EFFECTS OF A NEWLY CREATED MUSSEL BED AND HYDRODYNAMIC CONDITIONS ON THE BIODIVERSITY AND FUNCTIONING OF MACROBENTHIC COMMUNITIES

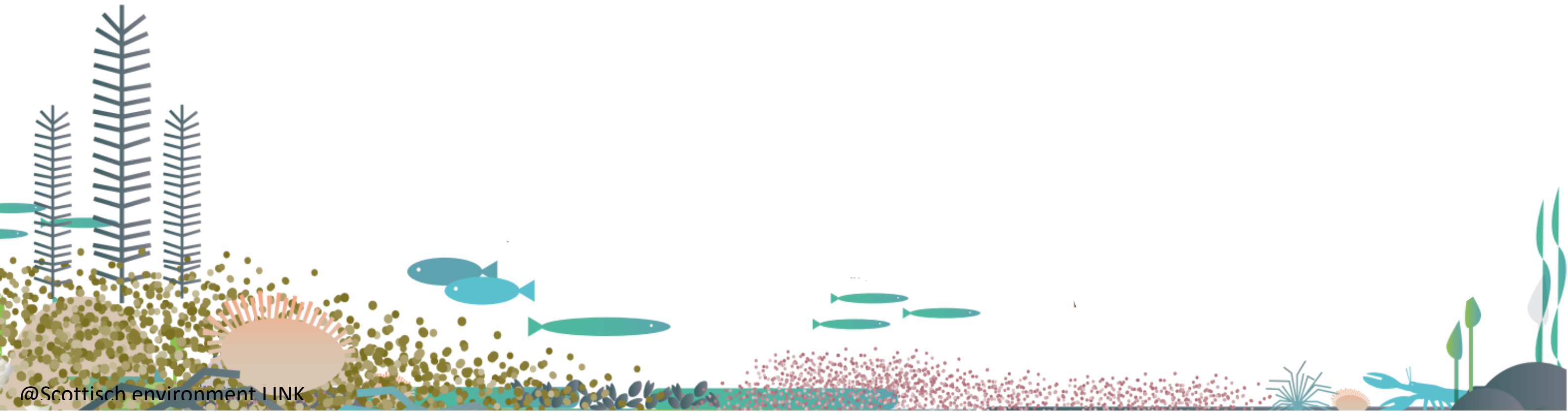
Arnaud Boulenger
Student number: 20191232

Promoter: Dr. Gert Van Hoey
Supervisor: Alexia Semeraro

Master thesis submitted to Ghent University for the partial fulfilment of the requirements for the degree of **International Master of Science in Marine Biological Resources (IMBRSea)**

Academic year: 2020 - 2021

Co-funded by the Erasmus+ Programme of the European Union



@Scottisch environment LINK

‘No data can be taken out of this work without prior approval of the thesis promoter’

'I hereby confirm that I have independently composed this Master thesis and that no other than the indicated aid and sources have been used. This work has not been presented to any other examination board.'

June 7th, 2021

Arnaud BOULENGER

Executive summary

As climate change is increasing the threat of erosion and flooding along the densely populated coastal areas, there is an urgent need to implement sustainable coastal protection. There has been an increasing interest to restore or create natural coastal ecosystems due to their coastal erosion and flood defences services. In the Belgian Part of the North Sea, the Coastbusters projects aim to develop nature-based coastal protection by favouring mussel bed establishment through dropper lines in situ installation. This was tested in a first finished project, and a mussel bed was formed during summer-autumn. In the second ongoing project, different hydrodynamic conditions were tested (sheltered versus exposed), as the successful development of this type of biogenic reefs will be dependent on the environmental conditions. Mussel beds are known to influence the structure and functioning of underlying macrofaunal communities. Therefore, the aim of this thesis was to determine the effects of the newly created mussel bed and differences in hydrodynamic conditions on the biodiversity and functioning of macrobenthic communities.

To detect these effects, a BACI (Before/After Control/Impact) approach was followed. Macrobenthic community structure was characterized by looking at density, biomass, and diversity. Functioning was assessed using secondary production estimates, biological trait analysis and functional diversity indices. Linear mixed models were used to determine statistical influences of the mussel bed and hydrodynamic conditions on those parameters.

The mussel bed had no effect on the secondary production but shifts in lifespan, feeding behaviour and development mode were indicated by the biological trait analysis. The functional diversity indices FEve and RaoQ suggested a better utilization of the different niches in the mussel bed compared to bare sediments but also lower trait differentiation, probably due to the higher abundance of oligochaetes in the mussel bed. The baseline characterization of the two Coastbusters 2.0 areas under different hydrodynamic conditions showed higher values of density, species richness and biomass in the sheltered area and high dissimilarity in community composition between the two conditions. Important differences in feeding, mobility, development mode and bioturbation were found between the two hydrodynamic conditions in response to different flow and food flux conditions. The functional diversity indices FRic, FEve, FDiv and RaoQ revealed a better resource-use efficiency in the sheltered area, indicating a more valuable ecosystem functioning.

Further studies with a long-lasting mussel bed are needed to draw strong conclusions on the influence of biogenic reef implementation for coastal protection on benthic ecosystems.

Abstract

Nature-based solutions, as shellfish reefs, can support natural coastal defence and be a potential solution for climate resilient shorelines in the future. They are dependent on environmental conditions, and both influence benthic ecosystems. This thesis analysed the effects of a newly created mussel bed and hydrodynamic conditions on the biodiversity and functioning of macrobenthic communities for the two Coastbusters projects. In a first finished project, a mussel bed was formed during summer-autumn. In the second ongoing project, different hydrodynamic conditions were tested (sheltered versus exposed). Shifts in lifespan, feeding behaviour and development mode were found. Functional diversity indices suggested a better utilization of the different niches, but lower trait differentiation compared to bare sediments, probably due to the higher abundance of oligochaetes in the mussel bed. Important differences in density, species richness, biomass and feeding, mobility, development, and bioturbation modes were found between the two hydrodynamic conditions in response to flow and food flux conditions. Moreover, functional diversity indices revealed a better resource-use efficiency in the sheltered area. Further studies with a long-lasting mussel bed are needed to draw strong conclusions on the influence of biogenic reefs under different hydrodynamic conditions on benthic ecosystems for the implementation of coastal protection.

Keywords: coastal protection, biogenic reefs, Mytilus edulis, soft sediment, macrofauna, hydrodynamics, biological traits, ecosystem functioning, benthic impact

Table of Contents

1. Introduction

1.1 Coastal demography and climate change

The settlement and expansion of human populations in coastal zones have always been intense because of the wide range of available services such as seafood, trade routes and transport, cultural and aesthetic value (Blackburn et al., 2019; Neumann et al., 2015). Nowadays, about 40% of the world's population lives within 100 km of the coastline (United Nations, 2017) and most megacities such as Shanghai, New York and Mumbai are located in coastal areas or large deltas (Blackburn et al., 2019; Neumann et al., 2015). Approximately 680 million people live in the low-lying coastal zone, coastal areas that are less than 10 meters above sea level (Adger et al., 2007), and this growing population is expected to reach one billion by 2050 (McMichael et al., 2020).

The densely populated coastal areas are being increasingly impacted by a number of threatening climate events, such as storms , floods and coastal erosion, being exacerbated by climate change (Harley et al., 2006; He & Silliman, 2019; Hinkel et al., 2014). Projections from the United Nations' Intergovernmental Panel on Climate Change (IPCC) find that global mean sea levels are expected to rise between 0.48m and 0.84m by the end of the century, relative to the period 1986-2005 (Adger et al., 2007). Even in the most optimistic mitigation scenarios, the impacts are likely to be major and will continue to rise over the next decades. Low-lying areas such as deltas, coastal wetlands, and coral islands will be impacted most by rising sea levels. Episodic flooding by storm surges and waves will penetrate farther inland causing damages to human habitations, salinizing aquifers and affecting agricultural production (Gornitz, 1991). An additional threat comes with coastal land loss. For instance, 24% of the world's sandy beaches are eroding at a rate exceeding 0.5 m/yr and the European shoreline has an expected retreat between 54m and 97m by 2100, relative to 2010 (Athanasiou et al., 2020; Luijendijk et al., 2018). Without shore and beach nourishment, the worldwide global land loss would sum up to approximately 6,000 – 17,000 km^2 during the 21st century, leading to 1.6–5.3 million people being forced to migrate with migration costs ranging between US$ 300–1000 billion (Hinkel et al., 2013). Therefore, there is an urgent need to further develop the appropriate coastal defence solutions to mitigate the effects of climate change and sea level rise on coastal populations.

1.2 Traditional coastal defence

Over the last century, coastal countries have implemented hard engineering structures to reduce the vulnerability of people, places, and resources against contemporary hazards. These built infrastructures, such as seawalls, groynes, and breakwaters, have been designed to maintain beach levels, intercept long-shore sand movement and resist severe exposure to climate events (Williams et al., 2018). Hard engineering structures are widely perceived as the ultimate solution to combat coastal erosion and flood risks (Temmerman et al., 2013). Nowadays, they are often combined with beach nourishment schemes and the association of both are the dominating form of coastal defence used worldwide (Spalding et al., 2014). However, while they have shown to be important and effective in some cases, they are also responsible of numerous adverse impacts and important financial costs due to maintenance and the need of sand replenishment every few years (Morris et al., 2018; Speybroeck et al., 2006; Temmerman et al., 2013; Williams et al., 2018). To protect its sandy coastline along the North Sea, Belgium spent € 419 million in coastal defence planning over the period 1998-2015 (Sterckx et al., 2019).

Besides their financial costs, these measures are also responsible for several ecological side effects. Coastal armouring is now well known to cause a steepening of the coast's intertidal profile (Masselink & Russell, 2013). Walker et al. (2008) studied the impact of groynes on the beach's dynamics and found that groynes create depositional conditions on the northern side and erosion on the southern side. Regarding seawalls, they are only efficient in maintaining a beach profile similar to the preconstruction shape if they are combined with beach nourishment (Kraus & McDougal, 1996). Moreover, the introduction of hard structures in the intertidal environment are responsible for many ecological consequences as modification of the trophic interactions, promotion of the settlement of invasive species, and changes in the native assemblages' diversity and functioning of the areas (Airoldi et al., 2005; Chapman & Bulleri, 2003; Riera et al., 2004; Walker et al., 2008).

1.3 Nature-based coastal defence

Salt marshes, seagrass and kelp beds, coral reefs, shellfish beds, mangroves and other diverse and productive coastal ecosystems have drastically declined over the last decades and are being lost at an alarming rate. It has been estimated that the loss rate of each of those ecosystems is faster than the global loss rate of tropical forests (Duarte et al., 2008). The impact of this loss is not only limited to an erosion of natural heritage, but also to a loss of valuable ecosystem services, such as water filtration, carbon sinks and coastal protection (Figure 1). Indeed, these ecosystems provide coastal erosion and flood defence services through ecological processes such as increased bed friction, localized water shallowing, sediment deposition and seabed stabilization (Figure 1) (Gracia et al., 2018; Morris et al., 2018). For instance, oysters and byssus threads-bearing bivalves beds have shown that they increase sediment deposition which can build up to form banks higher than the ambient substrate (Figure 1) (Gracia et al., 2018; Meadows et al., 1998). Furthermore, the use of these ecosystems for coastal protection can be more cost-effective in the long run than traditional hard engineering structures. In the Humber estuary in UK, Turner et al. (2007) revealed that, after 25 years, tidal marsh restoration on reclaimed land was more economically beneficial than maintaining dykes. Therefore, due to the additional benefits they provide alongside coastal protection and their cost-effectiveness, there has been an increasing interest in restoring or creating those ecosystems to replace or complement artificial structures (Spalding et al., 2014; Temmerman et al., 2013).

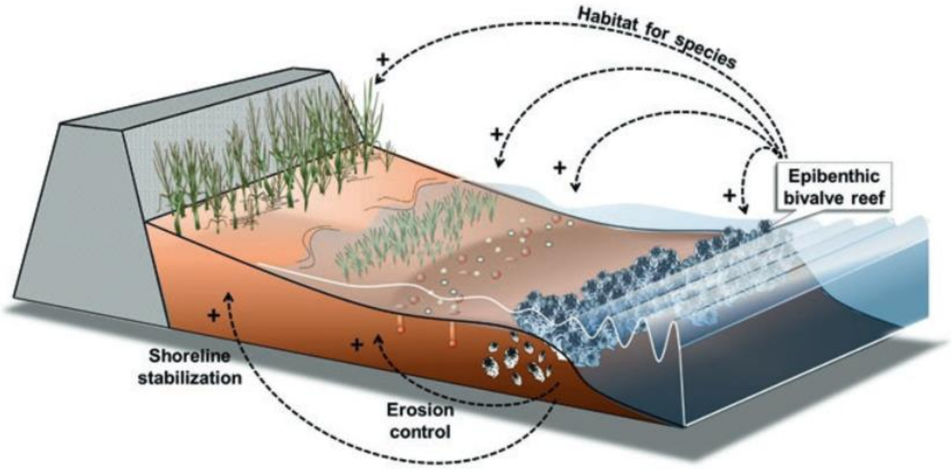


Figure 1: Visualisation of how epibenthic bivalve reefs provide coastal protection. From Ysebaert et al., 2018.

However, research in nature-based costal defence is still in its infancy and the lack of research limits their widespread expansion. The main limitations to their wider implementation are due to the lack of long-term studies on the effectiveness of those ecosystems for flood defence (Temmerman et al., 2013). Moreover, the variability in the results among the different studies highlights the fact that nature-based solutions are often dependent on the physical and biological conditions present at a specific site (Morris et al., 2018). In fact, the type of ecosystem that can be used in nature-based coastal protection management plans highly depend on the environmental conditions. In temperate regions, the most effective ecosystem to reduce wave height and protect the shoreline are salt marshes, but their distribution along the European coastline is limited (Narayan et al., 2016). Other solutions must therefore be considered to protect sandy coastlines such as the Belgian coast. The historical and current study of marine habitats in the Belgian part of the North Sea (BPNS) shows that bivalve and tube-building worms are the most suitable natured-inspired solutions for the environmental conditions of this region. Prior to their destruction by oyster dredgers in the 1860's, the European flat oyster (*Ostrea edulis*) was forming extensive reefs in the offshore gravel grounds. The last encounter with this emblematic species in Belgian waters dates to 1946. Following the disappearance of the flat oyster, the hard substratum also slowly disappeared and most of it has been replaced by sand, due to trawling disturbances (Houziaux et al., 2011). In the nearshore area, aggregations of the tube dwelling polychaetes *Lanice conchilega* are forming reefs on soft sediments (Degraer et al., 2008; Rabaut et al., 2009). Offshore, the windmill farm construction led to the introduction of new hard substrates. This new habitat has been colonized by several species, including the reef building blue mussel *Mytilus edulis*, which are not present on the sandy bottom of the BPNS (Degraer et al., 2019). However, its presence in the windmill farm suggests that the environmental conditions present in the BPNS are appropriate for mussel beds development.

1.4 The Coastbusters projects

The Coastbusters projects are a public-private partnership borne out of this need to develop ecologically sound solutions by combining nature-inspired designs in coastal protection systems.

1.4.1 Coastbusters 1.0

The Coastbusters 1.0 field pilot project was set up in the BPNS to test the feasibility of three types of biobuilder organisms as nature-inspired coastal protection elements to stabilize the shoreline (Sterckx et al., 2019). Bivalves (*M. edulis*), marine flora (seagrass and seaweed) and tube-dwelling sand mason worms (*L. conchilega*) were selected for their reef-building and sediment trapping capacities. The objectives of the project for the three types of reefs were that (1) the organisms should survive the hydrodynamic conditions and maintain their ecological functions, (2) the reef is stable and provides additional ecosystem services beside coastal protection, and (3) the development of the reef induces local sedimentation and stabilization of the foreshore. The results of the project showed that mussel reefs were the most suitable solution for the high energy coastal environment of the BPNS (Coastbusters, 2020). For the mussel bed setup, a typical aquaculture technique was adopted. A submerged aquaculture longline together with dropper lines were installed to capture the mussel larvae in the water column and favour their growth above a suitable site for a mussel bed development. Bags with shell material or stones were installed on the seabed underneath the dropper lines to investigate the use of hard substrates as reef-initiating structures. When the mussels on the dropper lines have reached a certain size and density, they detach in clumps and fall on the bottom where they can form a mussel bed if they persist long enough to establish a dense population. This three-year project (2017-2020) showed that a mussel bed developed under the dropper lines during summer and the beginning of fall but disappeared each winter season, probably due to predation and winter storms. Another important result from that project is the absence of significant differences between the control sandy site and the mussel reef site for macrobenthos density, species richness and community composition. Lower diversity indices values were found for the reef site. Longer time series are needed to draw strong conclusions on the impact of the bivalve reef on the underlying infauna communities (Goedefroo, 2020).

1.4.2 Coastbusters 2.0

The Coastbusters 2.0 project was launched following the promising results of the first project. This follow-up project (2020-2023) is looking closer at the feasibility of using mussel beds as coastal protection defence. It aims to (1) test different biodegradable and sustainable materials, (2) design new setups to favour the formation and survival of the reef, (3) determine the boundary conditions for reef development and (4) determine the added ecosystem values and services of such mussel bed. To answer those questions, the project also includes an important research component on the development of pioneering observation strategies to fully capture the spatio-temporal reef development and dynamics. The objective is to develop a high-level scientifically underpinned road map which can be applied in analogue environments in the rest of the world, including pioneering measurement setups. Compared to the first project, an additional experimental site has been added in a more exposed location further offshore compared to the original site. The aim is to study the mussel reef development under two different environmental conditions to better determine the boundary conditions and ecosystem services. A first estimation on the effects of such newly created mussel reefs on ecosystem services concluded that the main services are phosphorus retention, shrimp production, recreational diving, and coastal protection. It was estimated that the yearly added benefits of one hectare of this bivalve reef, compared to one hectare of unstructured sandy bottom, accounted for € 85,000 (Biest et al., 2020). However, important uncertainties are associated with that estimation and a long-term site-specific monitoring and research are needed to draw stronger conclusions on the ecosystem services provided by those reefs.

The acquired knowledge from this project will lead to the valorisation of sustainable nature-based solutions business opportunities for the industrial partners. However, to allow its commercial use, this concept of mussel reefs for coastal protection needs to fall within the EU environmental legislation, which is in place to ensure sustainable use of the environment. Several pieces of EU nature legislation specify that benthic habitats should not be adversely affected, and macrobenthos is an important part of the assessment process (Breine et al., 2018). Therefore, this second project will select an appropriate set of benthic indicators or evaluation criteria proposed by several EU environmental legislation such as Natura 2000 or the Marine Strategy Framework Directive. The aim will be that the Coastbusters concept is ready for the EU environmental impact assessment procedure.

1.5 The blue mussel

1.5.1 Ecology and life history

The blue mussel *M. edulis* is widely distributed in many subtidal and intertidal areas in the northern hemisphere. The growth and life-span of this species depends highly on the environmental conditions, but individuals up to 18 years and 8cm have been found in some subtidal reefs (Sukhotin et al., 2007). This semi-sessile epibenthic bivalve occurs both on hard substrates and soft sediments, and maintains its attachment to the substrate by producing byssal threads (Bologna et al., 2005; Moeser et al., 2006). At reproduction time, the males release the sperm in the water column and the eggs are fertilized externally. In the southern North Sea, this usually occurs between March and July and this is when the highest concentrations of larvae are found in the water column. To successfully grow mussels on an aquaculture longline, it is therefore essential to install the setup prior to the spawning event in March to successfully catch the mussel larvae. The pelagic larval stage lasts between 16 and 70 days after which the larva metamorphoses to the pediveliger stage during which it is able to settle on suitable substrates (Coolen et al., 2020). The metamorphosis is induced by environmental cues that indicate the presence of a suitable substrate to settle. Their preferred substrates to settle are filamentous substrate like seaweeds and seagrasses (Eyster & Pechenik, 1988). Another filamentous substrate are the aquaculture ropes deployed in the water column, which benefit the mussel larvae settlement (Benham, 2020). After this primary settlement, a second pelagic phase occurs, named secondary settlement. This latter process allows the juveniles to select preferred adult habitats, like adult mussels or shell debris (Bologna et al., 2005; Dolmer & Stenalt, 2010; Le Corre et al., 2013; McGrath et al., 1988).

1.5.2 The effects on benthic diversity and ecosystem functioning

The blue mussel is considered an ecosystem engineer, a species changing the surrounding abiotic conditions and affecting the abundance and distribution of other species (Koivisto et al., 2011). Through their three-dimensional architecture, mussels provide a complex habitat and a shelter from predation for many species of algae, crustaceans and worms (Wilcox et al., 2018; Ysebaert et al., 2009). They are also an important source of food for a wide range of animals like crabs, whelks, sea stars, fish and birds (Aaren S., 2007; Lappalainen et al., 2005; Smith & Jennings, 2000; Van der Heide et al., 2014). Being suspension feeders, mussels filter significant amounts of water and reduce the phytoplankton concentration in the water column (Fréchette et al., 1989; Ysebaert et al., 2009). This way, they play an important ecological role in the benthic-pelagic coupling, by transferring energy and nutrients from the pelagic to the benthic zone (Bologna et al., 2005; Griffiths et al., 2017; Ysebaert et al., 2009). Because of the intensity of this process, mussels play an essential role in the functioning of the ecosystem (Ysebaert et al., 2009). Furthermore, they have an important effect on the sediment properties by depositing large amount of organically enriched faeces and pseudofaeces. This biodeposition and the changes in near-bed hydrodynamic regime allow for the accumulation of fine organic particles (Norling & Kautsky, 2008; Ragnarsson & Raffaelli, 1999). This results in an increase in the microbial activity, which in turn causes decreased oxygen concentration in the sediment, increased denitrification and accumulation of free sulphides. The important modifications resulting from the mussel bed presence can affect the abundance, biomass and diversity of associated communities (Callier et al., 2009; Donadi, van der Heide, et al., 2015; Norling & Kautsky, 2007; Ysebaert et al., 2009).

Besides the structural effects on benthic communities resulting from mussel beds presence, few studies investigated their effects on the ecological functioning of the community of associated species (Norling & Kautsky, 2007). Studying ecosystem functioning, such as secondary production or nutrient fluxes, remains a time-consuming and logistically complex issue, However, it can be relatively easily described from numerical approaches based on traits exhibited by members of biological assemblages (Bolam et al., 2017). The presence and distribution of species-specific traits, such as life history, body size or feeding mode, determine how certain species contribute to ecosystem processes (Bremner, 2008). This approach can be particularly useful to monitor the effect of human activities and identify potential alteration or recovery of ecological functions (Breine et al., 2018; Bremner, 2008). Such analysis is also extremely important to determine the ecosystem functions, which are used for ecosystem services quantification (Armoškaitė et al., 2020). Previous studies have shown the importance of biological traits analysis of macrofauna, due to their importance in key ecosystem functions such as organic matter mineralization and cycling of oxygen and nutrients in surface sediments (Donadi et al., 2015; Norling et al., 2007). Therefore, to fully understand the effects of mussel beds on the benthic environment, it is essential to not limit the study to the structural aspects, but also to encompass functional aspects, which can be investigated by the proxy of biological traits.

1.6 Aims and objectives of the thesis

The first goal of this thesis will be to investigate the effects of the newly created mussel bed on the functioning of benthic communities. To assess the magnitude of the impacts, estimates of total secondary production, assemblages' biological trait composition and functional diversity indices were used. As it has been detailed previously, we hypothesized an increase in secondary production and a change in the benthic traits and functional diversity of the macrobenthos following the mussel bed implementation. This first part will be based on data retrieved from Coastbusters 1.0.

The second objective of this thesis is focused on the characterization of the sediment properties, macrobenthos assemblages' structure and functioning of the sheltered and exposed areas. This baseline characterization will be useful for the continuity of the project to assess the impact of mussel beds on the surrounding benthic ecosystem. As the sedimentological characteristics are known to be the major factor determining the distribution of benthic organisms, the influence of the granulometry on the community's composition and traits will also be determined (Van Hoey et al., 2014). Finally, this second part will also investigate which monitoring tools cover the key parameters in an optimal way. Therefore, the difference between the data obtained from the Van Veen grabs and the Sediment Profile Imaging (SPI) will be discussed. This second part will use data from Coastbusters 2.0.

2. Material and Methods

2.1 Sites description

2.1.1 Coastbusters 1.0

The bivalve reef setup was installed in the BPNS, 2km in front of the city of De Panne (N51°05’52.6’’, E2°35’37.2’’). It was established in a relatively sheltered location, south-west of the Broers Bank sandbank (N51°08’06.4’’, E2°35’17.8’’) (Figure 2), on the lee side of the Trapegeer bank to the Potje gully area. The sheltering from strong waves and winter storms was expected to benefit the reef development. Same as the whole BPNS, this area is subjected to semi-diurnal macro-tides with important height difference between spring and neap tides (De Moor, 1979). The experimental site is located in a subtidal area with a depth of 5m (Lowest Astronomical Tide, LAT) and subjected to a northeast subsurface current. This area is characterized by fine to medium sediment grain size with a high silt-clay fraction.

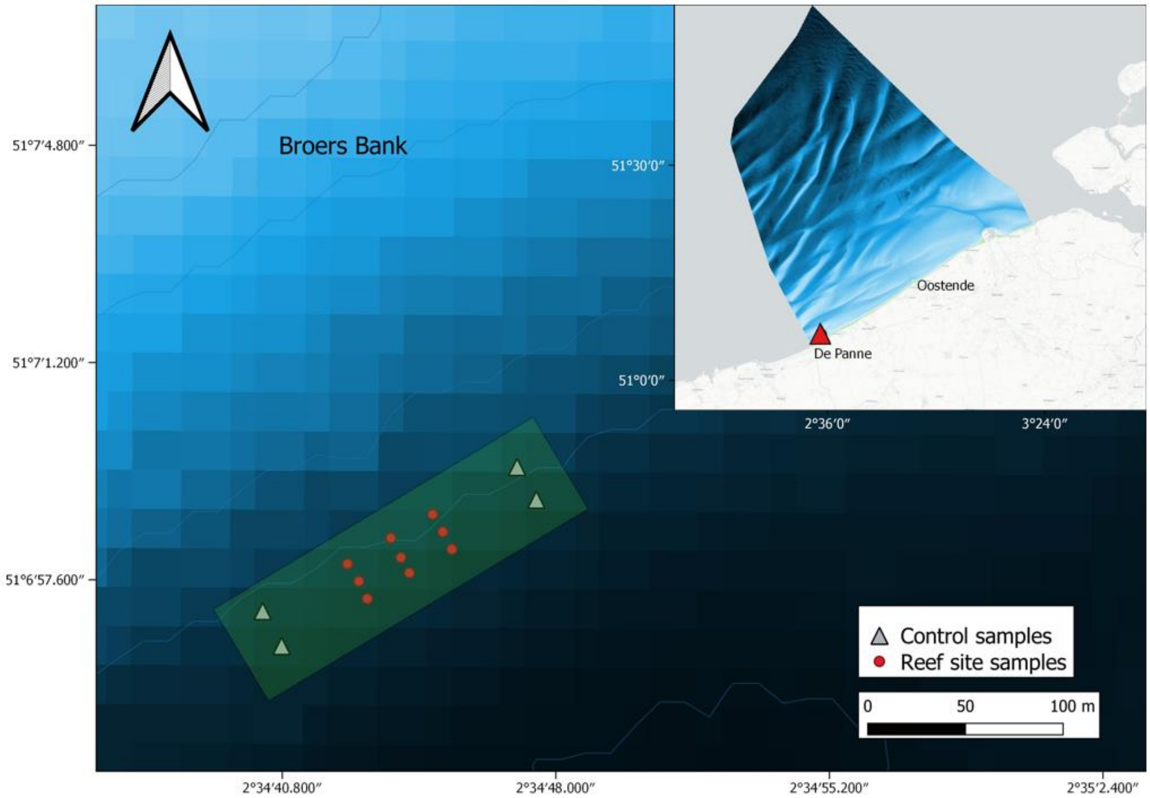


Figure 2: Location of Coastbusters 1.0 sampling stations. The overview map depicts the experimental site in the BPNS with its sandbanks system. The red triangle represents the location of the experimental sites.

The installation of the experimental setup started on the 24th of November 2017. Forty bags filled with stones and empty shells were spread out on the seafloor over a surface of approximately 500 m² to serve as a hard substrate for mussels’ settlement (Figure 3). The aquaculture system was deployed four months later, on the 14th of March 2018. It consisted of two buoys anchored to the seabed, that were connected by a submerged horizontal longline disposed parallel to the coast. The distance between the two anchoring points was 133 m and the longline measured 50m long. On this longline, 48 vertical dropper lines were installed to allow mussel larvae settlement. Each dropper line measured 3m and a 3kg metal weight was attached at the end to keep them vertical in the water column. The pilot reef was 20m wide and 50m long, resulting in an area of approximately 1000 m² (Figure 3).

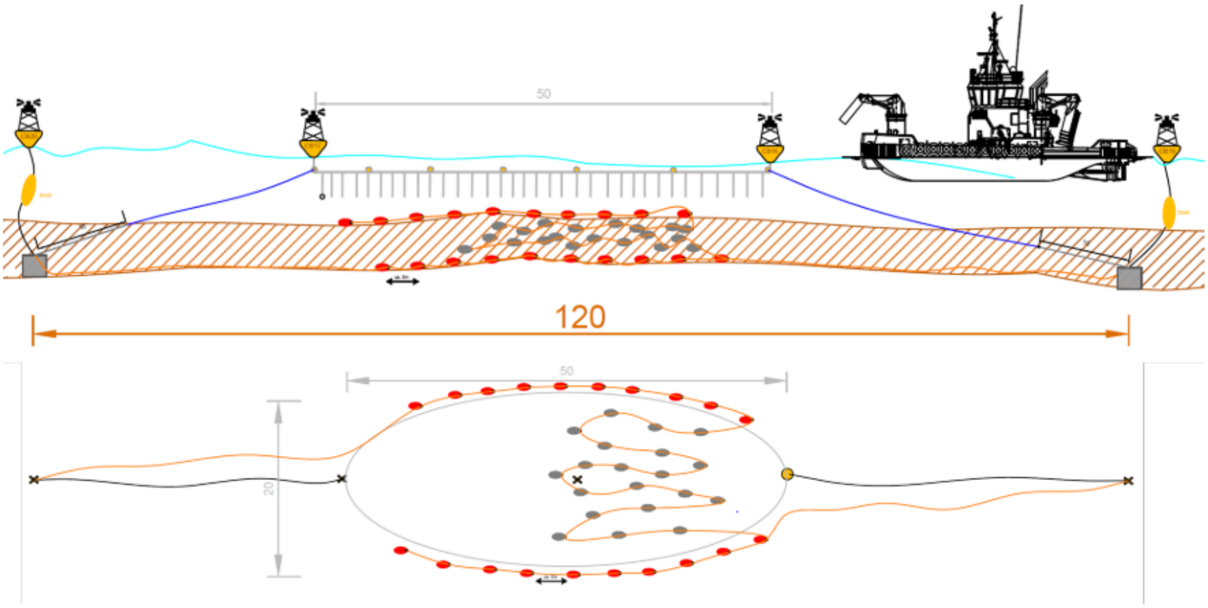


Figure 3: Setup of the longline, dropper lines and substrate bags. At the top, installation of the reef site and at the bottom, top view of the in-situ layout of the bags. From Sterckx et al., 2019.

2.1.2 Coastbusters 2.0

As Coastbusters 2.0 wanted to investigate the effects of different environmental conditions on the mussel reef development, a second site was added on the Northern slope of the Trapegeer sandbank (Figure 4). It is located 5km in front of the city of De Panne and 3km away from the sheltered site of Coastbusters 1.0, which was kept. Both sites have the same bathymetry and are characterised by fine to medium sand, probably with lower mud content in the exposed area, due to stronger hydrodynamic conditions.

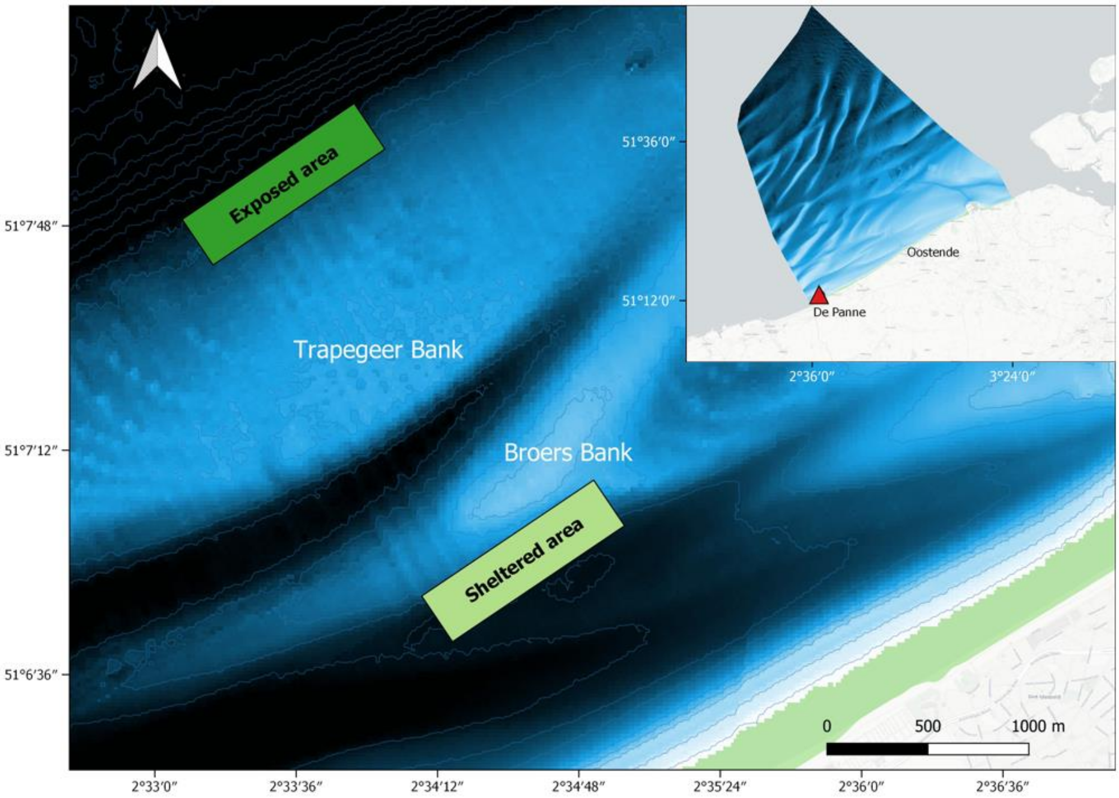


Figure 4: Location of Coastbusters 2.0 nearshore-sheltered area and offshore-exposed area. The overview map depicts the experimental sites in the BPNS with its sandbanks system. The red triangle in the overview represents the experimental sites.

For this follow-up project, no hard bottom substrates were used for any of the two pilot reefs. The hard substrates present at the sheltered site were removed prior to the new setups' installation. Because of the of the COVID-19 lockdown, the experimental setups could only be installed on the 26th of June 2020 and not in March as originally planned. As a result, major mussel spat recruitment of spring was missed, leading to no mussel bed development on the seafloor at the two experimental sites during the summer and fall months. In both setups, 36 droppers were used. Weights of approximately 10kg each were attached at the end of each dropper to keep them vertical in the water column.

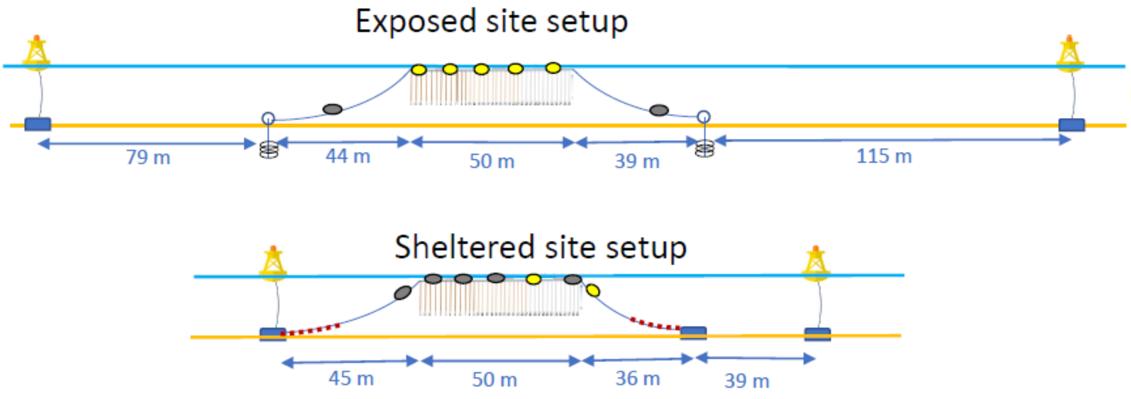


Figure 5: The two different setups used in Coastbusters 2.0. At the top, the installation of the exposed site setup and the sheltered site setup at the bottom.

2.2 Field sampling

2.2.1 Sampling protocol

The macrobenthos samples were collected by mean of a Van Veen grab (with a sampling surface of 0.1 m²). The sampling was conducted on board the Last Freedom (Allewerelt N.V., located in the Port of Nieuwpoort) which is suitable for sampling in shallow waters. At each sampling point, GPS data were recorded. All samples were taken during the day between sunrise and sunset to limit the variability due to vertical migration and day-night rhythms of various organisms. After collection by the Van Veen grab, the sample was dropped in a plastic box where a photo was taken to enable visual description of the sediment characteristics. Before rinsing the Van Veen samples over the sieve, sediment samples were collected using a PVC tube (core of 5cm diameter), stored, and further processed in the lab. After this step, the samples were washed over a 1mm mesh sieve and the residues were fixed in a 6% formaldehyde-seawater solution. Finally, the samples were labelled for species identification in the lab.

2.2.2 Sampling campaigns: Coastbusters 1.0

To test the effects of the mussel bed development on the benthic infauna life in and around the experimental site, five sampling campaigns were carried out between June 2017 and October 2019. The macrobenthos samples were collected following a Before/After – Control/Impact (BACI) design as it is commonly done in environmental monitoring (Underwood, 1992). The first sampling campaign was carried out before the bottom substrates and longline installation to characterize the benthic environment before reef implementation. Afterwards, four sampling campaigns were carried out to quantify the effects of the mussel bed development on the macrobenthic communities. Nine fixed stations within the reef development area were each sampled once during every campaign. Four fixed control stations, approximately 50 meters away from the reef, were also sampled once during each campaign. In conclusion, a total of 13 samples were collected during each sampling campaign, except for the campaign T2 (Table 1) where one reef site sampling point could not be sampled due to bad weather conditions.

Table 1: Installation of the Coastbusters 1.0 experimental setup and Van Veen sampling campaigns.

Sampling campaign	T0	Installation bottom substrates	Installation longline system	T1	T2	T3	T4
Date	22/06/17	24/11/17	14/03/18	17/04/18	13/07/18	24/04/19	25/10/19

2.2.3 Sampling campaigns: Coastbusters 2.0

For Coastbusters 2.0, the macrobenthos was also sampled before the reef setup installation to have a baseline of the benthic environment at the two sites. One sampling campaign has been carried out after the installation (T1) and two future sampling campaigns are planned before the end of the project in January 2023.

Table 2: Installation of the Coastbusters 2.0 experimental set up and Van Veen sampling campaigns.

Sampling campaign	T0	Installation longline system	T1
Date	15/06/20	26/06/20	07/09/20

The main difference between the field sampling protocol for Coastbusters 1.0 and 2.0 is that the second project has two experimental sites (Figure 4), and that the sampling stations are not the same. In Coastbusters 1.0, the control sites were located too close to the reef sites, and was probably influenced by the latter, especially the eastward control sites (Goedefroo, 2020). Furthermore, the first project revealed that the mussel drop-off and environmental influence of the installation is not only directly under the installation, but also wider and depending on the current. Therefore, the Van Veen grab sampling is organized along transects, at a certain distance from the backbone (Figure 6). For each campaign and for the two experimental sites, five samples were collected at random on the transect lines in the reef development area and five were taken at random in the reference area. Moreover, four random flexible stations at the edges of the reef survey area were sampled (Figure 6), which were the control stations used in Coastbusters 1.0. Two control stations were located at 80m from the eastern side of the reef, while two others were located at 20m from the western side. The aim of those stations is to measure and confirm changes observed by input from multibeam or backscatter data. In conclusion, a total of 14 samples were collected at each site, which means 28 samples for each sampling campaign.

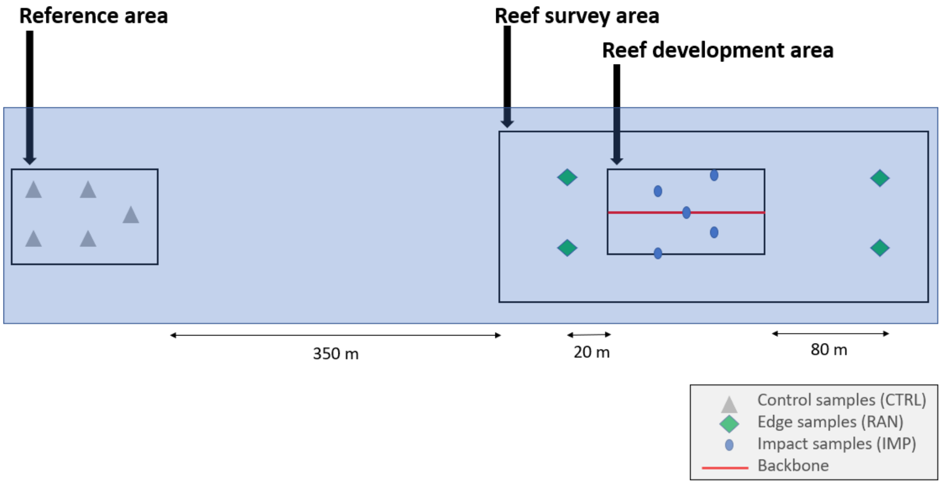


Figure 6: Sampling design of Coastbusters 2.0. The annotations in brackets are the names used for the three types of sites in the results.

2.3 Laboratory analysis

2.3.1 Macrobenthos

The samples were brought back to the lab and stained with eosine for easier visual detection of the benthic organisms. The samples were washed by decantation to separate the biota from the heavier sediment, which makes it easier to collect the macrobenthos. After this step, the sediment was further screened for potential remaining organisms. After sorting, the benthic organisms were identified to the lowest possible taxonomical level according to the Taxonomic Discrimination Protocol for impact studies used for all accredidated macrobenthos analysis at the Flanders Research Institute for Agriculture, Fisheries and Food. The organisms were counted and weighed per taxon. On the one hand, the weighing for Coastbusters 1.0 was done as Ash-Free Dry Weight (AFDW) obtained by incineration of the organisms at 450 to 500°C in a muffle furnace. The taxa were weighed to the nearest 0.0001g. On the other hand, taxa from Coastbusters 2.0 were weighed as Wet Weight biomass (WW) to the nearest 0.00001g. Two different methods were used as two different research institutes oversaw the biomass measurements. All organisms were subsequently stored in 70% ethanol. Density and biomass were standardized to m^{-2}.

2.3.2 Sediment

The samples were analysed by laser diffraction, using the Malvern Mastersizer for sediment composition (the percentages of clay, silt, sand and gravel) and median grain size. For Coastbusters 1.0, two different devices were used along the project. The Malvern Mastersizer 3000 was used for the sampling campaigns T1 and T2, while the Malvern Mastersizer 2000 with the Autosampler 2000 was used for the sampling campaigns T3 and T4. As the percentage of clay was not measured by the Malvern Mastersizer 3000, these percentages were calculated by assuming the missing percentages belonging to the clay fraction. For Coastbusters 2.0, the samples were analysed using a Malvern Mastersizer 2000. The sand fraction > 1000µm was sieved off before laser diffraction.

2.4 Data analysis

The datasets containing the macrobenthic abundances, biomass, and traits from Coastbusters 1.0 and Coastbusters 2.0 were used in the following analyses. The datasets were checked to ensure consistent taxonomic identification of all species among the different datasets. Prior any analyses, the datasets were standardized by removing all the species that were not sampled quantitatively by the Van Veen grab, namely all the species not considered as macrobenthos (i.e. hyperbenthos, meiobenthos and pelagic species). The datasets were checked for inconsistent species identifications and the different taxa that were difficult to distinguish from each other and/or identified to different taxonomical levels were grouped together to the lowest taxonomical level possible (e.g. Oligochaeta, *Owenia*, *Eteone*, etc). The abundance and biomass data from one sample in the impact sheltered area during the T0 sampling campaign from Coastbusters 2.0 data was discarded from the analyses because of bad conservation of the organisms, probably because not enough formaldehyde was added during the sampling campaign. For Coastbusters 1.0, since only two samples were taken per control site (Figure 2), both sites were grouped together as one location with four replicates in order to make any statistical analyses possible. The same was done for the edge sites for Coastbusters 2.0.

The univariate and multivariate analyses were performed with R Studio (version 1.4.1106). All the multivariate analyses were run using the 'ade4' and 'vegan' package. The 'lme4' package was used for the different linear mixed models' analyses. A significance level of $p < 0.05$ was used in all tests. All mean measurements are reported as mean ± standard error (SE). For Coastbusters 1.0, the structural characterisation (diversity, abundance, biomass) of the pilot study was already done in the study of Goedefroo (2020), wherefore we here only focus on the functional characterisation.

2.4.1 Structural characterisation of the pilot study Coastbusters 2.0

2.4.1.1 Density, diversity and biomass

The macrobenthic communities were characterized by the following structural parameters: density (ind.m^{-2}), species richness (spp.sample^{-1}), biomass (g.m^{-2}), Shannon index (H'(log$_e$)) and Simpson index (1-λ'). Species richness is the total number of species regardless of their abundance, Shannon index is sensitive to species richness while Simpson index is less sensitive to rare species but gives more weight to abundant species. The advantage of using 1-λ' to calculate the Simpson index is that it increases with greater diversity like the Shannon index. Those parameters were calculated using PRIMER v6 software.

2.4.1.2 Community composition

A Bray-Curtis similarity matrix based on abundance data was used to build the non-metric dimensional scaling (nMDS) which is an ordination method attempting to represent as closely as possible the pairwise dissimilarities between objects in a low dimensional space. The stress value provides information on the quality of the ordination plot. A PERMANOVA was performed on the Bray-Curtis similarity matrix using 'site' (impact, control, edge), 'hydrodynamic conditions' (exposed vs sheltered) and 'sampling campaign' (T0 vs T1) as factors. The PERMANOVA was followed by a PERMDISP to check for multivariate spread among factors. If significant differences were found in the community compositions between the impact, control, and edge sites, a post-hoc test was used to reveal the pairwise differences. The function 'pairwise.adonis' was used to run this pairwise test. A similarity of percentages (SIMPER) analysis was used to identify the most contributing taxa to the dissimilarities between exposed and sheltered areas and between the two sampling campaigns.

2.4.2 Functional characterisation of the pilot studies Coastbusters 1.0 and 2.0

2.4.2.1 Secondary production estimates

Secondary production estimates (kJ m^{-2} y^{-1}) were derived in a stepwise approach from the AFDW data according to the methodology described in Bolam et al. (2011, 2014) and Bolam (2012). Biomass data were converted to energy values (kJ m^{-2}) using conversion factors derived from Brey et al. (1988). The obtained energy values were converted to production values using the freely available spreadsheet from Thomas Brey handbook (http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html). As finite values were needed for the calculations, all the <0.0001 g inputs were changed to 0.0001 g to allow further calculations. It is important to point out that the estimates obtained are not as accurate as values obtained from more direct secondary production measurement methods (Bolam et al., 2016). The Brey model estimates the P:B ratio (in y^{-1}) for each taxon, which is a measure of the energy turnover of that taxon. The more productive a taxon is, the higher the P:B ratio is. Finally, each taxa was assigned to one of the three P:B classes: low (P:B < 2y $^{-1}$), medium (P:B 2–3.5 y $^{-1}$) and high (P:B > 3.5 y $^{-1}$) productivity (Bolam et al., 2016). Secondary production estimates were only calculated for Coastbusters 1.0 data.

2.4.2.2 Biological traits composition

To assess how the functional traits compositions of the study sites change due to the mussel longline system and the hydrodynamic conditions, a biological trait analysis was performed. Ten traits were considered and selected based on life history characteristics (maximum size, maximum longevity, larval development and egg development), morphology and behaviour (living habit, sediment position, feeding mode, mobility and bioturbation) (Breine et al., 2018). There is currently no accepted methodology to select traits for a given study and this selection mostly depends on the limited biological information available for benthic invertebrates (Bolam & Eggleton, 2014). Functional traits information was gathered from the traits' dataset of the Flanders Research Institute for Agriculture, Fisheries and Food and Breine et al. (2018). When specific traits information was missing, some local species were assigned to other species within the same respective genus or family after confirmation by an expert (Bolam & Eggleton, 2014; Hu et al., 2019). Each trait was divided into different modalities, which represent the different degrees of the trait (Table 3). This approach prevents the obligate assignment of a taxon to a single group, which can result in an incorrect representation of the biological data. Indeed, taxa can display different behaviour depending on the life stage, environmental conditions and resources available (Bolam et al., 2016; Bremner, 2008). Taxa were scored for each trait modality according to a fuzzy coding procedure with the score representing the affinity of a species for a trait, ranging from 0 (= no affinity) to 3 (= complete affinity). Those traits were then converted to proportions of one for each trait modalities (Breine et al., 2018). The resulting taxon-by-trait matrix was combined with the taxon abundance data to create a station-by-trait matrix based on abundance on which all further analyses were based (Bolam et al., 2016; Breine et al., 2018; Gusmao et al., 2016). This station-by-trait matrix was analysed using Fuzzy Correspondence Analysis (FCA) which is particularly appropriate for fuzzy coded data (Chevene et al., 1994). FCA was used to identify the differences in functional composition between sites and to estimate the contribution of each trait modalities to the trait patterns.

Table 3: Biological traits, modalities and labels used in the biological trait analysis.

Biological traits	**Trait modalities**	**Labels**
Maximum body size (sr)	>10mm	sr10
	10 - 20 mm	sr10-20
	21 – 100 mm	sr21- 100
	101 – 200 mm	sr101-200
	201 – 500 mm	sr201-500
Maximum longevity (l)	< 1 y	l<1
	1 – 3 y	l1-3
	3 – 10 y	l3-10
	> 10 y	l>10
Bioturbation (bt)	Surface deposition	btSurf
	Upward conveyor	btUp
	Downwards conveyor	btDown
	None	btNone
	Diffusive mixing	btMix
Feeding mode (fm)	Predator	fmPred
	Scavenger/Opportunist	fmScav
	Suspension feeder	fmSusp
	Surface depositor	fmSurf
	Subsurface depositor	fmSub
Larval development (ld)	Lecithotrophic	ldLec
	Planktotrophic	ldPla
	Direct	ldDir
Morphology (m)	Exoskeleton	mExo
	Soft	mSoft
Egg development (ed)	Sexual shed eggs- pelagic	edPel
	Asexual/Budding	edAsex
	Sexual shed eggs – benthic	edBen
	Sexual brood eggs	edBrood
Living habit (lh)	Attached	lhAttach
	Tube-dwelling	lhTube
	Burrow-dwelling	lhBurrow
	Free-living	lhFree
	Epi/endo zoic/phytic	lhEpi
	Crevice/hole/under stone	lhCrevice
Mobility (mb)	Sessile	mbSessile
	Swimmer	mbSwim
	Burrower	mbBurrow
	Crawler/climber	mbCrawl
Position in the sediment (sp)	Surface	spSurf
	Infauna: 0-5cm	sp0-5
	Infauna: 6-10cm	sp6-10
	Infauna: >10cm	sp10

2.4.2.3 Functional diversity

Different indices were calculated to consider the different components of functional diversity. Therefore, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and Rao's quadratic entropy (RaoQ) were selected and calculated as they are considered complementary measurements of functional diversity attributes for different environments and assemblages (Gusmao et al., 2016). Functional dispersion (FDis) was not calculated because of its high collinearity with RaoQ. The latter was selected because it is more commonly used in ecological studies (Gusmao et al., 2016). Those indices were calculated with the 'FD' package (Laliberte & Legendre, 2010). The definitions of the different indices are provided in Appendix 1.

Besides those four indices, the community bioturbation potential (BPc) was also calculated according to the methodology proposed by Solan et al. (2004) and Queirós et al. (2013). This index is based on abundance (A_i), biomass (B_i) and information on sediment reworking (R_i) and mobility (M_i) of a species/taxon present in a sample. It is calculated by the formula below:

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

In order to allow the comparison with previous research conducted in the BPNS, abundance and biomass data were used as count per sample (0.1 m²) and not standardized value per m² (Breine et al., 2018). Moreover, AFDW data from Coastbusters 1.0 was converted to WW using weight-to-weight conversion factors from Van Hoey et al. (2014) and Ricciardi & Bourget (1998). When the required Ri and Mi values were not defined, values from taxonomically close species were used. Ri and Mi values were obtained from Breine et al. (2018) and Queirós et al. (2013).

2.4.3 Statistical analyses

Linear mixed models (LMM) were used to explore whether the mussel reef has an effect on the secondary production and functional diversity indices values between impact and control site. Site was chosen as a categorical fixed effect (two levels: reef and control) and season as categorical random effect (four levels: spring, summer, autumn, and spring). To meet the normality assumption, FRic and RaoQ were cubic transformed (x^3). The secondary production data and BPc were square root transformed before any further calculations. The non-parametric Scheirer-Ray-Hare test was used for FDiv as no transformations allowed to meet the normality assumption. For FEve, no transformation was needed as the residuals were normally distributed.

To determine whether hydrodynamic condition, site and their interaction have an effect on the benthic characteristics and functional diversity indices, linear mixed models with hydrodynamic condition (two levels: exposed and sheltered) and site (three levels: control, impact and edge) were chosen as categorical fixed effects and sampling campaign as categorical random effect (two levels: T0 and T1).

If the site factor or the interaction between site and hydrodynamic condition was significant, a post-hoc test with the Bonferroni method was performed to determine which group means differ from the others. To meet the normality assumption, the density, species richness, and biomass were log transformed and Simpson index values were cubic transformed (x^3) before any further calculations. No transformation was needed for Shannon index as the residuals were normally distributed. To meet the normality assumption for some of the functional diversity indices, BPc data was log transformed and FRic was square root transformed. As no transformation managed FDiv to meet the normality assumption, the non-parametric Scheirer-Ray Hare was used with hydrodynamic condition and site as factors. For the sediment characteristics, the median grain size was squared transformed (x^2) to meet the normality assumption. For all these tests, the normality and linearity of the residuals was tested by visual inspection of the residuals versus fitted values plot and with a Shapiro-Wilks test, and homogeneity of variances was checked using a Levene's test.

3. Results

3.1 Coastbusters 1.0

3.1.1 Secondary production estimates

The total annual secondary production of the mussel reef was higher (232.66 ± 41.54 kJ m^{-2} y^{-1}) than the control site (222.78 ± 25.77 kJ m^{-2} y^{-1}), but no statistically significant difference (p=0.9286) was found. An important temporal variability was observed with the periods T2 and T4 showing the highest values while the periods T0, T1 and T3 showed lower values (Figure 7). The two summer periods T0 and T2 shows different values, with T2 having a much higher value than T0. Both the reef (126.63 ± 19.86 kJ m^{-2} y^{-1}) and the control site (139.10 ± 26.13 kJ m^{-2} y^{-1}) showed minimum values at T1. Maximum value was found at T4 for the reef (427.56 ± 62.23 kJ m^{-2} y^{-1}) and T2 for the control site (505.24 ± 85.04 kJ m^{-2} y^{-1}).

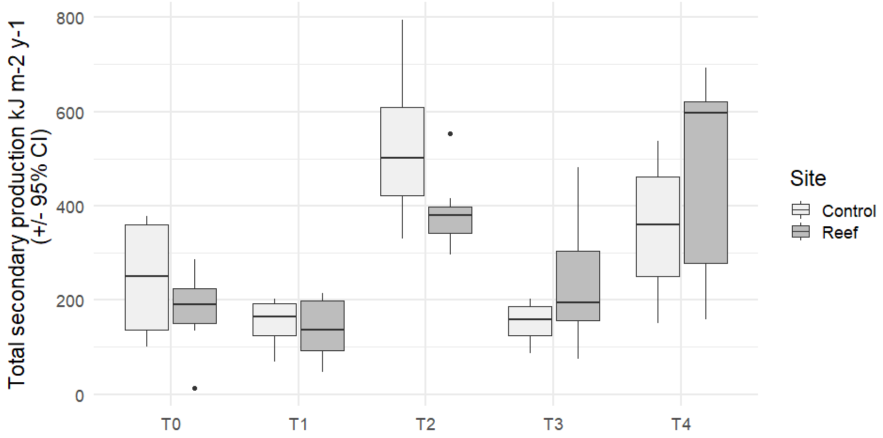


Figure 7: Total secondary production estimates (kJ m^{-2} y^{-1}) for the mussel reef and control site for each sampling campaign (T0 and T2: summer; T1 and T3: spring; T4: autumn).

No clear difference was found between the numerical contribution of the three productivity (P:B) classes to total abundance within the assemblages in the mussel reef and control site (Figure 8). Over the five sampling campaigns, the assemblages are always largely dominated by individuals with low productivity. In both reef and control site, a higher contribution of individuals with high productivity is noticeable for the sampling campaigns T2 and T4. The sampling campaigns T1 and T3 are almost entirely lacking individuals with high productivity.

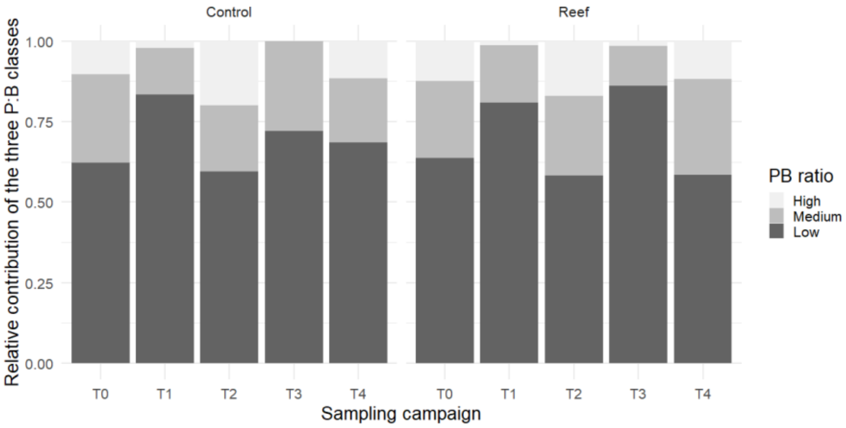
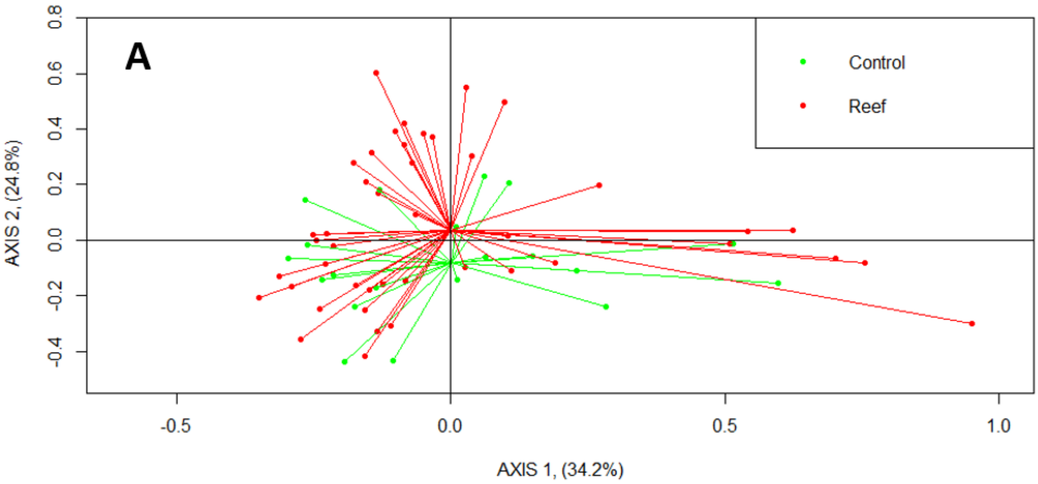


Figure 8: Relative contribution of the three productivity (P:B) classes to total abundance for the mussel reef and control site for each sampling campaign (T0 and T2: summer; T1 and T3: spring; T4: autumn).

3.1.2 Biological trait analysis

In the FCA, the first two axes accounted for 59% of the projected inertia (axis 1: 34.2% and axis 2: 24.8%) (Figure 9). The centroids of the two groups are mainly ordinated along the second axis but with relatively little separation between them (Figure 9A). On the one hand, the reef site has a greater numerical proportion of btNone (no bioturbation). On the other hand, the control site has a relatively greater numerical proportion of lhAttach (attached), l>10 (longevity longer than 10 years), lhEpi (Epi/endo zoic/phytic) and lhCrevice (Crevice/hole/under stone) (Figure 8B).



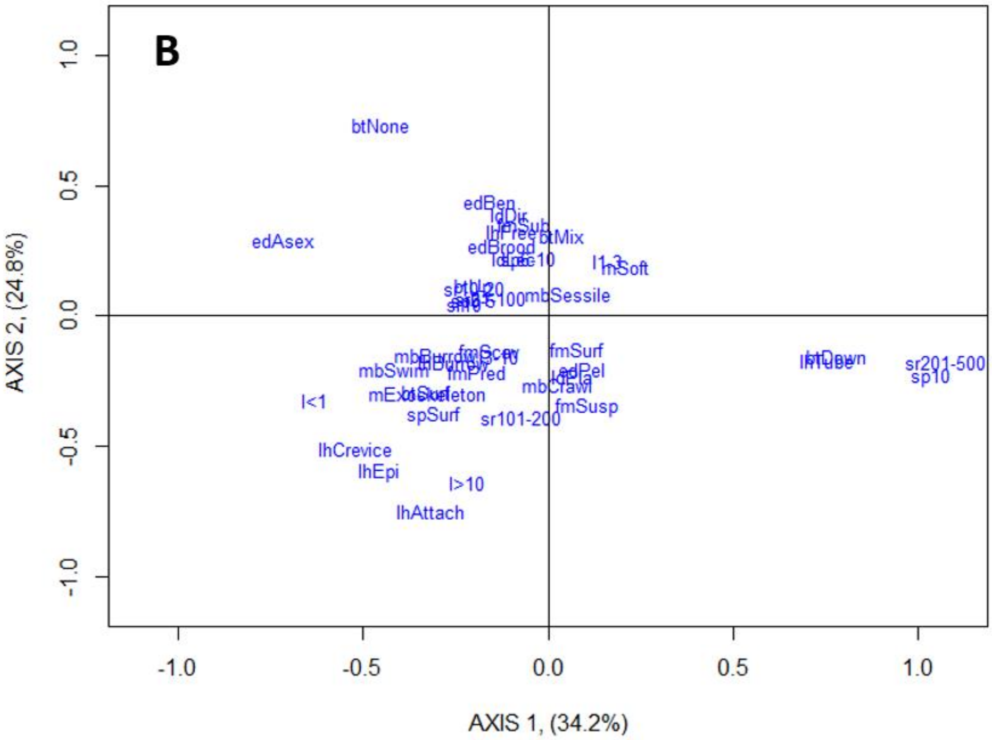


Figure 9: Two-dimensional biplots showing the dissimilarity between the mussel reef and control site based on their biological traits data ordinated along the two main axes of the Fuzzy Correspondence Analysis (FCA). The median location of the two sites is given by the centroid (the origin of the vector lines).

3.1.3 Functional diversity

A temporal variability could be observed for FRic and RaoQ but was less pronounced for FDiv and almost absent for FEve (Figure 10). No clear difference could be found between the mussel reef and the control site for FRic (no significant difference, p=0.186). This index was the highest at T2 for the reef site (10.22 ± 0.06) and at T0 for the control site (10.11 ± 0.16). Minimum values were found at T3 with 8.21 ± 0.40 and 8.30 ± 0.22 for the reef and control site, respectively. FEve values were similar with slightly changes over sampling campaigns and in most cases lowest in the control site (significant difference; p=0.01411). The highest value was recorded at T3 for the reef (0.65 ± 0.02) and T1 for the control site (0.61 ± 0.02). FEve presented minimum values at T4 (0.58 ± 0.02) and T2 (0.55 ± 0.03) for the mussel reef and control site, respectively. FDiv did not differ between the mussel bed and the control site (no significant difference, p=0.15577). The highest values of FDiv were found at T1 and T0 for both sites (0.90 ± 0.01). The lowest value was recorded at T3 for both sites (0.77 ± 0.02). The mussel reef had lower RaoQ than the control site (significant difference, p=0.00766). Like FRic, RaoQ had its highest values at T2 for the reef (0.71 ± 0.01) and T0 for the control site (0.71 ± 0.009). Minimum values were found at T3 with 0.58 ± 0.03 and T1 with 0.65± 0.003, for the reef and control site respectively. It is also important to point out that some outliers were detected for the different indices and may have influenced the results.

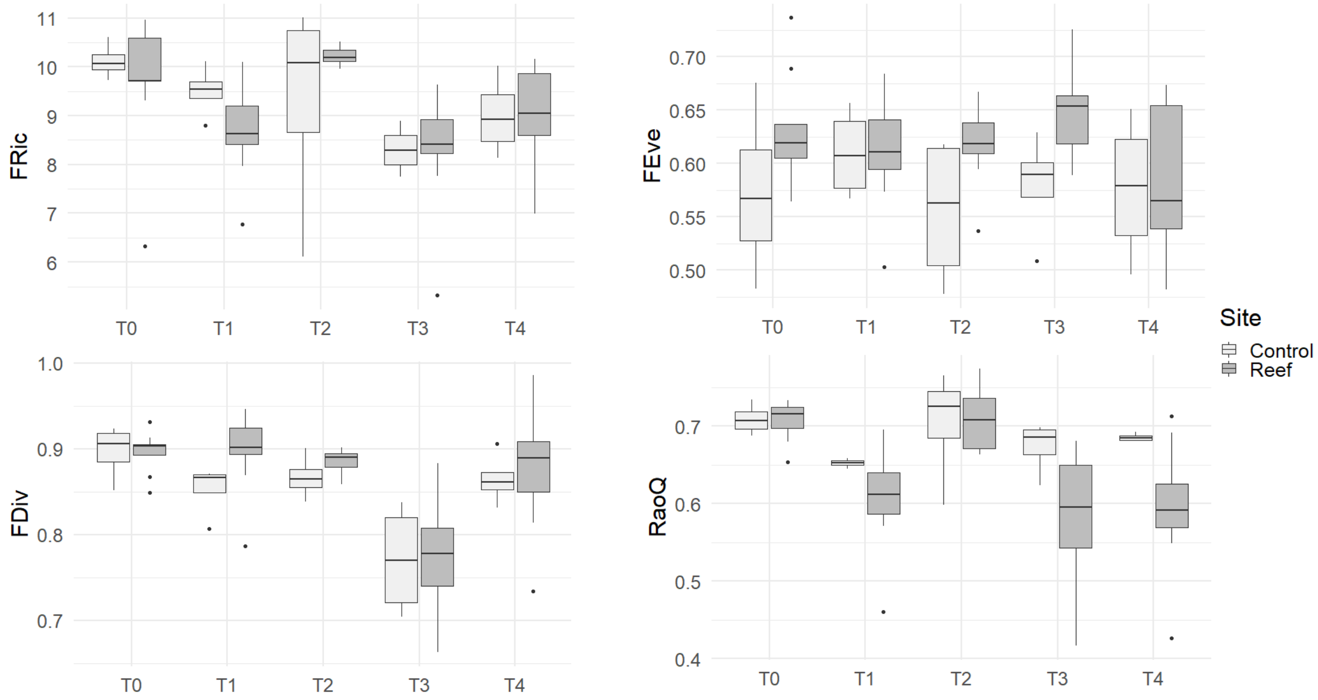


Figure 10: Functional richness (FRic), functional eveness (FEve), functional divergence (FDiv) and Rao's quadratic entropy (RaoQ) for the mussel reef and control site for each sampling campaign (T0 and T2: summer; T1 and T3: spring; T4: autumn).

The overall most important bioturbators were the same for the reef and the control site and were *Abra alba*, *Owenia* and *Echinocardium cordatum*. The reef (363.61±45.67) had an overall smaller BPc value than the control site (388.26±92.59). However, the BPc did not show any statistically significant difference (p=0.649829) between the mussel reef and the control site.

A temporal variability can clearly be observed for the BPc values with the highest values in summer (T0, T2) and the lowest values in autumn and spring (T4, T1 and T3) (Figure 11). The highest values were found for the mussel reef and the control site at T2 (721.29 ± 89.46; 918.32 ± 159.09). The reef had the lowest value at T1 (214.48 ± 46.74) and at T4 for the control site (177.66 ± 114.40).

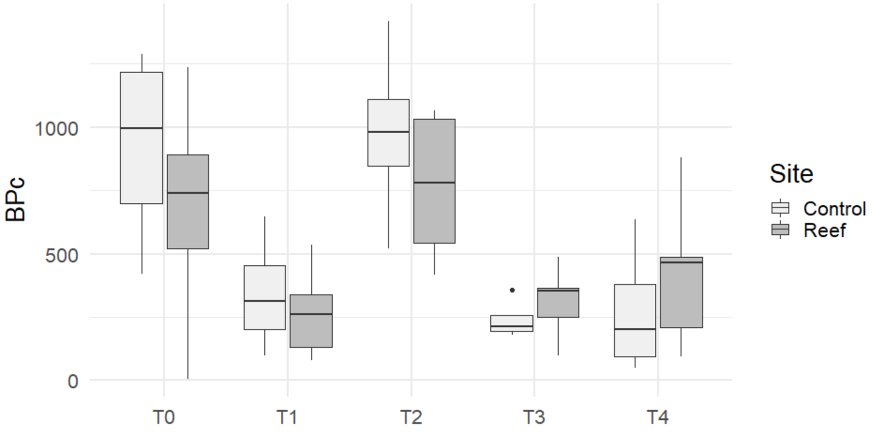


Figure 11: Bioturbation community potential (BPc) for the mussel reef and control site for each sampling campaign (T0 and T2: summer; T1 and T3: spring; T4: autumn).

3.2 Coastbusters 2.0

3.2.1 Assemblage structure

3.2.1.1 Density, diversity, and biomass

A total of 101 taxa were identified for the two sampling campaigns (Appendix 2). Density, species richness and biomass had higher values in the sheltered condition than in the exposed condition (significant differences: $p=3.582e^{-07}$, $p=1.275e^{-07}$ and $p=1.151e^{-09}$, respectively) (Figure 12). Site had a significant effect on the density and species richness (significant differences: p=0.01901, p=0.008909, respectively). The post-hoc tests for density and species richness revealed that the edge sites had higher values than the control sites (significant difference: p=0.0153, p=0.0100, respectively) (Figure 12). The density had its highest value at T0 in the sheltered edge site (24825.46±3977.29 ind.m-2) and its lowest value at T1 in the exposed control site (685.42±175.39 ind.m-2). Species richness had its highest and lowest values at T1, in the sheltered edge site with 34.70±0.89 species and in the exposed control site with 13±1.03 species. The interaction between hydrodynamic condition and site only affected the biomass (significant difference, p=0.006868). The post-hoc test revealed that, at the sheltered location, the control sites had lower values than the edge sites (significant difference, p=0.0051). The biomass was at its maximum and minimum at T0 in the edge sites, respectively in the sheltered condition (1943.78±249.35 g.m-2) and in the exposed condition (33.71±12.27 g.m-2). No significant differences for the hydrodynamic condition, site nor their interaction could be observed for the Shannon index. Simpson index had higher values for the exposed condition compared to the sheltered one (significant difference, p=0.008909) (Figure 12). The Simpson index had its highest and lowest value in the control site, respectively at T1 in the exposed condition (0.77±0.04) and t at T0 in the sheltered condition (0.46±0.08).

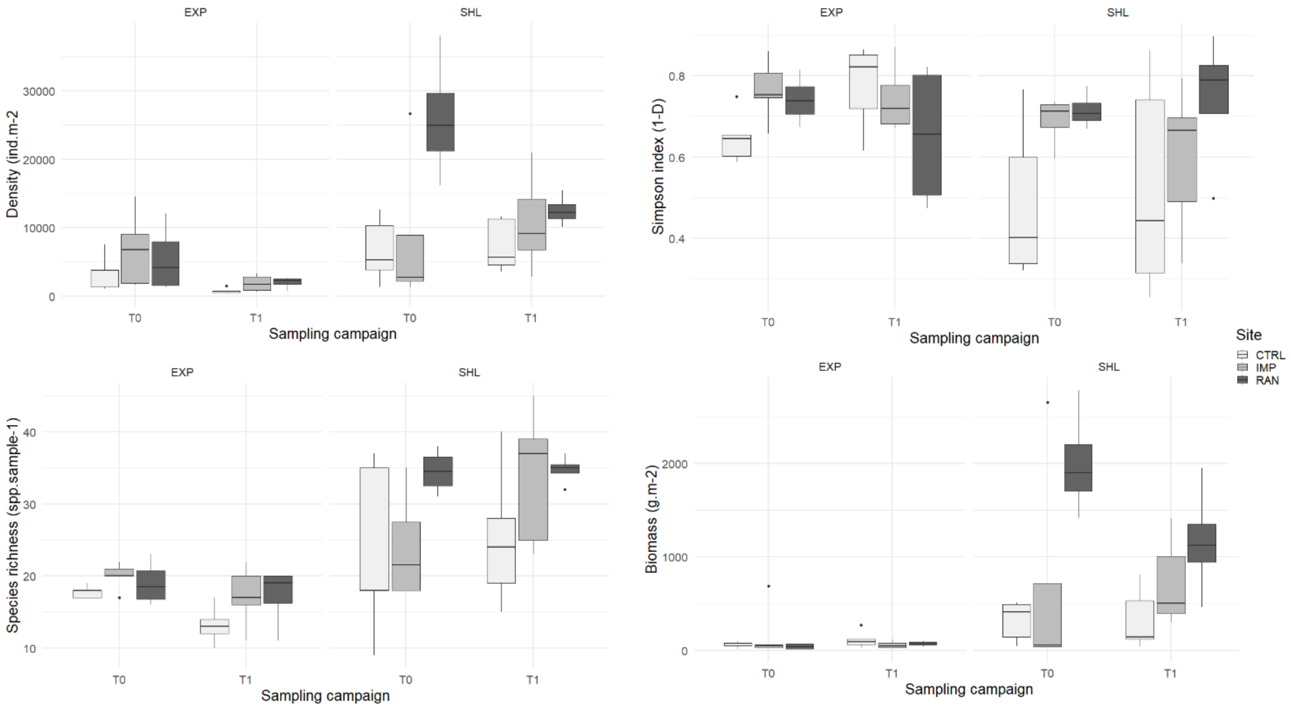


Figure 12: Effect of the hydrodynamic conditions on the density (ind.m^{-2}), species richness (spp.sample^{-1}), Simpson index (1-λ') and biomass (g.m^{-2}) for the impact (IMP), control (CTRL) and edge (RAN) sites at both sampling campaigns (T0 and T1).

3.2.1.2 Community composition

Macrobenthic community compositions were compared between both hydrodynamic conditions (exposed and sheltered) and sites (control, impact, and edge). The NMDS plot showed a clear separation between exposed and sheltered sites, as well as between the two time periods T0 and T1. However, no clear differences could be seen between the impact, control, and edge sites (Figure 13).

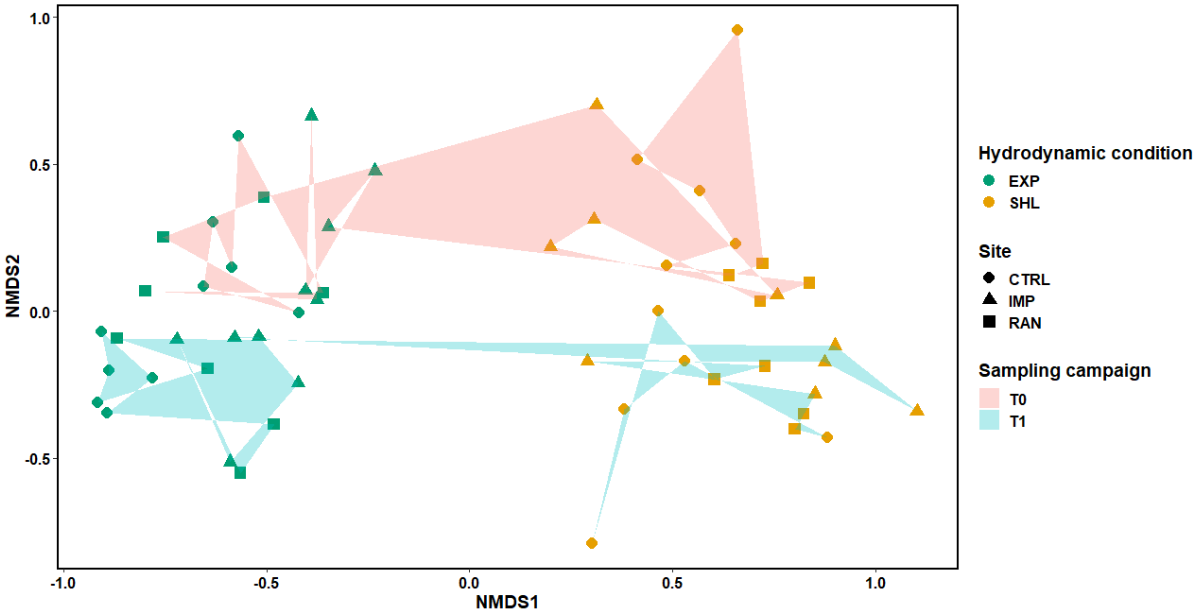


Figure 13: Non-metric multidimensional scaling (Bray-Curtis dissimilarity matrix) of macrobenthos abundance data separated by sites (IMP, CTRL and RAN), hydrodynamic conditions (EXP and SHL) and sampling campaigns (T0 and T1). Stress value: 0.17.

The PERMANOVA test revealed that the site (R^2=0.03965, p=0.016), the hydrodynamic condition (R^2=0.38407, p=0.001) and the sampling campaign (R^2=0.07224, p=0.001) have a significant effect on the community composition. Two of the interaction terms, hydrodynamic condition/sampling campaign (R^2=0.04822, p=0.003) and hydrodynamic condition/site (R^2=0.04568, p=0.008), also have a significant effect on the macrobenthos community. The R^2 values show that the hydrodynamics condition was the factor having the biggest contribution (38.41%) to the variance. The pairwise tests shows that there are no pairs of sites that differ in community composition (Table 4). This should be considered with caution as the number of observations is insufficient to make statistical inferences at a significant level of 0.05. The top five contributing taxa to the dissimilarities between sampling campaigns were Oligochaeta, *Spiophanes bombyx*, *Lanice*, *Magelona* juvenile and *Magelona johnstoni* while Oligochaeta, *Lanice*, *Spiophanes bombyx*, *Magelona johnstoni* and Cirratulidae were the top 5 taxa contributing to the dissimilarities between the hydrodynamic conditions. They contributed to 67.12% to the dissimilarity between the two sampling campaigns while 68.25% contributed to the dissimilarity between the exposed and sheltered areas. Oligochaeta was the main contributor to explain the differences between the two sampling campaigns (27.30%) and the exposed and sheltered areas (38.28%). The abundance of Oligochaeta was much higher in the sheltered sites compared to the the exposed sites, while it was only slightly different between the two time periods (Table 5).

Table 4: Results of the pairwise PERMANOVA showing the pairwise differences between impact, control, and edge sites.

Pairs	F.Model	R^2	p value
IMP vs RAN	0.8162624	0.02413816	0.5307
IMP vs CTRL	0.7368994	0.01952729	0.5800
RAN vs CTRL	1.6978802	0.04756249	0.1224

Table 5: Results of the SIMPER analysis showing the taxa that best discriminates between the samples collected at T0 and T1 (T1 vs T0) and between the exposed and sheltered sites (EXP vs SHL) across all time periods. The average abundances per variable and the contribution (%) to the overall dissimilarity between groups of the top 5 contributing taxa are also shown in the table.

	Top 5 contributing taxa	Av. abundances		Contribution (%)
		T1	**T0**	
T1 vs T0	Oligochaeta	2444.2857	2024.8148	27.30
	Spiophanes bombyx	233.9286	1238.5185	13.68
	Lanice	125.7143	2248.8889	9.78
	Magelona juvenile	1.4286	808.5185	8.28
	Magelona johnstoni	364.2857	426.2963	8.08
		EXP	**SHL**	
EXP vs SHL	Oligochaeta	2.5000	4557.0370	38.28
	Lanice	16.0714	2362.5926	9.33
	Spiophanes bombyx	1187.1429	250.0000	8.99
	Magelona johnstoni	724.6429	52.5926	6.24
	Cirratulidae	0.3571	778.5185	5.41

3.2.2 Assemblage functioning

3.2.2.1 Biological trait analysis

For the FCA, the first two axes explained 76.9% of the projected inertia (axis 1: 53.6% and axis 2: 23.3%) (Figure 14). The centroids of the six groups are mainly ordinated along the first axis with a clear separation between the exposed sites on the left and the sheltered sites on the right (Figure 14A). On the one hand, the trait attributes driving this pattern are mbBurrow (burrower) for the exposed sites (Figure 14B). On the other hand, the sheltered sites have a relatively greater numerical proportion of ldDir (direct larval development), edBrood (sexual brood eggs), lhCrevice (living in a crevice/hole/under stone) and edAsex (asexual/budding). While no separation between the three sites from the exposed area can be observed, there is a clear separation between the three sites of the sheltered area. The three groups are ordinated along the second axis in the following order: SHL_RAN, SHL_IMP and SHL_CTRL (Figure 14B). This separation can be explained by a greater numerical proportion of sp10 (position in the sediment deeper than 10cm), sr 201-500 (maximum body size between 201 – 500 mm) and btDown (downwards conveyor) in the SHL_RAN sites. A greater numerical proportion of edBrood (sexual brood eggs) and lDir (direct larval development) are found in the SHL_CTRL sites.

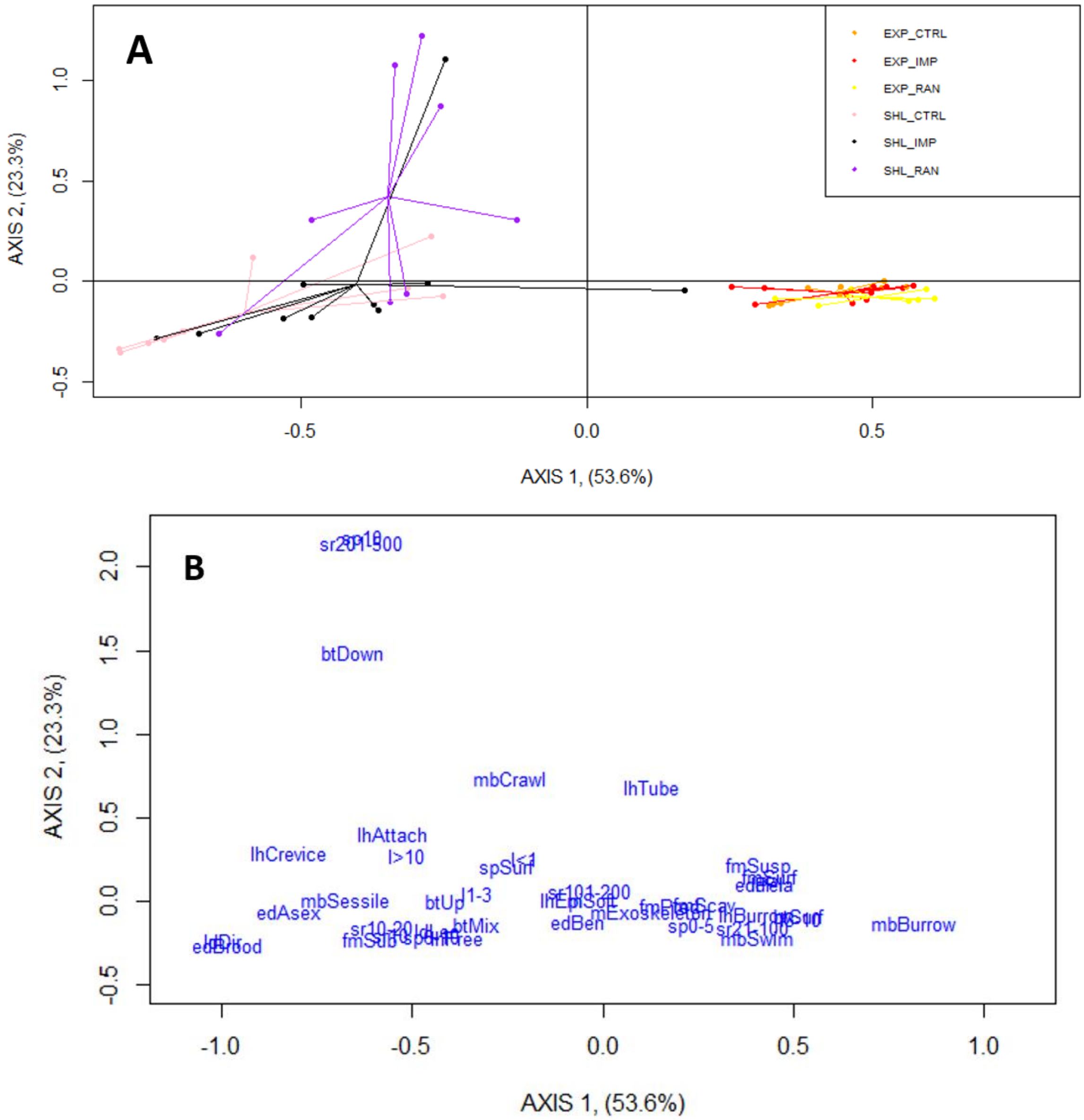


Figure 14: Two-dimensional biplots showing the dissimilarity between exposed and sheltered sites based on their biological traits data ordinated along the two main axes of the Fuzzy Correspondence Analysis (FCA). The median location of the sites is given by the centroid (the origin of the vector lines).

3.2.2.2 Functional diversity

Functional richness ($p=4.087e^{-06}$), functional evenness ($p=1.872e^{-05}$), functional divergence ($p=0.00004$), and Rao's quadratic entropy ($p=0.001157$) were all significantly affected by the hydrodynamic conditions. Although there is a significant difference between exposed and sheltered areas for all 4 indices, this difference is less marked for RaoQ. The exposed condition showed lower values than the sheltered condition for FRic, FEve, FDiv and RaoQ (Figure 15). The lowest values for FEve (0.42±0.03), FDiv (0.68±0.04) and RaoQ (0.27±0.05) were reached at T1 in the exposed edge site. The maximum values were reached at T1 for the sheltered control site (0.60±0.01) for FEve, at T0 for the sheltered impact site (0.94±0.02) for FDiv and at T1 for the sheltered impact site (0.60±0.02) for RaoQ. FRic had its lowest value and highest values at T0, respectively for the exposed control site

(3.99±0.27) and the sheltered edge site (10.06±0.50). It is also important to point out that some outliers were detected for the different indices and may have influenced the results.

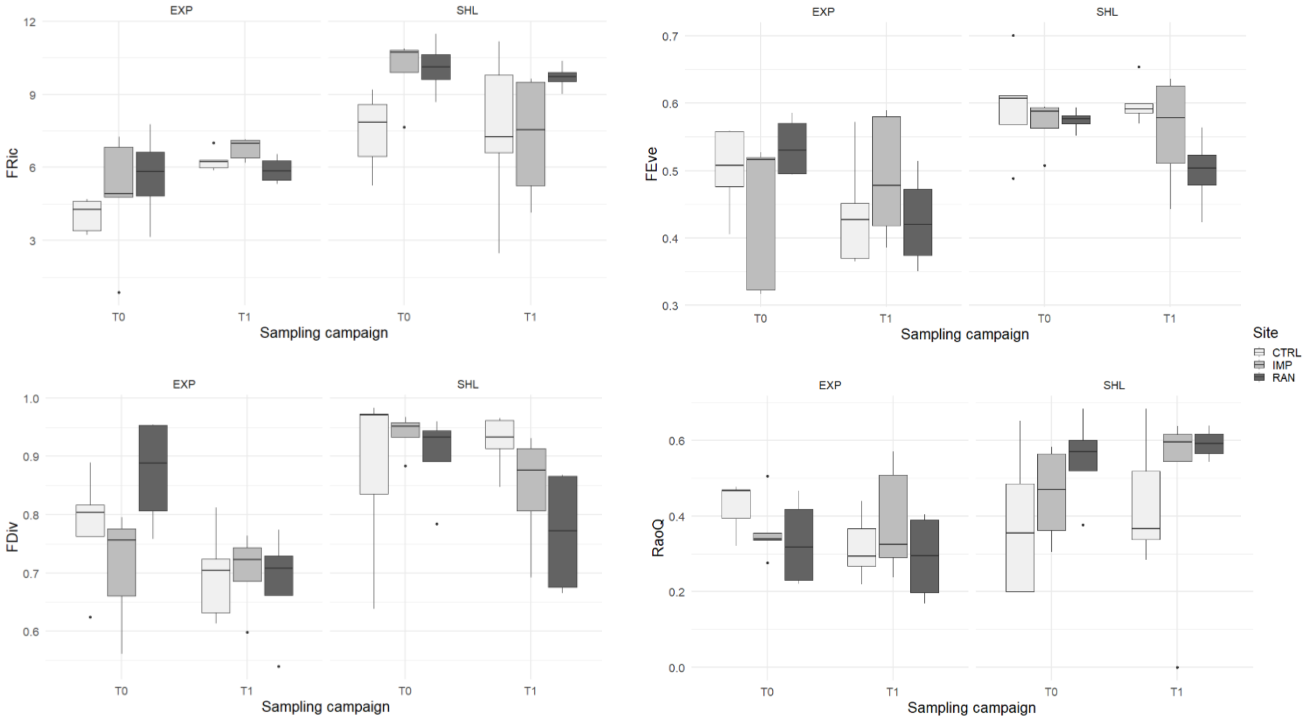


Figure 15: Effect of the hydrodynamic conditions on the functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and Rao's quadratic entropy (RaoQ) for the impact (IMP), control (CTRL) and edge (RAN) sites at both sampling campaigns (T0 and T1).

No temporal variability in the BPc could be observed (Figure 16). The overall most important bioturbators were *Nephtys cirrosa*, *Spiophanes bombyx* and *Tellina* for the exposed area while the most important ones were *Ensis*, *Lanice* and Oligochaeta for the sheltered area. The exposed condition had slightly lower values than the sheltered condition (significant difference, p=$7.486e^{-08}$). The site (p=0.009355) and the interaction between site and hydrodynamic condition (p=0.007387) had a significant effect on the community bioturbation potential. The post-hoc test for the site revealed that the control sites had in most cases lower values than the edge sites (significant difference, p=0.0104). The post-hoc test performed on the interaction showed that, at the sheltered condition, higher BPc values were found for the edge site compared to the impact (significant difference, p=0.0078) and the control site (significant difference, p=0.0015). The highest values were found both at T0, in the impact site for the exposed condition (123.90±49.87) and in the edge site for the sheltered condition (1277.77±229.90). The exposed condition had the lowest value at T1 for the control site (84.79±12.12) and at T0 in the impact site (121.38±324.13) for the sheltered condition.

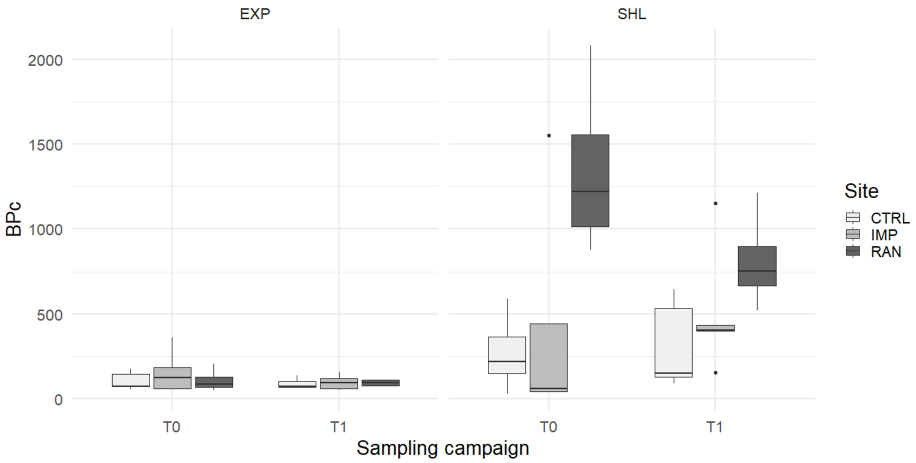


Figure 16: Bioturbation community potential (BPc) for the impact (IMP), control (CTRL) and edge (RAN) sites under the exposed (EXP) and sheltered (SHL) conditions at both sampling campaigns (T0 and T1).

3.2.3 Sediment characteristics

Sediment properties were the only abiotic factors that were quantitatively measured. A clear difference can be observed for the mud content percentages, with much higher mud content in the sheltered condition compared to the exposed condition (Figure 17). Mud content also varied greatly between the sites within the two hydrodynamic conditions. The mud content seems to have a temporal variability, with higher mud content present in T0 compared to T1. The maximum value was reached at T0 in the sheltered control site (20.27±7.77 %) while no mud content (0%) was found for the three sites at T1 in the exposed condition. The median grain size was higher in the exposed area (245.03±5.20 µm) than in the sheltered area (185.49±5.40 µm) (significant difference, $p=4.185e^{-12}$) and was relatively similar among sites in the same hydrodynamic condition (Figure 16). The median grain size reached its maximum and minimum at T0 in the control site, respectively in the exposed area (261.37±4.40 µm) and in the sheltered area (168.56±14.88 µm).

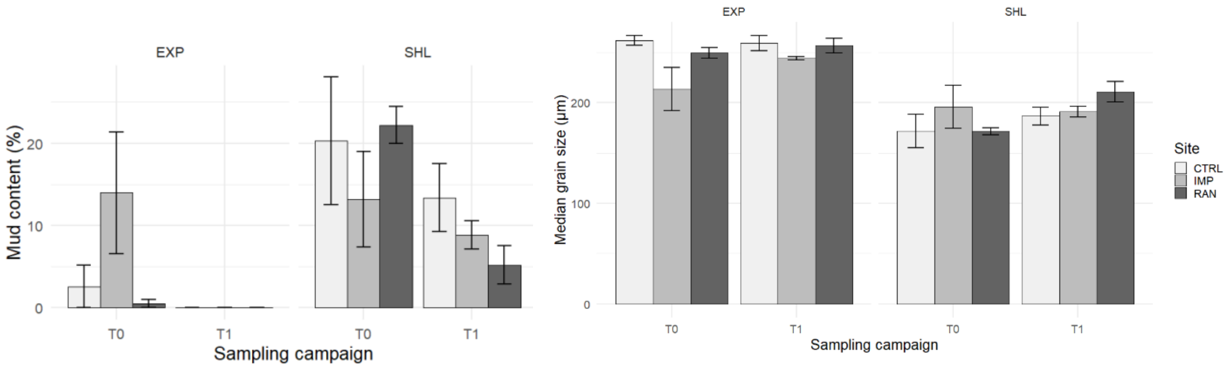


Figure 17: Mud content (0.01 µm < grain size < 63 µm) and median grain size (µm) for each site at the two hydrodynamic conditions for the two sampling campaigns (T0 and T1).

4. Discussion

One of the main objectives of the Marine Strategy Framework Directive (MSFD; 2008/56/EC) to achieve good environmental status is to ensure seafloor integrity at a level that safeguards both structural and functional aspects of benthic ecosystems (Van Hoey et al., 2010). Benthic macrofauna are an important component in ecosystem processes such as food web support to higher trophic levels and nutrient cycling. Moreover, as macrofauna are composed of species with different mobility, life cycle and tolerance to stress, they are important ecological indicator in environmental impact assessment (Patrício et al., 2009). Based on data gathered from Coastbusters 1.0 and 2.0, some observations and conclusions could be made on the spatio-temporal evolution of the macrobenthic communities to fully understand to what extent such newly created mussel reefs will impact the benthos under different environmental conditions.

4.1 Effects of the newly created mussel bed on macrofaunal communities

Mussel beds and suspended mussel cultures are known to influence the macroinvertebrate benthic communities through biodeposition and water filtration. In addition, mussel beds on soft-sediments provide a structurally complex habitat (McLeod et al., 2014; Ragnarsson & Raffaelli, 1999; Ysebaert et al., 2009). The biodeposition of organically enriched faeces and pseudo-faeces induce a change in the sedimentary habitat, which is a key descriptor for macrobenthic communities composition (Ysebaert et al., 2009). However, the results of Coastbusters 1.0 pilot project from Goedefroo (2020) showed little effects of the mussel bed and mussels on the longline dropper system on the structure of associated infaunal communities. Only diversity indices differed significantly between control and reef sites, with lower values observed in the reef site. Nevertheless, it was essential to take the study further and look at the potential effects of this newly created mussel bed on the functioning of macrobenthic assemblages. Indeed, following natural or anthropogenic disturbances, functional impacts on macrobenthic assemblages are not always matched by their structural counterparts (Bolam et al., 2016).

Secondary production studies have been recognized as an important tool to evaluate ecological changes in aquatic ecosystems due to environmental stress (Dolbeth et al., 2012). Although the total secondary production estimate of the infaunal assemblages in the mussel reef site was higher than in the control site, no significant difference was found. The community P:B (productivity) of the two sites was similar, with a higher proportion of low productive taxa and a relatively low proportion of medium and high productive taxa. This results in a reduced capacity to provide energy to the next trophic level (Bolam et al., 2016). While reef-building bivalves have been shown to have higher secondary production of the associated macrofauna than bare sands, this is the case for shellfish reef with no major seasonal fluctuations of the standing stock (Rodil et al., 2020; Wong et al., 2011). Moreover, Karp et al. (2018) concluded that macrofaunal productivity was high when the habitat complexity of shellfish was high.

The mussel bed at the Coastbusters 1.0 pilot site was not yet at such state, as it was characterized by a high seasonal variability and a limited habitat complexity as it was only present during the late summer months and the beginning of fall. Besides, the control sites (approximately 50m away from the mussel bed setup) were probably influenced by the mussels on the longline dropper system due to the relatively high local current velocity (Goedefroo, 2020). The non-persistence of the mussel bed throughout the year and the potential influence of the mussels on the control sites may provide an explanation to the absence of significant difference in secondary production estimates of macrofauna between the sites. Although the temporal variability was not statistically analysed, a seasonal variation was predominant. As for density and diversity, the highest values for secondary production were observed during the summer months while the lowest values were seen in the spring months, for both the control and reef sites (Goedefroo, 2020). A higher proportion of productive taxa was observed for the summer months, while the spring months were almost entirely lacking individuals with a high productivity. This seasonal variability is likely explained by larval recruitment and synergistic effects of factors like food quality and availability, water temperature, predation and hydrodynamical stress (Reiss & Kröncke, 2005).

While secondary production is an important metric for food web support, there are other essential functions that benthic organisms perform that are overlooked by this method and need to be investigated to understand the full extent of the potential impacts of anthropogenic or natural disturbances (Bolam et al., 2016). In this respect, it has been demonstrated that biological trait analysis is a useful tool to assess functioning in marine systems (Bremner, 2008). At the reef site, a high numerical presence of non-bioturbators was observed compared to the control site. This trait was one of the main traits responsible for most of the dissimilarity between the two sites. Based on these data, assemblages present at the control site had a greater bioturbatory capability relative to the reef site. The bioturbation potential community index (BPc) confirmed this, as it had lower values for the reef than for the control. However, no significant difference between the two sites was found.

Besides the importance of bioturbation traits in nutrient cycling and benthic-pelagic fluxes, lifespan, feeding behaviour and development mode are also important functional traits because of their relevance to the short- and long-term structure of macrofaunal assemblages (Pearson & Rosenberg, 1978). The control site possessed a higher proportion of long-lived (>10y) taxa, relative to the reef site. As longevity is closely linked with growth rates and energy turnover, the higher numerical proportion of organisms with longer longevity explains the lower energy turnover and then the slightly reduced secondary production in the control site compared to the reef site (Bolam et al., 2016). Taxa with longevity longer than 10y like *Ensis leei* or Anthozoa had a higher average abundance in the control sites and may perhaps be responsible of this result.

The production of faeces and pseudofaeces of mussels provides a rich food supply for deposit feeding organisms (Asmus, 1987), which was the main trophic guild in the reef site. In contrast, suspension feeding was the numerically dominant feeding mode in the control site. Organic matter has been shown to shape macrofauna functional traits by selecting for short-lived opportunistic fauna, like the oligochaetes, capable of deposit feeding (Dittmann, 1990; Lacson et al., 2019; Rodney & Paynter, 2006; Thiel & Ullrich, 2002). Thus, the proportion of long-lived suspension-feeding organisms decreases with organic matter content (Lacson et al., 2019). These observations from previous studies corroborate the results detailed above and the dominance of oligochaetes found by Goedefroo (2020).

Another important functional shift between both control and reef sites concerns the development mode. Indeed, direct development was the main development mode in the reef site and this trait was present in a relatively high proportion. A hypothesis put forward by Thiel and Ullrich (2002) suggests that organisms with direct development benefit from the interstitial spaces between the mussels as a shelter, for both parents and offspring. Therefore, large populations of species with direct development can be built because they directly release their offspring within the mussel bed.

The results of this study have shown that the mussel bed and the mussels on the longline dropper system in this pilot project caused a shift in bioturbation, feeding and development mode as well as longevity.

While BTA enables us to see changes for different types of traits, the analysis of functional diversity indices allows us to determine how the overall functioning is influenced. While functional richness and functional divergence did not show any difference between the reef and control site, the reef had higher functional evenness values than the control site. This result indicates a better utilization of the different niches in the mussel bed than in bare sediments. A more optimal occupation of the niche space can increase productivity, which is suggested by the slightly higher values of total secondary production estimate in the reef site (Llanos et al., 2020). Higher values of RaoQ were found in the control site which is consistent with the highest Simpson index values obtained in the control site by Goedefroo (2020). Indeed, RaoQ is a generalized form of Simpson diversity index, but taking into account functional dissimilarities between species from a community (Botta-Dukát, 2005). The lower values of RaoQ and Simpson index in the reef site might be the result of the oligochaetes starting to dominate the assemblages and contributing the most to the dissimilarities between sites (Goedefroo, 2020). The higher abundance of oligochaetes in the mussel bed may account for lower trait differentiation, and thus provide a hypothesis to the lower RaoQ values compared to the control site. As for the structural characteristics and secondary production estimates, a temporal variability was observed for FRic and RaoQ but was less pronounced for FDiv and almost absent for FEve. FRic and RaoQ followed the same pattern as the structural characteristics, with the highest values in the summer months and the lowest values in the spring months (Goedefroo, 2020). It was excepted as those two functional indices are closely related with macrobenthic species richness, abundance, and diversity.

The mussel bed influenced the diversity indices and functional diversity indices FEve and RaoQ. It was also responsible for minor shifts in longevity, bioturbation, feeding and development mode. These slight differences between the reef site and the control site are probably due to the modifications brought about by the mussel reef such as the modification of the organic content of the sediments and the provision of a more structurally complex habitat. Further studies with a permanent long-lasting mussel bed are needed to draw strong conclusions on the influence of biogenic reefs implementation on the structure and functioning of macrofaunal communities.

4.2 Effects of the hydrodynamic conditions on macrofaunal communities

As one of the goals of Coastbusters 2.0 is to determine the boundary conditions for the mussel bed development, two areas (nearshore and offshore) under different hydrodynamic conditions were selected to test the influence of the hydrodynamic climate. It is important to remember that the delayed experimental setups installation was delayed. Therefore, the major mussel spat recruitment was missed, leading to no mussel bed development at the two experimental areas on the seafloor during the summer and fall months. This thesis provides valuable information on the structural and functional characteristics of the existing macrobenthic communities under the two different hydrodynamic conditions. This baseline study is essential for the future of the project to understand if the mussel bed will induce any changes in the macrofaunal communities. The results of this thesis showed that the structural responses of infaunal assemblages to the different hydrodynamic climate were undeniable. Even though other parameters (site, sampling campaign, interaction between hydrodynamic condition/sampling campaign and hydrodynamic condition/site) also had an influence on the community composition, the hydrodynamic condition was the parameter contributing the most to the dissimilarities between stations at the nearshore and offshore areas (38% based on the PERMANOVA on community composition). Hydrodynamic condition was found to be a key descriptor for ecological richness, which includes, density, species richness and biomass. Those three parameters all had lower values in the exposed condition. This corroborates previous studies that showed higher density, species richness and biomass in low flow environments (Van Colen et al., 2010; van der Wal et al., 2017; Ysebaert et al., 2003). The two diversity indices used in this thesis were not similarly impacted by the hydrodynamic conditions. While Shannon index did not show any significant difference between exposed and sheltered areas, Simpson index had higher values in the exposed sites. On the one hand, the absence of significant differences for the Shannon index can be explained by the fact that, for a site with high species richness and low evenness, it may give you the same index value as a site with low richness but high evenness. On the other hand, Simpson index includes measures of evenness and species richness but gives greater weight to abundant species and is less sensitive to rare species than Shannon index. Therefore, higher evenness values found in the exposed condition might be explained by the dominance of some species in the sheltered sites, like Oligochaeta and *Lanice*. Both taxa contribute to almost half (47.51%) of the dissimilarity between the two hydrodynamic conditions. Those differences are also reflected in the differences in sediment composition between both sites, with higher mud content and lower median grain size in the sheltered sites compared to the exposed sites. It has been shown that organic carbon content increase with sediment mud content (Robertson et al., 2015). The model of Pearson and Rosenberg (1978) states that organically enriched sediment are dominated by opportunistic species. Therefore, the higher concentrations of organic matter found in sediments with a relatively high mud content are an explanation for the dominance patterns observed in the sheltered area and its lower Simpson index values than in the exposed site. These results clearly demonstrate the linkage between the hydrodynamic conditions and occurring sediment type, explaining the variability of benthic communities (Foulquier et al., 2020; Van Hoey et al., 2004).

The abiotic conditions which influence the environment are also important factors explaining the differences in the functional structure of macrobenthic communities. In exposed shallow subtidal areas, the strong hydrodynamic condition induce physical erosion and suspension of soft sediment which are factors known to favour assemblages dominated by active burrowers (Foulquier et al., 2020). The same conclusion was made from the biological trait analysis, with burrowers being the dominant trait in the exposed area, and responsible for most of the dissimilarity between the two hydrodynamic conditions.

Surface depositor and suspension feeding strategy were the main feeding guilds in the exposed area. While it was expected to have an important suspension feeder community due to their high dependency on higher oxygen concentration and the need of suspended particles in the water column for feeding purposes, it is surprising that surface deposit feeding was also an important feeding guild in the exposed area. Indeed, surface deposit feeders are usually associated with lower hydrodynamic condition as the strong currents limit their mobility and feeding (Foulquier et al., 2020; van der Wal et al., 2017). Although, other studies indicate that surface deposit feeders can also occur in high energy conditions (Dolbeth et al., 2009; Wildish and Kristmanson, 1997). It is also important to remember that the exposed area is located in the coastal zone, and therefore the hydrodynamic conditions at the exposed area, although more important compared to the sheltered area, are much less extreme than further offshore at sea. In response to food and flow conditions, several species may change their feeding mode (Dolbeth et al., 2009). The polychaetes *Spiophanes bombyx* and *Magelona johnstoni* were classified as surface deposit and suspension feeders and were two of the top five species contributing the most to the dissimilarity in community composition between the two hydrodynamic conditions. Their different trophic strategy may be a functional adaptation to different types of environmental conditions, and they may use only one feeding mode according to the hydrodynamics. This emphasizes a weakness of the trait classification regarding the lack of knowledge we have on traits that species exhibit in response to different environmental conditions (Bremner, 2008).

In addition to shifts in feeding and mobility modes, important differences in development mode are also present between the two hydrodynamic conditions. Indeed, the numerically dominant trait in the sheltered area was direct larval development, a type of development often observed in locations with limited planktonic food (Vance, 1973). As the sheltered condition is exposed to less stronger currents than the exposed, it was expected to find a dominance of this trait in the sheltered condition as less pelagic food is present. The main larval development mode in the exposed condition was planktotrophic, which agrees with the hypothesis above. Moreover, the numerical dominance of species with direct development in the sheltered area indicates higher environmental quality than in the exposed area as this mode of development requires a relatively stable environment (Llanos et al., 2020).

One of the most important traits of macrofauna species that influences ecosystem functioning is the bioturbation mode (Biles et al., 2002). Indeed, bioturbation, the biogenic modification of sediments through particle reworking, is a key factor in nutrient exchange across the sediment–water interface (Breine et al., 2018; Queirós et al., 2013; Volkenborn et al., 2007). To understand the differences in the various functional aspects between the exposed and sheltered conditions, the bioturbation potential of those areas was assessed by the calculation of the bioturbation potential community index BPc. This index had much lower values in the exposed condition than in the sheltered condition. Such result suggests reduced benthic-pelagic fluxes and nutrient cycling in the exposed area (Gusmao et al., 2016; van der Wal et al., 2017). Although the exposed area is dominated by burrowers which positively contribute to bioturbation (van der Wal et al., 2017), it is important to remember that BPc is positively correlated with abundance and biomass. Previous results demonstrate much higher values of those two structural characteristics in the sheltered area than in the exposed one. Thus, although some of the species present at the exposed sites have traits that benefit from bioturbation, the high abundance and biomass observed at the sheltered sites provide an explanation for the much higher BPc values.

In response to flow and food flux conditions, the above results illustrate shifts in mobility, trophic strategy, and development mode of the macrofauna communities. Those conclusions are corroborated by the study of the overall functional diversity which has been assessed by the indices' functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and Rao's quadratic entropy (RaoQ). They all behaved similarly to the hydrodynamic differences and indicated lower values in the exposed sites than in the sheltered sites. As FRic does not include information on relative abundances and is positively correlated with species richness, it was expected to find the same pattern as species richness which also had higher values in the sheltered area (Llanos et al., 2020). The lower FEve in the exposed area indicates that some parts of the niche space are under-utilized, indicating some redundancy in the functional traits among species and competition. A non-optimal use of the resources decrease the productivity and therefore food web support to higher trophic levels (Mason et al., 2005). The lower functional divergence in the exposed sites indicates assemblages with a lower relative abundance of species with extreme categories of functional traits (Gusmao et al., 2016). Therefore, this corroborates the results from FEve as it also suggests a lower niche differentiation in the exposed condition compared to the sheltered condition, and then more resource competition in strong hydrodynamic conditions (Mason et al., 2005). RaoQ is a measure based on the relative abundance of species in a community and some measure of trait dissimilarity among them. This index is highly correlated with Simpson index, but opposite results were found in this study. This is because the Simpson index used was 1-D which has the preferred property to increase with greater diversity as Shannon index. The Simpson index λ is the form used in RaoQ, explaining the opposite results for those two indices. The lower RaoQ values in the exposed condition suggests a community with low traits differentiation and low species abundance. The latter is confirmed by the analysis of the density with had much lower values in the exposed sites.

The integrated analysis of the four complementary functional diversity indices provided additional information to the biological trait analysis. While the BTA indicated a shift in the functional trait composition of the macrobenthic communities, the functional diversity indices revealed a lower functional diversity in the exposed area compared to the sheltered area. The main conclusion is that there is a better resource-use efficiency in the sheltered area, and therefore a more valuable ecosystem functioning (Cadotte et al., 2011).

4.3 Coastbusters 2.0: Monitoring applicability

4.3.1 Monitoring design

One of the main drawbacks of Coastbusters 1.0 was the location of the control sites. The latter were located only 50 meters away from the reef sites and may have experienced the influence of the bivalve reef setup (Goedefroo, 2020). For Coastbusters 2.0, the control sites were located 350m away from the bivalve reef survey area to avoid any potential influences from the reef on the control. Moreover, the control sites were located on the western side of the reef survey area, which avoids any influence from the reef as the area is subject to a northeast subsurface current. Due to the absence of mussel beds this year, the difference between the impact and control sites due to the reef effect could not be tested. However, a baseline characterization was done to assess potential differences between sites. No differences between control and impacts sites could be found for any of the structural and functional characteristics investigated previously. These results are reassuring because the absence of initial differences between the two sites will make it possible to better determine the influence of the mussel bed on the benthos in comparison with a control site not influenced by the latter.

4.3.2 Monitoring methods: Van Veen grabs vs Sediment Profile Imaging

To fully capture the dynamics of the newly created mussel beds and its influence on seafloor habitat and associated communities, Coastbusters 2.0 includes an important research component on the development of pioneering observation. Besides the traditional Van Veen grabs used in this thesis, Sediment Profile Imaging (SPI) and transect diving videos were used for the baseline monitoring of the exposed and sheltered areas (Lanza, 2021). The SPI is a camera delivering undisturbed images of the water-sediment interface and the presence of biotic structures (i.e. burrows, tubes) (Van Hoey et al., 2014). Such pictures can be analysed for biological, physical, and chemical parameters. Past studies have proven the usefulness of the combined use of benthic grabs and sediment-profile images to provide an accurate assessment of the biodiversity and functioning of benthic systems, as well as the response of those systems to disturbance (Birchenough et al., 2012; Van Hoey et al., 2014; Wilson et al., 2009). An important metric with regards to ecosystem functioning that can be derived from SPI images is the apparent redox discontinuity layer (aRPD), an estimate of the oxidized sediment depth. It is often related to BPc values, with deeper aRPDs associated with higher BPc values (Birchenough et al., 2012). However, Lanza (2021) found no differences in the aRPD between the two hydrodynamic conditions while the BPc index had much lower values in the exposed condition than in the sheltered condition. The absence of differences between the two hydrodynamic conditions is likely explained by the lack of a clear aRPD (only 29.52%) on the SPI pictures (Lanza, 2021). In contrast, tubeworms of *L. conchilega*, surface fauna, infauna, burrows, feeding mounds and pits were clearly more present in the sheltered area compared to the exposed one. This is corroborated by the higher macrofauna densities found in the sheltered condition. Moreover, community composition showed that *L. conchilega* was one of the dominant species in the sheltered area and was the taxon contributing the second most to the dissimilarities in community composition between the two hydrodynamic conditions. Based on a number of parameters retrieved from the SPI pictures, an adapted version of the Benthic Habitat Quality (BHQ) (Nilsson & Rosenberg, 1997) index was calculated. It uses the percentage of anoxic sediments rather than aRPD, which is an advantage in this case given the limited aRPD data collected from the SPI images. This index showed higher values in the sheltered area compared to the exposed area. Moreover, Pearson's correlation index between the number of *L. conchilega* and BHQ suggested a high degree of positive correlation (0.715) between those two parameters. The logarithmic regression showed that no other parameters had an influence on BHQ (Lanza, 2021). The dense *L. conchilega* aggregations responsible for a better habitat quality are also a likely explanation of the higher functional diversity (FRic, FEve, FDiv and RaoQ) in the sheltered condition. By increasing the structural complexity, those bio-builder polychaetes create more niches that can be utilized by species with different functional attributes (Rabaut et al., 2009).

Although the SPI has the advantage of being a quick tool with limited time and money needed for the analysis compared to the grab samples, the latter has the advantage of offering an extremely rich quantitative estimation of biological data (Van Hoey et al., 2014). Macrofauna density, diversity and biomass obtained with benthic grab samples can be used for structural characterization but also functional characterization if species traits datasets are available. While the information related to ecosystem functioning provided by SPI pictures mainly concerns bioturbation, trait-based approaches give more insight on additional aspects of functional diversity such as longevity, feeding or development mode. To conclude, each technique brings a different, yet complementary, approach to the assessment of physical, chemical and biological parameters that allow a better understanding of ecosystem processes (Birchenough et al., 2012; Van Hoey et al., 2014).

4.4 Considerations

The growing interest in nature-based solutions against coastal erosion offers interesting perspectives to tackle climate change and biodiversity erosion. However, the implementation of such solutions requires a rigorous environmental impact assessment protocol to ensure that no damage is caused to the existing habitat and associated communities. Metrics such as species richness, species diversity indices and distance-based ordination, like Bray Curtis, have been extensively used to assess human-driven disturbances on marine ecosystems. However, such metrics do not necessarily match their functional counterparts and therefore do not quantify the impacts on the functioning of the ecosystem (Bolam et al., 2016; Gusmao et al., 2016). Among the many different methods to assess functional diversity, biological trait analysis and functional diversity indices are the most commonly used methods and have been selected in this thesis (Gusmao et al., 2016). However, only an integrated approach to biological, chemical and physical components can truly provide a measure of benthic ecosystem functioning. BTA and functional diversity indices only provide a degree of information on the functioning of marine systems (Bremner, 2008). Therefore, the results obtained should be interpreted with the necessary caution. The success of those analyses depends on the reliability of underlying data, knowledge on natural history of marine taxa and the behaviour of species ‘traits to different environmental conditions (Bremner, 2008). Another aspect to consider cautiously when interpreting the results of this study is the sampling design. For Coastbusters 1.0, no fixed season or period in time was chosen for the sampling campaigns, therefore the seasonal variability within the samples possibly overshadowed the effects of the mussel bed on the infaunal communities. This issue has been solved in Coastbusters 2.0 where benthic grab samples will only ever be collected in fall. Furthermore, Coastbusters 1.0 and 2.0 datasets on which the LMM’s were performed were rather small in sample size which increases the chance of getting a type I error (i.e. rejecting a null. hypothesis when it is actually true) (Goedefroo, 2020). Longer time series and larger datasets, for example by sampling more replicates, may provide a better view on the structural and functional changes of macrobenthic communities due to biological and physical factors. Finally, it is important to consider that the mussel bed was non-persistent and only present for three months of the year. As changes in associated communities are triggered by changes in mussel density, patch size and bed thickness (Koivisto et al., 2011), the results of this study cannot be extended to a year-round persistent mussel bed. Further studies are needed to understand the influence of newly created mussel beds on structural and functional characteristics of associated benthic communities.

5. Conclusion

This thesis gives various insights on the influence of two different factors, mussel bed and hydrodynamic conditions, on the biodiversity and functioning of macrobenthic communities. It emphasizes the importance of combining structural and functional approaches to better understand the potential effects caused by physical and/or biological factors on macrofaunal communities. The monitoring design of Coastbusters 2.0 seems appropriate and the importance of using different methods to monitor the seafloor integrity was emphasized.

While the mussel bed had limited effects on the macrobenthic communities' structure and functioning, this thesis confirms that hydrodynamic conditions strongly affect the spatial distribution and the functional structure of macrobenthic fauna. Further studies with a permanent long-lasting mussel bed are needed to draw strong conclusions on the influence of biogenic reefs implementation for coastal protection on benthic ecosystems.

Acknowledgements

First, I would like to thank the Coastbusters consortium for letting me carry out this thesis on nature-based coastal protection. I learned a lot about this subject that was previously unknown to me. I wish to express my sincere gratitude to my supervisor Alexia Semeraro and my promoter Gert Van Hoey for their guidance throughout this thesis. Thank you, Alexia, for giving me the chance to participate in a Coastbusters sampling campaign. Thank you, Gert, for your suggestions and valuable feedback on my drafts throughout the project.

Thank you to all the macrobenthos lab at ILVO. I would like to express a special thanks to Jan Wittoeck for his supervision on my work on macrobenthos samples processing. Thank you for the training you gave me, your patience and for sharing your knowledge and passion for the macrofauna of the BPNS. A great thanks to Felien Festjens for all your help along this thesis, both for the processing of the samples and the data analysis. I do not think I would have been able to finish this thesis in time without your help.

A big thanks to my first semester biostatistics' assistant, Pieterjan Verhelst, who helped a lot for my statistical analyses all along this thesis. Thank you to Eric Thiebaut and Jean-Charles Leclerc for their help with functional diversity indices. Thank you to Kobus Langedock for the helpful tutorial on bathymetry mapping with QGIS.

I also want to thank Pablo Lanza, my friend, roommate, and fellow student working on the Diving Video Surveys and Sediment Profile Imaging for the Coastbusters 2.0 project. Thank you for being my driver to ILVO when I was invalid, your company, your advice, and your help. My experience at ILVO would definitely not have been the same without you.

To all people who have contributed to this thesis in one way or another, a much appreciated thank you.

Even though the pandemic made it not the best time to study an international master, I would like to thank everyone at the IMBRSea Coordination Office for making this master as enjoyable as possible during these difficult times.

Finally, I would like to thank my parents and brother for their support and interest in my research. Thank you for always believing in me and helping me to achieve my dreams.

References

Aaren S., F. (2007). Specificity of induced defenses in Mytilus edulis and asymmetrical predator deterrence. *Marine Ecology Progress Series*, *334*, 145–153. https://doi.org/10.3354/meps334145

Adger, N., & Coauthors including Fischlin, A. (2007). Summary for policymakers. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel of Climate Change (IPCC)*, *vii*, *973*, 7–22. https://doi.org/http://www.ipcc.ch/publications_and_data/ar4/wg2/en/spm.html

Airoldi, L., Abbiati, M., Beck, M. W., Hawkins, S. J., Jonsson, P. R., Martin, D., Moschella, P. S., Sundelöf, A., Thompson, R. C., & Åberg, P. (2005). An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coastal Engineering*, *52*(10–11), 1073–1087. https://doi.org/10.1016/j.coastaleng.2005.09.007

Armoškaitė, A., Puriņa, I., Aigars, J., Strāķe, S., Pakalniete, K., Frederiksen, P., Schrøder, L., & Hansen, H. S. (2020). Establishing the links between marine ecosystem components, functions and services: An ecosystem service assessment tool. *Ocean and Coastal Management*, *193*, 105229. https://doi.org/10.1016/j.ocecoaman.2020.105229

Asmus, H. (1987). Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. *Marine Ecology Progress Series*, *39*, 251–266. https://doi.org/10.3354/meps039251

Athanasiou, P., van Dongeren, A., Giardino, A., Vousdoukas, M. I., Ranasinghe, R., & Kwadijk, J. (2020). Uncertainties in projections of sandy beach erosion due to sea level rise: an analysis at the European scale. *Scientific Reports*, *10*(1), 11895. https://doi.org/10.1038/s41598-020-68576-0

Benham, P. (2020). The application of longline mussel aquaculture to establish subtidal reefs: New solutions in coastal defence.

Biest, K. Van Der, Meire, P., & Eiken, C. D. (2020). *Ecosystem services assessment of the COASTBUSTERS bivalve reef*. *020*, 1–33.

Biles, C. L., Paterson, D. M., Ford, R. B., Solan, M., & Raffaelli, D. G. (2002). Bioturbation, ecosystem functioning and community structure. *Hydrology and Earth System Sciences*, *6*(6), 999–1005. https://doi.org/10.5194/hess-6-999-2002

Birchenough, 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*(1), 8–16. https://doi.org/10.1016/j.ecolind.2011.03.015

Blackburn, S., Pelling, M., & Marques, C. (2019). Megacities and the Coast: Global Context and Scope for Transformation. In *Coasts and Estuaries: The Future*. Elsevier Inc. https://doi.org/10.1016/B978-0-12-814003-1.00038-1

Bolam, S. G., Barry, J., Bolam, T., Mason, C., Rumney, H. S., Thain, J. E., & Law, R. J. (2011).

Impacts of maintenance dredged material disposal on macrobenthic structure and secondary productivity. *Marine Pollution Bulletin*, *62*(10), 2230–2245. https://doi.org/10.1016/j.marpolbul.2011.04.012

Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M., & Stephens, D. (2014). Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. *Journal of Sea Research*, *85*, 162–177. https://doi.org/10.1016/j.seares.2013.05.003

Bolam, S. G., & Eggleton, J. D. (2014). Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. *Journal of Sea Research*, *88*, 47–58. https://doi.org/10.1016/j.seares.2014.01.001

Bolam, S. G., Garcia, C., Eggleton, J., Kenny, A. J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J. G., Sciberras, M., Smith, C., Papadopoulou, N., Gumus, A., Van Hoey, G., Eigaard, O. R., Bastardie, F., & Rijnsdorp, A. D. (2017). Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Marine Environmental Research*, *126*, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004

Bolam, S. G., McIlwaine, P. S. O., & Garcia, C. (2016). Application of biological traits to further our understanding of the impacts of dredged material disposal on benthic assemblages. *Marine Pollution Bulletin*, *105*(1), 180–192. https://doi.org/10.1016/j.marpolbul.2016.02.031

Bolam, Stefan G. (2012). Impacts of dredged material disposal on macrobenthic invertebrate communities: A comparison of structural and functional (secondary production) changes at disposal sites around England and Wales. *Marine Pollution Bulletin*, *64*(10), 2199–2210. https://doi.org/10.1016/j.marpolbul.2012.07.050

Bologna, P. A. X., Fetzer, M. L., McDonnell, S., & Moody, E. M. (2005). Assessing the potential benthic-pelagic coupling in episodic blue mussel (Mytilus edulis) settlement events within eelgrass (Zostera marina) communities. *Journal of Experimental Marine Biology and Ecology*, *316*(2), 117–131. https://doi.org/10.1016/j.jembe.2004.10.009

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, *16*(5), 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Breine, N. T., De Backer, A., Van Colen, C., Moens, T., Hostens, K., & Van Hoey, G. (2018). Structural and functional diversity of soft-bottom macrobenthic communities in the Southern North Sea. *Estuarine, Coastal and Shelf Science*, *214*(September), 173–184. https://doi.org/10.1016/j.ecss.2018.09.012

Bremner, J. (2008). Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology*, *366*(1–2), 37–47. https://doi.org/10.1016/j.jembe.2008.07.007

Brey, T., Rumohr, H., & Ankar, S. (1988). Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *Journal of Experimental Marine Biology and Ecology*, *117*(3), 271–278. https://doi.org/10.1016/0022-0981(88)90062-7

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. In *Journal of Applied Ecology* (Vol. 48, Issue 5, pp. 1079–1087). John Wiley & Sons, Ltd. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Callier, M. D., Richard, M., McKindsey, C. W., Archambault, P., & Desrosiers, G. (2009). Responses of benthic macrofauna and biogeochemical fluxes to various levels of mussel biodeposition: An in situ “benthocosm” experiment. *Marine Pollution Bulletin*, *58*(10), 1544–1553. https://doi.org/10.1016/j.marpolbul.2009.05.010

Chapman, M. G., & Bulleri, F. (2003). Intertidal seawalls - New features of landscape in intertidal environments. *Landscape and Urban Planning*, *62*(3), 159–172. https://doi.org/10.1016/S0169-2046(02)00148-2

CHEVENE, Fran., DOLEADEC, S., & CHESSEL, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, *31*(3), 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Coastbusters (2020). Coastbusters, ecosystem based coastal defence: A journey up to nature inspired solutions. https://www.blauwecluster.be/sites/default/files/coa_mar20_eindrapport_digitaal.pdf

Coolen, J. W. P., Boon, A. R., Crooijmans, R., van Pelt, H., Kleissen, F., Gerla, D., Beermann, J., Birchenough, S. N. R., Becking, L. E., & Luttikhuizen, P. C. (2020). Marine stepping-stones: Connectivity of Mytilus edulis populations between offshore energy installations. *Molecular Ecology*, *29*(4), 686–703. https://doi.org/10.1111/mec.15364

De Moor, G. (1979). Recent beach evolution along the Belgian North Sea coast. *Bulletin Societe Belge de Geologie de Paleontologie et d’Hydrologie, 88*, 143–157.

Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds). 2019. *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation*. Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management, 134 p.

Degraer, S., Moerkerke, G., Rabaut, M., Van Hoey, G., Du Four, I., Vincx, M., Henriet, J. P., & Van Lancker, V. (2008). Very-high resolution side-scan sonar mapping of biogenic reefs of the tube-worm Lanice conchilega. *Remote Sensing of Environment*, *112*(8), 3323–3328. https://doi.org/10.1016/j.rse.2007.12.012

Dittmann, S. (1990). Mussel beds - amensalism or amelioration for intertidal fauna? *Helgoländer Meeresuntersuchungen*, *44*(3–4), 335–352. https://doi.org/10.1007/BF02365471

Dolbeth, M., Cusson, M., Sousa, R., & Pardal, M. A. (2012). Secondary production as a tool for better understanding of aquatic ecosystems. In *Canadian Journal of Fisheries and Aquatic Sciences* (Vol. 69, Issue 7, pp. 1230–1253). NRC Research Press . https://doi.org/10.1139/F2012-050

Dolbeth, Marina, Teixeira, H., Marques, J. C., & Pardal, M. Â. (2009). Feeding guild composition of a macrobenthic subtidal community along a depth gradient. *Scientia Marina*, *73*(2), 225–237. https://doi.org/10.3989/scimar.2009.73n2225

Dolmer, P., & Stenalt, E. (2010). The impact of the adult blue mussel (Mytilus edulis) population on settling of conspecific larvae. *Aquaculture International*, *18*(1), 3–17. https://doi.org/10.1007/s10499-009-9266-2

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. *Marine Biology*, *162*(3), 675–685. https://doi.org/10.1007/s00227-015-2614-z

Donadi, S., van der Heide, T., Piersma, T., van der Zee, E. M., Weerman, E. J., van de Koppel, J., Olff, H., Devine, C., Hernawan, U. E., Boers, M., Planthof, L., & Klemens Eriksson, B. (2015). Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. *Oikos*, *124*(11), 1502–1510. https://doi.org/10.1111/oik.02100

Duarte, C. M., Dennison, W. C., Orth, R. J. W., & Carruthers, T. J. B. (2008). The charisma of coastal ecosystems: Addressing the imbalance. In *Estuaries and Coasts* (Vol. 31, Issue 2, pp. 233–238). Springer New York. https://doi.org/10.1007/s12237-008-9038-7

Eyster, L. S., & Pechenik, J. A. (1988). Attachment of Mytilus edulis L. larvae on algal and byssal filaments is enhanced by water agitation. *Journal of Experimental Marine Biology and Ecology*, *114*(2–3), 99–110. https://doi.org/10.1016/0022-0981(88)90131-1

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. https://doi.org/10.1155/2020/4674580

Fréchette, M., Butman, C. A., & Geyer, W. R. (1989). The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, Mytilus edulis L. *Limnology and Oceanography*, *34*(1), 19–36. https://doi.org/10.4319/lo.1989.34.1.0019

G. Van Hoey, J. Vanaverbeke, S. D. (2014). *STUDY RELATED TO THE REALIZATION OF THE WATER FRAMEWORK DIRECTIVE INTERCALIBRATION FOR THE BELGIAN COASTAL WATERS , TO DESIGN THE DESCRIPTIVE ELEMENTS 1 AND 6 OF THE MARINE STRATEGY FRAMEWORK DIRECTIVE AND THE NATURE OBJECTIVES OF THE HABITAT Study relate*.

Goedefroo, N. (2020). *The spatio-temporal evolution of a newly created mussel bed and its effects on benthic communities*. 2019–2020.

Gornitz, V. (1991). Global coastal hazards from future sea level rise. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *89*(4), 379–398. https://doi.org/10.1016/0031-0182(91)90173-O

Gracia, A., Rangel-Buitrago, N., Oakley, J. A., & Williams, A. T. (2018). Use of ecosystems in coastal erosion management. *Ocean and Coastal Management*, *156*, 277–289. https://doi.org/10.1016/j.ocecoaman.2017.07.009

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., Niiranen, S., & Winder, M. (2017). The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology*, *23*(6), 2179–2196. https://doi.org/10.1111/gcb.13642

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

Harley, C. D. G., Hughes, A. R., 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. In *Ecology Letters* (Vol. 9, Issue 2, pp. 228–241). John Wiley & Sons, Ltd. https://doi.org/10.1111/j.1461-0248.2005.00871.x

He, Q., & Silliman, B. R. (2019). Climate Change, Human Impacts, and Coastal Ecosystems in the Anthropocene. In *Current Biology* (Vol. 29, Issue 19, pp. R1021–R1035). Cell Press. https://doi.org/10.1016/j.cub.2019.08.042

Hinkel, J., Lincke, D., Vafeidis, A. T., Perrette, M., Nicholls, R. J., Tol, R. S. J., Marzeion, B., Fettweis, X., Ionescu, C., & Levermann, A. (2014). Coastal flood damage and adaptation costs under 21st century sea-level rise. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(9), 3292–3297. https://doi.org/10.1073/pnas.1222469111

Hinkel, J., Nicholls, R. J., Tol, R. S. J., Wang, Z. B., Hamilton, J. M., Boot, G., Vafeidis, A. T., McFadden, L., Ganopolski, A., & Klein, R. J. T. (2013). A global analysis of erosion of sandy beaches and sea-level rise: An application of DIVA. *Global and Planetary Change*, *111*, 150–158. https://doi.org/10.1016/j.gloplacha.2013.09.002

Houziaux, J. S., Fettweis, M., Francken, F., & Van Lancker, V. (2011). Historic (1900) seafloor composition in the Belgian-Dutch part of the North Sea: A reconstruction based on calibrated visual sediment descriptions. *Continental Shelf Research*, *31*(10), 1043–1056. https://doi.org/10.1016/j.csr.2011.03.010

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

Karp, M. A., Seitz, R. D., & Fabrizio, M. C. (2018). Faunal communities on restored oyster reefs: Effects of habitat complexity and environmental conditions. *Marine Ecology Progress Series*, *590*, 35–51. https://doi.org/10.3354/meps12470

Koivisto, M., Westerbom, M., & Riihimäki, A. (2011). Succession-driven facilitation of macrofaunal communities in sublittoral blue mussel habitats. *Marine Biology*, *158*(5), 945–954. https://doi.org/10.1007/s00227-010-1621-3

Kraus, N. C., & McDougal, W. G. (1996). The effects of seawalls on the beach: Part I, an updated literature review. *Journal of Coastal Research*, *12*(3), 691–701.

Kristmanson, D. W. and D. (1997). Benthic Suspension Feeders and Flow . David Wildish , David Kristmanson. In *Journal of the North American Benthological Society* (Vol. 17, Issue 1). https://doi.org/10.2307/1468062

Lacson, A. Z., Piló, D., Pereira, F., Carvalho, A. N., Cúrdia, J., Caetano, M., Drago, T., Santos, M. N., & Gaspar, M. B. (2019). A multimetric approach to evaluate offshore mussel aquaculture effects on the taxonomical and functional diversity of macrobenthic communities. *Marine Environmental Research*, *151*(June), 104774. https://doi.org/10.1016/j.marenvres.2019.104774

Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305. https://doi.org/10.1890/08-2244.1

Lappalainen, A., Westerbom, M., & Heikinheimo, O. (2005). Roach (Rutilus rutilus) as an important predator on blue mussel (Mytilus edulis) populations in a brackish water environment, the northern Baltic Sea. *Marine Biology*, *147*(2), 323–330. https://doi.org/10.1007/s00227-005-1598-5

Le Corre, N., Martel, A. L., Guichard, F., & Johnson, L. E. (2013). Variation in recruitment: Differentiating the roles of primary and secondary settlement of blue mussels Mytilus spp. *Marine Ecology Progress Series*, *481*, 133–146. https://doi.org/10.3354/meps10216

Lanza, P. (2021). Video and image analysis techniques to monitor mussel (*Mytilus edulis*) reef development under different hydrodynamic conditions.

Llanos, E. N., Saracho Bottero, M. A., Jaubet, M. L., Elías, R., & Garaffo, G. V. (2020). Functional diversity in the intertidal macrobenthic community at sewage-affected shores from Southwestern Atlantic. *Marine Pollution Bulletin*, *157*, 111365. https://doi.org/10.1016/j.marpolbul.2020.111365

Luijendijk, A., Hagenaars, G., Ranasinghe, R., Baart, F., Donchyts, G., & Aarninkhof, S. (2018). The State of the World’s Beaches. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-24630-6

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*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Masselink, G., & Russell, P. (2013). *Impacts of climate change on coastal erosion*. https://doi.org/10.14465/2013.arc09.071-086

McGrath, D., King, P., & Gosling, E. (1988). Evidence for the direct settlement of Mytilus edulis larvae on adult mussel beds. *Marine Ecology Progress Series*, *47*(Petersen 1984), 103–106. https://doi.org/10.3354/meps047103

McLeod, I. M., Parsons, D. M., Morrison, M. A., Van Dijken, S. G., & Taylor, R. (2014). Mussel reefs on soft sediments: A severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. *New Zealand Journal of Marine and Freshwater Research, 48*(1), 48–59. https://doi.org/10.1080/00288330.2013.834831

McMichael, C., Dasgupta, S., Ayeb-Karlsson, S., & Kelman, I. (2020). A review of estimating population exposure to sea-level rise and the relevance for migration. *Environmental Research Letters*, *15*(12). https://doi.org/10.1088/1748-9326/abb398

Meadows, P. S., Meadows, A., West, F. J. C., Shand, P. S., & Shaikh, M. A. (1998). Mussels and mussel beds (Mytilus edulis) as stabilizers of sedimentary environments in the intertidal zone. *Geological Society Special Publication*, *139*(1), 331–347. https://doi.org/10.1144/GSL.SP.1998.139.01.26

Moeser, G. M., Leba, H., & Carrington, E. (2006). Seasonal influence of wave action on thread production in Mytilus edulis. *Journal of Experimental Biology*, *209*(5), 881–890. https://doi.org/10.1242/jeb.02050

Morris, R. L., Konlechner, T. M., Ghisalberti, M., & Swearer, S. E. (2018). From grey to green: Efficacy of eco-engineering solutions for nature-based coastal defence. *Global Change Biology*, *24*(5), 1827–1842. https://doi.org/10.1111/gcb.14063

Narayan, S., Beck, M. W., Reguero, B. G., Losada, I. J., van Wesenbeeck, B., Pontee, N., Sanchirico, J. N., Ingram, J. C., Lange, G.-M., & Burks-Copes, K. A. (2016). The Effectiveness, Costs and Coastal Protection Benefits of Natural and Nature-Based Defences. *PLOS ONE*, *11*(5), e0154735. https://doi.org/10.1371/journal.pone.0154735

Neumann, B., Vafeidis, A. T., Zimmermann, J., & Nicholls, R. J. (2015). Future coastal population growth and exposure to sea-level rise and coastal flooding - A global assessment. *PLoS ONE*, *10*(3). https://doi.org/10.1371/journal.pone.0118571

Nilsson, H. C., & Rosenberg, R. (1997). Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment profile images. *Journal of Marine Systems*, *11*(3–4), 249–264. https://doi.org/10.1016/S0924-7963(96)00111-X

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

Norling, P, & Kautsky, N. (2008). Patches of the mussel Mytilus sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. *Aquatic Biology*, *4*(1), 75–87. https://doi.org/10.3354/ab00096

Norling, Pia, & Kautsky, N. (2007). Structural and functional effects of Mytilus edulis on diversity of associated species and ecosystem functioning. *Marine Ecology Progress Series*, *351*, 163–175. https://doi.org/10.3354/meps07033

Patrício, J., Neto, J. M., Teixeira, H., Salas, F., & Marques, J. C. (2009). The robustness of ecological indicators to detect long-term changes in the macrobenthos of estuarine systems. *Marine Environmental Research*, *68*(1), 25–36. https://doi.org/10.1016/j.marenvres.2009.04.001

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*(11), 3958–3985. https://doi.org/10.1002/ece3.769

Rabaut, M., Vincx, M., & Degraer, S. (2009). Do Lanice conchilega (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helgoland Marine Research*, *63*(1), 37–46. https://doi.org/10.1007/s10152-008-0137-4

Ragnarsson, S. Á., & Raffaelli, D. (1999). Effects of the mussel Mytilus edulis L. on the invertebrate fauna of sediments. *Journal of Experimental Marine Biology and Ecology*, *241*(1), 31–43. https://doi.org/10.1016/S0022-0981(99)00063-5

Reiss, H., & Kröncke, I. (2005). Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. *Estuarine, Coastal and Shelf Science*, *65*(1–2), 253–274. https://doi.org/10.1016/j.ecss.2005.06.008

Ricciardi, A., & Bourget, E. (1998). Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Marine Ecology Progress Series*, *163*, 245–251. https://doi.org/10.3354/meps163245

Riera, P., Stal, L., & Nieuwenhuize, J. (2004). Utilization of food sources by invertebrates in a man-made intertidal ecosystem (Westerschelde, the Netherlands): A δ13C and δ15N study. *Journal of the Marine Biological Association of the United Kingdom*, *84*(2), 323–326. https://doi.org/10.1017/S002531540400921Xh

Robertson, B. P., Gardner, J. P. A., & Savage, C. (2015). Macrobenthic-mud relations strengthen the foundation for benthic index development: A case study from shallow, temperate New Zealand estuaries. *Ecological Indicators*, *58*, 161–174. https://doi.org/10.1016/j.ecolind.2015.05.039

Rodil, I. F., Attard, K. M., Norkko, J., Glud, R. N., & Norkko, A. (2020). Estimating Respiration Rates and Secondary Production of Macrobenthic Communities Across Coastal Habitats with Contrasting Structural Biodiversity. *Ecosystems*, *23*(3), 630–647. https://doi.org/10.1007/s10021-019-00427-0

Rodney, W. S., & Paynter, K. T. (2006). Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology*, *335*(1), 39–51. https://doi.org/10.1016/j.jembe.2006.02.017

Rosenberg, R. (1978). Pearson TH , Rosenberg R .. Macrobenthic succession in relation to organic enrichment and pollution of the marine ... *Oceanography and Marine Biology: An Annual Review*, *16*(January), 229–331.

Smith, L. D., & Jennings, J. A. (2000). Induced defensive responses by the bivalve Mytilus edulis to predators with different attack modes. *Marine Biology*, *136*(3), 461–469. https://doi.org/10.1007/s002270050705

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*(5699), 1177–1180. https://doi.org/10.1126/science.1103960

Spalding, M. D., Ruffo, S., Lacambra, C., Meliane, I., Hale, L. Z., Shepard, C. C., & Beck, M. W. (2014). The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. *Ocean and Coastal Management*, *90*, 50–57. https://doi.org/10.1016/j.ocecoaman.2013.09.007

Speybroeck, J., Bonte, D., Courtens, W., Gheskiere, T., Grootaert, P., Maelfait, J. P., Mathys, M., Provoost, S., Sabbe, K., Stienen, E. W. M., Van Lancker, V., Vincx, M., & Degraer, S. (2006). Beach nourishment: An ecologically sound coastal defence alternative? A review. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *16*(4), 419–435. https://doi.org/10.1002/aqc.733

Sterckx, T., Lemey, E., Huygens, M., Fordeyn, J., Groenendaal, B., Delbare, D., Vanagt, T., Pycke, B., Semeraro, A., & Mascart, T. (2019). Coastbusters: Investigation of ecosystem based coastal stabilisation solutions. *22nd World Dredging Congress, WODCON 2019*, 813–822.

Sukhotin, A. A., Strelkov, P. P., Maximovich, N. V., & Hummel, H. (2007). Growth and longevity of Mytilus edulis (L.) from northeast Europe. *Marine Biology Research*, *3*(3), 155–167. https://doi.org/10.1080/17451000701364869

Temmerman, S., Meire, P., Bouma, T. J., Herman, P. M. J., Ysebaert, T., & De Vriend, H. J. (2013). Ecosystem-based coastal defence in the face of global change. *Nature*, *504*(7478), 79–83. https://doi.org/10.1038/nature12859

Thiel, M., & Ullrich, N. (2002). Hard rock versus soft bottom: The fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. *Helgoland Marine Research*, *56*(1), 21–30. https://doi.org/10.1007/s10152-001-0098-3

Turner, R. K., Burgess, D., Hadley, D., Coombes, E., & Jackson, N. (2007). A cost-benefit appraisal of coastal managed realignment policy. *Global Environmental Change*, *17*(3–4), 397–407. https://doi.org/10.1016/j.gloenvcha.2007.05.006

Underwood, A. J. (1992). Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology*, *161*(2), 145–178. https://doi.org/10.1016/0022-0981(92)90094-Q

United Nations (2017). Retrieved from https://www.un.org/sustainabledevelopment/wp-content/uploads/2017/05/Ocean-fact-sheet-package.pdf [24/01/21]

Van Colen, C., De Backer, A., Meulepas, G., Van Der Wal, D., Vincx, M., Degraer, S., & Ysebaert, T. (2010). Diversity, trait displacements and shifts in assemblage structure of tidal flat deposit feeders along a gradient of hydrodynamic stress. *Marine Ecology Progress Series*, *406*, 79–89. https://doi.org/10.3354/meps08529

Van der Heide, T., Tielens, E., van der Zee, E. M., Weerman, E. J., Holthuijsen, S., Eriksson, B. K., Piersma, T., van de Koppel, J., & Olff, H. (2014). Predation and habitat modification synergistically interact to control bivalve recruitment on intertidal mudflats. *Biological Conservation*, *172,* 163–169. https://doi.org/10.1016/j.biocon.2014.02.036

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., Birchenough, S. N. R., & Hostens, K. (2014). Estimating the biological value of soft-bottom sediments with sediment profile imaging and grab sampling. *Journal of Sea Research*, *86,* 1–12. https://doi.org/10.1016/j.seares.2013.10.010

Van Hoey, G., Borja, A., Birchenough, S., Buhl-Mortensen, L., Degraer, S., Fleischer, D., Kerckhof, F., Magni, P., Muxika, I., Reiss, H., Schröder, A., & Zettler, M. L. (2010). The use of benthic indicators in Europe: From the water framework directive to the marine strategy framework directive. *Marine Pollution Bulletin*, *60*(12), 2187–2196. https://doi.org/10.1016/j.marpolbul.2010.09.015

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*(4), 599–613. https://doi.org/10.1016/j.ecss.2003.11.005

Vance, R. R. (1973). More on reproductive strategies in marine benthic invertebrates. *American Naturalist*, *107*(955), 353–361. https://doi.org/10.1086/282839

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Volkenborn, N., Polerecky, L., Hedtkamp, S. I. C., Van Beusekom, J. E. E., & De Beer, D. (2007). Bioturbation and bioirrigation extend the open exchange regions in permeable sediments. *Limnology and Oceanography*, *52*(5), 1898–1909. https://doi.org/10.4319/lo.2007.52.5.1898

Walker, S. J., Schlacher, T. A., & Thompson, L. M. C. (2008). Habitat modification in a dynamic environment: The influence of a small artificial groyne on macrofaunal assemblages of a sandy beach. *Estuarine, Coastal and Shelf Science*, *79*(1), 24–34. https://doi.org/10.1016/j.ecss.2008.03.011

Wilcox, M., Kelly, S., & Jeffs, A. (2018). Ecological restoration of mussel beds onto soft-sediment using transplanted adults. *Restoration Ecology*, *26*(3), 581–590. https://doi.org/10.1111/rec.12607

Williams, A. T., Rangel-Buitrago, N., Pranzini, E., & Anfuso, G. (2018). The management of coastal erosion. In *Ocean and Coastal Management* (Vol. 156, pp. 4–20). Elsevier Ltd. https://doi.org/10.1016/j.ocecoaman.2017.03.022

Wilson, S. J. K., Fredette, T. J., Germano, J. D., Blake, J. A., Neubert, P. L. A., & Carey, D. A. (2009). Plan-view photos, benthic grabs, and sediment-profile images: Using complementary techniques to assess response to seafloor disturbance. *Marine Pollution Bulletin*, *59*(1–3), 26–37. https://doi.org/10.1016/j.marpolbul.2008.11.019

Wong, M. C., Peterson, C. H., & Piehler, M. F. (2011). Evaluating estuarine habitats using secondary production as a proxy for food web support. *Marine Ecology Progress Series*, *440*, 11–25. https://doi.org/10.3354/meps09323

Ysebaert, T., Herman, P. M. J., Meire, P., Craeymeersch, J., Verbeek, H., & Heip, C. H. R. (2003). Large-scale spatial patterns in estuaries: Estuarine macrobenthic communities in the Schelde estuary, NW Europe. *Estuarine, Coastal and Shelf Science*, *57*(1–2), 335–355. https://doi.org/10.1016/S0272-7714(02)00359-1

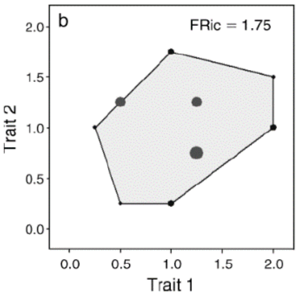
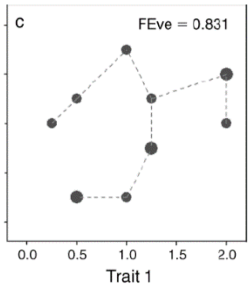
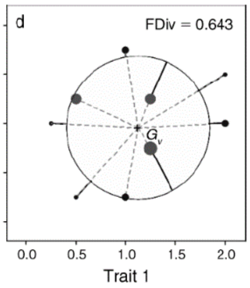
Ysebaert, Tom, Hart, M., & Herman, P. M. J. (2009). Impacts of bottom and suspended cultures of mussels Mytilus spp. on the surrounding sedimentary environment and macrobenthic biodiversity. *Helgoland Marine Research*, *63*(1), 59–74. https://doi.org/10.1007/s10152-008-0136-5

Ysebaert, Tom, Walles, B., Haner, J., & Hancock, B. (2018). Habitat modification and coastal protection by ecosystem-engineering reef-building bivalves. In *Goods and Services of Marine Bivalves* (pp. 253–273). Springer International Publishing. https://doi.org/10.1007/978-3-319-96776-9_13

Appendix

Appendix 1: Functional diversity indices.

Representations from Villéger et al., 2008.

Index	Label	Definition	Method of calculation
Functional richness	FRic	FRic measures how much of the niche space is filled by species present in the community. In the case of a 2-traits space, FRic is the surface filled by the community (i.e. convex hull area). This index is positively correlated with species richness.	
Functional evenness	FEve	FEve measures both the regularity of spacing between species in the multidimensional trait space and evenness in the distribution of species abundance or biomass in the trait space. On the one hand, a high FEve suggests an optimal use of resources and could result in higher stability and resilience. On the other hand, a low FEve suggests that the community is composed of clusters of species indicating some redundancy among species and competition.	
Functional divergence	FDiv	FDiv represents how abundance or biomass is dispersed in the multidimensional trait space. FDiv is low when the most abundant species have functional traits that are close to the centre of gravity of the functional space. It is high when the most abundant species have extreme trait values.	
Rao's quadratic entropy	RaoQ	RaoQ is the most common multivariate index. It is based on the Simpson diversity index and weighs the trait-based distances between pairs of species by the product of their relative abundance. RaoQ is high when a community has	RaoQ is calculated according to this formula: $RaoQ = \sum_{i}^{S} \sum_{j}^{S} dij\ pi\ pj$ with S, the number of species in an assemblage, d_{ij}, the

		high traits differentiation and high species abundance.	dissimilarity of species i and j, p_i, the proportion of species i and p_j the proportion of species j

Appendix 2: Macrobenthic species list of Coastbusters 2.0

Taxonomic group	**Taxon**
Amphipoda	*Abludomelita obtusata*
Amphipoda	*Aora gracilis*
Amphipoda	*Apolochus neapolitanus*
Amphipoda	*Bathyporeia elegans*
Amphipoda	*Bathyporeia guilliamsoniana*
Amphipoda	*Bathyporeia juv*
Amphipoda	*Corophium*
Amphipoda	*Corophium* juv
Amphipoda	*Jassa*
Amphipoda	*Leucothoe incisa*
Amphipoda	*Megaluropus agilis*
Amphipoda	*Microprotopus maculatus*
Amphipoda	*Nototropis swammerdamei*
Amphipoda	*Pariambus typicus*
Amphipoda	*Perioculodes longimanus*
Amphipoda	*Pontocrates*
Amphipoda	*Stenothoe monoculoides*
Amphipoda	*Tryphosella sarsi*
Amphipoda	*Urothoe brevicornis*
Amphipoda	*Urothoe* juv
Amphipoda	*Urothoe poseidonis*
Anthozoa	Anthozoa
Bivalvia	*Abra alba*
Bivalvia	*Aequipecten opercularis*
Bivalvia	*Donax vittatus*
Bivalvia	*Ensis*
Bivalvia	*Kurtiella bidentata*
Bivalvia	*Limecola balthica*
Bivalvia	*Mulinia lateralis*
Bivalvia	*Mya truncata*
Bivalvia	*Mytilus*
Bivalvia	*Spisula*
Bivalvia	*Tellimya ferruginosa*
Bivalvia	*Tellina*
Bivalvia	*Venerupis corrugata*
Cumacea	*Bodotria*
Cumacea	*Diastylis bradyi*
Cumacea	*Diastylis rathkei*
Cumacea	*Monopseudocuma gilsoni*
Cumacea	*Pseudocuma longicorne*
Decapoda	*Brachyura*
Decapoda	*Callianassa*
Decapoda	*Hippolyte varians*
Decapoda	*Liocarcinus*
Decapoda	*Liocarcinus holsatus*
Decapoda	*Liocarcinus navigator*
Decapoda	*Liocarcinus vernalis*
Decapoda	*Pisidia longicornis*
Decapoda	*Processa modica*
Decapoda	*Thia scutellata*
Echinodermata	*Echinocardium cordatum*
Echinodermata	*Ophiura juv*
Echinodermata	*Ophiura ophiura*
Gastropoda	*Crepidula fornicata*
Gastropoda	*Tritia reticulata*
Mysida	*Gastrosaccus spinifer*
Oligochaeta	Oligochaeta
Polychaeta	*Aonides oxycephala*
Polychaeta	*Aonides paucibranchiata*
Polychaeta	*Capitella*
Polychaeta	*Cirratulidae*
Polychaeta	*Dorvilleidae*
Polychaeta	*Eteone*
Polychaeta	*Eumida*
Polychaeta	*Eunereis longissima*
Polychaeta	*Glycera* juv
Polychaeta	*Glycera tridactyla*

Polychaeta	*Harmothoe*
Polychaeta	*Heteromastus filiformis*
Polychaeta	*Lagis koreni*
Polychaeta	*Lanice*
Polychaeta	*Magelona johnstoni*
Polychaeta	*Magelona* juv
Polychaeta	*Malmgrenia* juv
Polychaeta	*Mediomastus fragilis*
Polychaeta	*Myrianida*
Polychaeta	*Nephtys assimilis*
Polychaeta	*Nephtys caeca*
Polychaeta	*Nephtys cirrosa*
Polychaeta	*Nephtys hombergii*
Polychaeta	*Nephtys* juv
Polychaeta	*Nereis* juv
Polychaeta	*Notomastus latericeus*
Polychaeta	*Owenia fusiformis*
Polychaeta	*Pholoe*
Polychaeta	*Phyllodoce mucosa*
Polychaeta	*Phyllodoce rosea*
Polychaeta	*Poecilochaetus serpens*
Polychaeta	*Polydora*
Polychaeta	*Prionospio*
Polychaeta	*Proceraea*
Polychaeta	*Pseudopolydora pulchra*
Polychaeta	*Pygospio elegans*
Polychaeta	*Scoloplos armiger*
Polychaeta	*Sigalion mathildae*
Polychaeta	*Spio*
Polychaeta	*Spiophanes bombyx*
Polychaeta	*Spirobranchus*
Polychaeta	*Sthenelais* boa
Sipuncula	Sipuncula
Tainaidacea	*Tanaissus lilljeborgi*