



Variation in ecosystem services within biogenic reefs: The role of reef-building species under distinct hydrodynamic conditions

Rémi Dupont^{a,*}, Alexia Semeraro^{b,1}, Brecht Stechele^c, Tomas Sterckx^d, Gert Van Hoey^b, Thomas Vandorpe^e, Katrien Van der Biest^a

^a ECOSPHERE Research Group, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

^b Flanders Research Institute for Agriculture, Fisheries and Food (ILVO), Jacobsenstraat 1, 8400 Ostend, Belgium

^c Royal Belgian Institute of Natural Sciences (RBINS), Marine Ecology and Management (MARECO), Vautierstraat 29, 1000 Brussels, Belgium

^d Dredging, Environmental & Marine Engineering NV (DEME), Haven 1025, Scheldedijk 30, 2070 Zwijndrecht, Belgium

^e Flanders Marine Institute (VLIZ), Jacobsenstraat 1, 8400 Ostend, Belgium

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ABSTRACT

To enhance the climate resilience of coastlines, measures are being implemented to protect and restore coastal ecosystems, such as biogenic reefs and dunes. These measures, known as Nature-based Solutions (NbS), provide protection against storms, coastal erosion, and flooding. They are also recognised for increasing biodiversity and delivering a range of ecosystem services (ES). This study investigated the ES provided by biogenic reefs composed of two reef-building species (*Mytilus edulis* and *Lanice conchilega*) under distinct hydrodynamic conditions. Three ES were assessed at two sites in the Belgian part of the North Sea: (1) coastal protection, (2) carbon sequestration, and (3) water quality regulation. The two sites have different hydrodynamic conditions due to their relative locations in relation to local sandbanks, making one site more exposed and the other more sheltered. The ES were quantified and monetised using in-situ measurements and literature data based on the Sustainable Marine Ecosystem Services (SUMES) model. The results suggest that the provision of ES in biogenic reefs is determined by multiple factors, including environmental conditions (e.g. hydrodynamics) and reef-building species. (1) Sediment accumulation was only observed under low hydrodynamic conditions, due to the higher settlement success of *M. edulis* and the presence of *L. conchilega*. (2) *M. edulis* “produces” carbon under both low and high hydrodynamic conditions, due to high respiration and biocalcification rates. However, low hydrodynamic conditions are more conducive to carbon burial, thus enhancing carbon sequestration. (3) *M. edulis* patches exhibited higher denitrification rates under low hydrodynamic conditions than under high hydrodynamic conditions or in *L. conchilega* patches, due to divergent macrobenthic functional diversity. In conclusion, the level of ES provision is determined by location and associated environmental conditions, as well as temporal and spatial variation in biogenic reefs and the physiological characteristics of reef builders. Therefore, both aspects need to be carefully considered when planning coastal protection measures and determining the provision of ES. Finally, when implementing NbS along high-energy coastlines, sheltered sites should be prioritised.

1. Introduction

As coastal areas become increasingly vulnerable to erosion and flooding due to climate change, the implementation of sustainable solutions to build climate-resilient coastlines is paramount (Morris et al., 2018; Narayan et al., 2016; Temmerman et al., 2013). Traditional approaches to coastal defence include the use of hard engineering, such as

sea walls, groynes, and breakwaters, and soft engineering, such as beach nourishment (de Schipper et al., 2020; Morris et al., 2018). A combination of both approaches is also common. Although they are usually effective, traditional approaches are expensive and unsustainable due to the need for regular maintenance (Morris et al., 2018; Reguero et al., 2018; Sutton-Grier et al., 2015). In addition, the implementation of hard engineering can lead to habitat fragmentation, disruption of natural

* Corresponding author.

E-mail address: remi.dupont@uantwerpen.be (R. Dupont).

¹ Current affiliation: BLUEGent Innovations in Aquaculture & Blue Life Sciences, Coupure Links 653 - Blok F, 9000 Gent, Belgium.

dynamics (Walker et al., 2008), and the transformation of a natural coastline into a uniform habitat. This can result in changes to local and regional biodiversity and favour non-native species (Airoldi et al., 2015; Bulleri and Chapman, 2010). In contrast, beach nourishment (i.e. soft engineering) requires large amounts of sand, which can cause disturbances at the dredging and placement sites (de Schipper et al., 2020; Goedefroo et al., 2023; Wyns et al., 2021).

In recent years, the use of Nature-based Solutions (NbS) for coastal protection has therefore received increasing attention. Although NbS can be used independently, they are usually used alongside traditional coastal protection measures. NbS have been defined as “actions to protect, conserve, restore, sustainably use and manage natural or modified terrestrial, freshwater, coastal and marine ecosystems which address social, economic and environmental challenges effectively and adaptively, while simultaneously providing human well-being, ecosystem services, resilience and biodiversity benefits” (UNEA, 2022). Ecosystems that fall under this definition from a coastal protection perspective include biogenic reefs, mangroves, salt marshes, and dunes (Narayan et al., 2016). These ecosystems all provide coastal protection through natural processes such as increased bed friction, sediment deposition, and vertical biomass building (Gracia et al., 2018; Gutiérrez et al., 2011; Morris et al., 2018; Narayan et al., 2016). In contrast to traditional coastal defences, which often obstruct or disrupt natural processes, NbS work with these processes rather than against them. This makes NbS inherently more adaptive and responsive to external forces, such as storms and sea level rise (Cooper and McKenna, 2008; Van der Biest et al., 2020). This results in less maintenance and is the reason for the cost-effective and sustainable nature of NbS. In addition, NbS can offer a broader range of benefits than traditional coastal protection measures, including increased biodiversity and a variety of ecosystem services (ES) (Seddon et al., 2020a; Temmerman et al., 2013).

Compared to other ecosystems (e.g. mangroves, salt marshes, etc.), biogenic reefs are less commonly studied and used as NbS for coastal protection (Moraes et al., 2022; Paxton et al., 2024). They are defined as distinct geomorphological structures constructed by living organisms, known as reef builders (McManus, 2001). Reef builders include corals, bivalves (i.e. oysters and mussels), and polychaetes. As with ecosystems, some reef builders have been studied more extensively than others, such as corals and oysters (Giglio et al., 2024; Moraes et al., 2022; Paxton et al., 2024). In addition to providing coastal protection, biogenic reefs offer a variety of ES, including the direct provision of material and food (fisheries and aquaculture production), carbon sequestration, water quality regulation, and recreation (Barbier et al., 2011; Beck et al., 2011; Smaal et al., 2019).

Comprehensive ES assessments are needed to inform and encourage further investment in NbS for coastal protection. This is because ES assessments allow the benefits of NbS, such as biogenic reefs, to be weighed against the costs (i.e. the costs of creating and maintaining NbS) and allow more informed decision making where benefits can be maximised and trade-offs minimised (Seddon et al., 2020b, 2021). Therefore, changes in ecosystem function or service should be accompanied by monetary or non-monetary valuation in ES assessments. Furthermore, as the valuation of services and the relative value of different functions can vary considerably between locations and regions (Humphries and La Peyre, 2015), ES assessments should be location- and region-specific. In addition to providing a cost-benefit balance, demonstrating that the benefits of biogenic reefs in terms of ES (and biodiversity) exceed those of traditional coastal protection measures may increase public support and acceptance of biogenic reefs as a coastal protection measure. However, previous ES assessments in the scientific literature have focused on only one or two ES (e.g. Humphries and La Peyre, 2015; Scyphers et al., 2011; Westbrook et al., 2019), often without valuation, and have mainly focused on coral and oyster reefs (e.g. Grabowski et al., 2012; Smith et al., 2022). Therefore, more comprehensive ES assessments that include other reef builders are needed (Giglio et al., 2024).

In addition to the lack of comprehensive ES assessments, the widespread application of NbS for coastal protection is hampered by a lack of in-depth understanding of their long-term stability and morphological performance under different physical conditions (Bouma et al., 2014; Temmerman et al., 2013). Several studies have shown that the physical conditions in which NbS are installed affect their performance. For example, Salvador de Paiva et al. (2018) demonstrated this for coastal protection in *Crassostrea gigas* reefs. Their findings showed that oyster reefs in erosional conditions accumulated sediment, whereas those in accretionary conditions did not. This is true not only for coastal protection, but also for other ES, as demonstrated by Fodrie et al. (2017) for carbon sequestration in *Crassostrea virginica* reefs. Their findings showed that the location of oyster reefs determines whether they act as a carbon sink or source; intertidal sandflat reefs act as a source, whereas subtidal sandflat and intertidal salt marsh-fringing reefs act as a sink. In this context, the Coastbusters 2.0 project investigated the potential and boundary conditions for the development of biogenic reefs in the Belgian part of the North Sea (BPNS) for coastal protection. The development of biogenic reefs was facilitated by the installation of submerged mussel (Mytilidae, *Mytilus edulis*) longlines with vertical dropper lines (Boulenger et al., 2024; Goedefroo et al., 2022; Mazharul et al., 2024). The installation was placed at two locations in the BPNS with different hydrodynamic conditions. In addition to the introduced reef-building species, *M. edulis*, the area is also home to the naturally occurring reef-building species, *Lanice conchilega*.

The aim of this study is to provide a comprehensive assessment and comparison of the ES provided by biogenic reefs composed of *M. edulis* and *L. conchilega* under different hydrodynamic conditions. On the one hand, (1) the ES provided by biogenic reefs under high and low hydrodynamic conditions will be compared; on the other hand, (2) the ES provided by biogenic reefs composed of different reef-building species will be compared. ES will be quantified and monetised using in-situ measurements and literature data from the Coastbusters 2.0 project. The results of this study will highlight the role of site selection and reef builder selection in the provision of ES to support future implementation of biogenic reefs as NbS.

2. Materials and methods

2.1. Study area

The BPNS is located in the southern region of the North Sea (Fig. 1a) and covers an area of 3454 km², representing approximately 0.5 % of the total North Sea area (Dauwe et al., 2019; Verhalle and Van de Velde, 2020). The BPNS is characterised by high energy and dynamism, with the tidal regime and prevailing wind and wave patterns exerting a significant influence (Ivanov et al., 2020; Ruddick and Lacroix, 2006). The average depth of the BPNS is 20 m, and the seabed features a complex and dynamic system of channels and sandbanks running parallel to the coastline.

The study area is located in the western part of the BPNS, near the coastal town of De Panne (Fig. 1a). The study area consists of two sites (exposed and sheltered) where submerged mussel longlines with vertical dropper lines have been installed. Each site consists of a reference area (5000 m²) and an impact area (Fig. 1b). The latter is further subdivided into a reef survey area (45,000 m²) and a reef development area (1500 m²; the area of the mussel longline installation). The sizes of these areas were selected arbitrarily to facilitate comparison between the sites, encompass the variation within the study area, and allow the multibeam survey to be completed within the available monitoring time. The location of the sites relative to nearby sandbanks (Broers Bank and Trapegeer Bank) results in different hydrodynamic conditions; the current direction is the same, but the strength is slightly different (Fig. 1c). One of the sites is protected by a sandbank (i.e. sheltered site), whereas the other is not (i.e. exposed site). The sheltered site (51°07'19.2" N, 2°35'16.8" E) is located 2 km from the coast on the southern slope of the

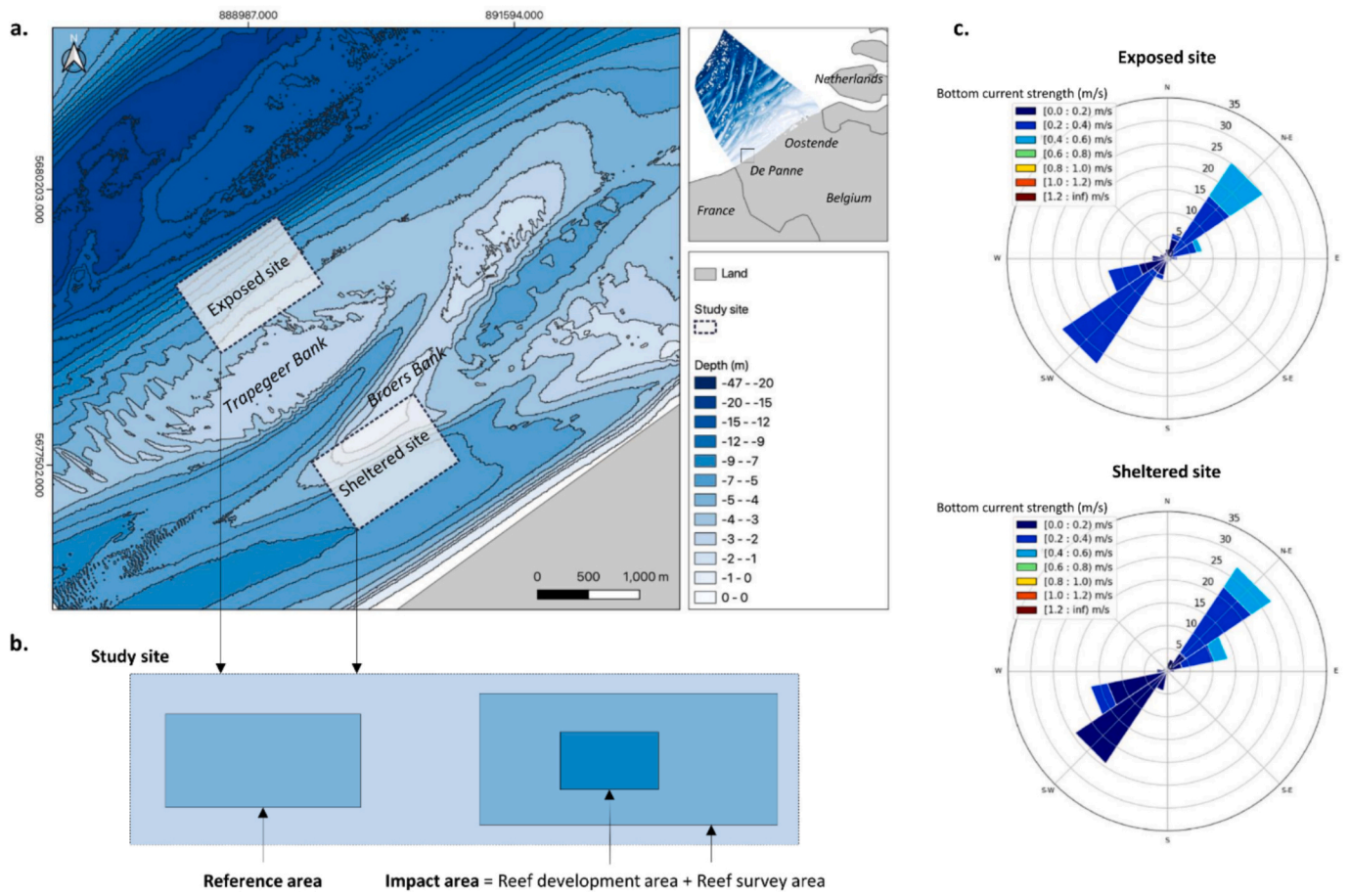


Fig. 1. a. Location and bathymetric data of the study area (exposed and sheltered sites) near the coastal town of De Panne (Belgium) (UTM-WGS84) (adapted from Mazharul et al., 2024). b. The exposed and sheltered sites each consist of a reference area and an impact area (reef survey area and reef development area). c. Direction and strength (m/s) of bottom currents at the exposed and sheltered sites (adapted from Langedock et al., 2020).

Broers Bank sandbank. The exposed site (51°07'22.2" N, 2°33'28.5" E) is located 5 km from the coast on the northern slope of the Trapegeer Bank sandbank. The two sites are 3 km apart but have similar bathymetry and sediment composition (i.e. fine to medium sand).

Dive surveys, during which video footage was taken, revealed that the mussel longline installation had successfully created small, intermittent, and sparsely distributed mussel patches in both exposed and sheltered sites (Appendix A: Fig. A.1). As these patches did not survive

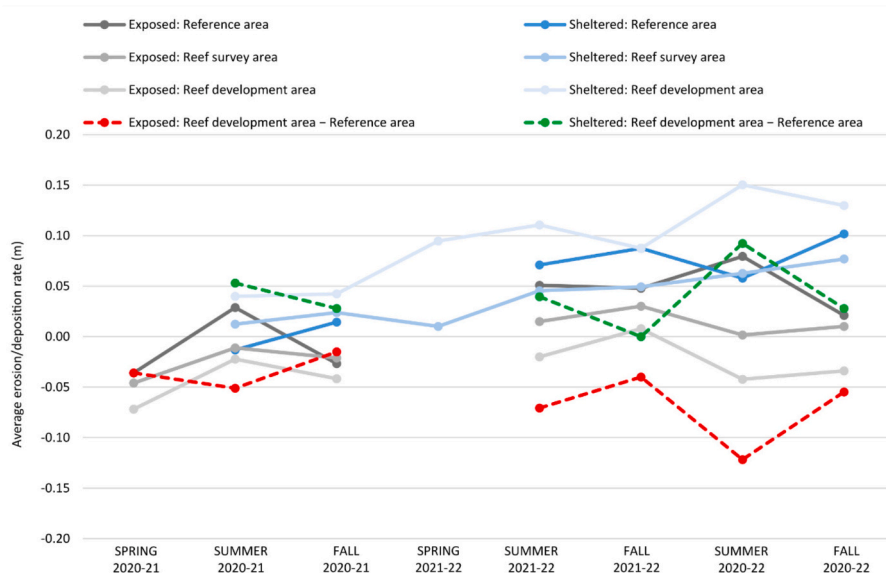


Fig. 2. Average erosion and deposition rates (m) for each season over one- and two-year periods (2020–2021, 2021–2022, and 2020–2022) at exposed and sheltered sites.

the winter, they are described as “intermittent” or “non-permanent”. This is not unexpected, given that new subtidal beds tend to disappear even in a natural environment (Smaal et al., 2021; Troost et al., 2022). Changes in bathymetry during the project (Vandorpe et al., 2025; Fig. 2), along with video footage from the dive surveys, suggest that the installation was more successful in developing mussel patches at the sheltered site (Appendix A: Fig. A.1). The sheltered site shows an average accretion of 3–5 cm; in contrast, no accretion was observed at the exposed site.

M. edulis reefs are conspecific aggregations that form complex, three-dimensional structures on the seabed (Gutiérrez et al., 2011; Ysebaert et al., 2019). These structures can range in size from small clumps and large patches to extensive beds and reefs. They are formed through the production of byssus threads, which enable the mussels to attach themselves to each other and to hard surfaces (Meadows et al., 1998; Ysebaert et al., 2019). The ability to shed these threads allows the structures to grow rapidly.

Like *M. edulis*, *L. conchilega* reefs consist of conspecific aggregations. However, unlike *M. edulis*, this species lives mostly buried in the sand and forms mounds. These mounds appear on the seabed at population densities of 500–1000 ind. m⁻² (Borsje et al., 2014; Carey, 1987; Passarelli et al., 2012; Rabaut et al., 2009). They are formed in response to the accumulation and consolidation of sand caused by the polychaetes, and can reach heights of up to 80 cm.

The BPNS hosts a variety of soft-bottom benthic communities, which can be distinguished based on their unique community composition (Breine et al., 2018; Van Hoey et al., 2004). Both exposed and sheltered sites host an *Abra alba* community, which is closely related to a *L. conchilega* community due to the high abundance of *L. conchilega* (Van Hoey et al., 2004). Although they belong to the same soft-bottom benthic community, the community composition differs slightly between the two sites (Mazharul et al., 2024). The sheltered site is characterised by a higher presence of *Oligochaeta* spp., *Cirratulidae* spp., and *L. conchilega*, whereas the exposed site is characterised by a higher presence of *Ensis leei* and *Magelona johnstoni*.

2.2. Biophysical quantification

A quantitative assessment of the ES provided by biogenic mussel (*M. edulis*) and, where possible, polychaete (*L. conchilega*) reefs in the western part of the BPNS was undertaken. This assessment involved the calculation of a biophysical value that quantifies the extent to which an ES is provided, expressed in units appropriate to the specific ES in question (e.g. coastal protection, m³ of sand). The quantitative assessment was based on the Sustainable Marine Ecosystem Services (SUMES) model. This comprehensive model has been developed to assess the impact of human activities at sea on marine ecosystems. The data for the quantification of ES included a range of in-situ measurements, including bathymetric, sedimentological, and biological data, as well as data derived from research conducted under environmental and social conditions similar to those in the study area (e.g. comparable landscape settings, climatic conditions, and socio-economic pressures).

The ES selected for quantification are the regulating ES coastal protection, carbon sequestration, and water quality regulation. Biogenic mussel and polychaete reefs provide coastal protection, carbon sequestration, and water quality regulation through several mechanisms and pathways (Bruschetti, 2019; Smaal et al., 2019). These, together with the similarities and differences between the reef-building species *M. edulis* and *L. conchilega*, are described in detail in Appendix A. The assessment excluded provisioning ES (i.e. fisheries and aquaculture production) and cultural ES (e.g. recreation). This exclusion was made because the monitoring focused on benthic (fish) species rather than commercial fish species, and because the reefs are not used for aquaculture or recreational activities.

2.2.1. Coastal protection

The coastal protection provided by the biogenic reefs, with considerations specific to this case study (Appendix A), was quantified as follows:

Bathymetric data were collected from both exposed and sheltered sites every three months between 2020 and 2023 using a multibeam sonar (Vandorpe et al., 2025) to assess whether the mussel longline installation and the underlying biogenic reefs (*M. edulis* and *L. conchilega*) had affected sand accumulation. Bathymetric maps showing changes in elevation (i.e. erosion and deposition patterns) were produced for the impact areas (reef survey areas and reef development areas) and reference areas over a two-year period (2020–2022). Based on the bathymetric maps, average erosion rates were calculated for both the impact areas and the reference areas (Vandorpe et al., 2025). The differences in average erosion rates were then calculated and multiplied by the total area of the impact areas to assess the extent to which the mussel longline installation and the underlying biogenic reefs influenced sand accumulation. Finally, as the bathymetric maps and calculations cover a two-year period, sand accumulation was averaged to represent a one-year period. All analyses were carried out using Global Mapper (Blue Marble Geophysics).

2.2.2. Carbon sequestration

The carbon burial and subsequent sequestration provided by the biogenic mussel reefs, with considerations specific to this case study (Appendix A), was quantified as follows:

A carbon budget based on Dynamic Energy Budget (DEB) modelling was used to assess the carbon sequestration capacity of *M. edulis*. Due to lack of data, a carbon budget comparable to *M. edulis* was not developed for *L. conchilega*. Individual-based models based on DEB theory quantify energy, mass, and elemental fluxes through the individual (Kooijman, 2010). DEB models can therefore be used as a basis for dynamic energy or nutrient budgets and for the quantification of regulating services (Kotta et al., 2023). Shell formation is an important aspect of bivalve carbon budgets (Filgueira et al., 2019), and can be included through the DEB rules for “product formation” (Kooijman, 2010; Stechele and Lavaud, 2024; Vaher et al., 2024). A DEB model for offshore cultivation of *M. edulis* was parameterised and validated for the BPNS (Stechele et al., 2022). Biocalcification parameters for *M. edulis* were parameterised in Stechele and Lavaud (2024).

Mussels play a direct role in the CO₂ cycle through five ecophysiological processes: respiration, biocalcification, food ingestion, rejection of uningested food (pseudofaeces), and egestion of unabsorbed food (faeces) (Filgueira et al., 2019). The DEB model presented here includes all ecophysiological processes except the rejection of uningested food (pseudofaeces) (Fig. 3). The model assumes a steady state; the standing

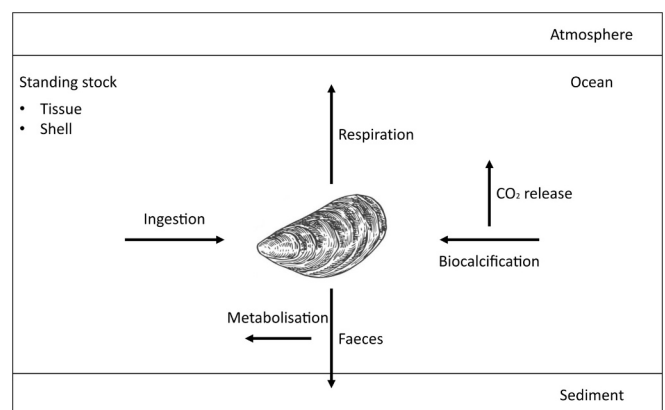


Fig. 3. Standing stock (i.e. carbon stored in tissue and shell) and carbon fluxes (ingestion/assimilation, respiration, biocalcification, and faeces) of *Mytilus edulis*.

stock (i.e. carbon stored in tissue and shell) remains constant over time. As mussels are not harvested, the model does not distinguish between carbon fluxes in tissue and shell. However, if mussels are harvested, a clear distinction between the two should be made when assessing carbon sequestration capacity (Filgueira et al., 2019). This is because, although both the tissue and the shell leave the marine system, they end up in different places. The tissue is consumed, whereas the shell may be discarded as waste or put to various uses, such as in agriculture or construction. The carbon budget of *M. edulis* was calculated by size class, as carbon fluxes vary with mussel size. As mussels range in size from 1 to 8 cm in both exposed and sheltered sites (Leinung, 2023; Sterckx, 2023; Appendix A: Table B.1), eight size classes were used in the carbon flux calculations.

Carbon is ingested (i.e. ingestion/assimilation flux) and after mobilisation, carbon is stored in tissue, shell (standing stock; organic matrix), reproductive tissue, and excreted in faeces (i.e. faecal flux). Assimilation, growth, excretion, and (in adults) reproduction all contribute to CO₂ respiration (i.e. respiration flux). In addition, CO₂ is also released through biocalcification, as *M. edulis* is a biocalcifying organism (i.e. biocalcification flux). The precipitation of 1 mol CaCO₃ releases approximately 0.6 mol CO₂ (Filgueira et al., 2019; Lee et al., 2024). During biocalcification, in addition to the release of CO₂, additional carbon is stored in the shell (standing stock; CaCO₃). Thus, the two processes/fluxes leading to the release of CO₂ are respiration and biocalcification. In contrast, the faecal flux when buried in seabed sediment is a process/flux that can lead to carbon burial (and subsequent sequestration). However, not all faecal matter reaches the seabed and is thus buried; some is metabolised prior to burial. As there is no specific value for faecal burial in the BPNS, a range of 10 % to 80 % is assumed based on studies of faecal deposition and burial in mussels (cf. Álvarez-Salgado et al., 2022; Aristegui et al., 2009; Carlsson et al., 2010; Filgueira et al., 2019; Hartstein and Stevens, 2005; Zúñiga et al., 2014). Carbon budgets were calculated as follows: % buried faeces - respiration - biocalcification - % metabolised faeces.

Carbon budgets were extrapolated to the mussel population using the estimated abundance and structure of mussel populations on the drop-per lines (Leinung, 2023; Sterckx, 2023; Appendix A: Table B.1). This was used as a proxy as data on the abundance and structure of mussel populations on the seabed were not available. Finally, using 3.67 tons of CO₂ as the equivalent of 1 ton of C, carbon budgets expressed in g C y⁻¹ were converted to g CO₂ y⁻¹.

2.2.3. Water quality regulation

The water quality regulation provided by the biogenic reefs, with considerations specific to this case study (Appendix A), was quantified as follows:

The multiple linear regression formula developed by Toussaint et al. (2021) was used to estimate sediment denitrification rates (D ; Eq. (1)). The formula estimates sediment denitrification rates based on abiotic variables related to sediment characteristics (total organic matter (TOM) and fine sediment fraction ($Fines$)) and biotic variables related to the macrobenthic community (irrigation rate ($IrrigationRate$) and irrigation potential of the macrobenthic community (IP_C)). The term “irrigation rate” is defined as the rate at which water is circulated within the sediments by the macrobenthic community (Meysman et al., 2006). Conversely, the term “irrigation potential” reflects the irrigation behaviour of the macrobenthic community and its impact on ecosystem functioning (Wrede et al., 2018).

$$D = 2.71 + 1.40 TOM + 0.10 Fines - 0.27 IrrigationRate - 1.09 \cdot 10^{-3} IP_C \quad (1)$$

with:

- D = denitrification (mmol N m⁻² d⁻¹)
- TOM = percentage of total organic matter in sediment (%)

- $Fines$ = percentage of sediment between 125 and 250 μm (%)
- $IrrigationRate$ = litre pore-water irrigated by macrobenthic organisms per day per surface area (L m⁻² d⁻¹)
- IP_C = irrigation potential of the macrobenthic community

During different campaigns (between 2020 and 2022), different locations (D0, REF1, etc.) within the exposed and sheltered sites (Fig. 4) were sampled for macrobenthic community abundance and biomass using a Van Veen grab sampler (Mazharul et al., 2024). Denitrification rates were calculated at sampled locations dominated by either *M. edulis* or *L. conchilega* (at their first, second, and third highest combined abundance and biomass) in order to best determine the effect of a biogenic reef on denitrification rates at both exposed and sheltered sites. For comparison, the same was done for the exposed and sheltered reference areas (only those with the first highest combined abundance and biomass). Details on the abundance, biomass, and species richness of the different locations for which denitrification rates were calculated can be found in Appendix A (Table C.1).

A core sample was taken at each sampled location (Fig. 4) to determine sediment total organic carbon (TOC) and grain size distribution (Mazharul et al., 2024). In addition to site-specific TOC and grain size distribution, average TOC and grain size distribution for each area (exposed and sheltered impact sites and exposed and sheltered reference areas) were used to calculate denitrification rates (Appendix A: Figs. C.1, C.2). This was done to reduce the effect of sediment characteristics and to better determine the effect of the macrobenthic community on denitrification rates. TOM was derived from TOC measurements, using a conversion factor of 1.724 (Pribyl, 2010; Schumacher, 2002), and sediment between 125 and 250 μm was derived from grain size distribution measurements.

As the irrigation rate ($IrrigationRate$) is not known for the sampled locations, it is not included in the calculation of denitrification rates. However, the irrigation potential of the macrobenthic community (IP_C ; Eq. (2)) is and was calculated using a formula provided by Wrede et al. (2018):

$$IP_C = \sum_{i=1}^n \left(\frac{B_i}{A_i} \right)^{0.75} A_i BT_i FT_i ID_i \quad (2)$$

with:

- IP_C = irrigation potential of the macrobenthic community
- B_i = ash-free dry biomass of species i (g m⁻²)
- A_i = abundance of species i (ind. m⁻²)
- BT_i = burrow type of species i (score: 1 - 2 - 3)
- FT_i = feeding type of species i (score: 1 - 2 - 3 - 4)
- ID_i = injection pocket depth of species i (score: 1 - 2 - 3 - 4)

Species biomass (B_i) and species abundance (A_i) were standardised per m² (Boulenger et al., 2024; Mazharul et al., 2024), after which species biomass was converted from wet mass (WW) to ash-free dry mass (AFDW) using conversion factors from Gogina et al. (2022).

Trait scores (BT_i , FT_i , and ID_i) were obtained from Wrede et al. (2018) and De Borger et al. (2020) (Appendix A: Tables C.2, C.3). In the absence of trait scores, scores were assigned based on the closest taxonomic relative, adjusted to correct for size and feeding type. Due to the uncertainty associated with their trait scores, 26 taxa were excluded from the calculations. The exclusion of these 26 taxa from the calculations is not expected to have a significant effect on the irrigation potential of the macrobenthic community (IP_C) and denitrification rates (D), as their abundance is consistently below 10 % of the total macrobenthic community abundance.

Finally, denitrification rates at each location (only those with the first highest combined abundance and biomass) were generalised to the total biogenic reef surface area and converted to kg per year using the average (and highest) observed *M. edulis* or *L. conchilega* cover between

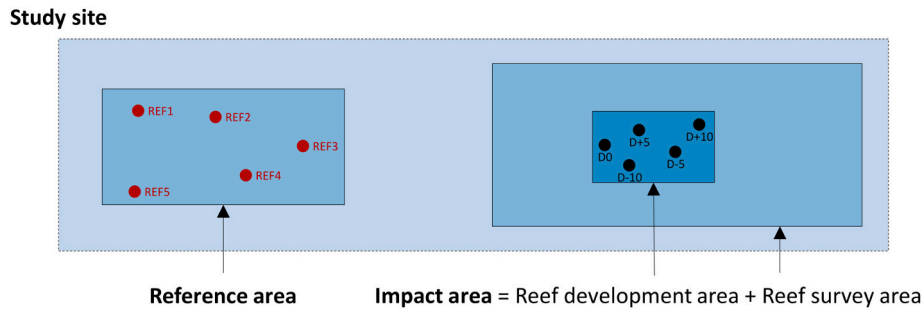


Fig. 4. Locations sampled between 2020 and 2022 for macrobenthic community abundance and biomass using a Van Veen grab sampler at exposed and sheltered impact sites and reference areas.

2020 and 2022 (Mazharul et al., 2024; Appendix A: Tables C.4, C.5).

2.3. Economic valuation

The biophysical units were converted into an economic value by applying monetary valuation techniques commonly used for ES. Each unit is assigned a monetary value (e.g. coastal protection, euros per m³ of sand), which is then multiplied by its biophysical value. The monetary values (and monetary valuation techniques) for each ES are presented in Appendix A (Table D.1).

3. Results

3.1. Coastal protection

3.1.1. Biophysical quantification

The reef development area and the reef survey area of the exposed site are characterised by sand waves that form a typical foreshore pattern (Fig. 5a). This foreshore pattern is not indicative of sediment accumulation. The reef development area experienced an average net erosion of 4.2 cm y⁻² (SD = 14.4 cm y⁻²), which is 12.2 cm y⁻² more than the reference area which experienced an average net accumulation of 7.9 cm y⁻² (SD = 12.5 cm y⁻²). This erosion results in a sand loss of 91.50 m³ per year at the exposed site.

In contrast to the exposed site, there is evidence of sand accumulation in the reef survey area of the sheltered site, particularly in the reef development area (Fig. 5b). The reef development area experienced an

average net accumulation of 15.0 cm y⁻² (SD = 9.1 cm y⁻²), which is 9.2 cm y⁻² more than the reference area which experienced an average net accumulation of 5.8 cm y⁻² (SD = 7.0 cm y⁻²). This accumulation results in a sand gain of 69 m³ per year at the sheltered site.

3.1.2. Economic valuation

The monetary value used to calculate coastal protection is 6.1 €/m³, derived using the shadow pricing method. At the sheltered site, the sand accumulation is anticipated to result in an annual saving of €420.90 on future foreshore nourishment. In contrast, an annual loss of €558.15 is anticipated at the exposed site.

3.2. Carbon sequestration

3.2.1. Biophysical quantification

Carbon fluxes and budgets were calculated for each size class and are presented in Table 1. Mussels in all size classes, assuming faecal burial between 10 % and 80 %, act as a carbon source at both exposed and sheltered sites. Applying this to the abundance and structure of the mussel populations at these sites, the biogenic mussel reefs produce between 0.52 and 0.54 tons of CO₂ at the exposed site and between 0.55 and 0.57 tons of CO₂ at the sheltered site.

3.2.2. Economic valuation

The monetary value used to calculate carbon sequestration is 61.8 €/t CO₂, derived using the avoided cost method. The annual CO₂ equivalent loss ranges from €32.43 to €33.48 per year at the exposed site

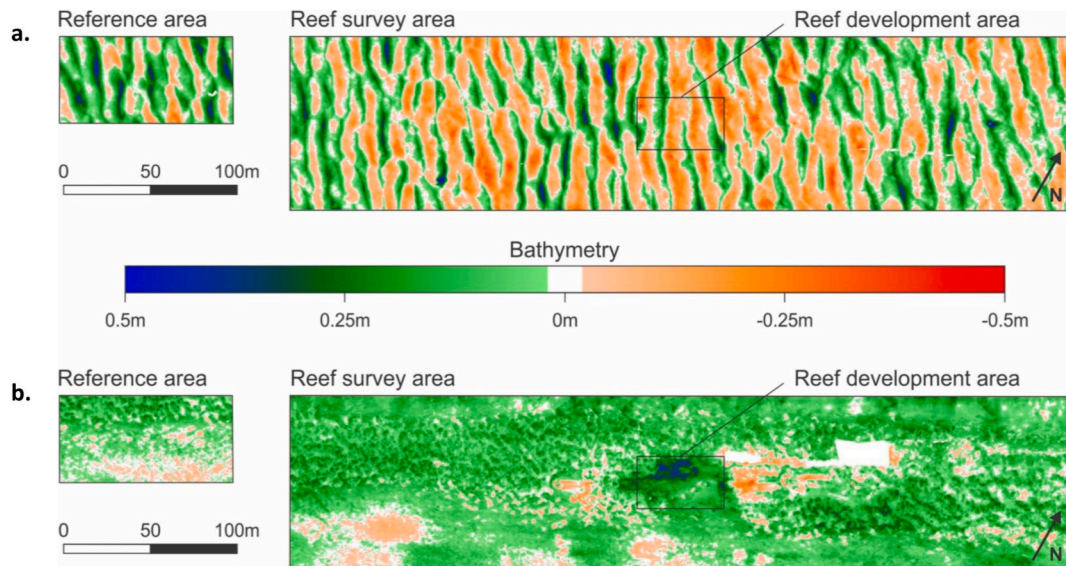


Fig. 5. Bathymetric map of erosion and deposition patterns between 2020 and 2022 (SUMMER) in the impact area (reef survey area and reef development area) at the a. exposed and b. sheltered sites and their respective reference areas.

Table 1

Dynamic Energy Budget (DEB) model output (carbon fluxes; g C y⁻¹) at exposed (grey) and sheltered (white) sites for *Mytilus edulis* of different size classes (1–8 cm). Carbon budgets: % buried faeces - respiration - biocalcification - % metabolised faeces (10 % / 80 % faecal burial).

Size (cm)	Respiration (g C y ⁻¹)		Biocalcification (g C y ⁻¹)		Ingestion (g C y ⁻¹)		Faeces (g C y ⁻¹)		Budget (g C y ⁻¹) 10% / 80%	
	Exposed	Sheltered	Exposed	Sheltered	Exposed	Sheltered	Exposed	Sheltered	Exposed	Sheltered
1	0.36	0.37	0.10	0.11	0.38	0.39	0.02	0.02	-0.42 / -0.40	-0.43 / -0.42
2	0.56	0.58	0.17	0.18	0.60	0.62	0.03	0.03	-0.67 / -0.64	-0.69 / -0.67
3	0.74	0.77	0.26	0.27	0.78	0.81	0.04	0.04	-0.89 / -0.86	-0.92 / -0.89
4	0.90	0.93	0.39	0.40	0.95	0.98	0.05	0.05	-1.12 / -1.09	-1.16 / -1.12
5	1.04	1.08	0.57	0.58	1.10	1.14	0.06	0.06	-1.37 / -1.33	-1.42 / -1.37
6	1.17	1.21	0.82	0.83	1.24	1.29	0.07	0.07	-1.66 / -1.61	-1.70 / -1.66
7	1.30	1.35	1.15	1.16	1.38	1.43	0.08	0.08	-1.98 / -1.93	-2.03 / -1.98
8	1.42	1.47	1.58	1.59	1.51	1.56	0.08	0.09	-2.36 / -2.30	-2.42 / -2.36

and from €34.26 to €35.38 per year at the sheltered site.

3.3. Water quality regulation

3.3.1. Biophysical quantification

The denitrification rates calculated for the sampled locations (at the exposed and sheltered impact sites and the exposed and sheltered

reference areas) dominated by either *M. edulis* or *L. conchilega* are presented in Table 2.

The denitrification rates are generalised to the total biogenic reef surface area, based on the average (and highest) cover of *M. edulis* and *L. conchilega* observed between 2020 and 2022. At the exposed and sheltered impact sites (locations 1 and 2), 0.06 and 1.08 kg N y⁻¹ (0.19 and 3.45 kg N y⁻¹) is denitrified by the macrobenthic community

Table 2

Denitrification rates (N m⁻² d⁻¹) at exposed (grey) and sheltered (white) impact sites and exposed (grey) and sheltered (white) reference areas at locations (D0, REF1, etc.) with the highest (first, second, and third highest) combined abundance and biomass of *Mytilus edulis* or *Lanice conchilega*. Between brackets are denitrification rates (N m⁻² d⁻¹) calculated from site-specific total organic carbon (TOC) and grain size distribution measurements rather than averages.

Abundance and biomass	Denitrification rate (N m ⁻² d ⁻¹)			
	Exposed impact site	Sheltered impact site	Exposed reference area	Sheltered reference area
Highest <i>M. edulis</i>	0.88 (0.65) (loc. 1; D0)	3.13 (2.89) (loc. 2; D-10)	2.68 (2.88) (loc. 13; REF4)	3.60 (3.50) (loc. 14; REF3)
Second highest <i>M. edulis</i>	3.20 (5.03) (loc. 3; D+5)	3.25 (2.96) (loc. 4; D-10)	-	-
Third highest <i>M. edulis</i>	2.93 (2.62) (loc. 5; D+10)	2.95 (3.11) (loc. 6; D+10)	-	-
Highest <i>L. conchilega</i>	1.11 (1.22) (loc. 7; D-5)	0 (0) (loc. 8; D+10)	2.73 (2.87) (loc. 15; REF5)	1.96 (1.77) (loc. 16; REF1)
Second highest <i>L. conchilega</i>	2.77 (2.60) (loc. 9; D-10)	0 (0) (loc. 10; D-10)	-	-
Third highest <i>L. conchilega</i>	0.88 (0.65) (loc. 11; D0)	2.40 (2.69) (loc. 12; D+10)	-	-

(including *M. edulis*), respectively. In the exposed and sheltered reference areas (locations 13 and 14), 0.07 and 0.05 kg N y⁻¹ (0.34 and 0.34 kg N y⁻¹) is denitrified by the macrobenthic community (including *M. edulis*), respectively. At the exposed and sheltered impact sites (locations 7 and 8), 0.01 and 0 kg N y⁻¹ (0.10 and 0 kg N y⁻¹) is denitrified by the macrobenthic community (including *L. conchilega*), respectively. In the exposed and sheltered reference areas (locations 15 and 16), 0.26 and 1.52 kg N y⁻¹ (1.83 and 3.77 kg N y⁻¹) is denitrified by the macrobenthic community (including *L. conchilega*), respectively.

3.3.2. Economic valuation

The monetary value used to calculate water quality regulation is 23.35 €/kg N, derived using different monetary valuation techniques (i.e. shadow pricing method and willingness to pay (WTP) method). The denitrification value for biogenic *M. edulis* reefs ranges from €1.48 to €25.28 (€4.42 to €80.49) per year at exposed and sheltered sites, while for biogenic *L. conchilega* reefs the denitrification value ranges from €0 to €0.33 (€0 to €2.23) per year at sheltered and exposed sites.

3.4. Total assessment

The biophysical quantification and economic valuation of the ES for the total biogenic reef, at both exposed and sheltered sites, are presented in Table 3.

4. Discussion

4.1. Coastal protection

Although the subtidal location of the biogenic reefs at both sites prevents them from providing wave attenuation, coastal protection is achieved through sediment accumulation and stabilisation. This effect is primarily observed at the sheltered site, which is believed to result from favourable local abiotic (i.e. hydrodynamic) and biotic (i.e. biogenic sedimentation) conditions that enable the formation of mussel patches. Firstly, favourable hydrodynamic conditions prevent the mussels from being washed away, allowing them to settle on the seabed and on aggregations of *L. conchilega*. Secondly, the greater abundance of *L. conchilega* provides *M. edulis* with a settlement substrate to which they can attach. Previous research has demonstrated the preference of *M. edulis* juveniles for complex habitat structures, as well as their interspecific facilitation with *L. conchilega* (Nauta et al., 2024; Schotanus et al., 2020). In contrast to the sheltered site, this effect is not observed at the exposed site. Furthermore, higher levels of erosion are observed at the exposed site than in its reference area. This is believed to be due to spatial and temporal variations (e.g. macro- and micro-relief), rather than the mussel longline installation.

As no permanent mussel reefs were formed during the project, more attention should be given to identifying the optimal combination of hydrodynamic conditions and settlement substrate, whether biogenic or non-biogenic. In addition, the potential impact of predation by invertebrates (e.g. starfish and crabs) on the formation of permanent reefs must be considered (Troost et al., 2022). Once permanent reefs have been established in the Belgian part of the North Sea (BPNS), their ability to provide coastal protection will depend on the prevailing hydrodynamic conditions (Chowdhury et al., 2019; Gutiérrez et al., 2011; Salvador de Paiva et al., 2018; Walles et al., 2015). Alongside these conditions, the characteristics of the reef itself must be considered, including its length, width, height, spatial density, and mussel density. Taking all these factors into account will enable the formation of permanent reefs optimised to provide coastal protection through sediment accumulation and stabilisation.

4.2. Carbon sequestration

This study shows that, when a Dynamic Energy Budget (DEB) model is used to calculate carbon sequestration potential, mussels are net “producers” of CO₂. This is true for both exposed and sheltered sites. The slight differences observed between the two sites can be attributed to the greater availability of food at the sheltered site, which is located closer to the coast. Other potential causes of difference are population age and physical conditions (Lee et al., 2020, 2024). However, these are not expected to have an effect in this case, as they are similar across both sites. Faecal burial (ranging from 10 % to 80 %) is insufficient to counteract the CO₂ released through the respiration of organic matter and biocalcification. This finding is consistent with other studies using both an “ecosystem-based approach” (e.g. cf. Filgueira et al., 2019; Jansen and van den Bogaart, 2020; Sea et al., 2022) and an individual-based approach (e.g. Hily et al., 2013; Lejart et al., 2012). In contrast to an individual-based approach, which only considers fluxes related to respiration and biocalcification, this study also considers the egestion of unabsorbed food (faeces). While this approach is more accurate, it cannot be considered a full “ecosystem-based approach”. To qualify as such, it would need to incorporate links to plankton dynamics and fish production, as well as other factors such as pseudofaecal production, ammonia excretion (Filgueira et al., 2019), shell dynamics (Fodrie et al., 2017), and reef characteristics (i.e. passive sedimentation) (Lee et al., 2020, 2024). Currently, there is no consensus on how to calculate the carbon sequestration potential of bivalves using carbon budget models, as authors differ on which carbon fluxes to include, especially with regard to the distinction between short-term and long-term carbon cycles (e.g. Lee et al., 2020, 2024; Martini et al., 2022; Sea et al., 2022; Tamburini et al., 2022). For example, respiration and pseudofaeces are not always included. Other differences in carbon budgets are related to

Table 3

Biophysical quantification and economic valuation of the ES provided by a *Mytilus edulis* and/or *Lanice conchilega* reef in the exposed and sheltered sites. In green: ES gain, in red: ES loss, and in black: no ES gain or loss.

Ecosystem service	Reef builder(s)	Biophysical quantification		Economic valuation	
		Exposed site	Sheltered site	Exposed site	Sheltered site
Coastal protection	<i>M. edulis</i> (and <i>L. conchilega</i>)	-91.50 m ³ y ⁻¹	69 m ³ y ⁻¹	-558.15 € y ⁻¹	420.90 € y ⁻¹
Carbon sequestration	<i>M. edulis</i>	-0.52 – -0.54 t CO ₂ y ⁻¹	-0.55 – -0.57 t CO ₂ y ⁻¹	-32.43 – -33.48 € y ⁻¹	-34.26 – -35.38 € y ⁻¹
Water quality regulation	<i>M. edulis</i>	0.06 – 0.19 kg N y ⁻¹	1.08 – 3.45 kg N y ⁻¹	1.48 – 4.42 € y ⁻¹	25.28 – 80.49 € y ⁻¹
Water quality regulation	<i>L. conchilega</i>	0.01 – 0.09 kg N y ⁻¹	0 – 0 kg N y ⁻¹	0.33 – 2.23 € y ⁻¹	0 – 0 € y ⁻¹
			TOTAL SUM	-588.77 – -584.98 € y⁻¹	411.92 – 466.01 € y⁻¹

whether the bivalves are cultured or not, as carbon budgets are then constructed from a different perspective. As carbon budgets are not static, it is recommended that carbon budgets are constructed as a function of time to account for carbon loss (e.g. erosion, resuspension, and bioturbation of sediment, degradation of tissue, shell, and pseudo-faeces, and weathering of shell). Taking these considerations and the ways in which the carbon sequestration potential of bivalves can be elevated towards a full “ecosystem-based approach” into account, a careful estimation was made based on the best available knowledge. However, further investigation is required.

In theory, the sheltered site should exhibit greater burial of both organic (biological deposits) and inorganic (shell) carbon than the exposed site for two reasons. Firstly, the hydrodynamic conditions in the sheltered area are less turbulent, which enables mussel patches to develop and allows sand to accumulate. This enables both organic and inorganic carbon to become buried (Middelburg, 2019). In addition, favourable hydrodynamic conditions should enable biological deposits to reach the seabed and become buried. The same applies to shells, which will either be displaced or buried on site, depending on the hydrodynamic conditions (i.e. currents). Secondly, the carbon content should be higher due to the greater success of mussel patch development and the higher presence of *L. conchilega* (Middelburg, 2019). However, the results of Mazharul et al. (2024) indicate that little to no organic carbon (inorganic carbon was not measured) was sequestered by the biogenic reefs in the sheltered site. This is most likely due to the transient nature of the mussel patches and the environmental conditions in the study area. The area is located within a shallow, dynamic coastal system where sand displacement occurs daily (Ivanov et al., 2020; Ruddick and Lacroix, 2006). This could result in the displacement of biological deposits and explain the absence of organic carbon burial in the sheltered site.

4.3. Water quality regulation

Denitrification rates are low at both exposed and sheltered sites, but are within the range observed in previous studies in the BPNS (Braeckman et al., 2014; Toussaint et al., 2021). These low rates are attributed to the high irrigation potential of the macrobenthic community (IP_C), rather than sediment composition or organic matter content, which are both influenced by hydrodynamic conditions. This is consistent with the finding that, in fine sediments, macrobenthic functional diversity has a greater impact on denitrification rates than sediment characteristics (Braeckman et al., 2014; Toussaint et al., 2021). However, as sediment characteristics and the species living in the sediment are inextricably linked, it remains difficult to attribute differences in denitrification rates to one or the other. As denitrification rates are calculated using the formula of Toussaint et al. (2021), which indicates that denitrification rates are negatively correlated with both IP_C and irrigation rate, the same reasoning is followed. As a result of NO_3^- and O_2 inputs (through bioturbation and bioirrigation), coupled nitrification-denitrification decreases.

Although high denitrification appears to be associated with low IP_C rather than a single species, previous research has demonstrated the positive contribution of mussels to denitrification. Mussels enhance denitrification in two ways: by increasing the supply of organic matter (biological deposits) through filter feeding and their physical structure, and by creating anoxic conditions in the sediment (Hillman et al., 2021; Sea et al., 2021; Smyth et al., 2016). Although it is true that the highest denitrification rates are observed in the reference area (due to differences in organic matter content and macrobenthic functional diversity), high denitrification rates are also observed under sheltered conditions with high densities of *M. edulis*. In contrast, high densities of *L. conchilega* (> 2000 ind. m^{-2}) show a lack of denitrification, which is directly related to bioturbation and bioirrigation. This decrease in denitrification at high densities of *L. conchilega* was previously demonstrated by Braeckman et al. (2010) under controlled conditions.

4.4. Reef-building species

Differences in temporal and spatial variation and physiological characteristics underlie the variation in ecosystem services (ES) provision between biogenic reefs composed of different reef builders. *M. edulis* and *L. conchilega* are both subject to considerable temporal and spatial variation. However, they differ in longevity, with *M. edulis* living up to 25 years (cf. Sukhotin et al., 2007) and *L. conchilega* living up to 1–2 years (Callaway et al., 2010; Rabaut et al., 2009). Although the survival of both biogenic reefs is highly dependent on recruitment, the success of which depends on many factors, the longevity of *M. edulis* gives it a slight advantage. The reef builders also differ in a number of physiological characteristics. For example, *M. edulis* forms byssus threads and is therefore able to form larger and more complex biogenic reefs (especially in terms of height). In addition, *M. edulis* forms a shell and is larger and therefore produces more CO_2 . Finally, when present in large numbers, *L. conchilega* hinders the denitrification process through bioturbation and bioirrigation, which is not the case for *M. edulis*. In conclusion, *M. edulis* appears to be the preferred option for coastal protection and water quality regulation. However, it is difficult to draw a similar conclusion regarding carbon sequestration. This is because no carbon budget has been established for *L. conchilega*, and the final destination of the biological deposits and shells of *M. edulis* in the BPNS remains unclear. As the reef builders *M. edulis* and *L. conchilega* also interact and benefit from each other (i.e. interspecific facilitation) (Nauta et al., 2024), further research on their combined effects on ES, as well as on ES not quantified in this study (e.g. fisheries production), is warranted.

4.5. Management implications

For the biogenic reefs that were the focus of this case study, the supply of ES at both sites was limited due to the reefs’ intermittent nature and the small area covered by the mussel longline installation. As demonstrated by Grabowski et al. (2012) for oyster reefs, coastal protection contributes the most to ES in both monetary and non-monetary terms. On average, 600,000–700,000 m^3 of sand is required each year to maintain the beaches along the Belgian coast (Verwaest et al., 2023). However, with an accumulation of less than 100 m^3 per year at the sheltered site, the contribution of the mussel longline installation is currently minimal. Nevertheless, future efforts should assess the potential of reef-building species along larger sections of the Belgian coast (20 %, 50 %, and 80 %) using modelling and extrapolation. This would enable broader conclusions to be drawn regarding the installation’s capacity for coastal protection through sediment accumulation and stabilisation.

4.6. Future research and knowledge gaps

The quantification of ES of Nature-based Solutions (NbS) (e.g. biogenic reefs) requires a comprehensive assessment based on a wide range of input data. ES were calculated using in-situ measurements from different measurement campaigns with different equipment (e.g. multibeam sonar, Van Veen grab sampler, etc.) and literature data. The in-situ measurements included bathymetric, sedimentological, and biological data. Due to limitations in the data collected for this study (e.g. lack of pelagic monitoring data) and existing knowledge gaps, literature data were used and assumptions were made in order to estimate the ES provided by biogenic reefs (mussels and polychaetes). In the hope of improving the quality of future research, this study openly acknowledges the limitations and knowledge gaps that have been identified.

Although evidence of seasonal variation exists, the uniform accumulation of sand over a two-year period was assumed for the purposes of **coastal protection**. Furthermore, as *M. edulis* and *L. conchilega* show interspecific facilitation (Nauta et al., 2024), it is difficult to define the proportional role of each reef-building species. Therefore, the combined

impact of the two species was evaluated. It is recommended that future ES assessments use models to evaluate sand accumulation and stabilisation for each species individually.

To calculate the **carbon sequestration potential** of biogenic mussel reefs, the estimated abundance and structure of mussel populations on the dropper lines was used. This approach was necessary because no population structure data were available for the biogenic reefs on the seabed. Therefore, the potential for carbon sequestration must be considered, based on the assumption that all the mussels on the dropper lines would have developed on the seabed. The carbon sequestration potential provides a range of values rather than a specific value due to uncertainty in the amount of biological deposits that reach the seabed, remain composed, and are buried. Factors that influence the burial of biological deposits include hydrodynamic conditions, water column depth, water temperature, and local fauna (Filgueira et al., 2019). High-energy conditions can result in biological deposits not reaching the seabed and being dispersed, as shown by Zúñiga et al. (2014), albeit in aquaculture. Once the biological deposits reach the seabed, they may be buried given that they are not metabolised by benthic (and pelagic) processes (Jansen et al., 2012; Sea et al., 2022). Given the highly energetic and dynamic nature of the BPNS, this amount is likely to be relatively limited (closer to 10 % than 80 %). Therefore, future studies should aim to determine whether biological deposits are indeed buried within the BPNS. Although the BPNS is nutrient rich and pseudofaeces are expected to be produced by mussels, a pseudofaeces flux was not part of the DEB model. The reasons for not including it are insufficient observations to calibrate pseudofaeces (at different chl_a/spm values) and insufficient observations to validate the pseudofaeces model. Finally, the potential for shells to contribute to carbon sequestration (i.e. standing stock; carbon stored in shell) in sediments is not considered. This could be done, but the values for shells reaching the seabed and being buried are even scarcer than for biological deposits, making it challenging to draw any definitive conclusions.

A DEB model for *L. conchilega* was not developed in this study and has not been developed to date. It is recommended that such a model be developed when sufficient data are available. This would allow more accurate comparisons to be made with *M. edulis*, for which a DEB model was developed in this study.

Water quality regulation was assessed by estimating sediment denitrification rates. As the irrigation rate for the BPNS has only been measured at a few sites (Pers. comm., Jan Vanaverbeke, 2024) and not at the sites included in this study, it was not included in the calculation of the denitrification rate. In addition, 26 taxa were not included in the IP_C calculation due to uncertainties in their traits. This, combined with the lack of total organic matter (TOM) measurements and the use of a conversion factor, results in less accurate denitrification rates. As the multiple linear regression formula of Toussaint et al. (2021) does not exclude other macrobenthic species and their influence on the denitrification process, the calculated denitrification rate is not solely determined by *M. edulis* or *L. conchilega*. To address this issue, experiments using benthic chambers should be conducted to directly measure individual species' nitrogen fluxes (Ray et al., 2021).

In addition to regulating ES (coastal protection, carbon sequestration, and water quality regulation), biogenic reefs have the potential to provide cultural and provisioning ES. In this case study, there is no demand for cultural ES; therefore this aspect was not assessed further. However, the recreational potential of biogenic reefs, mainly for diving or wildlife watching, can be assessed through approaches such as questionnaires. Fisheries and aquaculture production (i.e. provisioning ES) are other potential ES to be considered for biogenic reefs. Mussel longline installations can be considered within a nature-inclusive harvesting (NIH) model, which is aligned with broader bio-economy strategies and sustainability objectives (Murillas-Maza et al., 2023). However, it is not relevant to this case study to assess aquaculture production, as this conflicts with the primary function of the biogenic reef, which is to provide coastal protection. The ES of fisheries

production can be quantified through approaches such as food web modelling if additional data on commercial fish species are available. Quantifying fisheries production in this case study (and other ES related to biogenic reefs in other case studies) could provide a more comprehensive assessment of biogenic reefs, increasing potential investment in NbS and public acceptance. In conclusion, the primary function of NbS and the demand for ES should be carefully considered before undertaking an ES assessment.

5. Conclusion

This study shows that the ecosystem services provided by biogenic reefs composed of *M. edulis* and/or *L. conchilega* depend on the hydrodynamic conditions in which they are used as Nature-based Solutions. Sheltered sites with calmer conditions will offer greater benefits in this respect. This emphasises the importance of selecting sheltered locations (i.e. close to the shore or behind sandbanks) when establishing subtidal biogenic reefs in high-energy conditions. To sustain the provision of ecosystem services delivered by the biogenic reefs, long-term monitoring and adaptive management are further advised.

In addition to the direct and indirect impact of hydrodynamic conditions, reef-building species and the reefs they create, along with the associated macrobenthic communities, play a significant role in providing ecosystem services. This underlines the importance not only of selecting the right location, but also of selecting the right reef-building species. However, as the choice of reef builder (e.g. *M. edulis*, *L. conchilega*, *Crassostrea gigas*, *Sabellaria alveolata*, etc.) should be based on the location of the Nature-based Solutions, taking into account habitat suitability and the social challenges to be addressed, location remains the most important factor.

Finally, to maximise the potential of biogenic reefs formed by mussel longlines, further research is recommended into the optimal conditions (i.e. hydrodynamic conditions, settlement substrate, and levels of predation) for their development. Nevertheless, the biogenic reefs formed in this case study show promise, particularly with regard to coastal protection. This lends weight to the idea of modelling and extrapolating the use of mussel longlines along larger sections of the Belgian coast in future research.

CRedit authorship contribution statement

Rémi Dupont: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Alexia Semeraro:** Writing – review & editing. **Brecht Stechele:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Tomas Sterckx:** Writing – review & editing, Funding acquisition. **Gert Van Hoey:** Writing – review & editing, Project administration. **Thomas Vandorpe:** Writing – review & editing, Visualization, Methodology, Investigation. **Katrien Van der Biest:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2025.102650>.

Data availability

Data will be made available on request.

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