

Maïté P. Jacquot

Human Ecosystem Engineering

Effects and Feedback in Coastal Benthic Systems





Maïté P. Jacquot

Born 1991, in Longjumeau, France

Previous studies and degrees

Master, University of Western Brittany, France, 2016

Bachelor, University Rennes 1, France, 2014

Cover design and layout

© Maïté P. Jacquot



Human Ecosystem Engineering:

effects and feedback in coastal benthic systems

Maïté P. Jacquot

Environmental and Marine Biology
Faculty of Science and Engineering
Åbo Akademi University
Åbo, Finland, 2024

Supervised by

Docent, Associate Professor
Marie C. Nordström
Environmental and Marine Biology
Faculty of Science and Engineering
Åbo Akademi University
20500 Åbo, Finland

Ecosystems and Environment
Research Programme
Faculty of Biological and
Environmental Sciences
University of Helsinki
00790 Helsinki, Finland

Reviewed by

Professor **Simon Thrush**
Head of Institute of Marine Science
Science Centre 302 - Bldg 302
23 Symonds street, NZL
Auckland, 1010, New Zealand

Faculty opponent

Associate Professor
Laura L. Govers
Faculty of Science and Engineering
University of Groningen
Nijenborgh 4
9747 AG Groningen, The Netherlands

Co-supervised by

Docent **Martin Snickars**
Environmental and Marine Biology
Faculty of Science and Engineering
Åbo Akademi University
20500 Åbo, Finland

Reviewed by

Dr. **Henrik Nygård**
Marine Research Centre
Finnish Environment Institute SYKE
Latokartanonkaari 11
FI-00790 Helsinki, Finland

Author's address

Maïté P. Jacquot
Environmental and Marine Biology,
Faculty of Science and Engineering
Åbo Akademi University,
20500 Åbo, Finland
e-mail: Jacquot.Maite@gmail.com

© Maïté P. Jacquot

ISBN paperback: 978-952-12-4347-9
ISBN electronic: 978-952-12-4348-6

PDF version permanently hosted at www.doria.fi

Painosalama, Åbo, 2024

*"You cannot get through a single day without
having an impact on the world around you.*

*What you do makes a difference, and
**you have to decide what kind of
difference you want to make.**"*

Jane Goodall

Abstract

In the attempt to enhance their environment, humans are causing changes in ecosystems worldwide, by acting as ecosystem engineers. Changes in ecosystems, caused by any ecosystem engineering species, have the potential to feedback to the engineer. Humans are experiencing such feedback, affecting ecosystem goods and services. As today's feedback following human ecosystem engineering (HEE) are mostly negative, concerns are raising about the future of Earth's environment and its ability to provide the services required to maintain viable human civilizations. With 2.5 billion people living within 100 km of the coast, disproportionate pressure is placed on coastal ecosystems. Holding great environmental and economic value, concerns are consequently especially turned towards these coastal ecosystems. As humans are facing challenges related to climate change, biodiversity loss and increasingly threatened ecosystems, there is therefore a great need to understand human-induced pressures, effects and feedback processes in the environment.

This thesis explores the nature and consequences of HEE unintended effects on coastal ecosystems, through the study of a combination of three different areas worldwide: Sine Saloum in Senegal, West Africa, Åland Islands in Finland, Baltic Sea, and Mobile Bay in Alabama, Gulf of Mexico. It is well-known that unintended consequences following HEE can be detected using bioindicators, so in my thesis I focused on bioindicators particularly relevant in coastal ecosystems, namely macrofaunal organisms. Based on three papers, my PhD thesis first evaluates HEE effects on macrofaunal communities and ecosystem functioning by identifying effects on structural and functional properties of macrofaunal communities to different sets of anthropogenic and abiotic drivers, using a combination of taxonomic and trait-based approaches. Because macrofaunal organisms are central to several ecosystem functions and many of the ecosystem services provided by benthic macrofaunal communities are threatened directly via human-driven impacts, I also looked at how proxies for macrofauna-mediated ecosystem functions, which acts as biotic feedback for humans, responded to anthropogenic activities. I focused on macrofaunal ecological functions related to sediment reworking (i.e., bioturbation and bioirrigation potentials), to biogeochemical cycling and to their capacity to serve as essential role in energy acquisition for higher trophic levels while serving as central food resource for epibenthic predators and demersal fish.

The findings highlight that not only macrofauna was affected by the physical environment and sediment properties, but HEE was also highlighted as a significant driver. Indeed, in the three studied coastal ecosystems, drivers for macrofaunal community structure and functioning were always including variables not only describing the physical environment (*e.g., salinity, temperature, hydrodynamics, depth, dissolved oxygen, season*) and sediment properties (*e.g., grain size, CN content, organic content*) but also HEE (*e.g.,*

shellfish harvesting, heavy metals, hazardous substances, costal development and shoreline modification, eutrophication, fish farming, dredging). Results are showing that HEE is affecting macrofaunal communities (i.e., abundances, biomasses, diversity and species and trait composition) which translates to modifications in ecological functions and processes associated with macrofaunal communities, in turn having the potential to affect ecosystems services. Both spatial proximity to HEE and the type of HEE were shown to affect structure and functioning of macrofaunal communities. A concrete example of HEE effects and feedback was highlighted with shellfish harvesting in the Sine Saloum, Senegal.

This research provided additional evidence regarding the interest in using trait-based approaches in combination to the taxonomic approaches to better understand HEE effects and feedback. A novel index was found relevant to estimate the macrofaunal community quality as a food resource for consumers (e.g., benthic-feeding fish), reflecting an additional ecological function to sediment reworking. Moreover, this thesis demonstrates that the ecosystem engineering framework can be applied to the human species. The use of the HEE framework could represent a valuable step towards sustainability (e.g., helping reaching the UN Sustainable Development Goals (SDGs)). The findings of this thesis also bring a deeper understanding of HEE effects in coastal ecosystems and potential feedback for human society and economy. In order to preserve ecosystem services, particular attention should be paid towards human activities on coastal ecosystems.

KEYWORDS: COASTAL ECOSYSTEMS, COMMUNITY ECOLOGY, BIOLOGICAL TRAITS, ECOSYSTEM FUNCTIONING, ZOOBENTHOS, INFAUNA, MULTIPLE ENVIRONMENTAL STRESSORS, ECOLOGICAL FUNCTIONS, BIOTURBATION, FOOD RESOURCE, ECOSYSTEM SERVICES

Sammanfattning (Swedish abstract)

I strävan efter att förbättra sin livsmiljö, orsakar människan förändringar i ekosystem över hela världen. Detta sker till den grad att människan kan anses vara en ekosystemingenjör, dvs. en art med så omfattande inverkan på sin omgivning att ett stort antal andra arter och hela livsmiljöer påverkas. Förändringar i miljön har dock potential att länka tillbaka till människan via återkopplingsprocesser i ekosystemet och genom effekter på ekosystemvaror och -tjänster. Eftersom många mänskliga aktiviteter och de associerade återkopplingsprocesserna resulterar i förändringar som är negativa för människan, ökar farhågorna kring jordens framtida miljö och förmåga att tillhandahålla de tjänster som krävs för att upprätthålla livskraftiga mänskliga civilisationer. Då 2,5 miljarder människor bor inom 100 km från kusten läggs ett oproportionerligt stort tryck på kustnära ekosystem, vilka kännetecknas av särskilt höga ekologiska och ekonomiska värden. Emedan människan står inför utmaningar relaterade till klimatförändring, förlust av biologisk mångfald, samt alltmer hotade ekosystem, finns ett stort behov av att förstå människans effekter, samt möjliga återkopplingsprocesser, i den marina miljön.

Denna avhandling beskriver och undersöker konsekvenserna av mänskliga aktiviteter i kustnära ekosystem genom studier i tre olika områden: Sine Saloum i Senegal, Västafrika, Åland i Finland, Östersjön, och Mobile Bay i Alabama, Mexikanska golfen. Eftersom det är välkänt att effekter av mänskliga aktiviteter kan upptäckas med hjälp av indikatorer, fokuserade avhandlingen på bioindikatorer som är särskilt relevanta i kustnära ekosystem, nämligen bottenlevande makrofauna. I tre studier undersöktes mänsklig inverkan på kustnära makrofaunasamhällen och ekosystemfunktioner. Genom en kombination av taxonomiska och egenskapsbaserade tillvägagångssätt utvärderades både strukturella och funktionella egenskaper hos makrofaunasamhällena i förhållande till mänsklig påverkan såväl som olika abiotiska variabler. Eftersom bottenlevande makrofaunasamhällen är centrala för flera ekosystemfunktioner blir även många av de ekosystemtjänster som tillhandahålls av bottenlevande makrofaunasamhällen direkt hotade av mänsklig påverkan. Med hjälp av representativa variabler för makrofauna-associerade ekosystemfunktioner, studerades hur bottenfaunasamhällena reagerade på antropogena aktiviteter. I synnerhet studerades ekologiska funktioner relaterade till omarbetning av sedimentet (dvs. bioturbations- och bioirrigationspotential), till biogeokemiska flöden, samt till faunans roll i födoväven och dess funktion som en central födoresurs för epibentiska rovdjur och bottenlevande fiskar.

För samtliga av de tre studerade kustekosystemen, visade resultaten att makrofaunan inte bara påverkas av den fysiska miljön (t.ex. salthalt, temperatur, hydrodynamik, djup, syrehalt, årstid) och sedimentets egenskaper (t.ex. kornstorlek, organisk halt), utan även av mänskliga aktiviteter, såsom

skaldjursskörd, fiskodling, övergödning, tungmetaller, strand- och kustexploatering, samt muddring. Resultaten visar att mänskliga aktiviteter utgör styrmekanismer som påverkar makrofaunasamhällen (individdätheter, biomassor, biodiversitet, samt sammansättningen av arter och deras egenskaper), vilket medför förändringar i ekologiska funktioner och processer associerade med makrofaunasamhällena, vilket i sin tur har potential att vidare påverka ekosystemtjänster. Både typen av mänsklig aktivitet samt det geografiska avståndet till aktiviteten påverkar strukturen och funktionen hos makrofaunasamhällen. Forskningen i denna avhandling gav ytterligare stöd för fördelarna med att använda egenskapsbaserade metoder i kombination med taxonomiska metoder för att bättre förstå effekter och återkopplingsprocesser associerade med mänskliga aktiviteter. Ett nytt index användes för att uppskatta kvaliteten på makrofaunasamhället som en födoresurs för sekundärkonsumenter (t.ex. fiskar som äter bottenlevande organismer), vilket kompletterar studier som fokuserat på omarbetning av sediment.

Resultaten i avhandlingen ger i första hand en djupare förståelse av mänsklig påverkan i kustnära ekosystem, men utvärderar också potentiell feedback tillbaka till det mänskliga samhället. Slutligen visar denna avhandling att konceptet med ekosystemingenjörer kan tillämpas på människans effekter i havets ekosystem. Användningen av ett dylikt ramverk skulle kunna stöda hållbarhetsarbetet. För att bevara marina ekosystemtjänster bör särskild uppmärksamhet ägnas åt mänskliga aktiviteter som har konsekvenser för kustnära ekosystem.

NYCKELORD: KUSTEKOSYSTEM, SAMHÄLLSEKOLOGI, BIOLOGISKA EGENSKAPER, EKOSYSTEMFUNKTIONER, ZOOBENTHOS, INFAUNA, MILJÖSTRESSORER, BIOTURBATION, FÖDORESURS, EKOSYSTEMTJÄNSTER

Résumé (French abstract)

Afin d'améliorer son environnement, l'espèce humaine provoque des changements dans les écosystèmes du monde entier en agissant comme une espèce ingénieure des écosystèmes. Toute modification des écosystèmes, causée par une espèce ingénieure des écosystèmes, a le potentiel de rétroagir sur l'ingénieur. Les humains font l'expérience de ces rétroactions, affectant ainsi les biens et services écosystémiques. Comme les rétroactions actuelles suite à l'Ingénierie des Écosystèmes par l'espèce Humaine (IEH) sont principalement négatives, les inquiétudes s'intensifient concernant l'avenir de l'environnement et sa capacité à fournir les services nécessaires au maintien de civilisations humaines viables. Avec 2,5 milliards de personnes vivant à moins de 100 km de la côte, les écosystèmes côtiers sont soumis à une pression exacerbée. En raison de leur haute valeur environnementale et économique, les préoccupations se portent donc particulièrement sur ces écosystèmes côtiers. Alors que les humains font face à des défis liés au changement climatique, à la perte de biodiversité et aux écosystèmes de plus en plus menacés, il est donc impératif de comprendre les pressions induites par l'homme, les effets et les processus de rétroaction dans l'environnement.

Cette thèse explore la nature et les conséquences des effets involontaires de l'IEH sur les écosystèmes côtiers, à travers l'étude d'une combinaison de trois régions différentes à travers le monde : le Sine Saloum au Sénégal, en Afrique de l'Ouest, l'archipel d'Åland en Finlande, en mer Baltique, et la baie de Mobile en Alabama, dans le golfe du Mexique. Il est connu que l'on peut détecter les conséquences non voulues de l'IEH en utilisant des bioindicateurs, c'est pourquoi ma thèse porte sur l'étude de bioindicateurs particulièrement pertinents dans les écosystèmes côtiers, à savoir les organismes macrobenthiques. Sur la base de trois articles, ma thèse de doctorat évalue d'abord les effets de l'IEH sur les communautés macrobenthiques et le fonctionnement de l'écosystème en identifiant les effets sur les propriétés structurales et fonctionnelles des communautés macrobenthiques en réaction à différents ensembles de facteurs anthropiques et abiotiques, en utilisant une combinaison d'approches taxonomiques et basées sur les traits. Comme les organismes macrobenthiques sont au cœur de plusieurs fonctions de l'écosystème et que bon nombre des services écosystémiques fournis par les communautés macrofaunales benthiques sont directement menacés par les impacts causés par l'homme, j'ai également examiné la manière dont les proxies des fonctions écosystémiques médiées par les macrofaunes, agissant comme rétroactions biotiques pour les humains, sont affectés par les activités anthropiques. J'ai porté mon attention sur les fonctions écologiques macrobenthiques liées au remaniement des sédiments (c'est-à-dire les potentiels de bioturbation et de bioirrigation), au cycle biogéochimique et à leur capacité à jouer un rôle essentiel dans l'acquisition d'énergie pour les niveaux

trophiques supérieurs tout en servant de ressource alimentaire centrale pour les prédateurs épibenthiques et les poissons démersaux.

Mes résultats mettent en évidence que non seulement la macrofaune est affectée par l'environnement physique et les propriétés des sédiments, mais l'IEH a également été identifiée comme un facteur significatif. En effet, dans les trois écosystèmes côtiers étudiés, les facteurs influençant la structure et le fonctionnement des communautés macrobenthiques incluaient toujours des variables décrivant non seulement l'environnement physique (*par exemple la salinité, la température, l'hydrodynamique, la profondeur, l'oxygène dissous, la saison*) et les propriétés des sédiments (*par exemple la granulométrie, la teneur du sédiment en azote, en carbone et/ou en matière organique*), ainsi que des activités associées à l'IEH (*par exemple la récolte de coquillages, la pollution aux métaux lourds ou autres substances dangereuses, le développement côtier et la modification du littoral, l'eutrophisation, l'aquaculture, le dragage*). Les résultats montrent que l'IEH affecte les communautés macrobenthiques (en terme d'abondance, de biomasse, de diversité et de composition en espèces et en traits), ce qui se traduit par des modifications des fonctions écologiques et des processus associés aux communautés macrobenthiques, ayant ainsi le potentiel d'affecter les services écosystémiques. La proximité spatiale de l'IEH et le type d'IEH ont été démontrés comme influençant la structure et le fonctionnement des communautés macrobenthiques. Un exemple concret des effets de l'IEH et des rétroactions a été mis en évidence avec la récolte de coquillages dans le Sine Saloum, au Sénégal.

Cette recherche apporte des preuves supplémentaires de l'intérêt d'utiliser une approche basée sur les traits en parallèle de l'approche taxonomique afin de mieux comprendre les effets de l'IEH et leurs rétroactions. Un nouvel indice pertinent a été développé pour estimer la qualité de la communauté macrobenthique en tant que ressource alimentaire pour les consommateurs (par exemple les poissons benthiques), reflétant une fonction écologique supplémentaire par rapport aux proxies déjà existants liés au remaniement des sédiments. De plus, cette thèse démontre que le concept des espèces ingénieuses des écosystèmes peut s'appliquer à l'espèce humaine. L'utilisation de l'IEH pourrait représenter un framework avantageux en écologie scientifique, dans l'atteinte des Objectifs de Développement Durable (ODDs). Les conclusions de cette thèse apportent également une compréhension approfondie des effets de l'IEH dans les écosystèmes côtiers et des rétroactions potentielles pour la société humaine et l'économie. Afin de préserver les services écosystémiques, une attention particulière devrait être accordée aux activités humaines au niveau des écosystèmes côtiers.

MOTS-CLÉS : ÉCOSYSTÈMES CÔTIERS, ÉCOLOGIE DES COMMUNAUTÉS, TRAITS BIOLOGIQUES, FONCTIONNEMENT DES ÉCOSYSTÈMES, ZOOBENTHOS, ENDOFAUNE, STRESS ENVIRONNEMENTAL MULTIPLE, FONCTIONS ÉCOLOGIQUES, BIOTURBATION, RESSOURCE TROPHIQUE, SERVICES ÉCOSYSTÉMIQUES.

Table of contents

List of original papers	1
1. Introduction and background	3
1.1. The human species as an ecosystem engineer	3
1.2. Human ecosystem engineering in coastal ecosystems.....	5
1.3. Benthic macrofaunal communities as bioindicators in coastal ecosystems: combining taxonomic and functional approaches	6
1.4. Estimating macrofauna-mediated ecosystem functioning.....	7
1.5. Implied feedback for human society and economy.....	8
2. Aims and scope of the thesis	10
3. Material and methods	12
3.1. Study areas and data collection	13
3.1.1. Sine Saloum, Senegal, West Africa (I)	13
3.1.2. Åland Islands, Finland, Baltic Sea (II)	15
3.1.3. Mobile Bay, Alabama, Gulf of Mexico (III).....	16
3.2. Sample processing (I, II, III)	18
3.2.1. Sediment samples	18
3.2.1. Macrofaunal samples.....	18
3.3. Data analysis.....	19
3.3.1. Structural (I, II, III) and functional (I, II) diversity	19
3.3.2. Traits selection (I, II)	19
3.3.3. Macrofauna-mediated ecosystem functions (II, III)	23
3.3.4. Statistical analysis (I, II, III)	25
4. Results and discussion	28
4.1. Effects of direct drivers on the macrozoobenthos.....	28
4.1.1. Relationships between environmental descriptors and macrofaunal communities in different coastal ecosystems	28
4.1.2. Disentangling the main drivers for coastal macrozoobenthos	31
4.2. Effects on macrofauna-mediated ecosystem functions	39
4.2.1. Effects on sediment reworking (II, III).....	40
4.2.2. Effects on biogeochemical fluxes (III)	42
4.2.3. Effects on food availability for mesopredators (II).....	44
4.3. Potential feedback through macrofauna-mediated ecosystem functions	45

5. Conclusions and broader outlook..... 48

5.1. Key findings..... 48

5.2. Multidisciplinary perspectives on regulating human ecosystem
engineering effects and feedback 49

5.2.1. Broader perspective on root causes of the direct anthropogenic
drivers affecting nature..... 49

5.2.2. Rethinking the climate and biodiversity narrative to put nature
at the center of societal values, planning, and goals 50

5.3. Benefits with using the Human Ecosystem Engineering (HEE)
framework..... 54

Appendix..... 55

Terminology 58

Acknowledgments 62

References..... 66

ORIGINAL MANUSCRIPTS..... 84

List of original papers

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I. **Jacquot M.P.**, Nordström M.C., De Wever L., Ngom Ka R., Ka S., Le Garrec V., Raffray J., Sadio O., Diouf M., Grall J., Tito de Morais L., Le Loc'h F., 2023. Human activities and environmental variables drive infaunal community structure and functioning in West African mangroves. *Estuarine, Coastal and Shelf Science* 293. doi: [10.1016/j.ecss.2023.108481](https://doi.org/10.1016/j.ecss.2023.108481).
- II. **Jacquot M.P.**, Snickars M., Bonsdorff E., Nordström M.C. Trait responses to direct drivers and effects on multiple macrofauna-mediated ecosystem functions. (*submitted to Marine Ecology Progress Series*)
- III. **Jacquot M.P.**, Dorgan K.M., Mortazavi B., Kleinhuizen A.A., Clemo W.C. , 2018. Macrobenthic community structure and influence on denitrification capacity in soft sediments (Mobile Bay, Alabama, USA). *Marine Ecology Progress Series* 605: 17–35. doi: [10.3354/meps12759](https://doi.org/10.3354/meps12759).

Author contribution to individual papers:

	Paper I	Paper II	Paper III
Study design & methods	RNK, LTM, FLL	MPJ	MPJ , KMD, BM, AAK, CWC
Data collection	MPJ , LDW, RNK, SK, JR, OS, FLL	MPJ	MPJ , KMD, CWC
Data analysis	MPJ	MPJ	MPJ
Manuscript preparation	MPJ , MCN, LDW, RNK, SK, VLG, JR, OS, MD, JG, LTM, FLL	MPJ , MS, EB, MCN	MPJ , KMD, BM, AAK, CWC

Copyrights:

- © MPJ and co-authors (I, II)
- © Inter-Research Science Publisher (III)

1. Introduction and background

1.1. The human species as an ecosystem engineer

Many species attempt to enhance their environment, and humans have been trying to make the world a better place - for themselves - for thousands of years, often with unforeseen and unintended consequences (Gutiérrez et al., 2011; Smith, 2007). All organisms change their environment as they grow, live and reproduce. Some organisms, such as lugworms, elephants, beavers, and ants change their surroundings so much that they are called ecosystem engineers. As described by Jones et al. (1994), ecosystem engineers are “organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so, they modify, maintain and create habitats” (Fig. 1). Autogenic engineers (e.g., trees, corals) change the environment via their own physical structures (i.e., the engineer is part of the engineered environment through their living and dead tissues for example) (Jones et al., 1994). Allogenic engineers (e.g., fiddler crabs, beavers) change the environment by transforming living or non-living materials from one physical state to another, employing mechanical or other methods (Jones et al., 1994). All habitats on Earth support, and are influenced by, ecosystem engineers (Jones et al., 1994).

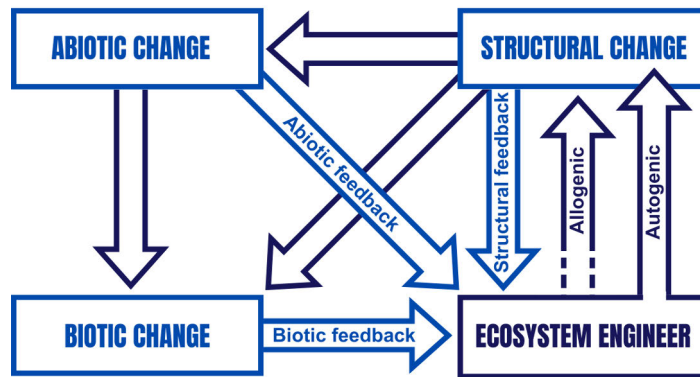


Fig. 1: Physical ecosystem engineering by organisms as conceptualized by Jones et al. (2010). This framework is based on the cause/effect relationships taking place in an engineered system and linking the engineer and the associated structural, abiotic and biotic change. The solid arrow for autogenic engineering represents the physical manifestation of the engineer in the environment. The broken arrow for allogenic engineering represents the action of the engineer on other living and nonliving structures. As described by Jones et al. (2010), the framework has four cause/effect relationships linking four components: 1. An engineer causes structural change; 2. Structural change leads to environmental modifications causing abiotic change; 3. Both structural and abiotic change can in turn cause biotic change; 4. Structural, abiotic and biotic change can all feedback to the engineer. The first two relationships describe an ecosystem engineering process and abiotic dynamics, while the second two describe biotic consequences for other species and the engineer. Structural change over time is the sum of structure formation by the engineer minus structural loss via decay.

Many human socio-economic activities (e.g., dredging and canalization of water courses, skyscraper construction, dam building, and forest clearing) correspond to cases in which humans act as ecosystem engineers (Chu and Karr, 2013; Gutiérrez et al., 2011; Jones et al., 1994), modulating the flow of resources to other species by causing physical or chemical state changes in abiotic or biotic materials (Berke, 2010; Jones et al., 1994). Jones et al. (1994) defined humans as allogenic engineers par excellence. From a functional perspective, Jones et al. (1994) did not identify fundamental differences between human and non-human engineering. The human species has the same way of affecting the ecosystem as any other ecosystem engineering species (Jones et al., 1994). The many types of human activities indeed fit the classification proposed by Berke (2010). In this classification of ecosystem engineers, emphasis was placed on how ecosystem engineers modulate the availability of resources to other organisms. Four non-exclusive functional classes of ecosystem engineers were distinguished, with structural engineers, bioturbators, light engineers, and chemical engineers having ecosystem-level effects corresponding to what is usually identified as “human impacts” (Tab. 1).

Table 1: Summary of the four functional classes of engineers as proposed by Berke (2010), with examples of ecosystem-level effects and associated human, marine and aquatic, as well as terrestrial ecosystem engineers.

Class of engineers	Examples of ecosystem effects	Human examples	Marine and aquatic examples	Terrestrial examples
Structural engineers	Create or destroy living space Reduce or enhance disturbance Alter hydrodynamics Alter diversity / richness	Construction Dam building Canalization of water courses Deforestation Wind farm	Corals Bivalves Tube-building invertebrates Macrophytes Macroalgae Mangroves	Most plants Mound-building insects Beavers
Bioturbators	Enhance disturbance Mix sediment Alter biogeochemistry Alter diversity / richness	Dredging Harvesting Agriculture Mining	Burrowing infauna (e.g., polychaetes, bivalves, crustaceans, echinoderms, nemerteans) Excavators (e.g., bottom-feeding fish, skates and rays, gray whales, crabs, echinoderms)	Burrowing vertebrates (e.g., fossorial rodents, mammals, lizards) Burrowing invertebrates (e.g., earthworms, ants, termites) Excavators (e.g., porcupines, skunks)
Light engineers	Alter light intensity, penetration, scatter Alter turbidity	Artificial lighting Aquaculture	Zooplankton Phytoplankton Filter feeders (e.g., bivalves, ascidians)	Any organism casting shade, most plants
Chemical engineers	Create biogeochemical gradients (physically or physiologically)	Aquaculture Climate change Chemical spill Agriculture runoff Industrial effluents	Microbes Seagrasses and aquatic plants Macroalgae Many burrowers (e.g., lugworms)	Most plants Mycorrhizal fungi Nutrient vectors (e.g., seabirds, bears)

Ecosystem effects mentioned in Tab. 1 correspond to structural, abiotic (e.g., altering turbidity) and biotic (e.g., altering diversity) changes in Fig. 1 and therefore have the potential to feedback to the engineers. As any other ecosystem engineering species, humans are also affected by both positive and/or negative structural, abiotic and biotic feedback, happening on the same or different time scales (Fig. 1) (Jones et al., 2010). Importantly, this feedback also represents “ecosystem services” and “nature’s contribution to people” (Brondizio et al., 2019).

What distinguishes humans from other species is the magnitude of the impact. Since the Industrial Revolution, the human species, through its socio-economic activities, has indeed become an ecosystem engineer on a whole new scale in time and space (Smith, 2007; Worm and Paine, 2016). The effects unfold faster and on a scale far greater than any effects of past ecosystem engineers. Over the past two centuries – representing barely more than two human lifetimes – humans have impacted living and nonliving systems everywhere. As a result, humans have even been described as a “hyperkeystone species” (Worm and Paine, 2016) and as “the ultimate ecosystem engineers” (Smith, 2007).

Climate change and many other human-driven changes to the environment are raising concerns about the future of Earth’s environment and its ability to provide the services required to maintain viable human civilizations (Worm and Paine, 2016). Today, as our efforts at ecosystem engineering are beginning to attempt to reduce and reverse human modification of environments (e.g., the UN decade on ecosystem restoration, <https://www.decadeonrestoration.org>), interest is also growing across diverse fields (including archaeology, biology, climatology, genetics, geography, psychology, sociology) in understanding the nature and consequences of human environmental impacts and managing these impacts to protect the well-being of human society and other life on Earth. Chu and Karr (2013) highlighted that: “understanding the environmental impacts of human actions is one of modern science’s greatest challenges” and that “understanding the consequences of those impacts, and managing them to protect the well-being of human society and other life on Earth, is humanity’s greatest challenge”.

1.2. Human ecosystem engineering in coastal ecosystems

Coastal ecosystems contribute with great environmental and economic value. They are associated with both important ecological functions (such as primary and secondary production and nutrient cycling) and highly valuable goods and services for human society (Barbier et al., 2011). Because coastal ecosystems are located at the interface between marine and terrestrial ecosystems, the ecosystem services provided by the biodiversity surpass the coastal area itself and benefit society in a wider spatial and historical context (Rodrigues-Filho et al., 2023). Not only are coastal areas important places for human well-being and

recreation, they are vital in terms of ecosystem functions, e.g., forming nurseries and feeding habitats for fish, providing a nutrient filtering function from land towards the open sea, sustaining important fishing grounds, and being zones responsible for a strong benthic-pelagic coupling (Griffiths et al., 2017; Miller-Way and Twilley, 1996).

Coastal ecosystems are influenced by pressures coming from land, adjacent open waters, the local atmosphere, and human socio-economic activities. Currently, 2.5 billion people live within 100 km of the coast, placing a disproportionate pressure on coastal and marine ecosystems (Brondizio et al., 2019; Dolbeth et al., 2007; Newton et al., 2020). Intense multiple uses result in physical and biological restructuring, mainly through (i) urban expansion and increased human population density, (ii) the fishing and aquaculture industries, (iii) maritime transport and associated infrastructures, and (iv) tourism and associated accommodations and facilities (Brondizio et al., 2019). Ecosystem responses to environmental changes can involve shifts in community dynamics as well as in the structure and function of marine ecosystems (Capasso et al., 2010; Frid et al., 2009).

1.3. Benthic macrofaunal communities as bioindicators in coastal ecosystems: combining taxonomic and functional approaches

Unintended consequences following human ecosystem engineering in coastal ecosystems can be detected using bioindicators. For example, macrofaunal organisms (invertebrates >0.5 mm) participate in intricate relationships with their environment, making them compelling bioindicators of environmental status (Perus et al., 2007). Due to their often restricted mobility, infauna are limited in their ability to avoid environmental and anthropogenic pressures. As a result, these organisms can be particularly impacted by human activities occurring in coastal ecosystems, such as overfishing as a result of the ever-increasing demand in marine resources (Pauly et al., 2005), topographical destruction of benthic habitats through dredging (Thrush and Dayton, 2002), or nutrient inputs from agriculture and industry leading to eutrophication and organic enrichment (e.g., HELCOM, 2013). The addition of climate-related pressures to direct anthropogenic impacts such as eutrophication often results in synergistic effects, exacerbating the impact (Blenckner et al., 2015; Harley et al., 2006; Kirby et al., 2009).

Human ecosystem engineering and environmental disturbances can impact macrofaunal communities leading to decreases in abundance, biomass and/or diversity (Corte et al., 2021; Dauer, 1993; Pearson and Rosenberg, 1978). For instance, in a eutrophication context, the response of benthic macrofauna exposed to low oxygen levels typically involve avoidance by, or mortality of, individuals. This results in an altered community structure, including increased

abundances of enrichment opportunists and shifts in species composition and trophic structure (Middelburg and Levin, 2009). Taxonomic diversity and composition (e.g., the total number of taxa within a community (species richness), the taxonomic identity of species and their abundance in an assemblage) have long been, and still are, cornerstones in community-ecology research. Linking changes in the environment to taxonomic-based attributes is common practice and provides ecologically valid insight into how environmental parameters influence a single species or entire communities.

Despite the high relevance of the taxonomic approach, the taxonomic identity of a species alone often offers limited information regarding its ecological role. Changes in taxonomic composition and diversity do not necessarily inform about other important ways in which communities are affected by human ecosystem engineering. Organisms are not influenced in a homogeneous or a random way; instead, certain organisms are much more affected than others. This is because the ecological traits (e.g., lifestyle, morphology, physiology, reproductive strategy, life span) of some organisms make them particularly vulnerable to human impacts, whereas other organisms, with different characteristics, thrive as a result of human activities. Díaz and Malhi (2022) highlighted two factors explaining this process: (1) humans involuntarily create habitat conditions that are distinctively favorable for some organisms but not for others and (2) people deliberately target certain organisms either by extracting them (e.g., fishing, selective harvesting, hunting) or by nurturing and deliberately transporting them over long distances (e.g., garden plants, pets, working animals). Evidence of the importance of functional biodiversity and species-specific traits of benthic fauna in explaining changes in ecosystem functioning is accumulating (Norling et al., 2007; Villnäs et al., 2011).

Moving beyond measures of taxonomic diversity to also consider trait characteristics of macrofaunal communities is important to evaluate potential ecosystem functions. Combining both approaches is key for understanding how ecosystem functions are affected due to human ecosystem engineering and for highlighting potential feedback for humans. Macrofaunal traits relate directly to their ecological processes and ecosystem function (Cadotte et al., 2011), and can respond rapidly to multiple pressures (Mouillot et al., 2013; Voß and Schäfer, 2017). During the past 20 years, many studies have used a combination of taxonomic and trait-based diversity approaches, which has developed our understanding of ecosystem function and supported efforts for better ecosystem management and conservation (Bremner et al., 2006; Henseler et al., 2019; Villnäs et al., 2019).

1.4. Estimating macrofauna-mediated ecosystem functioning

Besides serving as interesting bioindicators, macrofaunal organisms are central to several ecosystem functions. For instance, they facilitate the remineralization

of organic matter and enhance the depth of oxygen penetration in the sediments (Aller and Aller, 1998; Jovanovic et al., 2014). Additionally, they are essential in energy acquisition for higher trophic levels, serving as central food resource for epibenthic predators and demersal fish (Nilsen et al., 2006; Nordström et al., 2009; Salvanes et al., 1992). Many of ecosystem services provided by benthic macrofaunal communities are threatened directly via human-driven impacts. Looking at how proxies for macrofauna-mediated ecosystem functions respond to anthropogenic activities allows us to gain insights into potential feedback for human society and economy.

Benthic invertebrates contribute to sediment ecosystem functions by modifying their habitat through biological processes such as ingestion, digestion and excretion, as well as bioturbation and bioirrigation of the sediments (Levinton, 1995). These activities change sediment properties and enhance the transportation of particles and solutes. By increasing oxygen penetration into the sediment, the benthic infauna enhances the depth of the redox potential discontinuity (RPD) layer, and thus the availability of electron acceptors (such as O_2 , NO_3^- , Mn^{4+} and Fe^{3+}) within the sediment (Aller, 1979; Kristensen et al., 1991; Kristensen and Blackburn, 1987). Through their activities, benthic invertebrates can also enhance multiple sediment functions performed by microbial communities, such as organic matter mineralization and biogeochemical cycling, but also directly affect benthic primary production, as well as the energy transfer to higher trophic levels (Covich et al., 1999; Levinton, 1995; Lohrer et al., 2004). Quantitative proxies for the bioturbation (BP_c) (Queirós et al., 2013; Solan et al., 2004) and bioirrigation (BIP_c) (Renz et al., 2018) activity of communities were developed to evaluate effects of human engineering on the sediment physical structuring (Gogina et al., 2017; Tsikopoulou et al., 2021; Villnäs et al., 2013, 2012). Some studies go even further with direct measurements of ecosystem functions focusing on sediment-water interface fluxes and biogeochemical cycling (Norling et al., 2007; Villnäs et al., 2013, 2012).

1.5. Implied feedback for human society and economy

Changes in macrofaunal community structure due to human ecosystem engineering affect the coastal ecosystem functioning. Underpinning human welfare and livelihoods (Newton et al., 2014), these ecosystems provide several services, which are functions and products that benefit humans and society (Brondizio et al., 2019; Dasgupta, 2021). Changes in macrofauna-mediated ecosystem functions reflect on provisioning (e.g., food and raw material), regulating (e.g., carbon sequestration and water regulation), supporting (e.g., habitat for species and nutrient cycling) and cultural (e.g., aesthetic and educational values) services directly associated with coastal ecosystems (Tab. 2) (Rodrigues-Filho et al., 2023). For instance, a decrease in polychaete biomass following human activities could reflect a negative feedback since these macrofaunal organisms provide a supporting service as key prey to

INTRODUCTION & BACKGROUND

macrobenthic fish predators, with economic value, in coastal ecosystems (Weigel and Bonsdorff, 2018).

Table 2: Macrofaunal ecological functions (traits and mediated ecosystem functions) relating to different ecosystem services (categories according to Millennium Ecosystem Assessment (2005) (MEA cat.)) and underlying processes.

MEA cat.	Ecosystem services	Ecosystem processes	Macrofaunal ecological functions: traits and mediated ecosystem functions effects
Supporting	Nutrient cycling and sediment formation	Decomposition and mineralization, nutrient mobilization, biogeochemical cycle	Biomass production (detrital material converted into biomass) (+), body size (+), burrowing activity (+), sediment reworking (+), bioturbation and bioirrigation potential (multiple effects), diversity in substrate type, in life history and in species effects on soil processes (+), feeding habit and eco-morphology (multiple effects), movement habit, burrowing behavior and habitat use (<i>e.g., enhancing oxygen penetration and bacterial growth in sediment</i>) (multiple effects)
	Habitat provision	Secondary production / Ecological interactions	Prey biomass/abundance availability in foraging and nursery areas to mesobenthic predators (+)
	Primary production	Sediment formation / Biogeochemical cycle	Burrowing behavior (multiple effects), bioturbation potential (multiple effects)
Regulating	Water purification	Enhancing primary producers	Burrowing behavior and activity, bioturbation potential (multiple effects)
		Nutrient / Sediment retention	Abundance (+), biomass (+), feeding habits (<i>e.g., suspension feeders removing phytoplankton and controlling eutrophication or deposit feeders fostering bacterial activity in the water column</i>) (multiple effects), bioturbation potential (multiple effects)
		Oxygen regulation in water	
	Biological control	Decomposition	
Provisioning	Climate regulation	Herbivory control	Abundance, biomass and body size of grazers (multiple effects)
	Carbon sequestration in soil	Feeding habits enhancing photosynthetic rates and carbon sequestration (multiple effects), shell biomass production (+) as carbon long-term sink	
Provisioning	Primary production	Accumulation of standing biomass	Abundances (+), biomass (+)
	Biochemical material	Secondary production	Chitin biomass availability (+)
	Food	Secondary production / Ecological interactions	Abundance (+), biomass (+) availability supporting fishing activity (<i>e.g., shrimps, shellfish</i>)
Cultural	Aesthetic, inspirational values	Secondary production / Ecological interactions	Diversity (+), biomass (+), abundance (+) and size (+) of molluscs (<i>e.g., shells used to craft decoration artefacts or jewels</i>)
	Recreation and tourism		Biomass (+) and abundance (+) of fishing baits (<i>e.g., Polychaeta</i>), Biomass (+) and abundance (+) of molluscs supporting fishing activity, Biomass (+) of molluscs used as food and to build "Sambaquis" or used for floor covering in Senegal for example
	Sense of place, cultural heritage and diversity, social relationships, traditional knowledge		
	Educational, formal knowledge system		Biomass (+) and abundance (+) of bioindicator species, species used for classical studies
	Spiritual value		Shell biomass production (<i>e.g., gastropods shells named "Búzios" used in spiritual ceremonies</i>) (+)

The sign + indicates the most frequent direction of effects of traits on a given ecosystem process as found in the literature (De Bello et al., 2010; Rodrigues-Filho et al., 2023) and "multiple effects" indicates more complex relationships.

2. Aims and scope of the thesis

The overall aim of my thesis is to contribute to understanding “humanity's greatest challenge” by increasing our knowledge of the nature and consequences of human ecosystem engineering’s unintended consequences for benthic coastal ecosystems.

In this context, my PhD thesis aims at evaluating ecosystem engineering effects of humans on macrofaunal communities and ecosystem functioning by identifying (1) effects on structural (**I, II, III**) and functional (**I, II**) properties of macrofaunal communities to different sets of human ecosystem engineering and abiotic drivers, and (2) effects on multiple macrofauna-mediated ecosystem functions, acting as biotic feedback for humans (**II, III**) (Fig. 2).

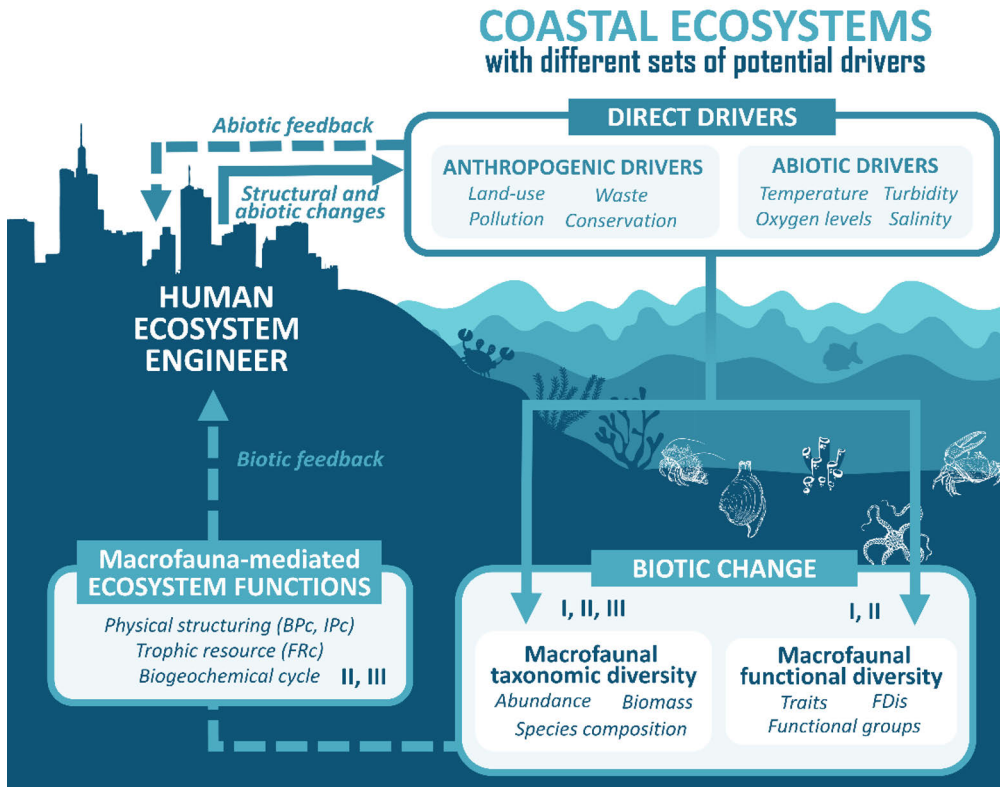


Fig. 2: Conceptual diagram of the thesis highlighting how the original papers (I, II, III) are interconnected. The figure from Jones et al. (2010) was modified and adapted to fit this thesis research and the human species as an ecosystem engineer.

Main questions:

1. How do different sets of anthropogenic and abiotic variables affect the structural (**I**, **II**, **III**) and functional (**I**, **II**) diversity of soft-sediment macrofaunal communities?
 2. Acting as biotic feedback for humans, how do changes in macrofaunal communities affect sediment ecosystem functioning in terms of physical structuring (through bioturbation and bioirrigation) (**II**), trophic resources (**II**), and biogeochemical cycling (**III**)?
-

I investigated these research questions in three studies (Fig. 2), exploring three different coastal benthic ecosystems in different parts of the world: a lagoon and an estuarine mangrove ecosystem (**I**), a complex archipelago system (**II**) and a shallow estuarine embayment (**III**). All these coastal benthic ecosystems are both valuable in terms of ecosystem functions and services and vulnerable to human ecosystem engineering (Brondizio et al., 2019; Dolbeth et al., 2007; Newton et al., 2020).

The combination of study areas allowed me to explore understudied areas (**I**, **III**) in addition to go deeper in the understanding of coastal communities in response to human ecosystem engineering and the resulting implications for coastal ecosystem functioning with a well-known study area (**II**). Indeed, different levels of knowledge were available regarding the macrofaunal communities in these three areas. Two of these coastal benthic ecosystems were not well studied in terms of macrofaunal communities, with the latest studies conducted in 1985 in the Sine Saloum, Senegal (**I**) (Ausseil-Badie and Monteillet, 1985; Leung Tack, 1985) and in 1988 in Mobile bay, Alabama (**III**) (Clarke and Miller-Way, 1992; Dardeau, 1988; Stout et al., 1998). An additional area I explored was one of the most extensively studied ecosystems in the world with the Åland Island archipelago in the Baltic Sea (**II**) (Reusch et al., 2018).

3. Material and methods



Sampling area			
Sampling years	2016	2007 -2008	2003 - 2022
Sampling in the intertidal area	✓	✓	✓
Sampling in the subtidal area	No	Yes	No
Tides	Shallow estuarine embayment	Reverse estuary	Complex archipelago system
Habitat type	Humid subtropical	Tropical	Humid continental
Climate			
Physical environment variables			
Temperature	✓	✓	✓
Salinity	✓	✓	✓
Depth	✓	✓	✓
Turbidity (Secchi Depth)	✓		✓
Dissolved oxygen levels (DO)	✓		✓
Location	✓	✓	✓
Year and Month / Season	✓	✓	✓
Wind-wave exposure			✓
Sediment properties variables			
Sediment type	✓	✓	✓
Grain size	✓	✓	
Organic content	✓		✓
Porosity	✓		
C:N and chlorophyll a content	✓		
Human ecosystem engineering factors			
Eutrophication	✓		✓
Coastal construction	✓		✓
Dredging	✓		✓
Shellfish harvesting		✓	
Potentially Toxic Elements (PTEs) (e.g., heavy metals)		✓	✓
Fish farming			✓
Bioindicators: macrofaunal community			
Abundance	✓	✓	✓
Biomass	✓	✓	✓
Taxonomic diversity	✓	✓	✓
Functional diversity		✓	✓
Ecosystem functions			
Biogeochemical processes			
Denitrification ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	✓		
NH_4^+ ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	✓		
$\text{NO}_2^- + \text{NO}_3^-$ ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	✓		
PO_4^{3-} ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	✓		
Sediment reworking			
Bioturbation potential (BP_c)	✓		✓
Bioirrigation potential (BIP_c)			✓
Trophic resource			
Food resource potential (FP_c)			✓

Fig. 3: Summary overview of all study areas and data included in papers I-III.

3.1. Study areas and data collection

Including different sets of potential drivers for macrofaunal communities, three different coastal benthic ecosystems were studied (Fig. 3).

3.1.1. Sine Saloum, Senegal, West Africa (I)

Two of the main mangrove areas in Senegal were explored: the Sine Saloum and the Petite Côte (Fig. 4). Located in Southwest Senegal, the Sine Saloum and the Petite Côte represent areas of great concern in terms of conservation and management due to the well-established traditional fishing activities carried out by Senegalese women, particularly the diverse harvesting of mangrove invertebrates. These areas are subject to a tropical climate characterized by two distinct seasons: (i) a long dry season from November to June, with air and water temperatures averaging around 17-25 °C and 20-22 °C, respectively, and dominated by hot and dry Harmattan wind, and (ii) a wet season from July to October, characterized by seasonal rainfall of approximately 600 mm, air and water temperatures of about 24-27 °C and 25-27 °C, respectively, and strong South-Eastern winds (Bodin et al., 2011). The Saloum Delta is recognized for its intricate network of small seawater creeks, locally referred to as “bolongs”. This “inverse estuary” is characterized by water salinity that is higher than that of seawater (Barusseau et al., 1985; Descroix et al., 2020). In this distinctive environment, salinity increases from downstream to upstream due to a combination of seawater intrusion linked to weak slope, limited freshwater inputs, and substantial evaporation. The upstream area experiences high levels of salinity, ranging from 60 to 120 (Simier et al., 2004). Consequently, where salinity is moderate, half the area is occupied by the mangrove forest, mainly *Rhizophora* and *Avicennia* species, but these trees rapidly disappear when salinity increases to more than 60. Upstream, mangroves are replaced by extensive intertidal sand and silt flats (Diop et al., 1997; Gning et al., 2010). The Petite Côte is located 20 km North of the Saloum Delta (Sambou et al., 2008). This lagoon-insular environment comprises extensive mangroves and mudflats, and is significantly impacted by coastal dynamics due to its opening to the sea. Lying on an island of clamshells, Joal-Fadiouth is the nearest town, with a population of 3500 inhabitants living on a small area of 500 meters in diameter. Both highly exposed to the sea, receiving minimal freshwater inputs, and experiencing hypersaline events during dry seasons, the Saloum inverse estuary and the lagoon in the Petite Côte have previously been characterized as similar marginal coastal environments (Guiral et al., 1999; Le Loeuff, 1999; Zabi and Le Loeuff, 1993, 1994).

Six stations were sampled between 2007 and 2008 in these two areas (Fig. 4). To assess macrofaunal variability depending on the exposure to human ecosystem engineering activities, which are more intense closer to the coast, sampling was conducted in: (1) the intertidal and (2) the subtidal areas. In these two tidal zones, stations were randomly selected in areas presenting different

exposure to shellfish harvesting and to heavy metals (Potentially Toxic Elements (PTEs)). In the Saloum delta, shellfish harvesting is based on the rotation of harvesting areas (Descamps, 1991; Sarr, 2005); areas left fallow for several months were considered non-exploited. Levels of PTEs were measured in a separate study conducted by Bodin et al. (2013), where concentrations of 12 trace elements (Li, V, Cr, Mn, Co, Ni, Cu, Zn, Ag, Cd, Pb, and Hg) were measured in surface sediment samples during the same sampling periods and in the same areas as in the present study. Anthropogenic contamination with Cd, Hg and Ni was measured in the Petite Côte (corresponding to station D), with Mn and Cr in Dionewar (corresponding to station W) and with Zn, Cu, V, Ag and Pb in both Dionewar (station W) and the Petite Côte (station D). These PTEs have previously been highlighted as presenting a potential ecological risk for macrofaunal communities (Dong et al., 2021; Piló et al., 2016; Ryu et al., 2011).

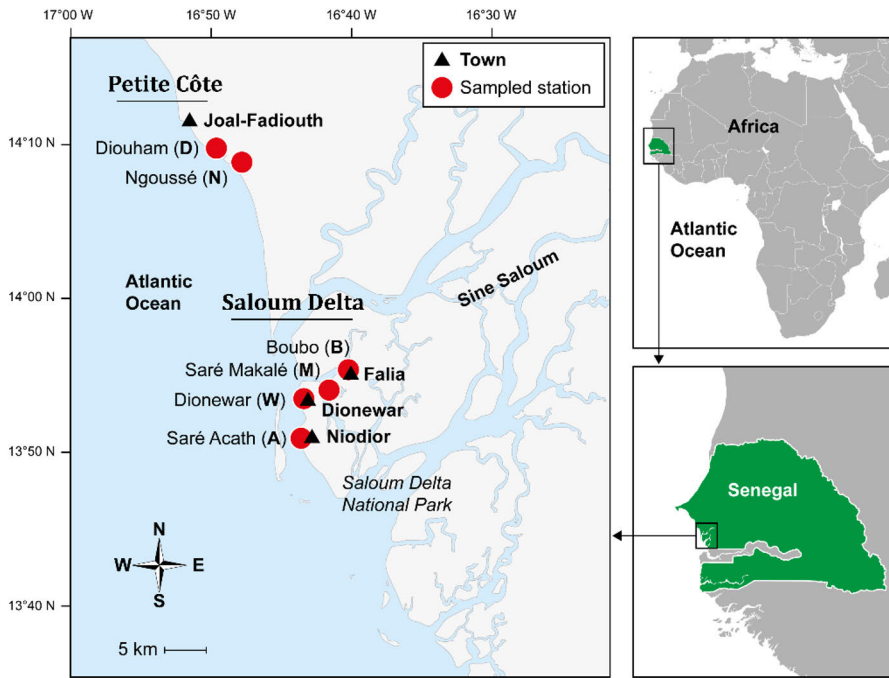


Fig. 4: Location of sampling stations in Southern West Senegal (I).

In the intertidal zone at low tide, a total of 87 samples were collected. Three to five replicates of 50 cm × 50 cm were sampled for macrofauna in December 2007 and February, April, June and October 2008 depending on stations. Sediment within the quadrat was scraped, using a hand shovel, to a depth of about 20 cm. Regarding the subtidal zone, a total of 56 macrofaunal samples were collected using a 0.1 m² Van Veen grab. Three to nine grab samples were taken at each station between 1 and 4 m depth in April, June and November 2008. Both sampling methods allow to collect infauna as well as sedentary and slowly moving species such as bivalves and gastropods, but is less accurate for estimating mobile animals, such as crabs. The recorded macrofaunal

communities in this study are therefore focused on a component of this community even if crabs were also caught and retained in the dataset. At each site and sampling event, three sediment samples were extracted for grain size analysis. In the subtidal zone, temperature and salinity measurements were taken at the bottom of the water column at each station using a YSI Multiparameter probe.

3.1.2. Åland Islands, Finland, Baltic Sea (II)

The Åland Islands archipelago is located in the Baltic Sea, at the junction of the northern Baltic Proper and the Bothnian Sea between Finland and Sweden (Fig. 5). Renowned as one of the most extensively studied ecosystems in the world and considered a simplified ecosystem, the Baltic Sea provides us with an “ideal” study area (Reusch et al., 2018). Due to its evolutionarily young age and prevailing brackish conditions, the Baltic Sea naturally presents low species diversity, facilitating in-depth analyses of community responses to human ecosystem engineering. Anthropogenic pressures on ecosystem structure and functioning have significantly fueled ecological interest in the Baltic Sea, for instance in regions such as the Åland Islands archipelago. Since the latter half of the 20th century, human-induced environmental changes have profoundly impacted the Baltic Sea ecosystem, leading to the classification of most Baltic Sea areas as having “moderate,” “poor,” or “bad” ecosystem health based on HOLAS (“tool of Holistic Assessment of Ecosystem Health Status”) (Andersen et al., 2017, 2011; HELCOM, 2023). The challenges faced by the Baltic Sea today encompass threats that many worldwide coastal and estuarine systems are and will likely be encountering in the near future (Reusch et al., 2018). Comprising over 6000 islands, the Åland coastal zone forms a highly heterogeneous land- and seascape, with underwater habitats ranging from shallow, sheltered bays to exposed open-sea areas. Gradients in environmental drivers, such as water temperature, salinity, oxygen concentration and organic content, can be steep from the inner to the outer coastal zone. Therefore, the Åland archipelago reflects broad environment types and can hence be considered a model area for understanding community structure and function across environmental gradients.

To spatially cover a wide range of environmental conditions and habitats and to pinpoint major environmental drivers for macrofaunal communities (traits and species), data for a total of 168 stations located throughout the Åland archipelago were compiled, for a total of 708 samples. Data on species composition, abundance and biomass of benthic macrofauna, along with environmental data, were collated from pre-existing scientific surveys that together cover the entire Åland Islands marine area. The analysis focused on the time period after 2000, given that this year corresponds to a large-scale community shift in the macrozoobenthos within the region, primarily attributed to the establishment of *Polychaeta Marenzelleria* spp. (Weigel et al., 2016). The datasets were obtained from Husö Biological Station (Åbo Akademi University, Finland), and our selection comprises data from years 2003 to 2022. Benthic

samples included were all obtained in a standardized way, using an Ekman-Birge grab sampler (289 cm²). The analysis only included stations with at least three replicate grab samples.

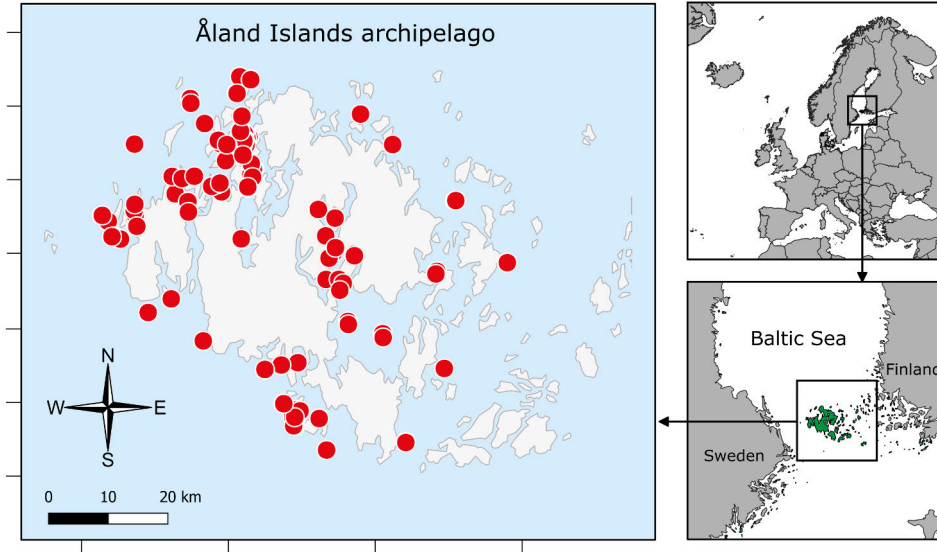


Fig. 5: Location of sampling stations in the Åland Islands archipelago (Finland, Baltic Sea) (II).

As environmental descriptors, I used available data on temperature (°C), salinity and oxygen concentration (mg L⁻¹) of bottom water (measured with a YSI Multi-parameter probe), sediment type (sand or mud), and sediment organic content (%). The extent of exposure to waves and wind, depth, and proximity to land were included through the EUNIS index, considering that they have been shown to be significant factors structuring biological communities (abundance, biomass, species composition) (Kilar and McLachlan, 1989; Pihl, 1986; Ricciardi and Bourget, 1999). Based on the established exposure index for the Northern Baltic Sea by Isæus (2004), the EUNIS index, I classified the stations *a priori* into sheltered, semi-exposed and exposed sites, accordingly. Research has demonstrated that fish-farm effluents impact both the water quality (Nordvarg and Johansson, 2002) and macrofaunal communities (Kraufvelin et al., 2001; Nordström and Bonsdorff, 2017) in the Åland Archipelago. As a proxy for fish-farm pollution, I estimated the distance to the nearest fish farm for each station. Human ecosystem engineering was further explored utilizing HELCOM data (<https://metadata.helcom.fi/>) (i.e., “Disturbance of species due to human presence”, “Physical disturbance”, “Integrated eutrophication status assessment”, and “Input of hazardous substances”).

3.1.3. Mobile Bay, Alabama, Gulf of Mexico (III)

Located in the northern Gulf of Mexico, Mobile Bay is a shallow estuarine embayment (Fig. 6) characterized by an average depth of 3 m and a 14 m deep

shipping channel running north–south. The lower part of the bay opens to the Gulf of Mexico and the Mississippi Sound. Due to the shallow water and variable freshwater inputs, salinity undergoes significant fluctuations, with strong vertical stratification under moderate to high river discharge and weak winds (Park et al., 2007). The tidal influence in Mobile Bay is limited, typically ranging from 0 to 20 cm on average. Mobile Bay experiences hypoxic and anoxic conditions, mostly during the summer months (Park et al., 2007). This study was carried out during predominately normoxic conditions (between January and May 2016). Given its nature as a shallow estuarine ecosystem, Mobile Bay is expected to experience substantial anthropogenic nitrogen loads (Lehrter, 2008). Estuaries, such as Mobile Bay, rank among the most productive ecosystems and provide habitats for many commercially and recreationally important species (e.g., oysters, crabs and shrimp). They also serve as active sites of sediment organic matter decomposition and associated nutrient regeneration.

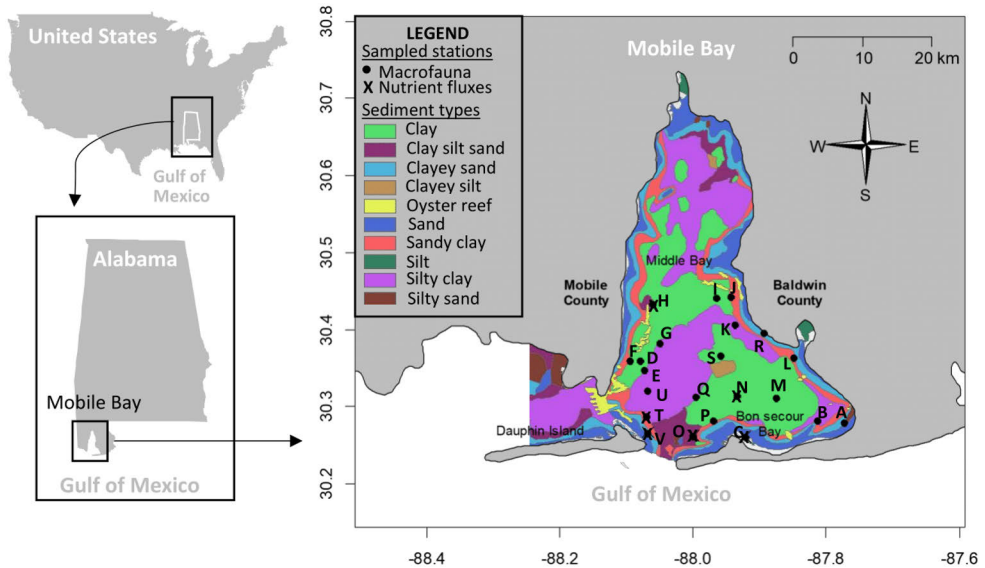


Fig. 6: Location of sampling stations in Mobile Bay covering different sediment types (sediment map based on Esri, HERE, De-Lorm, MapmyIndia, OpenStreetMap contributors and the GIS user community) (III).

To characterize variability in the macrofaunal community in Mobile Bay and determine the relationship between community structure and environmental variables, I sampled 22 stations randomly selected across a range of sediment types in the southern part of Mobile Bay between January and March 2016, during predominately normoxic conditions. At each station, three benthic infauna samples were collected using a 0.1 m² Petersen grab. Bulk sediment samples were collected using the same Petersen grab and haphazardly subsampled for grain size. Sediment cores (95 mm i.d.) were collected and the upper 10 cm was homogenized and analyzed for porosity and carbon to nitrogen (C:N) ratio and the top 1 cm was sampled for chlorophyll a (chl a) analysis and

frozen for later analysis. Temperature, salinity and DO of bottom water were also measured at each station with a YSI Multi - parameter probe, and turbidity was measured using a Secchi disk.

3.2. Sample processing (I, II, III)

3.2.1. Sediment samples

Depending on the knowledge regarding the sediment characteristics prior to our studies, two different methods were selected to analyze the sediment grain size. In areas with known-diverse sediment types **(I)**, sediment grain size was determined by water- (for 63 μm grain size fraction) and dry-sieving, using a series of 14 sieves from 63 μm to 10,000 μm . Sediment grain size was characterized through calculations for the median grain size, and the percentage of gravel, sand and mud. Gravel represents the fraction with particles larger than 2 mm, sand is the fraction ranging from 63 μm to 2 mm, and mud is defined as the sediment exhibiting grain sizes smaller than 63 μm and is described as the fine particle fraction (Blott and Pye, 2001). In areas with finer and organic-enriched sediments **(III)**, sediments were treated with a 30% hydrogen peroxide solution to oxidize organic matter prior to grain size analysis. Grain-size analysis followed the pipette method adapted from Folk (1974). To characterize the sediment type for each site, proportions of sand, clay and silt were plotted in a Shepard diagram **(I, III)** or estimated visually directly on site **(II)**. Organic matter in the sediment (%) was determined **(II)** by loss on ignition (3h at 500°C, dry weight). Sediment porosity was calculated **(III)** from the percentage of water in the sediment sampled at each station by weighing sediment before and after drying at 60°C for 24 h. Carbon and nitrogen content of the sediment (% wt) were measured **(III)** after homogenizing the dried sediment on a CHNSO elemental combustion system analyser (mod. ECS 4010; Costech Analytical Technologies). The molar C:N ratio (mol:mol) was used as a proxy for sediment organic matter quality (Blackburn and Henriksen, 1983). Sediment chl a content was determined **(III)** fluorometrically after cold extraction in 90% acetone in triplicate (Welschmeyer, 1994).

3.2.1. Macrofaunal samples

Regarding macrofaunal analysis, each replicate was treated separately to assess intra-station variability **(I, II, III)**. Benthic samples were washed through a sieve (with a mesh size of 1 mm **(I)** or 0.5 mm **(II, III)**), and retained material was preserved in either 7% formalin **(I)** or 70 to 95% ethanol **(II, III)**. Macrofaunal organisms were removed from all debris, identified and counted. Taxonomic identification was carried out at different taxonomic levels depending on the study: from family level **(III)** to the lowest possible taxonomic level for all taxa **(I, II)**. A thorough taxonomic quality assurance included verification of taxonomy and scientific names following several databases: MarBEF Data System - the European Register of Marine Species (ERMS) (Costello et al., 2023), WoRMS -

World Register of Marine Species (WoRMS Editorial Board, 2023) and ITIS - the Integrated Taxonomic Information System (ITIS, 2023).

Dry weights were obtained either by drying taxa of each sample at 60°C during 48 h (**I**, **II**) or using taxa-specific conversion factors provided by Brey (2001) from wet weight to dry weight (**I**, **II**, **III**). When conversion factors were applied, the wet weight was first measured to 0.001 g after blot-drying on tissue paper.

3.3. Data analysis

3.3.1. Structural (**I**, **II**, **III**) and functional (**I**, **II**) diversity

Macrofaunal taxonomic diversity was assessed (**I**, **II**, **III**) using the following primary community variables and diversity indices (Gray and Elliott, 2009): abundance (A), biomass (B), taxonomic richness (S), Shannon's diversity index (H'), Pielou's evenness (J') and Simpson's diversity index (1-D, hereafter D).

Functional diversity was assessed (**I**, **II**) with the following three multidimensional indices: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Laliberté and Legendre, 2010; Villéger et al., 2008). These indices were designed to complement each other (Villéger et al., 2008) and recognized as a relevant combination to cover the functional space of a community (Mouchet et al., 2010). FRic quantifies the extent of trait space occupied by species within a community, representing the number of expressed trait categories. FEve assesses the evenness of species abundances across the expressed trait categories, with a low value indicating under-utilization of certain parts of the niche space. FDiv characterizes the distribution of the abundance across the niche space, with a higher value indicating a high degree of niche differentiation (Mason et al., 2005).

3.3.2. Traits selection (**I**, **II**)

Traits reflect key components of functioning and act as proxies for ecological processes (Törnroos and Bonsdorff, 2012). For papers **I** and **II**, I selected a set of relevant traits reflecting key functions of macrofaunal communities within coastal ecosystems (Tab. 3). With the selected traits, I focused on two main functional aspects within coastal systems, with: 1) the quality of macrofauna as a food resource for higher trophic levels, with traits reflecting production, susceptibility to predation and palatability proxies (**II**); and 2) the role of macrofauna as ecosystem engineers, including traits related to habitat modification, bioturbation, spatial resource dynamics and nutrient cycling (**I**, **II**). The selection of traits depends on the level of knowledge available regarding the species in the specific area we were interested in. Indeed, a more extensive trait list was available for the extensively studied Åland Islands archipelago (**II**) compared to the not well-studied Sine Saloum system (**I**) (Tab. 3).

Table 3: Traits and functional categories included in the different studies (I, II) and their hypothesized relationships with factors responsible for spatial patterns in macrofaunal assemblages including traits helping to distinguish between natural and human-induced changes.

Traits	Categories and their definition	Key mechanisms and functions	Description and relevance	Hypothesized relationships with environment
Feeding mode	Scavenger: Feeding on carcasses.	Food acquisition, productivity, turnover, proxy for energy transfer, strength of benthic-pelagic coupling, prey accessibility	Feeding interactions have long been considered a central factor structuring macrofaunal communities (Pearson and Rosenberg, 1978). Feeding types contribute to production and trophic support, and play a role in nutrient uptake and recycling (Norling et al., 2007). It provides insights into the interactions between different species and their food sources. A diverse set of feeding modes indicates diverse food sources available in an area (Pacheco et al., 2011). The feeding mode is considered to be a proxy for energy fixation/transfer and ecosystem production (Tomroos and Bonsdorff, 2012). It has important implications for the transfer of carbon between the sediment and the water column and within the sediment. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995).	Predators and scavengers will be associated with areas with high availability of prey (Dolbeth et al., 2007). Scavengers are attracted to areas where physical disturbances occur and are expected to be more common in areas of high fishing or fish farming intensity. Organic enrichment caused by fish farming is expected to favor large deposit feeders (Donadi et al., 2015). Scrapers and grazers are more abundant in areas with high levels of primary producers, usually found in areas with low depth (Dolbeth et al., 2007) and potentially low hydrodynamics. Surface feeders are obtaining food from the surface of the substratum so they transport energy from the pelagos. They act on the pelagos-benthos elemental cycling. Sub-surface feeders obtain food within the sediment so energy transport stays within benthos.
	Predator: Feeding on living animals.			
	Parasite: Obtaining food from another animal (host)			
	Miner: Obtaining food through mining in, e.g., wood			
	Scraper, grazer: Feeding on leaves or other plant parts			
RESPONSE TRAIT (Resistance)	Surface deposit feeder: Feeding on phytoplankton, litter and organic matter in the sediment and water column.	Prey accessibility, susceptibility to cropping and predation, productivity, elemental cycling, space resource dynamics	Despite the generally restricted motility of benthic infauna, the small-scale motility of these organisms is crucial for the ecology of benthic communities. Not only motility provides insights into the ability to avoid physical disturbance (Hinchey et al., 2006) but also into the predatory-prey activities or the creation of biological structures. Mobility also affects the ability for adult recolonisation of disturbed areas. In addition, mobility may increase prey vulnerability or decrease it in case of strong escape response. Living habits are affecting habitat complexity, with the construction of biological structures for instance, and can influence nutrient recycling and trophic support (Brenner et al., 2006).	Infauna is expected to be less affected by wave exposure and to be found in higher proportions in deeper areas. Spatial overlap of predator and prey niches increases prey vulnerability. Indeed, infauna living in the top layer of the sediment, epibenthos and benthic-pelagic individuals are more accessible to cropping and predation than infauna living deeper in the sediment. If infauna is living deeper in the sediment, it suggests that there is a potential for water penetration into the sediment surface, which may provide organic matter to lower sediment layers where it can be decomposed and also incorporate oxygen in the sediment (Pacheco et al., 2011).
EFFECT TRAIT (Bioturbation)	Sub-surface deposit feeder: Feeding on phytoplankton, litter and organic matter.			
(I, II)	Passive suspension / filter feeder: Feeding on the suspended matter or food particles in the water column.			
	Surface deposit feeder: Feeding on the suspended matter or food particles in the water column.			
	Active suspension / filter feeder: Feeding on the suspended matter or food particles in the water column.			
Motility & Living habit	Motile Swimmer: Free-swimming organisms.	Mobility, dispersal, susceptibility to cropping / predation and environmental pressures	Sessile organisms are more subject to changes in the abiotic environment than motile species (Sarà, 1986). Motile species are expected to have a better ability to avoid stressors (e.g., fish farming, hypoxia events, eutrophication, physical disturbance...) and to be able to recolonize areas by migration (Gogina et al., 2014; Krause et al., 2010; Pacheco et al., 2011). Faster moving species (particularly swimmers) are more likely to evade local physical pressure, while those capable of movement within the sediment may regain sediment position following burial (Bolam, 2011). Burrow-dwellers and tubicolous are potentially less vulnerable to strong hydrodynamic disturbance, anoxic conditions and water pollution as opposed to free-living species because they can hide in their fixed tubes or burrow (Reise, 2002).	Infauna is expected to be less affected by wave exposure and to be found in higher proportions in deeper areas. Spatial overlap of predator and prey niches increases prey vulnerability. Indeed, infauna living in the top layer of the sediment, epibenthos and benthic-pelagic individuals are more accessible to cropping and predation than infauna living deeper in the sediment. If infauna is living deeper in the sediment, it suggests that there is a potential for water penetration into the sediment surface, which may provide organic matter to lower sediment layers where it can be decomposed and also incorporate oxygen in the sediment (Pacheco et al., 2011).
	Motile Rafter / Drifter: Rafting on, e.g., drifting algal mats			
	Motile Crawler: Move on the sediment surface.			
	Motile Burrower: Live in burrows within the sediment.			
	Semi-mobile Tubicolous: Lives in a tube.			
EFFECT TRAIT (Food resource, Bioturbation)	Sessile Byssus / Attached: Attached on the surface to a hard substrate.	Prey accessibility, susceptibility to cropping and predation, productivity, elemental cycling, space resource dynamics	Living habits are affecting habitat complexity, with the construction of biological structures for instance, and can influence nutrient recycling and trophic support (Brenner et al., 2006).	Infauna is expected to be less affected by wave exposure and to be found in higher proportions in deeper areas. Spatial overlap of predator and prey niches increases prey vulnerability. Indeed, infauna living in the top layer of the sediment, epibenthos and benthic-pelagic individuals are more accessible to cropping and predation than infauna living deeper in the sediment. If infauna is living deeper in the sediment, it suggests that there is a potential for water penetration into the sediment surface, which may provide organic matter to lower sediment layers where it can be decomposed and also incorporate oxygen in the sediment (Pacheco et al., 2011).
(I, II)	Infaua deep: Living within the substrate, deeper than 5 cm			
	Infaua middle: Living within the substrate between 2-5 cm			
	Infaua top: Living within the top 2 cm of the substrate			
	Epibenthic: Living on the surface of the substrate			
	Benthic-pelagic: Living in the water column and feeds on the bottom			

(Table 3 continued)

Traits	Categories and their definition	Key mechanisms and functions	Description and relevance	Hypothesized relationships with environment
Maximum adult body size	Very small: 0-0.01 g		The organism body size has a crucial relevance in the functioning and dynamics of aquatic systems (Woodward et al., 2005). Body size is correlated with many life-history traits and influences a wide range of biological and ecological functions (Bourassa and Morin, 1995; LaBarbera, 1989; Macdonald et al., 2012; Saiz-Salinas and Ramos, 1999; Warwick and Clarke, 1984). This biometric parameter can be more responsible for the trophic structure than taxonomic identity itself (Jennings et al., 2001). Body size has implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small bodied species (high turnover) (Pearson and Rosenberg, 1978).	Small-bodied species may characterize environments with high instability, the result of environmental/anthropogenic disturbances imposed on the organisms (Moullot et al., 2006). We expect small-sized species to be prevalent in high hydrodynamic areas (Donadi et al., 2015) and to have higher P/B ratios (Schwinghamer, 1983) with higher metabolic rates (Gillooly et al., 2001). Increases in organic matter in the sediment, e.g., due to fish farming, would favor larger individuals (Donadi et al., 2015). Hypoxia is also expected to act on the body size, sometimes favoring medium/large individuals (Gogina et al., 2014) and sometimes small size ones (Pacheco et al., 2011). Smaller prey body size increases prey vulnerability.
(I, II)				
Fragility	Fragile: Likely to crack as a result of physical impact	Prey accessibility, protection against predation and physical pressures, proxy for palatability, productivity, for litter quality, ease for ingestion and decomposition	Different morphologies vary in their relative susceptibility to damage from physical pressure (e.g., dredging).	Fragile individuals are likely to crack as a result of physical impact (e.g., dredging, submarine power cables installation) (Krause et al., 2010). Individuals with intermediate fragility are liable to suffer minor damage and robust individuals are unlikely to be damaged by physical impact (e.g., hard, leathery). Fragile individuals are expected to have a higher palatability and to decompose faster (Tornroos and Bonsdorff, 2012).
RESPONSE TRAIT (Resistance)				
EFFECT TRAIT (Food resource)				
(II)				
Longevity	Very short: < 1 year		Longevity represents the maximum lifespan of the adult stage (years). It indicates the relative investment of energy in somatic rather than reproductive growth and the relative age of sexual maturity, i.e., a proxy for relative r- and k- strategy (Pearson and Rosenberg, 1978).	Longer-lived species (k-strategy) are expected to be found in deeper waters where light, food availability, temperature and disturbance intensity drive highly predictable distributions (Montero-Serra et al., 2018). As long-living species are more common in undisturbed habitats, we further expect such species, particularly those of a larger body size, to be rarer in disturbed areas (Gogina et al., 2014; Pacheco et al., 2011).
RESPONSE TRAIT (Recovery potential)	Short: 1-2 years	Life cycle/lifespan, turnover rate, productivity, energy fixation		Long-living species have lower relative production due to slow growth and turnover rates (Moss et al., 2016; Ridgway et al., 2011).
EFFECT TRAIT (Food resource)	Long: 2-5 years			
(II)	Very long: 5-10 years			

(Table 3 continued)

Traits	Categories and their definition	Key mechanisms and functions	Description and relevance	Hypothesized relationships with environment
Reproductive Method RESPONSE TRAIT (Recovery potential)	Asexual-fragmentation: Asexual both fragmentation and budding		Species can reproduce asexually (fragmentation, budding), or eggs can be released into the water column (pelagic) or onto/into the bed either free or maintained by mucous (benthic) or eggs are maintained by adult for protection, either within parental tube or within body cavity (brood). These different mechanisms vary in their potential susceptibility to damage from physical pressures (Bolan et al., 2020).	Brooders (k-strategy) have fewer offspring but invest more time and resources in ensuring survival, both in gestation and rearing. Broadcast spawners (r-strategy) have numerous offspring to overwhelm the odds. This means that few resources and minimal energy are invested in the survival of each individual. We expect broadcast spawners to decrease with depth and an increase in species with other reproductive methods (Miletkovsky, 1971). Asexual reproduction may be an adaptation to unfavorable environmental conditions and for species where sexual reproduction is uncertain and/or infrequent (Foster et al., 2013; Wangenstein et al., 2016). We expect that asexual reproduction will dominate in areas that have been disturbed by anthropogenic pressures over a long period of time.
	Sexual broadcast spawner: Fertilized eggs laid or spawned	Reproduction, turnover, productivity		
	Sexual brooder: Egg layer/brooder			
	(II)			
Propagule dispersal RESPONSE TRAIT (Recovery potential)	Pelagic planktotrophic: Feeding on material captured from the plankton		This trait indicates the potential for dispersal of the larval stage prior to settlement from direct (no larval stage), lecithotrophic (larvae with yolk sac, pelagic for away from their egg after hatching (i.e., short periods) to planktotrophic (larvae feed and grow in water column). Dispersal is a fundamental ecological process that affects the organization of biological diversity at multiple temporal and spatial scales containing a high quantity of yolk, correlate with dispersal strongly with a short pelagic duration and settlement close to parents (Foster et al., 2013). Therefore, we expect that planktotrophic species can recolonize more easily areas that have been disturbed by anthropogenic pressures over a long period of time (e.g., physical disturbances, eutrophication, human presence, hazardous substances) (Gogina et al., 2014; Krause et al., 2010; Padheco et al., 2011). Additionally, we expect an increase of species with lecithotrophic or direct developing larvae with depth.	
	Pelagic lecithotrophic: Nourished on internal resources, yolk	Movement of resources, decomposition, productivity, proxy for recruitment success, elemental transport		
	Benthic direct development: Direct development of mini adults			
	(II)			
Degree of contagion EFFECT TRAIT (Food resource)	Solitary: Living alone		Macrofauna species act as food resources for larger benthic species, epifauna, or demersal fish species (Rosenberg, 1995). Therefore, the macrofaunal degree of contagion traits gives insights on food distribution thereby increase biodiversity for consumers (Ding et al., 2020).	
	Patchy: Living in groups (aggregated together) occasionally (e.g., mussels)	Consumption rate, elemental cycling, decomposition		
	Highly aggregated: Living in groups, growing in clusters, schooling			
	(II)			

Information on traits was collected for the lowest possible taxonomic level from a variety of published sources: literature (e.g., Törnroos and Bonsdorff, 2012) and online databases, such as Polytraits (Faulwetter et al., 2014), BIOTIC - Biology Traits Information Catalogue (MarLIN, 2006), and WoRMS - World Register of Marine Species (WoRMS Editorial Board, 2023). Since some species show plasticity in expressing certain trait categories, trait categories were scored using a fuzzy coding approach (Chevene et al., 1994), with a scoring range of 0 (no affinity) to 3 (total affinity towards trait category) (D'Alessandro et al., 2020; Hu et al., 2019; van der Linden et al., 2016). The fuzzy-coded species-trait matrix was then abundance-weighted using the average species abundances for each station.

3.3.3. Macrofauna-mediated ecosystem functions (II, III)

3.3.3.1. Estimate of benthic community quality as food resource for consumers (FP_c) (II)

Macrofauna inhabit the upper layers of the sediment and the interface between water and sediment, playing a vital role in benthic-pelagic coupling (Griffiths et al., 2017). These organisms serve as crucial food resources for larger benthic species, epifauna, and demersal fish species (Rosenberg, 1995). Weigel and Bonsdorff (2018) introduced a species-specific energy content proxy (EC, J g⁻¹) to estimate production, susceptibility to predation, palatability and overall quality as food resource (prey) for consumers (predators) in the ecosystem. Following the optimal foraging theory, predators are inclined to select prey that provide them with the highest energetic gain (EC_i) while losing minimal energy during the catching and handling process (expressed hereafter with Fr, Ep, Lp_i) (Pyke et al., 1977). Prey species with relatively high-energy content are likely to be preferred when their abundances and accessibility are comparable to those of lower energy species. Consequently, areas with such high-energy prey species that are easily accessible would present greater potential as a food resource.

For each sample, I multiplied the species-specific energy content (EC_i, J g⁻¹) by the mean individual biomass (expressed by the relation B_i/A_i, where B_i is a dry weight in g m⁻², and A_i is abundance in ind m⁻²) of each species in the sample and with standardized scores for prey vulnerability to predation based on its living position (Lp_i), standardized scores for the species ability to escape based on its motility (Ep_i) and standardized scores regarding the ease to be ingested by the predator based on the body fragility (Fr_i). The following index gives an estimate of food resource potential for each species (FP_i, J m⁻²) and for the community (FP_c, J m⁻²) food resource potential at each station as follows (Equation (1)):

$$FP_c = \sum_{i=1}^n FP_i = \sum_{i=1}^n \sqrt{\frac{B_i}{A_i}} \times A_i \times EC_i \times Fr_i \times Ep_i \times Lp_i$$

For the energy estimates (EC_i), I followed established biometric conversion factors from existing literature (Brey, 2001; Brey et al., 2010). Information on Fr_i , Ep_i and Lp_i was coded following my previous trait selection. In cases where there were no species-specific data available, I applied the values of the closest taxonomic level.

3.3.3.2. Estimate of the community bioturbation potential (BP_c) (II, III)

A frequently used approach to assess the ecosystem function related to the sediment reworking activity of macrofauna is the community bioturbation potential (BP_c) (Queirós et al., 2013; Solan et al., 2004). This index serves as a proxy for organic matter mineralization, providing indirect information on the oxygen penetration within the sediment. The community bioturbation potential has also been associated with sediment reworking (Morys et al., 2017), redox metrics (Birchenough et al., 2012), biogeochemical cycling (Braeckman et al., 2014), sediment chlorophyll a (Josefson et al., 2012), sediment total organic carbon (Solan et al., 2012), and chemical pollution (Mazik and Elliott, 2000).

This index includes quantitative measures of species biomass (B_i) and abundance (A_i), as well as qualitative considerations for mobility (M_i) and functional sediment reworking (R_i), two traits known to regulate biological sediment mixing, a key component of bioturbation (Solan et al., 2004). Information on mobility and sediment reworking mode was coded following Gogina et al. (2017) and Queirós et al. (2013). These data were used to estimate the species (BP_i) and community (BP_c) bioturbation potential, using the equation in Solan et al. (2004) (Equation (2)):

$$BP_c = \sum_{i=1}^n BP_i = \sum_{i=1}^n \sqrt{\frac{B_i}{A_i}} \times A_i \times M_i \times R_i$$

3.3.3.3. Estimate of the community bioirrigation potential (BIP_c) (II)

To quantify the potential for solute exchange at the sediment–water interface, community bioirrigation potential (BIP_c) was calculated, following Renz et al. (2018). In order to account for different underlying physical processes in mud and sand, BIP_c incorporates different scores for advective systems (corresponding to medium sand and coarser sediment types), and for diffusive benthic system (very fine and fine sand sediments, all other muddy and less permeable sediment types). Given that the sampling method adopted in this study is restricting the collection of fauna to only muddy to fine sand sediments, scores aligned with diffusive benthic systems were assigned to all taxa.

To calculate BIP_c , the mean individual biomass (expressed by the ratio B_i/A_i , where B_i is a dry weight in $g\ m^{-2}$, and A_i is abundance in $ind\ m^{-2}$) of each species within a sample is multiplied by the relevant scores for the trait categories feeding type (FT_i), burrow type (BT_i) and depth (L_i), and they are weighted in

turn by species abundance as given in the following equation. Subsequently, the results are summed up across all species present in the sample at a particular station (Equation (3)):

$$BIP_c = \sum_{i=1}^n BIP_i = \sum_{i=1}^n \sqrt{\frac{B_i}{A_i}} \times A_i \times BT_i \times FT_i \times L_i$$

In the cases where trait categories were deemed irrelevant or negligible regarding solute exchange across the sediment–water interface (e.g., epifauna), a score of “zero” was assigned. Information on BT_i modes, FT_i types and L_i (cm) were obtained from the literature (e.g., Renz et al., 2018) and databases (e.g., Faulwetter et al., 2014; MarLIN, 2006).

3.3.3.4. Measure of nutrient fluxes and denitrification rates (III)

Going further than estimating the bioturbation (BP_c) and bioirrigation (BIP_c) potentials, I also directly measured sediment–water interface nutrient fluxes and denitrification rates (III). These measures of biogeochemical fluxes correspond to direct measurements of ecosystem functions. Further information are accessible directly in **paper III**.

3.3.4. Statistical analysis (I, II, III)

Recognized as a robust approach to assess the relative influence of different ecological factors in driving community assembly (Jupke and Schäfer, 2020), a distance-based redundancy analysis (dbRDA) was performed (II, III). This method involves constrained ordinations on data using Bray-Curtis distances (Legendre and Gallagher, 2001). dbRDA synthesizes the complete dataset of taxa abundances at different sites with a triplot projection (sites, stations and explaining factors) on 2 axes. This analysis assessed the influence of the included variables on taxa abundances across stations. An ANOVA was performed on the model to ensure the significance of the dbRDA analysis (Legendre and Anderson, 1999). In case of an unbalanced design (I), non-metric multidimensional scaling (nMDS) was preferred in order to test the link between the macrofaunal assemblages based on their beta diversity and the different ecological factors. First, the Bray-Curtis coefficient was used to compute a dissimilarity matrix for species community structure analysis. The results were, then, visualized with nMDS. The environmental factors were fitted on the ordination diagrams after a permutation test (999 permutations) allowing to discriminate variables having a significant influence ($p < 0.05$). To ensure the interpretation of the nMDS results, stress values were calculated (Clarke, 1993). Hierarchical cluster analysis (I, II, III) was applied to abundance data to identify similarities among sites and build clusters on either dbRDA or nMDS plots. Cluster analysis (group-average linkage) was performed on a resemblance matrix of the transformed data based on Bray-Curtis distances.

Identified cluster groups were further described with boxplots for environmental variables (**I, II, III**). Boxplots for univariate data were also computed with samples pooled in testing groups based on the hierarchical cluster analysis results in order to assess macrofaunal taxonomic and functional diversity. Before performing statistical tests on univariate characteristics of macrofaunal α -diversity (A, B, S, H', J', 1-D) (**I, II, III**), functional diversity (FRic, FEve, FDiv) (**I, II**), and macrofauna-mediated ecosystem functions (FPc, BPc, BIPc, nutrient fluxes) (**II, III**), all faunal and environmental variables were checked for normality (graphically and using Agostino test) and fourth-root, $\log(x+1)$ or arcsine transformed if necessary. If data did not meet the assumptions for 1-way ANOVA, the Kruskal-Wallis 1-way ANOVA by ranks was used. If significant differences were detected by the main test ($p < 0.05$), post-hoc tests for pairwise multiple comparisons (Nemenyi's test) were used to identify differences between pairs of stations. In addition to species composition, community-level weighted means of trait values (CWM), representing the expressed trait categories weighted by abundances, were computed for each replicate and used to compare the trait composition between groups identified in the hierarchical cluster analysis (**I, II**). A SIMPER (similarity percentage) analysis was applied to examine the dissimilarity between the cluster groups concerning species and trait composition.

To investigate the correlation between the ecological traits of macrofaunal communities and environmental variables, a combination of RLQ (Dolédéc et al., 1996) and fourth-corner analysis (Legendre et al., 1997) according to Dray et al. (2014) was applied (**I, II**). For the RLQ analysis, tables representing environmental variables (R), species abundance (L), and traits (Q) were analyzed using Hill-Smith analysis, correspondence analysis (CA), and principal component analysis (PCA), respectively (Dray et al., 2014). The overall significance of this relationship was assessed through a global Monte Carlo test involving 49,999 random permutations of models 2 and 4 (Dray et al., 2014; Dray and Legendre, 2008). Model 2 tests whether the distribution of species with fixed traits is influenced by the environmental conditions while model 4 tests whether traits influence the composition of species assemblages found in samples, while keeping environmental conditions fixed (Dray et al., 2014). Additionally, given that RLQ analysis does not pinpoint which traits are impacted by specific environmental variables, fourth-corner analysis, with an adjusted p-value (false discovery rate method, FDR) (Benjamini and Hochberg, 1995) for multiple testing, was implemented. Furthermore, by combining both RLQ and fourth-corner analyses, the significance of the association between traits or environmental variables and the RLQ axes was investigated (Dray et al., 2014).

Variance partitioning analysis (VPA) was performed to evaluate the contribution of human ecosystem engineering, sediment properties and environmental factors to the variance in structural and functional diversity (**I, II, III**). Prior to this analysis, covariates were divided into three groups, one of

which was human ecosystem engineering (e.g., shellfish harvesting, heavy metals), another one was variables related to the physical environment (e.g., temperature and salinity) and the last one was sediment variables (e.g., sediment type, organic content). We computed adjusted R^2 following Peres-Neto et al. (2006) recommendations to produce unbiased estimates of the fractions of variation. Only variables explaining a significant variation ($p < 0.05$) were included in the VPA, after conducting a separate forward selection on each subset of environmental variables. To ensure the significance of the VPA, we tested all fractions independently using two-way ANOVA.

All analyses were performed using the R Statistical Software (R Core Team, 2022). The functional diversity indices (FRic, FEve, and FDiv) were calculated using the "FD" package in R (Laliberté and Legendre, 2010) based on the fuzzy coding matrix of the traits and the abundance of species. The dbRDA analysis was conducted using the "PMCMRplus" package (Legendre et al., 2013). For RLQ and fourth-corner analyses, the "ade4" R package was utilized (Dray and Dufour, 2007). Spearman correlation tests examining the relationships between taxonomic and functional indices and environmental variables were executed with the "corrplot" R package (Wei and Simko, 2017). nMDS and VPA were performed using the "vegan" package (Oksanen et al., 2011).

4. Results and discussion

4.1. Effects of direct drivers on the macrozoobenthos

4.1.1. Relationships between environmental descriptors and macrofaunal communities in different coastal ecosystems

Significant relationships between environmental descriptors and the macrofaunal community structure and functioning were identified in different coastal ecosystems: a lagoon and an estuarine mangrove ecosystem in the Sine Saloum (Senegal, West Africa) **(I)** (Fig. 7a), a complex archipelago system in Åland Islands (Finland, Baltic Sea) **(II)** (Fig. 7b), and a shallow estuarine embayment with Mobile Bay (Alabama, Gulf of Mexico) **(III)** (Fig. 7c).

4.1.1.1. In the Sine Saloum West African mangroves (I)

Original data of this study including infaunal abundances, biomasses, traits, and environmental variables are available at Mendeley Data (<https://doi.org/10.17632/xtdjv38vst.1>). In 142 samples collected in two of the main Southern West Senegal mangrove areas (the Sine Saloum and the Petite Côte), a total of 12,418 macrofauna individuals were identified belonging to 127 different taxa; with a total of 71 taxa found in the intertidal zone and 104 in the subtidal zone, including 48 taxa in common. Principal constraints for infaunal community structure and functioning were different depending on the tidal area (Fig. 7a).

Highly open to the sea and poorly supplied in freshwater, these studied West African marginal coastal ecosystems are subject to hypersaline events during dry seasons and therefore represent restrictive environments for infaunal communities. As a result, environmental variables characterized by a drastic change in seasons impacted the infaunal communities, especially in the subtidal zone (Fig. 7a). Closer to anthropogenic disturbances in the intertidal area, pressures related to human ecosystem engineering activities (shellfish harvesting and heavy metals) took precedence over environmental variables in explaining infaunal community structure and trait composition (Fig. 7a). In addition, in both intertidal and subtidal areas, sediment properties explained a significant part of the infaunal community structure and was associated with specific traits related to feeding mode (Fig. 7a).

4.1.1.2. In the Åland Islands complex archipelago system (II)

Original data of this study including macrofaunal abundances, biomasses, traits, and environmental variables are available at Mendeley Data (<https://doi.org/10.17632/6whtvfg3ds.1>). Among 168 stations and 708 samples, a total of 83,982 macrofauna individuals were identified belonging to 44 different taxa between 2003 and 2022 in the Åland archipelago. This large

dataset combining environmental and macrofaunal data allowed us to identify the exposure to wind-waves and to human-induced pressures, as well as the sediment characteristics, as the principal constraints for infaunal community structure and functioning (Fig. 7b).

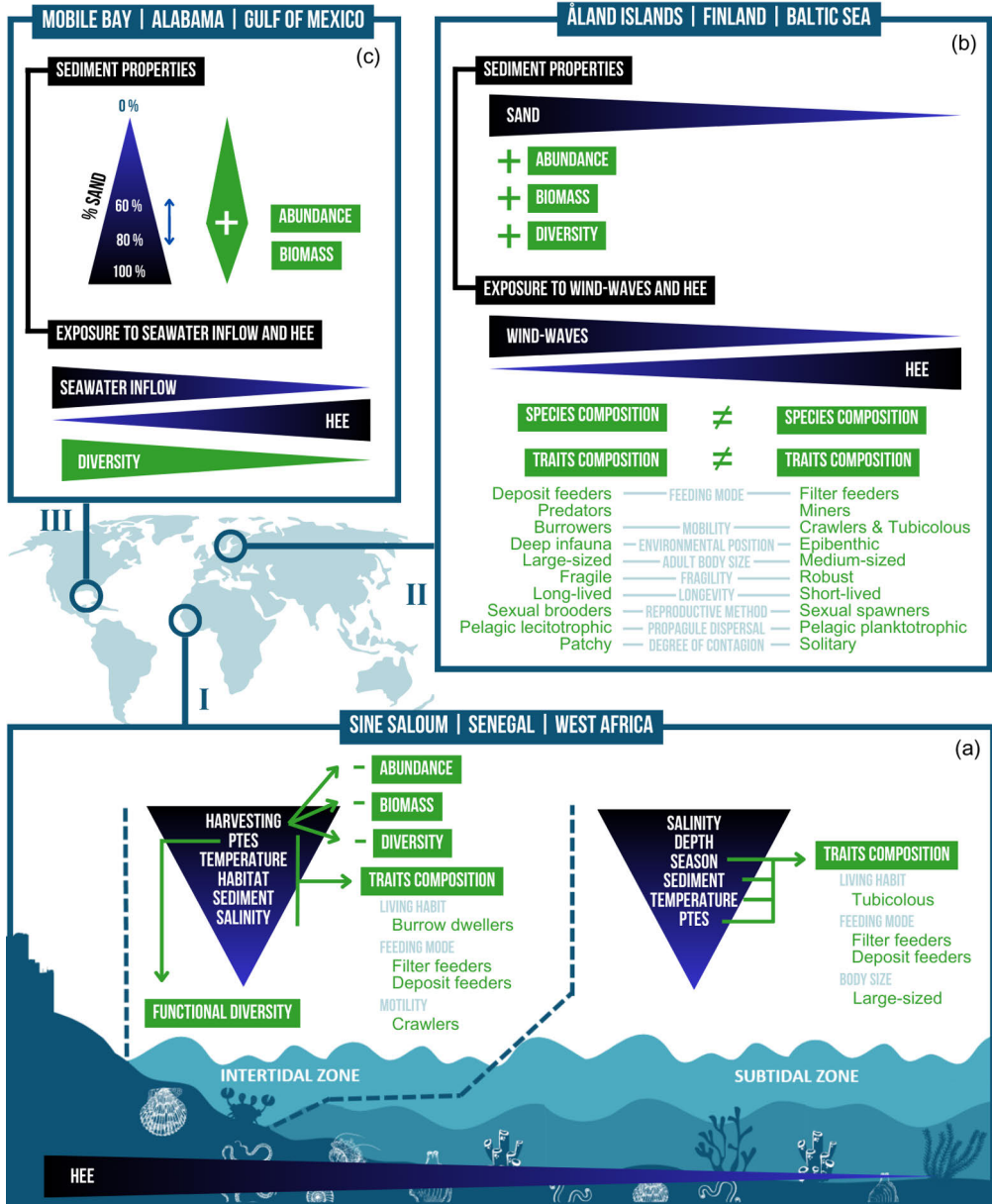


Fig. 7: Conceptual model summarizing the main drivers for macrofaunal communities in the different studied coastal ecosystems and their effects on communities structure and functioning. HEE = Human Ecosystem Engineering. PTEs = Potentially Toxic Elements (such as heavy metals). These results are based on multivariate analyses available in papers **I, II and III** (i.e., dbRDA, nMDS, RLQ and fourth-corner analyses).

In the Åland archipelago, the coastal zone comprises over 6,000 islands, forming a highly heterogeneous land- seascape, ranging from shallow, sheltered bays to exposed open-sea areas (Bonsdorff et al., 1996; Weigel et al., 2015). A gradient from the inner, sheltered and highly eutrophied archipelago to outer exposed areas was associated with a change in species and traits compositions (Fig. 7b and 8a). Sediment properties were also significant drives in explaining macrofaunal structural diversity patterns (Fig. 7b), with lower abundance, biomass and species richness in muddy sediments compared to sandy ones.

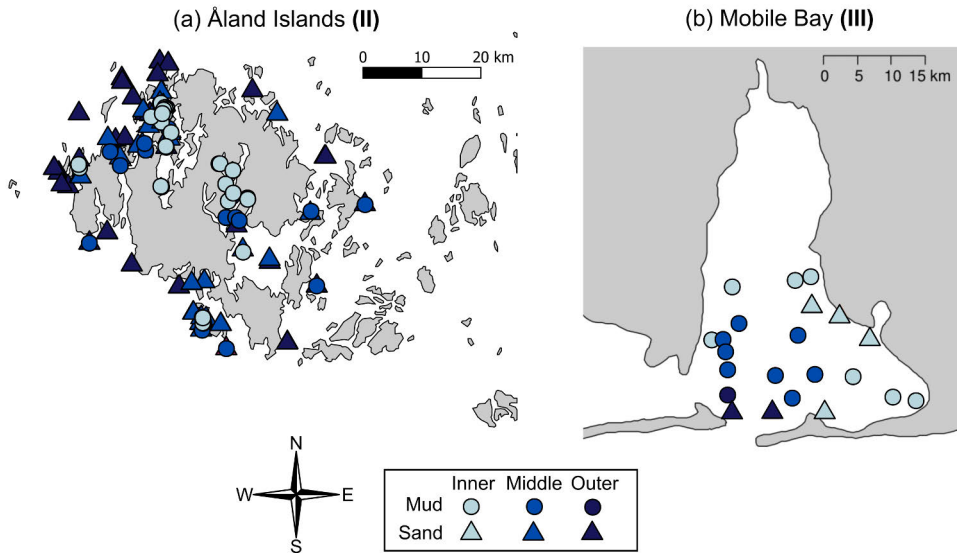


Fig. 8: Maps showing stations characteristics in sediment type (mud vs sand) and exposure (inner, middle and outer) in Åland islands (a) and Mobile Bay (b) based on results from multivariate analyses available in papers II and III (i.e., dbRDA, nMDS).

4.1.1.3. In the Mobile Bay shallow estuarine embayment (III)

Among 22 stations and 66 samples, a total of 7,299 macrofauna individuals belonging to 65 different families of infauna were identified in Mobile Bay. The exposure to seawater intake and to human ecosystem engineering in addition to the sediment characteristics were identified as the principal constraints for macrofaunal distribution and taxonomic composition (Fig. 7c).

Macrofaunal diversity in the bay was mostly dependent on the exposure to seawater inflow and to human ecosystem engineering (Fig. 7c), with the discrimination of three different zones: along the coastline, in the middle of the bay, and close to the mouth of the bay (Fig. 8b). While macrofauna exhibited a clear geographic pattern within Mobile Bay in terms of diversity, their abundances, biomass and taxonomic composition appear to depend mostly on sediment characteristics (i.e., sand content, quantity and quality of the organic matter, porosity and turbidity) (Fig. 7c).

4.1.2. Disentangling the main drivers for coastal macrozoobenthos

In the three studied coastal ecosystems, regardless of their specificities, drivers for macrofaunal community structure and functioning always included variables describing the physical environment, human ecosystem engineering and sediment properties (Fig. 7 and 9). Based on the independently selected variables for physical environment, human ecosystem engineering and sediment properties, I performed VPAs to investigate the amount of macrofaunal community variability uniquely linked to each variable category (Fig. 9).



Fig. 9: Variance (adjusted R^2) of the structural (a) and functional (b) diversity uniquely attributed to human ecosystem engineering activities (dark blue), to sediment properties (light blue) and to physical environmental characteristics (medium blue) in the intertidal and subtidal zones in Senegal (I), in Åland Islands (II) and in Mobile Bay (III). The residual variance is identified as “Other” (grey). All tested variables are listed on the right side of the corresponding histogram and significant variables ($p < 0.05$) included in the variance partitioning are highlighted.

4.1.2.1. Physical environment

In all studied subtidal zones, the physical environment was the main constraining factor for macrofaunal communities, explaining 22% of the variation in the structural diversity in the Sine Saloum, 31% in Åland Islands and 24% in Mobile Bay (Fig. 9a). Included in the parameters describing the physical environment, salinity and temperature were highlighted as significant constraints for macrofaunal communities in the three studied coastal ecosystems (I, II, III) (Fig. 9). Salinity and temperature are indeed well-known major driving variables for macrofaunal communities (Li et al., 2022). Salinity has been reported as the main environmental factor affecting benthic macrofauna community composition and structure in coastal and estuarine

ecosystems (Conde et al., 2013; Little et al., 2017; Verdelhos et al., 2015). For instance, in estuaries and lagoons of West Africa, Zabi and Le Loeuff (1993) showed that macrofaunal species distribution was linked to fluctuations in temperature and salinity. In our Sine Saloum study (**I**), variations in temperature and salinity were highlighted as drivers for traits related to motility, in the intertidal zone (Fig. 7a). Crawlers with their relatively high mobility were indeed found in different proportions depending on fluctuations in temperature and salinity. As noted by Dong et al. (2021), this trait is beneficial for macrobenthos to expand their range of activities, increase their access to food, and even help them to escape from disturbances quickly. Variability in salinity and temperature were also a prevailing factor for Mobile Bay macrofaunal diversity (**III**) (Fig. 9a). Higher diversity of macrofauna was found near the mouth of the bay whereas stations along the coastline were characterized by lower diversity and biomass, with communities dominated by a few, small and opportunistic (r-selected) taxa such as capitellids (Tsutsumi, 1987) and tolerant orbinids (Kruse et al., 2004) (Fig. 8b). Interestingly, communities inhabiting more variable environments (e.g., in salinity and temperature) tend to be dominated by high densities of relatively smaller-sized, r-selected species (Flint and Kalke, 1985). Temporal averages showed higher salinities at the mouth of the bay, although with considerable variability depending on rainfall. This salinity gradient has been previously identified as a prevailing structuring factor for benthic communities in Mobile Bay (Clarke and Miller-Way, 1992). Salinity has also been shown to affect benthic community structure in Nueces Bay, Texas (US), with higher biomass and diversity in the higher salinity region of the bay (Mannino and Montagna, 1997). In addition, on sunny days, bottom temperature can increase rapidly in shallow environments, and high bottom temperature can have a negative impact on macrofauna. Located close to freshwater inputs, the shallow-water stations therefore may experience higher variability in salinity and temperature (Flint and Kalke, 1985), and therefore higher stress inducing the observed decrease in diversity and change in community composition.

The critical importance of hydrodynamics for macrofaunal spatial distribution was reflected by the wind-wave exposure in the Åland archipelago (with the measure of the EUNIS index) (**II**) and the exposure to seawater inflow in the Mobile Bay shallow embayment (also indicated as distance to the mouth of the bay in paper **III**) (Fig. 7bc, 8 and 9). Clear spatial patterns were indeed identified in terms of diversity, species and traits compositions, in Åland Islands with the distinction of the inner *versus* exposed archipelago (**II**) (Fig. 8a) and in Mobile Bay with the distinction of the coast *versus* the mouth of the bay (**III**) (Fig. 8b). Foulquier et al. (2020) assessed impacts of wave action and freshwater outflow on soft-bottom benthic macrofauna spatial distribution and also highlighted that wave exposure strongly linked to estuarine inputs were the most relevant abiotic factors influencing distributional patterns and functional structure. Van Der Wal et al. (2017) also highlighted the importance of local hydrodynamic conditions regarding diversity and functional traits in subtidal

estuarine macrozoobenthic communities. The hydrological characteristics of Mobile Bay (**III**) have been identified as some of the potential factors explaining the gradient in the macrofaunal diversity from the mouth to the coast of the bay. The extent to which a marine species is able to penetrate into an embayment depends primarily on the amount and variability of the freshwater discharge relative to the tidal inflow of seawater (Ysebaert et al., 1993). The combination of small tidal ranges and long tidal periods that characterize Mobile Bay is expected to produce weak tidal currents at the estuary mouth (Lee et al., 2013; Stigebrandt, 1977). In addition, the shape of the Main Pass into Mobile Bay has the potential to support gyre formation on both sides of the estuary mouth (Lee et al., 2013) that can oxygenate and keep higher salinity levels in the area close to the mouth as well as transport and retain larvae from outside of the bay. As a consequence of the hydrodynamics occurring in the bay, larval transport patterns are another potential factor explaining the higher diversity of taxa near the mouth of the Mobile Bay.

In the subtidal areas (**I**, **II**, **III**), depth contributed in explaining the macrofaunal community structure (Fig. 7 and 9). This is consistent with previous studies indicating that benthic invertebrates are restricted to specific depths, which can be related to different hydrostatic pressures and food availability (Leung Tack, 1985; Warwick, 1984).

As expected, dissolved oxygen (DO) levels were also highlighted as a significant driver for macrofaunal communities in all areas where this parameter has been measured (i.e., in Åland Islands (**II**) and Mobile Bay (**III**)). DO is indeed known as a major driver because most organisms require oxygen to serve as the terminal electron acceptor in energy production (respiration) and to drive many redox reactions. Different taxa have specific tolerance ranges and, as a consequence, oxygen (normoxia, hypoxia, anoxia) is a strong predictor for species diversity and occurrence in the macrofaunal assemblage in general (Rousi et al., 2019; Weigel et al., 2015). All three studied areas are known or expected to be subject to anoxic events. Hypoxia ($<3.5 \text{ mg O}_2 \text{ L}^{-1}$) and anoxia ($0 \text{ mg O}_2 \text{ L}^{-1}$) are, for instance, two of the most important structuring factors for the macrofaunal communities of the Baltic Sea, leading to an impoverishment or complete loss of benthic macrofauna (Pearson and Rosenberg, 1978; Rousi et al., 2019). It is important to note that oxygen was already a significant driver in Mobile Bay with a sampling period focused on normoxic conditions, so we can expect a rather larger impact during hypoxic and anoxic conditions. The Sine Saloum study (**I**) would have gained from measuring dissolved oxygen concentrations in the subtidal zone (see Fig. A1), especially considering its larger residual variance in the VPA results (54% in the subtidal Sine Saloum compared to 46% in the intertidal Sine Saloum, 42% in the Åland Islands and 37% in Mobile Bay) (Fig. 9). DO is a particular relevant parameter because these environments could be facing anoxic events especially during the dry season.

The change in season highlighted as a significant driver in the Sine Saloum subtidal zone **(I)** (Fig. 7a and 9) reflects changes in several combined environmental variables including salinity and temperature. This parameter could also reflect hypersaline and anoxic events. The dry season was indeed characterized by higher proportions of organisms potentially less vulnerable to anoxic or hypersaline events with the ability to hide in their fixed tubes (Reise, 2002). The sampling period occurred between January and May in Mobile Bay **(III)** and during summer in the Åland Islands **(II)** so we did not cover a change in season. Therefore, this parameter would be relevant to consider in longer-term studies (e.g., seasonal studies or studies over a whole year), since we can expect changes along the year in both areas.

4.1.2.2. Human ecosystem engineering

Human ecosystem engineering (HEE) was the main driver in the Sine Saloum intertidal zone **(I)** explaining over 30% of the macrofaunal variation in species and traits (Fig. 9). It was also a significant constrain for both Åland Islands **(II)** and Mobile Bay **(III)** macrobenthos, contributing respectively to 19% and 18% of its variation in structure (Fig. 9a). Still significant but with a lower impact, human ecosystem engineering contributed to 6% of the macrofaunal community structure in the subtidal zone of the Sine Saloum, to 4% of its functional variability **(I)** and to 8% of the Åland Islands functional variability **(II)** (Fig. 9).

Spatial proximity to human ecosystem engineering

Regardless of the type of human ecosystem engineering, the spatial proximity to HEE was highlighted as particularly impacting macrofaunal community structure and functioning **(I, II, III)**.

In the Sine Saloum **(I)**, closer to anthropogenic disturbances in the intertidal zone compared to the subtidal zone, pressures related to HEE took precedence over environmental variables in explaining infaunal community structure and trait composition (Fig. 7a). This spatial difference in impact between tidal areas specifically attributed to harvesting may be due to the shellfish collection methods. Practiced at low tide, the collection was still mostly achieved by walking in the intertidal zone, at the time of the sampling. Sometimes, shellfish were also collected using pirogues allowing harvesters to go deeper and to carry heavier loads and to cross deep “bolongs” (Brenier et al., 2009; Descamps, 1991). In the subtidal zone, additional HEE would be interesting to explore in future research considering the higher residual variance pointed out in the VPA compared to other areas, especially considering trait-based approach (75% unexplained variability in the Sine Saloum subtidal zone macrofaunal traits *versus* 33% in the intertidal zone and 53% in Åland Islands) (Fig. 9).

Additionally, impacts of the proximity to human ecosystem engineering were highlighted with a gradient either from the inner sheltered to the deeper exposed Åland archipelago **(II)** (Fig. 8a) or from the coast to the mouth of the bay **(III)**

(Fig. 8b), the intensity of HEE being the strongest closer to the coast in both areas (Fig. 7 and 8). With similar patterns following these gradients, results in terms of macrofaunal community structure and functioning were similar in both the Åland Islands archipelago and the Mobile Bay shallow embayment (Fig. 7bc). These gradients were the result of a combination of environmental stability and exposure to HEE, both explaining a significant part of the macrofaunal structure and functioning variability (Fig. 9). The exposure to wind-waves **(II)** or to seawater inflow **(III)** in combination to the exposure to HEE contributed to spatial patterns in r- and K-strategists in both areas and to a decrease in diversity in Mobile Bay (Fig. 7bc).

In more detail, regarding the Åland Islands **(II)**, a gradient from the inner, sheltered and highly eutrophied archipelago to outer exposed areas was associated with a change in species and traits composition, and a change in dominance from r- to K-strategy in the infaunal invertebrate community (Fig. 7 and 8a). In the Åland archipelago, the coastal zone comprises over 6,000 islands, forming a highly heterogeneous land- and seascape, ranging from shallow, sheltered bays to exposed open-sea areas (Bonsdorff et al., 1996). Gradients in environmental drivers, such as exposure to wind-waves, water temperature, salinity and oxygen concentration, can therefore be steep from the inner/sheltered to the outer/exposed coastal zone. Alongside this environmental gradient, a gradient in HEE (i.e., eutrophication, physical disturbance, proximity to fish farms, human presence, inputs of hazardous substances) from the coast to the open sea is also noticeable. Higher eutrophication levels (i.e., HELCOM “Integrated eutrophication status assessment”) were indeed highlighted in sheltered areas, in addition to several environmental parameters known to describe eutrophication when considered together (i.e., Secchi depth, organic content and bottom oxygen). Macrofaunal species composition was influenced by these gradients from sheltered, characterized by e.g., higher temperatures, lower oxygen levels and higher eutrophication levels, to exposed areas being deeper and presenting higher water clarity and exposure to wind-waves, and the lowest exposure to human ecosystem engineering (Fig. 8a). Sheltered areas were dominated by pollution-tolerant insect larvae Chironomidae spp. (Leppäkoski, 1975) (Fig. 7). Described as not sensitive to nutrient enrichment (Leppäkoski, 1975) and to hypoxia (Gamenick et al., 1996), Oligochaeta spp. were found in higher proportions in organic-enriched sediments with higher levels of de-oxygenation, eutrophication, fish farm proximity and hazardous substances. Species particularly sensitive to pollution (e.g., *Monoporeia affinis* and *Halicryptus spinulosus*) were only present in outer stations, further from eutrophication and hazardous substances. Completely different sets of traits were highlighted in exposed versus sheltered areas (Fig. 7). Exposed areas were dominated by large, fragile individuals with long longevity, brooders, pelagic lecithotrophic larvae, sub-surface and surface deposit feeders and predators, burrowers, infauna (middle, deep and top), patchy organisms; whereas sheltered areas were dominated by medium size individuals with intermediate fragility, short longevity, spawners, benthic direct development,

passive filter feeders and miners, crawlers, tube builders and rafters/drifters, top infauna and epifauna, solitary organisms (Fig. 7). Semi-exposed areas showed an intermediate trait composition between sheltered and exposed areas, highlighting a switch in the macrofaunal trait composition from sheltered to exposed areas, occurring gradually along the exposure gradient related to wind-waves and to HEE. Combining traits from both sheltered and exposed areas, functional richness was the highest in this transition area with intermediate exposure to wind-waves and human-induced pressures, which is consistent with the intermediate disturbance hypothesis (Wilkinson, 1999). This change in the trait composition corresponds to a switch from a r-strategy, in sheltered areas affected by eutrophication, to a K-strategy, in exposed areas presenting a more stable environment. r-selected species with fast reproduction (planktotrophic larvae), short life cycle, numerous offspring (spawners) and smaller body size can indeed be at an advantage when an ecosystem is faced with severe or frequent disturbance, such as eutrophication or prolonged hypoxia, while K-selected species with lecithotrophic larvae, late sexual maturity and fewer offspring (brooders) will decrease in abundance (Jeschke et al., 2008; Pearson and Rosenberg, 1978).

Similarly to the Åland Islands, inner Mobile Bay stations **(III)** along the coastline were characterized by communities dominated by a few, small and opportunistic (r-selected) taxa such as capitellids (Tsutsumi, 1987) and tolerant orbinids (Kruse et al., 2004). In the case of Mobile Bay, the coastal area also showed lower biomass and higher diversity of macrofauna was found near the mouth of the bay (Fig. 7 and 8b). This is likely due to the hydrological characteristics of the bay described previously, in addition to distance from anthropogenic disturbances near the coast, indeed explaining on its own 18% of the macrofaunal community variability (Fig. 9). Natural stressors associated with the shallow coastal parts of Mobile Bay in which diversity was low may be exacerbated by human ecosystem engineering. Coastal development and shoreline modifications in Mobile Bay have led to transformation of 38% of the bay's shoreline into engineered structures (vertical walls and revetments) (Jones et al., 2009). Approximately 93% of the shoreline is experiencing erosion (Jones et al., 2009) and a loss of at least 5 to 10 hectares of intertidal habitat have been estimated in this microtidal bay (Douglass and Pickel, 1999). Moreover, as transitional areas between land and sea, estuaries receive large amounts of pollutants derived from urban, agricultural, industrial and domestic waste effluents (Lillebø et al., 2005; Paerl, 2006). Alteration of coastal habitats, discharge of pollutants due to coastal development, and fluctuations in salinity and temperature - characterized by low salinity, high temperatures, and substantial variability - may all contribute to stressful living conditions for macrofaunal communities.

Type of human ecosystem engineering

On top of highlighting the impact of the proximity to HEE, I was also able to disentangle specific effects of different types of human activities and pressures on macrofaunal community structure and functioning.

Specifically in the Sine Saloum intertidal area (**I**), shellfish harvesting resulted in a significant decrease ($p < 0.05$) in total macrofaunal abundance (933.79 ± 626.34 ind m^{-2} in unexploited stations compared to 140.92 ± 71.99 ind m^{-2} in exploited stations; mean $\pm$ SE) in addition to a decline in biomass and taxonomic richness. Shellfish harvesting inevitably leads to a physical disturbance of the substratum and its associated fauna (Skilleter et al., 2006; Spencer et al., 1998), thus affecting the population structure of marine invertebrates and altering nearshore coastal ecosystems (Kaiser et al., 2001; Leitão and Gaspar, 2007; Rick and Erlandson, 2009). The effect of harvesting is usually causing a reduction of infaunal species number and abundance (Aswani et al., 2015; Dirisu and Edwin-Wosu, 2022; Kaiser et al., 2001; Leitão and Gaspar, 2007; Spencer et al., 1998), which is in line with results in Fig. 7.

Heavy metals (PTEs) were also highlighted as a significant driver for macrofaunal community structure in the Sine Saloum intertidal area (**I**) (Fig. 7 and 9). Contamination with PTEs was associated with a significant decrease in functional diversity and particularly with a change in macrofaunal living habits in both tidal areas. Many other studies have shown that the presence of contaminants creates a harsh environment below the sediment surface affecting trait composition (e.g., Carvalho et al., 2011; Dong et al., 2021; Gaston and Young, 1992; Gusmao et al., 2016; Hu et al., 2019; Nunes et al., 2008; Piló et al., 2016; Selck et al., 1999).

4.1.2.3. Sediment properties

In addition to characteristics related to the physical environment and HEE, sediment properties were highlighted as significant constraints for macrofaunal communities, explaining 9% of the variation in the structural diversity in the intertidal Sine Saloum, 18% in the subtidal Sine Saloum (**I**), 8% in Åland Islands (**II**) and 21% in Mobile Bay (**III**) (Fig. 9). Differences in the sampled range of sediment grain sizes and in included descriptors could account for the differences in percentage of variation explained by sediment properties in the variation partitioning analysis (Fig. 9). The Ekman grab is known not to be as efficient as the Peterson or the Van Veen grab in retrieving samples in harder substrates, such as sand or gravel (Flannagan, 1970). As a consequence, the sediment fraction over 80% sand was most likely not sampled with an Ekman grab in Åland Islands whereas a wider range of sediment grain size was covered in Mobile Bay using a Peterson grab and in the Sine Saloum using a Van Veen grab. In addition, a lot more descriptors were included in the Mobile Bay study (i.e., sediment grain size, CN content, carbon content and porosity) than in the

Åland Islands one (i.e., sediment type and organic content). These different reasons could explain that sediment properties explained 8% of the Åland macrofaunal structural variability whereas contributing to explain 21% of the Mobile Bay variability (Fig. 9a).

Despite these differences in sampling efforts, sediment properties appeared consistently as a significant driver for macrofaunal community structure and functioning, regardless of the area, the sampled range of sediment grain size or the included descriptors (Fig. 9). Sediment characteristics represent a well-known significant explanatory factor for macrofaunal taxonomic and trait composition (Anderson, 2008; Mwakisunga et al., 2020) because benthic soft-sediment organisms generally show strong relationships with the grain-size characteristics of the sediments they inhabit (Gray, 1974). Our results specifically emphasized significant relationships between sediment characteristics and macrofaunal abundances (**II**, **III**), biomass (**II**, **III**), diversity (**II**) and species composition (**III**) (Fig. 7). Results from (**III**) related to species composition were also consistent with previous research from the northern Gulf of Mexico where sediment properties were shown to represent a significant explanatory factor in the taxonomic composition of infaunal communities (Coblentz et al., 2015). In addition, sediment properties were shown to be associated with specific traits in both Sine Saloum tidal zones (**I**). Different proportions in deposit- and filter feeders were following sediment median grain size. Both of these feeding strategies were expected to fluctuate with sediment properties because deposit-feeding is usually the dominant feeding strategy in muddy sediments and filter feeder tolerance to fine-grained sediments and turbid waters depend on their feeding structure (Shull, 2009; Steele-Petrovic, 1975).

Specifically regarding the relationship between sediment grain size and macrofaunal abundances, a similar pattern was found in both (**II**) and (**III**) with lower abundance and biomass in muddy sediments compared to sandy ones (Fig. 7bc). Results from the Åland Islands (**II**) were consistent with results from the Finnish coast (the Gulf of Finland) in the Baltic Sea showing that sediment type accounted for most of the variation in macrofaunal abundances (Rousi et al., 2019). Thanks to a larger number of sediment descriptors, a more in-depth pattern, needing some follow-up investigations (see Fig. A1), might have been uncovered in Mobile Bay (**III**). The highest abundances were found in sediments composed of 60 to 80% sand (Fig. 7), which are likely more stable environments than fine, easily resuspended mud. As sandier sediments are more highly oxygenated environments, they may be favored by macrofauna over organic-rich muds when hypoxic events occur with some frequency (Flint and Kalke, 1985; Wilson et al., 2008). Interestingly, the site with highest sand content had lower abundances and diversity, suggesting a non-linear relationship between community structure and sediment grain size with a peak at intermediate sand content. More sites with higher sand contents would be needed to determine the relationship between sediment type and community structure but this pattern is

consistent with previous studies (Anderson, 2008; Van Hoey et al., 2004). In the North Sea, macrofauna show maximum abundances at 6% mud and decrease with increasing median grain size and decreasing mud content (Van Hoey et al., 2004). Optimum percentage mud for most abundant macrofaunal taxa is estimated to $17 \pm 12\%$ in Auckland which is equivalent to a range from 71 to 95% sand (Anderson, 2008). In Neuces Bay, Texas (US), abundance and diversity were higher in >50% sand than in muds but did not, however, differ between 50-75% and 75-100% sands (Mannino and Montagna, 1997). This may reflect sediment stability resulting from a combination of cohesion by muds and compaction by heavier sand grains or a trade-off between oxygenated sands and higher food content of organic muds. It would be interesting to cover a larger range of sediment types using a Peterson grab (available at the Husö biological station) and expand the number of measured sediment descriptors in Åland Islands (II) to verify if the same pattern would be detected (see Fig. A1).

4.2. Effects on macrofauna-mediated ecosystem functions

Community reorganization due to environmental pressures and human ecosystem engineering, not only reshuffles species and trait composition, as described in the previous section (Fig. 7), but also has the potential to affect macrofauna-mediated ecosystem functions.

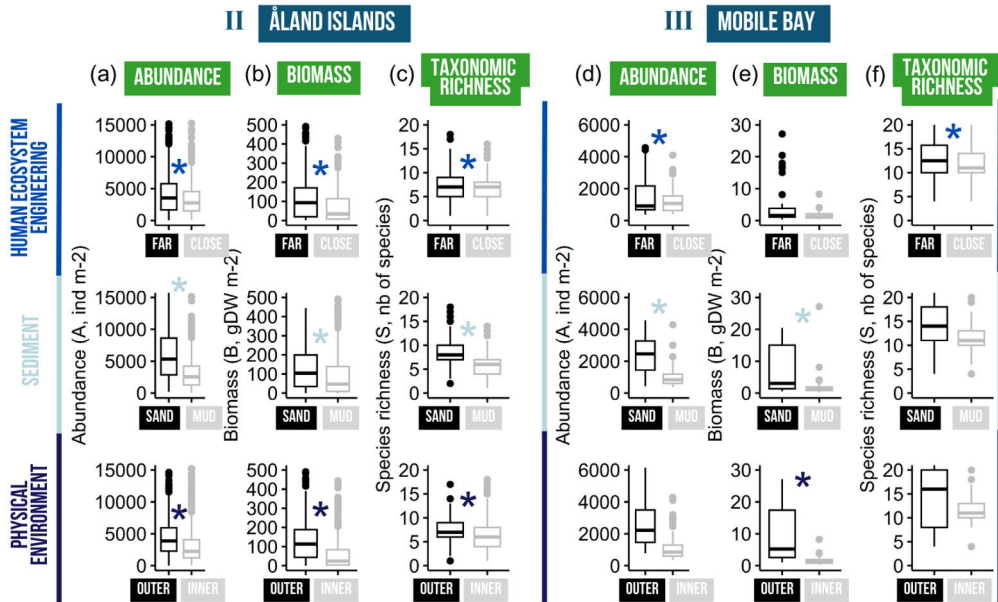


Fig. 10: Boxplots of macrofaunal (a, d) total abundance, (b, e) total biomass and (c, f) taxonomic richness in Åland Islands (II) (a, b, c) and Mobile Bay (III) (d, e, f). * indicates significant differences ($p < 0.05$, PERMANOVA tests) between groups composed of samples clustered together depending on their exposure to human ecosystem engineering (far vs close), on sediment type (sand vs mud) and hydrodynamics exposure (outer vs inner).

These functions range from promoting remineralization of organic matter and enhancing oxygen penetration depth in the sediments (Aller and Aller, 1998; Jovanovic et al., 2014), to playing an essential role in energy acquisition for higher trophic levels, serving as a central food resource for epibenthic predators and demersal fish (Nilsen et al., 2006; Nordström et al., 2009; Salvanes et al., 1992). Many of ecosystem functions and services provided by benthic infaunal communities are threatened directly by human-driven impacts.

Significant lower macrofaunal abundances, biomass and taxonomic richness were found in muddy innermost areas affected by HEE in the Åland Islands and Mobile Bay compared to sandy outer areas further away from HEE (Fig. 10), and these effects of the environment on macrofaunal communities are expected to reflect on the functions and services they are providing. Macrofaunal-mediated ecosystem functions were therefore explored in the Åland Islands (**II**) and Mobile Bay (**III**) (Fig. 11). In both **II** and **III**, I looked at how proxies for macrofauna-mediated ecosystem functions responded to HEE, sediment properties and the physical environment (Fig. 11), which offered insight into coastal ecosystem functioning.

4.2.1. Effects on sediment reworking (**II**, **III**)

Important ecosystem processes associated with macrofaunal communities are linked to their sediment bioturbation and bioirrigation capacities. Benthic invertebrates contribute to sediment ecosystem functions by modifying their habitat through biological processes such as ingestion, digestion and excretion, as well as bioturbation and bioirrigation of the sediments (Levinton, 1995) and these activities change sediment properties and enhance the transportation of particles and solutes. Quantitative proxies for the bioturbation (BP_c) (Queirós et al., 2013; Solan et al., 2004) and bioirrigation (BIP_c) (Renz et al., 2018) activity of communities were explored for the Åland Islands (**II**) and Mobile Bay (**III**) to evaluate effects of human ecosystem engineering on the sediment physical structuring (Fig. 11).

Environmental and anthropogenic shifts in macrofaunal community structure, taxonomic and trait composition as found in this thesis (e.g., Fig. 10), have the potential to affect bioturbation and bioirrigation potentials and in so doing to also impact ecosystem functioning (e.g., influencing sediment chlorophyll a (Josefson et al., 2012), total organic carbon (Solan et al., 2012), sediment reworking (Morys et al., 2017), redox metrics (Birchenough et al., 2012), and biogeochemical cycling (Braeckman et al., 2014)). Following the same trends as total abundances, biomass and taxonomic richness (Fig. 10), the bioturbation (BP_c) and bioirrigation (BIP_c) potentials were lower in muddy sediments and in the inner, more variable environment, closer to HEE in both coastal ecosystems (**II** and **III**) (Fig. 11). A reduction of community bioturbation and bioirrigation potential indices was therefore associated with a decrease in abundance, biomass and macrofaunal species richness. This is in line with

previous studies showing that the macrozoobenthic community structure influences bioturbation processes (Biles et al., 2002; Nasi et al., 2020).

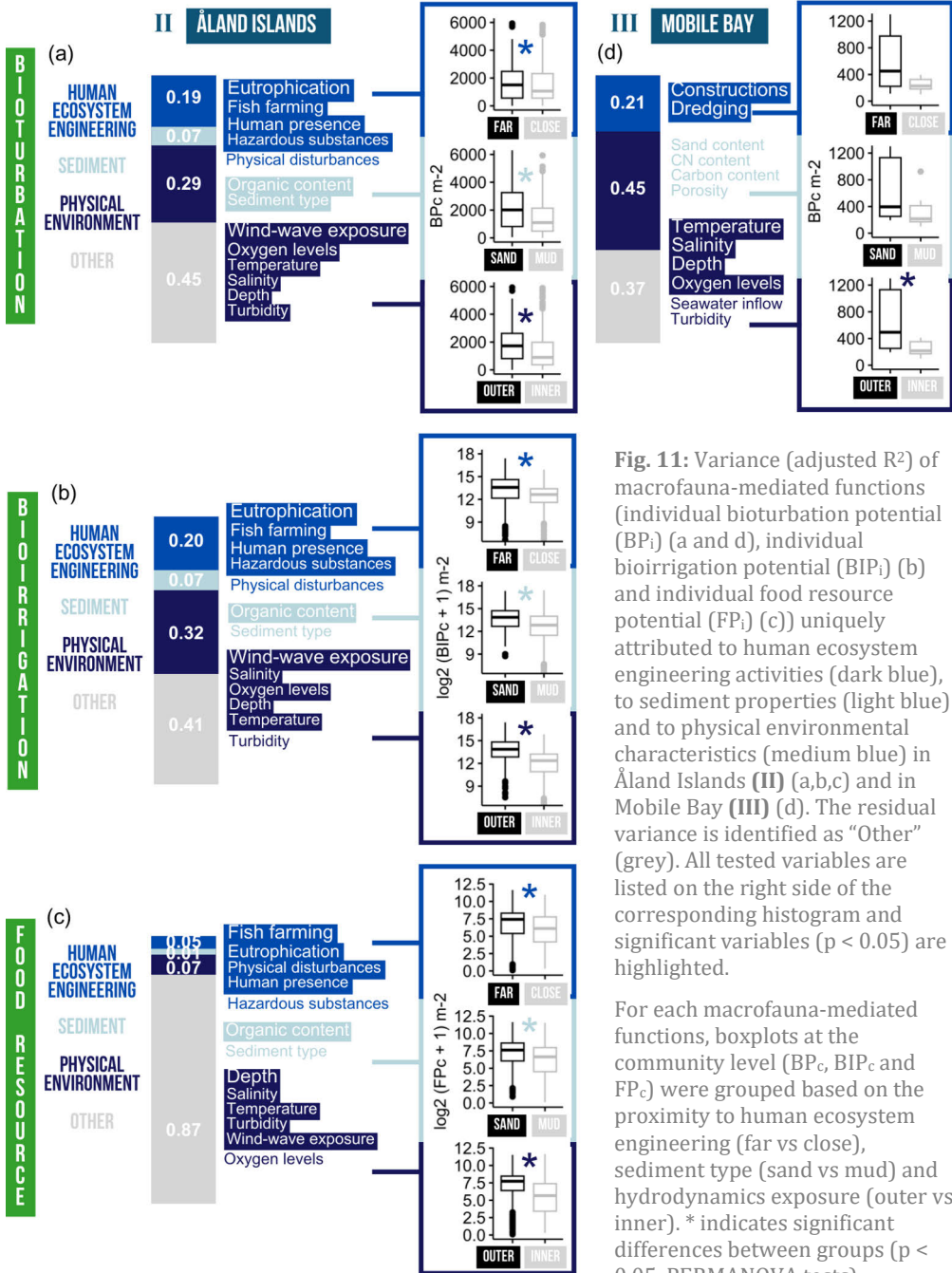


Fig. 11: Variance (adjusted R^2) of macrofauna-mediated functions (individual bioturbation potential (BP_i) (a and d), individual bioirrigation potential (BIP_i) (b) and individual food resource potential (FP_i) (c)) uniquely attributed to human ecosystem engineering activities (dark blue), to sediment properties (light blue) and to physical environmental characteristics (medium blue) in Åland Islands (II) (a,b,c) and in Mobile Bay (III) (d). The residual variance is identified as “Other” (grey). All tested variables are listed on the right side of the corresponding histogram and significant variables ($p < 0.05$) are highlighted.

For each macrofauna-mediated functions, boxplots at the community level (BP_c , BIP_c and FP_c) were grouped based on the proximity to human ecosystem engineering (far vs close), sediment type (sand vs mud) and hydrodynamics exposure (outer vs inner). * indicates significant differences between groups ($p < 0.05$, PERMANOVA tests).

Based on variables independently selected for the physical environment, human ecosystem engineering and sediment properties, I performed a variance partitioning to investigate the amount of variability of bioturbation (BP_i) and bioirrigation (BIP_i) potential uniquely linked to each variable category for the Åland Islands (**II**) (Fig. 10abc and 11ab) and Mobile Bay (**III**) (Fig. 10def and 11d). Variation in bioturbation and bioirrigation potentials were mainly explained by physical environment variables, indeed contributing, at the Åland Islands, to 29% of the variability in BP_i and 32% of the BIP_i and to 45% in the Mobile Bay BP_i (Fig. 11). While sediment had a rather low impact (explaining 7% of both the variability in BP_i and BIP_i in Åland and not significant in Mobile Bay), HEE was a significant constraint explaining around 20% of the variability in BP_i and BIP_i , in both areas (Fig. 11). This is evidence that human ecosystem engineering is important to consider regarding potential effects and feedback related to sediment reworking macrofauna-mediated functions and services. Human ecosystem engineering is affecting macrofaunal communities, which translates to modification in the ecological functions they are providing.

4.2.2. Effects on biogeochemical fluxes (**III**)

By increasing oxygen penetration into the sediment through bioturbation and bioirrigation activities, the benthic infauna enhances the depth of the redox potential discontinuity (RPD) layer, and thus the availability of electron acceptors (such as O_2 , NO_3^- , Mn^{4+} and Fe^{3+}) within the sediment (Aller, 1979; Kristensen et al., 1991; Kristensen and Blackburn, 1987). Through their activities, benthic invertebrates can also enhance multiple sediment functions performed by microbial communities, such as organic matter mineralization and biogeochemical cycling. In paper **III**, in addition to estimating quantitative proxies for the bioturbation (BP_c) activity of communities, I went further with direct measurements of an ecosystem process focusing on sediment-water interface fluxes and biogeochemical cycling.

Table 4: Pearson product-moment correlation matrix relating Mobile Bay station characteristics to biogeochemical process rates. No correlations were found significant ($p > 0.05$). (*Adapted from Table 2 in Paper III*).

	Fluxes					
	NH_4^+	NO_3^-	NO_2^-	D_{14}	D_{tot}	PO_4^{3-}
Total abundance (ind m^{-2})	-0.07	0.25	-0.28	0.12	-0.18	-0.20
Total biomass (gDW m^{-2})	0.06	-0.04	-0.02	0.41	0.12	-0.14
BP_c (m^{-2})	0.08	-0.03	-0.08	0.40	0.11	-0.14

Although macrofaunal abundance, biomass and diversity differed across stations in Mobile Bay (Fig. 7 and 10) and reflected differences in bioturbation potential (BP_c , Fig. 11d), we did not find a significant relationship between macrofaunal attributes (abundances, biomass and BP_c) and nutrient fluxes or denitrification capacity (**III**) (Tab. 4). Both abundance and biomass of infauna were low in Mobile Bay (< 4000 ind m^{-2} and < 5 gDW m^{-2} at most sites) (Fig. 12) compared to other studies which showed a positive relationship between

macrofaunal abundances and denitrification (Braeckman et al., 2014; Engelsen et al., 2008; Ferguson and Eyre, 2013; McTigue et al., 2016; Van Colen et al., 2012). The lack of a relationship between macrofauna and denitrification suggests that a threshold of abundance, biomass and/or burrowing activity is necessary to increase bioturbation or irrigation to sufficient levels to affect denitrification.

A relationship between macrofaunal abundances or biomass and nutrient fluxes has previously been documented in the Baltic Sea (Karlson et al., 2007; Tuominen et al., 1998) and more specifically in the Gulf of Finland (Tuominen et al., 1999). Despite lower taxonomic richness found in the Åland Island archipelago, higher abundances, biomass and consequently higher bioturbation potential were found around the Åland Islands compared to Mobile Bay (Fig. 12). Mazik and Elliott (2000) concluded that bioturbation is reduced as a result of decreasing species diversity and community biomass, as well as diversity of feeding and bioturbation groups. Considering my threshold hypothesis, my results could explain the significant relationship between macrofaunal community descriptors and nutrient fluxes found for the Åland Islands and not for Mobile Bay.

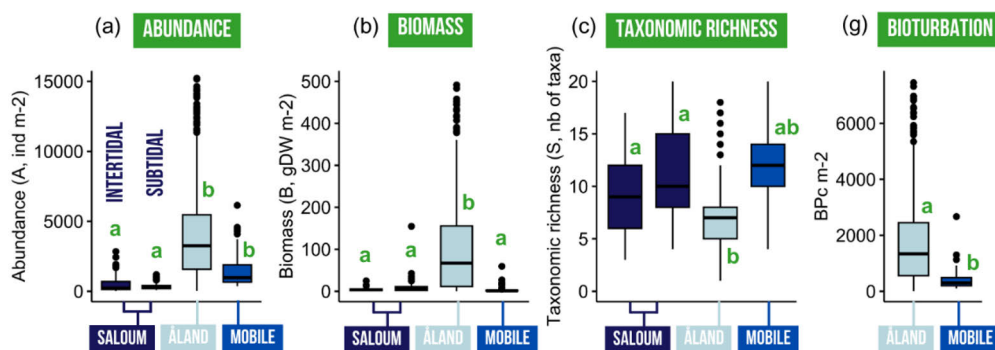


Fig. 12: Boxplots of macrofaunal (a) total abundance, (b) total biomass, (c) taxonomic richness and (d) community bioturbation potential (BP_c). Different lowercase letters above boxplots show significant differences ($p < 0.05$, Kruskal-Wallis tests with Nemenyir's post-hoc tests) between studied areas (Sine Saloum, Åland Islands and Mobile Bay). Note that significant differences in taxonomic richness are expected to be even stronger considering that Åland Island individuals were identified at the species level, Mobile Bay at the family level and Sine Saloum a mix of both.

This threshold hypothesis would need further exploration (see Fig. A1). For instance, it could be interesting to measure fluxes in the Sine Saloum to see if the results are similar to Mobile Bay because of the similarities in abundance and biomass or if the taxonomic and functional composition will determine nutrient fluxes (Fig. 12). Also considering meiofauna (invertebrates < 1 mm) would be valuable because their bioturbation has been previously shown to have a stimulating effect on nitrifying and denitrifying bacteria (Bonaglia et al., 2014; Bonaglia and Nascimento, 2023) (see Fig. A1).

4.2.3. Effects on food availability for mesopredators (II)

Community reorganization due to environmental pressures and human ecosystem engineering, reshuffling species and trait compositions (Fig. 7), also affects species interactions and trophic dynamics (Tylianakis et al., 2008). So, in addition to influencing macrofauna-mediated functions related to sediment reworking, the combination of main descriptors of the macrofaunal diversity (i.e., abundance, biomass and diversity) are expected to influence the potential for macrofauna to serve as a food resource for mesopredators, such as benthic feeding fish. What makes prey species suitable and/or favorable for their predators is a central question in ecology, especially in regards to accelerating rates of changing communities and shifting interactions (Both et al., 2009; Harley et al., 2006; Schmitz and Barton, 2014). In paper II, I applied a novel index to estimate the macrofaunal community quality as a food resource for consumers, such as benthic-feeding fish. The use of a trait-based approach was found relevant knowing that predators select their prey irrespective of taxonomic identities but based on a multitude of phenotypic characteristics, such as morphological, behavioral, and life history traits (Green and Côté, 2014; Rodríguez-Lozano et al., 2016; Spitz et al., 2014). Based on the relevant functional traits, this approach applied to our results succeeded in reflecting the optimal foraging theory: the highest index levels were indeed found in areas where predators are likely to find prey that provide them with highest energetic gain while losing minimal energy along the catching and handling process (II). The combination of both the energy content and the accessibility of the prey was central to the calculated FP_c : the highest values were associated with higher abundances and biomass in addition to large-sized, easily ingested, fragile individuals (e.g., *Marenzelleria* spp.) in exposed sandy areas, whereas the lowest FP_c values were found at sites with lower abundances and biomass where the fauna was mainly smaller and robust individuals (e.g., *Hydrobia* sp.) in semi-exposed muddy areas (II) (Fig. 11). Paper II also showed that FP_c values were equivalent between areas with higher abundance and biomass with robust individuals and areas with lower abundance and biomass including individuals with higher energy content (i.e., insect larvae) and higher accessibility (epifauna).

Based on variables independently selected for the physical environment, human ecosystem engineering and sediment properties, I performed a variance partitioning to investigate the amount of food resource potential variability uniquely linked to each variable category for the Åland Islands (II) (Fig. 11c). All categories were found to significantly contribute to explaining the variability in FP_i . However, with 87% residual variance, a significant part of this variability could not be explained, reflecting other processes involved related in this particular macrofauna-mediated function, such as trophic interactions (i.e., predation, competition).

4.3. Potential feedback through macrofauna-mediated ecosystem functions

Macrofauna-mediated ecosystem functions, explored in this thesis, are indicative of ecosystem health and resilience, and are intrinsically related to various ecosystem services that benefit society (Martins and Barros, 2022; Millennium Ecosystem Assessment, 2005; Strong et al., 2015). Through a cause-effect perspective, Fig. 13 clarifies how macrofauna habitat use (i.e., BP_c and BIP_c) and trophic interactions (i.e., FP_c) are intrinsically linked with ecosystem processes and services provided by coastal ecosystems. Based on the thorough review provided by Rodrigues-Filho et al. (2023), I was able to identify 20 ecosystem services associated with functions performed by macrofaunal organisms and categorized as supporting (4), regulating (3), provisioning (4) and cultural (9) services (Fig. 13). Macrofauna inhabiting coastal ecosystems perform a wide range of ecological functions and may have broad-scale implications for service provisioning (Rodrigues-Filho et al., 2023). A change in macrofaunal community structure or functioning (i.e., species or trait composition, species or trait loss, decrease in abundance, biomass or diversity) have the potential to affect both ecosystem processes and services (Fig. 13). Not only human activities affect macrofaunal communities and their ecological functions, but these in turn influence ecosystem processes and service provision, i.e., feedback to humans (Fig. 1 and 2).

Involving several ecosystem services, West African shellfish harvesting activities (I) represent a great example of human ecosystem engineering effects and feedback. The Sine Saloum and the Petite Côte areas are of great concern in terms of conservation and management because of the traditional and well-developed fishing activities of Senegalese women, particularly the harvesting of diverse mangrove invertebrates (Conchedda et al., 2011; Gallup et al., 2020). These activities play a significant role in artisanal and small-scale commercial fisheries, and are important in providing a source of protein and income to people in the coastal communities (Chapman, 1987; Matthews, 2002). The secondary production of invertebrate species (e.g., shellfish, shrimp, crabs) provides direct value as *food* (*provision service*), sustaining the livelihood of the local human communities that live in coastal areas. It is mainly intertidal Sine Saloum molluscs (e.g., arks (*Senilia senilis*), mangrove oysters (*Crassostrea tulipa*), *Cymbium* spp., *Murex* spp. and *Conus* spp.) harvested by artisanal fisheries and representing an important food item to human societies (Chapman, 1987; Matthews, 2002). These fisheries also have large social, economic, cultural and historical value, providing direct *cultural services* to social actors involved in this activity, such as *sense of place*, *social relationships*, aesthetics and *cultural heritage* values (e.g., in addition to serving as food, clam shells are used in local architecture and crafts). Despite the great cultural value of shellfish and their essential role as a resource for the livelihoods of local communities and to regional economy, its harvesting played a major role in determining the

structural diversity **(I)**, resulting in a significant decrease in total macrofaunal abundance as well as declines in biomass and taxonomic richness. These effects on macrofaunal communities have already led to consequences on provisioning services, forcing the local population to adapt. Conchedda et al. (2011) found that mangrove resources in Senegal contribute to one-third of the gross national income (GNI) per capita annually, and that the collection and sale of oysters and clams were the top two principal uses of mangrove resources. Constituting an important source of income especially for Senegalese women, concerns were raised regarding women's abilities to cope with shellfish decline (Bodin et al., 2013, 2011). Subsequently, women in the region have developed resilience strategies based on new socio-economic practices with a diversification in their activities (e.g., ecotourism, agriculture, aquaculture, market gardening, artisanal mining and sale of salt) (Diouf et al., 2020; Sarr, 2005).

Contamination of coastal water with heavy metals was also highlighted as a significant driver for the macrofaunal community structure and functioning, in particular affecting living habits in both tidal areas and feeding modes in the subtidal area in the Sine Saloum **(I)**. Reflecting ecological functions (i.e., movement, feeding), these changes in trait composition may underpin processes that benefit human societies (Fig. 13). Higher levels of deposit feeders and lower levels of suspension filter feeders in contaminated areas could reflect on regulating and supporting services, because of the suspension feeding key role in water column particles filtration (*water purification*) through the removal of phytoplankton and other particles in suspension and the deposit-feeding contribution to *nutrient cycling* through the enhancement of oxygen penetration and bacterial decomposition (i.e., releasing carbon and nitrogen) (Rodrigues-Filho et al., 2023).

Even though we did not find a significant relationship between macrofaunal bioturbation and biogeochemical cycles in Mobile Bay **(III)**, macrofaunal communities usually play a key role in *nutrient cycling* and *sediment formation* (both supporting services) (Martins and Barros, 2022), through their biomass production, movement, excretion, feeding and burrowing activities (Braeckman et al., 2014; Wrede et al., 2018) (Fig. 13). Lower bioturbation (BP_c) and bioirrigation (BIP_c) potentials found in muddy sediments and in inner, more variable environment, closer to HEE in the Åland archipelago **(II)** compared to sandy outer areas, at greater distance from HEE (Fig. 11), could affect biogeochemical cycles and involve feedback for the human society in terms of supporting services (Fig. 13).

The secondary production of macrofaunal species might be associated with several ecosystem services. Indeed, invertebrate organisms such as polychaetes or bivalves are key prey for benthic mesopredators in coastal ecosystems. Representing important food resource for fish (Mattila and Bonsdorff, 1988; Snickars et al., 2015; Weigel and Bonsdorff, 2018), macrofaunal biomass provide

a provisioning service (Fig. 13). Spatial differences in macrofaunal food resource availability in the Åland Islands **(II)** could reflect in a lower secondary production and food provision in muddy semi-exposed areas, resulting in a decrease in provisioning services for humans (Fig. 13).

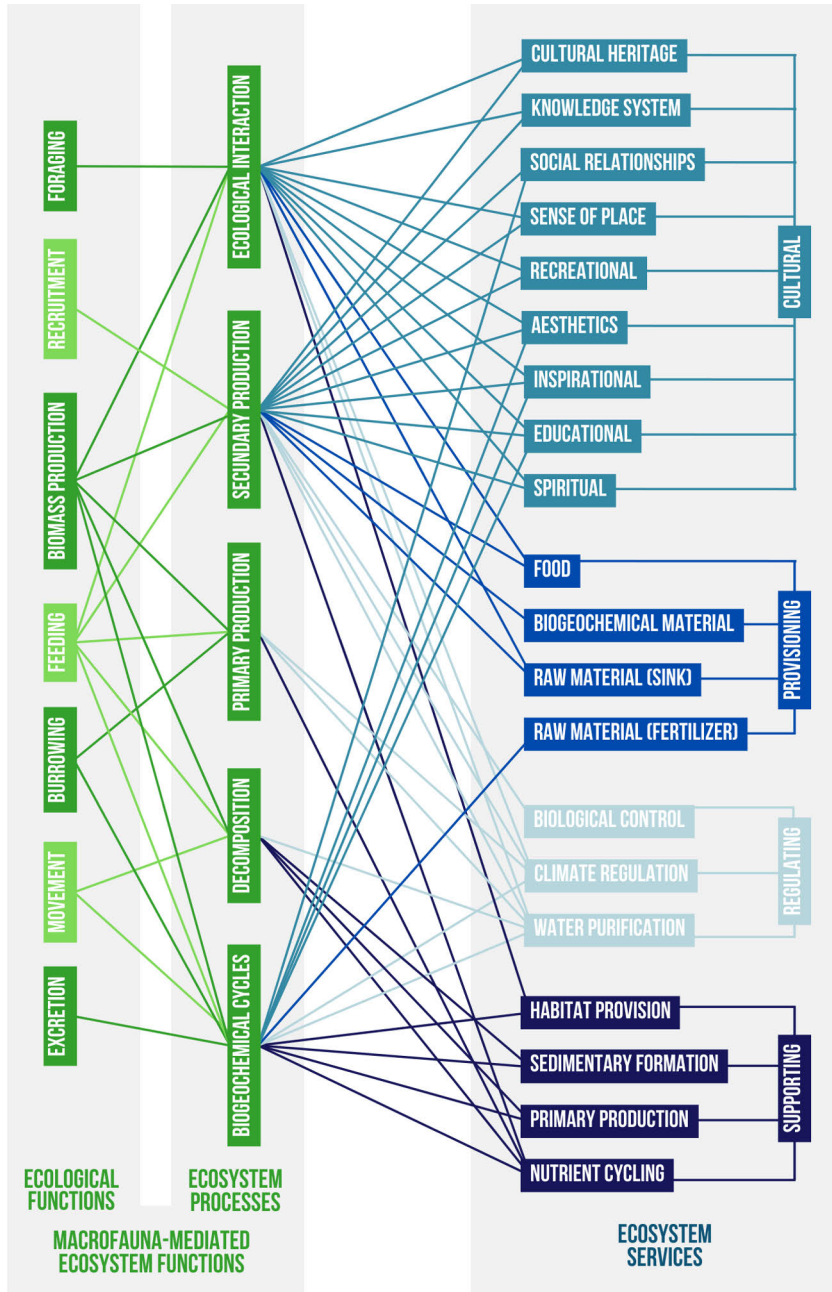


Fig. 13: Diagram of the pathways from macrofaunal ecological functions to ecosystem processes and services in coastal ecosystems. Arrows represent the links connecting pathways proposed by Rodrigues-Filho et al. (2023) and described in Tab. 2.

5. Conclusions and broader outlook

5.1. Key findings

- In the three studied coastal ecosystems, regardless of site specificities, drivers for macrofaunal community structure and functioning always included variables describing the physical environment (*e.g., salinity, temperature, hydrodynamics, depth, dissolved oxygen, season*), sediment properties (*e.g., grain size, C:N content, organic content*) and HEE (*e.g., shellfish harvesting, heavy metals, hazardous substances, coastal development and shoreline modification, eutrophication, fish farming, dredging*) (pages 30-38) **(I, II, III)**.
- Results from three different coastal areas show that HEE is affecting macrofaunal communities, which translates to modifications in ecological functions and processes associated with these communities, in turn with the potential to affect ecosystems services.
 - Both spatial proximity to HEE and the type of HEE were shown to affect macrofaunal community structure and functioning (pages 33-36) **(I, II, III)**.
 - Interlinkages of HEE effects and service feedback was exemplified using shellfish harvesting in the Sine Saloum, Senegal (pages 44-46) **(I)**.
 - Trait-based approaches in combination to the taxonomic approaches enabled us to better understand HEE effects and feedback (pages 27-38) **(I, II)**.
- The relationship between macrofaunal communities and sediment properties was explored. Macrofaunal abundances followed a non-linear relationship with grain size: increasing from mud to 60-80% sand and decreasing at over 80% sand (pages 36-38) **(II, III)**.
- A threshold of macrofaunal abundance, biomass and/or burrowing activity was found, above which bioturbation (BPc) or bioirrigation (BIPc) increased sufficiently to affect denitrification and nutrient fluxes (pages 41-42) **(III)**.
- The novel FPc index was found relevant for estimates of quality of the macrofaunal community as a food resource for consumers (*e.g., benthic-feeding fish*), and succeeded in reflecting the optimal foraging theory in the Åland Island soft-sediment system (page 43) **(II)**.

5.2. Multidisciplinary perspectives on regulating human ecosystem engineering effects and feedback

Although human ecosystem engineering is mostly intentional, its long-term consequences include some that are unforeseen and undesirable. There are many examples of human activities (e.g., shellfish harvesting, coastal constructions, fish farming) with unintended consequences for ecosystems (e.g., the proximity to human activities was associated with a decrease in macrofaunal taxonomic richness **(III)**, a decrease in macrofaunal abundances and biomass **(I)**, or a switch from a K- to a r-strategy **(II, III)**) and resulting in negative impacts on ecosystem goods and services for human society (e.g., shellfish harvesting resulted in consequences regarding provisioning services **(I)**) (Fig. 13). In addition to affecting ecosystem services for human society, HEE also has serious consequences on human physical health through pollution, the spread of disease, and food scarcity, as well as on mental health through the climate crisis causing feelings such as eco-anxiety.

Research in multiple disciplines (e.g., biology, sociology, and psychology) is allowing us to identify and better understand the unintended consequences of HEE on both nature and human wellbeing. This thesis contributes to this knowledge by uncovering the ecosystem engineering effects of humans on macrofaunal communities and coastal ecosystem functioning **(I, II, III)**. To support efforts to reduce and reverse human modification of environments, this understanding of the nature and consequences of human environmental impact is crucial. The next step is to put this knowledge in a broader multidisciplinary perspective for appropriate and efficient communication and management.

5.2.1. Broader perspective on root causes of the direct anthropogenic drivers affecting nature

Research in community ecology, such as the studies carried out in this thesis, usually focuses on direct drivers resulting in community changes. Direct drivers have direct physical impacts on nature, they can be abiotic (e.g., weather events, volcanic eruption, earthquakes), human-caused (e.g., harvesting, fishing, pollution, anthropogenic climate change), or a mixture of both (e.g., drastic seasonal change due to climate change) (Díaz and Malhi, 2022).

For a broader and deeper perspective on our ecological findings and their potential implications, it is crucial to also be aware of indirect drivers (Fig. 14) (see Fig. A1). Indirect drivers represent human actions and decisions that operate diffusely by altering and influencing direct drivers as well as other indirect drivers (Díaz and Malhi, 2022). They include e.g., economic, demographic, institutional, technological, and cultural drivers. Indirect drivers do not physically impact ecosystems nor their contributions to people. Rather, they are the root causes of the direct anthropogenic drivers that affect nature both positively and negatively (Díaz and Malhi, 2022). The distinction between

direct and indirect drivers is important conceptually and practically, because although direct drivers can be ameliorated or even temporarily stopped, these efforts are unlikely to succeed in the long term unless the indirect drivers - the root causes of the present negative impacts on ecosystems - are tackled (Díaz and Malhi, 2022) (see Fig. A1).

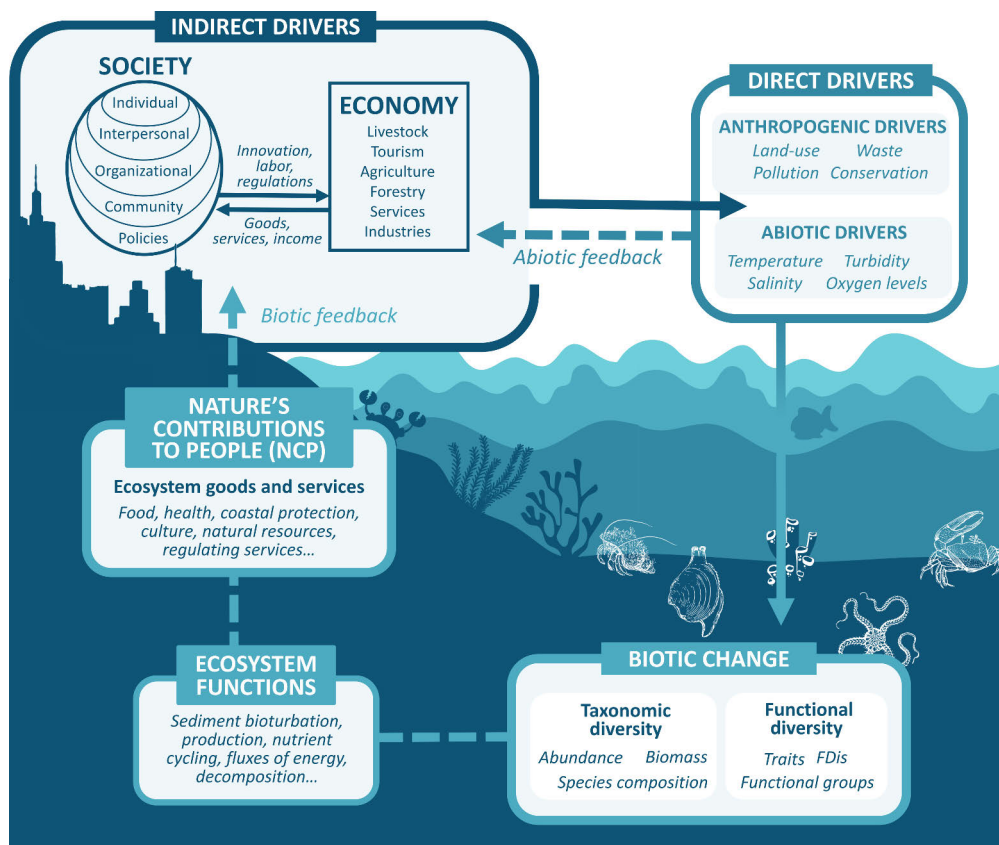


Fig. 14: Integrated socio-ecological system showing cause and effect relationships taking place in an ecosystem influenced by humans. A distinction is made between direct drivers, which have direct physical impact on biodiversity and ecosystems, and indirect drivers, which operate diffusely by affecting the level, direction, rate, and/or intensity of direct drivers (Brondizio et al., 2019; Díaz and Malhi, 2022). The social-ecological system theory defines society on different scales: “individual” (genotype, sex, age, health, knowledge, beliefs, experience), “interpersonal” (family, friends, social network), “organizational” (school, health services), “community” (local culture and politics, natural and built environment, mass media, social welfare services, industry) and “policies” (laws, attitudes and ideologies of the culture).

5.2.2. Rethinking the climate and biodiversity narrative to put nature at the center of societal values, planning, and goals

Addressing these underlying drivers requires system-wide rethinking and reorganization to put biodiversity at the center of societal values, planning, and goals (Díaz and Malhi, 2022). Communication is key for achieving such a shift. In

this communication, there is a need to take into account social challenges and human psychology and therefore to combine knowledge from multiple disciplines, e.g., biology, communication, sociology and psychology.

5.2.2.1. Outreach and education: a failing narrative

To fill the gap between knowledge acquired on the consequences of HEE and the implementation of sustainable actions to regulate them, it is common knowledge that scientific outreach is a key element (Fig. 15). Despite this awareness and efforts in communicating scientific results, there is still a gap between scientific knowledge and public motivation to respond to the highlighted challenges and/or solutions. Psychologists are identifying countless psychological “barriers” obstructing behavioral change despite knowledge about anthropogenic ecological degradation. To overcome such barriers around the topic of human ecosystem engineering, communicators must be critically aware of the essential role of emotions associated with behavior change. Emotions are a powerful motivator for human behaviors and they represent a missing link in effective communication (Salama and Aboukoura, 2018).

The current way of communicating knowledge about the ecological consequences of human activities is mostly contributing to enhance eco-anxiety and other eco-emotions (Fig. 15). Eco-anxiety is anxiety related to environmental degradation and its consequences, including but not limited to loss of biodiversity, increasing levels of pollution and the effects of climate change on current and future generations. Eco-anxiety is found to be closely connected to worry and fear. While eco-anxiety may manifest as “practical anxiety”, which leads to gathering of new information and reassessment of behavior options, paralyzing forms of eco-anxiety emerge as a problem (Kurth and Pihkala, 2022). The way people cope with these feelings affect their wellbeing and health, their willingness to acknowledge threatening information and take action to protect the environment. An excessive focus on the negative impacts of human activities with a severe “diagnosis”, without a balanced emphasis on solutions with a feasible “treatment”, often results in disengaging the audience (Salama and Aboukoura, 2018) (Fig. 15). Research into how humans cope with difficult environmental information reveals that some individuals respond with levels of worry that negatively affect their well-being and when falling into despair and helplessness, it cripples their capacity to act (Chawla, 2020) (Fig. 15). Most often, when highly worried about climate change, emotions are managed through distraction, deliberately thinking about something else, doing something else or avoiding disturbing information. Feeling hopelessness and helplessness, some people adopt a form of avoidance, concluding that action is pointless. Other people deny that climate change and its consequences exist or believe that it will only affect future generations or distant places. All of these psychological strategies are negatively associated with environmental action (Chawla, 2020) (Fig. 15).

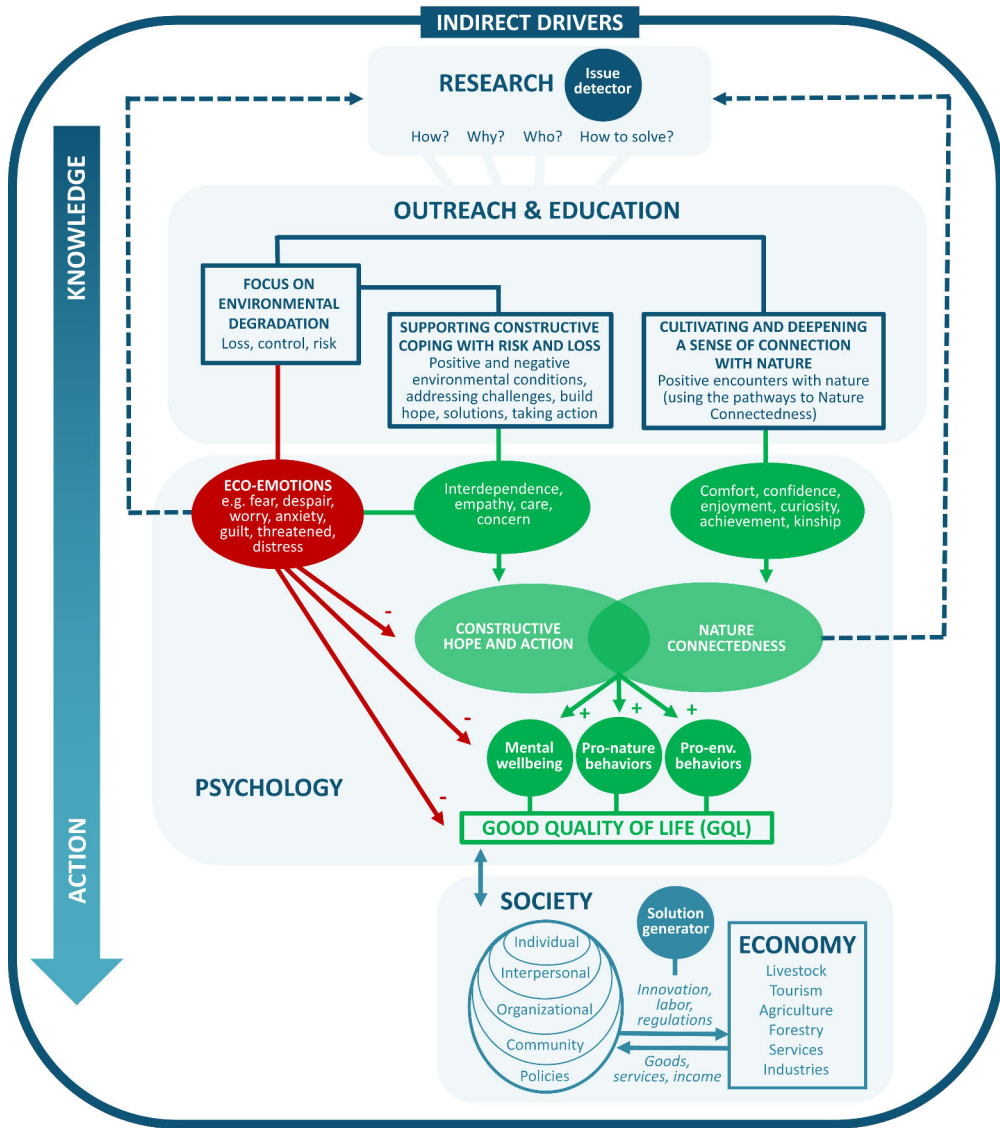


Fig. 15: Conceptual model showing how communication and psychology influence the gap between knowledge and action: from the detection of a socio-ecological issue to the implementation of a solution. Key: pro-env. = pro-environmental (e.g., carbon & resource use reduction); pro-nature = pro-nature conservation (e.g., wildlife habitat creation). Pro-environmental behavior is defined as “behavior that a person consciously chooses in order to minimize the negative impact of their actions on the environment” (Kollmuss and Agyeman, 2002). See Chawla (2020) for ideas on experiences promoting constructive hope and action and experiences cultivating and deepening a sense of connection with nature. See the “Terminology” section for definitions of terms such as “Good Quality of Life (GQL)”, “Nature Connectedness”, “Pathways to Nature Connectedness”...

5.2.2.2. Promoting constructive hope and action with nature connectedness to benefit both human wellbeing and pro-environmental behavior

For effective climate and biodiversity communication, we need to understand that emotions play a key role in motivating action. Markowitz and Shariff (2012) identify positive emotional appeals as one of the most promising strategies for climate and biodiversity communication. Indeed, emotional reactions to novel information happen effortlessly and almost instantaneously, shaping the subsequent cognitive processing of the information (Kahneman, 2011). Feelings of hope related to climate change and human activities likely increase the probability that individuals will choose to engage with the issue and adopt beliefs and behaviors consistent with efforts to stem the problem (Myers et al., 2012; Salama and Aboukoura, 2018). Feelings of hope and efficacy are strongly correlated with the willingness to engage in pro-environmental behaviors and to support climate change policies (Salama and Aboukoura, 2018). In addition to raise concern and inform about environmental degradation, there is a real interest in supporting constructive hope and action e.g., also informing about gain, solutions and addressing challenges (Chawla, 2020) (Fig. 15).

Moreover, research in psychology highlights that it is our connection with nature that supports human and environmental health and wellbeing. Improving people's relationship with nature, their nature connectedness, comes through simple, yet meaningful engagement with nature (Maiteny, 2002). The relationship between people and the rest of nature, "nature connectedness", is measurable. Research evidence shows that improved nature connectedness benefits both human wellbeing (Bakir-Demir et al., 2021; Seymour, 2016) and pro-environmental behaviors (Braitto et al., 2017; Richardson et al., 2020; Sulphrey and Faisal, 2021) (Fig. 15). Lumber et al. (2017) identified five distinct relationships activating people's connection with nature: (1) meaning (cultural relationship with nature), (2) emotion (feelings for nature), (3) compassion (care for nature), (4) beauty (noticing beauty of nature), and (5) contact (sensory interaction with nature). These pathways to nature connectedness offer a novel and applied approach to improving human-nature relations. They provide a flexible framework that can be implemented through straightforward adjustments across various applications and scenarios (from outdoor activities to the design of infrastructures), with the potential to significantly improve relationships between humans and nature on a large scale.

In natural sciences, we learn to observe and analyze objectively processes happening in nature. This happens to have repercussions on our nature connectedness as individuals: seeing nature as something we are not part of. Gaining awareness on our own relationship with nature and eco-emotions is important, especially as researchers, because it can affect our research questions and the way we communicate results (Fig. 15). Pihkala (2020) highlights the necessity for educators to "first practice self-reflection about eco-anxiety, after which they have many possibilities to help their audiences to develop emotional

resilience.” Practical guides (e.g., Richardson et al., 2020; Underhill, 2018) and online resources are now accessible in order to easily measure and reflect on our own Nature Connectedness (online test: <https://maitejacquot.com/measure-your-nature-connectedness/>) (Richardson et al., 2019), level of Climate Change Hope Scale (Li and Monroe, 2018) and level of eco-anxiety (Clayton and Karazsia, 2020) and to help others doing so.

5.3. Benefits with using the Human Ecosystem Engineering (HEE) framework

In sustainability science, reevaluating the paradigms that create a separation between humans and nature is considered a powerful “leverage point” for driving transformations (West et al., 2020). Categories of “humans” and “nature” should no longer be seen as disconnected and mutually exclusive, but rather as interconnected parts of holistic systems (West et al., 2020). However, West et al. (2020) point out that dichotomies persist in research practice. The proven disconnect to nature is inevitably intricately to the way we are currently framing ecological research. There is consequently a need to also rethink the human-nature relationship inside of ecological research. Instead of a framework with humans causing harm to nature, we could include humans as a species acting as any other species: causing changes in their environment and receiving feedback. This is exactly what I aim to achieve using the Human Ecosystem Engineering framework.

Using an already well-studied framework designed based on the observation of other species, this framework applied to the human species allows a higher nature connection, switching from human-centered to a more nature-centered way to frame research in ecology. Highlighting the similarity between human and non-human engineering (Jones et al., 1994), a framework originally designed based on the observation of other species and applied to humans allowed connecting naturally the already identified components of ecological research (i.e., anthropogenic pressures and ecosystem services). This provides us with a comprehensive and integrative framework to study human activities effects and feedback. Linking anthropogenic pressures and ecosystem services, this concept could be interesting for management, allowing communicating efficiently ecological research to policy makers and achieving the UN Sustainable Development Goals (SDGs). Moreover, needless to say that this framework goes beyond benthic systems and can be applied to all ecosystems (see Fig. A1).

Appendix

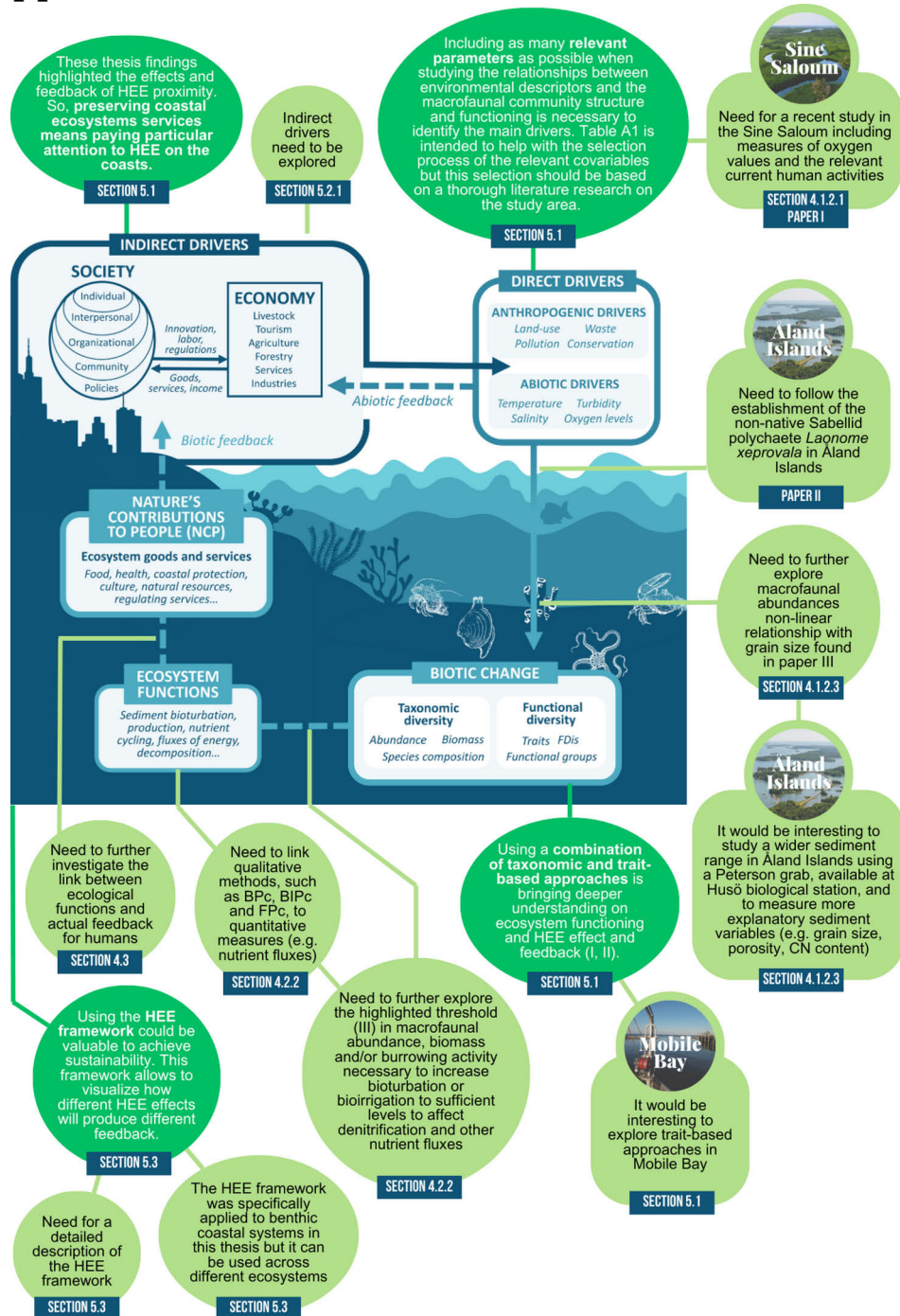


Fig. A1: Conceptual model summarizing recommendations considering these thesis findings (darker green) and the identified overall and area-specific knowledge gap (light green). Dark blue boxes are referring to sections and papers where more detailed information can be found.

APPENDIX

Table A1: Relevant covariates to consider for future research related to macrofaunal communities relationships with their environment in coastal ecosystems. Listed covariates were highlighted as significant drivers for macrofaunal communities structure and functioning in coastal ecosystems and are describing the following key categories: physical environment (a), sediment properties (b) and HEE (c). Expected relationship with structural and functional macrofauna vary depending on the study area.

(a) PHYSICAL ENVIRONMENT VARIABLES	
Covariate	Relevance
Salinity (PSU)	Reflecting climate, salinity and temperature are particularly important covariates to consider, especially in regard to the frequency and intensity increase of marine heatwaves with climate change (Kauppi and Villnäs, 2022). Salinity and temperature are well-known major driving variables for macrofaunal communities (Li et al., 2022). Reported as the main environmental factors affecting benthic macrofauna community composition and structure in coastal and estuarine ecosystems (Conde et al., 2013; Little et al., 2017; Verdelhos et al., 2015), they appeared as a significant drivers in the three studied coastal ecosystems (I, II, III) .
Temperature (°C)	
Hydrodynamics and/or Habitat (e.g., wind-wave exposure index (EUNIS))	Local hydrodynamic conditions is of critical importance for macrofaunal spatial distribution. Clear spatial patterns in diversity, species and traits compositions were both highlighted in previous studies (Kilar and McLachlan, 1989; Pihl, 1986; Ricciardi and Bourget, 1999; Van Der Wal et al., 2017; Weigel et al., 2015) and in my findings (II, III) . Established for northern Baltic Sea coasts by Isæus (2004) and improved by Weigel et al. (2016, 2015), an exposure index can be included as a covariate in this particular area, as an example. The exposure classification has been described as a habitat proxy. Habitat was shown as a driver in Sine Saloum (I) and Henseler et al. (2019) found distinct differences in community diversity and composition between the habitats.
Depth (m)	Benthic invertebrates are restricted to specific depth, which can be related to different hydrostatic pressures and food availability (Leung Tack, 1985; Warwick, 1984). Depth appeared as a significant driver in the three studied coastal ecosystems (I, II, III) .
Dissolved oxygen (DO) (e.g., DO concentration (mg L ⁻¹), DO saturation (%))	DO is known as a major driver because most organisms require oxygen to serve as the terminal electron acceptor in energy production (respiration) and to drive many redox reactions. Different taxa have specific tolerance ranges and, as a consequence, oxygen (normoxia, hypoxia, anoxia) is a strong predictor for species diversity and occurrence in the zoobenthic assemblage. The oxygenation status of the environment can be estimated by measuring dissolved oxygen. Hypoxia (<3.5 mg O ₂ L ⁻¹ , level recommended by Steckbauer et al. (2011) to designate hypoxic water masses) and anoxia (0 mg O ₂ L ⁻¹) are two of the most important structuring factors for the zoobenthic communities, leading to an impoverishment or complete loss of benthic macrofauna (Pearson and Rosenberg, 1978; Rousi et al., 2019). As expected, dissolved oxygen levels represented a significant driver for macrofaunal communities (II, III) .
(b) SEDIMENT PROPERTIES VARIABLES	
Covariate	Relevance
Sediment grain size (e.g., sediment type (sand/mud), median grain size (D50) (µm), sediment fractions (% in silt, clay, sand, gravel), porosity)	It is commonly recognized that the structure of the macrofaunal communities depends largely on sediment parameters (Rousi et al., 2019, 2011). Sediment characteristics are often a significant explanatory factor in macrofaunal taxonomic and trait composition, which was the case in the three studied areas (I, II, III) . Even if sediment type (mud/sand) was already highlighted as informative enough to detect its effect on macrofaunal communities (II) , when possible, I would recommend more detailed grain size analysis with the measure of the median grain size and of the different sediment fractions (% in silt, clay, sand and gravel) (I, III) . An interesting additional parameter to consider is porosity as it reflect the cohesion of sediment and the water penetration capacity.
Food availability and quality in the sediment (e.g., organic content, C:N ratio, chlorophyll a content)	The amount of organic content in the sediment can serve as a proxy for food availability for macrofaunal organisms and was highlighted as a significant driver for macrofaunal community structure and functioning (II) . The sediment-dwelling fauna is highly dependent on the energy produced in the photic zone, which is supplied to the soft-bottom as organic matter (Snoeijs-Leijonmalm et al., 2016). Additionally to the amount of organic content, C:N ratio gives information on the quality of the food availability (III) . Chlorophyll a is a proxy for microphytobenthos, which represents another source of food for macrozoobenthic organisms (III) .

APPENDIX

(c) HUMAN ECOSYSTEM ENGINEERING FACTORS (ACTIVITIES AND INDUCED PRESSURES)		
TYPE OF HEE (Tab. 1)	Covariate (Pressure and examples of associated human activities)	Relevance
STRUCTURAL HEE	Physical disturbance (e.g., dredging, harvesting, bottom trawling, constructions, fishing)	Many human activities are causing physical disturbance or damage to seabed: cables, dredging, extraction of sand and gravel, fishing intensity, pipelines, shipping density, etc. Such activities may cause erosion and resuspension of bottom sediments (Snoeijs-Leijonmalm et al., 2016) and have a direct physical impact on the benthic environment since it alters the sedimentary habitat structure and may harm the sediment-dwelling organisms by smothering (Snoeijs-Leijonmalm et al., 2016). Shellfish harvesting was found a key structuring driver for macrofaunal communities in the Sine Saloum intertidal zone (I) and dredging was a significant driver explaining macrofaunal spatial distribution in Mobile Bay (III) .
LIGHT HEE	Eutrophication (e.g., Fish farming, agriculture nutrient-rich runoff)	Coastal eutrophication caused by nutrient-rich runoff represents a major issue. Originating mainly from agriculture, riverine input, municipal wastewaters, aquaculture and airborne loading, nutrient inputs lead to increased primary production, decreased water clarity, increasing amounts of oxygen-consuming drifting algal mats and changes in zoobenthos and fish communities (Bonsdorff, 2021; Bonsdorff et al., 1997). One way to measure eutrophication together with other indicators is to measure the Secchi depth (Fleming-Lehtinen, 2016). Fish farming is an example of human activities representing "local point sources" for nutrient inputs and having a significant impact in terms of eutrophication (Bonsdorff et al., 1997). Both the Secchi Depth and the proximity to fish farms significantly contributed in structuring macrofaunal communities in Åland Islands (II) .
CHEMICAL HEE	Hazardous substances (e.g., heavy metals) (e.g., mining, industrial effluents, agriculture runoff, aquaculture, boating, chemical spills, sewage discharge)	Chemical substances, such as heavy metals (PTEs), can be considered hazardous if they are toxic, persistent and bioaccumulate or if they are highly persistent and bioaccumulate (Snoeijs-Leijonmalm et al., 2016). Chemical inputs arise from human activities, such as mining operations, industrial effluents, agriculture runoff, aquaculture, boating and recreational use of water bodies, chemical spills, and sewage discharge. Such activities are impacting the biogeochemical cycling, hence causing pollution, even in the most remote ecosystems of our planet (Majer et al., 2014). Hazardous substances were part of the HEE driving macrofaunal communities in Åland Islands (II) and PTEs have led to biodiversity and functional diversity loss in macrofaunal communities and particularly to a change in living habits in Sine Saloum (I) .
SOUND HEE	Underwater sound (e.g., submarine power cables, recreational boating)	Underwater sound creating acoustic pollution is derived from human activities such as: (1) boat traffic, (2) bathing sites, and (3) coastal urban land use (e.g., use of submarine power cables). Many invertebrates have been shown to be sound-sensitive, causing e.g., damage to sensory systems, stress, mortality, change in behavior (Solé et al., 2023). Underwater sound was part of the HEE affecting Åland Islands macrofaunal communities (II) .

Terminology

To help the understanding, important terms are described as interpreted by the author.

Good quality of life (GOL): the achievement of a fulfilled human life, a notion which may vary strongly across different societies and groups within societies. It is a context-dependent state of individuals and human groups, comprising aspects such as access to food, water, energy and livelihood security, and also health, good social relationships and equity, security, cultural identity, and freedom of choice and action. "Human wellbeing", "inclusive wealth", "living in harmony with nature", "living-well in balance and harmony with Mother Earth" are examples of different perspectives on a "Good quality of life". From Brondizio et al., (2019).

Ecological disturbance (anthropogenic and natural): an event that can disrupt any ecological level, environmental component as well as the organizational status of a biological cycle of organisms. Disturbances are an important aspect in the natural selection and the whole biological evolution, as they modify the environment in which every living being performs its vital functions (Graham et al., 2021).

Drivers: refer to all external factors affecting ecosystems, and, as a consequence, also affecting the supply of *nature's contribution to people (NCP)*. See Brondizio et al., (2019) for a detailed typology of drivers.

→ Direct drivers: both non-human induced and anthropogenic, affect nature directly in a physical sense. Direct anthropogenic drivers are those that flow from human institutions and governance systems and other indirect drivers. They include positive and negative *effects*,

such as habitat conversion, human-caused climate change, or species introductions. Direct non-human induced drivers can directly affect anthropogenic assets and quality of life (e.g., a volcanic eruption can destroy roads and cause human deaths).

→ Indirect drivers: human actions and decisions that operate diffusely by altering and influencing direct drivers as well as other indirect drivers. They do not physically *impact* nature or its contributions to people. Rather, they are the root causes of the direct anthropogenic drivers that affect nature both positively and negatively. Indirect drivers include e.g., economic, demographic, institutional, technological and cultural ones. Special attention is given, among indirect drivers, to the role of institutions and governance systems, including formal and informal systems of access to land and property rights as related to any component of nature, socially shared rules, legislative arrangements, international regimes such as agreements for the protection of endangered species, and economic policies.

Ecological trait / Biological trait: a well-defined, measurable property of organisms, usually at the individual level and used comparatively across species (de Juan et al., 2022; Lavorel et al., 1997; McGill et al., 2006; Reiss et al., 2009; Violle et al., 2007). Examples of frequently used biological traits in the marine realm are body size, mobility, and feeding habit (Degen et al., 2018).

→ Effect traits: traits of an organism that contribute to an *ecosystem function* or *process* (Hooper et al., 2005). As such, the presence or activity of a species, depending on its abundance or biomass, body size, and metabolic rate, influences the functioning of the system to different degrees (e.g., bioturbation, habitat provision, filtration rate).

→ Response traits: traits related with the response of species to environmental factors, including *disturbance*, or the potential recovery of the species under more favorable conditions (Hooper et al., 2005). These traits are directly related to the survival of species, populations, or communities in changing environmental conditions. An example could be the effect of fecundity on the species recovery from disturbance, with high fecundity having positive effects on recovery.

Ecosystem engineer: an organism that directly or indirectly modulates the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain and create habitats (Jones et al., 2010).

→ Autogenic engineer: (e.g., corals, or trees) change the environment via their own physical structures (i.e., their living and dead tissues).

→ Allogenic engineer: (e.g., woodpeckers, beavers) change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means.

Function: can be understood as the role that each component plays in the surrounding environment (i.e., control the fluxes of energy, nutrients, and organic matter) (Bellwood et al., 2019; Calow, 1987). But, in the ecological literature, the term is used in different ways depending on the scale (local or regional) and/or the object (individual, population, or ecosystem) (Drylie et al., 2020; Luiza-Andrade et al., 2017; Martins and Barros, 2022).

→ Ecological function: At the individual level, function is the role that an organism plays in the environment, and at the ecosystem level it refers to the combined effects of all natural processes that sustain an ecosystem and can result in global processes and ecosystem services (Degen et al., 2018; Snelgrove et al., 2014). From (Martins and Barros, 2022).

→ Ecosystem function: comprises the stocks and fluxes of energy and materials in the system and the relative stability over time (Paterson et al., 2012). Examples are primary production, nutrient fluxes and biogeochemical cycles, or sediment bioturbation. Absolute separation of ecosystem functions and ecosystem processes is not always possible, and in literature terms are often used synonymously (Paterson et al., 2012; Reiss et al., 2009).

Ecosystem process: any process of transformation that occurs in an ecosystem, theoretically whether measurable or not. This includes all metabolism, catabolism, and dynamic processes such as decomposition, sediment bioturbation, active resuspension, production, nutrient cycling and fluxes of nutrients and energy (De Bello et al., 2010).

Ecosystem functioning: The joint effects of all processes that sustain an ecosystem (Reiss et al., 2009).

Ecosystem services: *ecosystem functions* that have implicit value to humans. Ecosystem services are the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life. They maintain biodiversity and the production of ecosystems goods such as seafood, forage, timber, biomass fuels, natural fiber, and many pharmaceuticals, industrial products, and their precursors (Daily, 1997). These include provisioning services such as food and water; regulating services such as regulation of floods, drought, land degradation, and disease; supporting services such as soil formation and nutrient cycling; and cultural services such as recreational, spiritual, religious and other non-material benefits (De Bello et al., 2010).

Ecosystem services can adopt the classification system used under nature's contributions to people (NCP) in recognition that many services fit into more than one of the four categories used in the Millennium Ecosystem for example food may be both a provisioning service and a cultural service (Brondizio et al., 2019).

Effect: Human activities exert pressures, which have effects, which may lead to impacts on receptors. Therefore, pressure and effect are always coupled so that every pressure has an effect, but not every pressure necessarily leads to an impact. From Smith et al. (2022).

Human activities: Actions (potentially positive or negative) by society in an area or globally – what we do in the natural and built environment to fulfill societal basic needs; actions throughout all stages including creating, operating, using, removing infrastructure; creating an energy supply; obtaining food and water; being cognitive; using material by our presence (air), etc. From Smith et al. (2022).

Impact: refers to adverse *effects* on the environment caused by *pressures* from *human activities*. An “adverse effect” is defined as an alteration from natural conditions, whether permanent or temporary, in a physical, chemical or biological aspect of environment state that is considered undesirable and therefore needs to be avoided or reduced. From Smith et al. (2022).

Pressure: Resulting from [*human activities* – defined as the mechanisms (as rate processes) of change, in the way in which an activity will change the natural and societal systems, by modifying the structure and functioning of the systems. From Smith et al. (2022).

Stressor: A type of direct or indirect, natural or human related *driver* that causes undesired change in an ecosystem to any physical, chemical, or biological entity that can induce impacts on ecosystems or human health. In other words, a stressor can also be defined as a combination of activity/development pressure acting in a potentially negative manner on an ecosystem component. Often used interchangeably for “*activities*” and “*pressures*”. From Smith et al. (2022).

Nature: all different types of environments and organisms living in them. Within the *framing* of natural sciences, nature includes e.g., all dimensions of biodiversity, species, genotypes, populations, ecosystems, the biosphere, ecosystem functioning, communities, biomes, Earth life support's systems, and their associated ecological, evolutionary, biogeochemical processes and biocultural diversity.

→ Frame (e.g., framing nature): a conceptual term for interpretative storylines that communicate what is at stake in a science-related debate and why the issue matters. For additional information, see Blackmore et al. (2013) and Underhill (2018).

Nature connectedness (NC): psychological construct describing an individual's relationship with nature. The construct covers how we think about nature, our affective relationship with nature and the extent to which we see ourselves as part of nature. Nature Connectedness is measurable using psychometric scales containing carefully constructed sets of items and several studies suggest it can be increased through carefully designed interventions to prompt engagement with nature. For additional information, see Mayer and Frantz (2004) and Richardson et al. (2019). To measure your own nature connectedness:

<https://maitejacquot.com/measure-your-nature-connectedness/>.

→ The Pathways to nature connectedness (NC):

framework providing a new and applied approach to improving human-nature relations. This framework can be used to help design interventions to enhance human-nature connections bringing about benefits to pro-nature behaviors and human wellbeing. Five pathways to *nature connectedness* were identified with meaning (cultural relationship with nature), emotion (feeling for nature), compassion (care for nature), beauty (noticing beauty of nature) and contact (sensory interaction with nature). For additional information, see Lumber et al. (2017).

Nature's contribution to people (NCP): all the contributions, both positive and negative, of living nature (i.e., diversity of organisms, ecosystems, and their associated ecological and evolutionary processes) to the quality of life of humans as individuals, societies or humanity as a whole. Beneficial contributions from *nature* include such things as food provision, water purification, flood control, and artistic inspiration, whereas detrimental contributions include disease transmission and predation that damages people or their assets. Many of nature's contributions to people may be perceived as benefits or detriments depending on the cultural, temporal or spatial context. From Brondizio et al., (2019).

Acknowledgments

1 As a kid, I was lucky enough to spend my summer vacations camping along the Mediterranean Sea (France) with my family. I would spend almost the entire time in the water snorkeling. I would go back and forth: seeing a fish, looking at my identification book I bought at the aquarium, going back in the water. I noted the list of every fish I identified years after years. In the small amount of time I went on this same beach, I noticed the amount of people increasing drastically and the list of fish shortening. This is how my interest and passion started.

2 To pursue this passion, I started my journey in academia in Brittany (France). Drs. Alexandre Carpentier and Anne-Laure Barillé were the first ones to give me a chance by recruiting me as an intern.



3 My specific interest and passion for benthos started thanks to Dr. François Le Loc'h and Vincent Le Garrec in the LabexMER (Brest, France), with the analysis of samples collected in Senegal. This is when I realized how diverse worms could be, both morphologically and functionally. This was the first tangible seed of this thesis, which would turn into Paper I.

4 Dr. Kelly Dorgan has been the one granting me the resources and support to conduct my first ever complete research project, at the Dauphin Island Sea Lab (DISL) in Alabama (USA), which turned into Paper III of this thesis.

5 The name “Dr. Marie Nordström” came up several times during my research journey, way before officially starting my PhD. In Brest, her PhD student Dr. Nolween Quilien was the first one to tell me about her and later on, in Alabama, Kelly told me we would be a good fit! Such a small benthos world! So, it really feels like Marie and I were meant to work together. Ever since the moment we started to look for fundings for my PhD studies, she has been the best primary supervisor I could dream for.

6 During my PhD journey, I have been part of many fun adventures. It started on a small island at Askö Laboratory in Sweden with Dr. Tiina Salo and the Spigg°T team (Dr. Casey L. Yanos, Dr. Britas Klemens Eriksson, Dr. Johan S. Eklöf, Andrea De Cervo, Fiona Colgan Carey, Sorsha Passmore, and Inez Alsagoff) working with mesocosms.

7 In Åland Islands (Finland), at Husö Biological Station, I set-up the “DISCOBOX” experiment with the great help of Dr. Tiina Salo, Dr. Simon Gaultier and interns, Lisa Valkonen, Karl Weckström and Niilo Salmela. Later in Stockholm, I did metabarcoding analyses with the amazing Dr. Séréna Albert and Dr. Francisco Nascimento.

As a follow-up study to Paper II, the whole summer 2019, I have been sampling benthos in the Åland Islands with Erwan Aublet and the help of Viggo Henelius and Floriaan Eveleens Maarse.

I have also been part of two spectacular arctic cruises: 8 the ECOTIP West Greenland 2021 cruise (investigating ECOSystem TIPPING points and cascades in the Arctic Seas) with the benthos team, Dr. Anna Törnroos-Remes and Phoebe Armitage, and 9 the TUNU-VIII Expedition 2022 in NE Greenland (“TUNU” is the Greenlandic word for Northeast Greenland) with the benthos team composed of Dr. Bodil Bluhm, Dr. Marie Nordström, Dr. Erik Bonsdorff, and Ivan Cautain.

KEY ELEMENTS have determined the trajectory of this thesis:

A clear vision: During our PhD studies, most of us reach a point when we have to remind ourselves why our work is important. I was no exception. I needed a bigger vision to give purpose to my thesis. I have had the privilege to explore many exciting projects during my PhD and I needed to select the papers to include, to clarify what was fundamentally important for me and what was the

message I wanted to bring forward. I have Marie Nordström, Sandrine Carles and Olivia Victoria Sautereau to thank for that.

Reflecting on my relationship with nature: Part of clarifying my vision involved questioning my relationship with nature, which led me on a deep journey, eventually turning into the “Human Ecosystem Engineering” framework. I am so grateful to the Nature Connectedness Research Team working at the University of Derby and to the team of L’Université dans la Nature (University in Nature) who provided me with the key resources that fueled my reflection.

Teaching and Communicating: I had the opportunity to teach a couple of times, which I loved, thanks to my co-supervisor Dr. Martin Snickars. Teaching and communicating on social media has been the starting point of all my questioning on “nature connectedness”.

Passionate discussions: I have met amazing and passionate other PhD students and researchers during my journey and some of them became really good friends. Heidi, Pierre, Séréna, Christina, Bertille, Nadjeđa, Giovanna, Ivan we have had the best discussions together, this helped me in my thinking process.

SUPPORT:

Environmental and Marine Biology Research Department at ÅAU: the people inside the EMB department have been supporting my research and giving feedback with our Marine Seminars. Dr. Erik Bonsdorff has been a great advisor throughout my years of research at Åbo. I am also thankful to Dr. Christoffer Boström and Dr. Christian Pansch-Hattich who have been great coordinators, and to the whole PhD survival gang: Heidi, Pierre, Christina, Phoebe, Florian, Bertille, Ida, Jolle, Louise, Johanna, Viktor, Lucinda and many others.



Fundings and Infrastructures: My research would not have been possible without the support of the Åbo Akademi University doctoral network FunMarBio, and the MARmaED project, which received funding from the

European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 675997. This thesis used research infrastructure facilities provided by the Finnish Marine Research Infrastructure (FINMARI).

Staff: Research field stations would not be the same without their staff; their assistance and support are so precious. I am especially grateful to Vincent Le Garrec (LabexMER, IUEM), Cyrus W. Clemo and Alice A. Kleinhuizen (DISL), Tony Cederberg and Dennis Hellström (Husö Biological Station).

Supervision team: Knowing I had a supervision team with Marie and Martin was of great support for me through my PhD journey. I am especially thankful for Marie who has been a precious support in challenging times, the best advisor and a great person to celebrate and laugh with.

My own support team : No matter where I have been in the world, my love and rock, Simon, my oldest and closest friends (Marine, Gaëlle, Sylvain, Amanda), my closest "Finnish" friends (Heidi and Pierre), the DharmaCoach gang (Agnès, Éliane, Laure, Maï, Sandrine) and my family (Maman, Florian, Guillaume) have been my best support in this journey.

I am so grateful for every single one of you, for every research team, staff, lab, field stations, universities I have had the chance to collaborate with, and for many more people I haven't mentioned here but who are in my heart and memories.

Mille mercis.

Maïté P. Jacquot

References

- Aller, R.C., 1979. The effects of animal-sediment interactions on geochemical processes near the sediment-water interface, in: *Estuarine Interactions*. Academic Press, New York, pp. 157–172.
- Aller, R.C., Aller, J.Y., 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research* 56, 905–936.
- Andersen, J.H., Axe, P., Backer, H., Carstensen, J., Claussen, U., Fleming-Lehtinen, V., Järvinen, M., Kaartokallio, H., Knuuttila, S., Korpinen, S., Kubiliute, A., Laamanen, M., Lysiak-Pastuszek, E., Martin, G., Murray, C., Møhlenberg, F., Nausch, G., Norkko, A., Villnäs, A., 2011. Getting the measure of eutrophication in the Baltic Sea: towards improved assessment principles and methods. *Biogeochemistry* 106, 137–156. <https://doi.org/10.1007/s10533-010-9508-4>
- Andersen, J.H., Carstensen, J., Conley, D.J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B.G., Josefson, A.B., Norkko, A., Villnäs, A., Murray, C., 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea: Eutrophication in the Baltic Sea. *Biological Reviews* 92, 135–149. <https://doi.org/10.1111/brv.12221>
- Anderson, M.J., 2008. Animal-sediment relationships re-visited: characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *Journal of Experimental Marine Biology and Ecology* 366, 16–27. <https://doi.org/10.1016/j.jembe.2008.07.006>
- Aswani, S., Flores, C.F., Broitman, B.R., 2015. Human harvesting impacts on managed areas: ecological effects of socially-compatible shellfish reserves. *Rev Fish Biol Fisheries* 25, 217–230. <https://doi.org/10.1007/s11160-014-9376-4>
- Ausseil-Badie, J., Monteillet, J., 1985. Incidence des variations climatiques récentes enregistrées par la microfaune et la malacofaune des estuaires du Sénégal et du Saloum. *Océanographie Tropicale* 20, 151–160.
- Bakir-Demir, T., Berument, S.K., Akkaya, S., 2021. Nature connectedness boosts the bright side of emotion regulation, which in turn reduces stress. *Journal of Environmental Psychology* 76, 101642. <https://doi.org/10.1016/j.jenvp.2021.101642>
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81, 169–193. <https://doi.org/10.1890/101510.1>
- Barusseau, J.P., Diop, E.H.S., Saos, J.-L., 1985. Evidence of dynamics reversal in tropical estuaries, geomorphological and sedimentological consequences (Salum and Casamance Rivers, Senegal). *Sedimentology* 32, 543–552. <https://doi.org/10.1111/j.1365-3091.1985.tb00469.x>
- Bellwood, D.R., Streit, R.P., Brandl, S.J., Tebbett, S.B., 2019. The meaning of the term “function” in ecology: A coral reef perspective. *Funct Ecol* 33, 948–961. <https://doi.org/10.1111/1365-2435.13265>
- Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society: Series B (Methodological)* 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Berke, S.K., 2010. Functional Groups of Ecosystem Engineers: A Proposed Classification with Comments on Current Issues. *Integrative and Comparative Biology* 50, 147–157. <https://doi.org/10.1093/icb/icq077>
- Biles, C.L., Paterson, D.M., Ford, R.B., Solan, M., Raffaelli, D.G., 2002. Bioturbation,

- ecosystem functioning and community structure. *Hydrol. Earth Syst. Sci.* 6, 999–1005. <https://doi.org/10.5194/hess-6-999-2002>
- Birchough, S.N.R., Parker, R.E., McManus, E., Barry, J., 2012. Combining bioturbation and redox metrics: Potential tools for assessing seabed function. *Ecological Indicators* 12, 8–16. <https://doi.org/10.1016/j.ecolind.2011.03.015>
- Blackburn, T.H., Henriksen, K., 1983. Nitrogen cycling in different types of sediments from Danish waters. *Limnology and Oceanography* 28, 477–493.
- Blackmore, E., Underhill, R., McQuilkin, J., Leach, R., 2013. Common Cause for Nature: Finding values and frames in the conservation. Public Interest Research Centre, Machynlleth, Wales.
- Blenckner, T., Österblom, H., Larsson, P., Andersson, A., Elmgren, R., 2015. Baltic Sea ecosystem-based management under climate change: Synthesis and future challenges. *AMBIO* 44, 507–515. <https://doi.org/10.1007/s13280-015-0661-9>
- Blott, S.J., Pye, K., 2001. Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms* 26, 1237–1248. <https://doi.org/10.1002/esp.261>
- Bodin, N., N’Gom Ka, R., Le Loc’h, F., Raffray, J., Budzinski, H., Peluhet, L., Tito de Morais, L., 2011. Are exploited mangrove molluscs exposed to Persistent Organic Pollutant contamination in Senegal, West Africa? *Chemosphere* 84, 318–327. <https://doi.org/10.1016/j.chemosphere.2011.04.012>
- Bodin, N., N’Gom-Kâ, R., Kâ, S., Thiaw, O.T., Tito de Morais, L., Le Loc’h, F., Rozuel-Chartier, E., Auger, D., Chiffolleau, J.-F., 2013. Assessment of trace metal contamination in mangrove ecosystems from Senegal, West Africa. *Chemosphere* 90, 150–157. <https://doi.org/10.1016/j.chemosphere.2012.06.019>
- Bonaglia, S., Nascimento, F.J.A., 2023. Meiofauna Shaping Biogeochemical Processes, in: *New Horizons in Meiobenthos Research*. Springer, Cham.
- Bonaglia, S., Nascimento, F.J.A., Bartoli, M., Klawonn, I., Brüchert, V., 2014. Meiofauna increases bacterial denitrification in marine sediments. *Nature Communications* 5, 5133. <https://doi.org/10.1038/ncomms6133>
- Bonsdorff, E., 2021. Eutrophication: Early warning signals, ecosystem-level and societal responses, and ways forward: This article belongs to Ambio’s 50th Anniversary Collection. Theme: Eutrophication. *Ambio* 50, 753–758. <https://doi.org/10.1007/s13280-020-01432-7>
- Bonsdorff, E., Blomqvist, E.M., Mattila, J., Norkko, A., 1997. Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanologica Acta* 20, 319–329.
- Bonsdorff, E., Diaz, R.J., Rosenberg, R., Norkko, A., Cutter Jr, G.R., 1996. Characterization of soft-bottom benthic habitats of the Åland Islands, northern Baltic Sea. *Marine Ecology Progress Series* 142, 235–245.
- Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B., Visser, M.E., 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78, 73–83. <https://doi.org/10.1111/j.1365-2656.2008.01458.x>
- Braeckman, U., Foshtomi, M.Y., Van Gansbeke, D., Meysman, F., Soetaert, K., Vincx, M., Vanaverbeke, J., 2014. Variable importance of macrofaunal functional biodiversity for biogeochemical cycling in temperate coastal sediments. *Ecosystems* 17, 720–737. <https://doi.org/10.1007/s10021-014-9755-7>
- Braitto, M.T., Böck, K., Flint, C., Muhar, A., Muhar, S., Penker, M., 2017. Human-Nature Relationships and Linkages to Environmental Behaviour. *environ values* 26, 365–389.

- <https://doi.org/10.3197/096327117X14913285800706>
- Bremner, J., Rogers, S., Frid, C., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators* 6, 609–622. <https://doi.org/10.1016/j.ecolind.2005.08.026>
- Brenier, A., Henriques, A., Le Douguet, L., 2009. Des femmes et des coquillages. Expérience d'un projet de conservation dans le Delta du Saloum (Rapport FIBA, ENDA Graf Sahel & IRD).
- Brey, T., 2001. Population dynamics in benthic invertebrates. A virtual handbook.
- Brey, T., Müller-Wiegmann, C., Zittier, Z.M.C., Hagen, W., 2010. Body composition in aquatic organisms — A global data bank of relationships between mass, elemental composition and energy content. *Journal of Sea Research* 64, 334–340. <https://doi.org/10.1016/j.seares.2010.05.002>
- Brondizio, E., Diaz, S., Settele, J., Ngo, H.T., Gueze, M., Aumeeruddy-Thomas, Y., Bai, X., Geschke, A., Molnár, Z., Niamir, A., Pascual, U., Simcock, A., Jaureguiberry, P., 2019. Chapter 1 Assessing a planet in transformation: Rationale and approach of the IPBES Global Assessment on Biodiversity and Ecosystem Services, IPBES Global Assessment on Biodiversity and Ecosystem Services. Zenodo. <https://doi.org/10.5281/ZENODO.3831852>
- Cadotte, M.W., Carscadden, K., Mirotnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Calow, P., 1987. Towards a definition of functional ecology. *Functional Ecology* 1, 57. <https://doi.org/10.2307/2389358>
- Capasso, E., Jenkins, S.R., Frost, M., Hinz, H., 2010. Investigation of benthic community change over a century-wide scale in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom* 90, 1161–1172. <https://doi.org/10.1017/S0025315409991020>
- Carvalho, S., Pereira, P., Pereira, F., de Pablo, H., Vale, C., Gaspar, M.B., 2011. Factors structuring temporal and spatial dynamics of macrobenthic communities in a eutrophic coastal lagoon (Óbidos lagoon, Portugal). *Marine Environmental Research* 71, 97–110. <https://doi.org/10.1016/j.marenvres.2010.11.005>
- Chapman, M.D., 1987. Women's fishing in Oceania. *Human Ecology* 15, 267–288. <https://doi.org/10.1007/BF00888026>
- Chawla, L., 2020. Childhood nature connection and constructive hope: A review of research on connecting with nature and coping with environmental loss. *People and Nature* 2, 619–642. <https://doi.org/10.1002/pan3.10128>
- Chevene, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31, 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>
- Chu, E.W., Karr, J.R., 2013. Environmental Impact: Concept, Consequences, Measurement. *Encyclopedia of Biodiversity* 3, 278–296. <https://doi.org/10.1016/B978-0-12-809633-8.02380-3>
- Clarke, D., Miller-Way, T., 1992. An environmental assessment of the effects of open-water disposal of maintenance dredged material on benthic resources in Mobile Bay, Alabama. (Dredging Operations Technical Program No. Miscellaneous Paper D-92-1). U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecol* 18, 117–143.

- <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Clayton, S., Karazsia, B.T., 2020. Development and validation of a measure of climate change anxiety. *Journal of Environmental Psychology* 69, 101434. <https://doi.org/10.1016/j.jenvp.2020.101434>
- Coblentz, K.E., Henkel, J.R., Sigel, B.J., Taylor, C.M., 2015. Influence of sediment characteristics on the composition of soft-sediment intertidal communities in the northern Gulf of Mexico. *PeerJ* 3, e1014. <https://doi.org/10.7717/peerj.1014>
- Conchedda, G., Lambin, E.F., Mayaux, P., 2011. Between Land and Sea: Livelihoods and Environmental Changes in Mangrove Ecosystems of Senegal. *Annals of the Association of American Geographers* 101, 1259–1284. <https://doi.org/10.1080/00045608.2011.579534>
- Conde, A., Novais, J.M., Domínguez, J., 2013. Intertidal macrofauna and environmental stress at a riverine-marine boundary. *Marine Environmental Research* 92, 1–9. <https://doi.org/10.1016/j.marenvres.2013.07.002>
- Corte, G.N., Checon, H.H., Shah Esmaeili, Y., Lefcheck, J.S., Amaral, A.C.Z., 2021. Mangrove fragments as key coastal reservoirs of taxonomic and functional biodiversity. *Biodivers Conserv* 30, 1573–1593. <https://doi.org/10.1007/s10531-021-02158-y>
- Costello, M.J., Bouchet, P., Boxshall, G., Arvanitidis, C., Appeltans, W., 2023. European Register of Marine Species.
- Covich, A.P., Palmer, M.A., Crowl, T.A., 1999. The Role of Benthic Invertebrate Species in Freshwater Ecosystems. *BioScience* 49, 119. <https://doi.org/10.2307/1313537>
- Daily, G.C., 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington D.C., pp. 1–19.
- D'Alessandro, M., Porporato, E.M.D., Esposito, V., Giacobbe, S., Deidun, A., Nasi, F., Ferrante, L., Auriemma, R., Berto, D., Renzi, M., Scotti, G., Consoli, P., Del Negro, P., Andaloro, F., Romeo, T., 2020. Common patterns of functional and biotic indices in response to multiple stressors in marine harbours ecosystems. *Environmental Pollution* 259, 113959. <https://doi.org/10.1016/j.envpol.2020.113959>
- Dardeau, M.R., 1988. Mobile Bay trend station infaunal macroinvertebrates (winter 1987; spring 1988): life history and environmental requirements (Dauphin Island Sea Lab technical report No. 88– 004), A final report for the Alabama Department of Environmental Management. Dauphin Island Sea Lab, Dauphin Island, Alabama.
- Dasgupta, P., 2021. The economics of biodiversity: the Dasgupta review, Updated: 18 February 2021. ed. HM Treasury, London.
- Dauer, D.M., 1993. Biological criteria, environmental health and estuarine macrobenthic community structure. *Marine Pollution Bulletin* 26, 249–257. [https://doi.org/10.1016/0025-326X\(93\)90063-P](https://doi.org/10.1016/0025-326X(93)90063-P)
- De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins Da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers Conserv* 19, 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>
- de Juan, S., Bremner, J., Hewitt, J., Törnroos, A., Mangano, M.C., Thrush, S., Hinz, H., 2022. Biological traits approaches in benthic marine ecology: Dead ends and new paths. *Ecology and Evolution* 12. <https://doi.org/10.1002/ece3.9001>
- Degen, R., Aune, M., Bluhm, B.A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczyk, M., Zhulay, I., Albano, P.G., Bremner, J., Grebmeier, J.M.,

- Link, H., Morata, N., Nordström, M.C., Shojaei, M.G., Sutton, L., Zuschin, M., 2018. Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. *Ecological Indicators* 91, 722–736. <https://doi.org/10.1016/j.ecolind.2018.04.050>
- Descamps, C., 1991. La collecte des arches, une activité bi-millénaire dans le Bas-Saloum (Sénégal), in: *Dynamique et Usages de La Mangrove Dans Les Pays Des Rivières Du Sud, Du Sénégal à La Sierra Leone*. IRD Éditions, Marseille, pp. 107–113.
- Descroix, L., Sané, Y., Thior, M., Manga, S.-P., Ba, B.D., Mingou, J., Mendy, V., Coly, S., Dièye, A., Badiane, A., Senghor, M.-J., Diedhiou, A.-B., Sow, D., Bouaita, Y., Soumaré, S., Diop, A., Faty, B., Sow, B.A., Machu, E., Montoroi, J.-P., Andrieu, J., Vandervaere, J.-P., 2020. Inverse Estuaries in West Africa: Evidence of the Rainfall Recovery? *Water* 12, 647. <https://doi.org/10.3390/w12030647>
- Díaz, S., Malhi, Y., 2022. Biodiversity: Concepts, Patterns, Trends, and Perspectives. *Annu. Rev. Environ. Resour.* 47, 31–63. <https://doi.org/10.1146/annurev-environ-120120-054300>
- Diop, E.S., Soumare, A., Diallo, N., Guisse, A., 1997. Recent changes of the mangroves of the Saloum River Estuary, Senegal. *Mangroves and Salt Marshes* 1, 163–172. <https://doi.org/10.1023/A:1009900724172>
- Diouf, A.C., Cissokho, D., Somadjago, M., 2020. Analyse des stratégies de résilience développées par les femmes du Delta du Saloum (Sénégal) face aux changements climatiques. *Revue Espace Géographique et Société Marocaine* 135–143.
- Dirisu, A.-R., Edwin-Wosu, N.L., 2022. Environmental Influence on the Diversity and Composition of Benthic Macrofauna of Asarama Estuary at Adoni Flat in the Niger Delta. *American Journal of Marine Science* 10, 1–9. <https://doi.org/10.12691/marine-10-1-1>
- Dolbeth, M., Cardoso, P.G., Ferreira, S.M., Verdelhos, T., Raffaelli, D., Pardal, M.A., 2007. Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. *Marine Pollution Bulletin* 54, 576–585. <https://doi.org/10.1016/j.marpolbul.2006.12.005>
- Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environ Ecol Stat* 3, 143–166. <https://doi.org/10.1007/BF02427859>
- Dong, J.-Y., Zhao, L., Sun, X., Hu, C., Wang, Y., Li, W.-T., Zhang, P.-D., Zhang, X., 2021. Response of macrobenthic communities to heavy metal pollution in Laoshan Bay, China: A trait-based method. *Marine Pollution Bulletin* 167, 112292. <https://doi.org/10.1016/j.marpolbul.2021.112292>
- Douglass, S.L., Pickel, B.H., 1999. The tide doesn't go out anymore - the effect of bulkheads on urban shorelines. *Shore and Beach* 67, 19–25.
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. <https://doi.org/10.1890/13-0196.1>
- Dray, S., Dufour, A.-B., 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *J. Stat. Soft.* 22. <https://doi.org/10.18637/jss.v022.i04>
- Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412. <https://doi.org/10.1890/08-0349.1>
- Drylie, T.P., Lohrer, A.M., Needham, H.R., Pilditch, C.A., 2020. Taxonomic and functional response of estuarine benthic communities to experimental organic enrichment: Consequences for ecosystem function. *Journal of Experimental Marine Biology and Ecology* 532, 151455.

- <https://doi.org/10.1016/j.jembe.2020.151455>
- Engelsen, A., Hulth, S., Pihl, L., Sundbäck, K., 2008. Benthic trophic status and nutrient fluxes in shallow-water sediments. *Estuarine, Coastal and Shelf Science* 78, 783–795. <https://doi.org/10.1016/j.ecss.2008.02.018>
- Faulwetter, S., Markantonatou, V., Pavloudi, C., Papageorgiou, N., Keklikoglou, K., Chatzinikolaou, E., Pafilis, E., Chatzigeorgiou, G., Vasileiadou, K., Dailianis, T., Fanini, L., Koulouri, P., Arvanitidis, C., 2014. Polytraits: A database on biological traits of marine polychaetes. *BDJ* 2, e1024. <https://doi.org/10.3897/BDJ.2.e1024>
- Ferguson, A., Eyre, B., 2013. Interaction of benthic microalgae and macrofauna in the control of benthic metabolism, nutrient fluxes and denitrification in a shallow sub-tropical coastal embayment (western Moreton Bay, Australia). *Biogeochemistry* 112, 423–440. <https://doi.org/10.1007/s10533-012-9736-x>
- Flannagan, J.F., 1970. Efficiencies of various grabs and corers in sampling freshwater benthos. *Journal of the Fisheries Board of Canada* 27, 1691–1700. <https://doi.org/10.1139/f70-191>
- Fleming-Lehtinen, V., 2016. Secchi depth in the Baltic Sea - an indicator of eutrophication (Faculty of Biological and Environmental Sciences). University of Helsinki, Helsinki.
- Flint, R.W., Kalke, R.D., 1985. Benthos structure and function in a south Texas estuary. *Contributions Marine Science* 2, 33–53.
- Folk, R.L., 1974. *Petrology of Sedimentary Rocks*. Hemphill Publishing Company, Austin, Texas.
- Foulquier, C., Baills, J., Arraud, A., D'Amico, F., Blanchet, H., Rihouey, D., Bru, N., 2020. Hydrodynamic conditions effects on soft-bottom subtidal nearshore benthic community structure and distribution. *Journal of Marine Sciences* 2020, 1–16.
- Frid, C.L.J., Garwood, P.R., Robinson, L.A., 2009. Observing change in a North Sea benthic system: A 33 year time series. *Journal of Marine Systems* 77, 227–236. <https://doi.org/10.1016/j.jmarsys.2008.01.011>
- Gallup, L., Sonnenfeld, D.A., Dahdouh-Guebas, F., 2020. Mangrove use and management within the Sine-Saloum Delta, Senegal. *Ocean & Coastal Management* 185, 105001. <https://doi.org/10.1016/j.ocecoaman.2019.105001>
- Gamenick, I., Jahn, A., Vopel, K., Giere, O., 1996. Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonisation studies and tolerance experiments. *Mar. Ecol. Prog. Ser.* 144, 73–85. <https://doi.org/10.3354/meps144073>
- Gaston, G.R., Young, J.C., 1992. Effects of contaminants of macrobenthic communities in the upper Calcasieu Estuary, Louisiana. *Bull. Environ. Contam. Toxicol.* 49. <https://doi.org/10.1007/BF00203168>
- Gning, N., Le Loc'h, F., Thiaw, O.T., Aliaume, C., Vidy, G., 2010. Estuarine resources use by juvenile *Flagfin mojarra* (*Eucinostomus melanopterus*) in an inverse tropical estuary (Sine Saloum, Senegal). *Estuarine, Coastal and Shelf Science* 86, 683–691. <https://doi.org/10.1016/j.ecss.2009.11.037>
- Gogina, M., Morys, C., Forster, S., Gräwe, U., Friedland, R., Zettler, M.L., 2017. Towards benthic ecosystem functioning maps: Quantifying bioturbation potential in the German part of the Baltic Sea. *Ecological Indicators* 73, 574–588. <https://doi.org/10.1016/j.ecolind.2016.10.025>
- Graham, E.B., Averill, C., Bond-Lamberty, B., Knelman, J.E., Krause, S., Peralta, A.L., Shade, A., Smith, A.P., Cheng, S.J., Fanin, N., Freund, C., Garcia, P.E., Gibbons, S.M., Van Goethem, M.W., Guebila, M.B., Kempainen, J., Nowicki, R.J., Pausas, J.G.,

- Reed, S.P., Rocca, J., Sengupta, A., Sihi, D., Simonin, M., Słowiński, M., Spawn, S.A., Sutherland, I., Tonkin, J.D., Wisnoski, N.I., Zipper, S.C., Contributor Consortium, 2021. Toward a generalizable framework of disturbance ecology through crowdsourced science. *Front. Ecol. Evol.* 9, 588940. <https://doi.org/10.3389/fevo.2021.588940>
- Gray, J.S., 1974. Animal-sediment relationships. *Oceanography and Marine Biology Annual Review* 12, 223–261.
- Gray, J.S., Elliott, M., 2009. Ecology of marine sediments from science to management, second. ed. Oxford University Press, Oxford.
- Green, S.J., Côté, I.M., 2014. Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. *Journal of Animal Ecology* 83, 1451–1460. <https://doi.org/10.1111/1365-2656.12250>
- Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tاملander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., Winder, M., 2017. The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology*. <https://doi.org/10.1111/gcb.13642>
- Guiral, D., Albaret, J.-J., Baran, É., Bertrand, F., Debenay, J.-P., Diouf, P.S., Guillou, J.-J., Lœuff, P.L., Montoroi, J.-P., Sow, M., 1999. Chapitre II. Les écosystèmes à mangrove, in: Cormier Salem, M.-C. (Ed.), *Rivières du Sud*. IRD Éditions, pp. 63–130. <https://doi.org/10.4000/books.irdeditions.4985>
- Gusmao, J.B., Brauko, K.M., Eriksson, B.K., Lana, P.C., 2016. Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. *Ecological Indicators* 66, 65–75. <https://doi.org/10.1016/j.ecolind.2016.01.003>
- Gutiérrez, J.L., Jones, C.G., Byers, J.E., Arkema, K.K., Berkenbusch, K., Commiato, J.A., Duarte, C.M., Hacker, S.D., Lambrinos, J.G., Hendriks, I.E., Hogarth, P.J., Palomo, M.G., Wild, C., 2011. Physical Ecosystem Engineers and the Functioning of Estuaries and Coasts, in: *Treatise on Estuarine and Coastal Science*. Elsevier, pp. 53–81. <https://doi.org/10.1016/B978-0-12-374711-2.00705-1>
- Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems: Climate change in coastal marine systems. *Ecology Letters* 9, 228–241. <https://doi.org/10.1111/j.1461-0248.2005.00871.x>
- HELCOM, 2023. HELCOM Thematic assessment of biodiversity 2016-2021.
- HELCOM, 2013. State of the Baltic Sea - Second HELCOM holistic assessment 2011-2016. *Baltic Sea Environment Proceedings*.
- Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M., Bonsdorff, E., 2019. Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach. *Estuarine, Coastal and Shelf Science* 226, 106272. <https://doi.org/10.1016/j.ecss.2019.106272>
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35. <https://doi.org/10.1890/04-0922>
- Hu, C., Dong, J., Gao, L., Yang, X., Wang, Z., Zhang, X., 2019. Macrobenthos functional trait responses to heavy metal pollution gradients in a temperate lagoon. *Environmental Pollution* 253, 1107–1116. <https://doi.org/10.1016/j.envpol.2019.06.117>
- Isæus, M., 2004. Factors structuring *Fucus* communities at open and complex

- coastlines in the Baltic Sea. Stockholm University, Department of Botany, Stockholm.
- ITIS, 2023. Integrated Taxonomic Information System (ITIS). <https://doi.org/10.5066/F7KH0KBK>
- Jeschke, J.M., Gabriel, W., Kokko, H., 2008. r-Strategist/K-Strategists, in: Encyclopedia of Ecology. Elsevier, pp. 3113–3122. <https://doi.org/10.1016/B978-008045405-4.00648-0>
- Jones, C.G., Gutiérrez, J.L., Byers, J.E., Crooks, J.A., Lambrinos, J.G., Talley, T.S., 2010. A framework for understanding physical ecosystem engineering by organisms. *Oikos* 119, 1862–1869. <https://doi.org/10.1111/j.1600-0706.2010.18782.x>
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as Ecosystem Engineers. *Oikos* 69, 373–386.
- Jones, S.C., Tidwell, D.K., Darby, S.B., 2009. Comprehensive shoreline mapping, Baldwin and Mobile Counties, Alabama: Phase I (Open-File Report No. 0921), Geologic investigations program. Geological Survey of Alabama, Tuscaloosa, Alabama.
- Josefson, A., Norkko, J., Norkko, A., 2012. Burial and decomposition of plant pigments in surface sediments of the Baltic Sea: role of oxygen and benthic fauna. *Mar. Ecol. Prog. Ser.* 455, 33–49. <https://doi.org/10.3354/meps09661>
- Jovanovic, Z., Larsen, M., Organo Quintana, C., Kristensen, E., Glud, R., 2014. Oxygen dynamics and porewater transport in sediments inhabited by the invasive polychaete *Marenzelleria viridis*. *Marine Ecology Progress Series* 504, 181–192. <https://doi.org/10.3354/meps10737>
- Jupke, J.F., Schäfer, R.B., 2020. Should ecologists prefer model- over distance-based multivariate methods? *Ecol Evol* 10, 2417–2435. <https://doi.org/10.1002/ece3.6059>
- Kahneman, D., 2011. Thinking fast and slow, Farrar, Straus, and Giroux. ed. New York.
- Kaiser, M.J., Broad, G., Hall, S.J., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. *Journal of Sea Research* 45, 119–130. [https://doi.org/10.1016/S1385-1101\(01\)00052-1](https://doi.org/10.1016/S1385-1101(01)00052-1)
- Karlson, K., Bonsdorff, E., Rosenberg, R., 2007. The Impact of Benthic Macrofauna for Nutrient Fluxes from Baltic Sea Sediments. *AMBIO: A Journal of the Human Environment* 36, 161–167. [https://doi.org/10.1579/0044-7447\(2007\)36\[161:TIOBMF\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[161:TIOBMF]2.0.CO;2)
- Kauppi, L., Villnäs, A., 2022. Marine heatwaves of differing intensities lead to distinct patterns in seafloor functioning. *Proc. R. Soc. B.* 289, 20221159. <https://doi.org/10.1098/rspb.2022.1159>
- Kilar, J., McLachlan, J., 1989. Effects of wave exposure on the community structure of a plant-dominated, fringing-reef platform: intermediate disturbance and disturbance-mediated competition. *Mar. Ecol. Prog. Ser.* 54, 265–276. <https://doi.org/10.3354/meps054265>
- Kirby, R.R., Beaugrand, G., Lindley, J.A., 2009. Synergistic effects of climate and fishing in a marine ecosystem. *Ecosystems* 12, 548–561. <https://doi.org/10.1007/s10021-009-9241-9>
- Kollmuss, A., Agyeman, J., 2002. Mind the Gap: Why do people act environmentally and what are the barriers to pro-environmental behavior? *Environmental Education Research* 8, 239–260. <https://doi.org/10.1080/13504620220145401>
- Kraufvelin, P., Sinisalo, B., Bonsdorff, E., 2001. Changes in zoobenthic community structure after pollution abatement from @sh farms in the Archipelago Sea (N. Baltic Sea). *Marine Environmental Research*.
- Kristensen, E., Blackburn, T.H., 1987. The fate of organic carbon and nitrogen in experimental marine sediment systems: Influence of bioturbation and anoxia. *Journal of Marine Research* 45, 231–257.

- <https://doi.org/10.1357/002224087788400927>
- Kristensen, E., Hjorth Jensen, M., Aller, R.C., 1991. Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual polychaete (*Nereis virens*) burrows. *Journal of Marine Research* 49, 355–377. <https://doi.org/10.1357/002224091784995855>
- Kruse, I., Strasser, M., Thiermann, F., 2004. The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). *Journal of Sea Research* 51, 53–62. <https://doi.org/10.1016/j.seares.2003.05.004>
- Kurth, C., Pihkala, P., 2022. Eco-anxiety: What it is and why it matters. *Front. Psychol.* 13, 981814. <https://doi.org/10.3389/fpsyg.2022.981814>
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305. <https://doi.org/10.1890/08-2244.1>
- Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution* 12, 474–478. [https://doi.org/10.1016/S0169-5347\(97\)01219-6](https://doi.org/10.1016/S0169-5347(97)01219-6)
- Le Loeuff, P., 1999. La macrofaune d'invertébrés benthiques des écosystèmes à salinité variable le long des côtes atlantiques de l'Afrique tropicale ; variations de la biodiversité en relation avec les conditions climatiques actuelles (precipitations) et l'histoire climatique regionale. *Zoosystema* 21, 557–571.
- Lee, J., Webb, B.M., Dzwonkowski, B., Park, K., Valle-Levinson, A., 2013. Bathymetric influences on tidal currents at the entrance to a highly stratified, shallow estuary. *Continental Shelf Research* 58, 1–11.
- <https://doi.org/10.1016/j.csr.2013.03.002>
- Legendre, P., Anderson, M.J., 1999. Distance-based Redundancy Analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69, 1–24. <https://doi.org/10.2307/2657192>
- Legendre, P., Borcard, D., Blanchet, G., Dray, S., 2013. PCNM: MEM Spatial Eigen function and Principal Coordinate Analyses.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. <https://doi.org/10.1007/s004420100716>
- Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78, 547–562. [https://doi.org/10.1890/0012-9658\(1997\)078\[0547:RBTHST\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2)
- Lehrter, J.C., 2008. Regulation of eutrophication susceptibility in oligohaline regions of a northern Gulf of Mexico estuary, Mobile Bay, Alabama. *Marine Pollution Bulletin* 56, 1446–1460. <https://doi.org/10.1016/j.marpolbul.2008.04.047>
- Leitão, F.M.S., Gaspar, M.B., 2007. Immediate effect of intertidal non-mechanised cockle harvesting on macrobenthic communities: a comparative study. *Scientia marina* 71, 723–733. <https://doi.org/10.3989/scimar.2007.71n4723>
- Leppäkoski, E., 1975. Assessment of degree of pollution on the basis of macrozoobenthos in marine and brackish water environments. *Acta Academiae Åboensis, Series B* 35, 1–90.
- Leung Tack, D., 1985. La macrofaune benthique. In: Atelier régional UNESCO/COMAR (No. 32), Rapport UNESCO sur les Sciences de la Mer. Dakar (Sénégal).
- Levinton, J., 1995. Bioturbators as Ecosystem Engineers: Control of the

- Sediment Fabric, Inter-Individual Interactions, and Material Fluxes, in: Jones, C.G., Lawton, J.H. (Eds.), *Linking Species & Ecosystems*. Springer US, Boston, MA, pp. 29–36. https://doi.org/10.1007/978-1-4615-1773-3_3
- Li, C., Monroe, M.C., 2018. Development and Validation of the Climate Change Hope Scale for High School Students. *Environment and Behavior* 50, 454–479. <https://doi.org/10.1177/0013916517708325>
- Li, P., Liu, J., Bai, J., Tong, Y., Meng, Y., Diao, X., Pan, K., Zhu, X., Lin, G., 2022. Community Structure of Benthic Macrofauna and the Ecological Quality of Mangrove Wetlands in Hainan, China. *Front. Mar. Sci.* 9, 861718. <https://doi.org/10.3389/fmars.2022.861718>
- Lillebø, A.I., Neto, J.M., Martins, I., Verdelhos, T., Leston, S., Cardoso, P.G., Ferreira, S.M., Marques, J.C., Pardal, M.A., 2005. Management of a shallow temperate estuary to control eutrophication: the effect of hydrodynamics on the system's nutrient loading. *Estuarine, Coastal and Shelf Science* 65, 697–707. <https://doi.org/10.1016/j.ecss.2005.07.009>
- Little, S., Wood, P.J., Elliott, M., 2017. Quantifying salinity-induced changes on estuarine benthic fauna: The potential implications of climate change. *Estuarine, Coastal and Shelf Science* 198, 610–625. <https://doi.org/10.1016/j.ecss.2016.07.020>
- Lohrer, A.M., Thrush, S.F., Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431, 1092–1095. <https://doi.org/10.1038/nature03042>
- Luiza-Andrade, A., Montag, L.F.D.A., Juen, L., 2017. Functional diversity in studies of aquatic macroinvertebrates community. *Scientometrics* 111, 1643–1656. <https://doi.org/10.1007/s11192-017-2315-0>
- Lumber, R., Richardson, M., Sheffield, D., 2017. Beyond knowing nature: Contact, emotion, compassion, meaning, and beauty are pathways to nature connection. *PLoS ONE* 12, e0177186. <https://doi.org/10.1371/journal.pone.0177186>
- Maiteny, P.T., 2002. Mind in the Gap: Summary of research exploring “inner” influences on pro-sustainability learning and behaviour. *Environmental Education Research* 8, 299–306. <https://doi.org/10.1080/13504620220145447>
- Majer, A.P., Petti, M.A.V., Corbisier, T.N., Ribeiro, A.P., Theophilo, C.Y.S., Ferreira, P.A.D.L., Figueira, R.C.L., 2014. Bioaccumulation of potentially toxic trace elements in benthic organisms of Admiralty Bay (King George Island, Antarctica). *Marine Pollution Bulletin* 79, 321–325. <https://doi.org/10.1016/j.marpolbul.2013.12.015>
- Mannino, A., Montagna, P.A., 1997. Small-scale spatial variation of macrobenthic community structure. *Estuaries* 20, 159–173. <https://doi.org/10.2307/1352729>
- Markowitz, E.M., Shariff, A.F., 2012. Climate change and moral judgement. *Nature Clim Change* 2, 243–247. <https://doi.org/10.1038/nclimate1378>
- MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network.
- Martins, A.D., Barros, F., 2022. Ecological functions of polychaetes along estuarine gradients. *Front. Mar. Sci.* 9, 780318. <https://doi.org/10.3389/fmars.2022.780318>
- Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Matthews, D.D., 2002. Integrating women's subsistence fishing into Pacific fisheries conservation. *SPC Women in Fisheries Information Bulletin* 11, 13–14.

- Mattila, J., Bonsdorff, E., 1988. A quantitative estimation of fish predation on shallow soft bottom benthos in SW Finland. *Kieler Meeresforsch Sonderh* 6, 111–125.
- Mayer, F.S., Frantz, C.M., 2004. The connectedness to nature scale: A measure of individuals' feeling in community with nature. *Journal of Environmental Psychology* 24, 503–515. <https://doi.org/10.1016/j.jenvp.2004.10.001>
- Mazik, K., Elliott, M., 2000. The effects of chemical pollution on the bioturbation potential of estuarine intertidal mudflats. *Helgoland Marine Research* 54, 99–109. <https://doi.org/10.1007/s101520050008>
- Mcgill, B., Enquist, B., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- McTigue, N.D., Gardner, W.S., Dunton, K.H., Hardison, A.K., 2016. Biotic and abiotic controls on co-occurring nitrogen cycling processes in shallow Arctic shelf sediments. *Nature Communications* 7, 13145. <https://doi.org/10.1038/ncomms13145>
- Middelburg, J.J., Levin, L.A., 2009. Coastal hypoxia and sediment biogeochemistry. *Biogeosciences* 6, 1273–1293. <https://doi.org/10.5194/bg-6-1273-2009>
- Millennium Ecosystem Assessment, 2005. *Ecosystems and human well-being: synthesis*. Island Press, Washington, DC.
- Miller-Way, T., Twilley, R.R., 1996. Theory and operation of continuous flow systems for the study of benthic-pelagic coupling. *Marine Ecology Progress Series* 140, 257–269. <https://doi.org/10.3354/meps140257>
- Morys, C., Powilleit, M., Forster, S., 2017. Bioturbation in relation to the depth distribution of macrozoobenthos in the southwestern Baltic Sea. *Mar. Ecol. Prog. Ser.* 579, 19–36. <https://doi.org/10.3354/meps12236>
- Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional diversity measures. Functional Ecology* 24, 867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Mwakisunga, B., Machiwa, J.F., Pratap, H.B., 2020. Assessment of Sediment and Benthic Macrofauna Distribution at Dar es Salaam Harbour Channel. *GEP* 08, 133–147. <https://doi.org/10.4236/gep.2020.83010>
- Myers, T.A., Nisbet, M.C., Maibach, E.W., Leiserowitz, A.A., 2012. A public health frame arouses hopeful emotions about climate change: A Letter. *Climatic Change* 113, 1105–1112. <https://doi.org/10.1007/s10584-012-0513-6>
- Nasi, F., Ferrante, L., Alvisi, F., Bonsdorff, E., Auriemma, R., Cibic, T., 2020. Macrofaunal bioturbation attributes in relation to riverine influence: What can we learn from the Po River lagoonal system (Adriatic Sea)? *Estuarine, Coastal and Shelf Science* 232, 106405. <https://doi.org/10.1016/j.ecss.2019.106405>
- Newton, A., Icely, J., Cristina, S., Brito, A., Cardoso, A.C., Colijn, F., Riva, S.D., Gertz, F., Hansen, J.W., Holmer, M., Ivanova, K., Leppäkoski, E., Canu, D.M., Mocenni, C., Mudge, S., Murray, N., Pejrup, M., Razinkovas, A., Reizopoulou, S., Pérez-Ruzafa, A., Schernewski, G., Schubert, H., Carr, L., Solidoro, C., PierluigiViaroli, Zaldívar, J.-M., 2014. An overview of ecological status, vulnerability and future perspectives of European large

- shallow, semi-enclosed coastal systems, lagoons and transitional waters. *Estuarine, Coastal and Shelf Science* 140, 95–122.
<https://doi.org/10.1016/j.ecss.2013.05.023>
- Newton, A., Icely, J., Cristina, S., Perillo, G.M.E., Turner, R.E., Ashan, D., Cragg, S., Luo, Y., Tu, C., Li, Y., Zhang, H., Ramesh, R., Forbes, D.L., Solidoro, C., Béjaoui, B., Gao, S., Pastres, R., Kelsey, H., Taillie, D., Nhan, N., Brito, A.C., de Lima, R., Kuenzer, C., 2020. Anthropogenic, Direct Pressures on Coastal Wetlands. *Front. Ecol. Evol.* 8, 144.
<https://doi.org/10.3389/fevo.2020.00144>
- Nilsen, M., Pedersen, T., Nilssen, E., 2006. Macro-benthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. *Marine Ecology Progress Series* 321, 67–77.
<https://doi.org/10.3354/meps321067>
- Nordström, M., Aarnio, K., Bonsdorff, E., 2009. Temporal variability of a benthic food web: patterns and processes in a low-diversity system. *Marine Ecology Progress Series* 378, 13–26.
<https://doi.org/10.3354/meps07872>
- Nordström, M.C., Bonsdorff, E., 2017. Organic enrichment simplifies marine benthic food web structure. *Limnology and Oceanography*.
<https://doi.org/10.1002/lno.10558>
- Nordvang, L., Johansson, T., 2002. The effects of fish farm effluents on the water quality in the Åland archipelago, Baltic Sea. *Aquacultural Engineering* 25, 253–279. [https://doi.org/10.1016/S0144-8609\(01\)00088-7](https://doi.org/10.1016/S0144-8609(01)00088-7)
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E., 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* 332, 11–23.
<https://doi.org/10.3354/meps332011>
- Nunes, M., Coelho, J.P., Cardoso, P.G., Pereira, M.E., Duarte, A.C., Pardal, M.A., 2008. The macrobenthic community along a mercury contamination in a temperate estuarine system (Ria de Aveiro, Portugal). *Science of The Total Environment* 405, 186–194.
<https://doi.org/10.1016/j.scitotenv.2008.07.009>
- Oksanen, J., Blanchet, G.F., Kindt, R., Legendre, P., O'Hara, R.B., 2011. *Vegan: Community Ecology Package*.
- Paerl, H.W., 2006. Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: interactive effects of human and climatic perturbations. *Ecological Engineering* 26, 40–54.
<https://doi.org/10.1016/j.ecoleng.2005.09.006>
- Park, K., Kim, C.-K., Schroeder, W.W., 2007. Temporal variability in summertime bottom hypoxia in shallow areas of Mobile Bay, Alabama. *Estuaries and Coasts* 30, 54–65.
<https://doi.org/10.1007/BF02782967>
- Pauly, D., Watson, R., Alder, J., 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Phil. Trans. R. Soc. B* 360, 5–12.
<https://doi.org/10.1098/rstb.2004.1574>
- Pearson, T.H., Rosenberg, R., 1978. Macro-benthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review* 16, 229–311.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variance partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625.
[https://doi.org/10.1890/0012-9658\(2006\)87\[2614:VPOSDM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2)
- Perus, J., Bonsdorff, E., Bäck, S., Lax, H.-G., Villnäs, A., Westberg, V., 2007. Zoobenthos as indicators of ecological status in coastal brackish waters: A comparative study from the Baltic Sea. *AMBIO: A Journal of the Human Environment* 36, 250–256.
[https://doi.org/10.1579/0044-7447\(2007\)36\[250:ZAI0ES\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[250:ZAI0ES]2.0.CO;2)

- Pihkala, P., 2020. Eco-Anxiety and Environmental Education. *Sustainability* 12, 10149. <https://doi.org/10.3390/su122310149>
- Pihl, L., 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research* 20, 75–83. [https://doi.org/10.1016/0077-7579\(86\)90063-3](https://doi.org/10.1016/0077-7579(86)90063-3)
- Piló, D., Ben-Hamadou, R., Pereira, F., Carriço, A., Pereira, P., Corzo, A., Gaspar, M.B., Carvalho, S., 2016. How functional traits of estuarine macrobenthic assemblages respond to metal contamination? *Ecological Indicators* 71, 645–659. <https://doi.org/10.1016/j.ecolind.2016.07.019>
- Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology* 52, 137–154. <https://doi.org/10.1086/409852>
- Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution* 3, 3958–3985. <https://doi.org/10.1002/ece3.769>
- R Core Team, 2022. R: A language and environment for statistical computing.
- Reise, K., 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* 48, 127–141. [https://doi.org/10.1016/S1385-1101\(02\)00150-8](https://doi.org/10.1016/S1385-1101(02)00150-8)
- Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* 24, 505–514. <https://doi.org/10.1016/j.tree.2009.03.018>
- Renz, J.R., Powilleit, M., Gogina, M., Zettler, M.L., Morys, C., Forster, S., 2018. Community bioirrigation potential (BIPc), an index to quantify the potential for solute exchange at the sediment-water interface. *Marine Environmental Research* 141, 214–224. <https://doi.org/10.1016/j.marenvres.2018.09.013>
- Reusch, T.B.H., Dierking, J., Andersson, H.C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., Hasler, B., Hinsby, K., Hyytiäinen, K., Johannesson, K., Jomaa, S., Jormalainen, V., Kuosa, H., Kurland, S., Laikre, L., MacKenzie, B.R., Margonski, P., Melzner, F., Oesterwind, D., Ojaveer, H., Refsgaard, J.C., Sandström, A., Schwarz, G., Tonderski, K., Winder, M., Zandersen, M., 2018. The Baltic Sea as a time machine for the future coastal ocean. *Science advances* 17.
- Ricciardi, A., Bourget, E., 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Mar. Ecol. Prog. Ser.* 185, 21–35. <https://doi.org/10.3354/meps185021>
- Richardson, M., Dobson, J., Abson, D.J., Lumber, R., Hunt, A., Young, R., Moorhouse, B., 2020. Applying the pathways to nature connectedness at a societal scale: a leverage points perspective. *Ecosystems and People* 16, 387–401. <https://doi.org/10.1080/26395916.2020.1844296>
- Richardson, M., Hunt, A., Hinds, J., Bragg, R., Fido, D., Petronzi, D., Barbett, L., Clitherow, T., White, M., 2019. A Measure of Nature Connectedness for Children and Adults: Validation, Performance, and Insights. *Sustainability* 11, 3250. <https://doi.org/10.3390/su11123250>
- Rick, T.C., Erlandson, J.M., 2009. Coastal Exploitation. *Science* 325, 952–953. <https://doi.org/10.1126/science.1178539>
- Rodrigues-Filho, J.L., Macêdo, R.L., Sarmento, H., Pimenta, V.R.A., Alonso, C., Teixeira, C.R., Pagliosa, P.R., Netto, S.A., Santos, N.C.L., Daura-Jorge, F.G., Rocha, O., Horta, P., Branco, J.O., Sartor, R., Muller, J., Cionek, V.M., 2023. From ecological functions to ecosystem services: linking coastal lagoons

- biodiversity with human well-being. *Hydrobiologia* 850, 2611–2653. <https://doi.org/10.1007/s10750-023-05171-0>
- Rodríguez-Lozano, P., Verkaik, I., Maceda-Veiga, A., Monroy, M., De Sostoa, A., Rieradevall, M., Prat, N., 2016. A trait-based approach reveals the feeding selectivity of a small endangered Mediterranean fish. *Ecol Evol* 6, 3299–3310. <https://doi.org/10.1002/ece3.2117>
- Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands Journal of Sea Research* 34, 303–317. [https://doi.org/10.1016/0077-7579\(95\)90040-3](https://doi.org/10.1016/0077-7579(95)90040-3)
- Rousi, H., Korpinen, S., Bonsdorff, E., 2019. Brackish-water benthic fauna under fluctuating environmental conditions: the role of eutrophication, hypoxia, and global Change. *Front. Mar. Sci.* 6, 464. <https://doi.org/10.3389/fmars.2019.00464>
- Rousi, H., Peltonen, H., Mattila, J., Bäck, S., Bonsdorff, E., 2011. Impacts of physical environmental characteristics on the distribution of benthic fauna in the northern Baltic Sea. *Boreal Environment Research* 16, 521–533.
- Ryu, J., Khim, J.S., Kang, S.-G., Kang, D., Lee, C., Koh, C., 2011. The impact of heavy metal pollution gradients in sediments on benthic macrofauna at population and community levels. *Environmental Pollution* 159, 2622–2629. <https://doi.org/10.1016/j.envpol.2011.05.034>
- Salama, S., Aboukoura, K., 2018. Role of Emotions in Climate Change Communication, in: *Handbook of Climate Change Communication: Vol. 1., Climate Change Management*. Springer International Publishing, Cham.
- Salvanes, A.G.V., Aksnes, D.L., Giske, J., 1992. Ecosystem model for evaluating potential cod production in a west Norwegian fjord. *Marine Ecology Progress Series* 9–22.
- Sambou, V., Kébé, C.M.F., Dieve, E.H.B., 2008. Etude sur l'utilisation et la gestion alternative de l'énergie combustible à Fadiouth et dans les îles du Saloum. Fondation Internationale pour le Banc d'Arguin (FIBA) / ENDA GRAF Sahel, Dakar, Sénégal.
- Sarr, O., 2005. Aire marine protégée, gestion halieutique, diversification et développement local: le cas de la réserve de biosphère du Delta du Saloum (Sénégal).
- Schmitz, O.J., Barton, B.T., 2014. Climate change effects on behavioral and physiological ecology of predator–prey interactions: Implications for conservation biological control. *Biological Control* 75, 87–96. <https://doi.org/10.1016/j.biocontrol.2013.10.001>
- Selck, H., Decho, A.W., Forbes, V.E., 1999. Effects of chronic metal exposure and sediment organic matter on digestive absorption efficiency of cadmium by the deposit-feeding polychaete *Capitella* species I. *Environ Toxicol Chem* 18, 1289–1297. <https://doi.org/10.1002/etc.5620180631>
- Seymour, V., 2016. The Human–Nature Relationship and Its Impact on Health: A Critical Review. *Front. Public Health* 4. <https://doi.org/10.3389/fpubh.2016.00260>
- Shull, D.H., 2009. Bioturbation, in: *Encyclopedia of Ocean Sciences*. Elsevier, pp. 395–400. <https://doi.org/10.1016/B978-012374473-9.00656-1>
- Simier, M., Blanc, L., Aliaume, C., Diouf, P.S., Albaret, J.J., 2004. Spatial and temporal structure of fish assemblages in an “inverse estuary”, the Sine Saloum system (Senegal). *Estuarine, Coastal and Shelf Science* 59, 69–86. <https://doi.org/10.1016/j.ecss.2003.08.002>
- Skilleter, G., Cameron, B., Zharikov, Y., Boland, D., McPhee, D., 2006. Effects of physical disturbance on infaunal and epifaunal assemblages in subtropical, intertidal seagrass beds. *Mar. Ecol. Prog.*

- Ser. 308, 61–78.
<https://doi.org/10.3354/meps308061>
- Smith, B.D., 2007. The Ultimate Ecosystem Engineers. *Science* 315, 1797–1798.
<https://doi.org/10.1126/science.1137740>
- Smith, C., Papadopoulou, N., Elliott, M., Franco, A., Barnard, A., Borja, Á., Uyarra, M.C., 2022. Marine strategy framework directive terminology definitions and lists.
- Snelgrove, P.V.R., Thrush, S.F., Wall, D.H., Norkko, A., 2014. Real world biodiversity–ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution* 29, 398–405.
<https://doi.org/10.1016/j.tree.2014.05.002>
- Snickars, M., Weigel, B., Bonsdorff, E., 2015. Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. *Marine Biology* 162, 141–151.
<https://doi.org/10.1007/s00227-014-2579-3>
- Snøeijers-Leijonmalm, P., Schubert, H., Radziejewska (Eds.), 2016. *Biological oceanography of the Baltic Sea*. Springer Berlin Heidelberg, New York, NY.
- Solan, M., Aspden, R.J., Paterson, D.M. (Eds.), 2012. *Marine biodiversity and ecosystem functioning: frameworks, methodologies, and integration*, 1st ed. Oxford University Press, Oxford.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306, 1177–1180.
<https://doi.org/10.1126/science.1103960>
- Solé, M., Kaifu, K., Mooney, T.A., Nedelec, S.L., Olivier, F., Radford, A.N., Vazzana, M., Wale, M.A., Semmens, J.M., Simpson, S.D., Buscaino, G., Hawkins, A., Aguilar De Soto, N., Akamatsu, T., Chauvaud, L., Day, R.D., Fitzgibbon, Q., McCauley, R.D., André, M., 2023. Marine invertebrates and noise. *Front. Mar. Sci.* 10, 1129057.
<https://doi.org/10.3389/fmars.2023.1129057>
- Spencer, B.E., Kaiser, M.J., Edwards, D.B., 1998. Intertidal clam harvesting: benthic community change and recovery. *Aquaculture Research* 29, 429–437.
<https://doi.org/10.1046/j.1365-2109.1998.00221.x>
- Spitz, J., Ridoux, V., Brind'Amour, A., 2014. Let's go beyond taxonomy in diet description: testing a trait-based approach to prey-predator relationships. *J Anim Ecol* 83, 1137–1148. <https://doi.org/10.1111/1365-2656.12218>
- Steckbauer, A., Duarte, C.M., Carstensen, J., Vaquer-Sunyer, R., Conley, D.J., 2011. Ecosystem impacts of hypoxia: thresholds of hypoxia and pathways to recovery. *Environ. Res. Lett.* 6, 025003.
<https://doi.org/10.1088/1748-9326/6/2/025003>
- Steele-Petrovic, H.M., 1975. An Explanation for the Tolerance of Brachiopods and Relative Intolerance of Filter-Feeding Bivalves for Soft Muddy Bottoms. *Journal of Paleontology* 49, 552–556.
- Stigebrandt, A., 1977. On the effect of barotropic current fluctuations on the two-layer transport capacity of a constriction. *Journal of Physical Oceanography* 7, 118–122.
[https://doi.org/10.1175/1520-0485\(1977\)007<0118:OTEOBC>2.0.CO;2](https://doi.org/10.1175/1520-0485(1977)007<0118:OTEOBC>2.0.CO;2)
- Stout, J.P., Heck Jr, K.L., Valentine, J.F., Dunn, S.J., Spitzer, P.M., 1998. Preliminary characterization of habitat loss: Mobile Bay national estuary program. Dauphin Island Sea Lab, Dauphin Island, Alabama.
- Strong, J.A., Andonegi, E., Bizsel, K.C., Danovaro, R., Elliott, M., Franco, A., Garces, E., Little, S., Mazik, K., Moncheva, S., Papadopoulou, N., Patrício, J., Queirós, A.M., Smith, C., Stefanova, K., Solaun, O., 2015. Marine biodiversity and ecosystem function relationships: The potential for practical monitoring applications. *Estuarine, Coastal and Shelf Science* 161, 46–64.
<https://doi.org/10.1016/j.ecss.2015.04.008>
- Sulphey, M.M., Faisal, S., 2021. Connectedness to nature and

- environmental concern as antecedents of commitment to environmental sustainability. *IJEEP* 11, 208–219. <https://doi.org/10.32479/ijeep.10803>
- Thrush, S.F., Dayton, P.K., 2002. Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. *Annu. Rev. Ecol. Syst.* 33, 449–473. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150515>
- Törnroos, A., Bonsdorff, E., 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecological Applications* 22, 2221–2236. <https://doi.org/10.1890/11-2042.1>
- Tsikopoulou, I., Lampa, M., Tsiola, A., Pitta, P., Tsapakis, M., Karakassis, I., 2021. Functional adaptations of benthic communities to organic matter enrichment at the edge of an allowable zone of effect (AZE). *Estuarine, Coastal and Shelf Science* 262, 107596. <https://doi.org/10.1016/j.ecss.2021.107596>
- Tsutsumi, H., 1987. Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. *Marine Ecology Progress Series* 36, 139–149.
- Tuominen, L., Heinänen, A., Kuparinen, J., Nielsen, L., 1998. Spatial and temporal variability of denitrification in the sediments of the northern Baltic Proper. *Mar. Ecol. Prog. Ser.* 172, 13–24. <https://doi.org/10.3354/meps172013>
- Tuominen, L., Mäkelä, K., Lehtonen, K.K., Haahti, H., Hietanen, S., Kuparinen, J., 1999. Nutrient fluxes, porewater profiles and denitrification in sediment influenced by algal sedimentation and bioturbation by *Monoporeia affinis*. *Estuarine, Coastal and Shelf Science* 49, 83–97. <https://doi.org/10.1006/ecss.1999.0492>
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Underhill, R., 2018. Framing Nature Toolkit: A guide to how words can help wildlife. Public Interest Research Centre, Machynlleth, Wales.
- Van Colen, C., Rossi, F., Montserrat, F., Andersson, M.G.I., Gribsholt, B., Herman, P.M.J., Degraer, S., Vincx, M., Ysebaert, T., Middelburg, J.J., 2012. Organism-Sediment Interactions Govern Post-Hypoxia Recovery of Ecosystem Functioning. *PLoS ONE* 7, e49795. <https://doi.org/10.1371/journal.pone.0049795>
- van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H., Marques, J.C., 2016. The performance of trait-based indices in an estuarine environment. *Ecological Indicators* 61, 378–389. <https://doi.org/10.1016/j.ecolind.2015.09.039>
- Van Der Wal, D., Lambert, G.I., Ysebaert, T., Plancke, Y.M.G., Herman, P.M.J., 2017. Hydrodynamic conditioning of diversity and functional traits in subtidal estuarine macrozoobenthic communities. *Estuarine, Coastal and Shelf Science* 197, 80–92. <https://doi.org/10.1016/j.ecss.2017.08.012>
- Van Hoey, G., Degraer, S., Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science* 59, 599–613. <https://doi.org/10.1016/j.ecss.2003.11.005>
- Verdelhos, T., Marques, J.C., Anastácio, P., 2015. The impact of estuarine salinity changes on the bivalves *Scrobicularia plana* and *Cerastoderma edule*, illustrated by behavioral and mortality responses on a laboratory assay. *Ecological Indicators* 52, 96–104. <https://doi.org/10.1016/j.ecolind.2014.11.022>
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology.

- Ecology 89, 2290–2301.
<https://doi.org/10.1890/07-1206.1>
- Villnäs, A., Janas, U., Josefson, A., Kendzierska, H., Nygård, H., Norkko, J., Norkko, A., 2019. Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter. *Mar. Ecol. Prog. Ser.* 622, 31–48.
<https://doi.org/10.3354/meps13008>
- Villnäs, A., Norkko, J., Hietanen, S., Josefson, A.B., Lukkari, K., Norkko, A., 2013. The role of recurrent disturbances for ecosystem multifunctionality. *Ecology* 94, 2275–2287.
<https://doi.org/10.1890/12-1716.1>
- Villnäs, A., Norkko, J., Lukkari, K., Hewitt, J., Norkko, A., 2012. Consequences of Increasing Hypoxic Disturbance on Benthic Communities and Ecosystem Functioning. *PLoS ONE* 7, e44920.
<https://doi.org/10.1371/journal.pone.0044920>
- Villnäs, A., Perus, J., Bonsdorff, E., 2011. Structural and functional shifts in zoobenthos induced by organic enrichment - Implications for community recovery potential. *Journal of Sea Research* 65, 8–18.
<https://doi.org/10.1016/j.seares.2010.06.004>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892.
<https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Voß, K., Schäfer, R.B., 2017. Taxonomic and functional diversity of stream invertebrates along an environmental stress gradient. *Ecological Indicators* 81, 235–242.
<https://doi.org/10.1016/j.ecolind.2017.05.072>
- Warwick, R.M., 1984. Species size distributions in marine benthic communities. *Oecologia* 61, 32–41.
<https://doi.org/10.1007/BF00379085>
- Wei, T., Simko, V., 2017. R Package “Corrplot”: Visualization of a Correlation Matrix.
- Weigel, B., Andersson, H., Meier, H., Blenckner, T., Snickars, M., Bonsdorff, E., 2015. Long-term progression and drivers of coastal zoobenthos in a changing system. *Marine Ecology Progress Series* 528, 141–159.
<https://doi.org/10.3354/meps11279>
- Weigel, B., Blenckner, T., Bonsdorff, E., 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos* 125, 1421–1433.
<https://doi.org/10.1111/oik.02894>
- Weigel, B., Bonsdorff, E., 2018. Trait-based predation suitability offers insight into effects of changing prey communities. *PeerJ* 6, e5899.
<https://doi.org/10.7717/peerj.5899>
- Welschmeyer, N.A., 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography* 39, 1985–1992.
<https://doi.org/10.4319/lo.1994.39.8.1985>
- West, S., Haider, L.J., Stålhammar, S., Woroniecki, S., 2020. A relational turn for sustainability science? Relational thinking, leverage points and transformations. *Ecosystems and People* 16, 304–325.
<https://doi.org/10.1080/26395916.2020.1814417>
- Wilkinson, D.M., 1999. The Disturbing History of Intermediate Disturbance. *Oikos* 84, 145.
<https://doi.org/10.2307/3546874>
- Wilson, A.M., Huettel, M., Klein, S., 2008. Grain size and depositional environment as predictors of permeability in coastal marine sands. *Estuarine, Coastal and Shelf Science* 80, 193–199.
<https://doi.org/10.1016/j.ecss.2008.06.011>
- Worm, B., Paine, R.T., 2016. Humans as a Hyperkeystone Species. *Trends in Ecology & Evolution* 31, 600–607.
<https://doi.org/10.1016/j.tree.2016.05.008>

- WoRMS Editorial Board, 2023. World Register of Marine Species. <https://doi.org/10.14284/170>
- Wrede, A., Beermann, J., Dannheim, J., Gutow, L., Brey, T., 2018. Organism functional traits and ecosystem supporting services – A novel approach to predict bioirrigation. *Ecological Indicators* 91, 737–743. <https://doi.org/10.1016/j.ecolind.2018.04.026>
- Ysebaert, T., Meire, P., Maes, D., Buijs, J., 1993. The benthic macrofauna along the estuarine gradient of the schelde estuary. *Netherlands Journal of Aquatic Ecology* 27, 327–341. <https://doi.org/10.1007/BF02334796>
- Zabi, G.S.F., Le Loeuff, P., 1993. Benthic fauna in margino-littoral systems of West Africa, a review Part 2 Fauna and biotopes. *Revue d'Hydrobiologie Tropicale* 26, 19–51.
- Zabi, S.G.F., Le Loeuff, P., 1994. La macrofaune benthique, in: *Environnement et ressources aquatiques de Côte-d'Ivoire, Tome II: Les Milieux Lagunaires*. Paris, pp. 189–227.

ORIGINAL MANUSCRIPTS



Paper I

Jacquot M.P., Nordström M.C., De Wever L., Ngom Ka R., Ka S., Le Garrec V., Raffray J., Sadio O., Diouf M., Grall J., Tito de Morais L., Le Loc'h F, 2023.

Human activities and environmental variables drive infaunal community structure and functioning in West African mangroves.

Estuarine, Coastal and Shelf Science 293.



Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Human activities and environmental variables drive infaunal community structure and functioning in West African mangroves

M.P. Jacquot^{a,b,*}, M.C. Nordström^{b,c}, L. De Wever^a, R. Ngom Ka^d, S. Ka^e, V. Le Garrec^f, J. Raffray^a, O. Sadio^d, M. Diouf^g, J. Grall^{a,f}, L. Tito de Morais^a, F. Le Loc'h^a

^a IRD, Univ Brest, CNRS, Ifremer, LEMAR, IUEM, F-29280, Plouzané, France

^b Environmental and Marine Biology, Åbo Akademi University, AURUM, Henrikinkatu 2, 20500, Åbo, Finland

^c University of Helsinki, Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, PO Box 65 Viikinkaari 1, 00014, Helsinki, Finland

^d IRD, Univ Brest, CNRS, Ifremer, LEMAR BP, 1386, Dakar, Senegal

^e Département Gestion des Ressources Halieutiques, Pêche et Aquaculture, Université Du Sine Saloum El-Hadj Ibrahima Niass, Fatick, Senegal

^f Univ Brest, CNRS, UMS 3113, Observatoire Marin, Suivis Habitats Benthiques, OSU-IUEM, Rue Dumont D'Urville, 29280, Plouzané, France

^g Institut Universitaire de Pêche et D'Aquaculture, Université Cheick Anta Diop, Dakar, Senegal

ARTICLE INFO

Keywords:

Biological traits
Zooenthos
Shellfish harvesting
Potentially toxic elements
Intertidal and subtidal environments
Inverse estuary

ABSTRACT

In West African tropical estuaries, such as the Saloum Delta (Senegal), mangroves provide specific socio-economic functions including various natural food resources for local human populations. Mangrove-habitat loss is therefore of great concern, in terms of conservation and management, and highlights the need to study West African mangrove under human-induced pressures. Based on data from 2007 to 2008, this study aimed to establish a conditions report for two of the main Southern West Senegal mangroves areas: the Sine Saloum and the Petite Cote. We assessed the influence of environmental variables and human-induced pressures (i.e. shellfish harvesting and heavy metals (potentially toxic elements, PTEs)) on infaunal community structure and functions through trait-based approaches.

Reflecting for example changing seasons and hypersaline events, the Saloum environmental variables and their temporal dynamics greatly impacted infaunal communities in the subtidal zone. In the intertidal area, closer to anthropogenic disturbances, pressures related to human activities took precedence over environmental variables in explaining infaunal community structure. Shellfish harvesting resulted in a significant decrease ($p < 0.05$) in total macrofaunal abundance (933.79 ± 626.34 ind m^{-2} in unexploited stations compared to 140.92 ± 71.99 ind m^{-2} in exploited stations; mean $\pm$ SE) in addition to a decline in biomass and taxonomic richness. Intertidal species composition was affected by both shellfish harvesting and PTEs. PTEs were also associated with a significant decrease in functional diversity and particularly with a change in macrofaunal living habits. The combination of an RLQ and fourth-corner analysis highlighted a significant association between feeding modes and sediment grain size in both tidal areas.

This study provides a needed deeper understanding of the unintended effects of human activities on infaunal communities and their functioning, in a highly valuable system for humans. Pinpointed factors driving infaunal community structure and functions provide important insights for future research, as well as reference points for the implementation of management measures.

1. Introduction

Many human socio-economic activities, from dam-building and skyscraper construction to forest clearing and dredging and canalization of water courses, constitute cases where humans effectively act as

ecosystem engineers, modulating the flow of resources to other species by causing physical or chemical state changes in biotic and abiotic materials (Berke, 2010; Jones et al., 1994). Following their attempt to enhance their environment, humans are now facing unforeseen and unintended consequences (Gutiérrez et al., 2011; Smith, 2007), such as

* Corresponding author. Environmental and Marine Biology, Åbo Akademi University, AURUM, Henrikinkatu 2, 20500, Åbo, Finland.
E-mail address: maitejacquot@abo.fi (M.P. Jacquot).

<https://doi.org/10.1016/j.ecss.2023.108481>

Received 18 April 2023; Received in revised form 4 August 2023; Accepted 30 August 2023

Available online 30 August 2023

0272-7714/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

increasingly threatened ecosystems, e.g., mangroves (Duke et al., 2007; Walters et al., 2008). Today, in the context of conservation, our efforts are increasingly geared towards reducing and reversing human modification of environments. Interest is consequently growing in understanding the nature and consequences of the environmental impacts of human activities and managing these activities to protect the well-being of human society and other life on Earth. Chu and Karr (2013) describe these issues as “humanity’s greatest challenge”.

Due to their environmental and economic value, growing interest in coastal wetlands arises, in particular for mangrove ecosystems (Lee et al., 2014). Intertidal assemblages of trees and shrubs localized along coastlines and estuaries in tropical and subtropical regions, i.e., mangroves, are highly productive ecosystems (Alongi, 2002; Bouillon et al., 2008). They are associated with both important ecological functions (e.g. primary and secondary production and nutrient cycling) and highly valuable goods and services for human society (Costanza et al., 1997). Not only are mangrove areas important places for human well-being, they are fundamental ecosystem-service hotspots, e.g. forming nurseries and feeding habitats for fish, providing a nutrient filtering function from land towards the open sea, serving as protection against natural disasters and as coastline stabilization (Brito and Naia, 2020), and acting as important fishing and exploitation grounds (Griffiths et al., 2017; Miller-Way and Twilley, 1996).

Almost one-fifth of the world’s mangroves are found in Sub-Saharan Africa, and 70% of these are found in West Africa (Corcoran et al., 2007). Located in West Africa, Senegal harbors approximately 6000 km² of mangrove habitat, distributed along the Southern coast in three main areas: the Sine Saloum, the Petite Côte, and the Casamance. These mangroves contribute considerably to the social and economic well-being of inhabitants living in these regions. However, there was a loss of a quarter of the mangrove total surface area between 1980 and 2006 (Corcoran et al., 2007). The government of Senegal and the international community have since taken action to protect the biodiversity of these areas, because of the related socio-economic activities mainly dominated by fishing and its associated activities (from harvesting of the primary resource to commercialization of further processed fish and seafood products). The Sine Saloum and the Petite Côte areas are of great concern in terms of conservation and management because of the traditional and well-developed fishing activities of Senegalese women, particularly the harvesting of diverse mangrove invertebrates. These fisheries play a significant role in artisanal and small-scale commercial activities, and are important in providing a source of protein and income to coastal communities (Chapman, 1987; Matthews, 2002). Unfortunately, shellfish harvesting is considered a contributing factor of degradation for mangrove ecosystems. For example, techniques used to separate the West African mangrove oysters (*Crassostrea tulipa*) from the trees they are attached to, often injures or even kills the mangrove (Bousoo, 1996). In addition to negative impacts observed due to shellfish harvesting, Bodin et al. (2013) highlighted the exposure of these mangroves and associated commercially important marine species to anthropogenic pollution, particularly to heavy metals. Also called “Potentially Toxic Elements (PTEs)”, heavy metals are naturally occurring elements (e.g. cadmium (Cd), chromium (Cr), copper (Cu), lead (Pb), zinc (Zn), mercury (Hg), nickel (Ni)), but when present in elevated concentrations, they are typically associated with contamination and being potentially toxic to plants, animals and humans (Gustin et al., 2021; Zhang et al., 2022). Metallic enrichment of mangrove environments arises from human activities, such as mining operations, industrial effluents, agriculture runoff, aquaculture, boating and recreational use of water-bodies, chemical spills, and sewage discharge, associated with the use of artificial substances and fuels or production of waste and undesirable by-products containing heavy metals (C. Li et al., 2022). Such activities are impacting the biogeochemical cycling of heavy metals, hence causing pollution, in ecosystems such as West African mangroves (Bodin et al., 2013) and even in the most remote ecosystems on our planet (Majer et al., 2014).

Unintended consequences following human activities (such as heavy metal contamination) may be detected using bioindicators. Living within mangrove ecosystems, macrobenthic organisms (>1 mm) have intricate relationships with their environment, making them interesting as bioindicators of environmental status (Perus et al., 2007). Macrobenthic organisms are central to several ecosystem functions, e.g. promoting remineralization of organic matter, enhancing oxygen penetration depth in the sediments (Aller and Aller, 1998; Jovanovic et al., 2014), and playing an essential role in energy acquisition for higher trophic levels while serving as central food resource for epibenthic predators and demersal fish (Nilsen et al., 2006; Nordström et al., 2009). Due to their restricted mobility, macrofauna living in the sediment, called infauna, can have limited ability to avoid environmental and anthropogenic pressures. Many ecosystem functions and services provided by benthic infaunal communities are therefore threatened directly by human and terrestrial-driven impacts. As a result, infauna can be particularly impacted by stressors causing physical disturbances of the substratum such as shellfish harvesting (Skilleter et al., 2006; Spencer et al., 1998) or by stressors disrupting biogeochemical cycling of heavy metals and causing contamination (Dong et al., 2021; Ryu et al., 2011; Sizmur et al., 2019). Human ecosystem engineering and environmental disturbances can impact macrofaunal communities resulting in decreased abundance, biomass and/or diversity (Corte et al., 2021; Dauer, 1993; Pearson and Rosenberg, 1987). Moving beyond measures of basic taxonomic diversity to also consider the ecological characteristics of macrofaunal communities is important for evaluations of potential ecosystem functions. Combining both approaches is key in understanding how ecosystem functions are affected due to human activities and in highlighting potential feedback for humans. Ecological traits of macrobenthos (individual-level features of organisms, describing e.g., lifestyle, morphology, physiology, reproductive strategy, or life span) relate directly to their ecological processes and ecosystem function (Cadotte et al., 2011), and can respond rapidly to multiple stressors (Mouillot et al., 2013; Voß and Schäfer, 2017). In the past 20 years, many investigations have utilized a combination of taxonomic and trait diversity, which has developed our understanding of ecosystem function and supported efforts for better ecosystem management and conservation (Bremner et al., 2006; Henseler et al., 2019; Villnäs et al., 2019).

It is of great importance, in terms of conservation and management, to study the impacts of human activities on West African mangroves. Based on data from 2007 to 2008, our study aims to establish a conditions report for mangrove areas located in Southern West Senegal. We aim to disentangle structuring factors for macrobenthic communities at the time in Southern West Senegal by assessing the influence of environmental variables and human engineering impact (shellfish harvesting and heavy metal contamination) on infaunal community structure and functioning. Pinpointing factors driving infaunal community structure and functions in the past may provide important insights for future research, as well as reference points for the implementation of management measures. From a broader perspective, this study also aims to give insight into the unintended effects of human activities on infaunal communities and infauna-related functions through a trait-based approach.

2. Materials and methods

2.1. Study areas and sampling strategy

Two of the main mangrove areas in Senegal were investigated: the Sine Saloum and the Petite Côte (Fig. 1, Tab. A.1, Fig. A1), located in Southwest Senegal. As potential focal areas in terms of conservation and management, six stations were sampled between 2007 and 2008. Boubo (B) and Saré Makalé (M), near Falia, Dionewar (W), near the village of the same name, and Saré Acah (A), near Niodor, are located in the Sine Saloum region and more specifically in the Saloum Delta, and Diouham

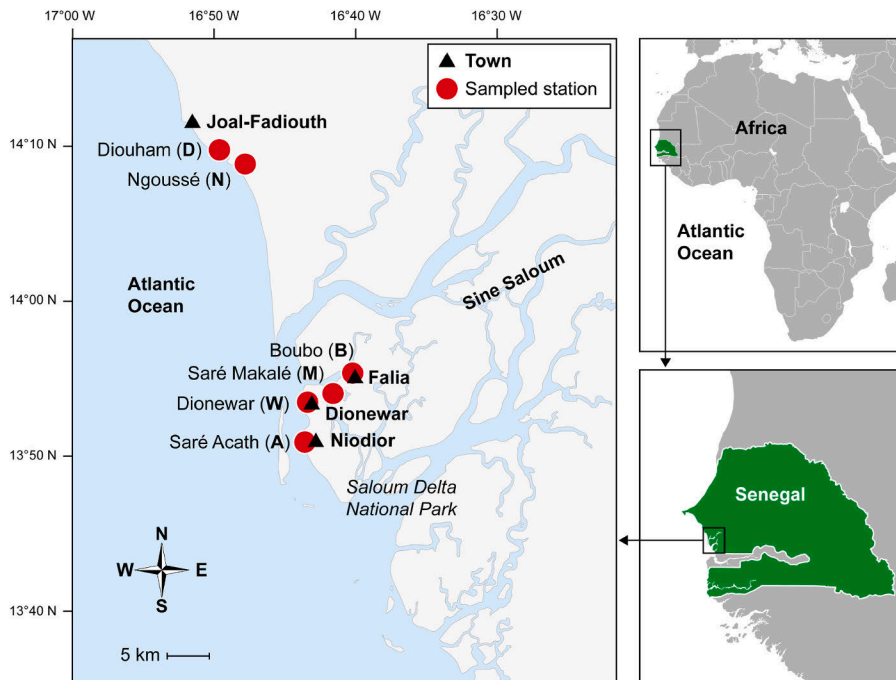


Fig. 1. Sampling stations location in Southern West Senegal.

(D) and Ngoussé (N), near Joal-Fadiouth, are located in the Petite Côte. These study areas are subject to a tropical climate with two alternate seasons: (i) a long dry season from November to June, characterized by air and water temperatures of about 17–25 °C and 20–22 °C, respectively, and dominated by hot and dry Harmattan wind, and (ii) a wet season extending from July to October, characterized by seasonal rainfall of about 600 mm, air and water temperatures of about 24–27 °C and 25–27 °C, respectively, and strong South-Eastern winds (Bodin et al., 2011).

The Saloum Delta is characterized by a dense network of small seawater creeks, locally named “bolongs”. This “inverse estuary” is distinguished by water salinity that is higher than that of seawater (Barusseau et al., 1985; Descroix et al., 2020). In this particular environment, salinity increases from downstream to upstream due to the combined effects of seawater intrusion linked to weak slope, lack of significant freshwater inputs, and intense evaporation. The upstream area is highly hyperhaline, with salinity reaching 60 to 120 (Simier et al., 2004). Consequently, where salinity is moderate, half the area is occupied by the mangrove forest, mainly *Rhizophora* and *Avicennia* species, but these trees rapidly disappear when salinity increases to more than 60. Upstream, mangrove is thus replaced by extensive intertidal sand and silt flats (Diop et al., 1997; Gning et al., 2010).

The Petite Côte is located 20 km North of the Saloum Delta (Sambou et al., 2008). This lagoon-insular environment is subject to coastal dynamics because of its seaward opening and is composed of extensive mangroves and mudflats. Lying on an island of clamshells, Joal-Fadiouth is the closest city with 3500 inhabitants living on the small area of 500 m in diameter. Both highly open to the sea, poorly supplied with fresh-water and subject to hypersaline events during dry seasons, the Saloum inverse estuary and the lagoon in the Petite Côte have previously been described as similar marginal coastal environments (Guiral et al., 1999;

Le Loeuff, 1999; Zabi and Le Loeuff, 1993, 1994).

To assess macrofaunal variability depending on the exposure to human activities, which occur more intensely closer to the coast, sampling was conducted in: (1) the intertidal and (2) the subtidal areas (Fig. 1). In these two tidal zones, stations were randomly selected in areas presenting different exposure to shellfish harvesting and to heavy metals, PTEs (see Fig. A1). In the Saloum delta, shellfish harvesting is based on the rotation of harvesting areas (Descamps, 1991; Sarr, 2005); areas left fallow for several months were considered non-exploited. Levels of PTEs were measured in a different study, conducted by Bodin et al. (2013), where they determined concentrations of 12 trace elements (Li, V, Cr, Mn, Co, Ni, Cu, Zn, Ag, Cd, Pb, and Hg) in surface sediment samples at the same sampling periods and in the same areas as in the present study. Because measurements were not from the exact same geographic coordinates and dates as the present study, we decided not to include the exact concentration values but the ecological conclusions instead (Table 2, Tab. A.1). Bodin et al. (2013) measured anthropogenic contamination with Cd, Hg and Ni in the Petite Côte (corresponding to station D), with Mn and Cr in Dionewar (corresponding to station W) and with Zn, Cu, V, Ag and Pb in both Dionewar (station W) and the Petite Côte (station D). These PTEs have already been shown as presenting a potential ecological risk for macrofaunal communities (Dong et al., 2021; Piló et al., 2016; Ryu et al., 2011).

In the intertidal zone at low tide, for a total of 87 samples, three to five 50 cm × 50 cm replicates were sampled for macrofauna in December 2007 and February, April, June and October 2008 (temporal sampling depended on stations, see Fig. A1). Sediment was scraped within the quadrat to a depth of about 20 cm using a hand shovel. Regarding the subtidal zone, a total of 56 macrofaunal samples were collected with a 0.1 m² Van Veen grab. Three to nine grab samples were taken at each station between 1 and 4 m depth in April, June and

Table 1
Traits and functional categories included in this study and their hypothesized relationships with factors responsible for special patterns in infaunal assemblages including traits helping to distinguish between natural and human-induced changes.

Traits	Categories	Label	Definition	Key mechanisms and functions	Description and relevance	Hypothesized relationships with environment
Feeding mode (feed)	Suspension/ filter feeder	stop	Feeding on the suspended matter or food particles in the water column.	Food acquisition, productivity, turnover, proxy for energy transfer, strength of benthic-pelagic coupling, prey accessibility	Feeding interactions have long been considered a central factor structuring macrobenthic communities (Pearson and Rosenberg, 1978). Feeding types contribute to production and trophic support, and play a role in nutrient uptake and recycling (Golding et al., 2007). It provides insights into the interactions between different species and their food sources. A diverse set of feeding modes indicates diverse food sources available in an area (Pacheco et al., 2011). The feeding mode is considered to be a proxy for energy fixation/transfer and ecosystem production (Ummoes and Janssen, 2012).	Scrapers and grazers are more abundant in areas with high levels of primary producers, usually found in areas with low depth (Dolbeth et al., 2007) and potentially low hydrodynamics. Predators and scavengers will be associated to areas with high availability of prey (Dolbeth et al., 2007). Scavengers are attracted to areas where physical disturbances occurs and are expected to be more common in areas of high fishing or harvesting intensity. Heavy metals are expected to favor large deposit-feeders (Dong et al., 2021; Pilo et al., 2016; Sedek et al., 1999).
	Scraper/grazer	graz	Feeding on leaves or other plant parts.			
	Predator/scavenger	pred	Feeding on living animals/carcasses.			
	Deposit feeder	depo	Feeding on phytoplankton, litter and organic matter in the sediment and water column.			
Motility (Mov)	Motile	swim	Free-swimming organisms.	Mobility, dispersal, susceptibility to cropping/predation and environmental pressures	Despite the generally restricted motility of benthic infauna, the small-scale motility of these organisms is crucial for the ecology of benthic communities. Not only motility provides insights into the ability to avoid physical disturbance (Hinckley et al., 2006) but also into the predator-prey activities or the creation of biological structures.	Sessile organisms are more subject to changes in the abiotic environment than motile species (Sara, 1986). Motile species are expected to have a better ability to avoid stressors (e.g. harvesting, heavy metals, drastic change in temperature and salinity ...) and to be able to recolonize areas by migration (Gagnia et al., 2014; Pacheco et al., 2011).
	Swimmer	crawl	Move on the sediment surface.			
	Crawler	burr	Live in burrows within the sediment.			
	Motile	sess	Sessile or very limited movement.			
	Burrower	free	Free-living in the sediment.			
Living habit (Liv)	Free-living	dwel	Lives in burrows constructed by other organisms or themselves.	Elemental cycling, productivity	Living habits are affecting habitat complexity, with the construction of biological structures for instance, and can influence nutrient recycling and trophic support (Brenner et al., 2006).	Burrow-dwellers and tubicolous are potentially less vulnerable to strong hydrodynamic disturbance, anoxic conditions and water pollution as opposed to free-living species because they can hide in their fixed tubes or burrow (Reise, 2002).
	Burrow dweller					
	Tubicolous	tubi	Lives in a tube of its own construction.			
	Attached	atta	Attached on the surface to hard substrate.			
Maximum adult size (Size)	Very small	VS	0-0.01 g	Growth rate, productivity, elemental cycling, metabolism, feeding interactions	The organism body size has a crucial relevance in the functioning and dynamics of aquatic systems (Woodward et al., 2005). Body size is correlated with many life-history traits and influences a wide range of biological and ecological functions (Bourassa and Morin, 1995; LaBarbera, 1989; Macdonald et al., 2012; Saliz-Salinas and Ramos, 1999; Warwick and Clarke, 1989). This biometric parameter can be more responsible for the trophic structure than taxonomic identity itself (Jennings et al., 2001). Biomass and biovolume affect the activity and function in the ecosystem (Brown et al., 2004).	Small-bodied species may characterize environments with high instability, the result of environmental/anthropogenic disturbances imposed on the organisms (Mouillot et al., 2006). We expect small-sized species to be prevalent in high hydrodynamic areas (Donadi et al., 2015) and to have higher P/B ratios (Schwinghamer, 1983) with higher metabolic rates (Gillooly et al., 2001). Harvesting and high levels of heavy metals in the sediment might favor smaller individuals, whereas low levels of heavy metals are expected to be dominated by large-sized individuals (Dong et al., 2021; Pilo et al., 2016).
	Small	S	0.01-0.1 g			
	Medium	M	0.1-1 g			
	Large	L	>1 g			

Table 2
Covariates with their assumed relevance and expected relationships to structural diversity and to functional diversity and the selected response traits.

Covariate Modalities or unit	Relevance		Expected relationships with:	
	Physical environment variables	Season	Structural diversity	Functional diversity and response trait
Sediment properties	Wet Dry	Habitat Estuary Lagoon	Season (Wet): Abundance (–) Diversity (–) Taxa composition (≠) (Melo et al., 2013) Habitat (Lagoon): Abundance (stable) Diversity (+) Giménez et al. (2014)	Season (Wet): Functional diversity (stable) Akoumianaki et al. (2013) –
	Salinity (PSU)	Temperature (°C)	Salinity (+): Abundance (+) Zhong et al. (2020) Salinity (Hypersaline): Abundance (–) Lam-Gordillo et al. (2022)	Salinity (Hypersaline): Functional diversity (–) Size: VS (+), S (+), M (–), L (–) Feeding mode: depo (+), susp (+) Living habit: dwell (–) Lam-Gordillo et al. (2013) Temperature (+): Size: VS (–), S (–), M (+), L (+) Lam-Gordillo et al. (2022) Alkinson and Sibly, 1997; van der Linden et al., 2016)
	Depth (m)	Fine particle fraction (%) Mud Clay	Depth (+): Biomass (–) Zhong et al. (2020) %Mud (–) and D50 (+) Abundance (+) Van Hooij et al., 2004; Zhong et al., 2020)	Depth (+): Size: VS (+), S (+), M (–), L (–) Labarbera (1989) %Mud (+): Feeding mode: susp (–), depo (+) (Shull, 2009; Steele-Petrovic, 1975)
Human ecosystem engineering structural factors	Harvesting Exploited Unexploited	Heavy metals (Potentially Toxic Elements, PTEs) Contaminated with Cd Hg Ni (yes/no) Contaminated with Zn Cu V Ag Pb (yes/no) Contaminated with Mn Cr (yes/no)	Harvesting (Yes): Abundance (–) Biomass (–) Aswan et al. (2015) PTEs (+): Abundance (–) Diversity (–) (Rabaoui et al., 2015; Ryu et al., 2011) Living habit: dwell (+), free (–) (Dong et al., 2021; Piló et al., 2016)	Harvesting (Yes): Size: VS (+), S (+), M (–), L (–) Jimenez et al. (2015) PTEs (+): Size: VS (+), S (+), M (–), L (–) Feeding mode: depo (+), pred (–) Living habit: dwell (+), free (–) (Dong et al., 2021; Piló et al., 2016)

November 2008, as indicated in Fig. A1. Both sampling methods allow collection of infauna as well as sedentary and slow mobile species such as bivalves and gastropods. This sampling approach is less accurate for estimating mobile animals, such as crabs, and using quadrats is restricted to fauna inhabiting the top 20 cm of the sediment. The recorded macrobenthic communities in this study are therefore focused on a component of the sediment community. Crabs that were caught were retained in the dataset. For each site and sampling occasion, three samples of sediment were extracted for grain size analysis. In the subtidal zone, measurements of temperature and salinity were recorded at the bottom of the water column at each station using a YSI Multiparameter probe.

2.2. Sample processing

Sediment samples were collected and analyzed for median grain size and fine particle fraction. Sediment grain size was determined by water- (for 63 μ m grain size fraction) and dry-sieving, using a series of 14 sieves from 63 μ m to 10,000 μ m. Sediment grain size characteristics were calculated for median grain size, percentage of gravel, sand and mud. Gravel represents the fraction with particles larger than 2 mm, sand is the fraction ranging from 63 μ m to 2 mm, and mud is defined as the sediment exhibiting grain sizes smaller than 63 μ m and is described as the fine particle fraction (Blott and Pye, 2001) (Fig. A2).

Regarding macrofaunal analysis, each replicate was treated separately to assess intra-station variability. For both intertidal and subtidal zones, sediments were washed through a 1 mm square-meshed sieve, and retained material was preserved in 7% formalin and stained with 1% Rose Bengal. Macrobenthic organisms were removed from all debris, identified and counted. Taxonomic identification was carried out at family level for polychaetes and at the lowest possible taxonomic level for all other taxa (Gerwing et al., 2020). Mollusca taxa for each sample were dried at 60 °C during 48 h, and dry weight was measured to 0.01 g. The wet weight of non-shellfish taxa for each sample was measured to 0.1 mg after blot-drying on tissue paper. Taxa-specific conversion factors provided by Brey (2001) were used to convert wet weight into dry weight.

Four ecological traits were selected based on their potential ability to reflect key biological and ecological processes with respect to human

ecosystem engineering and abiotic stressors. These traits, including feeding mode, motility, living habit and maximum adult size, were subdivided into 16 categories in total (Table 1). Information on these traits was collected for the lowest possible taxonomic level from a variety of published sources: literature (e.g. Jumars et al., 2015), species identification guides (e.g. Kornienko, 2013; Passos et al., 2005), and online databases, such as Polytraits (Faulwetter et al., 2014), BIOTIC—Biology Traits Information Catalogue (MarLIN, 2006), and WoRMS—World Register of Marine Species <http://www.marinespecies.org>. In cases where trait data for a species were not available, they were inferred from other species in the same genus or the same family (Boyé et al., 2019). Trait categories were then scored using a fuzzy coding approach (Chevene et al., 1994), with a scoring range of 0 (no affinity) to 3 (total affinity towards trait category) (D'Alessandro et al., 2020; Hu et al., 2019; van der Linden et al., 2016).

2.3. Statistical analyses

Data collected in the intertidal and the subtidal zones were analyzed separately in all statistical analyses described hereafter.

Macrofauna diversity was assessed employing the following primary community variables and diversity indices (Gray and Elliott, 2009): abundance (Ab), taxonomic richness (S) and Shannon's diversity index (H'), Pielou's evenness (J) and Simpson's diversity index (1-D, hereafter D). In addition to our interest in taxonomic diversity, three multidimensional indices were also considered in this study as components of functional diversity with the following: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Laliberté and Legendre, 2010; Villéger et al., 2008). These indices were built to be complementary (Villéger et al., 2008) and identified as a relevant combination to fill the functional space of a community (Mouchet et al., 2010). FRic describes the amount of trait space occupied by the species within a community and therefore represents the number of trait categories expressed. FEve refers to how evenly species abundances are distributed between the expressed trait categories (low value indicating that some parts of niche space are under-utilized). FDiv defines the distribution of the abundance across the niche space, with a higher value indicating a high degree of niche differentiation (Mason et al., 2005).

To test for significant differences in abundance and biomass (Bi)

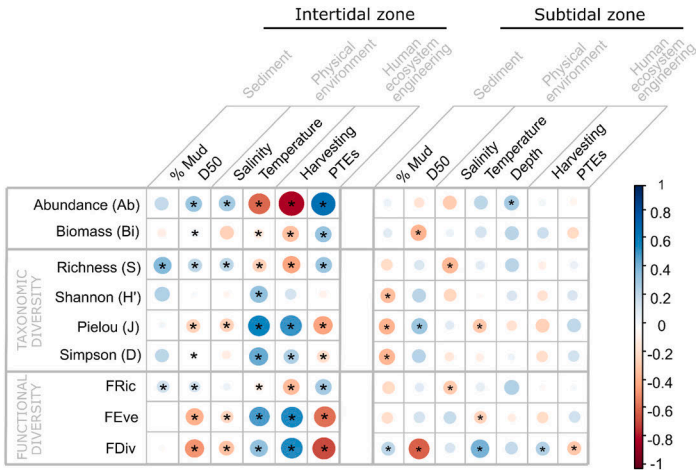


Fig. 2. Spearman correlation between structural and functional diversity indices and environmental variables (sediment, physical environment and human ecosystem engineering) in the intertidal and subtidal zone. * indicating $p < 0.01$. % Mud = fine particle fraction of sediment, D50 = sediment median grain size, PTEs = Potentially Toxic Elements, FRic = functional richness, FEve = functional evenness, FDiv = functional divergence. Covariates are further explained in Table 2.

between stations, the Kruskal-Wallis one-way analysis of variance by ranks was used because the data do not meet assumptions for one-way ANOVA. Since the sample sizes are not equal and the assumption of equal variances is not met, we performed this non-parametric test, equivalent to an ANOVA but much more robust to unequal sample sizes and unequal variances across treatment combinations. Provided that significant differences were detected by the test ($p < 0.05$), post-hoc tests for pairwise multiple comparisons (Nemenyi's test) were used to identify differences between pairs of stations.

To test the link between the macrofaunal assemblages based on their beta diversity and the different ecological factors, non-metric multidimensional scaling (nMDS) were performed. First, Bray-Curtis coefficient was used to calculate the dissimilarity matrix for species community structure analysis and then the results were visualized with nMDS. The environmental factors were fitted on the ordination diagrams after a permutation test (999 permutations) allowing to discriminate variables having a significant influence ($p < 0.05$). To ensure the interpretation of the nMDS results, stress values were calculated (Clarke, 1993). This analysis assesses the influence of the following variables on taxa abundances across samples: sampling date, sampling station, habitat, season, salinity, temperature, depth, sediment fine sediment particle fraction (% mud), sediment median grain size (D50), harvesting, and heavy metals (Mn and Cr, Cd, Hg and Ni and/or Zn, Cu, V, Ag and Pb) (Table 2).

To explore the relationship between the ecological traits of macrobenthos and environmental gradients, a combination of RLQ (Dolédéc et al., 1996) and fourth-corner analyses (Legendre et al., 1997) according to Dray et al. (2014) was applied. For the RLQ analysis, tables for environmental variables (R), species abundance (L), and traits (Q) were analyzed using Hill-Smith analysis, correspondence analysis (CA), and principal component analysis (PCA), respectively (Dray et al., 2014). The overall significance of this relationship was assessed using a global Monte Carlo test with 49,999 random permutations of models 2 and 4 (Dray et al., 2014; Dray and Legendre, 2008). Model 2 tests whether the distribution of species with fixed traits is influenced by the environmental conditions while model 4 tests whether traits influence the composition of species assemblages found in samples, keeping environmental conditions fixed (Dray et al., 2014). In addition, because RLQ analysis cannot determine which traits are affected by specific environmental variables, fourth-corner analysis, with an adjusted p-value (false discovery rate method, FDR) (Benjamini and Hochberg, 1995) for multiple testing, was applied. Furthermore, by combining both RLQ and fourth-corner analyses, the significance of the association between environmental variables or traits and the RLQ axes was investigated (Dray et al., 2014).

Variance partitioning analysis (VPA) was performed to evaluate the contribution of human ecosystem engineering, sediment properties and environmental factors to the variance in structural and functional diversity. Prior to this analysis, covariates were divided into three groups, one of which was human ecosystem engineering (i.e. shellfish harvesting and heavy metals), another one was variables related to the physical environment (i.e., season, habitat, depth, temperature and salinity) and the last one was sediment variables (i.e., fine particle fraction and median grain size). We computed adjusted R^2 following Peres-Neto et al. (2006) recommendations to produce unbiased estimates of the fractions of variation. Separate forward selection on each subset of environmental variables were conducted and only variables explaining a significant variation ($p < 0.05$) were retained in the VPA. To ensure the significance of the VPA, we tested all fractions independently using two-way ANOVA.

All analyses were performed using the R Statistical Software (R Core Team, 2022). The functional diversity indices (FRic, FEve, and FDiv) were calculated using the "FD" package (Laliberté and Legendre, 2010) based on the fuzzy coding matrix of the traits and the abundance of species. Spearman correlation tests between taxonomic and functional indices and environmental variables were performed in the "corrplot" R package (Wei and Simko, 2017). RLQ and fourth-corner analyses were

performed in the "ade4" R package (Dray and Dufour, 2007). Both the nMDS and the VPA were performed using the "vegan" package (Oksanen et al., 2011).

3. Results

Original data of this study including abundances, biomass, environmental variables and traits are available at Mendeley Data (<https://doi.org/10.17632/xtjdv38vst.1>). Among the 142 samples in the study, a total of 12,418 macrofauna individuals were identified belonging to 127 different taxa. A total of 71 taxa were found in the intertidal zone and 104 in the subtidal zone with 48 taxa found in both areas. Taxonomic richness was similar in both the Saloum Delta and the Petite Côte with a total of 54 and 51 taxa respectively, and 34 taxa in common.

3.1. Infaunal diversity patterns

Regarding diversity, a strong positive correlation was highlighted between temperature and most indicators of taxonomic and functional diversity in the intertidal zone, especially the Pielou index and functional evenness (FEve; Fig. 2). The same was observed for harvesting on diversity in the intertidal zone. On the contrary, temperature and harvesting had a significant negative impact on abundance and biomass in the intertidal zone. In the same zone, PTEs showed a positive relationship with abundance and biomass, while negatively affecting functional evenness and divergence (FDiv; Fig. 2). In the subtidal zone, median grain size (D50) negatively affected functional divergence, while the percentage of mud negatively affected mostly taxonomic diversity indices. Otherwise, temperature had a positive impact on functional divergence (Fig. 2). Overall, functional and taxonomic diversity were mostly affected by human ecosystem engineering variables and temperature in the intertidal zone, while sediment and variables describing the physical environment (salinity, temperature and depth) appeared as the most important factors for the subtidal zone.

3.2. Disentangling drivers of infaunal community composition and structure

Overall total abundances did not differ between the intertidal zone ($491.26 \pm 575.56 \text{ ind m}^{-2}$; mean $\pm$ SE) and in the subtidal zone ($369.10 \pm 244.50 \text{ ind m}^{-2}$; mean $\pm$ SE) (Kruskal-Wallis test with $p = 0.20$) (Fig. 3). In most of the stations of both zones, Annelida and Mollusca clearly dominated in terms of abundance and biomass (Fig. 3). However, the tidal zones were different in terms of species composition with an average between-group dissimilarity in species composition of 92.35%, as shown by SIMPER analysis. Indeed, Annelida and Mollusca species dominating the areas were different. In the intertidal zone, Annelida were mainly represented by Capitellidae (132 ind m^{-2} ; mean), *Golfingia (Golfingia) vulgaris* (96 ind m^{-2} ; mean) and Nereididae (24 ind m^{-2} ; mean) and Mollusca by bivalves with *Senilia senilis* (109 ind m^{-2} ; mean) and *Loripes orbiculatus* (34 ind m^{-2} ; mean). In the subtidal zone, Annelida were mainly represented by Orbiinidae (52 ind m^{-2} ; mean), Cirratulidae (21 ind m^{-2} ; mean) and Goniadidae (19 ind m^{-2} ; mean) and Mollusca again by bivalves but with *Diplodontia diaphana* (33 ind m^{-2} ; mean), *Senilia senilis* (33 ind m^{-2} ; mean) and *Moerella distorta* (30 ind m^{-2} ; mean). In the intertidal zone, total macrofaunal abundance (Kruskal-Wallis = 64.062, $p < 0.01$; Nemenyi's post-hoc, $p < 0.05$) and biomass (Kruskal-Wallis = 35.643, $p < 0.01$; Nemenyi's post-hoc, $p < 0.05$) were significantly higher at unexploited stations ($Ab = 933.79 \pm 626.34 \text{ ind m}^{-2}$, $Bi = 5.77 \pm 4.63 \text{ gDW m}^{-2}$; mean $\pm$ SE) compared to exploited stations ($Ab = 140.92 \pm 71.99 \text{ ind m}^{-2}$, $Bi = 3.33 \pm 2.46 \text{ gDW m}^{-2}$; mean $\pm$ SE) (Fig. 3). No significant difference was found between the different stations in the subtidal area ($p > 0.05$) (Fig. 3).

Variability among stations has been demonstrated in terms of taxonomic characteristics of macrobenthic communities. To identify factors underlying these differences, nMDS analyses were conducted for the

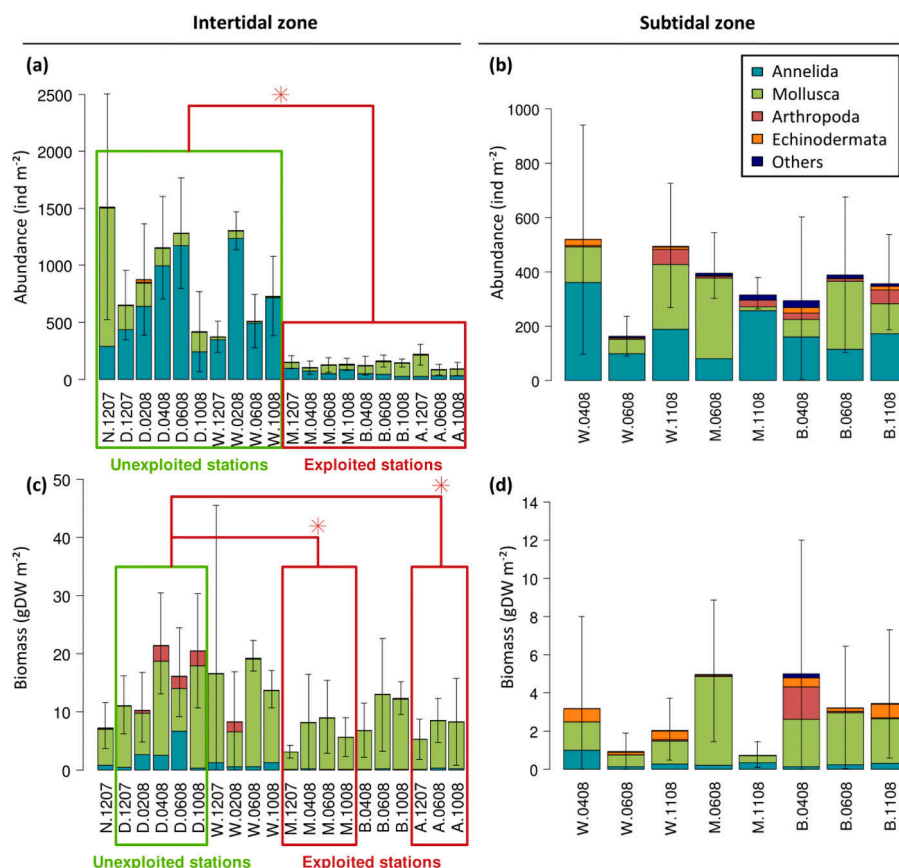


Fig. 3. Mean and standard error abundances [ind m⁻²] (a, b) and biomass [gDW m⁻²] (c, d) of macrofaunal taxa in intertidal zone (a, c) and subtidal zone (b, d) for stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N) and Dionewar (W)) and sampled date (December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)). Other taxa (Others) include Porifera, Cnidaria, Platyhelminthes, Nemertea and Chordata. Red stars indicate significant differences ($p < 0.05$) between stations, based on Kruskal-Wallis tests with Nemenyi's post-hoc tests. Please note the difference in scale between the intertidal and subtidal results. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

intertidal zone (Fig. 4a, c) and for the subtidal zone (Fig. 4b, d). In both tidal zones, nMDS presented stress values of 0.08 corresponding to “good ordinations with no real risk of drawing false inferences”, as explained in Clarke (1993). In the intertidal zone, the nMDS explained 63.56% of the total variability in the community structure (Fig. 4a, c). Specifically, factors having a significant influence on the community structure ($p < 0.05$) were mostly related to human activities with shellfish harvesting ($R^2 = 0.73$) and PTEs (contaminated with Zn, Cu, V, Ag and Pb ($R^2 = 0.77$), with Mn and Cr ($R^2 = 0.46$) and with Cd, Hg and Ni ($R^2 = 0.46$)) (Fig. 4a). Factors related to the physical environment characteristics (temperature ($R^2 = 0.35$), habitat ($R^2 = 0.31$), salinity ($R^2 = 0.11$) and season ($R^2 = 0.06$)) and the sediment properties (D50 ($R^2 = 0.13$), % Mud ($R^2 = 0.09$)) also significantly ($p < 0.05$) contributed to explain macrofaunal communities patterns (Fig. 4a). Clusters showed the major influence of shellfish harvesting (unexploited vs. exploited stations) in explaining the similarities between stations (Fig. 4c). In the subtidal zone, 36.97% of the total variability in the macrofaunal community structure was explained by the nMDS (Fig. 4b,

d). Factors having a significant influence on the subtidal community structure ($p < 0.05$) included physical environmental parameters with salinity ($R^2 = 0.16$), depth ($R^2 = 0.10$) and season ($R^2 = 0.05$) in addition to the sediment median grain size ($R^2 = 0.19$) (Fig. 4b). In the subtidal area, the macrobenthic community was more structured by seasons (Fig. 4d) than by shellfish harvesting.

3.3. Disentangling drivers of infaunal community traits

Regarding traits, both zones were dominated by deposit feeders, burrowers, sediment dwellers and medium-sized animals, whereas the subtidal zone also presented a high proportion in free-living individuals (Fig. 5b and c). Feeding modes were similar in both zones with a dominance of deposit feeders and suspension/filter feeders and the presence of predators/scavengers (Fig. 5b and c). In terms of motility, both zones were dominated by burrowers and crawlers were more abundant in the subtidal zone than in the intertidal (Fig. 5b and c). Dominance in terms of living habitats was balanced between burrow

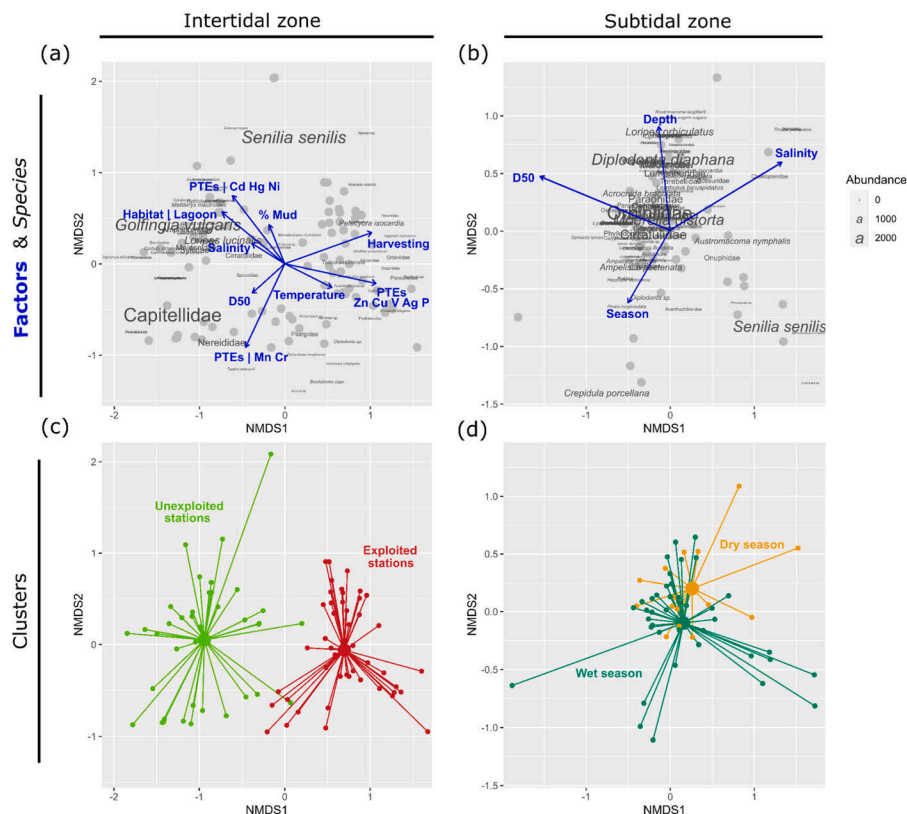


Fig. 4. nMDS ordination of untransformed macrofaunal community data (based on Bray–Curtis similarity) in the intertidal zone (a, c) and subtidal zone (b, d). Fitted environmental variables (a, b) with significant influence on the distribution of stations ($p < 0.05$) (blue arrows), macrofaunal taxa present in the different stations and having a significant influence on the distribution of these stations in the analysis (text in dark grey) and stations (grey points) sampled between December 2007 and November 2008. Clusters revealed by hierarchical clustering analysis based on transformed abundances data (Bray–Curtis), grouping unexploited and exploited samples in the intertidal zone (c) and grouping stations on season in the subtidal zone (d). Exploited stations are indicated in red and unexploited ones in light green, wet season in dark green and dry season in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

dweller and free-living individuals in the subtidal zone, whereas the intertidal zone presented higher proportions of burrow dwellers (Fig. 5b and c). Regarding maximum adult sizes, both areas were dominated by medium-sized individuals with a higher proportion of large individuals in the intertidal zone and the presence of small-sized individuals in the subtidal zone (Fig. 5b and c).

In both intertidal and subtidal zones, the RLQ analysis identified that feeding modes were associated with sediment median grain size (D50) (Fig. 6). More specifically, sediment median grain size (D50) presented a negative significant association with suspension/filter feeders (intertidal zone: $R^2 = -0.41$, $p < 0.05$; subtidal zone: $R^2 = -0.27$, $p < 0.05$) and a positive significant association with deposit feeders (intertidal zone: $R^2 = 0.40$, $p < 0.05$; subtidal zone: $R^2 = 0.33$, $p < 0.05$) (Fig. 6ab). In the subtidal zone, suspension/filter feeders were associated with higher temperatures ($R^2 = 0.23$, $p < 0.05$) and deposit feeders were also associated with other variables (Fig. 6b), indeed presenting a negative significant association with temperature ($R^2 = -0.30$, $p < 0.05$) and positive significant associations with the dry season ($R^2 = 0.29$, $p <$

0.05) (Fig. 6b). Also in both tidal areas, living habits were significantly associated with PTEs (Fig. 6). Stations contaminated with Cd, Hg and Ni were negatively associated with burrow dwellers in the intertidal zone ($R^2 = -0.50$, $p < 0.05$) (Fig. 6a) and in the subtidal stations contaminated with Mn and Cr presented a significant positive association with tubicolous ($R^2 = 0.21$, $p < 0.05$) (Fig. 6b). In the intertidal zone, burrow dwellers were also associated with habitat: the lagoon located in the Petite Côte showed fewer burrow dwellers than the Saloum estuary ($R^2 = 0.42$, $p < 0.05$) (Figs. 5a and 6a). In the subtidal zone, tubicolous individuals were also positively associated with the dry season ($R^2 = 0.24$, $p < 0.05$) (Fig. 6b). Motility was associated with both temperature and salinity in the intertidal zone, crawlers were significantly negatively associated with higher salinity ($R^2 = -0.13$, $p < 0.05$) and positively associated with higher temperature ($R^2 = 0.17$, $p < 0.05$) (Fig. 6a). Higher temperatures in the subtidal zone were associated with larger individuals ($R^2 = 0.25$, $p < 0.05$) (Fig. 6b).

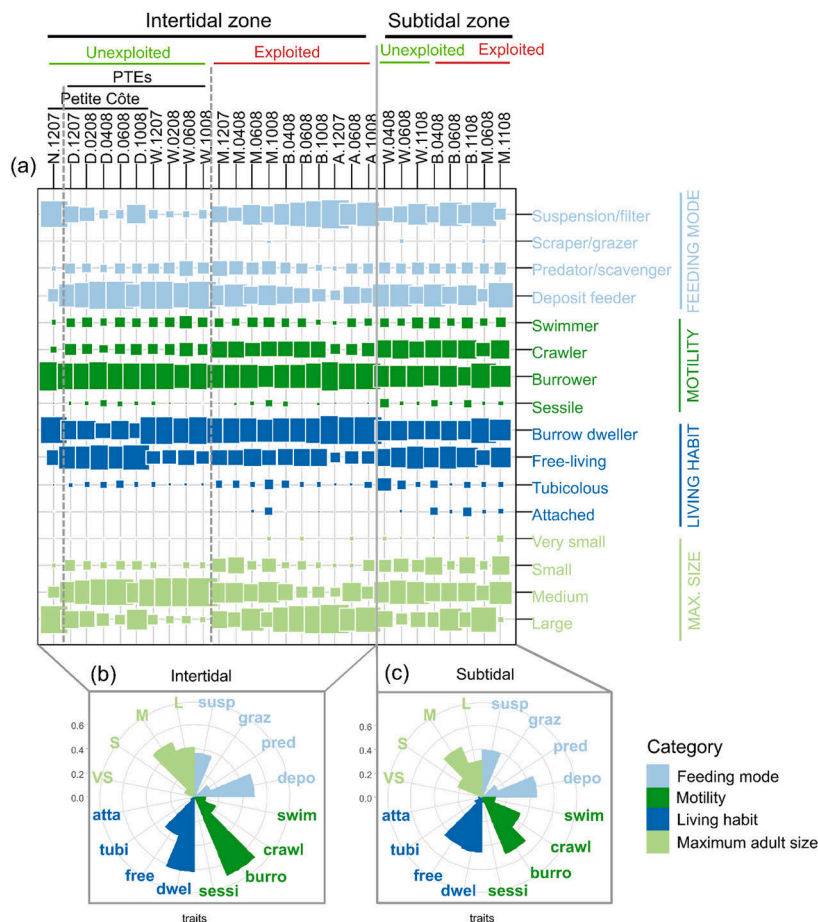


Fig. 5. Mean relative abundance [ind m^{-2} reduced in proportions] of the different traits in sampled stations (Saré Achat (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N), Dionewar (W)) at different sampling data (December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)) in intertidal and subtidal zone. Codes for traits are explained in Table 1.

3.4. Relative importance of drivers of infaunal structural and functional diversity

In the intertidal zone, results of the variance partitioning analysis showed that human ecosystem engineering (here exemplified through harvesting and PTEs) played a more important role in determining the structural and functional diversity than sediment properties and environmental variables (Fig. 7). The variation in structural diversity explained by human ecosystem engineering, sediment properties and environmental variables alone was 33%, 12% and 22%, respectively, and the variation explained in functional diversity was 35%, 9% and 10%, respectively (Fig. 7). In contrast, results of the VPA showed that sediment and environmental variables were the most important variables in the subtidal zone. The variation in structural diversity in this area explained by human ecosystem engineering, sediment properties and environmental variables alone was 4%, 7% and 14%, respectively. Regarding the functional diversity, the variation explained by human ecosystem engineering, sediment properties and environmental

variables alone was 6%, 18% and 22%, respectively (Fig. 7). Overall, drivers of abundance and traits are more explained with our set of variables in the intertidal than in the subtidal zone (Fig. 7).

4. Discussion

To our knowledge, this study is the first in this area to assess the influence of environmental variables and human activities (shellfish harvesting and PTEs) on infaunal community structure and functions through trait-based approaches. So far, studies in Southwest Senegal have mainly focused on fish communities (Diouf, 1996; Ecoutin et al., 2010; Simier et al., 2004), food webs (Faye et al., 2011; Gning et al., 2010), as well as persistent organic pollutants (POPs) and heavy metal contamination in bivalves and gastropods (Bodin et al., 2011, 2013). Only a few studies have focused on the whole invertebrate benthic communities, with the latest studies conducted in 1985 (Ausseil-Badie and Monteillet, 1985; Leung Tack, 1985) and the latest review in 1999 (Le Loeuff, 1999). Infauna data from 2007 to 2008 are thereby valuable

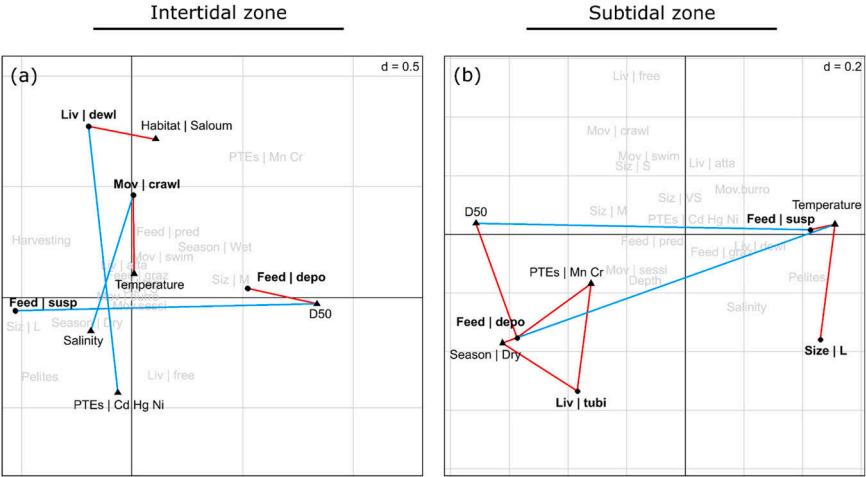


Fig. 6. Ordination biplot of significant ($p < 0.05$) associations identified by the fourth-corner method on the factorial map of RLQ analysis. The values of d give the grid size. Positive significant associations are represented by red lines and negative significant associations by blue lines. Traits are in boldface type and are represented by circles; environmental variables are in lightface type and are represented by triangles. Variables with no significant associations are shown in light grey. P values were adjusted for multiple comparisons using the FDR procedure. Codes for traits and environmental variables are explained in Tables 1 and 2, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

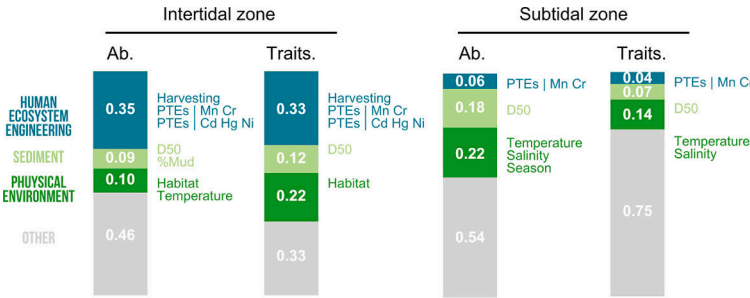


Fig. 7. Variance (adjusted R^2) of the structural (Ab.) and functional (Traits) diversity uniquely attributed to human ecosystem engineering activities (Human ecosystem engineering) (blue), to sediment variables (Sediment) (light green), and to physical environmental variables (Physical environment) (dark green) in the intertidal and subtidal zones. The residual variance is identified as “Other” (grey). Significant variables ($p < 0.05$) included in the variance partitioning are listed on the right side of the corresponding histogram. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

in filling a knowledge gap and constitute a valuable conditions report for follow-up research in this region. With environmental data and infaunal samples collected in two of the main Southern West Senegal mangroves areas, the Sine Saloum and the Petite Côte, the present study identified significant relationships between environmental descriptors and the infaunal community structure and functioning.

Six stations at the mouth of the Saloum Delta and a nearby lagoon of the Petite Côte highlighted a dominance of molluscs and polychaetes in terms of taxonomic diversity, abundance and biomass. This qualitative and quantitative dominance is consistent with previous studies on Senegalese macrofauna (Ausseil-Badie and Monteillet, 1985; Bouchet, 1977; Elouard and Rosso, 1977; Leung Tack, 1985; Seck, 1996; Zabi and Le Loeuff, 1993). Highly open to the sea, poorly supplied in freshwater and subject to hypersaline events during dry season, in addition to presenting high proportions of marine species compared to other marginal coastal ecosystems, the Saloum inverse estuary and the lagoon located at Petite Côte are described in the literature as similar ecosystems. Indeed, Zabi and Le Loeuff (1993) described six main marginal coastal habitats in West Africa based on major geomorphological and hydroclimatic parameters and on benthic communities, and one of their

groupings contained both our study areas. This explains our results showing similar taxonomic dominance and richness in both the Saloum Delta and the Petite Côte with a total of 54 and 51 taxa respectively. However, we also observed differences in taxonomic and trait composition, highlighting “habitat” as a driving factor for infaunal communities in the intertidal zone. Smaller proportions of burrow dwellers were found in the Petite Côte, which is mostly explained by the dominance of the free-living Sipuncula *Golfingia (Golfingia) vulgaris* in communities of the Petite Côte, whereas this taxa was found in low abundances in the Saloum Delta. Despite their overall similarities compared to other marginal coastal ecosystems, Guiral et al. (1999) also highlighted small differences in terms of species composition between the two areas, supporting our results.

Seasonal conditions were expected to be of high importance in explaining macrofaunal community structure and functioning; which was confirmed in the subtidal zone. Our results are consistent with previous studies conducted in the same area (Ausseil-Badie and Monteillet, 1985; Le Loeuff, 1999; Zabi and Le Loeuff, 1993) in the subtidal zone but not in the intertidal zone. Rather than focusing only on seasons, Dirisu and Edwin-Wosu (2022) and P. Li et al. (2022) highlighted the

importance of looking at the impact of human activities in the intertidal zone. Indeed, harvesting and PTEs played a major role in determining the structural and functional diversity in the intertidal zone.

Harvesting of intertidal molluscs (e.g. arks (*Senilia senilis*), mangrove oysters (*Crassostrea tulipa*), *Cymbium* spp., *Murex* spp. and *Conus* spp.) appeared as the main structuring factor for infaunal communities in the intertidal zone with a less significant impact in the subtidal zone. This spatial difference in impact may be due to the shellfish collection methods. Practiced at low tide, the collection was still mostly achieved by walking in the intertidal zone, at the time of the sampling. Sometimes, shellfish were also collected using pirogues allowing harvesters to go deeper and to carry heavier loads and to cross deep “bolongs” (Brenier et al., 2009; Descamps, 1991). Shellfish harvesting inevitably leads to a physical disturbance of the substratum and its associated fauna (Skilleter et al., 2006; Spencer et al., 1998). As a consequence, this human engineering activity has the ability to affect the population structure of marine invertebrates and alter nearshore coastal ecosystems (Kaiser et al., 2001; Leitão and Gaspar, 2007; Rick and Erlandson, 2009; Spencer et al., 1998). In our study, shellfish harvesting practices had indeed implications for a subset of community descriptors, namely abundance, biomass, taxonomic richness and composition. The effects of harvesting is usually causing a reduction of infaunal species number and abundance (Aswani et al., 2015; Dirisu and Edwin-Wosu, 2022; Kaiser et al., 2001; Leitão and Gaspar, 2007; Spencer et al., 1998), which is in line with results highlighted in the present study. Higher abundances, biomass and taxonomic richness were detected in stations permanently or temporarily closed to shellfish harvesting. The expected predominance of small-sized species in harvested areas (Jimenez et al., 2015) was only observed with higher levels of small-sized individuals in our exploited stations, but not detected as significant in the RLQ/Fourth-corner combined analyses.

An additional anthropogenic factor was also highlighted as one of the drivers for the macrofaunal community structure in the intertidal zone: the heavy metals studied by Bodin et al. (2013). In particular, areas with Mn and Cr were characterized by high abundances of Maldanid and Capitellid polychaetes. Being among the largest and deepest-dwelling species (Jacquot et al., 2018; Levin et al., 1997), Maldanid polychaetes are potentially less vulnerable to disturbances, such as PTEs, as opposed to free-living species because they can hide in their fixed tubes (Reise, 2002). Regarding Capitellids, they are well-known indicators of disturbance (Pearson and Rosenberg, 1978) and have been shown to dominate areas with extreme enrichment of heavy metals (Ryu et al., 2011). Capitellidae are also known indicators of organic enrichment (Checon et al., 2021). However, Bodin et al. (2011) found relatively low contamination levels of POPs in the sediments of the Petite Côte and the Saloum Delta, at the same period of time, which did not seem to represent an accurate toxicity threat to marine life. In addition to affecting species composition, PTEs also appeared as one of the factors explaining changes in infaunal community traits, in particular affecting living habits in both tidal areas. Sediment is reported to remarkably retain heavy metals, and thus is considered as especially subject to heavy metal pollution (Bodin et al., 2013). Living within these sediments, infauna is shown to be particularly affected as opposed to epifauna (Piló et al., 2016; Wang et al., 2022). These studies are consistent with our findings highlighting a decrease of infaunal burrow dwellers in areas contaminated with Cd, Hg and Ni, in the intertidal area. As previously mentioned, an increase of tubicolous taxa associated with a contamination with Mn and Cr, in the subtidal zone, can be explained by the capacity of these organisms to hide in their fixed tubes to avoid disturbances (Reise, 2002). On top of affecting living habits, PTEs were highlighted as explaining changes in feeding modes in the subtidal area. Feeding mode is a particularly interesting trait used as a proxy for changes in ecosystem functioning (Cardoso et al., 2004; Carvalho et al., 2011; Gaspar et al., 2009; Mistri et al., 2000). The category “deposit feeders” was dominant in contaminated areas. Many previous studies have shown that the presence of contaminants creates a harsh

environment below the sediment surface affecting mainly deposit feeders, and highlighted the association between this feeding mode and metal-contaminated areas (e.g. Carvalho et al., 2011; Dong et al., 2021; Gaston and Young, 1992; Gusmao et al., 2016; Hu et al., 2019; Nunes et al., 2008; Piló et al., 2015, 2016; Selck et al., 1999). It is important to note that grain size is known to influence feeding modes as well as PTE accessibility, bioavailability, bioaccumulation, concentration, and impact upon a system and individual invertebrates. Correlations have been previously reported between heavy metal concentrations and median grain size (Cabrini et al., 2017; El Tokhi et al., 2015), which is also the case in the present study.

As expected, both median grain size and percentage of fine particles (<63 µm) explained a significant part of the infaunal community structure in both intertidal and subtidal areas. Sediment characteristics are indeed often a significant explanatory factor in macrofaunal taxonomic and trait composition (Anderson, 2008; Jacquot et al., 2018; Mwakisunga et al., 2020). In addition, sediment properties were also associated with specific traits in both tidal zones, showing different proportions in deposit and filter feeders depending on sediment median grain size. Both of these feeding strategies were expected to fluctuate with sediment properties because deposit feeding is usually the dominant feeding strategy in muddy sediments and filter feeders tolerance to fine grained and turbid waters depend on their feeding structure (Shull, 2009; Steele-Petrovic, 1975).

In addition to human ecosystem engineering and sediment properties, variations in temperature and salinity were also highlighted as drivers for traits related to motility, in the intertidal zone. These two parameters are already known as major driving variables for macrofaunal communities (Conde et al., 2013; P. Li et al., 2022; Little et al., 2017; Verdelhos et al., 2015). In particular, studies such as Lam-Gordillo et al. (2022) showed that macrofaunal traits can be linked to fluctuations in salinity. Motile species were, for instance, expected to have a better ability to avoid stressors, such as changes in temperature and salinity, and to be able to recolonize areas by migration (Gogina et al., 2017; Pacheco et al., 2011). In the intertidal zone, crawlers with their relatively high mobility were indeed found in different proportions depending on fluctuations in temperature and salinity. As noted by Dong et al. (2021), this trait is beneficial for macrobenthos to expand their range of activities, increase their access to food, and even help them to escape from disturbances quickly. In the subtidal zone, which is further from human activities, physical environment variables take precedence over human activities occurring on the coast. Season, temperature and salinity appeared as significant structuring factors for infaunal communities and their functioning in the subtidal zone. Our study areas being under periodical severe conditions with hypersaline events during the dry season and potential rainfall events with decrease in salinity and temperature during the wet season, these physical environment variables were expected to impact infaunal communities. The dry season was characterized by higher proportions of tubicolous and deposit feeders, mainly represented by Terrebeldid and Maldanid polychaetes. With their ability to hide in their fixed tubes, such taxa are potentially less vulnerable to anoxic or hypersaline events occurring during the dry season (Reise, 2002). In addition to living habits, feeding modes again appeared as a particularly interesting trait to detect changes in ecosystem functioning, this time in response to seasonal change and temperature variations in the subtidal zone. Large filter feeders (e.g. *Senilia senilis*, *Loripes orbiculatus*, *Diplodonta diaphana*) were associated with high temperatures. Such a result can be explained by the remarkable adaptive response to the environment of some species like *Senilia senilis* (Zabi and Le Loeuff, 1993). Benthic invertebrates are also known to be restricted to specific depths, which can be related to different hydrostatic pressures and food availability (Warwick, 1984). In our area of interest, depth contributed in explaining the infaunal community structure in the subtidal zone. This is consistent with results by Leung Tack (1985), describing mollusc species distribution depending on depths in the Saloum Delta.

These different results helped to characterize infaunal communities in relation to the environment. Shellfish harvesting played a major role in determining the structural diversity in the intertidal zone. This human ecosystem engineering activity also constitutes an important source of income for Senegalese women (Conchedda et al., 2011; Gallup et al., 2020), as well as an important source of animal protein for local populations in West African mangroves. Conchedda et al. (2011) found that the annual revenues from mangrove resources in Senegal accounted for one-third of the gross national income (GNI) per capita, and that the collection and sale of oysters and clams were the top two principal uses of mangrove resources. At the time of sampling, concerns were raised regarding women's abilities to cope with shellfish decline (Bodin et al., 2011, 2013). Subsequently, women in the region have developed resilience strategies based on new socio-economic practices with a diversification in their activities (e.g. ecotourism, agriculture, aquaculture, market gardening, artisanal mining and sale of salt) (Diouf et al., 2020; Sarr, 2005). Considering management measures taken since the present study in addition to a diversification of human activities (Gallup et al., 2020; Sarr, 2005), it would be valuable to study potential changes in infaunal communities since 2008, both in terms of structure and functioning. Regarding future studies, we would also recommend identifying additional relevant parameters, such as measuring organic content, turbidity and oxygen levels. This would be especially interesting regarding the subtidal zone, where the environmental descriptors included in the present study could explain the structural and functional diversity in a much smaller proportion than in the intertidal zone, as seen in the variance partitioning analysis. Sediment and environmental variables were the most important variables in the subtidal zone and these variables will stay valuable to look at especially considering expected challenges related to climate change (e.g. aridification, sea level rise, and decrease in rainfall). In recent years, several studies have utilized a combination of taxonomic and trait-based diversity approaches, which has developed our understanding of ecosystem function and supported efforts for better ecosystem management and conservation (Henseler et al., 2019; Villnäs et al., 2019). The present study is again an example of the interest in using both taxonomy and traits, which is important to keep in mind for future work. Indeed, the effects of heavy metals would not have been highlighted using only a classic taxonomic approach. Like previous studies (Dong et al., 2021), trait composition of benthic infauna was not randomly distributed across communities and can reflect their strategies to respond to anthropogenic and environmental stressors.

5. Conclusion

Based on data collected in 2007–2008, the present study identifies significant relationships between environmental descriptors and the infaunal community structure and functioning in two of the main Southern West Senegal mangroves areas: the Sine Saloum and the Petite Côte. Highly open to the sea and poorly supplied in freshwater, these West African marginal coastal ecosystems are subject to hypersaline events during dry seasons and therefore represent restrictive environments for infaunal communities. As a result, environmental variables characterized by a drastic change in seasons impacted the infaunal communities, especially in the subtidal zone. Closer to anthropogenic disturbances in the intertidal area, pressures related to human ecosystem engineering activities (shellfish harvesting and heavy metals) took precedence over environmental variables in explaining infaunal community structure and trait composition. These results can now serve

for future research, providing both important insights and reference points for the implementation of management measures.

7. Research data for this article

[dataset] Jacquot, M.P., Nordström, M.C., De Wever, L., Ngom Ka, R., Ka, S., Le Garrec, V., Sadio, O., Diouf, M., Grall, J., Tito de Morais, L., Le Loc'h, F., 2023. Infaunal communities and environmental variables in Senegal, West Africa. Mendeley Data, V1, doi: 10.17632/xtjdv38vst.1.

CRediT authorship contribution statement

M.P. Jacquot: Methodology, Investigation, Formal analysis, Data curation, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **M.C. Nordström:** Methodology, Validation, Writing – review & editing. **L. De Wever:** Formal analysis, Data curation, Writing – review & editing. **R. Ngom Ka:** Methodology, Investigation, Data curation, Conceptualization, Writing – review & editing. **S. Ka:** Data curation, Investigation, Methodology, Writing – review & editing. **V. Le Garrec:** Formal analysis, Writing – review & editing. **J. Raffray:** Data curation, Investigation, Methodology, Writing – review & editing. **O. Sadio:** Methodology, Investigation, Data curation, Writing – review & editing. **M. Diouf:** Data curation, Writing – review & editing. **J. Grall:** Formal analysis, Writing – review & editing. **L. Tito de Morais:** Supervision, Resources, Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **F. Le Loc'h:** Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Original data of this study including abundances, biomass, environmental variables and traits are available at Mendeley Data (<https://doi.org/10.17632/xtjdv38vst.1>).

Acknowledgments

This study was part of the project « Femmes et Coquillages » implemented by the Fondation Internationale du Banc d'Arguin (FIBA) and the ENDA-GRAF NGO. Thanks to this project, research was conducted on traditional knowledge and practices in order to contribute to the sustainability harvest of shellfish resources from Sine Saloum and the Petite Côte, while improving management capacities, women's working conditions and living environment, as well as mangrove pollution sources. The authors would like to thank the Senegalese women from Falia and Fadiouth for their valuable help in sampling. We are also grateful to Michel Le Duff (IUEM) for his help with mollusc identification and to Sébastien Hervé (LEMAR/IUEM) for drawing the map and to Simon P. Gaultier for his inputs. MPJ was further supported by the Åbo Akademi University doctoral network FunMarBio, and MCN by the Åbo Akademi University Foundation.

APPENDICES.

Table A.1
General information and coordinates (latitude, longitude) of the sampling stations.

Station	ID	Exploitation	Region	Heavy metals	Town	Latitude	Longitude
Diouham	D	Unexploited	Petite Côte	Cd Hg Ni	Fadiouth	14.15750	−16.83306
Ngoussé	N	Unexploited	Petite Côte	Zn Cu V Ag Pb	Fadiouth	14.14167	−16.80222
Boubo	B	Exploited	Saloum Delta	No	Falia	13.90806	−16.70222
Saré Makalé	M	Exploited	Saloum Delta	No	Falia	13.92667	−16.68056
Dionewar	W	Unexploited	Saloum Delta	Mn Cr	Dionewar	13.88944	−16.73250
Saré Acath	A	Exploited	Saloum Delta	Zn Cu V Ag Pb	Niodior	13.84917	−16.73556

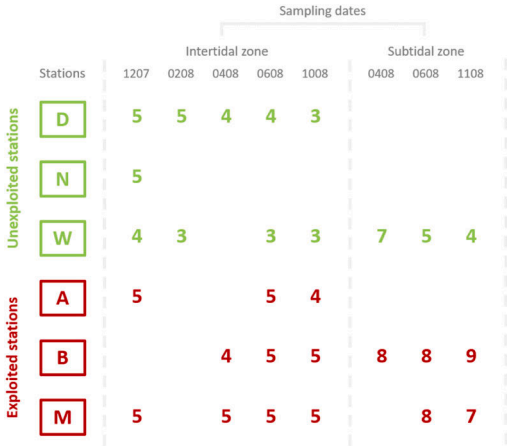


Fig. A.1. Number of samples collected for each station at the different sampling dates (December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)), including six sampling stations in the intertidal zone (A, B, D, M, N, W) and three sampling stations in the subtidal zone (B, M, W). Exploited stations are indicated in red and unexploited ones in green.

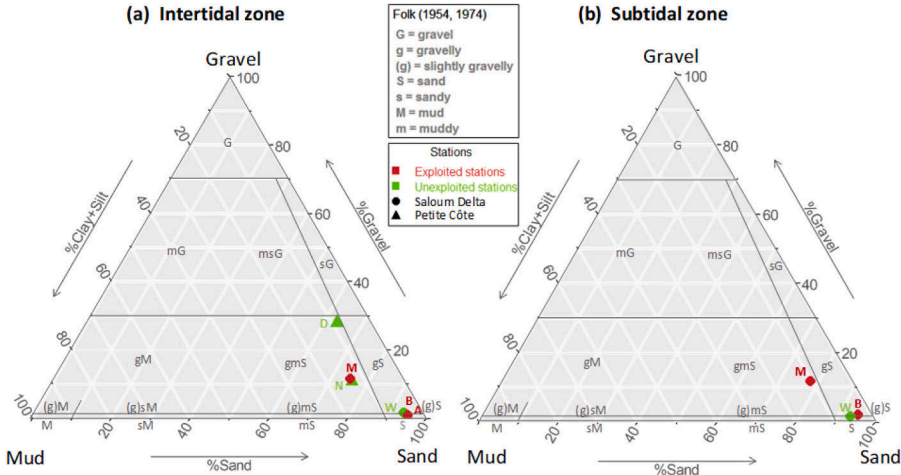


Fig. A.2. Ternary diagram of sediment classification scheme from Folk (1974) for (a) the intertidal area and (b) the subtidal area with the different stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N) and Dionewar (W)) depending on their proportion [%] of gravel, sand and mud (clay + silt). Exploited stations are indicated in red and unexploited ones in green with (●) for stations located in the Saloum Delta and (▲) for those located in the Petite Côte.

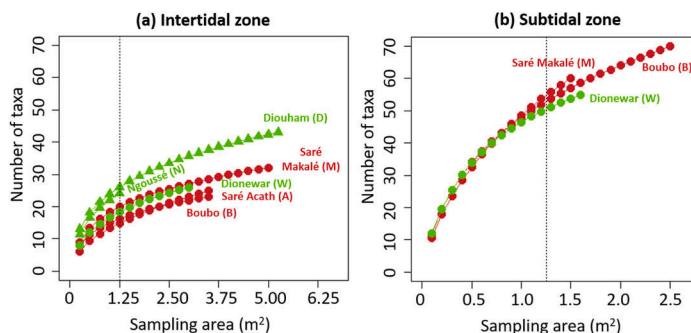


Fig. A.3. Rarefaction curves of the number of taxa depending on the number of samples based on intertidal stations (a) and subtidal stations (b) during December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)) at different stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Nguoussé (N) and Dionewar (W)). Exploited stations are indicated in red and unexploited ones in green with (●) for stations located in the Saloum Delta and (▲) for those located in the Petite Côte.

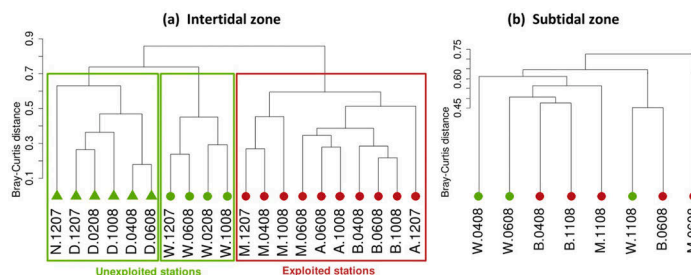


Fig. A.4. Dendrogram based on square-root transformation, Bray-Curtis distances, and group-average hierarchical clustering in the intertidal zone (a) and the subtidal zone (b) during December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)) at different stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Nguoussé (N) and Dionewar (W)). Exploited stations are indicated in red and unexploited ones in green with (●) for stations located in the Saloum Delta and (▲) for those located in the Petite Côte. The SIMPROF test identified three significant clusters ($p < 0.01$) for the intertidal zone (a) and no significant ones for the subtidal zone (b).

References

- Aller, R.C., Aller, J.Y., 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *J. Mar. Res.* 56, 905–936.
- Akoumianaki, I., Papaspyrou, S., Kormas, K.A., Nicolaïdou, A., 2013. Environmental variation and macrofauna response in a coastal area influenced by land runoff. *Estuar. Coast Shelf Sci.* 132, 34–44. <https://doi.org/10.1016/j.eess.2012.04.009>.
- Alongi, D.M., 2002. Present state and future of the world's mangrove forests. *Environ. Conserv.* 29, 331–349. <https://doi.org/10.1017/S0376892902000231>.
- Anderson, M.J., 2008. Animal-sediment relationships re-visited: characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *J. Exp. Mar. Biol. Ecol.* 366, 16–27. <https://doi.org/10.1016/j.jembe.2008.07.006>.
- Aswani, S., Flores, C.F., Broitman, B.R., 2015. Human harvesting impacts on managed areas: ecological effects of socially-compatible shellfish reserves. *Rev. Fish Biol. Fish.* 25, 217–230. <https://doi.org/10.1007/s11160-014-9376-4>.
- Atkinson, D., Sibly, R.M., 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* 12, 235–239. [https://doi.org/10.1016/S0169-5347\(97\)01058-6](https://doi.org/10.1016/S0169-5347(97)01058-6).
- Aussel-Badie, J., Monteillet, J., 1985. Incidence des variations climatiques récentes enregistrées par la microfaune et la malacofaune des estuaires du Sénégal et du Saloum. *Océanogr. Trop.* 20, 151–160.
- Barousseau, J.P., Diop, E.H.S., Saos, J.-L., 1985. Evidence of dynamics reversal in tropical estuaries, geomorphological and sedimentological consequences (Saloum and Casamance Rivers, Senegal). *Sedimentology* 32, 543–552. <https://doi.org/10.1111/j.1365-3091.1985.tb00469.x>.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Berke, S.K., 2010. Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integr. Comp. Biol.* 50, 147–157. <https://doi.org/10.1093/icb/iccq077>.
- Blott, S.J., Pye, K., 2001. Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surf. Process. Landforms* 26, 1237–1248. <https://doi.org/10.1002/esp.261>.
- Bodin, N., N'Gom Ka, R., Le Loc'h, F., Raffray, J., Budzinski, H., Peluhet, L., Tito de Morais, L., 2011. Are exploited mangrove molluscs exposed to persistent organic pollutant contamination in Senegal, West Africa? *Chemosphere* 84, 318–327. <https://doi.org/10.1016/j.chemosphere.2011.04.012>.
- Bodin, N., N'Gom-Ka, R., Kâ, S., Thiaw, O.T., Tito de Morais, L., Le Loc'h, F., Rozuel-Chartier, E., Auger, D., Chiffolleau, J.-F., 2013. Assessment of trace metal contamination in mangrove ecosystems from Senegal, West Africa. *Chemosphere* 90, 150–157. <https://doi.org/10.1016/j.chemosphere.2012.06.019>.
- Bouchet, P., 1977. Distribution des mollusques dans les mangroves du Sénégal. *Malacologia* 16, 67–74.
- Bouillon, S., Connolly, R.M., Lee, S.Y., 2006. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. *J. Sea Res.* 59, 44–58. <https://doi.org/10.1016/j.jseares.2007.05.001>.
- Bourassa, N., Morin, A., 1995. Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *J. North Am. Benthol. Soc.* 14, 393–403. <https://doi.org/10.2307/1467205>.
- Bouso, T., 1996. La pêche artisanale dans l'estuaire du Sine-Saloum (Sénégal) : Approches typologiques des systèmes d'exploitation.
- Boyé, A., Thiébaud, É., Grall, J., Legendre, P., Broudin, C., Houbin, C., Le Garrec, V., Maguer, M., Droual, G., Gauthier, O., 2019. Trait-based approach to monitoring marine benthic data along 500 km of coastline. *Divers. Distrib.* 25, 1879–1896. <https://doi.org/10.1111/ddi.12987>.
- Bremner, J., Rogers, S., Frid, C., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecol. Indic.* 6, 609–622. <https://doi.org/10.1016/j.ecolind.2005.08.026>.
- Brenier, A., Henriques, A., Le Douguet, L., 2009. Des femmes et des coquillages. Expérience d'un projet de conservation dans le Delta du Saloum (Rapport FIBA. ENDA Graf Sahel & IRD).
- Brey, T., 2001. Population Dynamics in Benthic Invertebrates. A Virtual Handbook.

- Brito, J.C., Naia, M., 2020. Coping with sea-level rise in African protected areas: priorities for action and adaptation measures. *Bioscience* 70, 924–932. <https://doi.org/10.1093/biosci/biaa087>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>.
- Cabrini, T.M.B., Barboza, C.A.M., Skinner, V.B., Hauser-Davis, R.A., Rocha, R.C., Saint Pierre, T.D., Valentin, J.L., Cardoso, R.S., 2017. Heavy metal contamination in sandy beach macrofauna communities from the Rio de Janeiro coast, Southeastern Brazil. *Environ. Pollut.* 221, 116–129. <https://doi.org/10.1016/j.envpol.2016.11.053>.
- Cadotte, M.W., Carscadden, K., Mirotnich, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>.
- Cardoso, P.G., Pardal, M.A., Lillebo, A.I., Ferreira, S.M., Raffaelli, D., Marques, J.C., 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *J. Exp. Mar. Biol. Ecol.* 302, 233–248. <https://doi.org/10.1016/j.jembe.2003.10.014>.
- Carvalho, S., Pereira, P., Pereira, F., de Pablo, H., Vale, C., Gaspar, M.B., 2011. Factors structuring temporal and spatial dynamics of macrobenthic communities in a eutrophic coastal lagoon (Obidos lagoon, Portugal). *Mar. Environ. Res.* 71, 97–110. <https://doi.org/10.1016/j.marenvres.2010.11.005>.
- Chapman, M.D., 1987. Women's fishing in Oceania. *Hum. Ecol.* 15, 267–288. <https://doi.org/10.1007/BF00888026>.
- Checon, H.H., Corte, G.N., Silva, C.F., Bicego, M.C., Amaral, A.C.Z., 2021. Using the Capitella complex to investigate the effects of sympatric cryptic species distinction on ecological and monitoring studies in coastal areas. *Mar. Biodivers.* 51, 48. <https://doi.org/10.1007/s12526-021-01185-w>.
- Chevone, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshw. Biol.* 31, 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>.
- Chu, E.W., Karr, J.R., 2013. Environmental impact: concept, consequences, measurement. *Encycl. Biodivers.* 3, 278–296. <https://doi.org/10.1016/B978-0-12-809633-8.02380-3>.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecol.* 18, 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>.
- Conchedda, G., Lambin, E.F., Mayaux, P., 2011. Between land and sea: livelihoods and environmental changes in mangrove ecosystems of Senegal. *Ann. Assoc. Am. Geogr.* 101, 1259–1284. <https://doi.org/10.1080/00045608.2011.579534>.
- Conde, A., Novais, J.M., Dominguez, J., 2013. Interstitial macrofauna and environmental stress at a riverine-marine boundary. *Mar. Environ. Res.* 92, 1–9. <https://doi.org/10.1016/j.marenvres.2013.07.002>.
- Corcoran, E., Ravilious, C., Skuja, M., 2007. Mangroves of western and central Africa, regional seas. In: *UNEP Regional Seas Reports and Studies*. UNEP World Conservation Monitoring Centre : UNEP, Regional Seas Programme, Cambridge, United Kingdom.
- Corte, G.N., Checon, H.H., Shah Esmaeili, Y., Lefcheck, J.S., Amaral, A.C.Z., 2021. Mangrove fragments as key coastal reservoirs of taxonomic and functional biodiversity. *Biodivers. Conserv.* 30, 1573–1593. <https://doi.org/10.1007/s10531-021-02158-y>.
- Costanza, R., d'Arge, R., De Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. <https://doi.org/10.1038/387253a0>.
- D'Alessandro, M., Porporato, E.M.D., Esposito, V., Giacobbe, S., Deidun, A., Nasi, F., Ferrante, L., Auriemma, R., Berto, D., Renzi, M., Scotti, G., Consoli, P., Del Negro, P., Andaloro, F., Romeo, T., 2020. Common patterns of functional and biotic indices in response to multiple stressors in marine harbours ecosystems. *Environ. Pollut.* 259, 113959. <https://doi.org/10.1016/j.envpol.2020.113959>.
- Dauer, D.M., 1993. Biological criteria, environmental health and estuarine macrobenthic community structure. *Mar. Pollut. Bull.* 26, 249–257. [https://doi.org/10.1016/0025-326X\(93\)90063-9](https://doi.org/10.1016/0025-326X(93)90063-9).
- Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Mar. Ecol. Prog. Ser.* 173, 67–83.
- Descamps, C., 1991. La collecte des arches, une activité bi-millénaire dans le Bas-Saloum (Sénégal). In: *Dynamique et Usages de La Mangrove Dans Les Pays Des Rivières Du Sud, Du Sénégal à La Sierra Leone*. IRD Editions, Marseille, pp. 107–113.
- Descroix, L., Sané, Y., Thior, M., Manga, S.-P., Ba, B.D., Mingou, J., Mendy, V., Coly, S., Dièye, A., Badiane, A., Senghor, M.-J., Diedhiou, A.-B., Sow, D., Bouaita, Y., Soumaré, S., Diop, A., Faty, B., Sow, B.A., Machu, E., Montoro, J.-P., Andrieu, J., Vanderveer, J.-P., 2020. Inverse estuaries in West Africa: evidence of the rainfall recovery? *Water* 12, 647. <https://doi.org/10.3390/w12030647>.
- Diop, E.S., Soumaré, A., Diallo, N., Guisse, A., 1997. Recent changes of the mangroves of the Saloum river estuary, Senegal. *Mangroves Salt Marshes* 1, 163–172. <https://doi.org/10.1023/A:1009900724172>.
- Diouf, P.S., 1996. Les peuplements de poissons des milieux estuariens de l'Afrique de l'Ouest : l'exemple de l'estuaire hyperhalin du Sine-Saloum (Thèse de Doctorat). Université de Montpellier II, Montpellier.
- Diouf, A.C., Cissokho, D., Somadjiago, M., 2020. Analyse des stratégies de résilience développées par les femmes du Delta du Saloum (Sénégal) face aux changements climatiques. *Revue Espace Géographique et Société Marocaine* 135–143.
- Dirisu, A.R., Edwin-Wosu, N.L., 2022. Environmental influence on the diversity and composition of benthic macrofauna of asarama estuary at adoni flat in the Niger delta. *Am. J. Mar. Sci.* 10, 1–9. <https://doi.org/10.12691/marine-10-1-1>.
- Dolbeth, M., Cardoso, P.G., Ferreira, S.M., Verdelhos, T., Raffaelli, D., Pardal, M.A., 2007. Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. *Mar. Pollut. Bull.* 54, 576–585. <https://doi.org/10.1016/j.marpolbul.2006.12.005>.
- Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* 3, 143–166. <https://doi.org/10.1007/BF02427859>.
- Donadi, S., Eriksson, B.K., Lettmann, K.A., Hodapp, D., Wolff, J.-O., Hillebrand, H., 2015. The body-size structure of macrobenthos changes predictably along gradients of hydrodynamic stress and organic enrichment. *Mar. Biol.* 162, 675–685. <https://doi.org/10.1007/s00227-015-2614-z>.
- Dong, J.-Y., Zhao, L., Sun, X., Hu, C., Wang, Y., Li, W.-T., Zhang, P.-D., Zhang, X., 2021. Response of macrobenthic communities to heavy metal pollution in Laoshan Bay, China: a trait-based method. *Mar. Pollut. Bull.* 167, 112292. <https://doi.org/10.1016/j.marpolbul.2021.112292>.
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. <https://doi.org/10.1890/13-0196.1>.
- Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Software* 22. <https://doi.org/10.18637/jss.v022.i04>.
- Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412. <https://doi.org/10.1890/08-0349.1>.
- Duke, N.C., Meynecke, J.-O., Dittmann, S., Ellison, A.M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K.C., Field, C.D., Koedam, N., Lee, S.Y., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? *Science* 317, 41–42. <https://doi.org/10.1126/science.317.5834.41b>.
- Ecoutin, J.M., Simier, M., Albaret, J.J., Laë, R., Tito de Morais, L., 2010. Changes over a decade in fish assemblages exposed to both environmental and fishing constraints in the Sine Saloum estuary (Senegal). *Estuarine, Coastal and Shelf Science* 87, 284–292. <https://doi.org/10.1016/j.eess.2010.01.009>.
- El Tokhi, M., Mahmoud, B., Alaabed, S., 2015. Distribution of heavy metals in the bottom sediments of the Arabian Gulf, United Arab Emirates. *Acta Phys. Pol., A* 128. <https://doi.org/10.12693/APhysPolA.128.B-103>. B-103-B-107.
- Elouard, P., Rosso, J.C., 1977. Biogéographie et habitat des mollusques actuels lagunaires du delta du Saloum (Sénégal). *Géobios* 10, 275–299. [https://doi.org/10.1016/S0016-6995\(77\)80094-6](https://doi.org/10.1016/S0016-6995(77)80094-6).
- Faulwetter, S., Markantonatou, V., Pavlou, C., Papageorgiou, N., Keldikoglou, K., Chatzinkolaou, E., Pafilis, E., Chatzigeorgiou, G., Vassileadou, K., Dailianis, T., Panini, L., Koulouri, P., Arvanitidis, C., 2014. Polytraits: a database on biological traits of marine polychaetes. *Biodivers. Data J.* 2, e1024. <https://doi.org/10.3897/BDJ.2.e1024>.
- Faye, D., Tito de Morais, L., Raffray, J., Sadio, O., Thiaw, O.T., Le Loc'h, F., 2011. Structure and seasonal variability of fish food webs in an estuarine tropical marine protected area (Senegal): evidence from stable isotope analysis. *Estuar. Coast Shelf Sci.* 92, 607–617. <https://doi.org/10.1016/j.eess.2011.02.017>.
- Folk, R.L., 1974. Petrology of Sedimentary Rocks. Hemphill Publishing Company, Austin, Texas.
- Gallup, L., Sonnenfeld, D.A., Dahdouh-Guebas, F., 2020. Mangrove use and management within the sine-saloum delta, Senegal. *Ocean Coast Manag.* 185, 105001. <https://doi.org/10.1016/j.ocecoaman.2019.105001>.
- Gaspar, M.B., Carvalho, S., Constantino, R., Tata-Regala, J., Cúrdia, J., Monteiro, C.C., 2009. Can we infer dredge fishing effort from macrobenthic community structure? *ICES (Int. Coun. Explor. Sea) J. Mar. Sci.* 66, 2121–2132. <https://doi.org/10.1093/icesjms/bsp202>.
- Gaston, G.R., Young, J.C., 1992. Effects of contaminants of macrobenthic communities in the upper Calcasieu Estuary, Louisiana. *Bull. Environ. Contam. Toxicol.* 49. <https://doi.org/10.1007/BF00203168>.
- Gerwing, T.G., Cox, K., Allen Gerwing, A.M., Campbell, L., Macdonald, T., Dudas, S.E., Juanes, F., 2020. Varying intertidal invertebrate taxonomic resolution does not influence ecological findings. *Estuar. Coast Shelf Sci.* 232, 106516. <https://doi.org/10.1016/j.eess.2019.106516>.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. *Science* 293, 2248–2251. <https://doi.org/10.1126/science.1061967>.
- Giménez, L., Venturini, N., Kandravicius, N., Hutton, M., Lanfranconi, A., Rodríguez, M., Brugnoli, E., Muniz, P., 2014. Macrofaunal patterns and animal-sediment relationships in Uruguayan estuaries and coastal lagoons (Atlantic coast of South America). *J. Sea Res.* 87, 46–55. <https://doi.org/10.1016/j.seares.2013.12.005>.
- Gning, N., Le Loc'h, F., Thiaw, O.T., Alliaume, C., Vidy, G., 2010. Estuarine resources use by juvenile Flaggfin mojarrá (*Eucinostomus melanopterus*) in an inverse tropical estuary (Sine Saloum, Senegal). *Estuar. Coast Shelf Sci.* 86, 683–691. <https://doi.org/10.1016/j.eess.2009.11.037>.
- Gogina, M., Darr, A., Zettler, M.L., 2014. Approach to assess consequences of hypoxia disturbance events for benthic ecosystem functioning. *J. Mar. Syst.* 129, 203–213. <https://doi.org/10.1016/j.jmarsys.2013.06.001>.
- Gogina, M., Morys, C., Forster, S., Gräwe, U., Friedland, R., Zettler, M.L., 2017. Towards benthic ecosystem functioning maps: quantifying bioturbation potential in the German part of the Baltic Sea. *Ecol. Indic.* 73, 574–588. <https://doi.org/10.1016/j.ecolind.2016.10.025>.
- Gray, J.S., Elliott, M., 2009. Ecology of Marine Sediments from Science to Management, second. Oxford University Press.
- Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M.,

- Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niranjan, S., Winder, M., 2017. The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biol.* <https://doi.org/10.1111/gcb.13642>.
- Guiral, D., Albaret, J.-J., Baran, É., Bertrand, F., Debenay, J.-P., Diouf, P.S., Guillou, J.-J., Lœuff, P.L., Montoroi, J.-P., Sow, M., 1999. Chapitre II. Les écosystèmes à mangrove. In: Cormier Salem, M.-C. (Ed.), *Rivières du Sud*. IRD Éditions, pp. 63–130. <https://doi.org/10.4000/books.irdeditions.4985>.
- Gusmao, J.B., Brauko, K.M., Eriksson, B.K., Lana, P.C., 2016. Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. *Ecol. Indic.* 66, 65–75. <https://doi.org/10.1016/j.ecolind.2016.01.003>.
- Gustin, M.S., Hou, D., Tack, F.M.G., 2021. The term “heavy metal(s)”: history, current debate, and future use. *Sci. Total Environ.* 789, 147951 <https://doi.org/10.1016/j.scitotenv.2021.147951>.
- Gutiérrez, J.L., Jones, C.G., Byers, J.E., Arkema, K.K., Berkenbusch, K., Commuto, J.A., Duarte, C.M., Hacker, S.D., Lambrinos, J.G., Hendriks, I.E., Hogarth, P.J., Palomo, M.G., Wild, C., 2011. Physical ecosystem engineers and the functioning of estuaries and coasts. In: *Treatise on Estuarine and Coastal Science*. Elsevier, pp. 53–81. <https://doi.org/10.1016/B978-0-12-374711-2.00705-1>.
- Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindgren, M., Bonsdorff, E., 2019. Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach. *Estuar. Coast Shelf Sci.* 226, 106272 <https://doi.org/10.1016/j.ecss.2019.106272>.
- Hinchee, E.K., Schaffner, L.C., Hoar, G.C., Vogt, B.W., Batte, L.P., 2006. Responses of estuarine benthic invertebrates to sediment burial: the importance of mobility and adaptation. *Hydrobiologia* 556, 85–98. <https://doi.org/10.1007/s10750-005-1029-0>.
- Hu, C., Dong, J., Gao, L., Yang, X., Wang, Z., Zhang, X., 2019. Macrobenthos functional trait responses to heavy metal pollution gradients in a temperate lagoon. *Environ. Pollut.* 253, 1107–1116. <https://doi.org/10.1016/j.envpol.2019.06.117>.
- Jacquot, M., Dorgan, K., Mortazavi, B., Kleinhuizen, A., Clemon, W., 2018. Macrobenthic community structure and influence on denitrification capacity in soft sediments (Mobile Bay, Alabama, USA). *Mar. Ecol. Prog. Ser.* 605, 17–35. <https://doi.org/10.3354/meps12759>.
- Jennings, S., Pinnegar, J., Polunin, N., Warr, K., 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Mar. Ecol. Prog. Ser.* 213, 127–142. <https://doi.org/10.3354/meps213127>.
- Jimenez, H., Dumas, P., Bigot, L., Ferraris, J., 2015. Harvesting effects on tropical invertebrate assemblages in New Caledonia. *Fish. Res.* 167, 75–81. <https://doi.org/10.1016/j.fishres.2015.02.001>.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jovanovic, Z., Larsen, M., Organo Quintana, C., Kristensen, E., Glud, R., 2014. Oxygen dynamics and porewater transport in sediments inhabited by the invasive polychaete *Marenzelleria viridis*. *Mar. Ecol. Prog. Ser.* 504, 181–192. <https://doi.org/10.3354/meps10737>.
- Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. *Ann. Rev. Mar. Sci.* 7, 497–520. <https://doi.org/10.1146/annurev-marine-010814-020007>.
- Kaiser, M.J., Broad, G., Hall, S.J., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. *J. Sea Res.* 45, 119–130. [https://doi.org/10.1016/S1385-1101\(01\)00052-1](https://doi.org/10.1016/S1385-1101(01)00052-1).
- Kornienko, E.S., 2013. Burrowing shrimp of the infraorders Gebiidea and Axidea (Crustacea: Decapoda). *Russ. J. Mar. Biol.* 39, 1–14. <https://doi.org/10.1134/S1063074013010033>.
- LaBarbera, M., 1989. Analyzing body size as a factor in ecology and evolution. *Annu. Rev. Ecol. Systemat.* 20, 97–117.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305. <https://doi.org/10.1890/08-2244.1>.
- Lam-Gordillo, O., Mosley, L.M., Simpson, S.L., Welsh, D.T., Dittmann, S., 2022. Loss of benthic macrofauna functional traits correlates with changes in sediment biogeochemistry along an extreme salinity gradient in the Coorong lagoon, Australia. *Mar. Pollut. Bull.* 174, 113202 <https://doi.org/10.1016/j.marpolbul.2021.113202>.
- Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. *Global Ecol. Biogeogr.* 23, 726–743. <https://doi.org/10.1111/geb.12155>.
- Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78, 547–562. [https://doi.org/10.1890/0012-9658\(1997\)078\[0547:RBTHST\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2).
- Le Loeuff, P., 1999. La macrofaune d'invertébrés benthiques des écosystèmes à salinité variable le long des côtes atlantiques de l'Afrique tropicale : variations de la biodiversité en relation avec les conditions climatiques actuelles (précipitations) et l'histoire climatique régionale. *Zoosystema* 21, 557–571.
- Leitão, F.M.S., Gaspar, M.B., 2007. Immediate effect of intertidal non-mechanised cockle harvesting on macrobenthic communities: a comparative study. *Sci. Mar.* 71, 723–733. <https://doi.org/10.3989/scimar.2007.71n4723>.
- Leung Tack, D., 1985. La macrofaune benthique. In: *Atelier Régional UNESCO/COMAR (No. 32). Rapport UNESCO sur les Sciences de la Mer, Dakar (Sénégal)*.
- Levin, L., Blair, N., DeMaster, D., Plaia, G., Fornes, W., Martin, C., Thomas, C., 1997. Rapid subduction of organic matter by maldivian polychaetes on the North Carolina slope. *J. Mar. Res.* 55, 595–611. <https://doi.org/10.1357/0022240973224337>.
- Li, C., Wang, H., Liao, X., Xiao, R., Liu, K., Bai, J., Li, B., He, Q., 2022. Heavy metal pollution in coastal wetlands: a systematic review of studies globally over the past three decades. *J. Hazard Mater.* 424, 127312 <https://doi.org/10.1016/j.jhazmat.2021.127312>.
- Li, P., Liu, J., Bai, J., Tong, Y., Meng, Y., Diao, X., Pan, K., Zhu, X., Lin, G., 2022. Community structure of benthic macrofauna and the ecological quality of mangrove wetlands in Hainan, China. *Front. Mar. Sci.* 9, 861718 <https://doi.org/10.3389/fmars.2022.861718>.
- Little, S., Wood, P.J., Elliott, M., 2017. Quantifying salinity-induced changes on estuarine benthic fauna: the potential implications of climate change. *Estuar. Coast Shelf Sci.* 198, 610–625. <https://doi.org/10.1016/j.ecss.2016.07.020>.
- Macdonald, T.A., Burd, B.J., van Roodelaar, A., 2012. Size structure of marine soft-bottom macrobenthic communities across natural habitat gradients: implications for productivity and ecosystem function. *PLoS One* 7, e40071. <https://doi.org/10.1371/journal.pone.0040071>.
- MacFarlane, G.R., Koller, C.E., Blomberg, S.P., 2007. Accumulation and partitioning of heavy metals in mangroves: a synthesis of field-based studies. *Chemosphere* 69, 1454–1464. <https://doi.org/10.1016/j.chemosphere.2007.04.059>.
- Mahe, G., Lienou, G., Desroix, L., Bamba, F., Patureau, J.E., Laraque, A., Meddi, M., Habaieb, H., Adeaga, O., Dieulin, C., Chahnez Kotti, F., Khomsi, K., 2013. The rivers of Africa: witness of climate change and human impact on the environment: HOW climate and human changes impacted river regimes in africa. *Hydrol. Process.* 27, 2105–2114. <https://doi.org/10.1002/hyp.9813>.
- Majer, A.P., Petti, M.A.V., Corbisier, T.N., Ribeiro, A.P., Theophilo, C.Y.S., Ferreira, P.A. D.L., Figueira, R.C.L., 2014. Bioaccumulation of potentially toxic trace elements in benthic organisms of Admiralty Bay (King George Island, Antarctica). *Mar. Pollut. Bull.* 79, 321–325. <https://doi.org/10.1016/j.marpolbul.2013.12.015>.
- MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network.
- Mason, N.W.H., Moullot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional diversity: the primary components of functional diversity. *Oikos* 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- Matthews, D.D., 2002. Integrating women's subsistence fishing into Pacific fisheries conservation. *SPC Women Fish. Inf. Bull.* 11, 13–14.
- Melo, K., dos, R., Tagliaro, C.H., Beasley, C.R., 2013. Seasonal changes in the subtidal benthic macrofauna of a mangrove coast in northern Brazil. *J. Coast Res.* 65, 87–92. <https://doi.org/10.2112/SI65-016.1>.
- Miller-Way, T., Twilley, R.R., 1996. Theory and operation of continuous flow systems for the study of benthic-pelagic coupling. *Mar. Ecol. Prog. Ser.* 140, 257–269. <https://doi.org/10.3354/meps140257>.
- Mistri, M., Fano, E.A., Rossi, G., Caselli, K., Rossi, R., 2000. Variability in macrobenthos communities in the valli di Comacchio, northern Italy, a hypereutrophized lagoonal ecosystem. *Estuarine. Coastal and Shelf Science* 51, 599–611. <https://doi.org/10.1006/ecss.2000.0697>.
- Mouchet, M.A., Villéger, S., Mason, N.W.H., Moullot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules: functional diversity measures. *Funct. Ecol.* 24, 867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>.
- Moullot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>.
- Moullot, D., Spatharis, S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A., Do Chi, T., 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water communities. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 16, 469–482. <https://doi.org/10.1002/aqc.769>.
- Mwakisinga, B., Machiwa, J.F., Pratap, H.B., 2020. Assessment of sediment and benthic macrofauna distribution at dar es salaam harbour channel. *J. Geosci. Environ. Protect.* 133–147. <https://doi.org/10.4236/gep.2020.83010>.
- Nilsen, M., Pedersen, T., Nilssen, E., 2006. Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. *Mar. Ecol. Prog. Ser.* 321, 67–77. <https://doi.org/10.3354/meps321067>.
- Nordström, M., Aarnio, K., Bonsdorff, E., 2009. Temporal variability of a benthic food web: patterns and processes in a low-diversity system. *Mar. Ecol. Prog. Ser.* 378, 13–26. <https://doi.org/10.3354/meps07872>.
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E., 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Mar. Ecol. Prog. Ser.* 332, 11–23. <https://doi.org/10.3354/meps332011>.
- Nunes, M., Coelho, J.P., Cardoso, P.G., Pereira, M.E., Duarte, A.C., Pardal, M.A., 2008. The macrobenthic community along a mercury contamination in a temperate estuarine system (Ria de Aveiro, Portugal). *Sci. Total Environ.* 405, 186–194. <https://doi.org/10.1016/j.scitotenv.2008.07.009>.
- Oksanen, J., Blanchet, G.F., Kindt, R., Legendre, P., O'Hara, R.B., 2011. *Vegan: Community Ecology Package*.
- Olivry, J.-C., 1987. Les conséquences durables de la sécheresse actuelle sur l'écoulement du fleuve Sénégal et l'hypersalinisation de la Basse-Casamance. Presented at the Influence of Climate Change and Climatic Variability on the Hydrologic Regime and Water Resources. In: *Proceedings of the Vancouver Symposium*. IAHs Publisher, Wallingford, UK, Vancouver, BC, Canada.
- Pacheco, A.S., González, M.T., Bremner, J., Oliva, M., Heimlyar, O., Laudien, J., Riascos, J.M., 2011. Functional diversity of marine macrobenthic communities from sublittoral soft-sediment habitats off northern Chile. *Helgol. Mar. Res.* 65, 413–424. <https://doi.org/10.1007/s10152-010-0238-8>.
- Passos, F.D., Domaneschi, O., Sartori, A.F., 2005. Biology and functional morphology of the pallial organs of the Antarctic bivalve *Myssella charcoti* (Lamy, 1906)

- (Galeommatoidae: lasaeidae). *Polar Biol.* 28, 372–380. <https://doi.org/10.1007/s00300-004-0702-5>.
- Pearson, T.H., Rosenberg, R., 1987. Feast and famine: structuring factors in marine benthic communities. In: *Organization of Communities, Past and Present*. Blackwell Scientific Publications, Oxford, pp. 373–395.
- Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Annu. Rev.* 16, 229–311.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625. [https://doi.org/10.1890/0012-9658\(2006\)87\[2614:VPOSDM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2).
- Perus, J., Bonsdorff, E., Bäck, S., Lax, H.-G., Villnäs, A., Westberg, V., 2007. Zoobenthos as indicators of ecological status in coastal brackish waters: a comparative study from the Baltic Sea. *AMBIO A J. Hum. Environ.* 36, 250–256. [https://doi.org/10.1579/0044-7447\(2007\)36\[250:ZAIOS\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[250:ZAIOS]2.0.CO;2).
- Piló, D., Ben-Hamadou, R., Pereira, F., Carrigo, A., Pereira, P., Corzo, A., Gaspar, M.B., Carvalho, S., 2016. How functional traits of estuarine macrobenthic assemblages respond to metal contamination? *Ecol. Indic.* 71, 645–659. <https://doi.org/10.1016/j.ecolind.2016.07.019>.
- Piló, D., Pereira, F., Carrigo, A., Cúrdia, J., Pereira, P., Gaspar, M.B., Carvalho, S., 2015. Temporal variability of biodiversity patterns and trophic structure of estuarine macrobenthic assemblages along a gradient of metal contamination. *Estuar. Coast Shelf Sci.* 167, 286–299. <https://doi.org/10.1016/j.ecss.2015.06.018>.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing.
- Rabaoui, L., El Zrelli, R., Ben Mansour, M., Balti, R., Mansour, L., Tlig-Zouari, S., Guerfel, M., 2015. On the relationship between the diversity and structure of benthic macroinvertebrate communities and sediment enrichment with heavy metals in Gabes Gulf, Tunisia. *J. Mar. Biol. Assoc. U. K.* 95, 233–245. <https://doi.org/10.1017/S0025315414001489>.
- Reise, K., 2002. Sediment mediated species interactions in coastal waters. *J. Sea Res.* 48, 127–141. [https://doi.org/10.1016/S1385-1101\(02\)00150-8](https://doi.org/10.1016/S1385-1101(02)00150-8).
- Rick, T.C., Erlandson, J.M., 2009. Coastal exploitation. *Science* 325, 952–953. <https://doi.org/10.1126/science.1178539>.
- Ryu, J., Khim, J.S., Kang, S.-G., Kang, D., Lee, C., Koh, C., 2011. The impact of heavy metal pollution gradients in sediments on benthic macrofauna at population and community levels. *Environ. Pollut.* 159, 2622–2629. <https://doi.org/10.1016/j.envpol.2011.05.034>.
- Saiz-Salinas, J., Ramos, A., 1999. Biomass size-spectra of macrobenthic assemblages along water depth in Antarctica. *Mar. Ecol. Prog. Ser.* 178, 221–227. <https://doi.org/10.3354/meps178221>.
- Sambou, V., Kébé, C.M.F., Dieve, E.H.B., 2008. Etude sur l'utilisation et la gestion alternative de l'énergie combustible à Fadiouth et dans les îles du Saloum. In: *Fondation Internationale pour le Banc d'Arguin (FIBA)/ENDA GRAF Sahel, Dakar, Sénégal*.
- Sará, M., 1986. Sessile macrofauna and marine ecosystem. *Ital. J. Zool.* 53, 329–337. <https://doi.org/10.1080/11250008609355518>.
- Sarr, O., 2005. Aire marine protégée, gestion halieutique, diversification et développement local: le cas de la réserve de biosphère du Delta du Saloum (Sénégal).
- Schwinghamer, P., 1983. Generating ecological hypotheses from biomass spectra using causal analysis: a benthic example. *Mar. Ecol. Prog. Ser.* 13, 151–166. <https://doi.org/10.3354/meps013151>.
- Seck, A.A., 1996. Le peuplement des mollusques et polychètes du littoral de Dakar (Baies de Hann et de Soumbédioune): impact et conséquences des perturbations du milieu sur la structure (Thèse de Doctorat). Université Cheikh Anta Diop de Dakar, Dakar, Sénégal.
- Selck, H., Decho, A.W., Forbes, V.E., 1999. Effects of chronic metal exposure and sediment organic matter on digestive absorption efficiency of cadmium by the deposit-feeding polychaete *Capitella* species I. *Environ. Toxicol. Chem.* 18, 1289–1297. <https://doi.org/10.1002/etc.5620180631>.
- Shull, D.H., 2009. Bioturbation. In: *Encyclopedia of Ocean Sciences*. Elsevier, pp. 395–400. <https://doi.org/10.1016/B978-012374473-9.00656-1>.
- Simier, M., Blanc, L., Aliaume, C., Diouf, P.S., Albaret, J.J., 2004. Spatial and temporal structure of fish assemblages in an “inverse estuary”: the Sine Saloum system (Senegal). *Estuar. Coast. Shelf Sci.* 59, 69–86. <https://doi.org/10.1016/j.ecss.2003.08.002>.
- Sizmur, T., Campbell, L., Dracott, K., Jones, M., O'Driscoll, N.J., Gerwing, T., 2019. Relationships between Potentially Toxic Elements in intertidal sediments and their bioaccumulation by benthic invertebrates. *PLoS One* 14, e0216767. <https://doi.org/10.1371/journal.pone.0216767>.
- Skilleter, G., Cameron, B., Zharikov, Y., Boland, D., McPhee, D., 2006. Effects of physical disturbance on infaunal and epifaunal assemblages in subtropical, intertidal seagrass beds. *Mar. Ecol. Prog. Ser.* 308, 61–78. <https://doi.org/10.3354/meps308061>.
- Smith, B.D., 2007. The ultimate ecosystem engineers. *Science* 315, 1797–1798. <https://doi.org/10.1126/science.1137740>.
- Spencer, B.E., Kaiser, M.J., Edwards, D.B., 1998. Intertidal clam harvesting: benthic community change and recovery. *Aquacult. Res.* 29, 429–437. <https://doi.org/10.1046/j.1365-2109.1998.00221.x>.
- Steele-Petrovic, H.M., 1975. An explanation for the tolerance of brachiopods and relative intolerance of filter-feeding bivalves for soft muddy bottoms. *J. Paleontol.* 49, 552–556.
- Törnroos, A., Bonsdorff, E., 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecol. Appl.* 22, 2221–2236. <https://doi.org/10.1890/11-2042.1>.
- van der Linden, P., Borja, A., Rodríguez, J.G., Muxika, I., Galparsoro, I., Patrício, J., Veríssimo, H., Marques, J.C., 2016. Spatial and temporal response of multiple trait-based indices to natural- and anthropogenic seafloor disturbance (effluents). *Ecol. Indic.* 69, 617–628. <https://doi.org/10.1016/j.ecolind.2016.05.020>.
- Van Hoey, G., Degraer, S., Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuar. Coast Shelf Sci.* 59, 599–613. <https://doi.org/10.1016/j.ecss.2003.11.005>.
- Verdelhos, T., Marques, J.C., Anastácio, P., 2015. The impact of estuarine salinity changes on the bivalves *Scrobicularia plana* and *Cerastoderma edule*, illustrated by behavioral and mortality responses on a laboratory assay. *Ecol. Indic.* 52, 96–104. <https://doi.org/10.1016/j.ecolind.2014.11.022>.
- Villéger, S., Mason, N.W.H., Moullot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301. <https://doi.org/10.1890/07-1206.1>.
- Villnäs, A., Janas, U., Josefson, A., Kendzierska, H., Nygård, H., Norkko, J., Norkko, A., 2019. Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter. *Mar. Ecol. Prog. Ser.* 622, 31–48. <https://doi.org/10.3354/meps13008>.
- Voß, K., Schäfer, R.B., 2017. Taxonomic and functional diversity of stream invertebrates along an environmental stress gradient. *Ecol. Indic.* 81, 235–242. <https://doi.org/10.1016/j.ecolind.2017.05.072>.
- Walters, B.B., Rönnbäck, P., Kovacs, J.M., Crona, B., Hussain, S.A., Badola, R., Primavera, J.H., Barbier, E., Dahdouh-Guebas, F., 2008. Ethnobiology, socio-economics and management of mangrove forests: a review. *Aquat. Bot.* 89, 220–236. <https://doi.org/10.1016/j.aquabot.2008.02.009>.
- Wang, Q., Shi, S., Liu, X., 2022. Functional diversity of macrofaunal assemblages as indicators to assess heavy metal pollution in the Bohai Sea, China. *Mar. Pollut. Bull.* 185, 114265. <https://doi.org/10.1016/j.marpolbul.2022.114265>.
- Warwick, R.M., 1984. Species size distributions in marine benthic communities. *Oecologia* 61, 32–41. <https://doi.org/10.1007/BF00379085>.
- Warwick, R.M., Clarke, K.R., 1984. Species size distributions in marine benthic communities. *Oecologia* 61, 32–41. <https://doi.org/10.1007/BF00379085>.
- Wei, T., Simko, V., 2017. R Package “Corrplot”: Visualization of a Correlation Matrix.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A., Warren, P., 2005. Body size in ecological networks. *Trends Ecol. Evol.* 20, 402–409. <https://doi.org/10.1016/j.tree.2005.04.005>.
- Zabi, G.S.F., Le Loeuff, P., 1993. Benthic fauna in margino-littoral systems of West Africa, a review Part 2 Fauna and biotopes. *Rev. Hydrobiol. Trop.* 26, 19–51.
- Zabi, G.S.F., Le Loeuff, P., 1994. La macrofaune benthique. In: *Environnement et ressources aquatiques de Côte-d'Ivoire, Tome II : Les Milieux Lagunaires*. Paris, pp. 189–227.
- Zhang, X., Barceló, D., Clougherty, R.J., Gao, B., Harms, H., Tefsen, B., Vithanage, M., Wang, H., Wang, Z., Wells, M., 2022. “Potentially toxic Element”—Something that means everything means nothing. *Environ. Sci. Technol.* 56, 11922–11925. <https://doi.org/10.1021/acs.est.2c03056>.
- Zhong, X., Qiu, B., Liu, X., 2020. Functional diversity patterns of macrofauna in the adjacent waters of the Yangtze River Estuary. *Mar. Pollut. Bull.* 154, 111032. <https://doi.org/10.1016/j.marpolbul.2020.111032>.



Paper II

Jacquot M.P., Snickars M., Bonsdorff E., Nordström M.C.

**Trait responses to direct drivers and effects on
multiple macrofauna-mediated ecosystem functions.**

(submitted to Marine Ecology Progress Series)



Paper III

**Jacquot M.P., Dorgan K.M., Mortazavi B.,
Kleinhuizen A.A., Clemo W.C., 2018.**

**Macrobenthic community structure and influence
on denitrification capacity in soft sediments
(Mobile Bay, Alabama, USA).**

Marine Ecology Progress Series 605: 17–35.

Macrobenthic community structure and influence on denitrification capacity in soft sediments (Mobile Bay, Alabama, USA)

M. P. Jacquot^{1,2,3}, K. M. Dorgan^{1,4,*}, B. Mortazavi^{1,5}, A. A. Kleinhuisen^{1,5}, W. C. Clemo^{1,4}

¹Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, AL 36528, USA

²Université de Bretagne Occidentale, Laboratoire des Sciences de l'Environnement Marin (LEMAR, UMR 6539, UBO/CNRS/IRD/Ifremer), Institut Universitaire Européen de la Mer (IUEM), 29280 Plouzané, France

³Environmental and Marine Biology, Åbo Akademi University, BioCity, Artillerigatan 6, 20520 Åbo, Finland

⁴Department of Marine Sciences, University of South Alabama, Mobile, AL 36688, USA

⁵Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA

ABSTRACT: Benthic macrofauna play important roles in coastal ecosystems through their impact on nutrient cycling and by serving as an important trophic link. This study investigated the influence of environmental stressors on macrofaunal community abundance, biomass and diversity and evaluated impacts of those benthic organisms on nutrient fluxes and denitrification capacity in Mobile Bay, a shallow subtropical estuary in the northern Gulf of Mexico. Between January and May 2016, 22 stations in the lower bay were sampled, and the distance from the sea and sediment characteristics were identified as the principal constraints for macrofaunal distribution and taxonomic composition. Higher diversity of macrofauna was found near the mouth of the bay, likely due to hydrological characteristics of the bay, in addition to distance from anthropogenic disturbances near coasts. Sediments comprised of 60–80% sand showed higher abundances, biomass and diversity compared to muddier or sandier sediments, potentially because these sediments were more stable. Although macrofaunal abundance, biomass and diversity differed across stations in the bay, we did not find a relationship between macrofaunal abundances or biomass and denitrification capacity. Both abundance and biomass of infauna were low in Mobile Bay (<4000 ind. m^{-2} and <5 g DW m^{-2} at most sites) compared to those in previous studies which showed a positive relationship between macrofaunal abundances and denitrification. The lack of the relation between macrofauna and denitrification suggests that a threshold of abundance, biomass and/or burrowing activity is necessary to increase bioturbation or irrigation to sufficient levels to affect denitrification.

KEY WORDS: Benthic macrofauna · Denitrification · Nitrogen flux · Sediments · Community diversity · Environmental stressors · Mobile Bay

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Estuaries are among the most productive ecosystems and provide habitats for many commercially and recreationally important species (e.g. oysters, crabs and shrimp). They are also active sites of sediment organic matter decomposition and associated nutrient regeneration. Benthic macrofauna, especially

deposit-feeders, play an important role in linking organic material with higher trophic levels and alter biogeochemical cycling in sediments through bioturbation and bioirrigation. Due to their restricted mobility, benthic macrofauna have limited ability to avoid environmental and anthropogenic stressors (Pearson & Rosenberg 1978, Dauer 1993), including eutrophication, hypoxia, salinity fluctuations and sedi-

*Corresponding author: kdorgan@disl.org

ment resuspension resulting from storms and tides. As a result, infauna can be particularly impacted by stressors that occur in estuarine ecosystems. Shallow areas subject to episodic storm disturbance are often dominated by opportunistic early colonizers (McCall 1978). Additionally, exposure to hypoxia (oxygen levels below 2 mg l^{-1}) can result in decreased functioning or mortality of benthic macrofauna and alteration in community structure, e.g. increased abundances of opportunists, shifts in species composition and trophic structure (Middelburg & Levin 2009).

Shallow coastal sediments can act as either a source or sink for nutrients. Nutrients regenerated in sediments can be a substantial component of those required for primary production in the water column (Nixon 1981, Fisher et al. 1982, Zimmerman & Benner 1994, Cowan et al. 1996, Fulweiler et al. 2010). Through their activities of feeding, burrowing, irrigation of burrows, excretion of wastes and locomotion, macrofauna can enhance the exchange of materials between the sediment and overlying water column and modify sediment redox conditions (Aller 1982, 1994, Aller & Yingst 1985). Burrow irrigation aerates sediments and increases the area of the oxic–anoxic interface and the transport of ions through the sediment, enhancing nutrient cycling rates (Kristensen et al. 1991, Gilbert et al. 1995). Natural and/or anthropogenic disturbances may influence nutrient fluxes by either disrupting macrofaunal activity or by directly affecting chemical processes (Middelburg & Levin 2009).

Due to their bioturbation, bioirrigation and feeding activities, the presence of macrofauna has been shown to enhance denitrification rates in laboratory experiments. Denitrification, the microbially driven stepwise reduction of nitrate (NO_3^-) to dinitrogen gas (N_2), represents an important nitrogen sink in estuarine systems (Seitzinger 1988) that is subject to complex interactions between organic matter supply, water column nitrate concentrations, sediment properties and bioturbation (Christensen et al. 1990, Risgaard-Petersen et al. 1994, Rysgaard et al. 1994). Increases in coupled nitrification–denitrification (Dn; 3-fold) and water column nitrate-driven denitrification (Dw; 5-fold) were measured in the presence of high densities of the amphipod *Corophium volutator* (19800 ind. m^{-2}) (Pelegri et al. 1994). Similarly, the presence of the amphipod *Monoporeia affinis* (1500 ind. m^{-2}) increased Dn in sediments 1.5-fold (Tuominen et al. 1999), and the polychaete *Nereis* spp. increased Dw 3-fold in estuarine sediments (Nizzoli et al. 2007). This enhancement of denitrification rates can be explained by the increased surface area of the oxic–anoxic transition where coupled ni-

trification–denitrification occurs (Gilbert et al. 1995) and the enhanced supply of water column nitrate into the anoxic sediments (Pelegri et al. 1994, Nizzoli et al. 2007).

Impacts of macrofauna on water–sediment exchanges, and therefore on denitrification rates, vary considerably among taxa, depending on species-specific feeding, ventilation and irrigation modes. Bonaglia et al. (2013) found that oxygenation of anoxic sediment increased denitrification rates, but addition of the deep-burrowing, irrigating spionid polychaete, *Marenzelleria* spp., reduced the enhancement of denitrification (Bonaglia et al. 2013). This reduction in denitrification in the presence of *Marenzelleria* spp. is likely due to enhanced bacterial reduction of sulfate to sulfide in the burrow walls, which can have a toxic effect on nitrifying bacteria, suppressing Dn (Bonaglia et al. 2013). The presence of the polychaete, *Nereis* sp., leads to higher aerobic respiration, Dw, and Dn than bivalves do (*Mya arenaria* and *Cerastoderma* sp.) (Pelegri & Blackburn 1995). This suggests that the impact of macrofauna on denitrification in sediments may depend strongly on the community composition (and traits) and sediment geochemistry, and that disturbances that impact macrofaunal species composition could consequently alter denitrification rates.

As a shallow estuarine ecosystem experiencing high anthropogenic nitrogen loads (Lehrter 2008), Mobile Bay, Alabama, is an ideal system in which to study the macrofaunal influence on sediment denitrification rates. Cowan et al. (1996) showed considerable intra-annual variability in nutrient fluxes and sediment oxygen consumption at a site in Mobile Bay, with variability that was best explained by bottom water dissolved oxygen (DO) concentrations and temperature. Cowan et al. (1996) did not examine macrofaunal communities in their study, and suggested that macrofauna were unlikely to be important because of their small size and therefore low biomass. Species-specific effects on benthic nutrient fluxes and denitrification rates (Pelegri et al. 1994, Tuominen et al. 1999, Nizzoli et al. 2007) have clearly demonstrated direct impacts of benthic organisms on sediment biogeochemistry. However, organisms selected for targeted studies tend to be larger-bodied and motile, i.e. the most likely taxa to impact nutrient fluxes. Moreover, given the dynamic feedbacks between diverse macrofaunal communities and sediment biogeochemistry in the natural environment, it is difficult to extrapolate these results to an ecosystem level such as natural infaunal communities within an estuary (Ferguson & Eyre 2013).

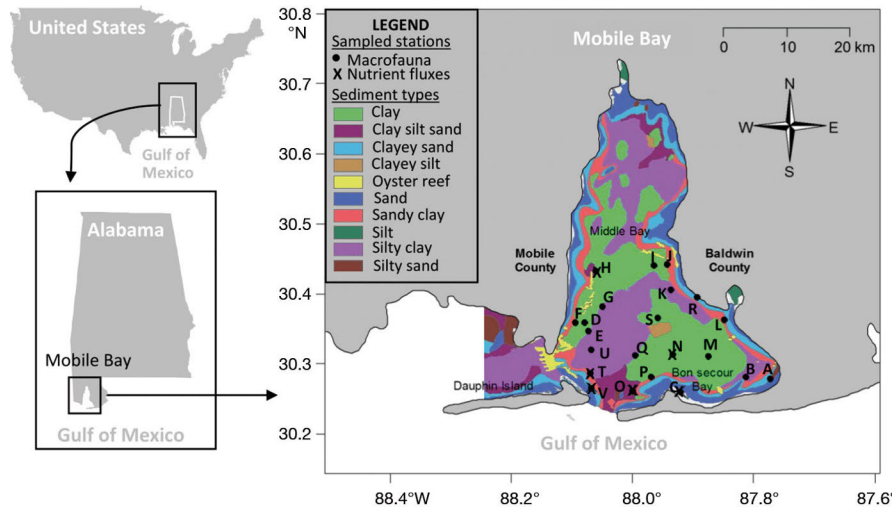


Fig. 1. Location of sampling stations in Mobile Bay covering different sediment types (sediment map based on Esri, HERE, De-Lorm, MapmyIndia, OpenStreetMap contributors and the GIS user community)

Since macrofaunal diversity of soft-sediment habitats within the Mobile Bay is not well studied, with the last survey conducted in 1988 (Dardeau 1988, Clarke & Miller-Way 1992, Stout et al. 1998), the first step of this study was to determine the distribution of macrofauna in the bay. Within this estuary, natural fluctuations in the physical environment play an important role in structuring the soft-sediment habitats (Stout et al. 1998).

This study aimed to determine the impact of location in the bay, sediment type, and potential stressors (bottom water salinity, DO levels) on the abundance, biomass and taxonomic diversity of infaunal communities in the lower region of Mobile Bay. Based on these results, we next evaluated impacts of natural macrofaunal communities with varying abundance and diversity on benthic nutrient fluxes and denitrification. This study therefore aimed to link potential stressors on macrofaunal communities to sediment denitrification rates in a shallow estuarine environment.

MATERIALS AND METHODS

Study area: Mobile Bay, Alabama

Mobile Bay is a shallow estuarine embayment located in the northern Gulf of Mexico (Fig. 1) with an average depth of 3 m and a 14 m deep shipping channel running north-south. The lower part of the bay opens to the Gulf of Mexico and the Mississippi

Sound. Because of the shallow water and variable freshwater inputs, salinity fluctuates dramatically, with strong vertical stratification under moderate to high river discharge and weak winds (Park et al. 2007). The tidal influence in Mobile Bay is small, with an average range of 0 to 20 cm. Mobile Bay experiences hypoxic and anoxic conditions, mostly during the summer months (Park et al. 2007). This study was conducted during predominately normoxic conditions (between January and May 2016).

To characterize variability in the macrofaunal community in Mobile Bay and determine the relationship between community structure and environmental parameters, 22 randomly selected stations were sampled across a range of sediment types in the southern part of Mobile Bay between January and March 2016 (Fig. 1). At each station, temperature, salinity and DO of bottom water were measured with a YSI Multi-parameter probe, and turbidity was measured with a Secchi disk. In the second phase of the study (April–May 2016), based on the initial survey of sediment type and macrofaunal abundance, biomass and diversity of 6 of the initial 22 stations were sampled for nutrient fluxes (Fig. 1).

Sediment analysis

For the initial sampling, bulk sediment samples were collected with a 0.1 m² Petersen grab and haphazardly subsampled for grain size, porosity and car-

bon to nitrogen (C:N) ratio. In the follow-up sampling for nutrient fluxes, sediment cores (95 mm i.d.) were collected and the upper 10 cm was homogenized and analyzed for grain-size, porosity and C:N content. The top 1 cm was sampled for chlorophyll *a* (chl *a*) analysis and frozen for later analysis.

Sediments were treated with a 30% hydrogen peroxide solution to oxidize organic matter prior to grain size analysis. Grain-size analysis followed the pipette method adapted from Folk (1974). Proportions of sand, clay and silt were plotted in a Shepard diagram to characterize the sediment type for each site. Sediment porosity was calculated from the percentage of water in the sediment sampled at each station by weighing sediment before and after drying at 60°C for 24 h. Care was taken to collect sediment that had been brought up in a cohesive clump from the middle of the Peterson grab rather than that near the edges that was often partially fluidized, but porosity measurements from those samples were likely less accurate than those from cores collected by divers during the 2nd sampling phase because of lower disturbance to the sediment during collection. Carbon and nitrogen content of the sediment (% wt) were measured after homogenizing the dried sediment on a CHNSO elemental combustion system analyser (mod. ECS 4010; Costech Analytical Technologies). The molar C:N ratio (mol:mol) was used as a proxy for sediment organic matter quality (Blackburn & Henriksen 1983). Sediment chl *a* content was determined fluorometrically after cold extraction in 90% acetone in triplicate (Welschmeyer 1994).

Macrofaunal sampling

Macrofaunal sampling strategy and laboratory procedures

Benthic infauna were collected using the same Petersen grab used for bulk sediment collection. Three grab samples were taken at each station. Each replicate was treated separately to assess intra-station variability. Sediments were washed through a 500 µm sieve, and retained material was preserved in 95% ethanol and stained with 1% Rose Bengal.

Macrobenthic organisms were removed from all debris, identified and counted. Taxonomic identification was carried out at family level. The wet weight of each taxon for each sample was measured to 0.001 g after blot-drying on tissue paper. Taxa-specific conversion factors provided by Brey (2001) were used to convert wet weight to dry weight.

Macrofaunal community analysis

Macrofauna diversity was assessed using the following primary community variables and diversity indices (Gray & Elliott 2009): abundance, biomass, taxonomic richness (*S*), Shannon's diversity index (*H'*), Pielou's evenness (*J'*) and Simpson's diversity index (1-*D*, hereafter *D*). Before performing statistical tests on these univariate characteristics of macrofaunal α -diversity, all faunal and environmental variables were checked for normality (graphically and using Agostino test) and fourth-root, log or arcsine transformed if necessary. If faunal data did not meet the assumptions for 1-way ANOVA, the Kruskal-Wallis 1-way ANOVA by ranks was used. If significant differences were detected by the test ($p < 0.05$), post-hoc tests for pairwise multiple comparisons (Conover's test) were used to identify differences between pairs of stations.

Hierarchical cluster analysis based on Bray-Curtis distances was applied to abundance and biomass data in order to identify similarities among sites. The same analysis was also applied to diversity metrics *S*, *H'*, *J'* and *D*, but these data were transformed based on Euclidean distances, which is more appropriate for index numbers. An agglomerative procedure was used beginning with discontinuous collection of objects, which were successively grouped into larger and larger clusters until a single, all-encompassing cluster was obtained (Legendre & Legendre 1998). The flexible clustering method proposed by Lance & Williams (1966) was used.

Distance-based redundancy analysis (db-RDA) provides a robust approach to identify the relative influence of different ecological factors in driving community assembly. This method is used for carrying out constrained ordinations on data using Bray-Curtis distances (Legendre & Gallagher 2001). The usual methods for constrained ordinations (canonical correspondence analysis [CCA], RDA) use Euclidean measures, but this distance measure has been found to be inappropriate for some types of data such as contingency tables gathering the species abundances as a function of sites (Legendre & Anderson 1999). db-RDA synthesizes the complete dataset of taxa abundances at different sites with a triplot projection (sites, stations and explaining factors) on 2 axes. This analysis assesses the influence of the following variables on taxa abundances across stations: sand content in sediment, mud composition (clay/clay+silt), sediment C:N ratio, total carbon content, porosity, temperature, salinity, turbidity, depth, dissolved oxygen, distance from the bay mouth, distance from the shore, distance from the channel, distance from fresh-

water input source and sampling date. To determine the significance of the analysis, an ANOVA was conducted (Legendre & Anderson 1999). Permutation tests were then conducted to assess significance of each of the constraint variables (Legendre & Anderson 1999). This last step returns a formula containing only variables with a significant influence on the community structure, independent from each other.

The rarefaction method allows for comparison of the number of species found in different regions when the sampling effort differed. Replication was not sufficient to plot rarefaction curves for individual stations, but rarefaction curves were plotted for aggregated samples from station clusters identified by the db-RDA results. All analyses were performed using R Statistical Software (R Core Team 2013) using the Vegan (Oksanen et al. 2011) and PCNM (Legendre et al. 2013) packages.

Nutrient fluxes and denitrification rates

Sampling strategy

Sampling sites were chosen based on the results obtained in the first part of the study (see Fig. 1, Table 1, Table S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m605p017_supp.pdf). To span the range of variability in Mobile Bay, sites with relatively high, low and intermediate values of abundance, biomass and diversity (*S*) were selected for both mud and sand. Samples were collected over 2 d, with muddy sites on one day and sandy sites on the other. At each of the 6 sites, triplicate sediment cores were collected by divers (18 cores in total) in 95 mm i.d. × 270 mm long clear Plexiglas tubes, retaining approximately 190 mm sediment and 50 mm overlying water. Care was taken to ensure that no air bubbles remained on the inside of the Plexiglas tubes before coring and to select only cores with an undisturbed sediment surface. An additional diver-collected core was processed for sediment analysis. A

150 l sample of bottom water was also collected from each site and used to replenish the overlying water in the core throughout the duration of the laboratory experiment.

Benthic *ex situ* incubation set-up

Cores were transported within 8 h of collection to the laboratory, where they were placed uncapped in buckets with aerated water from the corresponding site in an environmental chamber maintained at the average bottom temperature of the 3 sites. Cores were capped underwater, ensuring that no air bubbles were trapped, and continuous flow of water collected from the site through the cores was established. Overlying water in the core was gently stirred with a magnetic stir bar. Water collected from each site ('inflow') was filtered (0.7 µm), enriched to ~100 µM Na¹⁵NO₃⁻ (99 atom%) and pumped into the overlying water of each core at a flow rate of 1.2 ml min⁻¹ with a multi-channel proportioning pump. The positive displacement of the overlying water forced water through the outflow tubing, which, following a 24 h pre-sampling incubation period, was collected for analyses ('outflow'). Incubations were carried out in the dark to prevent both interference by photosynthetic algae (An & Joye 2001) and air bubble formation, which alters gas concentrations in water (Reeburgh 1969).

Nutrient fluxes

After a 24 h pre-sampling incubation period (Eyre et al. 2002), triplicate water samples for nutrient analysis were collected from the outflow and inflow lines from each core, GF/F filtered and immediately frozen. Nutrient concentrations were analyzed for dissolved inorganic nitrogen (DIN) (NO₂⁻, NO₃⁻, NH₄⁺) and PO₄³⁻ on a Skalar autoanalyzer. Benthic nutrient fluxes (*F*) were calculated using the standard flux equation (Miller-Way & Twilley 1996):

Table 1. Characteristics of selected sites (see Fig. 1) according to sediment type, showing macrofaunal abundance, biomass and taxonomic richness. Data are classified as low, medium and high, and values are mean ± SE

Sediment type	Site	Abundance (ind. m ⁻²)	Biomass (gDW m ⁻²)	Taxonomic richness (no. taxa)
Mud	N	Low (721.98 ± 74.66)	Medium (1.50 ± 0.17)	Medium (11.67 ± 2.08)
	H	Medium (897.99 ± 213.99)	Low (0.27 ± 0.02)	Low (10.00 ± 1.00)
	T	High (1429.60 ± 224.32)	High (2.88 ± 1.32)	High (19.67 ± 1.52)
Sand	C	High (3444.68 ± 568.81)	Medium (3.32 ± 0.44)	Medium (17.00 ± 3.00)
	O	High (2816.09 ± 541.09)	High (16.13 ± 0.96)	High (31.33 ± 4.04)
	V	Low (790.23 ± 12.44)	Low (1.58 ± 0.53)	Medium (18.67 ± 1.53)

$$F = \frac{(C_e - C_i) \times V}{A} \quad (1)$$

where C_e is the outflow concentration (μM), C_i is the inflow concentration (μM), V the flow rate (l h^{-1}) and A the surface area of the sediment (m^2). Nutrient fluxes were measured after $^{15}\text{NO}_3^-$ was added, and this increased nitrate in the water column may have affected fluxes. We opted to measure both fluxes and denitrification simultaneously to minimize the time between collection of sediments and measurement of denitrification rates.

Oxygen concentrations in inflow and outflow water were measured with calibrated microelectrodes and a Unisense multimeter and used to calculate the sediment oxygen demand (SOD). Outflow water overflowed exetainers by $\sim 2.5\times$ the volume immediately before oxygen was measured.

Denitrification

Triplicate samples from the inflow and outflow lines were collected in 12 ml exetainers by overflowing the volume of the vial twice and preserving them with 250 μl of 50 % (w/v) ZnCl_2 . Samples were capped and stored underwater in the environmental chamber until dissolved gas analysis on a membrane inlet mass spectrometer (MIMS). The MIMS was equipped with a copper reduction column set at 600°C to remove oxygen upstream (O_2) (Eyre et al. 2002). Rates of denitrification in the cores were determined following the isotope pairing technique (IPT) (Nielsen 1992) with standard gas concentrations determined by Hamme & Emerson (2004). Denitrification is explicitly calculated from the $^{29}\text{N}_2$ and $^{30}\text{N}_2$ fluxes calculated from dissolved $^{29}\text{N}_2/^{28}\text{N}_2$ and $^{30}\text{N}_2/^{28}\text{N}_2$ measured with the MIMS (Kunu et al. 1998). Denitrification from added $^{15}\text{NO}_3^-$ (D_{15}) was calculated directly:

$$D_{15} = F^{29} + 2 F^{30} \quad (2)$$

where F^{29} and F^{30} represent the steady-state fractions of dissolved $^{29}\text{N}_2$ and $^{30}\text{N}_2$ gas fluxes relative to that of $^{28}\text{N}_2$. *In situ* denitrification from water column $^{14}\text{NO}_3^-$ and $^{14}\text{NO}_3^-$ produced from nitrification (D_{14}) was calculated (to exclude the contribution from added $^{15}\text{NO}_3^-$) according to Nielsen (1992):

$$D_{14} = \frac{F^{29}}{2 F^{30}} D_{15} \quad (3)$$

Total denitrification, henceforth referred to as denitrification capacity, was then calculated as the sum of D_{14} and D_{15} .

Denitrification and benthic fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) were determined from the inflow and outflow concentrations, flow rate, and the surface area of the sediment according to Eq. (1). All rates and fluxes pertaining to N species are expressed on a N atom basis. A positive flux indicates release from the sediments to the water column, and a negative flux indicates uptake by the sediment.

Macrofauna extraction and quantification

At the end of the incubation, the sediment cores were sectioned by depth (0–2 cm, 2–5 cm, 5–10 cm, >10 cm). Each segment was sieved through a 500 μm sieve for macrofauna. Macrofaunal samples were then processed following methods for field samples (see 'Macrofaunal sampling strategy and laboratory procedures'). Additionally, to relate the potential activity of the community to the impact on nutrients, the bioturbation potential index (BP_i) for each taxon and the summed community bioturbation potential index (BP_c) were calculated taking into account the population biomass of each species based on the macrofauna samples and the species' impact on sediment bioturbation through its specific mobility and sediment reworking traits (Solan et al. 2004, Queirós et al. 2013).

Statistical analysis

Pearson product-moment correlation analyses were conducted to determine correlations among parameters. When correlations were significant, linear regressions were plotted. All analysis were performed using R Statistical Software (R Core Team 2013).

RESULTS

Identification of factors structuring benthic infaunal communities

Sediment characteristics in Mobile Bay

Sediment composition in Mobile Bay ranges from sandy in nearshore to muddy throughout much of the bay (Fig. 1, Fig. S1 and Table S1 in the Supplement). Our results (Fig. S1, Table S1) followed published data fairly well (Fig. 1). Muddy sites were more clayey than silty, and sites tended to be mixtures of sand and clay (Fig. S1, Table S1). Organic matter quantity var-

ied from 0.0048 mmol C at the sandiest site near the mouth of the bay (V) to ~0.04 mmol C at silty clay sites (P,Q) in the middle of the bay (Table S1). Organic matter quality (C:N) was fairly consistent (9.6–11.4), except for one sandy site (O) near the mouth of the bay, with C:N = 19.6 (Table S1).

Macrobenthic taxonomic composition

A total of 65 different families of infauna were identified in Mobile Bay, a third of which were Annelida (Table S2). Annelids dominated the abundance and biomass of the macrobenthic community (Fig. 2, Tables S2 & S3), except at Stns O and T, located near the mouth of the bay, where other taxa such as Mollusca and Arthropoda were more abundant. The high biomass of Echinodermata in Stn O was due to a few individual brittle stars (Amphiuridae) and the high biomass of other taxa (others) in Stn L was mostly attributed to Platyhelminthes (Fig. 2b, Table S3).

Differences in abundance (Kruskal-Wallis = 57.253, $p < 0.01$) and in biomass (Kruskal-Wallis = 57.197, $p < 0.01$) were significant among stations (Fig. 2). Macrofaunal abundance ranged from 474 to 3444 ind. m^{-2} (1192 ± 814 ; mean $\pm$ SE) and biomass from 0.27 to 16.13 gDW m^{-2} (2.16 ± 3.28 ; mean $\pm$ SE) (Fig. 2). Significantly higher abundances (Conover's post-hoc, $p < 0.05$) were found in stations composed of 60–80 % sand, and higher biomass (Conover's post-hoc, $p < 0.05$) at Stn O, which had a few large brittle stars (Fig. 2, Tables S2 & S3).

Hierarchical clustering analysis conducted on abundance data grouped sites with similar abundances and species compositions (Fig. 3a). The resulting clusters reflected both sediment characteristics of sites and their locations in the bay. Muddy sites, excluding Stn T at the mouth of the bay, grouped together and formed 2 clusters split by location in the bay (Fig. 3a). Another cluster included coastal sites with 60–80 % sand, and Stn O was distinct from other sites with the highest abundance (Fig. 3a). Hierarchical cluster analysis conducted on biomass data did not show strong

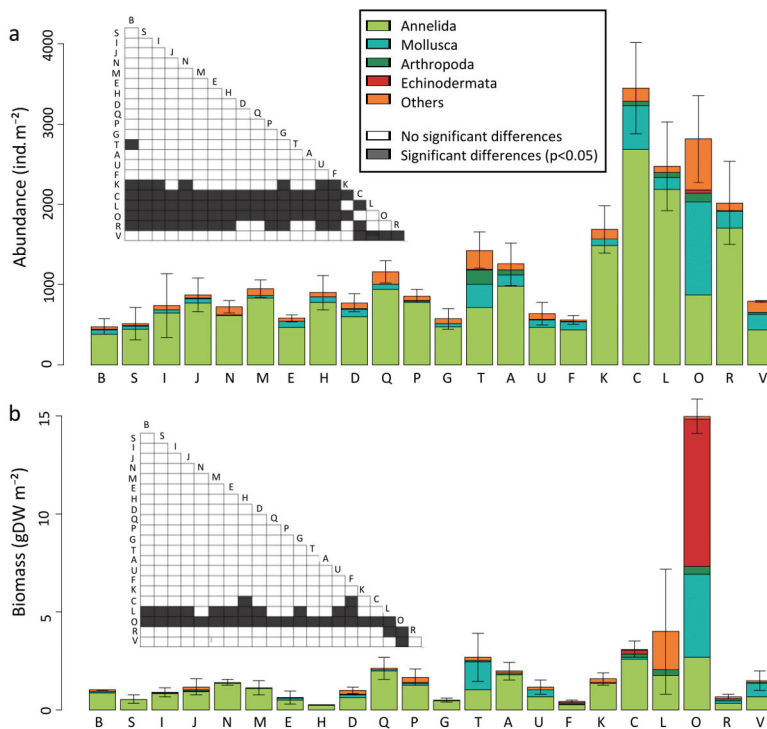


Fig. 2. Mean $\pm$ SE ($n = 3$) (a) abundance and (b) biomass of macrofaunal taxa in Mobile Bay. Other taxa (others) include Cnidaria, Hemichordata, Nemertea, Oligochaeta and Platyhelminthes. Stations are ordered by increasing sand content. The matrix insets show significant differences ($p < 0.05$) between stations, based on Kruskal-Wallis tests with Conover's post-hoc tests

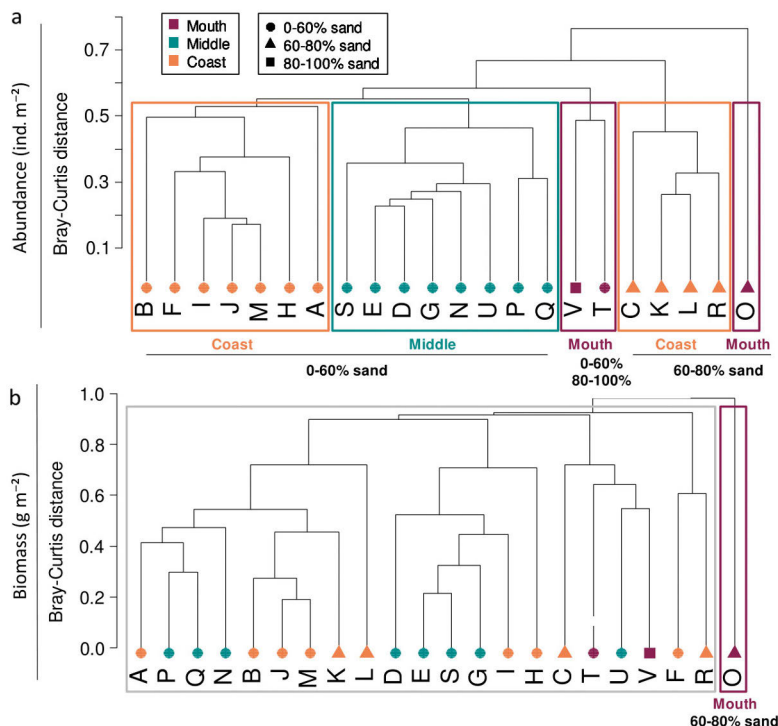


Fig. 3. Dendrogram from group-averaged hierarchical cluster analysis based on Bray-Curtis distances, produced using transformed macrofaunal (a) abundances and (b) biomass (data at 22 sites in Mobile Bay, grouped according to location in the bay (coast, middle, mouth) and sand content). Clusters grouped in the gray box show stations that cannot be explained by sediment characteristics or location in the bay

clustering based on sediment and location, but Stn O was, again, distinct from all other stations (Fig. 3b).

Macrofaunal diversity

The sand content and location in the bay both influenced macrofaunal abundance, biomass and diversity metrics (S , H' , D and J') (Fig. 4, Table S4). There was considerable variability in abundance and biomass within sediment types and locations in the bay (Fig. 4ab). Taxonomic richness ranged from 9 to 35 families (13.76 ± 4.94 ; mean $\pm$ SE) and was higher in stations close to the mouth of the bay (Fig. 4c). Of note is the high taxonomic richness at Stn O (total of 35 families) with 60–80 % sand and near the mouth of the bay (Table S2). H' varied from 1.32 to 2.95 (2.06 ± 0.35 ; mean $\pm$ SE) (Fig. 4d), D varied from 0.52 to 0.92 (0.81 ± 0.09 ; mean $\pm$ SE) (Fig. 4f) and J' varied from 0.52 to 0.94 (0.80 ± 0.10 ; mean $\pm$ SE) (Fig. 4e). Diversity increased from the coastline to the mouth (S , H' ,

D : Coast < Middle < mouth; $p < 0.01$) (Fig. 4c,d,f, Table S4). Lower values of evenness were found in sediments containing 60–80 % sand than in 0–60 % sand (Fig. 4e, Table S4). Despite a differential sampling effort, macrofaunal communities from stations close to the mouth of the bay and containing 60–80 % sand showed a higher taxonomic richness on rarefaction curves (not shown). Diversity metrics were not higher for sites with 60–80 % sand (Fig. 4), so the lack of difference in diversity among sediment types likely resulted from there being more sites with 60–80 % sand near the coast (with lower diversity) than near the mouth (with higher diversity); a more even sampling effort may have shown differences.

Influence of environmental factors on macrobenthic community structure

The db-RDA (Fig. 5) highlights the influence of the sediment characteristics, notably the sand content

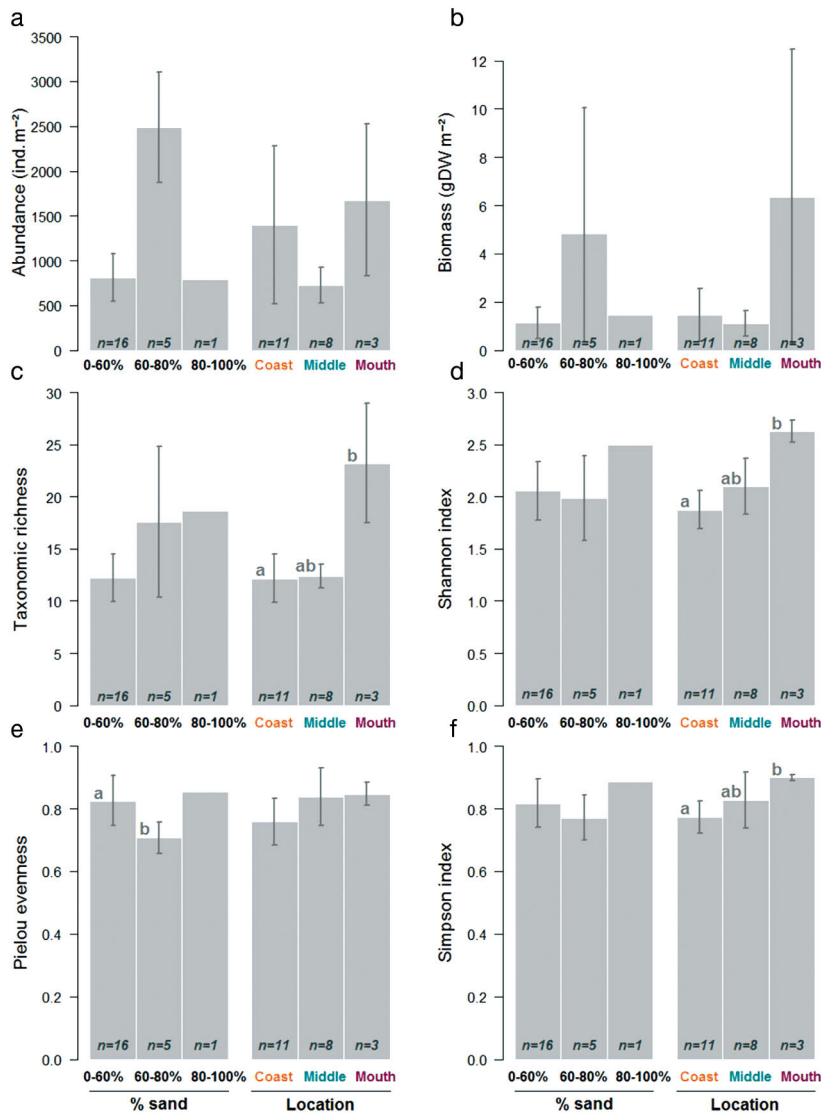


Fig. 4. Mean $\pm$ SE (a) total abundance, (b) total biomass, (c) taxonomic richness, (d) Shannon's diversity, (e) Pielou's evenness, (f) Simpson's diversity index of macrofauna sampled at 22 sites classified depending on their sand content (<60%, 60–80%, >80%) and their location (stations near the coast in orange, stations in the middle of the bay in blue and stations near the mouth of the bay in violet). Different lowercase letters above the bars show significant differences ($p < 0.05$) (Kruskal-Wallis tests with Conover's post-hoc tests). Replicates are pooled together for each station, and numbers of stations (n) are indicated at the bottom of the bars

(Fig. 5a,c) and location in the bay (Fig. 6a,d), on macrobenthic community structure. The ANOVA performed on the db-RDA analysis showed the significance of the results ($p = 0.001$). Permutation tests were conducted to assess the significance of constraints with

fauna abundances as a function of environmental parameters (% sand, distance from the sea, total carbon content, C:N ratio, distance from the channel, salinity, temperature, turbidity, porosity, clay/clay + silt). This analysis showed that the combination of these envi-

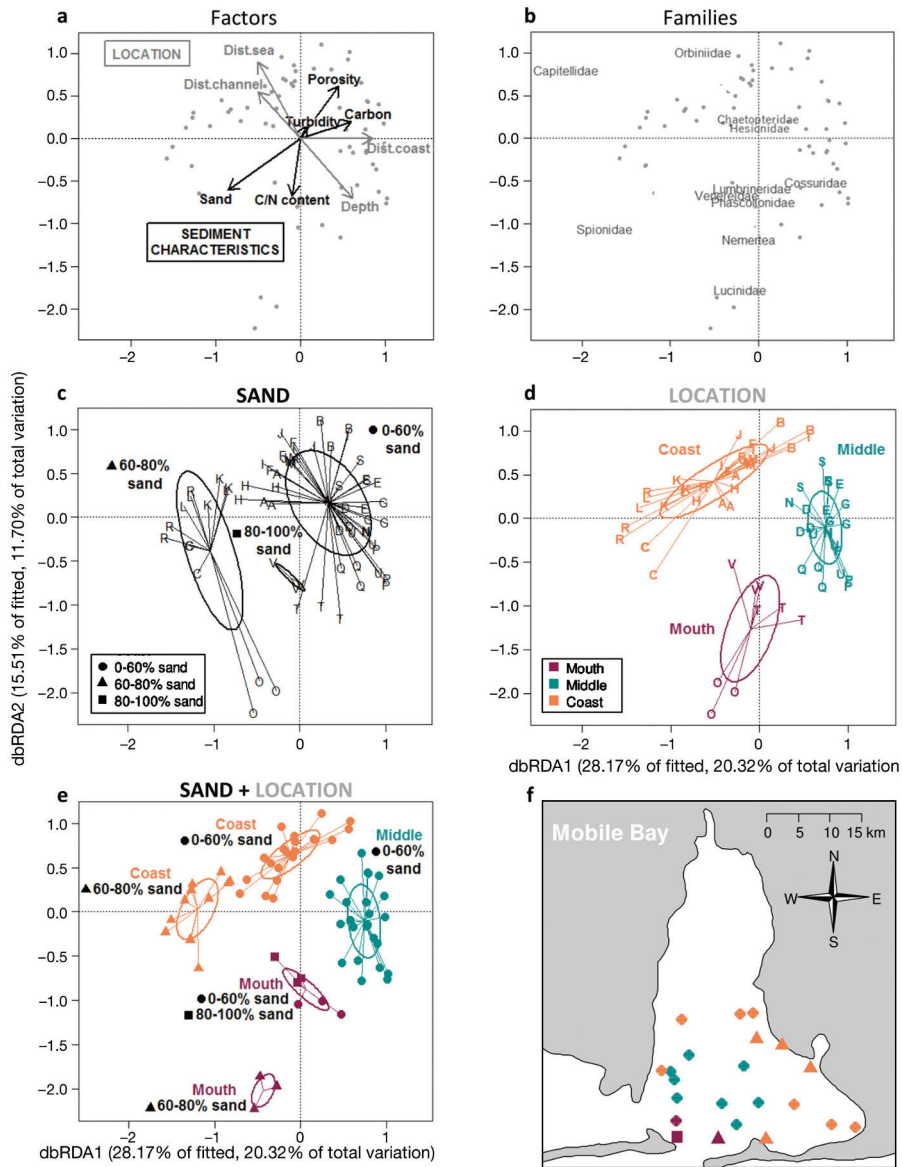


Fig. 5. Distance-based redundancy analysis (db-RDA) resulting from macrobenthos data based on Bray-Curtis similarities. This analysis has been divided into 5 graphs for clarity. (a) Environmental variables with a significant influence on the distribution of sites: distance from the sea (Dist.sea, m), distance from the channel (Dist.channel, m), distance from the coast (Dist.coast, m), water column depth (Depth, m), sand content (Sand, %), C:N content (C/N content, mol mol⁻¹), turbidity (Turbidity, m), porosity (Porosity) and carbon content (Carbon, mol). See Table S1 in the Supplement for additional information on environmental variables. (b) Macrofaunal families present in the different sites and showing a significant influence on the distribution of those sites in the analysis. Possible clusters have been highlighted depending on (c) sand content, (d) location in the bay and (e) the combination of both % sand and location in the bay, revealed by hierarchical clustering analysis based on transformed abundances data (Bray-Curtis). (f) Map showing stations' characteristics in % sand and location in the bay. 43.68 % of fitted and 32.02 % of the total information is summarized with the first 2 axes (dbRDA1 and dbRDA2) (Table S5).

This analysis is significant (ANOVA, $p = 0.001$)

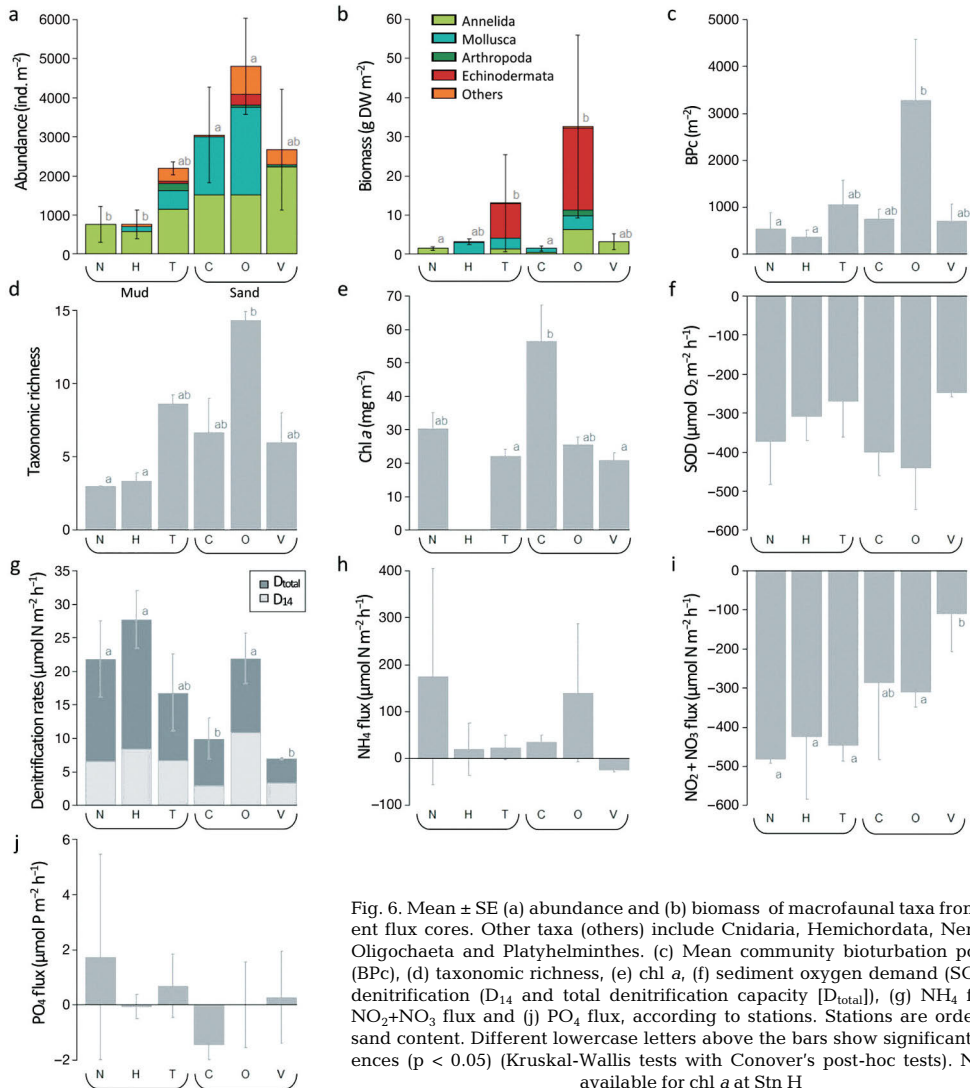


Fig. 6. Mean $\pm$ SE (a) abundance and (b) biomass of macrofaunal taxa from nutrient flux cores. Other taxa (others) include Cnidaria, Hemichordata, Nemertea, Oligochaeta and Platyhelminthes. (c) Mean community bioturbation potential (BPC), (d) taxonomic richness, (e) chl a, (f) sediment oxygen demand (SOD), (g) denitrification (D_{14}) and total denitrification capacity [D_{total}], (h) NH_4 flux, (i) $NO_2 + NO_3$ flux and (j) PO_4 flux, according to stations. Stations are ordered by sand content. Different lowercase letters above the bars show significant differences ($p < 0.05$) (Kruskal-Wallis tests with Conover's post-hoc tests). No data available for chl a at Stn H

ronmental variables explained 62.1% of the variability in community structure (Table S5). Specifically, community structure (Table S2) was significantly influenced by sediment characteristics (Table S1) (sand content: 12.5%, $p < 0.01$; total carbon content: 6.4%, $p < 0.01$; C:N ratio: 5.0%, $p < 0.01$; turbidity: 3.8%, $p < 0.05$; porosity: 3.4%, $p < 0.01$; clay/clay+silt: 2.9%, $p < 0.01$), the location in the bay (distance from the sea: 14.2%, $p < 0.01$; distance from the channel: 4.5%, $p < 0.01$), salinity (5.5%, $p < 0.01$) and temperature (3.8%, $p < 0.01$) (Table S5).

Higher abundances of Spionidae were found in stations with 60–100% sand, whereas Chaetopteridae and Hesionidae were more abundant in stations with 0–60% sand (Fig. 5b,c). Capitellidae and Orbiniidae were particularly abundant in stations located along the coastline, whereas stations close to the mouth of the bay were characterized by the presence of 3 families of annelids (Lumbrineridae, Cossuridae and Phascolionidae [Sipuncula]), a bivalve (Lucinidae) and nemerteans (Nemertea) (Fig. 5b,d). Clusters identified with the hierarchical

cluster analysis were also clearly identified in the db-RDA (Fig. 5e), supporting the combined effects of sediment characteristics and location in the bay explaining the similarities in macrofaunal community structure among sites (Fig. 5f).

Influence of macrofaunal community structure on nutrient fluxes

Patterns of macrofaunal abundance (Fig. 6a) and biomass (Fig. 6b) in cores collected for nutrient fluxes followed those of the earlier sampling (Fig. 2) with the same significant differences among sites (Figs. 6a,b & 2). Absolute values for both abundance and biomass were slightly higher, although the sampling was done later in the spring and sample size was much smaller—a 0.007 m² core rather than the 0.1 m² Petersen grab. Macrofaunal biomass at Stns O and T were largely driven by a few brittle stars (Amphiuridae) (Table S6).

BPC (Fig. 6c) showed a similar pattern to biomass, as expected from the calculation. Both BPC (Fig. 6c) and *S* (Fig. 6d) were higher in Stn O (*RS* = 15, BPC = 3291 ± 1273 m⁻²) than in N (*RS* = 3, BPC = 537 ± 348 m⁻²) and H (*RS* = 3, BPC = 379 ± 132 m⁻²) (Table S7). Highest benthic chl *a* concentrations were found in Stn C and averaged 56.4 ± 10.9 (SE) mg m⁻² (Fig. 6e, Table S7). Due to a problem during sample processing, no chl *a* data for Stn H are available. Higher denitrification rates were measured at the muddy stations, N and H, and the sandy station, O (Fig. 6g). Nitrate (plus nitrite) fluxes were higher in the muddy sites than the sandiest site (V), although these fluxes were likely enhanced by the added nitrate for denitrification measurements (Fig. 6i). Sediment oxygen consumption (Fig. 6f), NH₄⁺ fluxes (Fig. 6h), or PO₄³⁻ fluxes (Fig. 6j) did not differ among sites.

Denitrification capacity (*D*_{total}) and *in situ* denitrification (*D*₁₄) increased with increasing sediment oxygen demand (*r*² = 0.40 and 0.44, respectively, *p* < 0.01) (Fig. S2a,e, Table 2). Neither macrofaunal abundance, biomass, nor BPC, however, were correlated with either *in situ* or total denitrification (Fig. S2b–d, f–h, Table 2) or correlated with any nutrient fluxes (all *p* > 0.05) (Table 2, Fig. S2).

Table 2. Pearson product-moment correlation matrix relating station characteristics to biogeochemical process rates. Correlations in **bold** are significant. Positive values show a positive relationship and negative values a negative relationship. SOD: sediment oxygen demand; BPC: community bioturbation potential. **p* < 0.05, ***p* < 0.01, ****p* < 0.001

	SOD	Fluxes					
		NH ₄ ⁺	NO ₃ ⁻	NO ₂ ⁻	<i>D</i> ₁₄	<i>D</i> _{total}	PO ₄ ⁻
SOD	1.00						
Fluxes							
NH ₄ ⁺	-0.108	1.00					
NO ₃ ⁻	0.270	-0.274	1.00				
NO ₂ ⁻	-0.369	-0.023	-0.514*	1.00			
<i>D</i> ₁₄	-0.660**	0.084	-0.396	0.345	1.00		
<i>D</i> _{total}	-0.631**	0.077	-0.635**	0.416	0.878***	1.00	
PO ₄ ⁻	-0.204	0.091	-0.084	0.309	0.211	0.247	1.00
Bottom water							
Salinity	0.254	0.390	-0.813	0.813	0.252	0.675	0.844
Temp. (°C)	0.300	0.291	-0.841	0.890*	0.315	0.755	0.764
DO (mg l ⁻¹)	-0.159	-0.529	0.623	-0.517	-0.161	-0.458	-0.928
Sediment:							
C:N	-0.620	0.528	-0.024	-0.282	0.807	0.371	-0.028
Chl <i>a</i> (mg m ⁻²)	-0.514	0.007	-0.009	0.031	-0.393	-0.393	-0.695
Macrofauna							
Abundance (ind. m ⁻²)	-0.259	-0.066	0.245	-0.277	0.118	-0.179	-0.200
Biomass (gDW m ⁻²)	-0.038	0.058	-0.036	-0.024	0.410	0.121	-0.136
BPC (m ⁻²)	-0.163	0.084	0.027	-0.083	0.404	0.107	-0.135

DISCUSSION

Macrobenthic community structure depends on sediment characteristics and location in Mobile Bay

Influence of location in the bay on macrofaunal diversity

Macrofaunal abundance and biomass were comparable to samples collected from Mobile Bay in August 1988 (Clarke & Miller-Way 1992). Although abundance and biomass from several of our sites exceeded their ranges of 443–1410 ind. m⁻² and 0.07–0.95 gWW m⁻², respectively, those sites tended to be near coasts or the mouth of the bay, whereas sampling by Clarke & Miller-Way (1992) followed transects across the middle of the bay (cf. Fig. 1 in Clarke & Miller-Way 1992). *S*, *H'* and *J'* were higher but fairly comparable to values determined by Clarke & Miller-Way (1992) (*S* = 7–20, *H'* = 1.11–2.21 and *J'* = 0.39–0.73). These differences could also be due to differences in sampling locations or to lower oxic and thermal stress during the spring in our sampling, but could also represent temporal or inter-annual variability. Our study found high abundances of similar taxa found in the 1988 survey (Clarke & Miller-Way 1992), including polychaetes (Capitellidae, Goniadi-

dae, Pilargidae and Spionidae) and bivalves (Tellinidae) (Table S2).

The lower region of the bay close to the mouth is characterized by the highest diversity, similar to previous sampling (Dardeau 1988, Clarke & Miller-Way 1992). Macrofaunal diversity in the bay is mostly dependent on the distance from the sea, with the discrimination of 3 different zones: along the coastline, in the middle of the bay, and close to the mouth of the bay. Stations along the coastline are characterized by lower diversity and biomass, with communities dominated by a few, small and opportunistic (r-selected) taxa such as capitellids (Tsutsumi 1987) and tolerant orbinids (Kruse et al. 2004) (Fig. 5).

Communities inhabiting more variable environments (e.g. in salinity and temperature) tend to be dominated by high densities of relatively smaller-sized, r-selected species (Flint & Kalke 1985). Even though our time-point measurements of the salinity at our sites were not always higher near the mouth (Table S1), time-averaged salinity shows higher salinities at the mouth of the bay, although with considerable variability depending on rainfall. This salinity gradient has been previously identified as a prevailing structuring factor for benthic communities in Mobile Bay (Clarke & Miller-Way 1992). Salinity has also been shown to affect benthic community structure in Nueces Bay, Texas, USA, with higher biomass and diversity in the higher-salinity region of the bay (Mannino & Montagna 1997). In addition, on sunny days, bottom temperature can increase rapidly in shallow environments, and high bottom temperature can have a negative impact on macrofauna. Located close to freshwater inputs, the shallow-water stations therefore may experience higher variability in salinity and temperature (Flint & Kalke 1985) and therefore higher stress.

Natural stressors associated with the shallow coastal parts of Mobile Bay in which diversity was low may be exacerbated by anthropogenic factors. Coastal development and shoreline modification in Mobile Bay have led to the transformation of 38% of the bay's shoreline into engineered structures (vertical walls and revetments) (Jones et al. 2009). Approximately 93% of the shoreline is experiencing erosion (Jones et al. 2009), and a loss of at least 5 to 10 ha of intertidal habitat has been estimated in this microtidal bay (Douglass & Pickel 1999). Moreover, as a transitional area between land and sea, estuaries receive large amounts of pollutants derived from urban, agricultural, industrial and domestic waste effluents (Lillebø et al. 2005, Paerl 2006). Coastal habitat alteration, release of pollutants from coastal

development, and low salinity and high temperatures with high variability in both salinity and temperature may all contribute to stressful living conditions for macrofaunal communities.

The extent to which a marine species is able to penetrate into an estuary depends primarily on the amount and variability of the freshwater discharge relative to the tidal inflow of seawater (Ysebaert et al. 1993). The combination of small tidal ranges and long tidal periods that characterize Mobile Bay is expected to produce weak tidal currents at the estuary mouth (Stigebrandt 1977, Lee et al. 2013). In addition, the shape of the mouth of Mobile Bay has the potential to support gyre formation on both sides (Lee et al. 2013) that can oxygenate and keep higher salinity levels in the area close to the mouth as well as transport and retain larvae from outside of the bay. Larval transport patterns and reduced variability in oxygen, salinity and temperature are potential factors explaining the higher diversity of taxa near the mouth, including the polychaetes Lumbrineridae and Phascolionidae, ophiuroids, and bivalves (e.g. Lucinidae, Pandoridae).

Influence of sediment characteristics on macrofaunal abundance, diversity and taxonomic composition

Whereas diversity showed a clear geographic pattern within Mobile Bay, macrofaunal abundances and taxonomic composition appear to depend more on sediment characteristics, including sand content as well as quantity and quality of the organic matter, porosity and turbidity. Benthic soft-sediment organisms generally show strong relationships with the grain-size characteristics of the sediments they inhabit (Gray 1974). Sediment characteristics are a significant explanatory factor in the taxonomic composition of northern Gulf of Mexico infaunal communities (Coblentz et al. 2015). Highest macrofaunal abundances are found in 60–80% sand, which are likely more stable environments than fine, easily resuspended muds. As sandier sediments are more highly oxygenated environments, they may be favored by macrofauna over organic-rich muds when hypoxic events occur with some frequency (Flint & Kalke 1985, Wilson et al. 2008). Interestingly, the site with highest sand content had lower abundances and diversity, suggesting a non-linear relationship between community structure and sediment grain size, with a peak at intermediate sand content. More sites with higher sand contents would be needed to determine

the relationship between sediment type and community structure, but this pattern is consistent with previous studies (Van Hoey et al. 2004, Anderson 2008). In the North Sea, macrofauna show maximum abundances at 5.8% mud and decrease with increasing median grain size and decreasing mud content (Van Hoey et al. 2004). Optimum percentage mud for most abundant macrofaunal taxa is estimated to $17.3 \pm 11.8\%$ in Auckland (New Zealand) which is equivalent to a range from 70.9 to 94.6% sand (Anderson 2008). In Neuces Bay, abundance and diversity were higher in >50% sand than in muds but did not, however, differ between 50–75% and 75–100% sands (Mannino & Montagna 1997). This may reflect sediment stability resulting from a combination of cohesion by muds and compaction by heavier sand grains or a trade-off between oxygenated sands and higher food content of organic muds.

Macrofaunal abundance and biomass do not significantly impact nutrient fluxes in Mobile Bay

We hypothesized that the differences in macrofaunal abundance, biomass and diversity observed in Mobile Bay would result in differences in nutrient fluxes and denitrification. Although macrofauna have been shown to affect denitrification in laboratory experiments (Svensson et al. 2001, Bonaglia et al. 2013), the present study did not show a relationship between natural macrofaunal abundances or biomass and nutrient fluxes in Mobile Bay.

There was no detectable impact of the macrofauna on nutrient and oxygen fluxes. Fluxes of ammonium, phosphate and SOD were within ranges of reported values for Mobile Bay (Cowan et al. 1996), Weeks Bay, a sub-estuary of Mobile Bay (Mortazavi et al. 2012), and other Gulf of Mexico estuaries (Twilley et al. 1999). SOD is low in these systems compared to many other estuaries, with the majority of organic matter processing occurring in the water column (Mortazavi et al. 2012). However, because the water column was enriched with $^{15}\text{NO}_3^-$ (~100 μM), nitrate + nitrite fluxes were much higher than previously measured fluxes in Mobile Bay (–14 to 67 $\mu\text{mol N m}^{-2} \text{ h}^{-1}$) or in Weeks Bay (–30 $\mu\text{mol N m}^{-2} \text{ h}^{-1}$). Interestingly, only a fraction of the nitrate + nitrite uptake by the sediments was denitrified, suggesting that most of the N uptake by the sediments is retained within the sediments either through dissimilatory nitrate reduction to ammonium (DNRA) or assimilation by microorganisms. While we do not have the data to address the role of DNRA in this system, these results

are consistent with the findings of Hou et al. (2012), who used a mass balance for sediments in a Texas estuary to show that 50–70% of the sediment uptake of $^{15}\text{NO}_3^-$ was assimilated by microorganisms.

Numerous laboratory studies have shown species-specific effects on benthic fluxes by comparing inhabited sediments with a control of defaunated cores (Pelegrini et al. 1994, Tuominen et al. 1999, Karlson et al. 2005, Nizzoli et al. 2007, Bonaglia et al. 2013) (Table 3). This approach helps to understand direct impacts of benthic organisms on processes by quantifying the impacts of an active burrower or irrigator such as nereid polychaetes (Henriksen et al. 1980, Sayama & Kurihara 1983, Kristensen & Blackburn 1987, Kristensen et al. 1991, Gilbert et al. 1995, 1998) and corophium amphipods (Henriksen et al. 1980, Pelegrini et al. 1994, Rysgaard et al. 1995, Gilbert et al. 1998) but differences do not necessarily represent fluxes driven by natural assemblages. Several studies, however, have also found enhancement of denitrification and nutrient fluxes from sediments with higher densities of infauna compared to lower-density sediments (Table 3). Communities studied by Engelsen et al. (2008) and Van Colen et al. (2012), enhanced nutrient fluxes at high densities, but at abundances that were much higher than those in Mobile Bay (>35 000 versus <4800 ind. m^{-2}) (Table 3). Macrofaunal abundances in the present study were similar to those measured in Mobile Bay (Dardeau 1988, Clarke & Miller-Way 1992), as well as in Perdido Bay, a nearby estuary (Flemer et al. 1998), and the coastal northern Gulf of Mexico (Baustian & Rabalais 2009, Engle et al. 2009). These low macrofaunal abundances in Mobile Bay and nearby regions that also experience fluctuating oxygen and salinity may be insufficient to substantially influence nutrient fluxes. The idea that there may be a threshold in macrofaunal abundance above which denitrification and nutrient fluxes are enhanced but below which the impact is low is supported by results from a controlled experimental and modeling study by Gilbert et al. (2003). Their aim was to determine the influence of macrofaunal density on sedimentary denitrification by simulating different distances between oxygenated burrow centers using sediment plugs of different thicknesses immersed in aerated seawater reservoirs (Gilbert et al. 2003). Highest denitrification/nitrification occurred for the intermediate plug thickness representing burrow spacing of 5000 ind. m^{-2} of large animals (burrow radius of 5 mm), likely because this density allows both O_2 flux from burrows and NH_4^+ flux from anoxic zones between burrows to fuel nitrification. Thicker plugs correspon-

Table 3. Summary of macrofaunal impact on nutrient fluxes in different experimental conditions and with variation in abundance, biomass and community bioturbation potential (BPC). Y: yes; N: no; blank: absence of information. I: impact on denitrification rate but calculation of the stimulation rate not possible with available data; F: denitrification rate not measured but impact on other nutrient fluxes shown; X: no impact on denitrification rate or other nutrient fluxes shown. See Gilbert et al. (1998) and Karlson et al. (2005) for additional information on denitrification stimulation rate

Bioturbating organism	Abundance (ind. m ⁻²)		Biomass (gWW m ⁻²)		BPC (m ⁻²)		Control used (defaunated sediment)	Denitrification stimulation rate (%)	Source
	Min.	Max.	Min.	Max.	Min.	Max.			
Laboratory									
<i>Oligochaeta</i>	0	12000					Y	180	Chatarpaul et al. (1980)
<i>Nereis virens</i>	0	2000					Y	171	Henriksen et al. (1980)
<i>Nereis virens</i>	0	1810					Y	240	Kristensen & Blackburn (1987)
<i>Nereis virens</i>	0	875					Y	300	Kristensen et al. (1991)
<i>Nereis diversicolor</i>	0	1430					Y	114	Gilbert et al. (1995)
<i>Nereis</i> sp.	0	2000					Y	500	Pelegrí & Blackburn (1995)
<i>Hediste japonica</i>	0	1000					Y	300	Sayama & Kurihara (1983)
<i>Corophium volutator</i>	0	6000					Y	161	Henriksen et al. (1980)
<i>Corophium volutator</i>	0	19800					Y	300 to 500	Pelegrí et al. (1994)
<i>Monoporeia affinis</i>	0	1500					Y	866	Tuominen et al. (1999)
<i>Monoporeia affinis</i>	0	5000					Y	141	Karlson et al. (2005)
<i>Mya arenaria</i>	0	1100					Y	163	Pelegrí & Blackburn (1995)
<i>Cerastoderma</i> sp.	0	1100					Y	254	Pelegrí & Blackburn (1995)
<i>Macoma baltica</i>	0	1200					Y	253	Karlson et al. (2005)
Field									
<i>Corophium</i> spp.	300	9000					N	950	Rysgaard et al. (1995)
Assemblage	0	3160					Y	160 to 529	Gilbert et al. (1998)
Assemblage (high nereids abundances)	0	1130					N	I	Ferguson & Eyre (2013)
Assemblage	0	70000					N	I	Van Colen et al. (2012)
Assemblage	1800	35350	5	180			N	F	Engelsen et al. (2008)
Assemblage (high maldanids abundances)	500	7000			100	6000	N	I	McTigue et al. (2016)
Assemblage	527	4600	17	412	100	5500	N	I	Braeckman et al. (2014)
Assemblage	430	4800	7	107	379	3291	N	X	Present study

ding to lower densities of 1600 and 400 ind. m⁻² did not differ in denitrification, likely because both were limited by NO₃⁻, which was formed closer to the sediment–water interface, rather than at the oxic–anoxic boundary around burrow walls, and thus more likely to diffuse to the water column. These results are consistent with a minimum density, in this case between 1600 and 5000 large burrows, being necessary to substantially enhance denitrification rates.

Macrofaunal abundance is not the only factor that needs to be taken into account. The burrow spacing predicted by Gilbert et al. (1998) to enhance denitrification near the maximum of the range of abundances found in Mobile Bay, and other studies have shown an influence of macrofauna on nutrient fluxes at abundances comparable to this study (Ferguson & Eyre 2013, Braeckman et al. 2014). Differences in biomass and taxonomic composition are likely important as well. However, we found no relationship between denitrification and nutrient fluxes and either biomass or BPC. BPC depends heavily on biomass (and therefore, unsurprisingly, shows a similar trend in our study) but includes species mobility and sediment reworking traits (Solan et al. 2004, Queirós et al. 2013) and therefore would be more likely to correlate with nutrient fluxes. High macrofaunal biomass at a couple of sites in Mobile Bay was driven by a few individual brittle stars (Table S6). Brittle stars have been shown to increase the sediment release of nitrite and nitrate with higher densities (Wood et al. 2009). All other individuals, however, are small, limiting their bioturbation impact.

At abundances similar to those found in Mobile Bay, an active burrower such as *Corophium* spp. enhances denitrification rates, in contrast to our findings for the macrofaunal community of Mobile Bay (cf. Fig. 7 of Rysgaard et al. 1995). A macrofaunal community including high abundances of taxa that irrigate deep burrows or actively bioturbate sediments may have a greater impact on denitrification. Potentially, the fewer bioturba-

tors in the community, the greater the abundance that would be needed to have an impact. Functionally contrasting species of macrofauna stimulate microbial nitrogen transformations to different extents or can even decrease denitrification (Bonaglia et al. 2014): for instance, impacts on oxygen and nutrient fluxes by shallow biodiffusers (*Cerastoderma edule*) are much less than those by deeper gallery-diffusers (*Corophium volutator* and *Nereis diversicolor*) (Mer-millod-Blondin et al. 2004).

Microbial processing should be higher in muddy sediments with higher organic content than in sand, potentially explaining the higher levels of denitrification in muds in this study (Figs. 6g & S2a–h) (Deutsch et al. 2010, Braeckman et al. 2014). The one sandy site with higher denitrification rates, O (Fig. 6g), also had much higher biomass than the other 2 sandy sites (Fig. 6b). Higher macrofaunal biomass could potentially explain the high denitrification, however; if biomass were driving denitrification, we would expect to also see higher SOD at that site (Fig. 6f). SOD is often used as a proxy for the quality of the organic matter that is being remineralized (Eyre et al. 2013a). It is somewhat surprising that SOD did not differ between muddy and sandy sites (Fig. 6f), although the organic matter quantity and quality did not differ substantially between the sandy and muddy sites (Table S1). The higher denitrification rates at sites with higher SOD, but a lack of correlation between denitrification and the macrofauna abundance or biomass, is consistent with prior investigations suggesting that the quality of the organic matter is a major driver of denitrification rates (Eyre et al. 2013b, Fulweiler et al. 2013).

One of the sandy sites near the bay mouth (Stn O), however, appears to be an outlier in the bay with higher macrofaunal abundance, biomass, diversity and denitrification rates. All replicates have fairly high denitrification rates (Fig. S2). The core that had the highest denitrification rate had the lowest abundance at this site but contained a large tube-building worm (Polychaeta: Maldanidae) (Table S6). Not only do maldanids irrigate their burrows, but *in situ* tracer experiments revealed that maldanids can rapidly subduct freshly deposited algal carbon and inorganic materials to at least 10 cm below the surface (Levin et al. 1997). As a result of this transport, relatively fresh organic matter becomes available to deep-dwelling microbes rapidly after deposition. Both aerobic and anaerobic processes may be enhanced by maldanid activity (Levin et al. 1997), which therefore has the potential to impact nutrient fluxes. *Maldane sarsi* at high densities (5057 ± 484 ind. m^{-2}) and high BPC

in shallow Arctic shelf sediments contribute to enhanced denitrification (McTigue et al. 2016). However, based on the results of the first part of the present study, this family of polychaetes appears to be rare in the bay (Table S2).

This study shows that, given unfavorable abundance, biomass and/or bioturbation or irrigation activity, an enhancement of fluxes by benthic macrofauna does not become measurable or statistically detectable. In this study, it seems that small numbers of burrows associated with low biomass result in macrofauna not being a predominant factor to explain variability of nutrient fluxes and denitrification rates in the bay. Our community analysis suggests that sandy-mud sites and those near the mouth of the bay with higher macrofaunal abundance and diversity are the most promising regions for future study to determine whether seasonal or environmental variables interact with macrofaunal community structure to impact nutrient cycling. However, on a bay-wide scale, our study indicates rather that physical processes and microbial communities drive nutrient cycling in Mobile Bay.

Acknowledgements. Research reported in this manuscript was supported by an Early-Career Research Fellowship to K.M.D from the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine. The content is solely the responsibility of the authors and does not necessarily represent the official views of the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine. Thanks to the support of the international mobility of the LabexMER, a cluster of Excellence funded by the French 'Investment for the future' program, supported by the French Ministry of Research and Education (reference ANR-10-LabX-19-01). We are very grateful to Grant Lockridge, Sarah Frankenberg, Ryan Parker and Alex Leynse for their help in the field. We also thank Steve Dykstra for help with Fig. 1.

LITERATURE CITED

- Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tevesz MJ (eds) Animal-sediment relations. Plenum Press, New York, NY, p 53–102
- ✦ Aller RC (1994) Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chem Geol* 114:331–345
- ✦ Aller RC, Yingst JY (1985) Effects of the marine deposit-feeders *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia), and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates, and microbial distributions. *J Mar Res* 43:615–645
- ✦ An S, Joye SB (2001) Enhancement of coupled nitrification-denitrification by benthic photosynthesis in shallow estuarine sediments. *Limnol Oceanogr* 46:62–74
- ✦ Anderson MJ (2008) Animal-sediment relationships revisited: characterising species' distributions along an en-

- vironmental gradient using canonical analysis and quantile regression splines. *J Exp Mar Biol Ecol* 366:16–27
- ✦ Baustian MM, Rabalais NN (2009) Seasonal composition of benthic macroinfauna exposed to hypoxia in the northern Gulf of Mexico. *Estuaries Coasts* 32:975–983
- ✦ Blackburn TH, Henriksen K (1983) Nitrogen cycling in different types of sediments from Danish waters. *Limnol Oceanogr* 28:477–493
- ✦ Bonaglia S, Bartoli M, Gunnarsson JS, Rahm L and others (2013) Effect of reoxygenation and *Marenzelleria* spp. bioturbation on Baltic Sea sediment metabolism. *Mar Ecol Prog Ser* 482:43–55
- ✦ Bonaglia S, Nascimento FJA, Bartoli M, Klawonn I, Brüchert V (2014) Meiofauna increases bacterial denitrification in marine sediments. *Nat Commun* 5:5133
- ✦ Braeckman U, Foshtomi MY, Van Gansbeke D, Meysman F, Soetaert K, Vincx M, Vanaverbeke J (2014) Variable importance of macrofaunal functional biodiversity for biogeochemical cycling in temperate coastal sediments. *Ecosystems* 17:720–737
- ✦ Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. <http://www.thomas-brey.de/science/virtualhandbook>
- ✦ Chatarpaul L, Robinson JB, Kaushik NK (1980) Effects of tubificid worms on denitrification and nitrification in stream sediment. *Can J Fish Aquat Sci* 37:656–663
- ✦ Christensen PB, Nielsen LP, Sørensen J, Revsbech NP (1990) Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism. *Limnol Oceanogr* 35:640–651
- ✦ Clarke D, Miller-Way T (1992) An environmental assessment of the effects of open-water disposal of maintenance dredged material on benthic resources in Mobile Bay, Alabama. US Army Engineer Waterways Experiment Station, Vicksburg, MS
- ✦ Coblenz KE, Henkel JR, Sigel BJ, Taylor CM (2015) Influence of sediment characteristics on the composition of soft-sediment intertidal communities in the northern Gulf of Mexico. *PeerJ* 3:e1014
- ✦ Cowan JLW, Pennock JR, Boynton WR (1996) Seasonal and interannual patterns of sediment-water nutrient and oxygen fluxes in Mobile Bay, Alabama (USA): regulating factors and ecological significance. *Mar Ecol Prog Ser* 141:229–245
- ✦ Dardeau MR (1988) Mobile Bay trend station infaunal macroinvertebrates (winter 1987; spring 1988): life history and environmental requirements. Technical report 88-004. Dauphin Island Sea Lab, Dauphin Island, AL
- ✦ Dauer DM (1993) Biological criteria, environmental health and estuarine macrobenthic community structure. *Mar Pollut Bull* 26:249–257
- ✦ Deutsch B, Forster S, Wilhelm M, Dippner JW, Voss M (2010) Denitrification in sediments as a major nitrogen sink in the Baltic Sea: an extrapolation using sediment characteristics. *Biogeosciences* 7:3259–3271
- ✦ Douglass SL, Pickel BH (1999) The tide doesn't go out anymore—the effect of bulkheads on urban shorelines. *Shore Beach* 67:19–25
- ✦ Engelsen A, Hulth S, Pihl L, Sundbäck K (2008) Benthic trophic status and nutrient fluxes in shallow-water sediments. *Estuar Coast Shelf Sci* 78:783–795
- ✦ Engle VD, Hyland JL, Cooksey C (2009) Effects of Hurricane Katrina on benthic macroinvertebrate communities along the northern Gulf of Mexico coast. *Environ Monit Assess* 150:193–209
- ✦ Eyre BD, Rysgaard S, Dalsgaard T, Christensen PB (2002) Comparison of isotope pairing and N₂:Ar methods for measuring sediment denitrification—assumption, modifications, and implications. *Estuaries* 25:1077–1087
- ✦ Eyre BD, Maher DT, Squire P (2013a) Quantity and quality of organic matter (detritus) drives N₂ effluxes (net denitrification) across seasons, benthic habitats, and estuaries. *Global Biogeochem Cycles* 27:1083–1095
- ✦ Eyre BD, Santos IR, Maher DT (2013b) Seasonal, daily and diel N₂ effluxes in permeable carbonate sediments. *Biogeosciences* 10:2601–2615
- ✦ Ferguson A, Eyre B (2013) Interaction of benthic microalgae and macrofauna in the control of benthic metabolism, nutrient fluxes and denitrification in a shallow subtropical coastal embayment (western Moreton Bay, Australia). *Biogeochemistry* 112:423–440
- ✦ Fisher TR, Carlson PR, Barber RT (1982) Sediment nutrient regeneration in three North Carolina estuaries. *Estuar Coast Shelf Sci* 14:101–116
- ✦ Flemer DA, Kruczynski WL, Ruth BF, Bundrick CM (1998) The relative influence of hypoxia, anoxia, and associated environmental factors as determinants of macrobenthic community structure in a northern Gulf of Mexico estuary. *J Aquat Ecosyst Stress Recovery* 6:311–327
- ✦ Flint RW, Kalke RD (1985) Benthos structure and function in a south Texas estuary. *Contrib Mar Sci* 2:33–53
- ✦ Folk RL (1974) Petrology of sedimentary rocks. Hemphill Publishing Company, Austin, TX
- ✦ Fulweiler RW, Nixon SW, Buckley BA (2010) Spatial and temporal variability of benthic oxygen demand and nutrient regeneration in an anthropogenically impacted New England estuary. *Estuaries Coasts* 33:1377–1390
- ✦ Fulweiler R, Brown S, Nixon S, Jenkins B (2013) Evidence and a conceptual model for the co-occurrence of nitrogen fixation and denitrification in heterotrophic marine sediments. *Mar Ecol Prog Ser* 482:57–68
- ✦ Gilbert F, Bonin P, Stora G (1995) Effect of bioturbation on denitrification in a marine sediment from the West Mediterranean littoral. *Hydrobiologia* 304:49–58
- ✦ Gilbert F, Stora G, Bonin P (1998) Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: an *in situ* experimental approach. *Mar Ecol Prog Ser* 163:99–107
- ✦ Gilbert F, Aller RC, Hulth S (2003) The influence of macrofaunal burrow spacing and diffusive scaling on sedimentary nitrification and denitrification: an experimental simulation and model approach. *J Mar Res* 61:101–125
- ✦ Gray JS (1974) Animal-sediment relationships. *Oceanogr Mar Biol Annu Rev* 12:223–261
- ✦ Gray JS, Elliott M (2009) Ecology of marine sediments from science to management, 2nd edn. Oxford University Press, Oxford
- ✦ Hamme RC, Emerson SR (2004) Measurement of dissolved neon by isotope dilution using a quadrupole mass spectrometer. *Mar Chem* 91:53–64
- ✦ Henriksen K, Hansen JL, Blackburn TH (1980) The influence of benthic infauna on exchanges rates of inorganic nitrogen between sediment and water. *Ophelia* 1:249–256
- ✦ Hou L, Liu M, Carini SA, Gardner WS (2012) Transformation and fate of nitrate near the sediment–water interface of Copano Bay. *Cont Shelf Res* 35:86–94
- ✦ Jones SC, Tidwell DK, Darby SB (2009) Comprehensive shoreline mapping, Baldwin and Mobile Counties, Alabama: Phase I. Open-file report 09210. Geological Survey of Alabama, Tuscaloosa, AL

- ✦ Karlson K, Hulth S, Ringdahl K, Rosenberg R (2005) Experimental recolonisation of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling. *Mar Ecol Prog Ser* 294:35–49
- ✦ Kristensen E, Blackburn TH (1987) The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. *J Mar Res* 45:231–257
- ✦ Kristensen E, Hjorth Jensen M, Aller RC (1991) Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual polychaete (*Nereis virens*) burrows. *J Mar Res* 49:355–377
- ✦ Kruse I, Strasser M, Thiermann F (2004) The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). *J Sea Res* 51:53–62
- ✦ Kunu TM, Sullivan MB, Cornwell JC, Groxzkowski KM (1998) Denitrification in estuarine sediments determined by membrane inlet mass spectrometry. *Limnol Oceanogr* 43:334–339
- ✦ Lance GN, Williams WT (1966) A generalized sorting strategy for computer classifications. *Nature* 212:218
- ✦ Lee J, Webb BM, Dzwonkowski B, Park K, Valle-Levinson A (2013) Bathymetric influences on tidal currents at the entrance to a highly stratified, shallow estuary. *Cont Shelf Res* 58:1–11
- ✦ Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24
- ✦ Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (1998) Numerical ecology, 2nd English edition. Elsevier, Amsterdam
- ✦ Legendre P, Borcard D, Blanchet G, Dray S (2013) PCNM: MEM spatial eigen function and principal coordinate analyses. R package version 2.1-2/r109. <http://R-Forge.R-project.org/projects/sedar/>
- ✦ Lehrter JC (2008) Regulation of eutrophication susceptibility in oligohaline regions of a northern Gulf of Mexico estuary, Mobile Bay, Alabama. *Mar Pollut Bull* 56:1446–1460
- ✦ Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. *J Mar Res* 55:595–611
- ✦ Lillebø AI, Neto JM, Martins I, Verdelhos T and others (2005) Management of a shallow temperate estuary to control eutrophication: the effect of hydrodynamics on the system's nutrient loading. *Estuar Coast Shelf Sci* 65:697–707
- ✦ Mannino A, Montagna PA (1997) Small-scale spatial variation of macrobenthic community structure. *Estuaries* 20:159–173
- McCall PL (1978) Spatial-temporal distributions of Long-Island Sound infauna: the role of bottom disturbance in a nearshore marine habitat. In: Wiley ML (ed) *Estuarine interactions*. Academic Press, New York, NY, p 191–219
- ✦ McTigue ND, Gardner WS, Dunton KH, Hardison AK (2016) Biotic and abiotic controls on co-occurring nitrogen cycling processes in shallow Arctic shelf sediments. *Nat Commun* 7:13145
- ✦ Mermillod-Blondin F, Rosenberg R, François-Carcaillet F, Norling K, Mauclaire L (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. *Aquat Microb Ecol* 36:271–284
- ✦ Middelburg JJ, Levin LA (2009) Coastal hypoxia and sediment biogeochemistry. *Biogeosciences* 6:1273–1293
- ✦ Miller-Way T, Twilley RR (1996) Theory and operation of continuous flow systems for the study of benthic-pelagic coupling. *Mar Ecol Prog Ser* 140:257–269
- ✦ Mortazavi B, Riggs AA, Caffrey JM, Genet H, Phipps SW (2012) The contribution of benthic nutrient regeneration to primary production in a shallow eutrophic estuary, Weeks Bay, Alabama. *Estuaries Coasts* 35:862–877
- ✦ Nielsen LP (1992) Denitrification in sediment determined from nitrogen isotope pairing. *FEMS Microbiol Lett* 86:357–362
- Nixon SW (1981) Remineralization and nutrient cycling in coastal marine ecosystems. In: Neilson BJ, Cronin LE (eds) *Estuaries and nutrients*. Springer, New York, NY, p 111–138
- ✦ Nizzoli D, Bartoli M, Cooper M, Welsh DT, Underwood GJC, Viaroli P (2007) Implications for oxygen, nutrient fluxes and denitrification rates during the early stage of sediment colonisation by the polychaete *Nereis* spp. in four estuaries. *Estuar Coast Shelf Sci* 75:125–134
- ✦ Oksanen J, Blanchet GF, Kindt R, Legendre P, O'Hara RB (2011) Vegan: community ecology package. <https://cran.r-project.org/web/packages/vegan/index.html>
- ✦ Paerl HW (2006) Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: interactive effects of human and climatic perturbations. *Ecol Eng* 26:40–54
- ✦ Park K, Kim CK, Schroeder WW (2007) Temporal variability in summertime bottom hypoxia in shallow areas of Mobile Bay, Alabama. *Estuaries Coasts* 30:54–65
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Annu Rev* 16:229–311
- ✦ Pelegri SP, Blackburn TH (1995) Effect of bioturbation by *Nereis* sp., *Mya Arenaria* and *Cerastoderma* sp. on nitrification and denitrification in estuarine sediments. *Ophelia* 42:289–299
- ✦ Pelegri SP, Nielsen LP, Blackburn TH (1994) Denitrification in estuarine sediment stimulated by the irrigation activity of the amphipod *Corophium volutator*. *Mar Ecol Prog Ser* 105:285–290
- ✦ Queirós AM, Birchenough SNR, Bremner J, Godbold JA and others (2013) A bioturbation classification of European marine infaunal invertebrates. *Ecol Evol* 3:3958–3985
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Reeburgh WS (1969) Observations of gases in Chesapeake Bay sediments. *Limnol Oceanogr* 14:368–375
- ✦ Risgaard-Petersen N, Rysgaard S, Nielsen LP, Revsbech NP (1994) Diurnal variation of denitrification and nitrification in sediments colonized by benthic microphytes. *Limnol Oceanogr* 39:573–579
- ✦ Rysgaard S, Risgaard-Petersen N, Sloth NP, Jensen K, Nielsen LP (1994) Oxygen regulation of nitrification and denitrification in sediments. *Limnol Oceanogr* 39:1643–1652
- ✦ Rysgaard S, Christensen PB, Nielsen LP (1995) Seasonal variation in nitrification and denitrification in estuarine sediment colonized by benthic microalgae and bioturbating infauna. *Mar Ecol Prog Ser* 126:111–121
- ✦ Sayama M, Kurihara Y (1983) Relationship between burrowing activity of the polychaetous annelid, *Neanthes japon-*

- ica (Izuka) and nitrification-denitrification processes in the sediments. *J Exp Mar Biol Ecol* 72:233–241
- Seitzinger SP (1988) Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. *Limnol Oceanogr* 33:702–724
- ✦ Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180
- ✦ Stigebrandt A (1977) On the effect of barotropic current fluctuations on the two-layer transport capacity of a constriction. *J Phys Oceanogr* 7:118–122
- Stout JP, Heck KL Jr, Valentine JF, Dunn SJ, Spitzer PM (1998) Preliminary characterization of habitat loss: Mobile Bay national estuary program. Dauphin Island Sea Lab, Dauphin Island, AL
- ✦ Svensson JM, Enrich-Prast A, Leonardson L (2001) Nitrification and denitrification in a eutrophic lake sediment bioturbated by oligochaetes. *Aquat Microb Ecol* 23:177–186
- ✦ Tsutsumi H (1987) Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. *Mar Ecol Prog Ser* 36:139–149
- ✦ Tuominen L, Mäkelä K, Lehtonen KK, Haahti H, Hietanen S, Kuparinen J (1999) Nutrient fluxes, porewater profiles and denitrification in sediment influenced by algal sedimentation and bioturbation by *Monoporeia affinis*. *Estuar Coast Shelf Sci* 49:83–97
- Twilley RR, Cowan J, Miller-Way T, Montagna P, Mortazavi B (1999) Benthic nutrient fluxes in selected estuaries in the Gulf of Mexico. In: Bianchi TS, Pennock JR, Twilley RR (eds) *Biogeochemistry of Gulf of Mexico estuaries*. John Wiley & Sons, New York, NY, p 163–209
- ✦ Van Colen C, Rossi F, Montserrat F, Andersson MGI and others (2012) Organism–sediment interactions govern post-hypoxia recovery of ecosystem functioning. *PLOS ONE* 7:e49795
- ✦ Van Hoey G, Degraer S, Vincx M (2004) Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuar Coast Shelf Sci* 59:599–613
- ✦ Welschmeyer NA (1994) Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnol Oceanogr* 39:1985–1992
- ✦ Wilson AM, Huettel M, Klein S (2008) Grain size and depositional environment as predictors of permeability in coastal marine sands. *Estuar Coast Shelf Sci* 80:193–199
- ✦ Wood HL, Widdicombe S, Spicer JI (2009) The influence of hypercapnia and the infaunal brittlestar *Amphiura filiformis* on sediment nutrient flux—Will ocean acidification affect nutrient exchange? *Biogeosciences* 6: 2015–2024
- ✦ Ysebaert T, Meire P, Maes D, Buijs J (1993) The benthic macrofauna along the estuarine gradient of the Schelde estuary. *Neth J Aquat Ecol* 27:327–341
- ✦ Zimmerman AR, Benner R (1994) Denitrification, nutrient regeneration and carbon mineralization in sediments of Galveston Bay, Texas, USA. *Mar Ecol Prog Ser* 114: 275–288

Editorial responsibility: Erik Kristensen, Odense, Denmark

Submitted: November 26, 2017; Accepted: September 17, 2018
Proofs received from author(s): October 19, 2018

Macrobenthic community structure and influence on denitrification capacity in soft sediments (Mobile Bay, Alabama, USA)

M. P. Jacquot, K. M. Dorgan*, B. Mortazavi, A. A. Kleinhuizen, W. C. Clemons

*Corresponding author: kdorgan@disl.org

Marine Ecology Progress Series 506: 17–35 (2018)

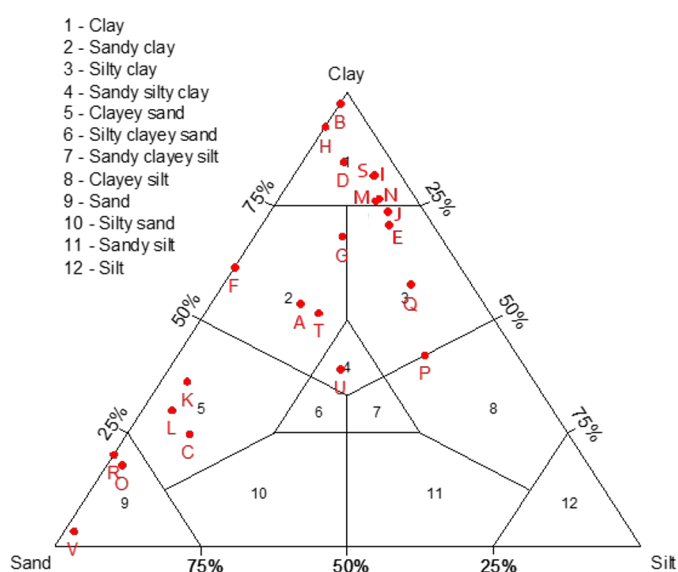


Figure S1: Shepard diagram with the different stations (A to V) in red indicating their sediment type (1-Clay, 2-Sandy clay, 3-Silty clay, 4-Sandy silty clay, 5-Clayey sand, 6-Silty clayey sand, 7-Sandy clayey silt, 8-Clayey silt, 9-Sand, 10-Silty sand, 11-Sandy silt, 12-Silt) depending on their proportion (%) of silt, clay and sand. Station locations are given in Fig. 1.

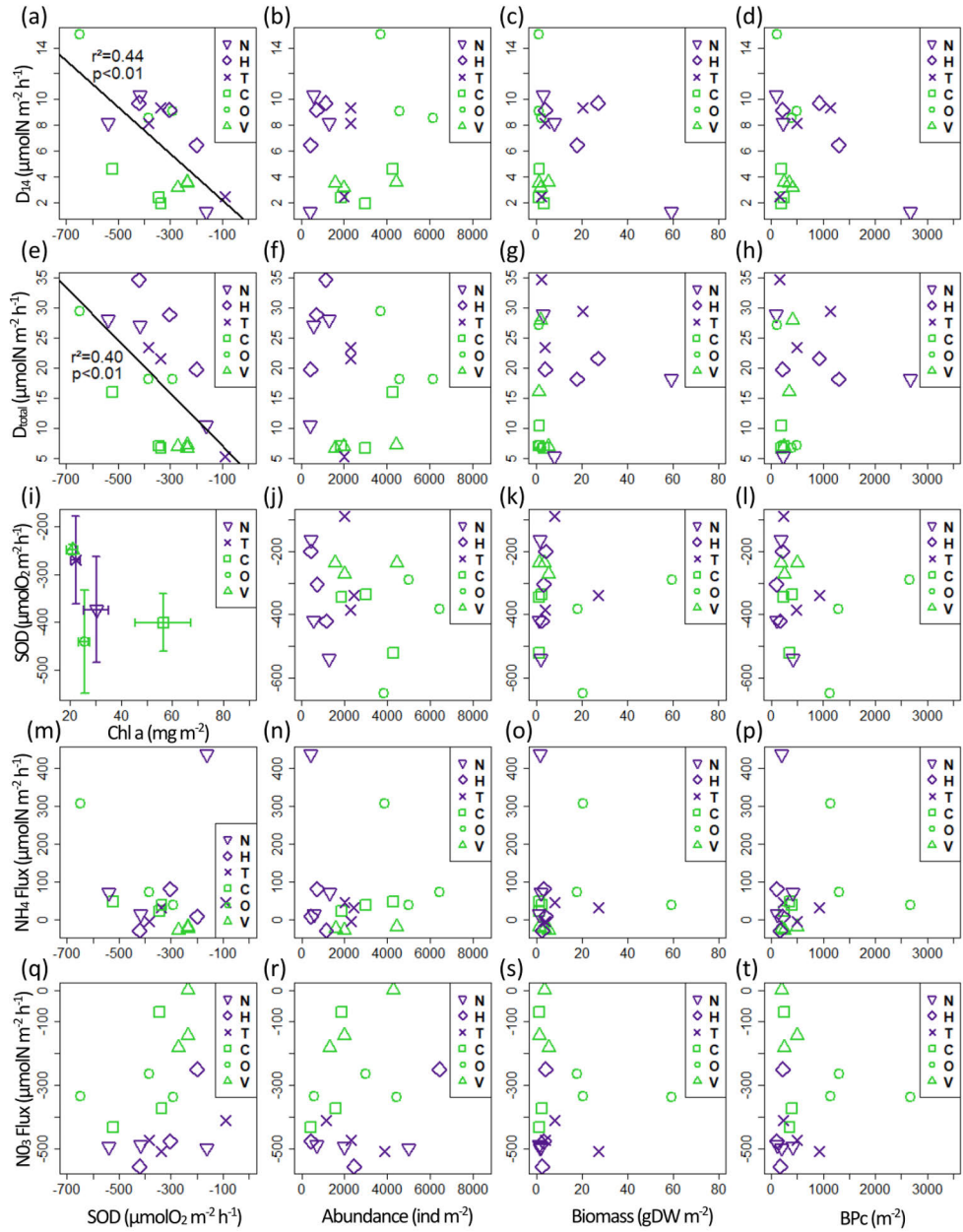


Figure S2: Denitrification rates (D_{14}) [$\mu\text{molN m}^{-2} \text{h}^{-1}$] (a, b, c, d) and (D_{total}) [$\mu\text{molN m}^{-2} \text{h}^{-1}$] (e, f, g, h) for individual cores depending on macrofaunal descriptors with oxygen consumption (SOD) [$\mu\text{molO}_2 \text{m}^{-2} \text{h}^{-1}$] (a,e), abundances [ind m^{-2}] (b,f), biomass [gDW m^{-2}] (c,g) and community bioturbation potential (BPC) [m^{-2}] (d,h) (Table S7). Oxygen consumption (SOD) [$\mu\text{molO}_2 \text{m}^{-2} \text{h}^{-1}$] depending on benthic parameters with chlorophyll *a* (Chl *a*) [mg m^{-2}] (i), plotted as mean for each site, abundances [ind m^{-2}] (j), biomass [gDW m^{-2}] (k) and community bioturbation potential (BPC) [m^{-2}] (l). Nutrient fluxes (ammonium flux (NH_4 flux) [$\mu\text{molN m}^{-2} \text{h}^{-1}$] (m-p) and nitrates flux (NO_3 flux) [$\mu\text{molN m}^{-2} \text{h}^{-1}$] (q-t) depending on macrofaunal descriptors with oxygen consumption (SOD) [$\mu\text{molO}_2 \text{m}^{-2} \text{h}^{-1}$] (m,q), abundances [ind m^{-2}] (n,r), biomass [gDW m^{-2}] (o,s) and community bioturbation potential (BPC) [m^{-2}] (p,t) (Table S7). Sites in purple are muddy and in green are sandy. Linear regression lines are shown only if significant ($p < 0.05$).

Table S1: Environmental data for each site with sampling date (Date), latitude, longitude, depth [m], temperature (T) [°C], salinity (S), dissolved oxygen of bottom water (DO) [%], secchi disk depth (Secchi) [cm], sediment type (Sed type), porosity, grain size (%sand, silt, clay) [%], carbon content (C) [% weight], nitrogen content (N) [% weight], C:N [mol:mol], location in the bay (Location), distance from freshwater input source (dist fresh) [m], distance from bay mouth (dist sea) [m], distance from shore (dist coast) [m] and distance from channel (dist chan) [m].

Site	Date	Latitude	Longitude	Depth	T	S	DO	Secchi	Sed type	Porosity	%Sand	%Silt	%Clay	N	C	C/N	Location	dist fresh	dist sea	dist coast
A	20.01.16	30.27875	-87.77315	1.6	11.6	8.5	110	90	Sandy-Clay	0.75	31.31	15.27	53.42	0.19	1.68	10.31	Coast	51.91	28.93	1.45
B	20.01.16	30.282017	-87.813533	2.3	10.7	7.5	100	30	Clay	0.74	2.51	0.00	111.43	0.19	1.66	10.14	Coast	48.47	25.41	3.05
C	20.01.16	30.260667	-87.92135	2.4	13.2	21.1	83.6	60	Clayey-sand	0.66	64.68	10.60	24.72	0.28	2.26	9.60	Coast	45.49	14.15	0.7
D	12.02.16	30.358683	-88.079833	3.5	12	6.8	87	50	Clay	0.67	8.20	7.06	84.74	0.17	1.64	11.19	Middle	36.21	14.67	3.15
E	12.02.16	30.346967	-88.073333	3.4	11.9	2.9	99.1	30	Silty-Clay	0.72	7.31	21.82	70.88	0.19	1.80	10.82	Middle	37.37	13.11	4.19
F	12.02.16	30.359183	-88.09505	2.8	12.4	6.1	96	40	Sandy-Clay	0.65	38.48	0.00	61.52	0.14	1.30	10.63	Coast	37.18	15.24	1.75
G	12.02.16	30.382367	-88.049733	3.6	12.5	6.5	102.2	60	Sandy-Clay	0.67	16.67	15.16	68.17	0.17	1.68	11.43	Middle	32.45	17.44	5.54
H	12.02.16	30.43335	-88.061133	3.4	12.4	5.9	102.8	40	Clay	0.73	7.63	0.00	92.37	0.20	2.01	11.75	Coast	28.91	22.91	4.29
I	18.02.16	30.4441183	-87.964967	3.1	14.8	8.6	83	50	Clay	0.71	4.76	13.61	81.63	0.21	2.00	11.29	Coast	25.41	25.32	4.85
J	18.02.16	30.442267	-87.943383	2.9	14.5	4.8	81.2	60	Silty-Clay	0.71	6.17	20.11	73.72	0.19	1.86	11.37	Coast	25.17	26.64	2.83
K	18.02.16	30.40545	-87.93745	3.2	13.1	2.8	91.7	40	Clayey-sand	0.49	59.07	4.55	36.38	0.06	0.55	11.21	Coast	29.32	25.35	2.92
L	18.02.16	30.363567	-87.848	1.8	14.9	4.3	124	40	Clayey-sand	0.60	64.88	5.02	30.10	0.11	1.05	10.77	Coast	39.84	25.47	1.12
M	18.02.16	30.311067	-87.874383	2.8	14.7	19.1	53.1	50	Clay	0.71	7.10	16.90	76.00	0.21	1.92	10.72	Coast	45.5	20.12	6.28
N	18.02.16	30.31375	-87.93435	3.2	14.7	25.7	70.7	60	Clay	0.72	6.31	17.04	76.65	0.22	2.01	10.63	Middle	39.8	15.25	5.96
O	16.03.16	30.261583	-88.0011	4.5	20	2.9	15.1	20	Sand	0.38	79.38	2.58	18.04	0.06	0.97	19.64	Mouth	44.63	6.73	3.29
P	16.03.16	30.282067	-87.970183	3.4	20.4	3.2	72.7	25	Silty-Clay	0.73	15.62	42.21	42.17	0.30	2.73	10.84	Middle	43.03	10.55	3.6
Q	16.03.16	30.3126	-87.99505	3.3	19.8	1.6	81.1	40	Silty-Clay	0.70	10.37	32.02	57.60	0.21	1.99	11.21	Middle	39.74	11.67	8.89
R	16.03.16	30.395767	-87.894333	2.1	21.8	4.1	75.5	20	Sand	0.49	79.69	0.00	23.70	0.09	0.77	10.31	Coast	32.1	24.83	0.64
S	16.03.16	30.365667	-87.95845	3.7	19.5	0.8	82.6	40	Clay	0.63	4.37	13.67	81.96	0.17	1.53	10.77	Middle	33.5	18.3	7.01
T	16.03.16	30.2872	-88.070033	4.5	20.7	10.5	81.2	60	Sandy-Clay	0.64	29.22	19.31	51.46	0.18	1.63	10.60	Mouth	43.34	6.96	3.59
U	16.03.16	30.320883	-88.069117	4.5	20.7	3.2	90	50	Sandy-Silty-Clay	0.61	31.72	29.28	39.01	0.19	1.61	9.89	Middle	39.55	10.62	5.88
V	16.03.16	30.26495	-88.0685	4.4	19.7	7.8	85.9	70	Sand	0.24	94.89	1.70	3.40	0.03	0.26	9.66	Mouth	45.61	4.32	1.81

Table S2: Average family abundances [# ind] for each station (3 replicates) collected using a 0.1 m² Petersen grab.

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	Mean
Annelida	Amphinomidae	0.00	0.00	0.00	4.33	5.00	0.67	7.67	0.67	0.33	0.00	0.00	0.00	0.00	8.33	1.00	5.67	10.33	0.00	2.67	0.33	7.33	0.00	2.47
Annelida	Capitellidae	7.67	2.00	66.33	4.33	0.33	19.00	2.00	43.33	27.33	21.33	80.00	85.00	27.33	8.33	10.67	0.67	1.00	80.00	5.67	13.33	0.00	14.67	23.65
Annelida	Chaetopteridae	1.33	1.00	0.33	1.67	1.00	0.33	1.00	0.00	2.00	3.33	7.33	3.00	6.00	1.67	0.00	0.00	0.33	0.00	1.33	0.33	0.00	0.67	1.48
Annelida	Cirratulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.02
Annelida	Cossuridae	0.00	4.00	8.33	10.00	8.00	0.00	12.67	2.00	5.33	5.67	1.67	4.67	8.00	8.00	1.00	47.67	33.67	0.00	5.33	17.33	9.00	0.67	8.77
Annelida	Eunicidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Annelida	Glyceridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Annelida	Goniadidae	10.67	1.67	34.00	9.33	9.00	2.33	5.33	13.00	5.33	11.33	17.33	15.33	6.67	5.67	8.67	1.33	7.33	0.00	8.67	9.33	3.33	1.67	8.52
Annelida	Hesionidae	1.67	7.00	5.67	2.00	2.33	1.33	2.00	0.00	3.67	2.33	3.67	2.67	1.00	1.33	0.00	0.33	0.33	0.00	0.00	0.67	0.67	0.67	1.79
Annelida	Lumbrineridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.33	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.80
Annelida	Magelonidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.33	0.00	0.00	0.00	3.00	0.33	5.33	0.67
Annelida	Maldanidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.05
Annelida	Nephtyidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Annelida	Nereididae	0.67	0.33	6.67	0.33	0.00	1.33	0.00	0.33	0.00	0.00	0.67	2.00	0.00	0.00	3.33	0.00	0.00	1.00	0.00	0.67	0.00	3.33	0.94
Annelida	Onuphidae	0.00	0.00	1.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Annelida	Orbiniidae	33.67	13.00	7.00	3.33	5.33	8.67	2.00	1.67	8.33	16.33	9.33	42.33	17.00	4.33	0.33	3.33	6.00	7.33	6.33	0.00	3.00	0.67	9.06
Annelida	Oweniidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.33	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.17
Annelida	Pectinariidae	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.33	0.00	1.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.15
Annelida	Phyllodoctidae	0.67	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	1.33	0.00	0.33	0.00	0.33	0.00	1.00	1.00	0.32
Annelida	Pilargidae	21.33	1.33	2.00	5.33	5.00	1.67	3.00	1.33	2.67	2.67	5.67	15.67	4.33	6.67	10.00	7.67	10.33	12.33	7.33	8.33	8.67	2.00	6.61
Annelida	Sigalionidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Annelida	Spionidae	13.00	4.67	116.67	14.33	7.33	4.67	7.67	10.00	4.67	8.00	12.00	30.00	6.33	12.33	14.67	5.00	17.33	57.33	3.67	10.67	11.00	9.00	17.29
Annelida	Sternaspidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.02
Mollusca	Acteocinidae	0.67	0.33	0.00	0.33	1.67	0.00	0.67	1.00	0.67	0.67	1.33	0.00	0.00	0.33	8.33	0.00	0.67	0.00	0.33	3.67	1.33	6.33	1.29
Mollusca	Arcidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.03
Mollusca	Eulimidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Mollusca	Hydrobiidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	6.00	0.00	0.00	0.00	0.30	
Mollusca	Juv Gastropoda	3.00	1.67	4.67	0.33	0.67	0.00	0.00	0.00	0.00	0.33	1.33	4.33	0.00	0.00	0.00	0.00	3.00	6.00	1.67	0.00	0.33	0.33	1.26
Mollusca	Lasaeidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21
Mollusca	Lucinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	52.67	0.00	0.00	0.00	0.00	0.00	0.33	0.33	2.42
Mollusca	Macluridae	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	3.33	0.00	0.33	0.20
Mollusca	Nassaridae	0.00	0.67	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	1.00	0.67	0.00	0.33	0.00	0.00	0.00	0.17
Mollusca	Naticidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Mollusca	Nuculanidae	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.33	0.00	0.33	0.00	0.00	3.67	1.33	1.00	0.74
Mollusca	Pandoridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Mollusca	Pyramidellidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Mollusca	Rissoidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.02
Mollusca	Solecurtidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Mollusca	Tellinidae	9.67	2.67	4.00	7.33	3.33	9.00	3.00	5.00	3.33	4.33	5.00	9.33	3.00	0.00	16.33	0.00	1.00	7.00	1.33	7.33	3.33	4.67	5.00
Mollusca	Tornidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Mollusca	Veneridae	0.00	0.00	41.33	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.00	0.33	0.00	0.00	0.33	4.00	2.36	
Mollusca	Yoldiidae	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	4.00	0.67	0.67	0.00	0.00	8.33	1.67	0.67	0.76
Arthropoda	Anthuridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Arthropoda	Axiidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Arthropoda	Bodotriidae	2.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	1.33	0.27
Arthropoda	Callinassidae	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.05
Arthropoda	Caprellidae	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Arthropoda	Corophiidae	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Arthropoda	Diastylidae	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Arthropoda	Gammaridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Arthropoda	Isaeidae	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Arthropoda	Leuconidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	16.33	0.33	0.00	0.79
Arthropoda	Ogyridae	0.00	0.00	0.00	0.67	0.33	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	4.33	0.00	0.00	0.00	0.00	0.33	0.00	0.	

Table S3: Mean macrofaunal biomass [g WW] for each station (3 replicates) collected using a 0.1 m² Petersen grab.

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	Mean
Annelida	Amphinomidae	0.00	0.00	0.00	0.02	0.02	0.01	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.03	0.03	0.00	0.01	0.00	0.02	0.00	0.01
Annelida	Capitellidae	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.03	0.03	0.01	0.00	0.13	0.00	0.00	0.02	0.00	0.08	0.00	0.00	0.02
Annelida	Chaetopteridae	0.03	0.01	0.01	0.02	0.02	0.01	0.01	0.00	0.07	0.09	0.21	0.14	0.13	0.03	0.00	0.00	0.01	0.00	0.04	0.00	0.00	0.00	0.04
Annelida	Cirratulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Cossuridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03	0.01	0.00	0.00	0.01	0.00	0.00	0.00
Annelida	Eunicidae	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Glyceridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Goniadidae	0.02	0.00	0.05	0.01	0.01	0.00	0.01	0.02	0.01	0.01	0.04	0.04	0.01	0.01	0.01	0.00	0.01	0.00	0.01	0.01	0.01	0.00	0.01
Annelida	Hesionidae	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Lumbrineridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Annelida	Magelonidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00
Annelida	Maldanidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Nephtyidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Nereididae	0.03	0.00	0.16	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.03	0.10	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00	0.04	0.00	0.02
Annelida	Onuphidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Orbiniidae	0.44	0.23	0.06	0.11	0.15	0.06	0.09	0.01	0.26	0.18	0.12	0.27	0.22	0.13	0.00	0.15	0.20	0.02	0.13	0.00	0.03	0.01	0.13
Annelida	Oweniidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.01	0.01	
Annelida	Pectinariidae	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	
Annelida	Phyllodocidae	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00
Annelida	Pilargidae	0.04	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.02	0.04	0.08	0.01	0.22	0.00	0.03	0.04	0.06	0.01	0.00	0.02	0.00	0.03
Annelida	Sigalionidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Annelida	Spionidae	0.34	0.17	0.92	0.12	0.04	0.02	0.07	0.07	0.05	0.16	0.21	0.20	0.15	0.24	0.45	0.39	0.69	0.02	0.04	0.37	0.25	0.22	0.24
Annelida	Sternaspidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Arcidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00
Mollusca	Acteocinidae	0.00	0.01	0.00	0.00	0.02	0.00	0.01	0.00	0.02	0.01	0.01	0.00	0.00	0.00	0.26	0.00	0.01	0.00	0.00	0.04	0.01	0.11	0.02
Mollusca	Eulimidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Hydrobiidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Mollusca	Juv Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Lasaeidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Lucinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.03
Mollusca	Mactridae	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.49	0.00	0.05	0.03
Mollusca	Nassariidae	0.00	0.03	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.03	0.00	0.01	0.00	0.00	0.00	0.01
Mollusca	Naticidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Nuculanidae	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.01	0.00	0.00	0.28	0.08	0.02	0.03
Mollusca	Pandoridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pyramidellidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Rissoidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Solecurtidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Mollusca	Tellinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.54	0.00	0.00	0.07	0.00	0.01	0.00	0.16	0.04	0.00
Mollusca	Tornidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Veneridae	0.00	0.00	0.04	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.02
Mollusca	Yoldiidae	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Anthuridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Axiidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Bodotriidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Callianassidae	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Arthropoda	Caprellidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Corophiidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Diastylidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Gammaridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Isaeidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Leuconidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Arthropoda	Ogyrididae	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00
Arthropoda	Pinnotheridae	0.02	0.0																					

Table S4: Kruskal Wallis test results for total abundance [individuals m⁻²], total biomass [g m⁻²], taxonomic richness, Shannon's diversity, Pielou's evenness and Simpson's diversity index of macrofauna sampled at 22 sites classified depending on their % sand (<60% sand, 60-80% sand or >80% sand) and their location (stations near the coast (Coast), stations in the middle of the bay (Middle) and stations near the mouth of the bay (Mouth)). p-value is significant with "*" when p < 0.05, "**" when p < 0.01 and "***" when p < 0.001.

	% sand			Location		
	chi ²	df	p-value	chi ²	df	p-value
Abundance	5.24	2	0.073	0.59	2	0.75
Biomass	4.73	2	0.094	3.99	2	0.14
Taxonomic richness	4.84	2	0.089	8.04	2	0.018 *
Shannon's diversity	2.76	2	0.25	12.36	2	0.0021 **
Pielou's evenness	6.16	2	0.046 *	6.10	2	0.047 *
Simpson's diversity	3.10	2	0.21	12.04	2	0.0024 **

Table S5: Parsimonious distance-based redundancy analysis (db-RDA) results (see plots in Fig. 7): (a) model summary, (b) marginal effects of terms with variables analysed separately, (c) marginal effects of terms with analysis including all variables and (d) variation explained by individual axes with proportion explained by axes (Prop.). The response is a dissimilarity matrix computed on macrofaunal abundances in all samples of each station. Environmental variables having a significant impact on macrofaunal communities are % Sand, distance from the sea, total carbon content, C/N ratio, distance from the channel, salinity, temperature, turbidity, porosity, Clay/Clay+Silt. Statistical significance is indicated with “***” when $p < 0.001$, “**” when $p < 0.01$, “*” when $p < 0.05$, “ ” when $p > 0.05$.

(a)	df	var.	F	p		
Model	10	7.5573	8.8548	0.001	***	
Residual	55	4.6941				
R ² = 62%						
Adj. R ² = 55%						
(b)	df	var.	F	p		
% Sand	1	1.2648	14.8197	0.001	***	
Distance from the sea	1	0.6551	7.6760	0.001	***	
Total carbon content	1	0.2298	2.6921	0.011	*	
C/N ratio	1	0.5907	6.9217	0.001	***	
Distance from the channel	1	0.4968	5.8204	0.001	***	
Salinity	1	0.2564	3.0047	0.013	*	
Temperature	1	0.3031	3.5513	0.003	**	
Turbidity	1	0.3484	4.0819	0.002	**	
Porosity	1	0.2887	3.3826	0.001	***	
Clay/Clay+Silt	1	0.2479	2.9050	0.009	**	
Residual	55	4.6941				
(c)	df	AIC.	F	p		
% Sand	1	156.62	12.4661	0.005	**	
Distance from the sea	1	145.17	14.2357	0.005	**	
Total carbon content	1	140.69	6.3955	0.005	**	
C/N ratio	1	137.46	5.0297	0.005	**	
Distance from the channel	1	134.67	4.5245	0.005	**	
Salinity	1	130.80	5.4821	0.005	**	
Temperature	1	128.63	3.7885	0.005	**	
Turbidity	1	126.34	3.8283	0.005	**	
Porosity	1	124.45	3.4001	0.010	**	
Clay/Clay+Silt	1	123.05	2.9050	0.010	**	
(d)	df	var.	F	Prop.	p	
dbRDA1	1	2.9724	28.1709	0.2032	0.001	***
dbRDA2	1	1.6361	15.5063	0.1170	0.001	***
dbRDA3	1	1.0986	10.4117	0.07991	0.001	***
dbRDA4	1	0.7101	6.7302	0.03949	0.001	***
dbRDA5	1	0.3346	3.1710	0.02365	0.001	***
dbRDA6	1	0.3180	3.0137	0.02091	0.003	**
dbRDA7	1	0.2156	2.0433	0.01477	0.018	*
dbRDA8	1	0.1632	1.5464	0.01205	0.065	
dbRDA9	1	0.1396	1.3226	0.00792	0.158	
dbRDA10	1	0.0829	0.7859		0.775	
Residual	55	5.8031				

dbRDA, distance-based redundancy analysis axes

Table S6: Macrofaunal family abundances [ind], biomass [g WW] in each core (0.00708 m²), mobility (Mi) and sediment reworking (Ri) of each taxa (Solan et al. 2004, Queirós et al. 2013).

	Ri	Mi	Abundance (ind/0.00708 m ²)													Biomass (gWW/0.00708 m ²)																				
			T1	T2	T3	C1	C2	C3	O1	O2	O3	V1	V2	V3	Mean	N1	N2	N3	H1	H2	H3	T1	T2	T3	C1	C2	C3	O1	O2	O3	V1	V2	V3	Mean		
Annelida			Amphinomidae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	12,00	0,00	0,67	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Capitellidae	3,00	2,00	1,00	2,00	5,00	1,00	2,00	0,00	0,00	1,00	13,00	5,00	2,00	4,00	3,00	9,00	10,00	3,72	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,01	0,16	0,04	0,00	0,00	0,00	0,00
Annelida			Cossuridae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00	1,00	0,00	0,00	0,00	0,00	0,17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Echiura	3,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Goniadidae	4,00	3,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	2,00	0,00	0,00	0,00	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,01	0,00	0,00	0,00	0,00	
Annelida			Hesionidae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Lumbrineridae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,00	2,00	0,00	0,00	0,33	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Magelonidae	2,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00	0,00	1,00	2,00	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Maldanidae	3,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Nereididae	4,00	4,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00	0,00	0,00	1,00	0,00	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Orbinidae	4,00	3,00	1,00	0,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,28	0,04	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Owenitidae	2,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,00	0,00	1,00	0,00	0,17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Phyllodoctidae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Platydoridae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00	0,00	0,00	2,00	0,00	0,56	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Polinoidea	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Annelida			Spionidae	3,00	2,00	1,00	1,00	1,00	0,00	1,00	7,00	2,00	6,00	2,00	1,00	0,00	1,00	3,00	1,00	2,06	0,01	0,04	0,01	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Mollusca			Acteocinidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Juv Gastropoda	NA	NA	0,00	0,00	0,00	0,00	0,00	0,00	1,00	1,00	3,00	0,00	0,00	0,00	0,00	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Lucinidae	2,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,94	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Macruridae	2,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Naticidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Nuculanidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,00	0,00	0,00	0,00	0,33	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Pandoridae	2,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Rissoiidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Tellinidae	2,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,67	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Veneridae	2,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7,00	13,00	6,00	8,00	4,00	5,00	0,00	2,39	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Mollusca			Yoldiidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Arthropoda			Bobotriidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,11	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Arthropoda			Leucoidae	2,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Arthropoda			Pinnotheridae	1,00	4,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Echinodermata			Amphipuridae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Echinodermata			Ophiactidae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,11	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Others			Actinidia	1,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,06	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Others			Nemertea	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,94	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Others			Phascolionidae	4,00	3,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00																				

Table S7: Summary table for all the sediment replicate cores with sediment type (Sed), macrofaunal total abundance (A) [ind m⁻²], biomass (B) [gWW m⁻²], community bioturbation potential (BPc) [m⁻²], chlorophyll *a* (Chl *a*) [mg m⁻²], Carbon content (C) [% wt], Nitrogen content (N) [% wt], C:N [mol:mol], sediment oxygen demand (SOD) [μmol O₂ m⁻² h⁻¹], NO₃⁻ flux (NO₃) [μmol N m⁻² h⁻¹], NH₄⁺ flux (NH₄) [μmol N m⁻² h⁻¹] and denitrification rate (D₁₅, D₁₄ and D_{total}) [μmol N m⁻² h⁻¹].

Site	Sed	Chl <i>a</i>	C	N	C:N	SOD	NO ₃	NH ₄	D ₁₅	D ₁₄	D _{total}	A	B	BPc
N.core1	Mud	30.22	2.0067	0.2200	10.63	-163.96	-497.22	438.87	9.24	1.26	10.51	429	1.39	192.6
N.core2						-418.37	-487.46	14.23	16.73	10.32	27.05	571	1.05	113.1
N.core3						-538.86	-492.57	69.88	19.80	8.15	27.96	1286	2.04	411.7
H.core1	Mud	NA	2.0100	0.2000	11.75	-199.87	-249.35	7.54	13.31	6.44	19.75	429	4.03	215.8
H.core2						-304.41	-476.14	81.05	19.64	9.17	28.81	714	3.24	101.2
H.core3						-420.94	-555.26	-29.64	24.89	9.70	34.59	1143	2.44	170.9
T.core1	Mud	22.17	1.6333	0.1800	10.60	-338.36	-507.81	30.92	12.21	9.36	21.57	2286	27.14	923.7
T.core2						-89.09	-409.52	45.04	2.97	2.42	5.38	2000	8.12	232.0
T.core3						-384.39	-471.97	-4.90	15.29	8.16	23.45	2286	3.95	489.6
C.core1	Sand	56.39	2.2600	0.2767	9.60	-343.78	-69.78	21.62	4.75	2.36	7.11	1857	1.08	241.5
C.core2						-336.29	-372.77	37.79	4.79	1.91	6.69	3000	2.30	395.3
C.core3						-521.83	-432.51	47.57	11.41	4.61	16.02	4286	1.11	353.3
O.core1	Sand	25.56	0.9667	0.0567	19.64	-382.55	-264.49	72.63	9.56	8.57	18.13	6143	17.98	1300.4
O.core2						-290.53	-337.37	37.87	9.02	9.11	18.13	4571	59.47	2668.1
O.core3						-648.71	-334.30	307.77	14.41	15.02	29.42	3714	20.44	1131.7
V.core1	Sand	20.82	0.2567	0.0333	9.66	-236.32	0.49	-24.53	3.27	3.47	6.74	1571	3.33	195.0
V.core2						-236.99	-143.69	-19.43	3.68	3.55	7.23	4429	1.18	493.0
V.core3						-271.13	-181.16	-28.27	3.88	3.12	7.01	2000	5.25	251.9

Maïté P. Jacquot

Human Ecosystem Engineering

Effects and Feedback in Coastal Benthic Systems

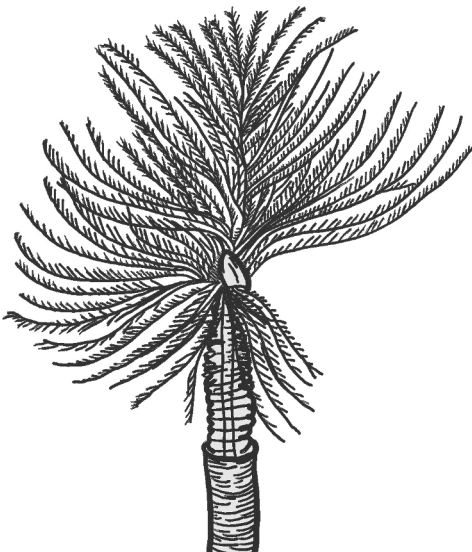
As humans are facing challenges related to increasingly threatened ecosystems through climate change and biodiversity loss, there is a great need to understand human-induced pressures, effects and feedback processes in the marine environment.

This doctoral research explores the effects of humans, as an engineer species, on the functioning of macrofauna in coastal ecosystems in multiple parts of the world: Sine Saloum in Senegal, West Africa, Åland Islands in Finland, Baltic Sea, and Mobile Bay in Alabama, Gulf of Mexico. As any other species whose presence and activities significantly modify the availability of resources for other species, humans can indeed be described as “ecosystem engineers”.

The overall aim of this thesis is to contribute to a deeper understanding of the effects of human ecosystem engineering on coastal ecosystems and potential feedback to human society through functioning.

About the author

Maïté P. Jacquot’s main research interests are biodiversity and ecosystem functioning, and a particular interest in human-nature relationships. During her PhD, she has participated in quantitative field-based observational studies in different parts of the world (Senegal, Alabama, Finland, Greenland). Since she discovered the realm of macrofaunal communities with their wide diversity in species, shapes and functions, her research focus has been on benthic ecology. Her approach combines traditional taxonomic and trait-based assessments.



ISBN 978-952-12-4348-6