Check for updates

Received: 28 February 2024 | Accepted: 9 October 2024

DOI: 10.1002/pan3.10757

PEOPLE AND NATURE
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Hotspots in peril: Misalignment of conservation efforts and ecological values in a shallow coastal sea

Kasper J. Meijer[1] | Oscar Franken[1,2] | Sterre Witte[2] | Sander J. Holthuijsen[3] | Tjisse van der Heide[1,2] | Laura L. Govers[1,2] | Han Olff[1]

[1]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands

[2]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands

[3]Rijkswaterstaat Noord Nederland, Utrecht, The Netherlands

Correspondence
Kasper J. Meijer
Email: k.j.meijer@rug.nl

Funding information
Exacte en Natuurwetenschappen, Grant/Award Number: 016. Veni.181.087; Waddenfonds, Grant/Award Number: WF2018-187059

Handling Editor: Andrea Belgrano

Abstract

1. Misalignment between the location of marine protected areas (MPAs) and ecologically valuable areas, here defined as low conservation conformity, may arise due to conflicting socioeconomic and ecological demands, diminishing MPA effectiveness. Such conflicts are especially found in coastal areas with high human population density and high natural productivity. Here, we aim to provide a framework to quantitatively and qualitatively assess conservation conformity using multiple indicators to identify hotspots of ecological quality.
2. We use the subtidal Dutch Wadden Sea as a case study due to its unique natural, cultural, and economic values and the availability of high-resolution spatial data. We focus on macrozoobenthic communities (larger animals living in and on the seafloor), a vital group experiencing significant ecological degradation due to a long history of human activity. A complex set of restrictions has been implemented to prevent further macrozoobenthos degradation and to stimulate recovery. We first spatially overlay and translate the different protection measures to international standards. We then determine hotspots of ecological quality based on nationally and internationally used indicators of biodiversity and seafloor status and map their overlap with protected areas.
3. We found that in 2024, 37% of the 134,466 ha subtidal Dutch Wadden Sea has some level of protection. However, due to the poor spatial overlap of implemented measures, the IUCN-based guidelines would classify only 10% as an MPA, while only 2% of the subtidal is truly free of human bottom-disturbing activities. Of this total subtidal area, 19% was classified as an ecological hotspot based on multiple indicators. However, the protection measures in place overlapped very poorly with these ecological hotspots. Overall, only in 2% of the total subtidal area, IUCN-classified MPAs overlapped with locations identified as ecological hotspots for at least six indicators, indicating poor overlap of MPAs with ecological hotspots.
4. Because the whole Wadden Sea is subject to several international protection schemes (e.g. Natura 2000, OSPAR convention, Ramsar Convention, and

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.
© 2024 The Author(s). *People and Nature* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

UNESCO World Heritage), these results call for substantial adjustment of the current conservation layout. We thus emphasise the importance of quantitatively evaluating potential misalignment between protected areas and ecologically valuable areas in coastal zones.

KEYWORDS
ecological quality indicators, hotspots, Macrozoobenthos, marine protected areas, sensitivity, Wadden Sea

1 | INTRODUCTION

Marine protected areas (MPAs), discrete marine areas managed through legal or other effective means, hold immense potential for the long-term conservation and recovery of natural values. They are among the most effective measures to protect and restore marine biodiversity (Dudley et al., 2008; Rising & Heal, 2014; Sala & Giakoumi, 2018). However, many currently established MPAs are ineffective (Lubchenco & Grorud-Colvert, 2015; Sala et al., 2018), either through poor regulations, too little enforcement of existing regulations or due to misplacement. Fully protected and enforced MPAs, also known as no-take zones, are considered the most effective at protecting marine biodiversity (Lubchenco & Grorud-Colvert, 2015; Sala & Giakoumi, 2018; Zupan et al., 2018). Nevertheless, ineffective placement of MPAs in areas with little ecological value or low recovery potential, regardless of the protection level, diminishes the ecological benefits of MPA establishment (Devillers et al., 2015). This is because the establishment of new MPAs is often opportunistic rather than based on sound ecological analysis (Rabaut et al., 2009; Sundblad et al., 2011), and trade-offs between socioeconomic interests and nature are often biased towards resource utilisation rather than preservation (Joppa & Pfaff, 2009; Venter et al., 2018). This trade-off emerges because ecologically valuable areas (hotspots, such as high biodiversity areas) often coincide with areas of high primary and secondary productivity and hence high economic value (Beukema & Dekker, 2011; Van der Reijden et al., 2018; Venter et al., 2018), This ultimately results in limited overlap between ecological hotspots and protected areas (Lindegren et al., 2018; Rodrigues et al., 2004; Venter et al., 2018). Here, we define such poor overlap of MPAs with ecological hotspots as a low "conservation conformity".

Quantifying conservation conformity can support decision-making on natural resource planning and management (Myers et al., 2000). Moreover, it can be used within the assessment of ecological coherence for MPA networks where limited overlap (low conservation conformity) would negatively impact the adequacy criteria of MPA networks (Ardron, 2008), as well as to evaluate the effectiveness of singular MPAs in protecting natural values (i.e. ecological hotspots). But while the criteria for an economic hotspot are often clear (e.g. high fishing or energy revenues), identifying ecological hotspots is more complex, given the wide range of conservation regulations, targets and available indices. Traditionally, standard biodiversity measures, calculated using species ranges, are used to identify areas with high biodiversity or areas with a high proportion of rare or endemic species (i.e. hotspots) (Myers et al., 2000; Reid, 1998). Alternatively, ecological hotspots can also be defined based on functional significance, which do not necessarily match with biodiversity hotspots (Stuart-Smith et al., 2013). This variation highlights the urgency of adopting a more strategic approach that combines multiple hotspot indicators, such as biodiversity and functionality, into an integrated assessment. Moreover, a clear overview of which areas are protected in which way is often lacking in coastal areas due to multiple and complex regulations, hindering a good quantification of conservation conformity.

In marine ecosystems, evaluating the spatial placement of protected areas in relation to ecological hotspots is especially important in coastal areas, where conflicts between socioeconomic interests and nature are ubiquitous. Benthic fauna is an interesting group to evaluate for conservation conformity, as it represents several good indicators of ecosystem health (Jayachandran et al., 2022). Macrozoobenthos (benthic invertebrates larger than 1 mm) are especially good ecological indicators as they are largely sedentary and have relatively fast life cycles through which they respond quickly to changes or perturbations (Tillin et al., 2006). Additionally, macrozoobenthos forms an important ecological foundation and food source for birds and fish in many rocky and soft-bottom ecosystems (Bouma et al., 2009; Choat, 1982; Mathot et al., 2018; Rabaut et al., 2007; Underwood, 2000), with a key role in physio-chemical processes (Reiss & Kröncke, 2005). Therefore, we focus on macrozoobenthos as ecological quality indicators to identify hotspots of ecological quality (hereafter ecological hotspots).

In Europe, multiple legal and policy frameworks exist that incorporate macrozoobenthos, such as the Water Framework Directive (WFD, 2000) and the Marine Strategy Framework Directive (MSFD, 2008). Here, macrozoobenthos are indicators of pollution and disturbance levels (WFD), as well as seafloor integrity (MSFD). Important aspects within these frameworks are measures of biodiversity (MSFD Descriptor 1), functioning (MSFD Descriptor 6) and food web status (MSFD Descriptor 4). In addition, important benthic habitats and species are described in the Habitat Directive (Council Directive 92/43/EEC, 1997). These different policy frameworks, therefore, provide multiple perspectives relevant to defining ecological hotspots using macrozoobenthos as indicators.

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

In this study, we aim to provide a unified approach to quantitatively and qualitatively assess conservation conformity (the degree of overlap of MPAs with ecological hotspots) using a multiple-indicator approach for macrozoobenthos. As a case study, we use the Dutch Wadden Sea, a UNESCO World Heritage Site and Natura 2000 area that is assessed under the EU Water Framework Directive. The Wadden Sea has a long history of human interventions and resource use (Lotze, 2007), and several area-based conservation measures have been implemented to enhance and preserve its natural values. Such an assessment is highly necessary because the Natura 2000 objectives for the Dutch Wadden Sea have still not been met, and its ecological qualities are even degrading in some cases (Heidinga et al., 2023). We first assess the current area-based restrictions using the MPA guide classification framework based on the allowed impact of human activities (Grorud-Colvert et al., 2021). This provides a framework to classify these restrictions as MPA and their associated protection level. Next, we assess the conservation conformity of combined hotspots of 12 macrozoobenthic-based ecological quality indicators. We combine diversity indicators that are traditionally used to identify hotspots with indicators that reflect quality descriptors in various policy frameworks. We use five diversity-related indices: Hill's diversity, Margalef diversity, Rao's Q, Shannon diversity, and species richness; and seven habitat quality indices: AZTI's Marine Biotic Index (AMBI), Benthic Ecosystem Quality Index 2 (BEQI2), benthic species indicator index (BISI), Benthic Quality Index (BQI), food web connectance, Infaunal trophic index (ITI), and sensitivity, together capturing all policy frameworks relevant for this system. This yields a unified approach to quantify conservation conformity as the degree of overlap between ecological hotspots and MPA placement.

2 | METHOD

2.1 | Study site

The Wadden Sea is an extensive shallow tidal sea ranging from the Netherlands to Denmark, hosting unique biodiversity and is an important foraging area for migratory bird and fish species (Boere & Piersma, 2012; Wolff, 2013). For these reasons, the Wadden Sea has been designated UNESCO World Heritage and is protected through the European Natura 2000 framework. This study focuses on the Dutch Wadden Sea (hereafter referred to as the Wadden Sea), ranging from the westernmost Marsdiep tidal inlet to the Eems-Dollard tidal basin (Figure 1a,b). The Wadden Sea comprises 47.7% subtidal and 52.3% intertidal areas (Baptist et al., 2019, 2022). Most subtidal (permanently inundated) areas are found in the Western tidal basins Marsdiep, Vlie, and Borndiep (Figure 1b). Here, subtidal is defined as being exposed <4% of the time (Baptist et al., 2019, 2021; Ricklefs et al., 2022). The median depth in the subtidal is −2.96 m, and 50% of the area (between the 25% and 75% quantiles) ranges between −1.60 and −7.47 m NAP (Dutch Ordnance Datum). The intertidal parts of the Wadden Sea are hardly used for industrial activities besides non-extractive tourism, small-scale hand-cockle fishery and mechanical lugworm fishery. The subtidal parts of the Dutch Wadden Sea are among the most heavily affected areas, where bottom-disturbing activities such as dredging and bottom trawling fisheries are spatially ubiquitous. Restrictions have mostly focused on hydrodynamically calm areas with the predisposition that these areas host the most vulnerable communities (Hiddink et al., 2007; Robert et al., 2021). At the same time, ecological knowledge on subtidal habitats in this ecosystem is limited (Ricklefs et al., 2022; Wolff et al., 2010), and a clear historical baseline to assess degradation or conservation success is lacking. Therefore, we focus on the subtidal (permanently submerged) areas.

2.2 | Ecotopes

Management decisions are often based on delineated units of biological importance, such as ecosystems or habitats. An ecotope map for the trilateral Wadden Sea was created (Baptist et al., 2019, 2022) to delineate the system's main ecotopes for management purposes. The Dutch Ministry of Water & Infrastructure has adopted this ecotope map with minor changes to the parameters used in delineating each ecotope (Rijkswaterstaat) to guide management decisions (van Donk & Baptist, 2021). The ecotope map is updated annually with the newest parameters and ecotope classifications. We used the ecotope map based on data from 2017, as this is the latest, most complete ecotope map for all tidal basins (Figure 1b).

2.3 | Human activities

Despite the Wadden Sea's relatively strong potential protection status (Bastmeijer et al., 2023), various activities with potential ecological impacts are allowed (Rippen et al., 2020), though the cumulative effects remain unclear. To assess actual protection, we mapped all human activities in the subtidal Wadden Sea that are known to directly impact seafloor integrity (Appendix S1). Shrimp fishery for brown shrimp (*Crangon crangon*) is widespread (Figure A1G). Shrimp and mussel seed fishery (*Mytilus edulis*) (Figure A1E) use bottom trawling methods (Craeymeersch et al., 2023; Smaal & Lucas, 2000; Tulp et al., 2020). Mechanical lugworm fishery (Figure A1C) employs a digging machine to harvest lugworms (*Arenicola marina*) (Beukema, 1995; Ministerie van Infrastructuur en Milieu, Rijkswaterstaat Noord-Nederland, 2016), and dredging (Figure A1B) occurs regularly to maintain navigation channels open with designated deposition areas for dredged material (Figure A1B). Shell extraction for cycling paths and isolation material occurs in deeper gullies (Figure A1F) (Rippen et al., 2020; Schans et al., 2003), and anchoring is generally allowed except in restricted areas (Figure A1A). We mapped the legal extent to which all activities are allowed. Still, for the mussel seed fishery, we restricted the activity to the two tidal basins where they occur, and the extent of the shrimp fishery overlaps with fishing pressure maps (Eijsackers et al., 2023). Other than

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

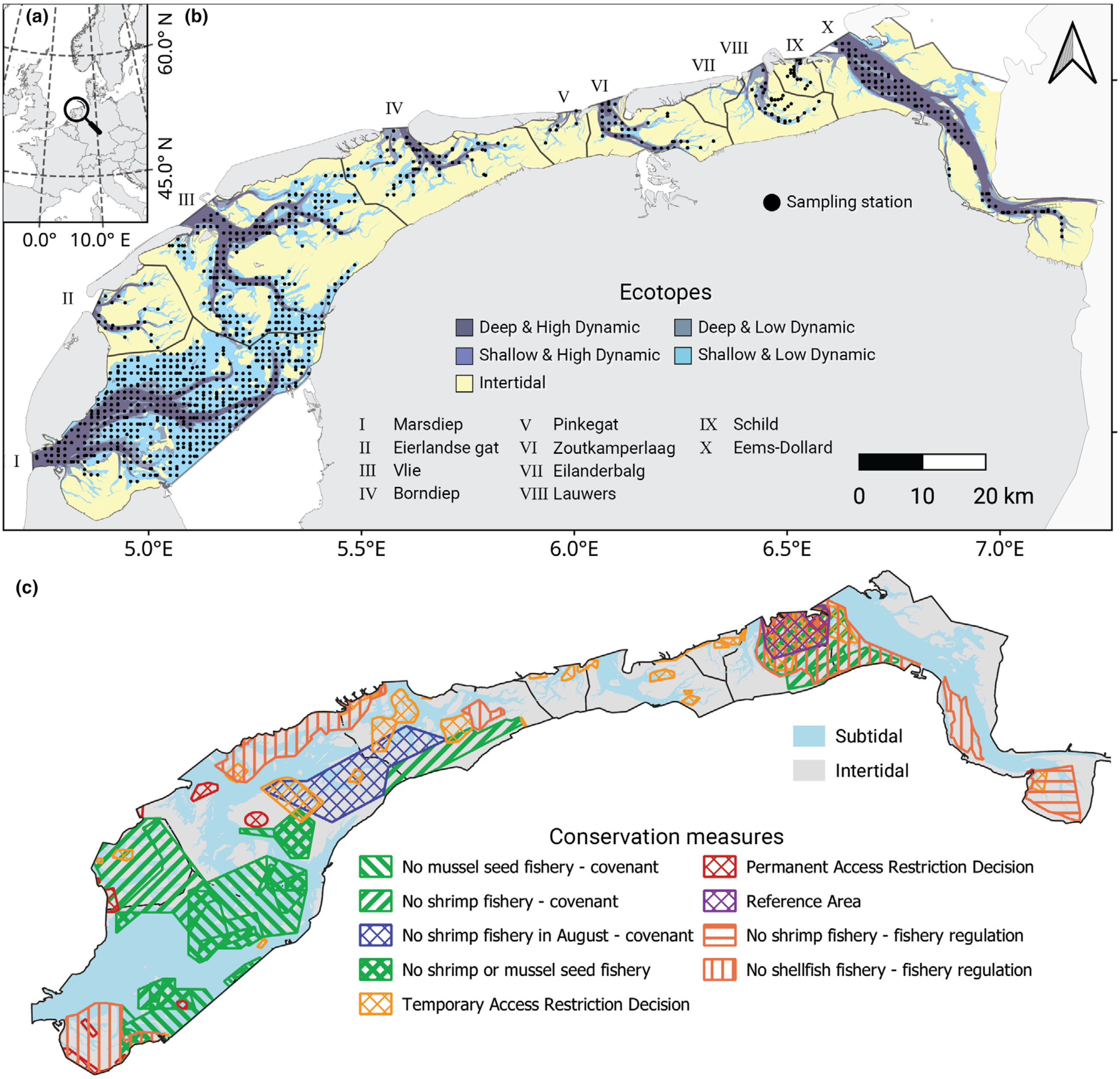


FIGURE 1 Overview map study site. (a) Location of the study site within Europe. (b) Dutch Wadden Sea, divided into 10 tidal basins (labelled with Roman numerals) and underlying ecotopes (van Donk & Baptist, 2021). Dots mark sampling locations from the 2019 subtidal Wadden Mosaic sampling campaign. (c) Map of all identified areas with nature conservation restrictions and their overlap with the subtidal zone. The reference area, established in 2005, excludes all human activities. Zones with fisheries restrictions are based on agreements between fisheries sectors, government, and nature organisations, as well as through the Fishery Implementation Regulation. Under Article 2.45 of the Environment and Planning Act, some areas (Access Restriction Decision areas) are temporarily or permanently closed to most activities to support Natura 2000 goals. Further details can be found in Table 1 and Appendix S1.

the shell extraction, all activities happen daily, though not with the same frequency in all locations. See Appendix S1 for more details.

2.4 | Legal framework for nature conservation

The activities listed above are not permitted everywhere in the Wadden Sea due to various restrictions (Table 1). It remains unclear whether these area-based restrictions can be classified as MPAs. The nature and goals of these restrictions can differ from pure conservation focussed to managing fish stocks or preventing damage to underground infrastructure. Only areas that can be classified as an IUCN-defined MPA are considered here (Figure 1c): "…*a clearly defined geographical space, recognised, dedicated and managed through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem*

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Overview of the different area-based conservation measures and their legal framework in the Dutch Wadden Sea. The marine protected areas (MPA) classification refers to the MPA guide where the MPA classification for each conservation measure is described (Grorud-Colvert et al., 2021).

Conservation measures	Legal framework	Closed for	MPA classification
No mussel seed fishery	Covenant between the fishery sector, nature organisations, and Ministry of Agriculture, Nature and Food Quality (LNV, 2020), Natura2000 measure (Appropriate Measure with Implementation Obligation)	Closed for mussel seed trawling unless insufficient mussel seed is available in open areas. The most recently closed areas can then be fished	Dependent on overlap with other conservation measures and the impact of allowed activities
No shrimp fishery	Covenant between the fishery sector, nature organisations, northern provinces, and Ministry of Agriculture, Nature and Food Quality (PRW, 2014), Natura 2000 measure (Appropriate Measure with Implementation Obligation)	Closed for shrimp trawling	Dependent on overlap with other conservation measures and the impact of allowed activities
Access Restriction Decision	Article 2.45 Environment and Planning Act (Omgevingswet, Dutch Law; previously: art. 2.5 Wet natuurbescherming)	Closed for all activities, except for shrimp trawling (LNV, 2023)	Incompatible due to exception for shrimp trawling
Fishery implementation regulation	Articles 20 and 35 of the fishery implementation regulation (Uitvoeringsregeling Visserij, 2008)	Closed for either shrimp fishery or for tickler chain, mussel seed, oyster and hand-cockle fishery	Dependent on overlap with other conservation measures and the impact of allowed activities
Reference area	Trilateral agreement between Denmark, Germany and the Netherlands (CWSS, 2017; Ministerial Council of the Trilateral Governmental Conference on the Protection of the Wadden Sea, 1991)	Closed for all activities	Fully protected

services and cultural values" (Dudley et al., 2008). Conservation in the Wadden Sea is partly arranged through the European Natura 2000 framework and partly through restrictions for certain types of activities (Table 1). A fully protected reference area has been established in the Eastern Dutch Wadden Sea (Figure 1c) since 2005 following trilateral agreements between the Netherlands, Germany, and Denmark (CWSS, 2017; Ministerial Council of the Trilateral Governmental Conference on the Protection of the Wadden Sea, 1991). Several agreements between nature organisations, the Ministry of Agriculture, Nature and Food Quality, and fishery sectors are in place to further safeguard and enhance underwater nature (LNV, 2020; PRW, 2014). As a result, shrimp and/or mussel seed trawling is prohibited in various areas (Figure 1c). By law, both trawling activities are prohibited in the intertidal (LNV, 2020, 2023). In addition, areas are restricted based on an Access Restriction Decision under Article 2.45 Environment and Planning Act (Aanvullingswet natuur Omgevingswet, 2024), following the European habitat- and bird directive (Figure 1c). These restrictions may be temporary, year-round, or enacted under certain circumstances. Additional closures for shrimp and shellfish fishery are enforced under the Fishery implementation regulation (Uitvoeringsregeling Visserij, 2008) (Figure 1c). See Appendix S1 for more details. Defining discrete protected areas remains challenging, given the complex patchwork of protection statuses and allowed activities, and was, up till now, still missing (Fieten et al., 2022). To assess the protection level and whether these areas can be classified as MPAs, we categorised the subtidal Dutch Wadden Sea using the internationally broadly accepted MPA guide decision tree (Grorud-Colvert et al., 2021).

2.5 | MPA classification

The spatial extent of human activities was overlaid with restriction measures (Figure 1c) to assess the accumulation of activities and classify areas according to the MPA guide (Grorud-Colvert et al., 2021). Here, four different levels of protection are recognised: Minimally protected, lightly protected, highly protected, and fully protected, based on the impact of allowed activities (Grorud-Colvert et al., 2021). Areas where activities exceed allowable impact limits cannot be classified as MPAs and are deemed incompatible (Grorud-Colvert et al., 2021).

Dredging and deposition of dredged material are incompatible with MPA management, as is any form of mining (Grorud-Colvert et al., 2021). Only artisanal or low-impact forms of fishery can be compatible with some MPAs. However, industrial fishing (e.g. ships >12m long×6m

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

wide or any ship towing or dragging gear across the seafloor) is considered incompatible with MPA management (Grorud-Colvert et al., 2021; International Union for the Conservation of Nature, 2020). Thus, except for anchoring, all activities described above (i.e. bottom trawling, dredging, shell extraction, and mechanical lugworm fishing) are incompatible with MPA management due to their destructive impact.

Anchoring can have impacts similar to bottom trawling, though more localised, as the anchors' penetration depth often supersedes trawling gear. However, since the frequency of anchoring and specific effects of anchoring in the Wadden Sea have not yet been investigated, we have categorised the impact of anchoring as low due to its localised nature (Broad et al., 2020; Grorud-Colvert et al., 2021).

For this study, we only included activities with a clear, direct impact on seafloor communities. While salt extraction and gas mining, classified as industrial activities, are also incompatible with MPA management, these are done remotely from land or the North Sea through pipes under the seafloor, and their direct impact on seafloor communities remains unclear (de la Barra et al., 2023; Fokker et al., 2018). de la Barra et al. (2023) concluded changes in sediment composition due to gas mining but found no clear effect on macrozoobenthic communities. Regardless, including these areas minimally affects the assessment of MPA protection levels (Appendix S3).

2.6 | Sampling and data collection

The subtidal area of the Wadden Sea was sampled in 2019 as part of the Wadden Mosaic sampling campaign between February and May on a 1 km grid with an additional 26% random samples, totalling 1060 sampling stations (Figure 1b). Shallow areas were sampled by RIB (rigid inflatable boat) using four long-cores (⌀ 10.4 cm) and combined (0.035 m^2). Deeper areas were sampled using a single 20×30 cm (0.060 m^2) hydraulic boxcore from the NIOZ Research Vessel Navicula to a depth of ~25 cm. Each sample was sieved over a 1 mm round mesh. Larger shellfish and crustaceans were frozen at −20°C. The remainder of the sample was stored in a borax-buffered 6% formalin:seawater solution with ~2 mg L^{-1} Rose Bengal (CAS no. 632-68-8). In the lab, organisms were sorted, counted, and identified to the highest possible taxonomic level (Bijleveld et al., 2012; Compton et al., 2012, 2013; Meijer et al., 2022). The abundance of the genus was added to the species level in case both genus and species levels of the same genus were found in a sample. This was done in the ratio with which each species occurred in the sample in case multiple species of the same genus were found. Genus level was used if no species from that genus was identified in the sample. In total, 149 taxa were identified, and abundances were standardised to densities per m^2.

2.7 | Ecological quality indices

Ecological quality indices are calculated to assess various aspects of macrozoobenthic communities in the Wadden Sea as described in policy frameworks, including biodiversity, functioning, integrity, sensitivity, and food web dynamics. These indicators can be separated into diversity-related indices (Margalef diversity, Hill's diversity, Rao's *Q*, Shannon diversity, and species richness) and quality-related indices (AMBI, BEQI2, BISI, BQI, food web connectance, ITI, and sensitivity). Hellinger transformed (Legendre & Gallagher, 2001; Rao, 1995) abundance data was used for all calculations except for BISI, species richness, Rao's *Q*, sensitivity, and food web connectance.

2.7.1 | Community diversity-related indices

To assess biodiversity, we calculated Margalef diversity, Hill's diversity, Shannon diversity, and species richness, all of which are commonly used in benthic fauna quality assessments (van Loon et al., 2018). Margalef diversity values were $\log(x+1)$ transformed to normalise the distribution. To assess the functional diversity of macrozoobenthic communities, we calculated Rao's Quadratic Entropy (Rao's *Q*) (Botta-Dukát, 2005) using functional trait data from a comprehensive database covering 10 life history traits (adult body size, adult burrowing depth, adult locomotion, age of sexual maturation, fecundity, larval development location, longevity, offspring size, reproductive frequency, and reproductive mode; Appendix S2) (Gusmao et al., 2022; Meijer et al., 2023). Rao's *Q* is then calculated using the "*rao.diversity*" function from the 'SYNCSA' package (Debastiani & Pillar, 2012).

2.7.2 | Habitat-quality-related indices

AMBI (Borja et al., 2000) was determined based on pre-classified species' sensitivities to a eutrophication and water quality gradient (Borja et al., 2000; Gittenberger & van Loon, 2013). This indicator is included within the WFD to assess the ecological and chemical quality of water bodies (Boon et al., 2011). We inverted the AMBI scores so that high scores correspond to high water quality to make the scores more intuitive and ease the comparison with the other indices.

The BEQI2 is the Dutch framework applied to the Wadden Sea within the WFD to evaluate the macrozoobenthic community (Backx et al., 2018). The BEQI2 framework utilises ecological quality ratios of species richness, Shannon-Wiener biodiversity, and AMBI scores (Backx et al., 2018). BEQI2 values for all sampling stations were calculated following the procedures described by Backx et al. (2018) and van Loon et al. (2015).

The BISI was developed to evaluate benthic habitat quality, seafloor integrity, and ecological functioning of macrozoobenthic communities (Wijnhoven & van Avesaath, 2019). This indicator was developed for North Sea macrozoobenthos assessments within the MSFD and was optimised for the Wadden Sea (Wijnhoven & van Avesaath, 2019). We calculated index scores for ecotope-specific characteristic species following the protocol in

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Wijnhoven (2018) and using indicator values in Wijnhoven and van Avesaath (2019).

The BQI is the Swedish national benthic indicator under the WFD (Rosenberg et al., 2004) and was shown to respond to trawling for nearshore benthic samples (Gislason et al., 2017; McLaverty et al., 2023; Sköld et al., 2018). The BQI index following calculations by Leonardsson et al. (2009) and Rosenberg et al. (2004) requires the use of pristine habitats as a reference for calculating the sensitivity value of individual species. Given the long history of human activities in the study system, we believe we do not have ample sample replications containing pristine habitats to calculate appropriate sensitivity values. Instead, we have calculated a modified BQI (hereafter referred to as BQI_m) using the functional sensitivity indicator described below instead of the conventional abundance-weighted sensitivity score. This sensitivity score uses literature-based expectations of species responses to mechanical bottom disturbance (Appendix S2).

As an indicator for food web elements following Descriptor 4 of the MSFD we calculate the food web connectance. Food web connectance (total number of links/total number of species^2) can be used as a proxy for the resistance of communities to press disturbances (Wootton & Stouffer, 2016). Communities with a higher connectance are generally considered more robust and thus less sensitive than more complex communities with a lower connectance (Dunne et al., 2002). To calculate this indicator, we retrieved trophic interactions between all taxonomic groups in the sampling campaign from an existing database (Witte et al., 2024). This database contains all potential trophic interactions between taxonomic groups in the Wadden Sea. The interaction matrix of this database was subsetted to create an adjacency matrix for the species found in each benthic sample. Zooplankton, phytoplankton, sediment Particulate Organic Matter, and water column Particulate Organic Matter were added to every sub-interaction matrix to form the basis of the food web. A food web was created from each adjacency matrix using the 'igraph' package (Csárdi et al., 2023), and connectance was determined for each community. The connectance score was inverted, so high scores correspond with more sensitive communities to facilitate more intuitive interpretation.

An additional food-web-related indicator is the ITI. This indicator is based on benthic trophic classes where the presence of species is subdivided over major feeding types (Gittenberger & van Loon, 2013; Lavaleye, 1999; Word, 1978). The index takes a value between 0 and 100, where low values indicate domination by deposit feeders and high values indicate domination by suspension feeders, indicating generally less disturbed environments (Gittenberger & van Loon, 2013) (Appendix S2).

Finally, we calculate a sensitivity indicator for the sensitivity of macrozoobenthos to bottom abrasion. Several methods have been described to measure the sensitivity of a community to a disturbance using functional traits (Bolam et al., 2014; Butt et al., 2022; Hinz et al., 2021; Kenny et al., 2018). Incidentally, most methods compare similarly when applied to the same dataset (Appendix S2). Here, we calculated a sensitivity indicator based on Bolam et al. (2014) and Kenny et al. (2018). All modalities were given an accreting score based on the sensitivity to bottom abrasion and used to calculate a community-weighted sensitivity indicator (Appendix S2). This sensitivity score is also used for the BQI_m calculations.

See Appendix S2 for a more detailed description of these indicators.

2.8 | Statistical analysis

Statistical analysis was done in RStudio, R version 4.3.1. (R Core Team, 2023). Figures were created in RStudio and QGIS version 3.26.2 (QGIS Development Team, 2023). First, we overlapped MPA protection levels with the ecotopes to determine how well different ecotopes are protected. Means were calculated for all ecological quality indicators per ecotope and protection level and tested separately using a one-way ANOVA to test whether there is a predisposition for higher values of certain indicators within ecotopes or MPAs. BISI and Rao's *Q* were tested using a Kruskal–Wallis test and post hoc using a Dunn test due to a violation of homoscedasticity and normality following a Bartlett's and Shapiro–Wilkinson test. Species richness was tested using a generalised linear model assuming Poisson distribution of residuals.

Next, local indicators of spatial autocorrelation (LISA's) were calculated for all ecological quality indicators. First, a spatial weights matrix was constructed from all sampling stations using the 'spdep' package (Bivand & Wong, 2018), where the neighbours were determined based on the minimum distance for which all sampling stations have at least a single neighbour. Hotspot analysis was then performed using a spatial weights matrix, where each sampling station itself is included as a neighbour in calculating the average neighbour value to compute Getis-Ord Gi* scores for local spatial autocorrelation (Getis & Ord, 1992). Here, Getis-Ord Gi* scores return *z*-scores representing local clusters of hot- or cold spots. Values were then converted into significance scores where values above 1.65 or below −1.65 respectively represent samples belonging to a hot- or cold spot with 90% confidence, values above 1.96 or below −1.96 with 95% confidence, and values above 2.58 or below −2.58 with 99% confidence (Getis & Ord, 1992). Next, sampling stations were scored for each indicator, either as hotspot (1), not significant (0), or as coldspot (−1). Mean values and 95% confidence intervals were determined for each indicator for the samples that scored a hot- or coldspot and those that were not significant, respectively. The total number of indices for which a sampling station scored a hotspot (1) or coldspot (−1) was determined and divided by the total number of indices to get a value ranging from 0 to 1. This value indicates the proportion of indicators for which a sampling station can be considered a hotspot. This was done for all indices together, as well as only considering the community diversity indices (Margalef diversity, Hill's diversity, Rao's Q, Shannon diversity, and species richness) and habitat-quality-related indices (AMBI, BEQI2, BISI, BQI_m, connectance, ITI, and sensitivity). To investigate whether hotspots or coldspots occur more frequently in certain ecotopes or within

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

MPAs, the proportion of sampling stations classified as hot- or coldspots within an ecotope and MPA class were determined for each indicator and all combined categories. Because not all ecotopes and MPA classes were sampled with the same frequency, a habitat selection index (*E*) was calculated to determine the selection strength for hot- and coldspots of all indices for certain ecotope types or MPA classes. This habitat selection index corrects for the unequal distribution of sampling points over ecotopes and MPA classes and represents a score between −1 and 1. Values near 1 indicate a strong positive selection for a certain level of a variable (i.e. an ecotope or an MPA class), values near −1 a strong negative selection, and values around 0 no selection (or random preference) (Wang et al., 2018). The selection coefficient and index were calculated following van der Ploeg and Scavia (1979) and Wang et al. (2018). Finally, we determined the overlap between protected areas and ecological hotspots (conservation conformity) per ecotope and for the entire subtidal Wadden Sea. Ecological hotspots for multiple indicators were classified as sampling stations that scored a hotspot for at least 50% of all indicators. The overlap between these areas and MPAs was determined relative to the number of sampling locations within MPAs and ecotopes. The same was done with coldspots, considering only the grouped diversity- and quality-related indicators and each indicator separately (Appendix S4).

3 | RESULTS

3.1 | Human activities and MPAs

We found that 48,889 ha (37%) of the subtidal Wadden Sea has some level of protection. Access Restriction Decision areas, which are closed based on the Dutch nature law 2.45, primarily aim to provide resting areas for seals and birds. Consequently, these areas are mainly found in the intertidal zone (77% intertidal, 23% subtidal) (Figure 1c). The reference area aims to protect an entire tidal basin and contains 17% subtidal habitat but represents only 0.4% of the entire subtidal Wadden Sea (Figure 1c; Table A1). By law, mussel seed and shrimp fisheries are only allowed in the subtidal Wadden Sea (LNV, 2020, 2023). Areas closed to mussel seed fisheries align with the regions where this activity is legally permitted, resulting in 76% of the closed areas being subtidal (Figure 1c). In contrast, only 31% of shrimp fishery closures are located in the subtidal, with the remaining 69% in the intertidal (Figure 1c). This is similar to shrimp-fishery-free zones following fishery regulations, where 85% of the area falls in the intertidal and 15% in the subtidal (Figure 1c).

The number of overlapping bottom-disturbing human activities in the Wadden Sea ranges from zero to six (Figure 2a; Figure A1), with the highest cumulative activity in the deeper gulleys of the western part (Figure 2a). Only 2% of the subtidal area is entirely free of bottom-disturbing human activities. Most of the subtidal Wadden Sea is subject to either two (39%) or three (35%) different activities. In contrast, 16% of the area is impacted by one type of activity, 8% by four, 0.4% by five, and only 0.008% by six activities.

Following the MPA guide and IUCN guidelines (Grorud-Colvert et al., 2021), fully protected areas remain where no human activities are permitted (2%; Figure 2b,c). Highly protected areas, where only low-impact activities such as anchoring are allowed, make up 8% (Figure 2b,c). The remaining areas, representing 27% of the subtidal, allow activities incompatible with MPA management as defined by the MPA guide and IUCN guidelines (Grorud-Colvert et al., 2021).

Among the different ecotopes, the shallow and low dynamic ecotope is the best protected, with 2% of its area fully protected, 12% highly protected, and 39% subject to restrictions that still permit incompatible activities (Figure 2c). The shallow and high dynamic ecotope is similarly protected, with 3% fully protected, 9% highly protected, and 21% of the area allowing incompatible activities (Figure 2c). The deep sublittoral ecotopes are less well protected. The low dynamic deep sublittoral has 3% fully protected, 5% highly protected, and 32% restricted but incompatible areas. In comparison, the high dynamic deep sublittoral is covered by 2% fully protected, 2% highly protected, and 7% restricted areas allowing incompatible activities (Figure 2c).

3.2 | Ecological quality indices to assess ecological hotspots

The different ecotopes showed strong differences in biodiversity and habitat quality indices (Appendix S2). Generally, biodiversity and habitat quality were highest in the shallow low dynamic ecotope, except for AMBI, which had the highest values in the deep and high dynamic ecotope (Appendix S2). Significant Getis Ord G*-scores revealed clear ecological hot- and coldspots across all indicators (Figure 3), with hotspots generally located further inward of the tidal basins and coldspots near the tidal inlets (Figure 3). Moreover, hotspots were primarily found in the western parts of the Wadden Sea, whereas coldspots occurred throughout the entirety of the Wadden Sea (Figure 3).

Combining the hot- and coldspots from the individual indicators revealed broader patterns (Figure 4). Ecological hotspots were most pronounced in the western tidal basins (Marsdiep and Vlie) and some in the east primarily focussed in the tidal basin Schild (Figure 4a). Diversity-related hotspots were primarily found in the Marsdiep tidal basin, the northern channels of the Vlie tidal basin (Noord- and Zuid Meep), and Schild (Figure 4b). In contrast, quality-related hotspots were more widespread over the larger tidal basins (Figure 4c). Coldspots were mostly located at the tidal basin inlets (Figure 4d), a pattern that held for diversity-related indicators, with a minor exception in the southern part of the Marsdiep and Vlie tidal basin (Figure 4e).

The shallow and low dynamic ecotope is generally best protected and had the most hotspots, housing 52% of all hotspots, 72% of the diversity-related hotspots, and 52% of the quality-related hotspots (Figure 5a). However, there was no strong ecotope preference for the hotspots of these combined indicators to occur in a specific ecotope (Figure 5a). Similar patterns are found

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

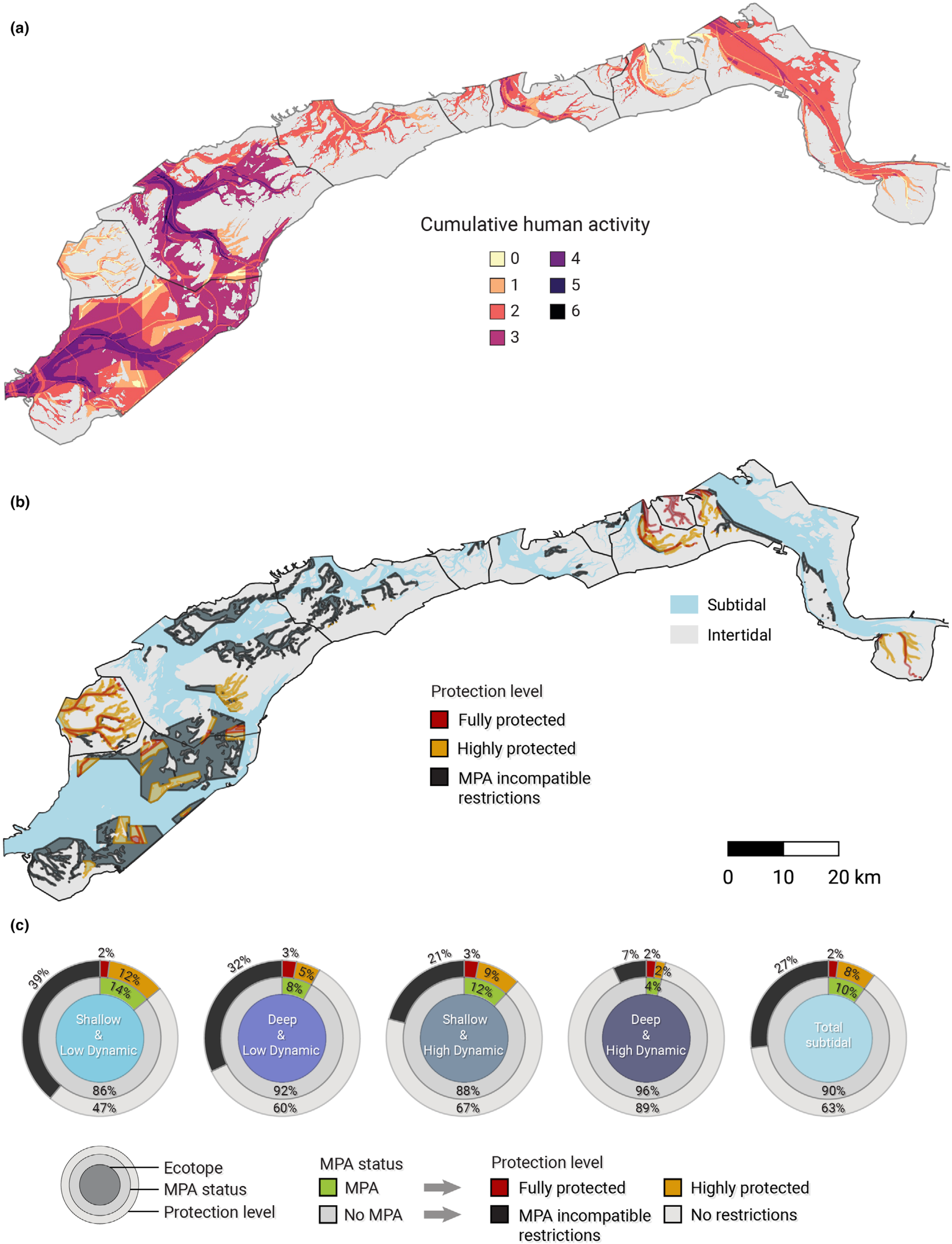
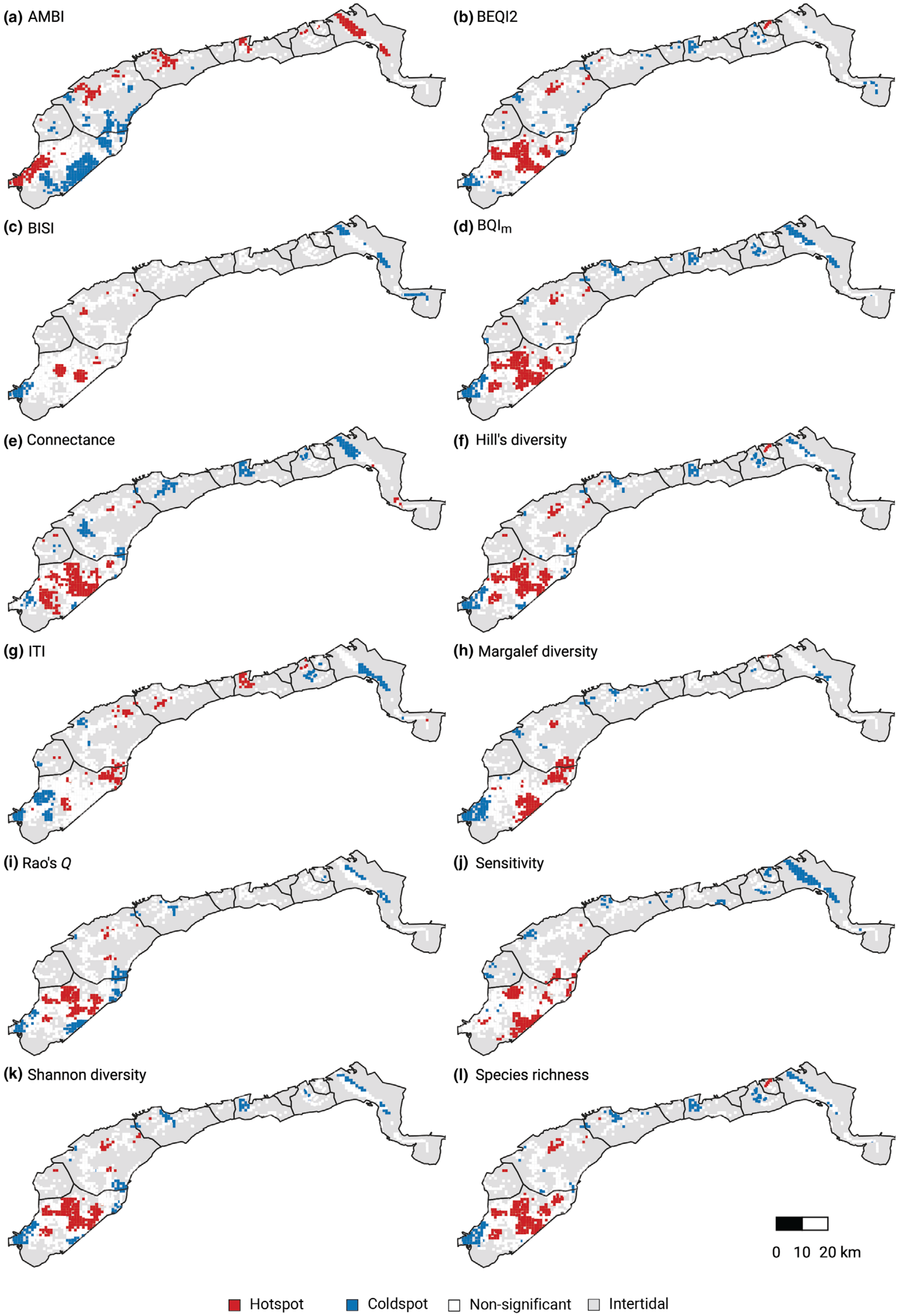


FIGURE 2 (a) Map of the cumulative seafloor impacting human activities in the subtidal Dutch Wadden Sea. (b) Distribution of marine protected area (MPA) protection levels across the Dutch subtidal Wadden Sea. (c) Donut charts showing the relative coverage of MPAs and protection levels across all ecotopes and the total subtidal.



25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

FIGURE 3 Hot- and coldspots for (a) AMBI, (b) BEQI2, (c) BISI, (d) BQI_m, (e) connectance, (f) Hill's diversity, (g) ITI, (h) Margalef diversity, (i) Rao's Q, (j) sensitivity, (k) Shannon diversity, and (l) species richness. Here, 90% confidence was used as a cut-off value for determining statistically significant hot- or coldspots. AMBI, AZTI's Marine Biotic Index; BEQI2, Benthic Ecosystem Quality Index 2; BISI, benthic species indicator index; BQI_m, modified Benthic Quality Index; ITI, Infaunal trophic index.

for the individual indicators except for AMBI, for which hotspots mostly (65%, $E=0.4$) occur in the deep and high dynamic ecotope. In comparison, hotspots of sensitivity were rare in this ecotope (3%, $E=-0.8$). Coldspots were more evenly distributed over the shallow and low dynamic (45% for all coldspots, 43% for diversity-related coldspots, and 44% for quality-related coldspots) and deep and high dynamic areas (36% for all coldspots, 40% for diversity-related coldspots, and 37% for quality-related hotspots) with no strong selection for the coldspots of these combined indicators to occur in a specific ecotope (Figure 5b). Overall, coldspots of individual indicators were mostly found in the deep and high dynamic ecotope (Figure 5b), except for AMBI, for which coldspots were mostly found in the shallow and low dynamic ecotope (76%). However, this was not reflected in the selection index for this ecotope ($E=0.2$) (Figure 5b).

3.3 | Conservation conformity

We assessed conservation conformity by evaluating the spatial overlap of the identified MPA classifications (i.e. fully protected, highly protected, and areas with restrictions incompatible with MPA management) with hot- and coldspots of ecological quality. Hotspots can be considered areas for conservation priority due to their significantly high natural values, whereas coldspots, though less immediately valuable, may have recovery potential. Only marginal percentages of ecological hotspots in the Wadden Sea are currently covered by protection measures (Figure 5a).

Of all combined indicators, just 3% of hotspots are fully protected, 8% are highly protected, and 65% remain unprotected (Figure 5a). The remaining 24% are covered by restrictions incompatible with MPA management (Figure 5a). Habitat-quality-related indicators mirror this pattern, while diversity-related indicators are slightly better covered, with 4% fully protected and 11% highly protected (Figure 5a). No clear preference was found for hotspots to be located within MPAs, indicating a random distribution of hotspots relative to the protection statuses (Figure 5a). Coverage of ecological coldspots from the combined indicators are likewise marginally covered by protection measures. Of all coldspots, 5% is covered by fully protected areas, 8% by highly protected areas, and 21% by restrictions incompatible with MPA management (Figure 5b). Coldspots of diversity-related and quality-related indices were similarly covered (both 5% fully protected, 7% and 8% highly protected, 19% and 21% restrictions incompatible with MPA management, and 68% and 64% unprotected, respectively; Figure 5b). Again, no strong selection is found for these coldspots to be covered by a protection measure (Figure 5b).

Areas with high ecological and chemical quality, as indicated by the AMBI index, are the least protected. Only 2% of these hotspots are fully protected ($E=-0.1$), 1% are highly protected ($E=-0.7$), 8% ($E=-0.3$) are covered by areas with restrictions incompatible with MPA management, but 89% remains unprotected ($E=0.4$) (Figure 5a). In contrast, areas sensitive to bottom abrasion are better protected. Still, 47% remain unprotected ($E=-0.2$), only 2% are fully protected ($E=-0.3$), and 12% are highly protected ($E=0.1$) (Figure 5a). Coldspots of low ecological quality (BISI) only occurred in non-protected areas ($E=0.5$), and low-diversity areas (Margalef diversity) were absent from fully protected areas ($E=-1$) (Figure 5b). The highest overlap is found between low sensitivity areas and fully protected areas, at 12% ($E=0.4$) (Figure 5b).

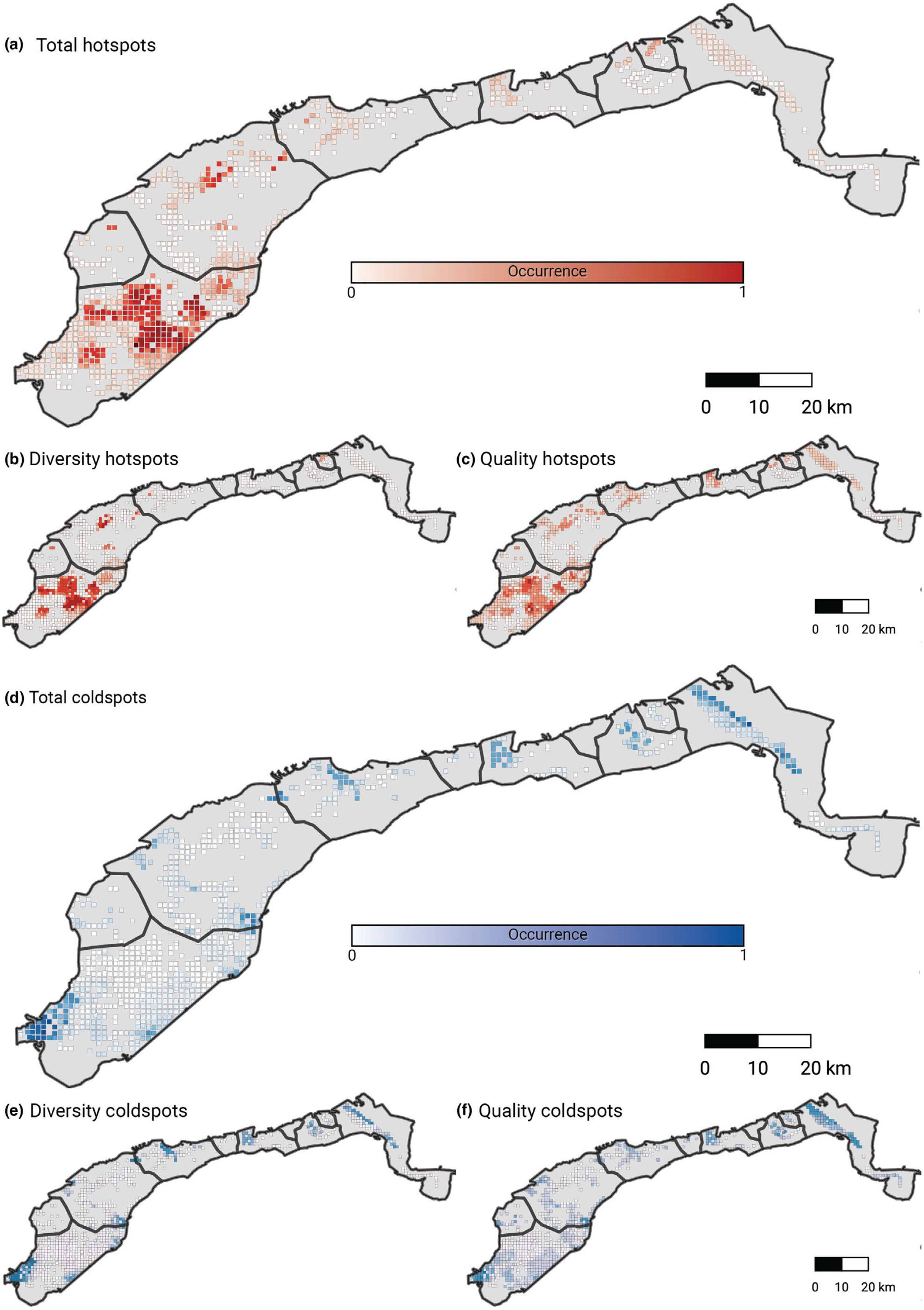
Hotspots identified at more than 50% of sampling stations show poor conformity in the alignment with MPAs. Only 14% of sampling stations within MPAs (i.e. fully and highly protected areas) are classified as hotspots, while 19% of all sampling stations (inside and outside MPAs) are considered ecological hotspots, with just 2% falling within MPAs (Figure 6; Appendix S4). When separating this into the different ecotopes, the deep and low dynamic ecotope has the highest percentage of ecological hotspots (31%), but none are protected by MPAs (Figure 6). Similarly, no ecological hotspots in the deep and high dynamic ecotope are covered by MPAs (Figure 6).

In contrast, the shallow and low dynamic ecotope has relatively better protection, but only 18% of its sampling stations in MPAs are classified as hotspots (Figure 6). The spatial overlap of coldspots with MPAs is even lower, with just 6% of sampling stations in MPAs classified as coldspots for at least half of the indicators (Appendix S4).

4 | DISCUSSION

Our study provides a comprehensive assessment of the current placement of area-based conservation measures in the Dutch Wadden Sea, a shallow coastal area of high biological value with significant socioeconomic and cultural uses. We introduce the concept of conservation conformity, which quantifies the spatial alignment of area-based conservation measures with ecological hotspots. We develop a novel set of tools and approaches to map ecologically valuable areas based on multiple indicators for macrozoobenthos, as described in EU policy frameworks such as the WFD and MSFD. Applying these methods, we reveal a concerning lack of conservation conformity in the Dutch Wadden Sea. By applying the MPA guide framework (Grorud-Colvert et al., 2021) to the area-based conservation measures in the subtidal Wadden Sea, we find that only a small percentage (10%) of the subtidal Wadden Sea falls under an MPA protection status. Furthermore, these protected areas are not strategically placed in the most ecologically valuable areas when considering a multitude

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License



25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

FIGURE 4 Maps of relative occurrences of hot- and coldspots for all indices combined, diversity-related indices (Margalef diversity, Hill's diversity, Rao's Q, Shannon diversity, and species richness), and quality-related indices (AMBI, BEQI2, BISI, BQI_m, connectance, ITI, and sensitivity). (a) Hotspot occurrence for all indices combined; (b) Hotspot occurrence for diversity-related indices; (c) Hotspot occurrence for quality-related indices; (d) Coldspot occurrence of all indices combined; (e) Coldspot occurrence for diversity-related indices; (f) Coldspot occurrence of quality-related indices. AMBI, AZTI's Marine Biotic Index; BEQI2, Benthic Ecosystem Quality Index 2; BISI, benthic species indicator index; BQI_m, modified Benthic Quality Index; ITI, Infaunal trophic index.

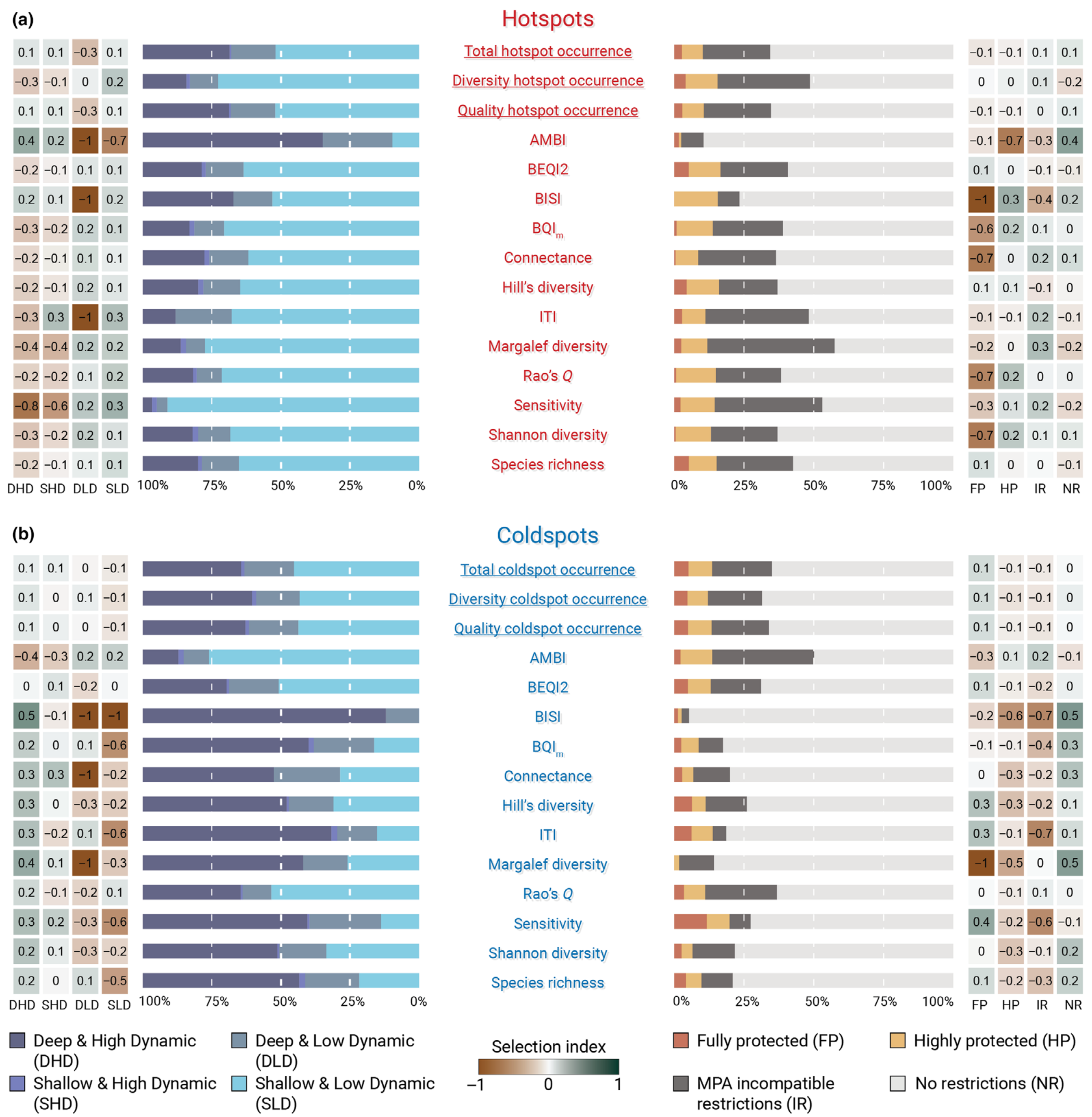


FIGURE 5 Relative occurrence (horizontal bars) and selection indices (*E*; coloured blocks on both sides) of (a) hot- and (b) coldspots of combined indices (underlined) and individual benthic ecological quality indicators for all ecotopes and protection levels. The relative occurrences indicate the distribution of the hot- and coldspots per used index over the ecotopes (horizontal bars on the left side) and the protective status (horizontal bars on the right side). The selection index represents selection strength for ecotopes or protection levels ranging from −1 (strong negative selection, brown colour) to 1 (strong positive selection, teal colour) and corrects for the inequality of sampling stations within ecotopes and marine protected area (MPA) classes to indicate whether hot- or coldspots are consistently found within an ecotope or MPA class. AMBI, AZTI's Marine Biotic Index; BEQI2, Benthic Ecosystem Quality Index 2; BISI, benthic species indicator index; BQI_m, modified Benthic Quality Index; ITI, Infaunal trophic index.

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

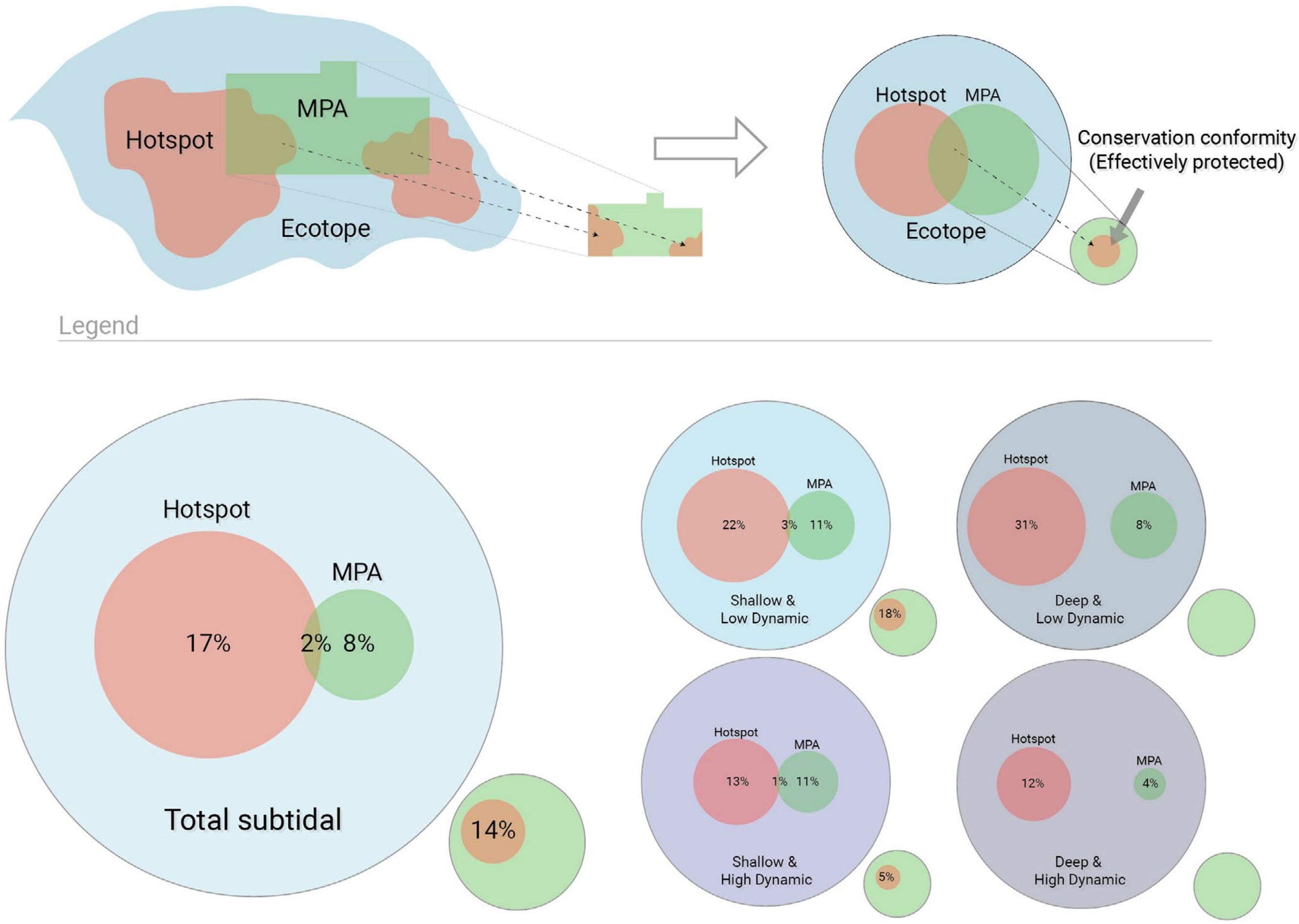


FIGURE 6 Venn diagram showing the degree of conservation conformity through the spatial overlap between ecological hotspots and marine protected areas (MPAs) across the subtidal zone and by ecotope. Hotspots are determined from sampling stations that score as a hotspot for 50% or more of the macrozoobenthic-centred biodiversity and habitat quality indicators. Percentages reflect the proportion of sampling locations classified as hotspots (red circle) and those located within an MPA (green circle). The overlap between the circles represents the percentage of sampling locations that are both hotspots and within an MPA relative to all stations within each ecotope. A smaller circle in the lower right corner shows the percentage of hotspots within MPAs relative to the total number of stations inside MPAs for each ecotope. The areas of overlap in the Venn diagrams are not to scale.

of indicators for seafloor integrity. Using the Dutch Wadden Sea as a case study, we present a quantitative method to evaluate the current conservation conformity of MPAs, providing valuable insights for local and global conservation efforts. Our findings have practical implications for the management and planning of conservation measures in the Dutch Wadden Sea, and provide a framework that can be applied to other systems and indicators, thereby enhancing the effectiveness of area-based conservation strategies.

4.1 | Macrozoobenthos indicating ecological hotspots

We use macrozoobenthos to identify ecological hotspots and assess their conservation conformity with protected areas as they are perfect indicators of environmental quality and change (Jayachandran et al., 2022; Tillin et al., 2006) as changes in macrozoobenthos stock can cascade into higher trophic levels (Rabaut et al., 2007). Considering macrozoobenthos within the spatial planning of MPAs can also assure safe havens for birds and fish (Rolet et al., 2015). Macrozoobenthos are, therefore, excellent signals for adaptive management approaches where they can be used to assign and monitor new MPAs and management interventions (Dolbeth et al., 2007; Laurino et al., 2021). Nevertheless, our method could also be applied to spatially explicit datasets of other species groups. For example, the Wadden Sea is an important nursery habitat for commercially important fish species (van der Veer et al., 2015) and an important area for birds protected under Natura 2000 regulations (Boere & Piersma, 2012). Standardised monitoring, in combination with hotspot analysis, can delineate effective conservation areas for specific species groups, or be combined for a holistic ecosystem assessment.

Different policy frameworks include macrozoobenthos as an indicator of seafloor integrity and ecosystem health. The Habitat Directive recognises large areas of the subtidal Dutch Wadden Sea under type H1110A—permanently submerged sandflats. However,

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

neither the Annexes nor the national interpretation lists any species that can be assessed with the data we currently have or include any species we found (Council Directive 92/43/EEC, 1997; Ministerie van Infrastructuur en Milieu, Rijkswaterstaat Noord-Nederland, 2016). Still, the WFD and MSFD do recognise macrozoobenthos as important indicators of ecosystem health. Individually, these indicators highlight varying areas as ecological hotspots in the Wadden Sea, confounding clear choices for conservation prioritisation. This study does not aim to evaluate the quality of singular indicators and draw conclusions on which indicators are best to use. Other studies have concluded that the suitability of indicators differs depending on the conservation goal and threats of the system (Hiddink et al., 2020; McLaverty et al., 2023; van Loon et al., 2018). Rather, we show how combining multiple indicators merits the use over singular indicators. We find large areas that overlap as ecological hotspots for multiple facets described by the different policy frameworks (MSFD, 2008; WFD, 2000). A combined indicator approach then delineates clear ecological hotspots over the scattered hotspots identified by singular indicators.

4.2 | People and policy in the Wadden Sea

The EU Marine Spatial Planning Directive (Directive 2010/41/EU) requires human activities to be organised in such a way as to achieve ecological, economic and social objectives (Smith, 2015). Due to a lack of knowledge of the subtidal areas of our study system, management of the Wadden Sea so far has aimed to reduce human activities in the low dynamic ecotopes as these are hypothesised to host the most diverse and sensitive communities (Hiddink et al., 2007; Robert et al., 2021). However, the current distribution of hotspots over the ecotopes indicates a greater biotic heterogeneity than the current abiotic delineation based on the ecotope classification of Baptist et al. (2019, 2022). As such, zonation based on abiotic delineation does not always adequately cover areas of biotic conservation value. On the other hand, this heterogeneity in ecological values might also arise due to the degradation through anthropogenic impacts, which might obscure the true potential of natural values. However, proper baseline measurements are often missing to adequately compare the current state to a historical baseline (Mihoub et al., 2017). Coldspots may actually represent areas with potential for recovery and can provide significant benefits in attaining biodiversity targets (Sacre et al., 2019), especially in the low dynamic ecotopes. Nevertheless, ecological coldspots are even less well represented within current conservation measures than hotspots. Still, situating protection measures to safeguard areas hypothesised to host the most diverse or sensitive communities is a sensible approach in data-poor circumstances.

Large coastal areas remain heavily impacted by human activities despite strong conservation efforts. In the Wadden Sea, we find a large overlap of ecological hotspots with intensively used areas. We here mapped the theoretically and lawfully available areas for certain human activities. The addition of high spatial resolution data using Automatic Identification System or Vessel Monitoring System data, but also clearer information on indirect effects such as the redistribution of sediment through dredging activities, can aid in accurately mapping the realised cumulative human impact in a system. Still, this does not remove the fact that human activities are spatially ubiquitous throughout the area. A big remaining question is whether these activities have already reduced the natural values to their current state and hamper recovery, e.g. the areas previously had even higher ecological values, whether these hotspots are currently in their maximum state, or instead, whether the ecological values are caused by high human activities, equivalent to terrestrial ecosystems where low-intensity human use can locally promote biodiversity (Bakker, 1989). The last hypothetical situation seems unlikely given the many recorded negative effects of bottom-disturbing activities on macrozoobenthic communities that have been found in the trilateral Wadden Sea (e.g. Fock et al., 2023; Klunder et al., 2021; Tulp et al., 2020). We therefore recommend to improve the overlap between the protected areas and these ecological hotspots, both to safeguard the current conditions (when the ecological values are at their maximum) and to facilitate recovery (when the system is degraded).

We cannot conclude whether current MPAs in the Wadden Sea effectively improve the ecological status of seafloor communities. We analysed a single year of landscape-wide benthos sampling data and therefore cannot assess the development, nor the stability, of ecological hotspots over time. The lack of reference data also makes it impossible to assess whether coldspots do indeed provide areas with recovery potential. Moreover, most of the area-based conservation measures have only recently been established (Table A2). Improvements in macrozoobenthos in the reference area Schild could only be observed after 10 years of closure (Glorius et al., 2018). This highlights the importance of repetitive monitoring of ecological communities over longer time spans and the accessibility of existing spatially and temporally extensive monitoring programs to understand the dynamics of coastal systems.

4.3 | Broader lessons for MPA design

Conservation prioritisation ultimately requires weighing ecological, social, cultural, and economic interests. But when conservation is a priority, as is for the Wadden Sea due to it being a Natura 2000 area, then also the ecologically most important areas should be best protected. Coastal seas are among the most heavily used and debated marine ecosystems worldwide (Halpern et al., 2019), and generally, multiple stakeholders participate in the MPA design process (Grorud-Colvert et al., 2021). The interplay among many stakeholders and their varied interests in the Dutch Wadden Sea has resulted in a strong mosaic of different area-based conservation measures (Fieten et al., 2022). This also applies to the wider international Wadden Sea. The Danish parts are largely closed off for all bottom-disturbing activities, and most resource extraction is prohibited but with notable local exceptions (Fieten et al., 2022). In the

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

German parts of the Wadden Sea, national parks have been implemented, where protection levels depend on the ecological value of each area, and the strongest restrictions typically apply to the areas with the highest ecological values (Fieten et al., 2022). However, also within these zones, specific disturbing activities are allowed locally despite high ecological values (Fieten et al., 2022). In Belgian MPAs, a similar situation is found where MPA establishment was based on ecological information and overlapped with ecological hotspots but still allowed fishing activities in many places due to legal exceptions (Rabaut et al., 2009). Such resulting convoluted patchworks of different conservation measures will inadvertently diminish any realistic effect of ecosystem-wide protection. This is mostly due to multiple exceptions to resource extraction, each with its own historical, cultural, and economic motivations. But often leaving it unclear how they all add up and multiply. In the case of the Dutch Wadden Sea, this has resulted in a very low conservation conformity.

We recommend that our approach be applied to other productive and densely inhabited coastal areas to determine if this is a general pattern. Of course, other guidelines or frameworks can be applied to map the MPA status for other areas. Other definitions of MPAs could have been used in our case, perhaps leading to more optimistic conclusions on conservation conformity. Nevertheless, effective MPA establishment will benefit from a clear and transparent legal framework to prevent misalignment of conservation areas from both an ecological and management perspective.

We conclude that assessing conservation conformity based on quantifying and combining the maps of MPAs, and ecological hot- and coldspots adds vital information for improving the effectiveness of conservation measures for specific areas such as the Dutch Wadden Sea. Still, the resulting conclusions should also be viewed in a wider international context of seascape connectivity, as marine systems are intricately spatially connected and interdependent. The Wadden Sea ecosystem is in constant exchange with both the North Sea and terrestrial ecosystems through estuarine influxes and exports, making it part of a network of internationally connected MPAs. Therefore, an assessment of ecological coherence at the scale of the southern North Sea should be conducted to evaluate the coverage of habitats, functions and connectivity by this larger network (Ardron, 2008).

5 | CONCLUSION

In this study, we developed a comprehensive approach to quantify conservation conformity (i.e. the spatial alignment of area-based conservation measures with ecological hotspots) using multiple indicators. When applied to the Dutch subtidal Wadden Sea, we find a strong misalignment between area-based conservation measures and ecological hotspots based on macrozoobenthos. This misalignment is even greater (lower conservation conformity) when only considering area-based conservation measures that qualify as MPAs. It remains unclear yet if ecological hotspots or coldspots have the potential for further recovery due to the lack of proper undisturbed reference data. Nevertheless, should coldspots indeed have the greatest recovery potential, the overlap of MPAs with ecological coldspots is even less than with ecological hotspots. Since the Dutch Wadden Sea is formally strongly protected as both a Natura 2000 and a UNESCO World Heritage area, our finding of low conservation conformity calls for substantial adjustment of its current spatial conservation schemes and further exploration of similar marine planning problems elsewhere.

AUTHOR CONTRIBUTIONS

Kasper J. Meijer conceived ideas and designed methodology. Kasper J. Meijer, Oscar Franken, Laura L. Govers, Tjisse van der Heide, and Han Olff conceptualised the study. Kasper J. Meijer, Oscar Franken, and Sander J. Holthuijsen collected the data. Kasper J. Meijer and Sterre Witte analysed the data. Kasper J. Meijer led the writing of the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors would like to thank Karin J. van der Reijden and Quirin Smeele for their advice and critical thoughts on an earlier version of the manuscript. This study was funded by Waddenfonds grant “Waddentools: WaddenMozaiek”, registered under reference number WF2018-187059. Laura L. Govers was additionally funded by NWO grant 016. Veni.181.087.

CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

The codes and data produced for this manuscript will be available in the dataverseNL (DANS) repository through https://doi.org/10.34894/8AOOQJ. The analysis was done using RStudio version 2023.09.1+494 and R version 4.3.1.

ORCID

Kasper J. Meijer https://orcid.org/0000-0002-3904-2510
Oscar Franken https://orcid.org/0000-0001-8361-3117
Sterre Witte https://orcid.org/0009-0007-3890-7387
Sander J. Holthuijsen https://orcid.org/0000-0002-7454-6933
Tjisse van der Heide https://orcid.org/0000-0002-3664-8904
Laura L. Govers https://orcid.org/0000-0003-4532-9419
Han Olff https://orcid.org/0000-0003-2154-3576

REFERENCES

Aanvullingswet natuur Omgevingswet. (2024). BWBR0044063. http://wetten.overheid.nl/jci1.3:c:BWBR0044063

Ardron, J. A. (2008). Three initial OSPAR tests of ecological coherence: Heuristics in a data-limited situation. *ICES Journal of Marine Science*, *65*(8), 1527–1533. https://doi.org/10.1093/icesjms/fsn111

Backx, J. J. G. M., Baretta-Bekker, J. G., van den Berg, M. S., Bijkerk, R., Duijts, R., Hartholt, J. G., Jager, Z., de Jong, D., Klinge, M., Knoben,

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

R. A. E., Kranenbarg, J., van Loon, W. M. G. M., Stikvoort, E. C., Twisk, F., & Walvoort, D. (2018). *Referenties en maatlatten voor natuurlijke watertypen voor de kaderrichtlijn water 2021–2027 (2018-49)*. STOWA.

Bakker, J. P. (1989). *Nature management by grazing and cutting*. Springer. https://doi.org/10.1007/978-94-009-2255-6

Baptist, M., van der Wal, J. T., Gräwe, U., Folmer, E., & Elschot, K. (2021). Data for: An ecotope map of the trilateral Wadden Sea (Version 2) [Dataset]. *Mendeley Data*. https://doi.org/10.17632/27mysx289g.2

Baptist, M. J., van der Wal, J. T., Folmer, E. O., Gräwe, U., & Elschot, K. (2019). An ecotope map of the trilateral Wadden Sea. *Journal of Sea Research*, *152*, 101761. https://doi.org/10.1016/j.seares.2019.05.003

Baptist, M. J., van der Wal, J. T., Folmer, E. O., Gräwe, U., & Elschot, K. (2022). Corrigendum to "An ecotope map of the trilateral Wadden Sea" [*Journal of Sea Research* 152 (2019) 101761]. *Journal of Sea Research*, *182*, 102176. https://doi.org/10.1016/j.seares.2022.102176

Bastmeijer, K., Boerema, L., Gilissen, H. K., Kistenkas, F., Miltenburg, L., van Rijswick, M., Trouwborst, A., Verschuuren, J., & Zwier, W. (2023). *De Europees- en internationaalrechtelijke status van de Waddenzee. Een analyse van de relevantie van EU-richtlijnen en internationale verdragen voor de bescherming en het beheer van de Waddenzee met een doorkijk naar de Nederlandse implementatie*. Waddenacademie.

Beukema, J. J. (1995). Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research*, *33*(2), 219–227. https://doi.org/10.1016/0077-7579(95)90008-X

Beukema, J. J., & Dekker, R. (2011). Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. *Helgoland Marine Research*, *65*(2), 155–164. https://doi.org/10.1007/s10152-010-0210-7

Bijleveld, A. I., van Gils, J. A., van der Meer, J., Dekinga, A., Kraan, C., van der Veer, H. W., & Piersma, T. (2012). Designing a benthic monitoring programme with multiple conflicting objectives. *Methods in Ecology and Evolution*, *3*(3), 526–536. https://doi.org/10.1111/j.2041-210X.2012.00192.x

Bivand, R. S., & Wong, D. W. S. (2018). Comparing implementations of global and local indicators of spatial association. *Test*, *27*(3), 716–748. https://doi.org/10.1007/s11749-018-0599-x

Boere, G. C., & Piersma, T. (2012). Flyway protection and the predicament of our migrant birds: A critical look at international conservation policies and the Dutch Wadden Sea. *Ocean and Coastal Management*, *68*, 157–168. https://doi.org/10.1016/j.ocecoaman.2012.05.019

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

Boon, A. R., Gittenberger, A., & van Loon, W. M. G. M. (2011). *Review of Marine Benthic Indicators and Metrics for the WFD and design of an optimized BEQI (1203801-000-ZKS-0007)*. Deltares.

Borja, A., Franco, J., & Pérez, V. (2000). A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin*, *40*(12), 1100–1114. https://doi.org/10.1016/S0025-326X(00)00061-8

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

Bouma, T. J., Olenin, S., Reise, K., & Ysebaert, T. (2009). Ecosystem engineering and biodiversity in coastal sediments: Posing hypotheses. *Helgoland Marine Research*, *63*(1), 95–106. https://doi.org/10.1007/s10152-009-0146-y

Broad, A., Rees, M. J., & Davis, A. R. (2020). Anchor and chain scour as disturbance agents in benthic environments: Trends in the literature and charting a course to more sustainable boating and shipping. *Marine Pollution Bulletin*, *161*, 111683. https://doi.org/10.1016/j.marpolbul.2020.111683

Butt, N., Halpern, B. S., O'Hara, C. C., Allcock, A. L., Polidoro, B., Sherman, S., Byrne, M., Birkeland, C., Dwyer, R. G., Frazier, M., Woodworth, B. K., Arango, C. P., Kingsford, M. J., Udyawer, V., Hutchings, P., Scanes, E., McClaren, E. J., Maxwell, S. M., Diaz-Pulido, G., … Klein, C. J. (2022). A trait-based framework for assessing the vulnerability of marine species to human impacts. *Ecosphere*, *13*(2), e3919. https://doi.org/10.1002/ecs2.3919

Choat, J. H. (1982). Fish feeding and the structure of benthic communities in temperate waters. *Annual Review of Ecology and Systematics*, *13*, 423–449.

Compton, T. J., Holthuijsen, S., Koolhaas, A., Dekinga, A., Horn, J. T., Brugge, M., Smith, J., Ysbrand Galema, Meer, J. V. D., Veer, H. W. V. D., & Piersma, T. (2012). *SYNOPTIC INTERTIDAL BENTHIC SURVEY, SIBES, accros the Dutch Wadden Sea. Report on data collected from 2008 to 2010 (2012.1.SIBES.NIOZ)*. Royal Netherlands Institute for Sea Research. http://rgdoi.net/10.13140/2.1.4295.8405

Compton, T. J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., Galama, Y., Brugge, M., van der Wal, D., van der Meer, J., van der Veer, H. W., & Piersma, T. (2013). Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *Journal of Sea Research*, *82*, 103–116. https://doi.org/10.1016/j.seares.2013.02.002

Council Directive 92/43/EEC. (1997). *Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora*. http://data.europa.eu/eli/dir/1992/43/oj

Craeymeersch, J. A., van Stralen, M. R., & Smaal, A. C. (2023). Impact of mussel seed fishery on subtidal sediment and macrozoobenthos in the western Wadden Sea. *Journal of Sea Research*, *192*, 102353. https://doi.org/10.1016/j.seares.2023.102353

Csárdi, G., Nepusz, T., Müller, K., Horvát, S., Traag, V., Zanini, F., & Noom, D. (2023). igraph for R: R interface of the igraph library for graph theory and network analysis (v1.6.0) [Computer software]. *Zenodo*. https://doi.org/10.5281/ZENODO.7682609

CWSS. (2017). *Introduction (Wadden Sea quality status report)*. Common Wadden Sea Secretariat. qsr.waddensea-worldheritage.org

de la Barra, P., Aarts, G., & Bijleveld, A. (2023). The effects of gas extraction under intertidal mudflats on sediment and macrozoobenthic communities. *Journal of Applied Ecology*, *61*, 390–405. https://doi.org/10.1111/1365-2664.14530

Debastiani, V. J., & Pillar, V. D. (2012). SYNCSA—R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics*, *28*, 2067–2068.

Devillers, R., Pressey, R. L., Grech, A., Kittinger, J. N., Edgar, G. J., Ward, T., & Watson, R. (2015). Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*(4), 480–504. https://doi.org/10.1002/aqc.2445

Dolbeth, M., Cardoso, P. G., Ferreira, S. M., Verdelhos, T., Raffaelli, D., & Pardal, M. A. (2007). Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. *Marine Pollution Bulletin*, *54*(5), 576–585. https://doi.org/10.1016/j.marpolbul.2006.12.005

Dudley, N., & Andalusia (Spain), IUCN World Commission on Protected Areas, Fundación Biodiversidad, & IUCN—The World Conservation Union (Eds.). (2008). *Guidelines for applying protected area management categories*. IUCN.

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

connectance. *Ecology Letters*, *5*(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Eijsackers, H. J. P., Eriksson, B. D. H. K., Van Der Heide, T., Herman, P. M. J., Van Der Meer, J., Polet, H., & Tulp, I. (2023). *Beoordeling van ecologische effecten van garnalenvisserij op bodem en biota: Mate van wetenschappelijke onderbouwing (C056/23)*. Wageningen Marine Research & Waddenacademie. https://doi.org/10.18174/637595

Fieten, N., Frauendorf, M., & Walter, E. (2022). *Inventory of protected area restrictions in the trilateral Wadden Sea a comparison of the existing different protection regimes (A&W-rapport 22-146)*. Altenburg & Wymenga ecologisch onderzoek.

Fock, H., Dammann, R., Mielck, F., Kraus, G., Lauerburg, R. A. M., López González, A., Nielsen, P., Nowicki, M., Pauli, M., & Temming, A. (2023). *Auswirkungen der Garnelenfischerei auf Habitate und Lebensgemeinschaften im Küstenmeer der Norddeutschen Bundesländer Schleswig- Holstein, Hamburg und Niedersachsen (CRANIMPACT) (Thünen report 107)*. Johann Heinrich von Thünen-Institut. https://doi.org/10.3220/REP1681989003000

Fokker, P. A., Van Leijen, F. J., Orlic, B., Van Der Marel, H., & Hanssen, R. F. (2018). Subsidence in the Dutch Wadden Sea. *Netherlands Journal of Geosciences*, *97*(3), 129–181. https://doi.org/10.1017/njg.2018.9

Getis, A., & Ord, J. K. (1992). The analysis of spatial association by use of distance statistics. *Geographical Analysis*, *24*(3), 189–206. https://doi.org/10.1111/j.1538-4632.1992.tb00261.x

Gislason, H., Bastardie, F., Dinesen, G. E., Egekvist, J., & Eigaard, O. R. (2017). Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. *Ecological Indicators*, *82*, 260–270. https://doi.org/10.1016/j.ecolind.2017.07.004

Gittenberger, A., & van Loon, W. (2013). Sensitivities of marine macrozoobenthos to environmental pressures in The Netherlands. *Nederlandse Faunistische Mededelingen*, *41*, 79–112.

Glorius, S. T., Tulp, I. Y. M., Meijboom, A., Bolle, L. J., & Chen, C. (2018). *Developments in benthos and fish in gullies in an area closed for human use in the Wadden Sea: 2002–2016 [WOt-technical report 129]*. Wettelijke Onderzoekstaken Natuur & Milieu. https://doi.org/10.18174/464873

Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta e Costa, B., Pike, E. P., Kingston, N., Laffoley, D., Sala, E., Claudet, J., Friedlander, A. M., Gill, D. A., Lester, S. E., Day, J. C., Gonçalves, E. J., Ahmadia, G. N., Rand, M., Villagomez, A., Ban, N. C., … Lubchenco, J. (2021). The MPA guide: A framework to achieve global goals for the ocean. *Science*, *373*(6560), eabf0861. https://doi.org/10.1126/science.abf0861

Gusmao, J. B., Thieltges, D. W., Dekker, R., Govers, L. L., Meijer, K. J., & Klemens Eriksson, B. (2022). Comparing taxonomic and functional trait diversity in marine macrozoobenthos along sediment texture gradients. *Ecological Indicators*, *145*, 109718. https://doi.org/10.1016/j.ecolind.2022.109718

Halpern, B. S., Frazier, M., Afflerbach, J., Lowndes, J. S., Micheli, F., O'Hara, C., Scarborough, C., & Selkoe, K. A. (2019). Recent pace of change in human impact on the world's ocean. *Scientific Reports*, *9*(1), 11609. https://doi.org/10.1038/s41598-019-47201-9

Heidinga, D., Schilt, B., Versloot, F., Gotjé, W., Bijkerk, W., & Latour, J. B. (2023). *Ecologische evaluatie Natura 2000 beheerplannen (128201)*. Witteveen+Bos.

Hiddink, J. G., Jennings, S., & Kaiser, M. J. (2007). Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *Journal of Applied Ecology*, *44*(2), 405–413. https://doi.org/10.1111/j.1365-2664.2007.01274.x

Hiddink, J. G., Kaiser, M. J., Sciberras, M., McConnaughey, R. A., Mazor, T., Hilborn, R., Collie, J. S., Pitcher, C. R., Parma, A. M., Suuronen, P., Rijnsdorp, A. D., & Jennings, S. (2020). Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. *Journal of Applied Ecology*, *57*, 1199–1209. https://doi.org/10.1111/1365-2664.13617

Hinz, H., Törnroos, A., & de Juan, S. (2021). Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions. *Ecological Indicators*, *126*, 107692. https://doi.org/10.1016/j.ecolind.2021.107692

International Union for the Conservation of Nature. (2020). *Motion 066—Guidance to identify industrial fishing incompatible with protected areas*. IUCN World Conservation Congress 2020. https://www.iucncongress2020.org/motion/066

Jayachandran, P. R., Bijoy Nandan, S., Jima, M., Philomina, J., & Vishnudattan, N. K. (2022). Benthic organisms as an ecological tool for monitoring coastal and marine ecosystem health. In *Ecology and biodiversity of benthos* (pp. 337–362). Elsevier. https://doi.org/10.1016/B978-0-12-821161-8.00004-0

Joppa, L. N., & Pfaff, A. (2009). High and far: Biases in the location of protected areas. *PLoS One*, *4*(12), e8273. https://doi.org/10.1371/journal.pone.0008273

Kenny, A. J., Jenkins, C., Wood, D., Bolam, S. G., Mitchell, P., Scougal, C., & Judd, A. (2018). Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. *ICES Journal of Marine Science*, *75*(3), 1080–1092. https://doi.org/10.1093/icesjms/fsx205

Klunder, L., Van Bleijswijk, J., Kleine Schaars, L., Van Der Veer, H., & Luttikhuizen, P. (2021). Impact of mechanical Arenicola dredging on the benthic fauna communities: Assessed by a morphological and molecular approach. *Marine Ecology Progress Series*, *673*, 17–28. https://doi.org/10.3354/meps13816

Laurino, I. R. A., Serafini, T. Z., Costa, T. M., & Christofoletti, R. A. (2021). The role of estuarine macrofaunal patterns for the management of marine protected areas in a changing world. *Journal for Nature Conservation*, *63*, 126042. https://doi.org/10.1016/j.jnc.2021.126042

Lavaleye, M. S. S. (1999). *Rapport Graadmeters van de Noordzee. Infaunal trophic index (ITI) van het macrobenthos en Structuur macrobenthos gemeen schap (verhouding r en Kstrategen) [GONZ-Rapport]*. Nederlands Instituut voor Onderzoek der Zee (NIOZ).

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Leonardsson, K., Blomqvist, M., & Rosenberg, R. (2009). Theoretical and practical aspects on benthic quality assessment according to the EU-Water Framework Directive—Examples from Swedish waters. *Marine Pollution Bulletin*, *58*(9), 1286–1296. https://doi.org/10.1016/j.marpolbul.2009.05.007

Lindegren, M., Holt, B. G., MacKenzie, B. R., & Rahbek, C. (2018). A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. *Scientific Reports*, *8*(1), 4099. https://doi.org/10.1038/s41598-018-22419-1

LNV. (2020). *Addendum op Convenant transitie mosselsector en natuurherstel Waddenzee*. https://open.overheid.nl/

LNV. (2023). *Wet natuurbescherming; gedoogbeschikking; garnalenvisserij—Natuurvergunningen*. Puc.Overheid. https://puc.overheid.nl/natuurvergunningen/doc/PUC_748958_17/1/

Lotze, H. K. (2007). Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. *Fisheries Research*, *87*(2), 208–218. https://doi.org/10.1016/j.fishres.2006.12.009

Lubchenco, J., & Grorud-Colvert, K. (2015). Making waves: The science and politics of ocean protection. *Science*, *350*(6259), 382–383. https://doi.org/10.1126/science.aad5443

Mathot, K. J., Piersma, T., & Elner, R. W. (2018). Shorebirds as integrators and indicators of mudflat ecology. In P. G. Beninger (Ed.), *Mudflat ecology* (pp. 309–338). Springer International Publishing. https://doi.org/10.1007/978-3-319-99194-8_12

McLaverty, C., Eigaard, O. R., Olsen, J., Brooks, M. E., Petersen, J. K., Erichsen, A. C., van der Reijden, K., & Dinesen, G. E. (2023). European coastal monitoring programmes may fail to identify impacts on benthic macrofauna caused by bottom trawling. *Journal*

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of Environmental Management, *334*, 117510. https://doi.org/10.1016/j.jenvman.2023.117510

Meijer, K. J., Franken, O., van der Heide, T., Holthuijsen, S. J., Visser, W., Govers, L. L., & Olff, H. (2022). Characterizing bedforms in shallow seas as an integrative predictor of seafloor stability and the occurrence of macrozoobenthic species. *Remote Sensing in Ecology and Conservation*, *9*(3), 323–339. https://doi.org/10.1002/rse2.312

Meijer, K. J., Gusmao, J. B., Bruil, L., Franken, O., Grimm, I. A., van der Heide, T., Hijner, N., Holthuijsen, S. J., Hübner, L., Thieltges, D. W., Olff, H., Eriksson, B. K., & Govers, L. L. (2023). The seafloor from a trait perspective. A comprehensive life history dataset of soft sediment macrozoobenthos. *Scientific Data*, *10*(1), 808. https://doi.org/10.1038/s41597-023-02728-5

Mihoub, J.-B., Henle, K., Titeux, N., Brotons, L., Brummitt, N. A., & Schmeller, D. S. (2017). Setting temporal baselines for biodiversity: The limits of available monitoring data for capturing the full impact of anthropogenic pressures. *Scientific Reports*, *7*(1), 41591. https://doi.org/10.1038/srep41591

Ministerial Council of the Trilateral Governmental Conference on the Protection of the Wadden Sea. (1991). *Declaration of the 6th Trilateral Governmental Conference on the Protection of the Wadden Sea: With adoption of the guiding principle, common management principles and objectives for human use*. https://www.waddensea-worldheritage.org

Ministerie van Infrastructuur en Milieu, Rijkswaterstaat Noord-Nederland. (2016). *Natura 2000-beheerplan Waddenzee Periode 2016–2022*. Ministerie van Infrastructuur en Milieu Rijkswaterstaat Noord-Nederland.

MSFD. (2008). *Directive 2008/56/EC of the European Parliament and of the council of 17 June 2008; establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive)*. Official Journal of the European Communities.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

PRW. (2014). *Convenant transitie garnalenvisserij en natuurambitie Rijke Waddenzee*.

QGIS Development Team. (2023). *QGIS geographic information system (3.26.2)* [Computer software].

R Core Team. (2023). *R: A language and environment for statistical computing (4.3.1.) [Computer software]*. R Foundation for Statistical Computing. https://www.R-project.org/

Rabaut, M., Degraer, S., Schrijvers, J., Derous, S., Bogaert, D., Maes, F., Vincx, M., & Cliquet, A. (2009). Policy analysis of the 'MPA-process' in temperate continental shelf areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(5), 596–608. https://doi.org/10.1002/aqc.985

Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M., & Degraer, S. (2007). A bio-engineered soft-bottom environment: The impact of Lanice conchilega on the benthic species-specific densities and community structure. *Estuarine, Coastal and Shelf Science*, *75*(4), 525–536. https://doi.org/10.1016/j.ecss.2007.05.041

Rao, C. R. (1995). A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. *Questiio*, *19*, 23–63.

Reid, W. V. (1998). Biodiversity hotspots. *Trends in Ecology & Evolution*, *13*(7), 275–280. https://doi.org/10.1016/S0169-5347(98)01363-9

Reiss, H., & Kröncke, I. (2005). Seasonal variability of benthic indices: An approach to test the applicability of different indices for ecosystem quality assessment. *Marine Pollution Bulletin*, *50*(12), 1490–1499. https://doi.org/10.1016/j.marpolbul.2005.06.017

Ricklefs, K., Franken, O., Glorius, S., Mascioli, F., Nielsen, P., Reimers, H.-C., & Trampe, A. (2022). *Subtidal habitats (Wadden Sea quality status report)*. Common Wadden Sea Secretariat. qsr.waddensea-worldheritage.org/reports/subtidal-habitats

Rippen, A., van der Zee, E., Fieten, N., Latour, J., & Wymenga, E. (2020). *Review effecten natuurlijke bodemdynamiek en menselijke bodemberoering in de sublitorale Waddenzee*. Altenburg & Wymenga ecologisch onderzoek.

Rising, J., & Heal, G. (2014). *Global benefits of marine protected areas (w19982)*. National Bureau of Economic Research. https://doi.org/10.3386/w19982

Robert, A. E., Quillien, N., Bacha, M., Caulle, C., Nexer, M., Parent, B., Garlan, T., & Desroy, N. (2021). Sediment migrations drive the dynamic of macrobenthic ecosystems in subtidal sandy bedforms. *Marine Pollution Bulletin*, *171*, 112695. https://doi.org/10.1016/j.marpolbul.2021.112695

Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D. C., Da Fonseca, G. A. B., Gaston, K. J., Hoffmann, M., Long, J. S., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., … Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, *428*(6983), 640–643. https://doi.org/10.1038/nature02422

Rolet, C., Spilmont, N., Dewarumez, J.-M., & Luczak, C. (2015). Linking macrobenthic communities structure and zonation patterns on sandy shores: Mapping tool toward management and conservation perspectives in Northern France. *Continental Shelf Research*, *99*, 12–25. https://doi.org/10.1016/j.csr.2015.03.002

Rosenberg, R., Blomqvist, M., C Nilsson, H., Cederwall, H., & Dimming, A. (2004). Marine quality assessment by use of benthic species-abundance distributions: A proposed new protocol within the European Union Water Framework Directive. *Marine Pollution Bulletin*, *49*(9), 728–739. https://doi.org/10.1016/j.marpolbul.2004.05.013

Sacre, E., Bode, M., Weeks, R., & Pressey, R. L. (2019). The context dependence of frontier versus wilderness conservation priorities. *Conservation Letters*, *12*(3), e12632. https://doi.org/10.1111/conl.12632

Sala, E., & Giakoumi, S. (2018). No-take marine reserves are the most effective protected areas in the ocean. *ICES Journal of Marine Science*, *75*(3), 1166–1168. https://doi.org/10.1093/icesjms/fsx059

Sala, E., Lubchenco, J., Grorud-Colvert, K., Novelli, C., Roberts, C., & Sumaila, U. R. (2018). Assessing real progress towards effective ocean protection. *Marine Policy*, *91*, 11–13. https://doi.org/10.1016/j.marpol.2018.02.004

Schans, H., Mulder, H. P. J., & de Vlas, J. (2003). *Opvulsnelheid, gedragen effect van schelpenwinputten in de Waddenzee. Vervolgonderzoek Schelpenwinning (NN-ANW-03-01)*. Ministerie van Verkeer en Waterstaat.

Sköld, M., Göransson, P., Jonsson, P., Bastardie, F., Blomqvist, M., Agrenius, S., Hiddink, J., Nilsson, H., & Bartolino, V. (2018). Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Marine Ecology Progress Series*, *586*, 41–55. https://doi.org/10.3354/meps12434

Smaal, A. C., & Lucas, L. (2000). Regulation and monitoring of marine aquaculture in The Netherlands. *Journal of Applied Ichthyology*, *16*(4–5), 187–191. https://doi.org/10.1046/j.1439-0426.2000.00266.x

Smith, R. (2015). Directive 2010/41/EU of the European Parliament and of the Council of 7 July 2010. In R. Smith (Ed.), *Core EU Legislation* (pp. 352–355). Macmillan Education UK. https://doi.org/10.1007/978-1-137-54482-7_33

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., Stuart-Smith, J. F., Hill, N. A., Kininmonth, S. J., Airoldi, L., Becerro, M. A., Campbell, S. J., Dawson, T. P., Navarrete, S. A., Soler, G. A., Strain, E. M. A., Willis, T. J., & Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, *501*(7468), 539–542. https://doi.org/10.1038/nature12529

Sundblad, G., Bergström, U., & Sandström, A. (2011). Ecological coherence of marine protected area networks: A spatial assessment

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

using species distribution models. *Journal of Applied Ecology*, *48*(1), 112–120. https://doi.org/10.1111/j.1365-2664.2010.01892.x

Tillin, H., Hiddink, J., Jennings, S., & Kaiser, M. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, *318*, 31–45. https://doi.org/10.3354/meps318031

Tulp, I., Glorius, S., Rippen, A., Looije, D., & Craeymeersch, J. (2020). Dose-response relationship between shrimp trawl fishery and the macrobenthic fauna community in the coastal zone and Wadden Sea. *Journal of Sea Research*, *156*, 101829. https://doi.org/10.1016/j.seares.2019.101829

Uitvoeringsregeling Visserij. (2008). BWBR0024539. http://wetten.overheid.nl/jci1.3:c:BWBR0024539

Underwood, A. J. (2000). Experimental ecology of rocky intertidal habitats: What are we learning? *Journal of Experimental Marine Biology and Ecology*, *250*(1), 51–76. https://doi.org/10.1016/S0022-0981(00)00179-9

van der Ploeg, H. A., & Scavia, D. (1979). Calculation and use of selectivity coefficients of feeding: Zooplankton grazing. *Ecological Modelling*, *7*(2), 135–149. https://doi.org/10.1016/0304-3800(79)90004-8

Van der Reijden, K. J., Hintzen, N. T., Govers, L. L., Rijnsdorp, A. D., & Olff, H. (2018). North Sea demersal fisheries prefer specific benthic habitats. *PLoS One*, *13*(12), e0208338. https://doi.org/10.1371/journal.pone.0208338

van der Veer, H. W., Dapper, R., Henderson, P. A., Jung, A. S., Philippart, C. J. M., Witte, J. I. J., & Zuur, A. F. (2015). Changes over 50 years in fish fauna of a temperate coastal sea: Degradation of trophic structure and nursery function. *Estuarine, Coastal and Shelf Science*, *155*, 156–166. https://doi.org/10.1016/j.ecss.2014.12.041

van Donk, S., & Baptist, M. (2021). *Validatie van het Zoute wateren EcotopenStelsel (ZES.1) in de Waddenzee (C093/21)*. Wageningen Marine Research. https://doi.org/10.18174/557468

van Loon, W. M. G. M., Boon, A. R., Gittenberger, A., Walvoort, D. J. J., Lavaleye, M., Duineveld, G. C. A., & Verschoor, A. J. (2015). Application of the Benthic Ecosystem Quality Index 2 to benthos in Dutch transitional and coastal waters. *Journal of Sea Research*, *103*, 1–13. https://doi.org/10.1016/j.seares.2015.05.002

van Loon, W. M. G. M., Walvoort, D. J. J., van Hoey, G., Vina-Herbon, C., Blandon, A., Pesch, R., Schmitt, P., Scholle, J., Heyer, K., Lavaleye, M., Phillips, G., Duineveld, G. C. A., & Blomqvist, M. (2018). A regional benthic fauna assessment method for the Southern North Sea using Margalef diversity and reference value modelling. *Ecological Indicators*, *89*, 667–679. https://doi.org/10.1016/j.ecolind.2017.09.029

Venter, O., Magrach, A., Outram, N., Klein, C. J., Possingham, H. P., Di Marco, M., & Watson, J. E. M. (2018). Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. *Conservation Biology*, *32*(1), 127–134. https://doi.org/10.1111/cobi.12970

Wang, P., Teng, M., He, W., Tang, C., Yang, J., & Yan, Z. (2018). Using habitat selection index for reserve planning and management for snub-nosed golden monkeys at landscape scale. *Ecological Indicators*, *93*, 838–846. https://doi.org/10.1016/j.ecolind.2018.05.070

WFD. (2000). Directive 2000/60/EC of the European Parliament and of the council of 23 October 2000; establishing a framework for community action in the field of water policy. *Official Journal of the European Communities*, *327*, 1–73. https://eur-lex.europa.eu/eli/dir/2000/60/oj

Wijnhoven. (2018). *Protocol Benthic Indicator Species Index (BISI): Protocol BISI for generic application (BISI v2), v181218 (2018-04)*. Ecoauthor. http://ecoauthor.net/wp-content/uploads/2019/09/Protocol-BISI-v2-for-Generic-Application-v181218.pdf

Wijnhoven, S., & van Avesaath, P. (2019). *Benthische Indicator Soorten Index (BISI) voor mariene habitattypen in natura 2000-gebieden. Itwerking beoordelingsmethodiek inclusief monitoringvoorstel voor mariene habitattypen van de Habitatrichtlijn gelegen in de Deltawateren, het Waddenzeegebied en de kustzone van de Noordzee (2019-03)*. Ecoauthor.

Witte, S., Dickson, J., Franken, O., Holthuijsen, S., Govers, L. L., Olff, H., & Van Der Heide, T. (2024). Enhancing ecological complexity in soft-bottom coastal ecosystems: The impact of introducing hard substrates. *Restoration Ecology*, *32*, e14126. https://doi.org/10.1111/rec.14126

Wolff, W. J. (2013). Ecology of the Wadden Sea: Research in the past and challenges for the future. *Journal of Sea Research*, *82*, 3–9. https://doi.org/10.1016/j.seares.2013.03.006

Wolff, W. J., Bakker, J. P., Laursen, K., & Reise, K. (2010). *The Wadden sea quality status report—Synthesis report 2010*. Common Wadden Sea Secretariat.

Wootton, K. L., & Stouffer, D. B. (2016). Species' traits and food-web complexity interactively affect a food web's response to press disturbance. *Ecosphere*, *7*(11), e01518. https://doi.org/10.1002/ecs2.1518

Word, J. Q. (1978). *The Infaunal trophic index* [Southern California coastal water research project annual report, Southern California Coastal Water Research Project].

Zupan, M., Fragkopoulou, E., Claudet, J., Erzini, K., Horta e Costa, B., & Gonçalves, E. J. (2018). Marine partially protected areas: Drivers of ecological effectiveness. *Frontiers in Ecology and the Environment*, *16*(7), 381–387. https://doi.org/10.1002/fee.1934

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Restrictions and activities.

Appendix S2. Indicator calculations.

Appendix S3. Gas extraction and salt solution mining.

Appendix S4. Hotspots, coldspots and conservation conformity.

How to cite this article: Meijer, K. J., Franken, O., Witte, S., Holthuijsen, S. J., van der Heide, T., Govers, L. L., & Olff, H. (2025). Hotspots in peril: Misalignment of conservation efforts and ecological values in a shallow coastal sea. *People and Nature*, *7*, 160–179. https://doi.org/10.1002/pan3.10757

25758314, 2025, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10757 by Centrum Voor Wiskunde En Info (Cwi), Wiley Online Library on [14/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License