Specifically, the use of the diversity index $\exp(H'_{bc})$ based on benthic foraminifera showed good performance in detecting the impact of pollution in different contexts. This method was originally tested along a decreasing gradient of bottom-water oxygen concentration in SE Norwegian fjords and we showed it may work against most pollution sources like aquaculture, dike construction and heavy metals. Furthermore, our effort to assign foraminiferal species to ecological groups of sensitivity to total organic carbon showed that the classification reflects differences in species tolerance of organic load-related stress. We then obtained good evaluation of the ecological quality status with the use of the sensitivity-based Foram-AMBI index. Our experiments on the motion-behavior showed that benthic foraminifera displayed a high variability in their travelled distance but also in their motion behavior, *e.g.* tortuosity, vertical position; exhibiting typical responses of stressed organisms. Last, we reported that despite their minute size benthic foraminifera may play a significant role, though still largely overlooked, in intertidal mudflats sediment reworking. In details, bioturbation by benthic foraminifera is the result of the complex interplay between species-specific features such as motion behavior, phenotypic plasticity and functional classification, *i.e.* bioturbation mode.

In conclusion, we believe that benthic foraminifera offer a putatively endless sets of opportunities to tackle the question of the potential effects of new global stressors, from the physiological to the ecosystem level. We plea here to embrace the opportunity to see in these minute organisms a unique prospect to refine our understanding of the effects of the new environmental threats of the "Anthropocene" on the structure and functions at play behind the future of transitional and intertidal ecosystems under climate change.