Journal of Sea Research 210 (2026) 102666

Contents lists available at ScienceDirect

Journal of Sea Research

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

Long-term changes in the subtidal macrozoobenthos of the western Dutch Wadden Sea☆

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ARTICLE INFO

Dataset link: https://doi.org/10.25850/nioz/7b.b.vg, https://live.aquadesk.nl

Keywords:
Ecosystem function
Macrobenthos
Introduced species
Temporal data

ABSTRACT

The comparison of two large-scale surveys (1981/82 and 2008), combined with annual monitoring of the subtidal macrofauna in the western Dutch Wadden Sea from 1990 to 2018, revealed pronounced temporal changes in macrobenthic community composition over the past four decades. In the early 1980s, mussels (*Mytilus edulis*) dominated the macrobenthic biomass, but their contribution had strongly declined by 2008. This decline was evident both on natural mussel beds and on culture plots, pointing to a widespread reduction in mussel biomass across the subtidal western Dutch Wadden Sea. Likewise, the biomass of the bivalves *Macoma balthica* and *Cerastoderma edule* also declined strongly in the course of the study period. In contrast, biomass of several non-native species, such as the bivalves *Mya arenaria* and *Ensis leei*, increased strongly in the same period and became the dominating species. Other invaders, such as the polychaete *Marenzelleria viridis*, experienced considerable fluctuations during the early 2000s. Typical for invasion trajectories, it increased dramatically to the dominating macrozoobenthos species, but soon after decreased to marginal levels (boom and bust dynamics). Despite the large changes in the species composition there were very little changes in the distribution of biomass among the different feeding and taxonomic groups. This study shows that the macrozoobenthos of the subtidal western Dutch Wadden is prone to considerable temporal fluctuations. As a result of species introductions, the benthic community has changed from a predominantly native species dominated community to one where introduced species make up a prominent part of the community.

1. Introduction

Coastal areas are amongst the most productive ecosystems in the world. They provide diverse habitats (e.g., open waters, subtidal gullies, and intertidal flats) that support a rich marine species community (e.g. Herman et al., 1999). The Wadden Sea is the largest temperate coastal ecosystem worldwide, bordering the Danish, Dutch and German North Sea coast (e.g. Reise et al., 2010). The majority of the Wadden Sea is dominated by intertidal flats, which are intersected by extensive areas that remain continuously submerged (e.g. Dijkema, 1991; Reise et al., 2010). Such submerged or subtidal areas are especially important in the western Dutch Wadden Sea that harbours considerable shallow subtidal areas, covering about 70% of the total area (Baptist et al., 2019, 2022).

An integral component of coastal areas such as the Wadden Sea is formed by the macrozoobenthos, which is defined as the invertebrate community that lives in or on the sediment and is retained on a 1 mm^2 mesh sieve. It provides key services through nutrient cycling, decomposing organic matter and serves as important food source for birds, fish and other invertebrates (Pihl and Rosenberg, 1982; Zwarts and Wanink, 1993; van de Kam et al., 2004). Most knowledge of the macrobenthic fauna within coastal areas generally stems from intertidal flats, where the benthos is regularly monitored (e.g. Beukema and Dekker, 2020; Bijleveld et al., 2025). Long-term studies have shown that the benthos is subject to considerable temporal fluctuations (Beukema, 1989; Reise et al., 1989; Schückel and Kröncke, 2013; Compton et al., 2017). The variability is on the one hand driven by natural causes such as winter mortality and episodic recruitment events (Beukema et al., 2010) and on the other hand by anthropogenic influences, such as eutrophication, pollution, exploitation of marine life (e.g., towed bottom fishing), habitat alteration, climate change and the introduction of non-native species (Cloern, 2001; Levin et al.,

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☆ This article is part of a Special issue entitled: 'Subtidal benthos dynamic' published in Journal of Sea Research.

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https://doi.org/10.1016/j.seares.2025.102666
Received 31 July 2025; Received in revised form 18 December 2025; Accepted 30 December 2025
Available online 30 December 2025
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2001; Lotze et al., 2006; Katsanevakis et al., 2014; Reise et al., 2023; Buschbaum et al., 2024).

In contrast to the intertidal areas, quantitative studies exploring the macrobenthos of subtidal zones are far less common, due to more difficult logistics and higher costs. This is also true for the Wadden Sea, where only a few studies focussed on the macrozoobenthos in subtidal areas (Dekker, 1989; Armonies and Reise, 2003; Schückel et al., 2015; Armonies et al., 2023). As a consequence, very little is known about the long-term variability of the macrozoobenthos in subtidal areas of the Wadden Sea. Some information on the long-term development of subtidal macrozoobenthos is available from the western Dutch Wadden Sea, where an extensive large-scale survey on the subtidal macrozoobenthos has been conducted in the early 1980s (Dekker, 1989). This study revealed that mussels (*Mytilus edulis*) were dominating the benthic biomass, with the mud snail (*Peringia ulvae*), the polychaete (*Heteromastus filiformis*), the shore crab (*Carcinus maenas*) and the Baltic tellin (*Macoma balthica*) as other important species. A subsequent monitoring program at much smaller spatial scale that started in 1990 pointed to considerable temporal fluctuations in the subtidal benthic community (e.g. Dekker and de Bruin, 2000). For instance, some species like the bivalves *M. edulis* and *M. balthica* showed declining trends, while introduced species, such as the spionid polychaete *Marenzelleria viridis* and the American Razor clam (*Ensis leei*) developed high densities shortly after their introduction (Dekker and de Bruin, 2000; Essink and Dekker, 2002; Dekker and Beukema, 2012; Jung et al., 2020).

In order to explore the temporal changes of the macrozoobenthic community in the subtidal western Dutch Wadden Sea in detail, we compared the large-scale survey in the early 1980s with a survey from 2008 that revisited the original sampling stations. Although the surveys cover a large spatial area of the subtidal zone of the western Dutch Wadden Sea, they only offer two snapshots of the long-term development of the macrozoobenthos. Therefore, we also consider results of the previously mentioned monitoring program (e.g. Dekker and de Bruin, 2000) in the shallow subtidal that was conducted in the period 1990–2018. This program consists of three fixed transects that are sampled each year in winter and summer and therefore offer, albeit restricted in spatial area, a high temporal resolution. By integrating the results of over almost four decades from the two large-scale surveys and from the monitoring program in the period 1990–2018, we aim to answer following questions: (1) How did the species composition, biomass and community structure of the macrozoobenthos in the subtidal western Dutch Wadden Sea change over time? (2) Did certain groups (i.e. feeding groups, species preferring certain substratum types or taxonomic groups) show considerable changes in the study period? And (3) how was the development of introduced species over the last decades in the subtidal Dutch Wadden Sea?

2. Material and methods

2.1. Study area

The western Dutch Wadden Sea is generally characterized by vast subtidal areas, stretching over the Marsdiep and Vlie tidal basins (Fig. 1). In contrast, the small tidal basin Eierlandse Gat, located north of the Marsdiep and south-west of the Vlie, holds comparatively small amounts of subtidal area. The tidal basins are connected to the North Sea via tidal inlets. The salinity of the water shows a gradual decrease away from the inlets and a high variability, due to freshwater discharges from sluices in the “Afsluitdijk”, the dam separating the Wadden Sea from the freshwater Lake IJssel (van Aken, 2008; Duran-Matute et al., 2014). The seafloor of the subtidal area mainly consists of sandy and silty sediments. The more seaward parts generally show coarser sediments than the more inner parts, as a result of increasing current velocities towards the tidal inlets. For a more detailed description of the area see Dekker (1989).

2.2. Large-scale surveys of the subtidal macrobenthos

2.2.1. Survey in 1981/82

The survey in 1981/82 focused on the soft-sediment infauna of the subtidal western Dutch Waddem Sea. Apart from the Eierlandse Gat, the entire western Dutch Wadden was investigated between September 1981 and July 1982. In total, 459 stations along 45 transects, extending perpendicular to the direction of the tidal channels, were sampled (Fig. 1). Most of the stations (~90%) were located in shallow areas up to a depth of 5 m in mean tide level (MTL). At each station, samples were taken with two different gears: a 0.18 m^2 Van Veen grab for the top layer (up to 8–10 cm in depth) of the sediment and a 0.02 m^2 modified flushing sampler connected to a 5 m long hose (van Arkel and Mulder, 1975) for deeper sediment layers down to 40 cm in depth. Per station, three samples with the flushing sampler, pooled to one sample of 0.06 m^2, and one Van Veen grab sample were taken. The samples collected with the Van Veen grab were deep frozen, in order to allow easy sample processing. However, a proper identification and biomass determination of polychaetes was often not possible with this type of preservation. To allow a more proper processing of the often deep burrowing polychaetes, the samples collected with the flushing sampler were preserved in formalin. At deeper stations, and stations were the flushing sampler could not obtain a proper sample, only the Van Veen grab sample (16% of the samples) was taken and preserved in formalin. For details see Dekker (1989).

2.2.2. Survey in 2008

The survey of 2008 was initially intended to revisit all 459 stations of the survey from 1981/82. However, logistic reasons, budget constraints and the fact that some of the sampling stations from the 1980s survey became elevated up to the level that the former subtidal character changed into an intertidal one, resulted in a reduced sample number. Overall 397 samples were taken in October during the 2008 survey, of which 392 samples were taken at the identical locations of the initial survey from the 1980s (Fig. 1). Samples were taken with a 0.06 m^2 Reineck boxcorer. Depending on the sediment penetrability, the core depth of the samples varied between 15 and 45 cm. In those cases where many visible small organisms (*Peringia ulvae*, juvenile bivalves) were present at the sediment surface, a sub-sample with a small corer (Ø 4.25 cm; 0.0014 m^2) was taken to a depth of 4 cm. All samples were sieved on board over 1-mm sieves, stored in jars with buffered formaldehyde and stained with Rose Bengal for further analysis.

2.3. Annual monitoring of the subtidal macrozoobenthos

In summer 1989 a monitoring program on the macrozoobenthos of the shallow parts of the subtidal western Dutch Wadden Sea was initiated. After slightly adjusting the sampling method in winter 1990 (e.g. Dekker and de Bruin, 2000), the macrozoobenthos was monitored each year at three fixed subtidal transects (each consisting of 15 sampling stations with a distance of 100 m between the stations). The stations are located at depths between 1.5 and 4.7 m below MTL. In this study, we focus on the period 1990–2018. The two transects O and P remained unchanged in position during the entire period, whereas transect Q was partly relocated from 2014 onward due to rising above low water levels and thus getting an intertidal character. The transect was shifted counterclockwise at an angle of about 45° (Fig. 1). The majority of the transect stations (2–11, stations that were fallen dry) were relocated in the summer 2014. The remaining stations (12–15) were subsequently moved (one per year), resulting in the complete repositioning of the transect to its new location by summer 2018. The stations of the transects were sampled with a 0.06 m^2 Reineck boxcorer (0.9 m^2 sampling area per transect) twice a year (late winter: mostly March and late summer: mostly August). Depending on the sediment penetrability, sample depth varied between 15 and 45 cm. In cases

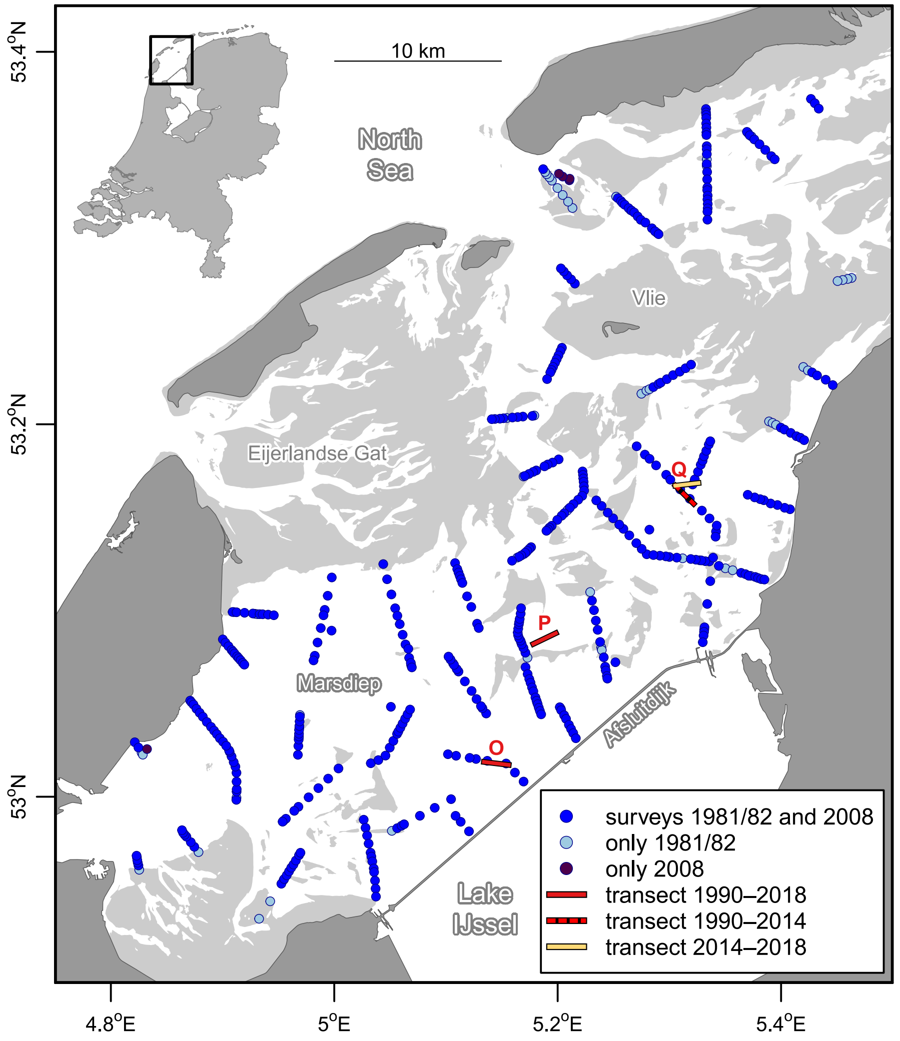

Fig. 1. Locations of subtidal sampling sites in the western Dutch Wadden Sea: circles indicate stations from the large-scale surveys (1981/82 and 2008), and lines show transects (O, P, Q) of the twice-annual monitoring program (winter/summer). Solid lines denote operational transects, and the dashed line marks the transect discontinued in 2014. Permanently submerged areas are shown in white, tidal flats in light grey, and land in dark grey.

of extremely high abundances (e.g. *Peringia ulvae*, *Marenzelleria viridis*) sub-samples were taken and conserved in 6% buffered formaldehyde. All samples were sieved on board over 1-mm sieves. After sieving, bivalves were separated from the other species for later analysis in the laboratory. The residue was preserved in buffered formaldehyde and stained with Rose Bengal for further analysis.

2.4. Laboratory analyses

In the laboratory the samples were sorted and all organisms were identified up to species level, except nemerteans and oligocheates (identified to the lowest taxonomic level possible). The soft parts of all bivalves were removed from the shells for biomass measurements. Apart from colony-forming hard substrate species: bryozoans (e.g. *Alcyonidioides mytili*, *Conopeum reticulum*, *Electra pilosa*, *Smittoidea prolifica*) and some hydrozoans (e.g. *Clytia hemisphaerica*, *Hartlaubella gelatinosa*, *Obelia longissima*) that are difficult to remove conveniently from their substrate, biomass was determined for all species as ash-free dry mass (AFDM) by drying at 60 °C to constant weight, weighing, incinerating at 560 °C and reweighing to obtain by subtraction the AFDM. While for the two large-scale surveys biomass was measured per separate station, biomass of the monitoring stations was pooled per transect. As hard substrate species (barnacles, bryozoans, hydroids) were not quantified during the survey in 1981/82 (only presence registered for barnacles), no biomass information is available for these species from the survey in 1981/82.

2.5. Data analyses

Prior to data analysis, all species names were checked against the standard World Register of Marine Species (WoRMS; www.marinespecies.org) ensuring that all names were consistent within and between the two surveys and the monitoring program. Each species was assigned to taxonomic phylum, environmental position (in- or epifauna), substratum preferences (soft, hard, heterogeneous) and functional feeding groups (deposit feeders, suspension feeders, omnivores, predators) based on the following online databases: BIOTIC (www.marlin.ac.uk/biotic), Marine Species Traits (www.marinespecies.org/traits), SeaLifeBase (www.sealifebase.org), Marine Species Identification Portal (www.species-identification.org) and from expert knowledge. Species were categorized as native or introduced (species of exotic origin introduced by human activity) according to Buschbaum et al. (2012) and Gittenberger et al. (2023). Biomass data were standardized to g per m^{-2} AFDM.

Cumulative species numbers and arithmetic means of the biomass of native and introduced species grouped to either the in- or epifauna were calculated separately for each large-scale survey and the different years of the monitoring program.

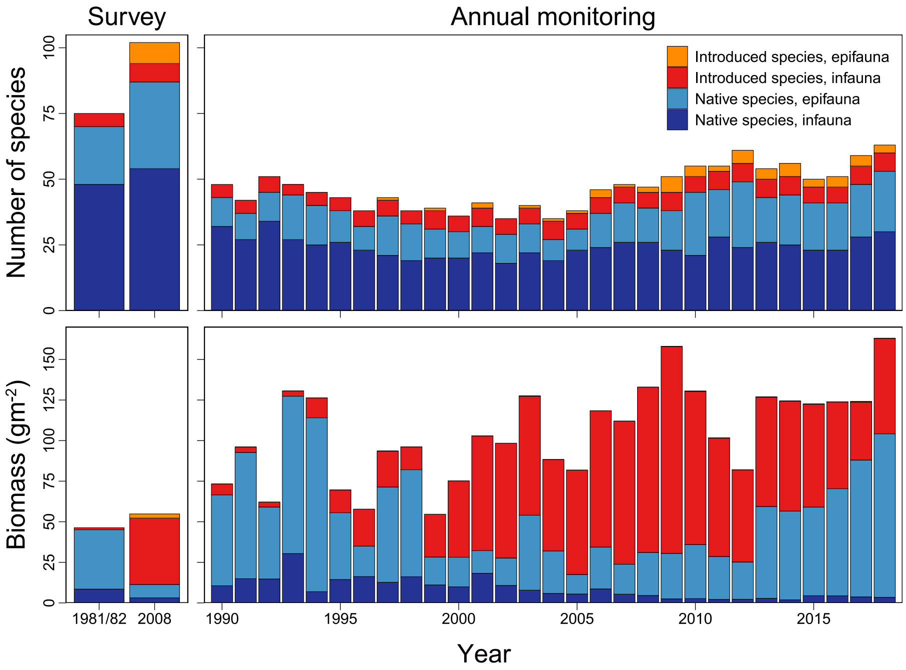

Fig. 2. The cumulative number of species (top panels) and average biomass (lower panels) for the large-scale surveys (left panels) and the annual monitoring in the period 1990–2018 (right panels). Shown are the values for native and introduced species grouped to the in- and epifauna. Although several epifaunal species of exotic origin were present during the last recent years of the annual monitoring, their biomass was in general comparably low so that the biomass values are almost unrecognizable in the graph. Note that numbers of the monitoring are given per separate year. For seasonal figures (winter/summer) see Fig. S2.

The monitoring time series was further split in two different time periods (one situated between the two surveys: 1990–2008, and the other after the second survey: 2009–2018) in order to assess whether pronounced differences in the benthic community occurred in the period between the two large scale surveys and in the period after the last survey in 2008. The differences in biomass of the different taxonomic groups (phylum level) and functional groups (substratum and feeding type) were analysed in detail for the two surveys in 1981/82 and 2008 as well as for the two monitoring periods.

To determine the change in community structure over time of the two large-scale surveys and 29 years of monitoring, the progression of individual species was analysed. A non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity was performed on square-root transformed biomass data of the 25 most common benthic species, occurring in at least 10% of all 856 stations of both large scale surveys. Furthermore, the biomass contribution of the ten most dominant species in relation to the total biomass (other species) was analysed for each long-term survey and each year of the monitoring program.

All statistical analyses were performed using the R platform (R Development Core Team, 2024), supplemented by the vegan package for the multivariate analysis.

3. Results

A total of 144 species was found in the subtidal western Dutch Wadden Sea at which 115 different species were discovered in the surveys and 118 species during the annual monitoring. On average 7 to 11 species were found per separate sample (Fig. S1). In the first survey 75 species were recorded, whereas 102 species were found in the second survey in 2008 (Fig. 2). The numbers of species encountered at the three monitoring transects within a single year was on average 46.2 (± 7.5 SD) species, with lowest numbers observed during the late 1990s and early 2000s and highest numbers in the most recent years (Fig. 2). In respect to the different seasons, a higher species number was generally observed during summer (Fig. S2).

During the entire study period, the number of introduced species steadily increased. While in 1981/82 and during the early 1990s, only a few introduced — exclusively infaunal — species were encountered, an increase in introduced species (both infaunal and epifaunal) was observed in the late 1990s and the 2000s.

The average total biomass was remarkably similar between the surveys of 1981/82 and 2008 (46.3 to 54.8 gm^{-2}), but showed a remarkable shift towards a dominance of introduced species in 2008 (Fig. 2). In contrast to the native fauna, where the main share of biomass was in epibenthic species, infaunal species contributed most to the biomass of introduced species.

Likewise, infaunal introduced species also dominated the macrobenthic biomass since the early 2000s in the transects of the annual monitoring, where generally higher average biomass values were observed than in the large-scale surveys. Only in the more recent years (from 2015 onward) biomass of introduced species decreased slightly and native species became dominant again (Fig. 2).

In general, the highest biomass with respect to functional feeding groups was observed in the suspension feeders followed by deposit feeders, whereas carnivores and omnivores generally only contributed little to the total biomass in the surveys and the monitoring (Fig. 3). The biomass contribution of deposit feeders declined slightly, whereas the biomass contribution of suspension feeders increased in both the surveys and the monitoring periods.

The majority of the biomass was found in species associated to the soft-sediment macrofauna. Exceptions are the carnivores (e.g. shore crab (*Carcinus maenas*), or the polychaets *Alitta succinea*, *Alitta virens*, and *Nepthtys* sp.), where a high biomass is attributed to species that are equally found on soft and hard substrates (heterogeneous substrate species). Moreover, biomass of suspension feeders was dominated by hard substrate species during the survey in 1981/82, but this shifted towards a dominance of soft-sediment species in the survey of 2008 and in both monitoring periods.

The differences in biomass among the different taxonomic groups were relatively consistent over the entire study period. The highest biomass by far was observed in the mollusks, followed by annelids and arthropods, whereas biomass of the other groups was generally marginal (Fig. 4). In all three dominant macrobenthic groups (mollusks,

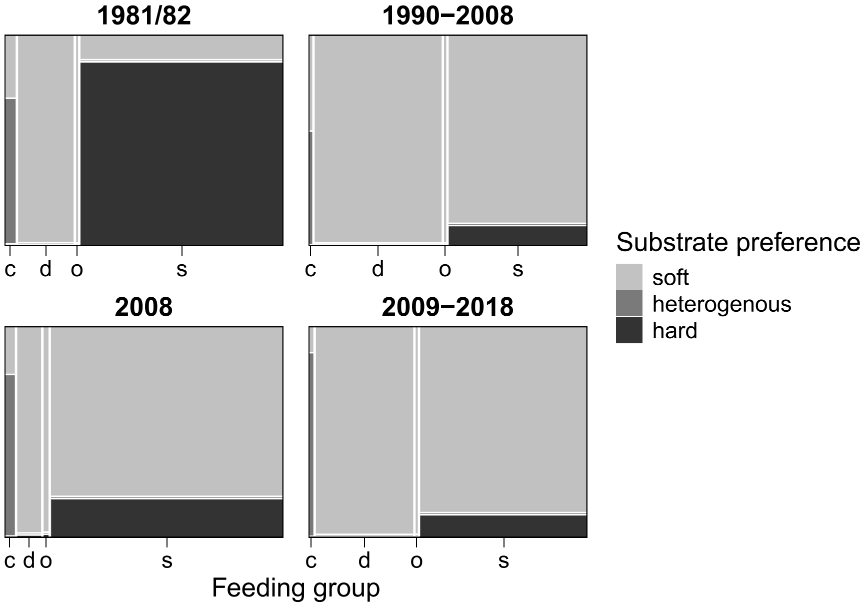

Fig. 3. Mosaic plots of the macrozoobenthos biomass from the large scale surveys in 1981/82 and in 2008 (left panels) and the annual monitoring between 1990 and 2018 (right panels) in the subtidal western Dutch Wadden Sea, distributed by feeding groups (c: carnivores; d: deposit feeders; o: omnivores; s: suspension feeders; horizontal axis) and substrate preferences (vertical axis: soft, heterogeneous, hard). The area of each rectangle is proportional to the relative biomass of each feeding group–substrate combination. Note that the monitoring was split into a period between the two large-scale surveys (1990–2008) and the period after the last survey (2009–2018).

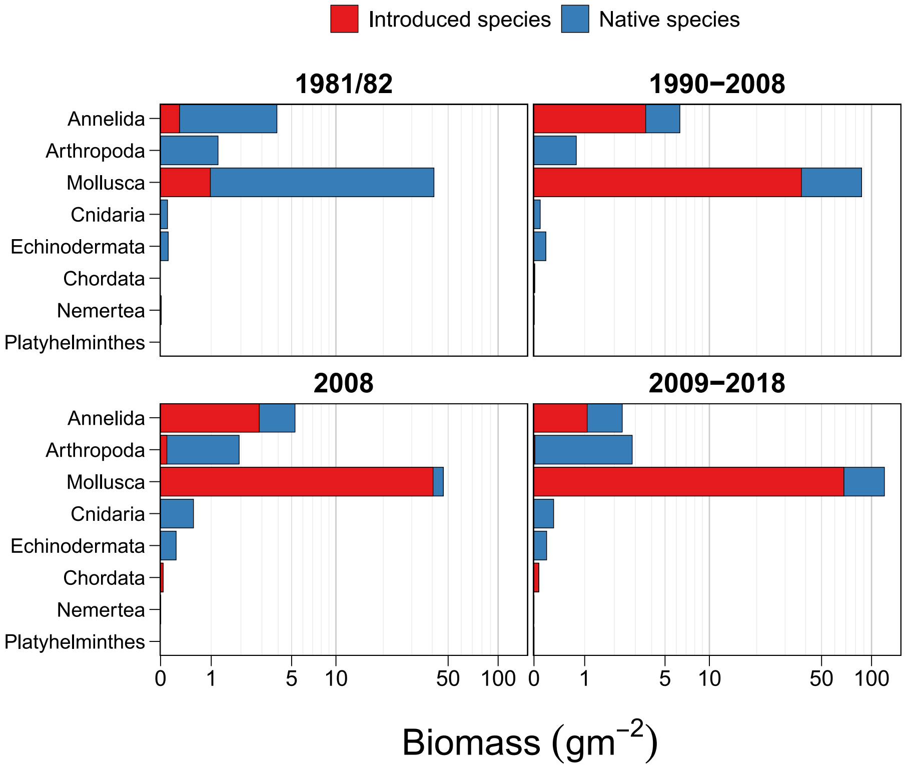

Fig. 4. Summary of the average macrozoobenthos biomass (AFDM, log scale) of native and introduced species aggregated per taxonomic group for the large scale surveys in 1981/82 and in 2008 (left panels) and the annual monitoring between 1990 and 2018 (right panels) of the subtidal western Dutch Wadden Sea. The monitoring was split into a period between the two large-scale surveys (1990–2008) and the period after the last survey (2009–2018). Note that no biomass was estimated for colony-forming bryozoans and hydrozoans, resulting in an underestimation (Cnidaria) and no information (Bryozoa) of the specific biomass. Therefore, Bryozoa are not listed in this plot. For an overview of the cumulative species numbers within each taxonomic group per survey and monitoring period, see Fig. S3.

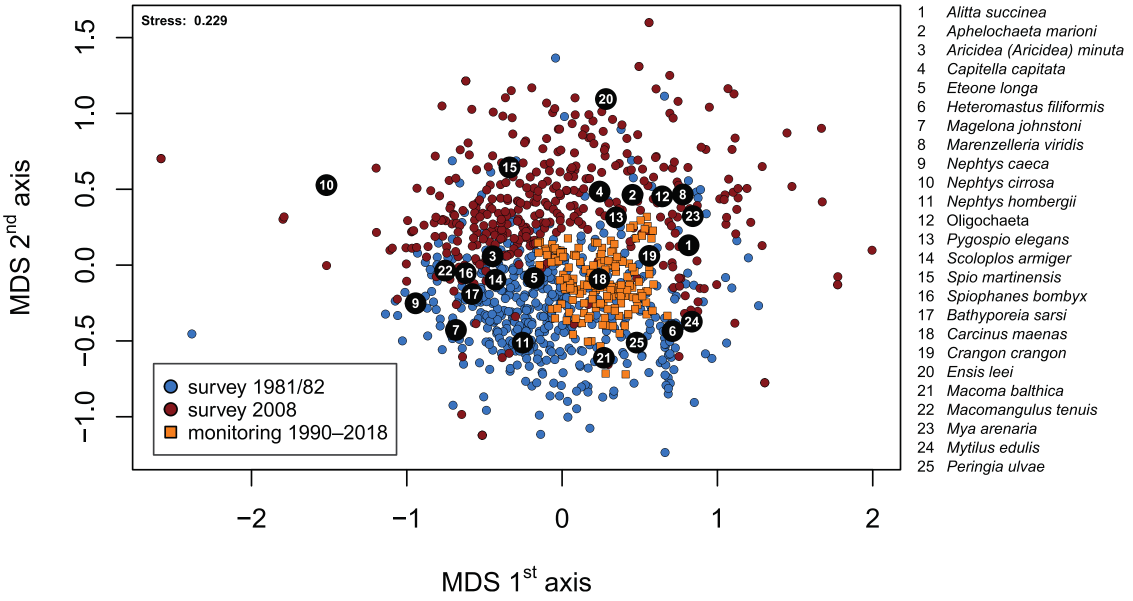

Fig. 5. Nonmetric multidimensional scaling (nMDS) plot of stations in the large-scale surveys of 1981/82 and 2008 and of the monitoring between 1990–2018 based on a Bray Curtis similarity matrix of square root transformed biomass data of the 25 most common macrozoobenthos species (occurring in at least 10% of all 856 stations of the two large-scale surveys) from the subtidal western Dutch Wadden Sea. The closer two stations are in the ordination plot, the more similar their macrobenthic communities. The centroids of the 25 considered species (black circles) are shown to illustrate the general distribution of the different species within the ordination plot and to depict the differences in species composition among the stations. For direct comparisons of the two large-scale surveys see Fig. S4. For details on the monitoring stations see Fig. S5.

annelids, arthropods), biomass increased between the two large-scale surveys (1981/82 and 2008). In the monitoring program, biomass also increased for mollusks and arthropods, whereas annelids showed a slight decrease between the two monitoring periods. The general picture of biomass increase of the different groups is to a certain extend based on the rise of introduced species. Although only comparatively few species were of non-native origin in the later sampling periods (Fig. S3), they often were dominating in terms of biomass (Fig. 4).

The subtidal macrozoobenthos community experienced pronounced changes since the first survey in 1981/82. Results from the multivariate data analysis revealed clear differences in macrofauna community structure among species commonly occurring in the two large-scale surveys in 1981/82 and in 2008 (Fig. 5). The species communities at the different stations of the two surveys are clearly separated in the nMDS plot, particularly in respect of the second axis (see also Fig. S4). The species communities of the monitoring transects showed much less variation than those of the two large-scale surveys. This is largely due to the fact that the monitoring biomass values represent averages from 15 separate stations and that the transects are restricted to smaller areas near the Afsluitdijk, where environmental conditions are relatively homogeneous compared to the broader survey areas.

The transects are generally arranged mainly within the stations of the survey from 1981/82, but a closer inspection reveals a similar temporal shift in the second axis of the MDS analysis (Fig. 6, Fig. S4).

Important species of the early sampling campaigns are for example *Macoma balthica*, *Peringia ulvae*, *Nephtys hombergii*, *Magelona johnstoni*, *Heteromastus filiformis*, and *Mytilus edulis* (Fig. 5). Characteristic species of the species communities of the recent sampling campaigns are among others the introduced species *Ensis leei*, *Mya arenaria*, *Marenzelleria viridis*, and *Aphelochaeta marioni* (Fig. 5).

Likewise, the share in total biomass of the most dominant species also showed that the communities have changed considerably (Fig. 7). One of the most remarkable changes in the large-scale surveys was the strong decrease of mussels (*Mytilus edulis*) from a relative high biomass contribution of 29.9 gm^{-2} AFDM (64.6% of the total biomass) in 1981/82 to 5.2 gm^{-2} AFDM (9.5% of the total biomass) in 2008. This decline was apparent for mussels on naturally occurring beds (5.7 gm^{-2} AFDM in 1981/82 to 0.5 gm^{-2} AFDM in 2008) as well as for individuals that were stocked on culture plots (24.2 gm^{-2} AFDM in 1981/82 to 4.8 gm^{-2} AFDM in 2008) (Fig. 7).

In contrast, the introduced species *Mya arenaria* and *Ensis leei* that had a comparably low biomass (*M. arenaria*) or were absent (*E. leei*) during the early 1980s became dominant (16.9 gm^{-2} AFDM/ 30.8% of total biomass and 21.1 gm^{-2} AFDM/ 38.5% of total biomass, respectively) in the survey of 2008. With respect to the transects monitored every year, which were initially dominated by *Peringia ulvae*, a shift towards dominance by introduced species such as *E. leei*, *M. arenaria* (Fig. 7 and Fig. S8), *Marenzelleria viridis* (Fig. 7 and Fig. S6), and *Aphelochaeta marioni* (Fig. S6) is also apparent.

4. Discussion

The macrozoobenthos of the subtidal Western Dutch Wadden Sea experienced considerable changes since the early 1980s. The benthic community changed from a dominance of native species to a community that shows a high biomass of introduced species. While a few species of non-native origin proliferated enormously and established dominant populations, several native species that were formerly dominant and present with high biomass values became less abundant in the course of 4 decades. For instance, blue mussels were common and dominant during the large-scale survey in 1981/82, but were of minor importance in subsequent sampling campaigns. The relatively high mussel biomass during the 1980s is the result of an exceptional strong mussel recruitment in 1979 (Beukema et al., 2015) and of the extensive use of the area for mussel farming that is practised since 1950 (Dijkema, 1997). Although mussel beds have occurred regularly up to a depth of about 20 m in the Wadden Sea prior to mussel cultivation (Verwey, 1954), mussel culture intensified the mussel presence by transplanting seed mussels from subtidal and intertidal areas and regulating predator abundances by selectively removing voracious predators, such as sea stars (e.g. Barkhouse et al., 2007). As a result, biomass in these culture areas is generally higher than in wild mussel beds (Dekker, 1989; Capelle et al., 2017; Waser et al., 2025, see also Fig. 7). The densely populated culture plots may, in turn, also increase the mussel biomass

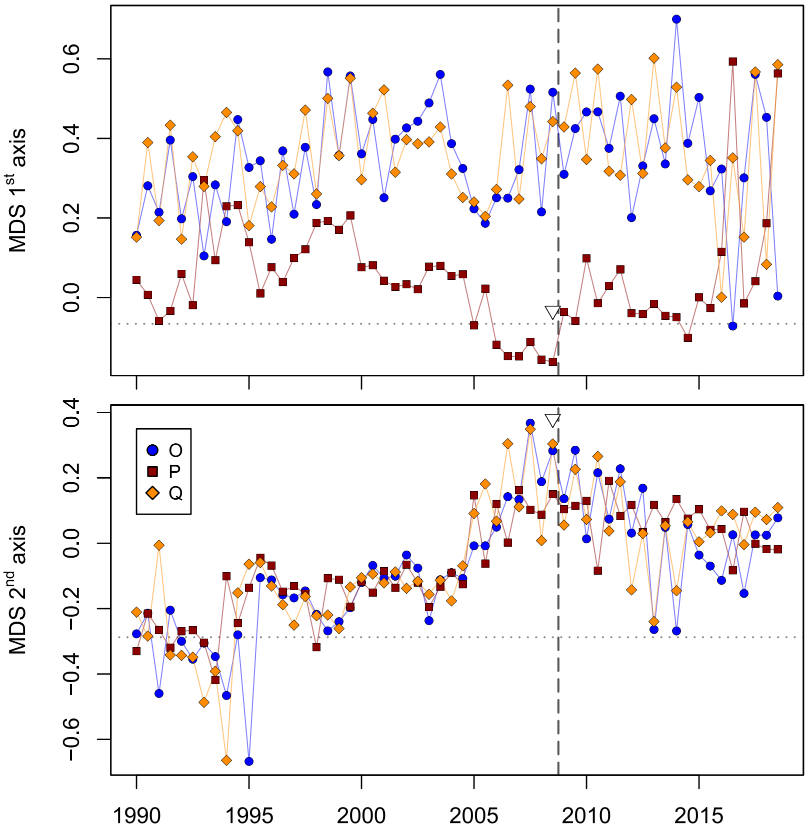

Fig. 6. Temporal change of the subtidal macrozoobenthos community at three transects (O,P, and Q) during winter (x = year) and summer (x = year + 0.5) for the period 1990–2018. Shown are the first (top panel) and second (lower panel) axes of the nMDS analysis for the three monitoring stations, plotted against the year of sampling. The vertical grey dashed line marks the survey conducted in autumn 2008, which was used to divide the monitoring series into two periods (1990–2008 and 2009–2018). Reference averages from the large-scale surveys are marked by the dotted light grey horizontal line (1981/82) and the white triangle (2008).

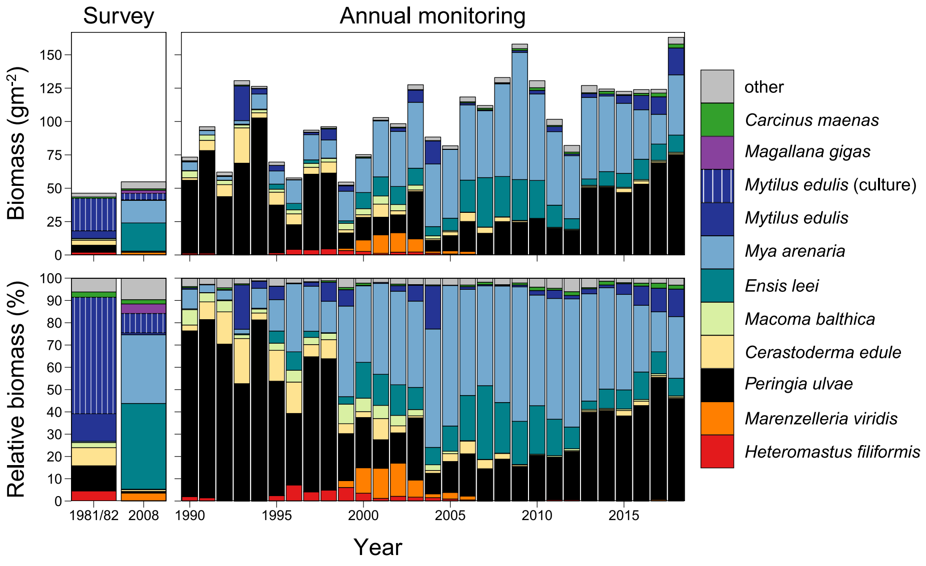

Fig. 7. Changes in biomass over time for the ten most dominant species. Shown are the absolute biomass (gm^{-2}, top panels) and the relative share (%) of each species on the total biomass (lower panels) for the two large-scale surveys (left panels) and per year for the annual monitoring (right panels). Note that the average mussel biomass was divided into individuals originating from inside culture plots (*M. edulis* (culture)) and outside (*M. edulis*). For details on the most important groups (annelids, arthropods, and mollusks) see Figs. S6–S8. Further details on the species-specific annual biomass patterns for the monitored transects are shown in Fig. S9.

of nearby subtidal areas by supplying larvae and mussels washed away during storms. During the monitoring program, for example, an increase in mussel biomass in 1993 was attributed to an input of mussels flushed from neighbouring culture plots, as evidenced by the sudden appearance of larger, older individuals in the subtidal areas (Dekker and de Bruin, 2000). It remains uncertain to what extent the biomass assessed in 1981/82 is representative for this time period and if it resembles biomass in pre- or succeeding years, as there is a lack of comparable biomass data. However, data on the fishery yield indicate that the period where sampling took place (1981/82) was seemingly a period with relatively high mussel biomass (Dankers and Zuidema, 1995; Dijkema, 1997) so that the average mussel biomass during the 1970s and 1980s was presumably slightly lower than observed during the survey in 1981/82.

Starting with the late 1980s and early 1990s the conditions began to change as a result of recruitment failures accompanied by declines in the mussel population (Obert and Michaelis, 1991; Herlyn and Millat, 2000; Dankers et al., 2001; Ens, 2006). The combination of low mussel recruitment and ongoing fisheries lead to the disappearance of almost all intertidal mussel beds in the Dutch Wadden Sea in 1990 (Beukema and Cadée, 1996; Dankers et al., 2001; Ens, 2006). In order to promote intertidal mussel bed recovery, fishing quotas were introduced and intertidal areas were closed for mussel fisheries. The subtidal areas remained open for fisheries and were the only source for stocking the culture plots before suspended seed mussel collectors (e.g. van Broekhoven et al., 2024; Zhao et al., 2024) were introduced in 2009. After the 1990s, recruitment remained comparably low (Beukema and Dekker, 2014; Beukema et al., 2015; van Stralen and van den Ende, 2018). Natural losses (e.g. storms) and losses caused by mussel and cockle fisheries in the subtidal area (Dekker, 1995; Dekker and de Bruin, 1998, 2000) often could not be compensated by the low recruitment, leading to considerably lower mussel occurrence and biomass than in the early 1980s. The decline in mussel biomass also implied the decline of complex three-dimensional structures, which are known to provide settlement and refuge for other organisms in the surrounding soft sediments (Saier, 2002; Norling and Kautsky, 2008; Buschbaum et al., 2009). However, only minor differences in the benthic fauna were observed, which may have resulted from variation in the presence of epibenthic habitat structures.

Similar to the decline of the mussel, declines were also observed for the two endobenthic bivalves, the cockle (*Cerastoderma edule*) and the Baltic tellin (*Macoma balthica*). While both bivalves contributed 8.1% and 2.3%, respectively of the total benthic biomass during the survey in the 1980s and could reach shares up to 20% and 9%, respectively observed during the monitoring in the 1990s, their biomass decreased to relatively low levels in the 2000s and 2010s. The declines of the three bivalves are amongst other things likely related to increasing water temperatures during winter that promoted epibenthic predators (crabs, shrimps). High predator numbers succeeding a mild winter, in turn, generally resulted in low recruitment of *M. balthica*, *C. edule*, and *M. edulis* (Beukema and Dekker, 2014).

Despite the strong declines of the three bivalve species, only little taxonomic or functional changes occurred and suspension feeding bivalves remained dominant in the subtidal western Dutch Wadden Sea. This can be explained by the proliferation of two introduced species: the American Razor clam (*Ensis leei*) and the sand gaper (*Mya arenaria*). *Mya arenaria* once widely occurred on both North Atlantic coasts during the Pliocene. It has disappeared from European coasts during the glaciation of the Pleistocene, while it survived along the Atlantic coasts of North America. It was reintroduced to European coasts in the 13th to 15th century, most likely by Vikings travelling between Greenland and North America (Strasser, 1999; Essink and Oost, 2019). *Ensis leei*, originating from the east coast of North America, was first recorded in the Wadden Sea area in the late 1970s and early 1980s (Essink, 1985; Armonies and Reise, 1999; Dekker and Beukema, 2012). In the 2000s, both species increased dramatically and established dominant populations in the subtidal Dutch Wadden Sea. It is not known what factors explicitly favoured their proliferation and whether the declines in the native bivalves facilitated their initial establishment by reducing predation risk on the *E. leei* and *M. arenaria* larvae (Möller and Rosenberg, 1983; André and Rosenberg, 1991).

Besides the two bivalves, also other introduced species invaded the subtidal parts of the western Dutch Wadden Sea. In contrast to the two bivalves, however, most of these invaders showed a rather low biomass and local occurrence. For example, the Pacific oyster (*Magallana gigas*), which established a considerable population across intertidal areas of the Dutch Wadden Sea (Troost, 2010; Waser et al., 2016; van der Meer et al., 2019), occurred only at a few sites in the large-scale survey in 2008 and was negligible during the annual monitoring. It remains to be seen if the species will further expand its subtidal occurrence in the future, but annual surveys on the subtidal shellfish stocks suggest a more or less stable population of Pacific oysters in the subtidal western Dutch Wadden Sea (Vorberg et al., 2017).

Other invaders may be subject to considerable fluctuations in population size, such as the polychaete *Marenzelleria viridis*. This species, originating from Atlantic coasts of North America, increased dramatically at the subtidal monitoring transects during the early 2000s, but decreased substantially soon after. A similar boom and bust pattern of *M. viridis* has been described earlier from intertidal areas of the Wadden Sea (Essink et al., 1998; Essink and Dekker, 2002).

Another example of a species showing extensive fluctuations was the mud snail (*Peringia ulvae*). While in the early 1980s it contributed more than 10% of the total macrobenthic biomass, declining numbers resulted in markedly lower biomass in 2008. Even more remarkable are the extensive variations observed at the monitoring transects, where the snail was dominating the benthos by far during the 1990s till experiencing a population collapse in the late 1990s. Only in 2013, *P. ulvae* increased to levels as observed during the 1990s. The reasons for the fluctuations are not well understood, but could be partly based on differences in organic matter content of the sediment (Bick and Zettler, 1994).

The example of *P. ulvae* (e.g. very high average biomass values in the monitoring program and comparably much lower values during the large scale surveys) also points to specific differences between the monitoring transects and the entire set of stations sampled in the large-scale surveys. The survey stations are widely scattered throughout the subtidal western Dutch Wadden Sea, resulting in a high variability of sediments, water depths and habitats. The monitoring transects, in contrast, are confined to shallow areas with low hydrodynamic forces, resulting in a relatively high sedimentation of silt and organic material. The relatively high amount of deposited material favours particularly deposit feeders, such as amongst others *P. ulvae*. Consequently, comparably high biomass values and high proportions of deposit feeders are observed on the transects compared to the large scale surveys. Apart from this difference, however, both programs show a similar trend of change in benthic community composition. The monitoring transects corroborate the drastic change in the benthos community observed in the surveys between the 1980s and 2008.

In the course of the last decades, the species number recorded in the subtidal western Dutch Wadden Sea has increased considerably. In the survey of 2008, the total inventory was with 102 species almost 30 species higher than in the first survey in 1981/82. This difference, however, needs to be interpreted with caution due to growing taxonomic skills and the fact that both surveys were initially conceived with somewhat different goals. The first survey particularly focused on the soft-sediment infauna, while the second survey aimed to gain a more thorough picture on the entire subtidal macrozoobenthos. It is therefore very likely that the differences in the number of epibenthic species that are often associated to hard substrata are partly due to differences in survey accuracy. However, an increase in species richness is also apparent when focusing only on the infaunal species that live almost exclusively in soft sediments. These observations concur with the general picture of increased species richness in intertidal areas of the Wadden Sea (e.g. Beukema and Dekker, 2011; Schückel and Kröncke, 2013), driven by immigration of exotic species and increasing water temperatures (Beukema, 1992; Beukema and Dekker, 2011). The increase in species richness seems to be a common phenomenon in coastal marine ecosystems, as a study of 471 time series from coastal areas across the globe found that increases in the number of species predominated in the analysed data sets (Elahi et al., 2015).

For the entire Wadden Sea, numbers of macrozoobenthic newcomers generally exceed those of species known to have disappeared (Lotze et al., 2005). However, detailed information on historic distributions and occurrences of the macrobenthos in the Dutch Wadden Sea is scarce (see Wolff, 2000). Quantitative data on the macrozoobenthos exist only from the 1970s onward for the intertidal parts of the Wadden Sea (e.g. Beukema and Dekker, 2011). Older records are often incomplete and/or contain only qualitative information of a few selected species. For the subtidal parts, quantitative historic data lack completely and only little is known on the subtidal macrozoobenthos of the distant past.

Our study shows that the macrozoobenthos of the subtidal western Dutch Wadden is prone to considerable temporal fluctuations. Based on our analyses, we cannot make reliable predictions about the future development of the subtidal macrozoobenthic community as a whole. Nevertheless, species diversity may continue to increase. For instance, species invasions, such as the recently introduced dwarf surf clam (*Mulinia lateralis*) (Craeymeersch et al., 2019; Klunder et al., 2019), the Manila clam (*Ruditapes philippinarum*) (Reise et al., 2024), or the mud blister worm (*Polydora websteri*) (Waser et al., 2020) will presumably further diversify the macrozoobenthos of the subtidal western Dutch Wadden Sea with unpredictable effects on the native community and existing species interactions.

CRediT authorship contribution statement

Andreas M. Waser: Writing – original draft, Visualization, Formal analysis, Conceptualization. **Rob Dekker:** Writing – review & editing, Investigation, Data curation. **Jan Drent:** Writing – review & editing, Formal analysis. **Jaap van der Meer:** Writing – review & editing, Formal analysis.

Funding

This study was carried out as part of the PRODUS project, which was funded by the Producers' Organization of the Dutch Mussel Culture, the Netherlands (PO Mossel) and the Dutch Ministry of Economic Affairs, the Netherlands. The annual benthos monitoring was financially supported by the Dutch Ministry of Infrastructure and Water Management (Rijkswaterstaat). AMW acknowledges support from the project MARBEFES of the European Union's Horizon Europe Programme (Grant No. 101060937, www.marbefes.eu).

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.

Acknowledgements

We thank the crew of the RV Navicula for the logistical support during field work. We thank Bert Brinkman and Chris Abbink for assisting during the benthic sampling. Lodewijk van Walraven, Evelien Dekker, Sjoerd Duijns, Jeremy Smith, Lise Klunder, Janneke Bakker, Sander Holthuijsen, Job ten Horn and Chris Abbink are thanked for helping sorting and identifying the samples. We further appreciate the valuable feedback on an earlier draft by 2 anonymous reviewers.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.seares.2025.102666.

Data availability

The data from the two large-scale surveys are archived in the NIOZ Dataverse repository and can be accessed at https://doi.org/10.25850/nioz/7b.b.vg. Data from the annual macrobenthic long-term monitoring up to 2011 are available on AquaDesk (https://live.aquadesk.nl, Dutch Rijkswaterstaat MWTL). The remaining data from 2012 to 2018 will be made available upon request.

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