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Trophic modelling as a pathway to ecosystem-based management – the Marine Protected Area "Sylt Outer Reef - Eastern German Bight"

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ABSTRACT

The Marine Protected Area of the Sylt Outer Reef – Eastern German Bight (SOR), located in the German Exclusive Economic Zone of the North Sea, is an ecologically important region that provides essential habitats for numerous species and supports high benthic faunal diversity. In this study, we developed the first mass-balanced food web model for the SOR covering the period 2010–2020, using Ecopath with Ecosim (EwE), in order to understand ecosystem functioning, structure, and energy flows prior to the implementation of management measures. The model included 44 functional groups and 8 fishing gear types. We found that the SOR is dominated by low trophic levels and strong benthic recycling, with detritus and primary producers contributing 33.43% and 20.41% of total system throughput (TST), respectively. Ecosystem indicators highlight that the system is detritus-driven with high internal recycling. It has multiple alternative pathways for energy and biomass flow, supporting a complex trophic structure and potentially being resilient to disturbance. Keystone groups and species included surface-feeding birds and harbour porpoise, whereas key structuring groups included carnivorous polychaetes, phytoplankton, herbivorous zooplankton, and sandeels. Fishing gears in the SOR target both pelagic and demersal groups, primarily forage fish such as sandeels and sprat. The static food web model of the SOR is a baseline for evaluating the effect of the implemented management measures on the ecosystem as the next step, supporting ecosystem-based management decisions for the Sylt Outer Reef such as the exclusion of bottom trawling from many areas of the SOR in March 2023.

1. Introduction

The North Sea is a highly productive marine region of great ecological and economic importance (Walday and Kroglund, 2002; Andersen et al., 2013). It supports major human activities, including fisheries, maritime shipping, and offshore renewable energy development, particularly wind farms. The simultaneous activities place substantial anthropogenic pressure on the ecosystem (Álvarez et al., 2019; Stelzenmüller et al., 2022; OSPAR Commission, 2023). As a result of intense previous use such as fishing, the region has experienced declines in biodiversity, degradation of benthic habitats, reduction in fish stocks and seabird populations, inducing pressure on populations of marine mammals (OSPAR Commission, 2023). Given the increasing disturbances to global marine ecosystems (Halpern et al., 2015) and, at the same time, the economic importance of marine resources and associated sectors to the EU blue economy (European Commission, 2025), there is an urgent need for EU member states to adopt sustainable practices in the management of marine environments. The implementation of ecosystem-based management approaches is needed for sustainable management and utilisation of marine resources (O'Hagan, 2020; AORA, 2017). In the North Sea, seabed disturbance and mortality of target and non-target species by commercial fishing, particularly bottom trawling, rank among the most significant human pressures on the ecosystem (Rijnsdorp et al., 2016).

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Marine Protected Areas (MPAs) are common tools for the conservation of marine biodiversity, promoting the sustainable use of ocean resources (Grorud-Colvert et al., 2021). Evidence shows that both fully and partially protected MPAs benefit fish and invertebrate populations compared to open-access areas (Lester and Halpern, 2008; Sciberras et al., 2015). The provision of benefits is particularly important in marine conservation zones within the MPAs, where stricter management measures reduce human pressure, facilitating a balance between conservation goals and sustainable human activities (Sciberras et al., 2013). In the German Exclusive Economic Zone (EEZ) of the North Sea, three MPAs have been designated in the Natura 2000 framework: the Borkum Reef Ground, the Dogger Bank, and the Sylt Outer Reef- Eastern German Bight (SOR), which is the largest of all German MPAs (Krause et al., 2011; Pedersen et al., 2009). The SOR was subject to anthropogenic pressure from bottom trawling fisheries, which have been shown to negatively affect benthic faunal diversity (Lindeboom and De Groot, 1998; Neumann et al., 2016). Research has shown that the impact of bottom trawling on benthic and demersal communities can be complex (Van De Wolfshaar et al., 2020), and indeed its negative effects on benthic habitats and associated fauna have been documented for decades (e.g., Kaiser, 1998; Rijnsdorp et al., 2016). In addition to fishing pressure, the SOR is also affected by other human activities, including sand extraction, heavy ship traffic, surrounding offshore constructions (Alessandrini et al., 2017; Kenny et al., 2018), eutrophication, and warming (Amorim et al., 2023; Balkoni et al., 2026). Many of these activities occur across extensive parts of the SOR area, and a management plan was implemented by the German Federal Agency for Nature Conservation (BfN) in March 2023. In the frame of the European Natura 2000 program, to reduce human impact, restore habitats, and strengthen cooperation between relevant authorities in response to the growing concerns about the impact of fisheries and the conservation of species and habitats, different fisheries management measures have been implemented in the SOR, including a ban on bottom trawling over large areas, with complete exclusion of all bottom trawling fisheries in the largest part of the western region, albeit with an exemption for shrimp fisheries in the eastern region. In both the western and eastern parts, fishing effort with passive gear was reduced, and a no-take zone was designated at the Amrum Bank, a sand bank in the eastern part of the SOR. However, a corridor persists without any exclusions in the EU Regulation 2023/340 (European Commission, 2023). Although MPAs, such as the Sylt Outer Reef Eastern German Bight, play an important role in conserving biodiversity and maintaining ecosystem resilience (Bildstein et al., 2021; Hahn et al., 2022), a significant knowledge gap on their effectiveness and the suitability of implemented management measures remains.

The assessment of the efficiency of management measures is challenging because of limited knowledge of the ecosystem's structure and functioning inside the MPAS. Accordingly, a comprehensive baseline model is needed to properly interpret the responses of the ecosystem to the exclusion of bottom trawling and other management measures. In this context, ecosystem-based modelling as a support to management has received attention from fisheries managers and scientists (Rodriguez-Perez et al., 2023). In this regard, food web models serve as a useful tool to simplify complex ecosystems, interactions between species, and for the assessment of the effectivity of management strategies (Walters and Martell, 2004; Link et al., 2005; Heymans et al., 2014). Food web interactions determine the energy flow in ecosystems, which are controlled by a complex interplay of biological and environmental factors. Important factors include the bottom-up regulation of predator populations by prey availability, and also the top-down control through predation and exploitation (Frederiksen et al., 2006; Lynam et al., 2017).

The trophic mass-balanced Ecopath with Ecosim (EwE) modelling framework built upon the work of Polovina (1984) and developed further by (Christensen and Pauly, 1992), is an effective tool for ecosystem modelling that provides an overview of the ecosystem's trophic state (Christensen et al., 2005). Ecological Network Analysis (ENA) is a major output of EwE and can be used to evaluate food web structure and function by analysing trophic dynamics and energy flows. It is used to inform ecosystem-based management, assess the impact of fisheries, and evaluate ecosystem health (Christensen and Pauly, 1993). The ecological network indicators also serve as a valuable tool for environmental decision-makers and stakeholders (De La Vega et al., 2018; Fath et al., 2019). EwE food web models have already been applied to larger areas, such as the greater North Sea (Mackinson and Daskalov, 2007), the southern and northern North Sea (Püts et al., 2020; Hill et al., 2021), the southern Bight of the North Sea (Pint et al., 2024), as well as individual MPAs, such as the three MPAs in the Southern Mediterranean Sea (Vilas et al., 2020). A food web model for the Sylt Outer Reef is important as a baseline for understanding ecosystem functioning prior to the implementation of management measures. In this study, we applied the ecosystem model Ecopath to develop an initial, comprehensive trophic model of the Sylt Outer Reef – Eastern German Bight for the period 2010–2020. We investigated the trophic structure and functioning of the SOR MPA, identified keystone species and essential trophic interactions, and assessed the ecosystem's state.

2. Material and methods

2.1. Study area

The Sylt Outer Reef - Eastern German Bight (54°55′N, 007°20′E) west of the North Frisian Island of Sylt is the largest MPA in the German EEZ and a Special Area of Conservation (SAC) under both the EU Habitats Directive and the Birds Directive (Fig. 1). The SOR covers an area of 5603 km^2, with a water depth ranging from 8 to 48 m (Fig. 1C). As part of the southern North Sea (Statistical area IVb of the International Council of the Exploration of the Sea, ICES), the region features significant riverine inflow, tidal currents, and shallow waters, leading to a consistently well-mixed water column throughout the year (Sündermann and Pohlmann, 2011). The input of fine-grained and organic matter from the Elbe river carried along the river's paleo valley and other major rivers created extensive muddy seabed areas in the south-eastern North Sea, including offshore parts of the SOR (Papenmeier and Hass, 2020; Galvez et al., 2021). The ecosystem of the SOR is characterized by a complex, dynamic sedimentary environment dominated by sandy habitats with patches of coarse habitats and stone fields forming reef-like structures that support diverse benthic communities (Fig. 1C).

2.2. Sylt Outer Reef – Eastern German Bight food web model

2.2.1. The Ecopath model overview and balancing

In this study, we developed a mass-balanced trophic model of the SOR using the Ecopath software (EwE) version 6.7 (Christensen and Steenbeek, 2026). Ecopath is based on two main equations for energy conservation (1) and mass balance (2) (Polovina, 1984; Christensen and Pauly, 1992)

$$Qi = Pi + Ri + Ui \quad (1)$$

Where Q_i is the consumption of group i, Pi is the production, R_i is the respiration, and U_i is the unassimilated food.

$$P_i = Y_i + B_i(M2_i) + E_i + BA_i + P_i\,(1 - EE_i) \quad (2)$$

With P_i being the total production of group i, Y_i is the total fishery catch rate; B_i is the biomass; ($M2_i$) is the predation mortality rate, E_i is the net migration rate (immigration and emigration), BA_i is the biomass accumulation rate, EE_i is the ecotrophic efficiency, and Pi (1 - EE_i) is the other mortality rate.

The food web is structured by functional groups that include different trophic levels and species, ranging from detritus, bacteria,

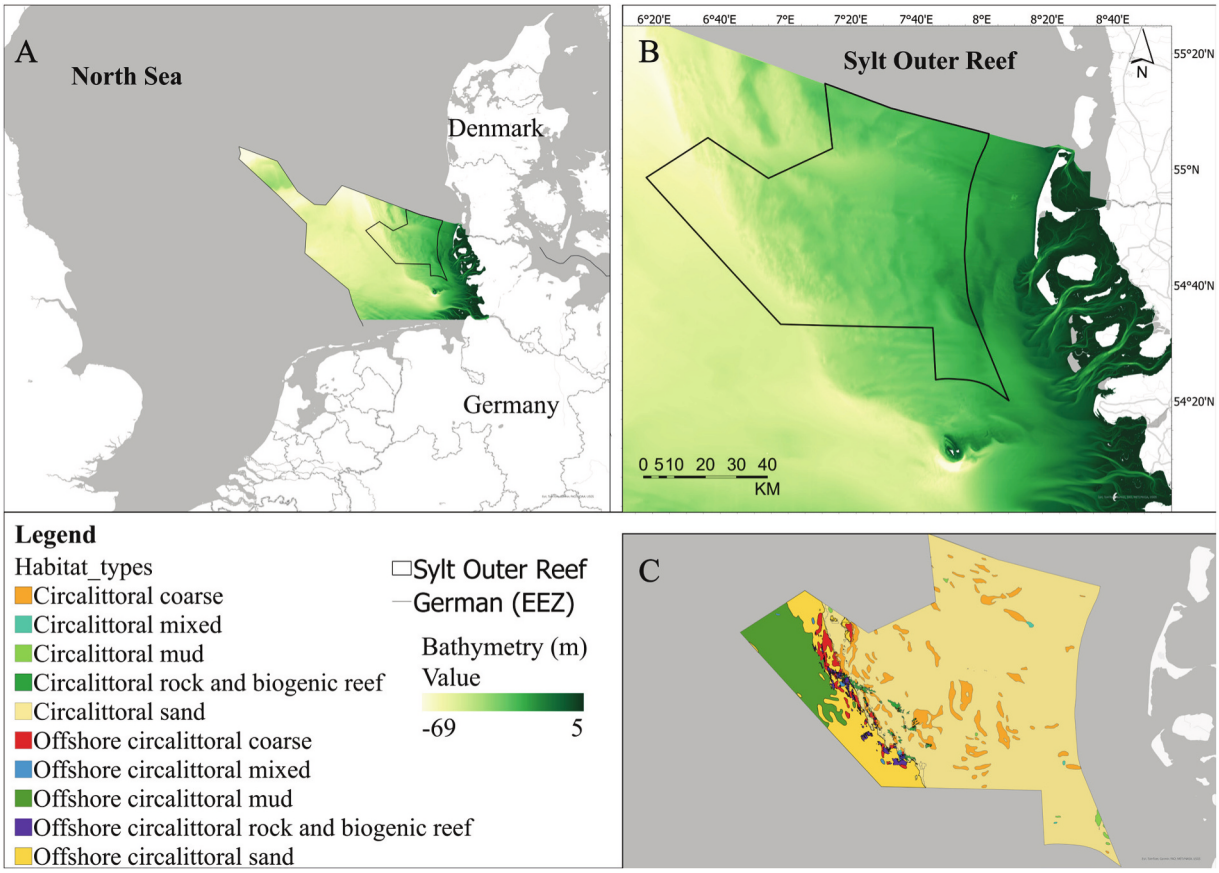

Fig. 1. Location of the Sylt Outer Reef-Eastern German Bight, within the German exclusive economic zone (EEZ) of the North Sea (A). The map for bathymetry (B) and for seafloor habitat types (C). The classification of habitat was based on the EUSeaMap (Vasquez et al., 2021), and the bathymetry of the German EEZ was provided by the Federal Maritime and Hydrographic Agency (BSH, 2020).

primary producers, to invertebrates, fish, birds and mammals. These groups were classified by taxonomic class (e.g., fish, birds, mammals), habitat (e.g., demersal, pelagic, benthic), and/or species diet (e.g., detritivorous, carnivorous). Fish were classified as pelagic or demersal, while invertebrates were grouped by habitat (epifauna and/or infauna), major taxa (e.g., bivalves, echinoderms), and further divided based on feeding behaviour (e.g., detritivorous polychaetes, suspension-feeding bivalves). Birds were also classified by their feeding behaviour (diving and surface-feeding).

The model comprised 44 groups: 2 groups of birds, 1 group of mammals, 12 groups of fish, 19 groups of invertebrates, 3 groups of zooplankton, 1 group of phytoplankton, 1 group of meiofauna, 2 groups of bacteria, and 3 groups of detritus (Table 1). In the model, detritus fates were defined by functional group. The non-utilized production and egestion in the benthic and pelagic compartments were assumed to enter the particulate organic matter (POM) and dissolved organic matter (DOM) pools proportionally (Table S1). We did not select a single year but a time span for 2010–2020, to make maximum use of the available data. We used catch data for 2013, which includes data from 8 fleets (i.e., beam trawl, bottom otter trawl, bottom pair trawl, demersal seine, midwater otter trawl, pelagic pair trawl, boat dredge, set gillnet, and pots).

2.2.2. Data sources and parameter estimation

For the construction of the Ecopath model, information was required on biomass (B; t km^{-2} y^{-1}), the production/biomass ratio (P/B; y^{-1}), the consumption/biomass ratio (Q/B; y^{-1}) of different groups of organisms, the ecotrophic efficiency (EE), and the production/consumption ratio (P/Q; y^{-1}) for different functional groups. Ecopath requires three of these four basic input parameters and estimates the remaining parameter during model balancing. Furthermore, the diet composition for each group in the ecosystem had to be defined, and data on fisheries landings and discards had to be compiled (t km^{-2} y^{-1}).

2.2.3. Biomasses

Different data sources were used to obtain biomass values. The biomass of harbour porpoises was estimated by multiplying the abundance from aerial and shipboard surveys conducted during the SCANS-III project in the summer of 2016 in European Atlantic waters (Hammond et al., 2017). by the average body mass of an individual (Lockyer, 1995).

Seabird abundance data from 2010 to 2020 were collected from ship- and aerial-based surveys in the German North Sea, carried out by the University of Kiel and the German Marine Biodiversity Monitoring program of the BfN. For the aerial-based survey, visual observations were conducted simultaneously with a digital imaging survey along identical transects (Borkenhagen et al., 2021). The dataset included geo-referenced observations of species' presence, abundance, and group size. The observations were conducted within transects of predefined width in the German EEZ across all four seasons. The average body mass of both surface and diving-feeding birds was compiled from the scientific literature (Cramp and Simmons, 1983; Bezzel, 1985; Pierotti et al., 1994; Bauer and Glutz von Blotzheim, 1996; Rizzolo et al., 2015; Bordage and Savard, 2011).

The biomass of Herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) were estimated using HERAS acoustic survey data from 2014 to 2020 (ICES, 2021). Acoustic measurements combined with pelagic trawl hauls provided biological data, which were used to calculate total biomass within predefined strata. Biomass values for each stratum were obtained from reports of the Working Group of International Pelagic Survey

Table 1
List for relevant taxonomic division the species/groups included and the dominant species for the Sylt Outer Reef as used in the Ecopath model.

Taxonomic division	Species/groups included	Composition of dominant species
Mammals	Harbour porpoise	*Phocoena phocoena*
Birds	Diving feeding birds	*Larus minutus, Larus fuscus, Larus canus, Larus argentatus, Rissa tridactyla*
	Surface feeding birds	*Melanitta nigra, Uria aalge, Gavia* spp., *Gavia stellata, Sterna sandvicensis, Sula bassana*
Demersal fish	Sandeels	*Ammodytes* spp., *Ammodytes tobianus*
	Whiting	*Merlangius merlangus*
	Dragonet	*Callionymus lyra*
	Hooknose	*Agonus cataphractus*
	Grey gurnard	*Eutrigla gurnardus*
	Scaldfish	*Arnoglossus laterna*
	Solenette	*Buglossidium luteum*
	Plaice	*Pleuronectes platessa*
	Dab	*Limanda limanda*
	Cod	*Gadus morhua*
Pelagic fish	Herring	*Clupea harengus*
	Sprat	*Sprattus sprattus*
Squid	Squid	*Loligo forbesii*
		Allotheuthis subulata
Epifaunal benthos	Brown shrimp	*Crangon crangon*
	Edible crab	*Cancer pagurus*
	Swimming crabs	*Polybius holsatus, Polybius depurator*
	Paguridae	*Paguridae* spp., *Pagurus bernhardus*
	Sand star	*Astropecten irregularis*
	Common starfish	*Asterias rubens*
Infaunal benthos	Masked crab	*Corystes cassivelaunus*
	Phoronids	*Phoronis muelleri*
	Nemertea	*Nemertea* indet, *Tubulanus polymorphus*
	Detritivorous amphipods	*Autonoe longipes, Cheirocratus sundevallii,*
	Omnivorous decapods	*Thia scutellata*
	Lancelet	*Branchiostoma lanceolatum*
	Detritivorous polychaetes	*Aonides paucibranchiata, Eunereis longissima, Mediomastus fragilis, Notomastus latericeus, Scoloplos armiger, Spiophanes bombyx.*
	Carnivourous polychaetes	*Glycera lapidum, Nephtys caeca, Nephtys cirrosa, Pholoe baltica, Pisione remota, Protodorvillea kefersteini*
	Suspension feeding polychaetes	*Lanice conchilega, Polycirrus medusa, Polygordius appendiculatus, Polygordius lacteus*
	Deposit feeding echinoderms	*Amphipholis squamata, Amphiura filiformis, Echinocardium* spp., *Echinocardium pennatifidum, Echinocyamus pusillus*
	Deposit feeding bivalves	*Abra alba, Fabulina fabula, Kurtiella bidentata*
	Suspension feeding bivalves	*Dosinia exoleta, Ensis ensis, Ensis leei, Ensis magnus, Phaxas pellucidus*
Zooplankton	Herbivorous zooplankton	
	Carnivorous zooplankton	
	Gelatinous zooplankton	
Primary producers	Phytoplankton	
Bacteria	Pelagic and benthic Bacteria	
Detritus	Detritus (DOM) – Detritus (POM)	

(WGIPS) and standardized by the area to yield biomass per square meter (details in supplementary materials). The epibenthos and demersal fish data were collected using a beam trawl from 2010 to 2020 (Thünen-Institute of Sea Fisheries, with personal communication with Holger Haslob).

The infauna was sampled with a van Veen grab (0.1 m^2) from 116 sites in the SOR area using the German research vessel 'Heincke' (2014–2018). The samples were sieved (mesh size: 1000 μm) and the retained benthic macrofauna was stored in buffered 4% formalin-seawater solution. In the laboratory, the benthic macrofauna was identified to the lowest taxonomic level possible, and abundances and biomasses (wet weight in g) were determined. The taxonomy was matched against the World Register of Marine Species (WoRMS Editorial Board 2024, https://www.marinespecies.org). Species biomass was first classified according to habitat association and subsequently normalized to the total study area based on the proportional extent of each habitat type (a detailed description of the methodology, Slila et al.in prep.). Biomass data for zooplankton groups, phytoplankton, bacteria, detritus, and discards compartments were assumed to be the same as those used in the model of the Greater North Sea (Mackinson and Daskalov, 2007), and were used unchanged in the present model.

2.2.4. Production/biomass (P/B) and consumption/biomass (Q/B)

The production/biomass ratio (P/B) and (Q/B) for harbour porpoise were added from (Mackinson and Daskalov, 2007). The birds (Q/B) were calculated using the empirical equation of Nilsson and Nilsson (1976), and the (P/B) was estimated from (Pint et al., 2024). For fish groups, the (P/B) was estimated as follows:

$$\frac{P}{B} = Z = M + \left(\frac{C}{B}\right) \tag{3}$$

where Z is the total mortality, (M, y^{-1}) is natural mortality, and the catch/biomass ratio (C/B) corresponds to fishing mortality (F, t km^{-2}).

Natural mortality (M, y^{-1}) was obtained from the online database Fishbase (www.fishbase.se; Froese and Pauly, 2024), and the total mortality (Z) of the exploited fish species was determined by the sum of fishing and natural mortalities.

For the consumption/biomass ratio (Q/B), we used the empirical Eq. (4) of Pauly et al. (1990):

$$Log\left(\frac{Q}{B}\right) = 7.964 - 0.204 \times \log(W\infty) - 1.1965 \times T^{'} + 0.083A + 0.532 + 0.398 \times h \tag{4}$$

Where $W\infty$ is the asymptotic weight, $T^{'}$ is (°C + 273.15), A is the aspect ratio, h *is* the length of the tail fin of a fish, and it is found in (www.fishbase.se).

The (P/B) ratio for invertebrates, such as crabs, and benthic infauna, was calculated using the network model of Brey (2001), which requires as inputs temperature, depth, and other parameters such as taxonomic classification and mobility, and for brown shrimp and edible crab, it was estimated based on Eq. (3).

For the production/consumption ratio (P/Q), we assumed a P/Q gross efficiency of 20% for sand star, common starfish, swimming crabs, and masked crab. For all infaunal groups and brown shrimp, we assumed a gross efficiency of 30% (Mackinson and Daskalov, 2007). The gross food conversion efficiency (P/Q) ranged from 0.1 to 0.3, except for small, fast-growing organisms such as bacteria (Darwall et al., 2010; Heymans et al., 2016).

2.2.5. Fisheries and diet composition

Fisheries data for the SOR were obtained from the EU Data Collection Framework (DCF) and Fisheries Dependent Information (FDI) (European Commission, Joint Research Centre, 2026a). Landing data were collected based on predefined strata. The data were obtained for each stratum overlapping the SOR and then adjusted according to the proportion of the stratum that overlapped the SOR. These values were subsequently standardized by area to calculate landings per km^2. All gear types, such as beam trawl, bottom otter trawl, bottom pair trawl, demersal seine, midwater otter trawl, pelagic pair trawl, boat dredge, set gillnet, and pots, were included. The most targeted fisheries were

sandeels and sprat. Discard ratios, calculated from ICES rectangle 27.4.B catch data, were applied to estimate species and gear-specific discards in the SOR, and bycatch data were not considered (European Commission, Joint Research Centre, 2026b). Diets of different species and groups were collected from FishBase (www.fishbase.se; Froese and Pauly, 2024) and from scientific literature. For multispecies groups with multiple sources of diet information, diets were adapted from the nearest geographic area (Table S5).

2.3. Model balancing and data quality

We considered the model balanced when the ecotrophic efficiency, which is the fraction of its production that is consumed (EE < 1) for all groups, and the respiration/biomass (R/B) ratio was within 1–10 year^{-1} for fish. Production/respiration (P/R) <1 for all groups besides bacterial groups and gelatinous zooplanktons (Heymans et al., 2016). The integrated pedigree routine was assigned to assess the data and parameters (biomass, P/B, Q/B, diet composition, and catches) and the model's quality. The pedigree indicates the quality and confidence interval of a parameter. It gives an index ranging from 0 to 1, with 1 indicating high confidence based on locally accurate sampling data of the modelled system (Christensen et al., 2005; Christensen et al., 2005).

2.4. Ecosystem indicators and energy flows

Ecological Network Analysis (ENA) provides a set of ecosystem indices for understanding ecosystem functioning, structure, and status (Ulanowicz, 1986; Christensen et al., 2005). We used relative ascendency (A/C), which is the ratio between ascendency (A), a measure of the system's ability to process energy or material structurally and efficiently, to development capacity (C), which is the system's growth capacity. A/C is an index of the organization and efficiency in the transfer of energy and matter from primary producers to high trophic levels. Higher relative ascendency suggests more orderly flows and a greater presence of dietary specialists (Ulanowicz, 1986; Canning and Death, 2018). Conversely, the overhead (O) is the difference between the system development capacity (C) and the ascendency (A), which refers to the ecosystem's reserve capacity and flexibility, and the relative overhead (O/C) is the ratio of the total calculated overhead (O) and the development capacity (C). Systems with a high relative overhead (O/C) have more complex structures, including multiple pathways and redundant connections that enhance long-term stability and adaptability. These systems also tend to show prevalence of generalists (Ulanowicz, 1986; Heymans et al., 2014; Fath et al., 2019). Relative ascendency and relative overhead are counterparts, and the trade-off between organization and flexibility is central to assessing the ecosystem health (Ulanowicz, 2004).

The calculated Finn Cycling Index (FCI) measures the fraction of total system throughput that is recycled. A high FCI indicates a greater degree of internal recycling of energy or matter within the ecosystem (Finn, 1976). We also took into account the average path length (APL), which is the average number of compartments an inflow passes through the system (Finn, 1976). A longer APL suggests greater structural complexity as energy passes through more compartments before exiting the system (Finn, 1980). Moreover, APL tends to be greater in ecosystems with a wider variety of flow pathways and lower in systems with shorter pathways or simpler food webs (Christensen, 1995). It is also affected by the system's number of trophic levels, the amount of cycling, and the model's resolution and complexity (Finn, 1980). Finally, the system omnivory index (SOI) was used to understand the degree to which consumers feed across multiple trophic levels, with a high SOI reflecting trophic complexity (Libralato, 2008).

Energy transfer across trophic levels was assessed using the Lindeman trophic spine, which simplifies complex food webs to a linear chain (Lindeman, 1942). The Lindeman spine enables the tracking of energy as it moves from producers to higher trophic levels, and quantifies energy losses due to respiration, export, or transfer to detritus. From this, trophic transfer efficiency (TE) was calculated to quantify how much energy passes across trophic levels in a linear food chain, and how much is diverted to detritus (Christensen et al., 2005; Christensen et al., 2005). To compare the SOR model with other published models covering adjacent areas, the Southern Bight of the North Sea (Pint et al., 2024) and the Greater North Sea (Mackinson and Daskalov, 2007) models we used the following robust indicators based on the total system throughput (TST), which is the total of all energy flows in the food web, as identified by Heymans et al. (2016) for comparing different marine ecosystem models. These indicators are all based on total system throughput (TST), total primary production to TST (PP/TST), consumption to TST (Q/TST), flow to detritus to TST (FD/TST), and export to TST (EX/TST) (Table S6).

2.4.1. Mixed trophic impact (MTI) and keystone analysis (KS)

The Mixed Trophic Impact (MTI) was originally developed by Leontief (1951) and implemented in Ecopath with Ecosim (EWE) by Ulanowicz and Puccia (1990). It describes the combined direct effects (e.g., predation) and indirect interactions (e.g., competition) among groups in the food web (Eq. (5)). MTI quantifies the positive or negative relative impact that a change in the biomass of one group has on other groups, based on prey-predator interactions (Ulanowicz and Puccia, 1990; Christensen et al., 2005), and is calculated as follows:

$$MTI_{ji} = DC_{ji} - FC_{ij} \tag{5}$$

where DC_{ji}(Diet Composition) represents the proportion of the prey group i in the diet of predator group j, and FC_{ij} indicates the proportion of total mortality of the prey i, that is caused by predator j.

Keystone groups are defined as functional groups or species with relatively low biomass and a functioning and structuring role in shaping the food web (Power et al., 1996). Keystone groups were identified using the keystoneness index proposed by Libralato et al. (2006) index (Eq. (6)):

$$KS_i = log[E_i(1 - p_i)] \tag{6}$$

Where E_i is the total trophic impact of group *i* on all other groups in the food web, and p_i is the biomass proportion of the species to the total biomass of the food web. This index integrates both the magnitude of trophic impact and the relative biomass of each functional group. Following the keystoneness analysis, KS values were interpreted together with the relative biomass of the functional groups. Groups with high keystoneness and low relative biomass were considered keystone groups. In contrast, groups with high trophic impact and relatively high biomass were interpreted as key or structuring groups because of their important roles in ecosystem functioning and energy flow (Piraino and Fanelli, 1999).

3. Results

3.1. Food web trophic organization, structure, and energy flow

The balanced Ecopath model included 44 functional groups spanning four trophic levels (TLs) (Fig. 2; Table 2). The basal trophic level of the food web was formed by phytoplankton and particulate and dissolved organic detritus, which together provided the foundation for energy input into the system. The ecotrophic efficiency for detritus was high (DOM = 0.93; POM = 0.72), while phytoplankton had a low EE of 0.26. Groups with TLs between 2.0 and 2.5 included herbivorous zooplankton, benthic and pelagic invertebrates feeding mainly on detritus, phytoplankton, and ingested bacteria. These groups consisted of both suspension feeding bivalves (e.g., *Dosinia exoleta, Ensis leei,* and *Ensis ensis*), and deposit feeding bivalves (e.g., *Fabulina fabula* and *Abra alba*), as well as suspension feeding polychaetes (e.g., *Lanice conchilega,* and *Polycirrus medusa*), deposit feeding echinoderms (e.g.,

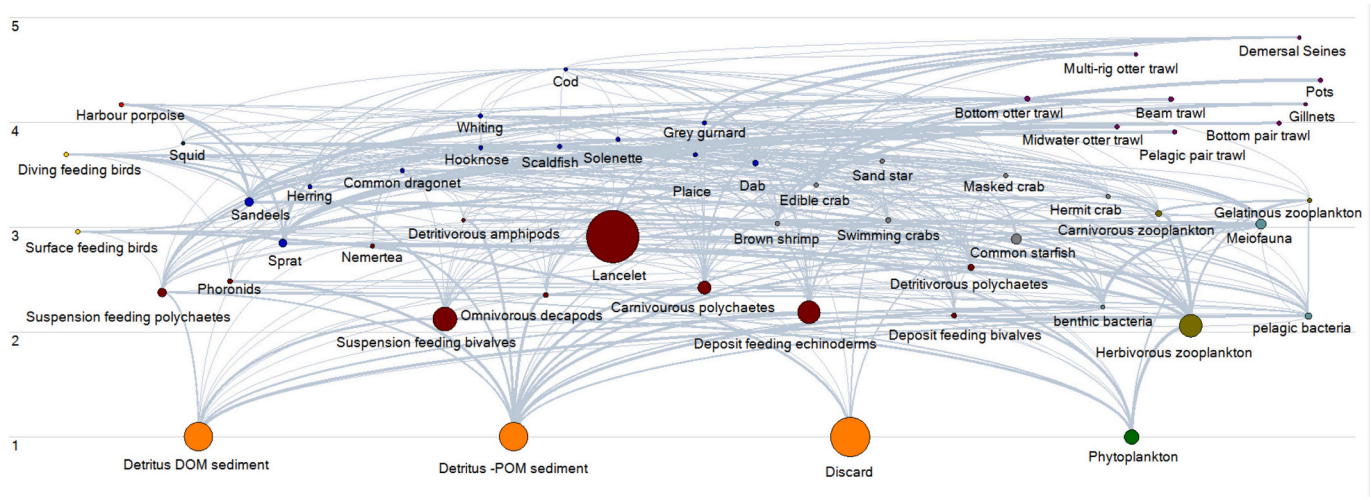

Fig. 2. Food web diagram of the MPA Sylt Outer Reef. The size of the circle is proportional to the group's biomass, and the lines represent the flow of energy between groups. The trophic level is represented on the y-axis. Taxonomic groups are colour-coded as follows: orange for detritus, green for phytoplankton, olive green for zooplankton, light blue for bacteria and meiofauna, brown for infauna, grey for epifauna, blue for fish, red for mammals, and yellow for birds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Echinocardium spp. and *Echinocardium pennatifidun*), and phoronids. The detritivorous and carnivorous polychaetes, phoronids, and deposit- and suspension-feeding bivalves showed relatively high ecotrophic efficiencies (EE $>$ 0.6), except for the lancelet, whose EE was exceptionally low (0.01) due to its high biomass and limited predation.

Intermediate trophic levels (TL $\approx$ 2.8–3.8) were constituted by planktivorous fish, predatory and omnivorous invertebrates, small demersal fish, and zooplankton. These include common starfish, *Nemertea,* brown shrimp, gelatinous and carnivorous zooplankton, and decapods such as masked crab, hermit crab, and edible crab. Groups of sea birds ranged from (TL 2.9) for surface feeding- birds to (TL 3.7) for diving feeding- birds. Demersal fish, such as the common dragonet, plaice, and dab, occupied TLs of 3.6. Other small pelagic fish, such as sprat (TL 2.8) and herring (TL 3.38), were also presented in the mid trophic level. Dominant predatory fish and marine mammals, such as the grey gurnard, whiting, harbour porpoise, and cod, occupied the highest trophic level (3.99–4.5). This trophic structure is consistent with the typical fundamental TLs of marine food webs (Fig. 2).

The Lindeman spine indicated that most of the energy flow in the SOR food web occurred at the first trophic level, with detritus and primary producers contributing up to 33.4% and 20.42% of TST, respectively. In contrast, the second trophic level (TL2) accounted for 36.92% of TST and 51.24% of the total biomass excluding detritus (Fig. 3). The functional groups with high biomass at TL 2 included the lancelet *B. lanceolatum* (101 t km^{-2}), suspension feeding bivalves (17.75 t km^{-2}), deposit feeding echinoderms (16.35 t km^{-2}), and herbivorous zooplankton (16 t km^{-2}) (Table 2). The TL3 accounted for 31.95% of total biomass and 7.6% of TST. Among the groups with high biomass, sandeels had the highest estimated biomass (3 t km^{-2}), followed by carnivorous zooplankton (1.11 t km^{-2}), meiofauna (4 t km^{-2}), and dab (1.07 t km^{-2}). The groups in the food web with the lowest biomass were detritivorous amphipods (0.0015 t km^{-2}) and cod (0.0038 t km^{-2}). The estimated mean transfer efficiency (TE) from primary producers was 10.54%, from detritus 16.90%, and the total transfer efficiency was 16.26% (Table 3).

In terms of fisheries, the four most intensively exploited groups were sandeels (0.48 t km^{-2}), sprat (0.31 t km^{-2}), brown shrimp (0.34 t km^{-2}), plaice (0.09 t km^{-2}), and dab (0.06 t km^{-2}) (Table 2). Bottom trawls and pelagic pair trawls mainly target sandeels and sprat (Table 2). Brown shrimp is targeted mainly by beam trawl, whereas brown shrimp, dab, and plaice were the most discarded species (Tables S2 and S3). Overall, the highest fisheries catches were associated with beam trawl, bottom otter trawl, and pelagic pair trawls. Functional groups such as brown shrimp, herring, whiting, sandeels, and plaice exhibited a high EE value ranging from 0.9 to 0.99.

3.2. Mixed trophic impact and keystone analyses

The mixed trophic impact (MTI) analyses showed both positive and negative impacts of one group on another in the ecosystem (Fig.4). The analyses indicated negative impacts of intraspecific competition and predation pressure on benthic fauna, particularly benthic invertebrates such as crustaceans, echinoderms, bivalves, and polychaetes. On the other hand, detritus POM and DOM had a positive impact on many pelagic and benthic groups, supporting the growth of various marine groups. Carnivourous polychaetes had a strong negative impact on their prey, including phoronids, detritivorous polychaetes, and suspension-feeding bivalves. Moreover, diving- feeding birds had strong direct negative impacts on sandeels. In turn, sandeels positively impacted top predators such as diving and surface-feeding birds and harbour porpoises.

Commercial fishing fleets impacted species across a wide range of trophic levels (2.8–4.48). For example, beam trawl had a relatively strong impact on several species, including brown shrimp, dab, plaice, and cod. Additionally, pelagic pair trawl, midwater trawl, and bottom otter trawl had a negative impact on demersal fish. Demersal seines showed a substantial negative impact on grey gurnard.

Keystoneness analysis (Table 4; Fig. 5) identified several functional groups with high ecological impact within the SOR food web. Carnivourous polychaetes showed the highest keystone index (KS = −0.06) and relative total impact (RTI = 1), followed by phytoplankton (KS = -0.08), diving-feeding birds (KS = -0.08), sandeels (KS = -0.11), herbivorous zooplankton (KS = -0.15), and harbour porpoise (KS = -0.18). These groups comprised both potential keystone groups and biomass-dominant groups that play important structuring roles within the food web.

3.3. Ecological indicators

The model's output parameters (Table 5) indicated that the total community biomass excluding detritus was 191.59 t km-^{2}, and the total system throughput (TST) was 10,930.05 t km-^{2}. yr^{-1}). The total consumption, respiratory flow, and flow to detritus represented 48%, 13%, and 38% of the TST, respectively. The primary production flow was 19%

Table 2
Basic estimates of the trophic model of the MPA Sylt Outer Reef: Group name, trophic level (TL); biomass (B; t km^{-2}), production/biomass ratio (P/B; y^{-1}), consumption/biomass ratio (Q/B; y^{-1}), ecotrophic efficiency (EE), production/consumption (P/Q; y^{-1}), biomass accumulation (BA; t km^{-2}), fisheries catch (C; t km^{-2} $year^{-1}$). Ecopath estimated the values in bold.

ID	Group name	TL	B	P/B	Q/B	EE	P/Q	BA	C
1	Surface feeding birds	2.96	0.03	0.10	75.73	**0.00**	**0.00**	0	
2	Diving feeding birds	3.70	0.14	1.12	66.00	**0.00**	**0.02**	0	
3	Harbour porpoise	4.17	0.01	0.02	17.63	**0.00**	**0.00**	0	
4	Squid	3.80	0.01	4.00	20.00	**0.82**	**0.20**	0	0
5	Herring	3.39	0.38	0.61	4.59	**0.98**	**0.13**	0	0.03
6	Cod	4.51	0.0038	0.42	2.58	**0.61**	**0.16**	0	0
7	Sandeels	3.24	**3.00**	2.28	10.10	0.90	**0.23**	0	0.48
8	Sprat	2.85	2.67	0.81	8.00	0.66	**0.10**	0	0.31
9	Whiting	4.06	0.01	0.50	2.60	0.96	**0.19**	0	0
10	Common dragonet	3.54	0.03	0.69	6.10	0.31	**0.11**	0	0
11	Hooknose	3.76	0.03	1.42	3.70	0.02	**0.38**	0	0
12	Grey gurnard	4.00	0.04	0.26	3.70	0.49	**0.07**	0	0.01
13	Scaldfish	3.77	0.02	1.42	3.70	0.09	**0.38**	0	0
14	Solenette	3.84	0.08	1.42	3.70	**0.66**	**0.38**	0	0
15	Plaice	3.69	0.39	0.31	3.42	**0.95**	**0.09**	0	0.09
16	Dab	3.61	1.08	0.37	3.69	**0.57**	**0.10**	0	0.06
17	Brown shrimp	3.04	**0.09**	4.62	**15.42**	0.99	0.30	0	0.34
18	Edible crab	3.40	0.08	1.98	**9.88**	0.37	**0.20**	0	0.04
19	Swimming crabs	3.06	0.66	0.55	**2.77**	**0.62**	0.20	0	
20	Masked crab	3.49	0.14	0.55	**2.77**	**1.00**	0.20	0	
21	Hermit crab	3.29	0.32	0.60	**3.00**	**0.74**	0.20	0	
22	Sand star	3.63	0.29	0.70	**3.50**	**0.72**	0.20	0	
23	Common starfish	2.89	4.20	0.23	**1.15**	**0.50**	0.20	0	
24	Phoronids	2.48	0.46	1.30	**4.33**	**1.00**	0.30	0	
25	Nemertea	2.82	0.26	0.60	**2.00**	**0.06**	0.30	0	
26	Detritivorous amphipods	3.07	0.0015	2.80	**9.34**	**0.61**	0.30	0	
27	Lancelet	2.91	101.10	1.08	**3.60**	**0.01**	0.30	0	
28	Omnivorous decapods	2.35	0.58	1.25	**4.18**	**0.88**	**0.30**	0	
29	Detritivorous polychaetes	2.62	1.44	1.97	**6.55**	**0.83**	0.30	0	
30	Carnivourous polychaetes	2.42	6.32	2.30	**7.66**	**0.59**	0.30	0	
31	Suspension feeding polychaetes	2.38	2.91	1.84	**6.13**	**0.34**	0.30	0	
32	Deposit feeding echinoderms	2.19	16.35	0.83	**2.76**	**0.13**	0.30	0	
33	Deposit feeding bivalves	2.16	0.48	1.73	**5.78**	**0.67**	0.30	0	
34	Suspension feeding bivalves	2.13	17.75	0.55	**1.84**	**0.98**	0.30	0	
35	Gelatinous zooplankton	3.26	0.07	2.86	**6.35**	**0.10**	0.45	0	
36	Herbivorous zooplankton	2.06	16.00	9.20	30.00	**0.35**	0.31	0	
37	Carnivorous zooplankton	3.13	**1.12**	4.00	**12.50**	0.99	0.32	0	
38	Meiofauna	3.03	**4.01**	35.00	125.00	0.99	0.28	0	
39	pelagic bacteria	2.16	1.46	571.00	**1142.00**	**0.53**	0.50	0	
40	benthic bacteria	2.24	0.11	9470.00	18,940.00	**0.71**	0.50	0	
41	Phytoplankton	1.00	7.50	286.67		**0.26**		0	
42	Detritus DOM sediment	1.00	25.00			**0.94**		103.091	
43	Detritus -POM sediment	1.00	25.00			**0.72**		681.189	
44	Discard	1.00	50.00			**0.02**		0	

of TST, and the export flow out of the system was very low (0.00013 t km^{-2}. yr^{-1}). Furthermore, the total net primary production (NPP) was (2150 t km^{-2}. yr^{-1}), and the ratio of total primary production to total respiration (TPP/TR) was 1.47. The system showed a low degree of organization, with a relative ascendency (A/C; 22.73%) compared to its capacity to buffer perturbations (O/C; 77.27%), and an omnivory index of 0.3. Approximately one-third of the system's energy was recycled, as indicated by Finn's cycle index (FCI) of 32.79%, and Finn's mean path length (APL) was 7.4. Finally, the mean trophic level of the catch (MTL) was 3.15, and the pedigree index was 0.4.

4. Discussion

4.1. Holistic view of the food web structure and functioning of the Sylt Outer Reef

The balanced Ecopath model provided the first detailed description of the Sylt Outer Reef food web structure and functioning, which comprises 44 recognized functional groups spanning trophic levels from 1.0 to 4.5. The model integrates diverse pelagic and benthic components connected through both grazing and detritus-based food chains. The import of non-living material was not explicitly included, as the information available on-import and export of detritus and other compartments from outside the Sylt Outer Reef is thin. Thus, the fate to detritus and discards was defined to be the unassimilated biomass from the functional groups, which was assumed to partition proportionally into particulate organic matter (POM) and dissolved organic matter (DOM) and to represent the principal pathways by which organic matter is retained and recycled within the system (Table S3). Most fish groups in the model were represented at the species level, and benthic invertebrates were aggregated into 20 functional groups. The improved resolution of the benthic groups is important in the SOR, where functional groups such as detritivorous polychaetes, deposit-feeding bivalves, swimming crabs, and brown shrimp obtain their primary energy from detrital particles (POM and DOM), supporting the dominant role of detritus-based pathways in structuring the energy flow of the system. This improved inclusion of these functional groups enhances the link between living and non-living compartments, and the relatively high ecotrophic efficiencies observed for these groups (EE $>$ 0.60) further indicate that a large fraction of their production is utilized within the food web (Table 1), supporting their role in energy transfer to higher trophic levels. The important role of these complex macrobenthic communities in the North Sea has been recognized, as they increase the complexity of trophic interactions and support the stability of the food

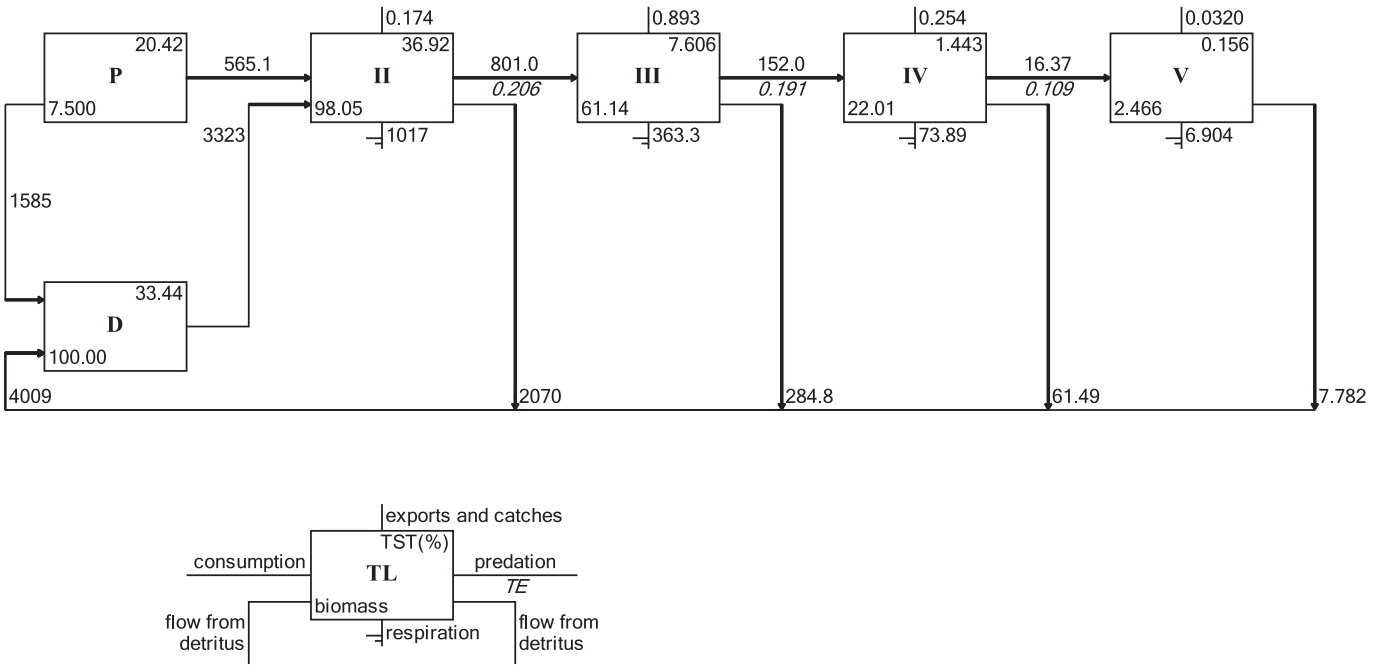

Fig. 3. Lindeman's spine diagram of the SOR model. P: Primary producers, D: Detritus; TST, Total system throughput, TL: Trophic level, TE: Trophic efficiency.

Table 3
Transfer efficiency (mean values) from different trophic levels of the Sylt Outer Reef ecosystem.

Source \ Trophic level	TE
Transfer efficiencies (calculated as geometric mean for TL II-IV)	
From primary producers:	10.54%
From detritus:	16.90%
Total:	16.26%

chain web (Sokołowski et al., 2012). The functional role of benthic invertebrates is highlighted by the presence of key bioturbators such as *Echinocardium* spp., which enhance recycling of organic matter in the sediment and transfer energy-rich food to higher trophic levels (Wrede et al., 2017; Beermann et al., 2023).

The model also highlights the ecological importance of suspension and filter feeders, such as suspension-feeding bivalves and polychaetes, in supporting the grazing food chain as prey for benthivorous fish (Table S5). It also applies to small planktivorous fish (e.g., sprat, sandeels, herring) that feed mainly on zooplankton, and constitute a major prey for predatory fish and birds in the area (Table S5). However, the results show that the lancelet (*B. lanceolatum*) had the highest biomass in the system (101 t km-2), and the limited ecological information on this species in the SOR and particularly on its predators introduces uncertainty in the representation of the trophic link of *B. lanceolatum*. Consequently, a high proportion of its production remained unused (EE = 0.01; Table 1). Future studies focusing on the role of the lancelet in the food web could substantially improve models for areas where the biomass is dominated by this species.

The improved representation of benthic invertebrates, therefore, influences energy flows in the system. The mean transfer efficiency (TE) of the SOR (16.26%; Table 4) exceeds the theoretical (10%) benchmark suggested by Pauly and Christensen (1995) and aligns more closely with the average TE values reported for ecosystems such as the Greater North Sea and the Irish Sea (Lees and Mackinson, 2007; Mackinson and Daskalov, 2007). Notably, TE from detritus (16.90%) surpasses that of primary production (10.54%), likely due to the inclusion of microbial groups and a better representation of detritus groups, and the benthic detritivores and deposit feeders. This enhances the recycling of particulate and dissolved organic matter, making energy more accessible to their predators. Consequently, the food web of the SOR is primarily detritus-driven, supporting a diverse array of groups that contribute to the overall system throughput. While reliance on detritus dynamics enhances ecosystem stability (Moore et al., 2004), long-term modification of detrital input or dynamics can reshape benthic communities, influence system energy reserve, and alter the structure of the food web (Essink, 1999; Jorge-Romero et al., 2019).

4.2. Comparison between the models of the Sylt Outer Reef, Southern Bight of the North Sea, and the Greater North Sea

A general assessment of the Sylt Outer Reef model was made by comparing it with models of the Southern Bight of the North Sea (SBoNS; Pint et al., 2024) and the Greater North Sea (GNS; Mackinson and Daskalov, 2007), using the most robust ecosystem-level indices recommended for comparative analysis (Heymans et al., 2014; Table 5). The Ecopath model generates a range of ecosystem-level outputs, which are sensitive to model structure, spatial scale, and input resolution and must, therefore, be interpreted cautiously (Christensen et al., 2005). However, ecosystem biomass, total system throughput (TST), and TST-based indicators are recognized to be robust indicators of the ecosystem's overall size and function (Heymans et al., 2014). The total system throughput, which measures the size and activity of the food web (Ulanowicz, 1986), were lower in the SOR (TST; 10,930.58 t km^{-2}. $year^{-1}$) and in the SBoNS (TST; 10,248.01 t km^{-2}. $year^{-1}$) than in the GNS (TST; 12,150.01 t $km^{-2.}$ $year^{-1}$). The SBoNS and SOR are smaller sub-regions and shallower areas of GNS, with a maximum water depth in southeastern North Sea of 50 m depth (Stäbler et al., 2018). The difference is probably due to the GNS having a larger spatial extent, greater depth, and greater habitat complexity, which make its food web more productive. Most TST-based indicators are similar across the SOR, with comparable ratios such as Q/TST, FD/TST, PP/TST, and R/TST (Table 5). However, the relative export of biomass (Ex/TST) is almost four times lower in the SOR (0.12 0.10^{-3}; Table 5) than in the GNS and the SBoNS, as data on exports and imports between the SOR and other areas were not included. This may suggest that the SOR is a more retentive system and a larger fraction of energy is recycled internally rather than exported, or it may reflect a bias in model construction. This

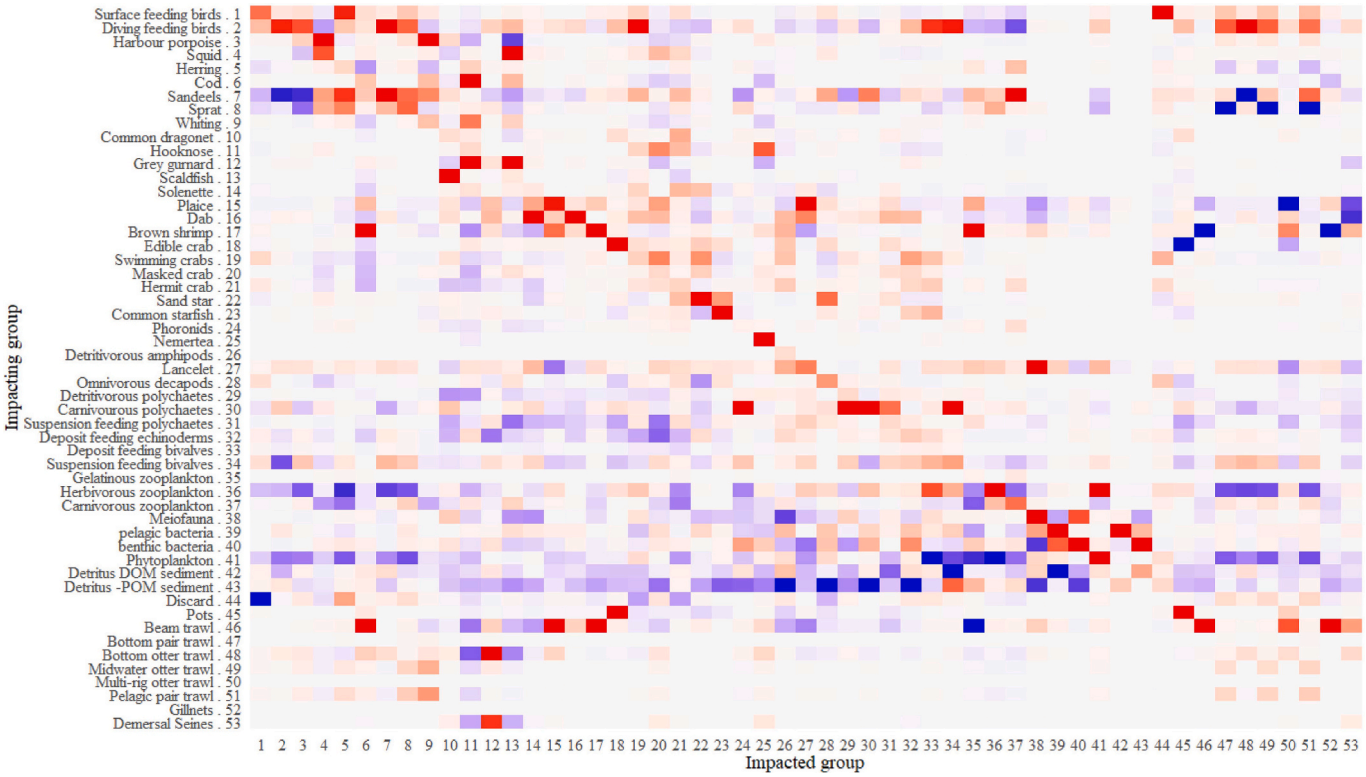

Fig. 4. Mixed trophic impact matrix of the MPA Sylt Outer Reef. Impacted groups are shown on the x-axis, and the impacting groups are shown on the y-axis. Positive impact (blue) and negative impact (red). The colour's transparency indicates the magnitude of the impact. Low transparency has a low impact. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Keystone index 1 (Libralato et al., 2006) for the group with a keystone index > −0.2.

ID	Group name	Keystone index #1	Relative total impact
30	Carnivourous polychaetes	−0.06	1
41	Phytoplankton	−0.08	0.96
2	Diving feeding-birds	−0.08	0.92
7	Sandeels	−0.11	0.87
36	Herbivorous zooplankton	−0.15	0.87
3	Harbour porpoise	−0.18	0.74

pattern is consistent with the results from the models analysed by Heymans et al. (2014) (Fig. 5 b), where relative exports tend to increase with the spatial extent of the ecosystem, in contrast to the Finn cycling index, which tends to be higher in smaller systems. Higher recycling (FCI) and longer cycles (APL) in the SOR (Table 5) further indicate that this system is self-reliant, with an extended energy pathway and robust matter recycling. This is important because systems, which recycle detritus more effectively, tend to be more resilient and recover better from disturbances (Vasconcellos et al., 1997).

A noticeable difference is the total biomass of the communities (excluding detritus), which is three times lower in the SOR model (Table 5). The difference is likely due to methodological differences rather than ecological contrasts, as the SOR model biomass values for the infauna, epifauna, and fish are based on locally collected, field-sampled data for each group (see section 2.2.3), whereas the larger-scale models rely more on averaged biomass datasets (c.f. Mackinson and Daskalov, 2007; Pint et al., 2024).

Three ratio indicators, relative ascendency (A/C), relative overhead (O/C), and the system omnivory index (SOI), were also used for comparison because these metrics are unaffected by network size or complexity (Heymans et al., 2014; Baird et al., 2009). The three models had low relative ascendency (A/C) and high relative overhead (O/C), indicating low predictability in energy flows, as numerous alternative routes exist for energy to move from primary producers to higher trophic levels. This indicates that the food web of the SOR is sustained by a wide range of first- and second-order consumers using similar food sources, which together facilitate energy transfer and buffer the ecosystem against disturbances (Ulanowicz, 1980; Lewis et al., 2001). The aggregated functional groups of the SOR model at lower trophic levels, such as the keystone groups, carnivorous polychaetes, which feed on a variety of benthic and pelagic prey (e.g., phytoplankton, DOM, POM, discards, and infauna), and planktivorous fish (e.g., sandeels, sprat, herring), that primarily consume zooplankton and phytoplankton, together link primary producers and benthic production simultaneously to predatory fish, birds, and crustaceans through numerous parallel routes. In this context, high overhead enables mid- and top-predator species to access redundant prey resources, thereby increasing the robustness of the food web. Therefore, the SOR likely is resilient, with more alternative pathways for energy and biomass flow, reinforcing the complexity of its trophic interactions (Ulanowicz, 1986; Christensen, 1995; Fath et al., 2019). The system omnivory index (SOI) was calculated by averaging the omnivory index across all functional groups, thereby indicating the variance of the trophic levels in the predators' diets within the food web (Pauly et al., 1993). The SOI was higher in the SOR (0.3) than in the SOR of the SBoNS and the GNS (0.22; 0.26) and higher than in other systems such as the Mediterranean Sea (Coll et al., 2006), the Adriatic Sea (Coll et al., 2007), and the Portuguese continental shelf (Veiga-Malta et al., 2019) where SOI ranged from 0.19 to 0.22. This demonstrates that the SOR has more groups with an unspecialized diet (Pauly et al., 1993), and a web-like structure of trophic flows (Ulanowicz, 1986; Christensen, 1995), which further supports the high relative overhead in the system. The three food-web models are expressed in identical area-standardized units, represent systems of similar size, and highlight some similarities. However, the ability to draw broader conclusions

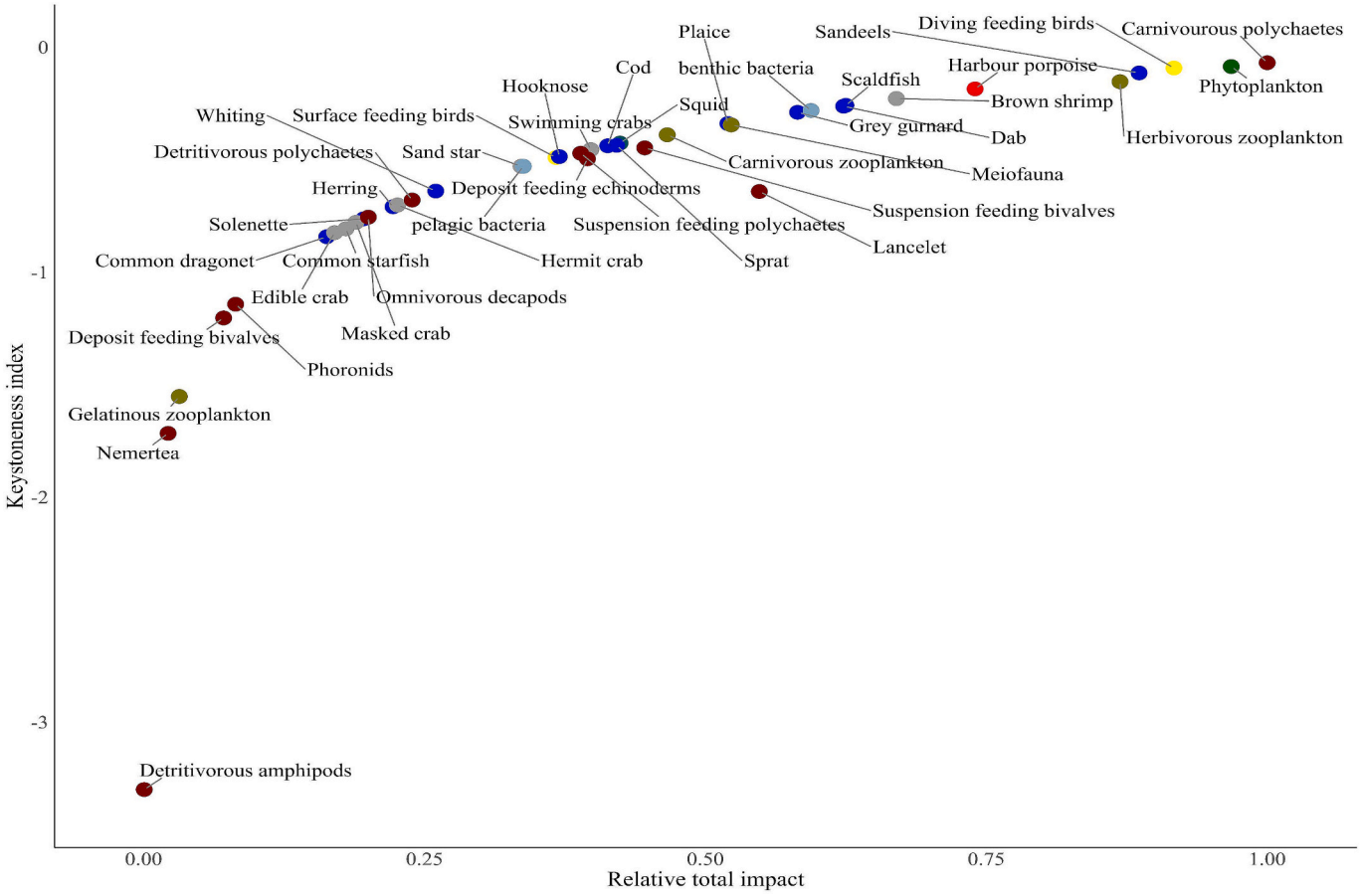

Fig. 5. Keystone index for the Sylt Outer Reef, keystone index vs Relative total impact. For the colour code, see the caption of Fig. 2.

from the models might be affected by different spatial extents and structure of the ecosystems, the time periods they represent, and underlying ecosystem characteristics. Ecosystem indicators from the SOR model provide only a temporal snapshot value, making it difficult to draw broad, conclusive interpretations of ecosystem stability and state. The use of multiple models across different time frames may allow for a more complete picture of ecosystem health and change over time, under different management measures. For example, a future model excluding bottom trawling, compared with the current model, would enable a holistic assessment of ecosystem changes before and after the exclusion of bottom trawling, given that a healthy ecosystem requires a balance between ascendency (the ability to maintain its organization) and overhead (resilience and adaptation to disturbances) (Costanza and Mageau, 1999; Ulanowicz, 2004; Ulanowicz, 2020).

4.3. Keystone groups, fisheries, and management implications

The results showed that none of the keystone functional groups had values close to or greater than zero (Libralato et al., 2006), indicating the absence of groups with high ecological impact relative to their biomass. Nevertheless, several functional groups showed relatively high relative total impact and were identified as either potential keystone groups or structuring groups within the SOR food web (Table 4; Fig. 5). The latter included carnivorous polychaetes, phytoplankton, herbivorous zooplankton, and sandeels, whereas diving-feeding birds and harbour porpoise were identified as potential keystone groups. Among the structuring groups, carnivorous polychaetes were identified likely due to their positive trophic impact, as shown in (MTI; Fig. 4). They feed on a variety of benthic prey across different trophic levels while they are preyed upon by different predatory fish and birds. Therefore, their trophic impact can extend through different trophic levels. Species in this group (e.g., *Nephtys caeca*) exert a regulatory influence through predation on other populations within their community (Caron et al., 2004). At the mid-trophic level, sandeels were identified as another important structuring group. They derive their energy from a broad range of zooplankton and, in turn, constitute a major prey for many fish, birds, and mammals. Several predators in the North Sea are trophically highly dependent on sandeels as prey, such as the black-legged kittiwake (*Rissa tridactyla)* and the harbour porpoise (*Phocoena phocoena*). Both species are threatened and declining in the North Sea (Reilly et al., 2014; Lewis et al., 2001). The ecological importance of sandeels is further emphasized by their role as conduits for energy transfer from zooplankton to top predators, as is the case for other forage fish (e.g., sprat, herring), emphasizing the need for efficient control of sandeels, which is the most intensively fished species in the SOR. So far, the identified keystone and structuring key groups suggest that the ecosystem of the SOR is primarily bottom-up-regulated, where predators are limited by the availability of their prey (Reilly et al., 2014). In ecosystems with bottom-up limitations, a decline in key species, such as sandeels and forage fish, can severely affect predators, especially predators with limited capacities to exploit alternative food sources (Rindorf et al., 2000; Daunt et al., 2008; Yaragina and Dolgov, 2009; Reilly et al., 2014). However, the identification of keystone groups, such as diving-feeding birds and harbour porpoise, with high trophic levels (3.5–4.17; Fig. 5, Table 4) might also indicate top-down effects within the food web. These findings highlight that maintaining prey availability and the integrity of low trophic levels is essential for sustaining higher trophic levels, including commercially and ecologically important predators. The SOR is ecologically significant for its high benthic faunal diversity (Hahn et al., 2022) and provides crucial habitat for numerous

Table 5
Comparison between the Sylt Outer Reef food and other North Sea models using ecological network analysis, Odum (1969) attributes as calculated by Christensen (1995), with robust indicators as suggested by Heymans et al. (2014).

Area	Sylt Outer Reef (SOR)	The Southern Bight of the North Sea (SBoNS)	The Great North Sea (GNS)
Model characteristics			
Area (km^2)	6503 km^2	63,633 km^2	570,000 km^2
Depth range (m)	8–48 m	<50 m	50 m – 100 m
Number of groups	44	43	68
Ecosystem properties ($t.km^{-2}.year^{-1}$)			
Total system throughput	10,930.01	10,248.01	12,150.01
Total biomass of the community	191.34	569.26	551.8
Total net primary production	2150	2150	2150
total primary production/total respiration	1.47	No data	1.11
total primary production / total Biomass	11.23	3.77	3.89
Total export/Total system throughput	0.13 0.10^{-3}	$0.44 \cdot 10^{-3}$	$0.46 \cdot 10^{-3}$
Total consumption/ Total system throughput	0.48	0.48	0.51
Total respiration/ Total system throughput	0.13	0.2	0.16
Flows to detritus / Total system throughput	0.38	0.32	0.32
Primary production/ Total system throughput	0.19	0.21	0.17
Food web structure			
Relative Ascendency	22.73	23.63	21.2
Relative Overhead	77.27	76.37	78.74
System omnivory index	0.30	0.22	0.26
Finn's cycle index	32.79	25.25	20.24
Finns' mean path length	7.4	No data	No data
Fishery indices			
Mean trophic level of the catch	3.15	3.55	3.6
Information index			
The pedigree index	0.4	No data	No data

species, including seabirds such as Kittiwakes (*Rissa tridactyla*), marine mammals such as harbour porpoise (*Phocoena phocoena*) and harbour seal (*Phoca vitulina*), and numerous fish. Notably, it serves as a nursery ground and migration corridor, particularly for harbour porpoises with juveniles (Bundesamt für Naturschutz (bfN), 2020). Management measures, including the exclusion of bottom trawling in large parts of the SOR, have been implemented to safeguard habitat types and to achieve a favourable conservation status for species such as harbour porpoise and seabirds (Article 11 and 18 No 1380/2013). Bottom trawling was banned in large parts of the area in March 2023, while other pressures still persist (EU Regulation 2023/340). These management measures could also help preserve the overall ecosystem structure and function and should address the protection of keystone and key structuring species across different trophic levels, which is crucial for ensuring ecosystem resilience and stability and for improving conservation status. In this study, a first step toward developing a baseline model for ecosystem-based management in the SOR was taken.

4.4. Model limitations and future implications

The SOR food-web model was developed as a baseline representation of the marine protected area, as a snapshot for the time period from 2010 to 2020. Biomass estimates for major taxonomic groups were obtained either from local sampling campaigns or from a regional model with spatial overlap with the SOR. However, temporal inconsistencies arise because the biomass of different functional groups was sampled at different time frames. For example, biomass of infaunal benthos and pelagic fish were sampled at high-resolution from 2014 to 2018, and pelagic fish data are similarly restricted (see Supplementary Material for methodological details), whereas biomass data for demersal fish and benthic epifauna cover the full period of 2010–2020. Moreover, the infauna was sampled in different areas of the SOR in different years. Hence, the period with the most complete data coverage was selected for the model. Catchability limitations of the beam trawl survey likely underestimated the biomass of species such as sandeels and brown shrimp. These inputs were thus estimated by Ecopath. Although dietary information is relatively well documented for certain groups of fish, mammals, or some invertebrate species (e.g., Hinz et al., 2005; Schückel et al., 2012; Jansen et al., 2013), it remains limited or generalized for many invertebrate groups, as no local dietary data is available and no experiments were conducted. Likewise, data on lower trophic groups, such as detritus, bacteria, meiofauna, and zooplankton, are scarce, despite their recognized importance in nutrient cycling and energy transfer (De Jonge et al., 2006; Van Der Heijden et al., 2020); Improved monitoring of these compartments would substantially enhance future food-web analyses. Fishery landings and discard data were obtained from the EU Data Collection Framework (DCF) and Fisheries Dependent Information (FDI) (European Commission, 2025). These data are reported by administrative boundaries and reflect multinational fishing activities, thereby limiting access to local catch data. Therefore, the catch was assumed to be evenly distributed and normalized based on ICES squares and the proportion of the catch allocated to the MPA. This introduces additional uncertainty, and related results should accordingly be interpreted with caution. Note that model accuracy generally depends on the availability and quality of data (Plagányi, 2007). Consequently, following Heymans et al. (2016) advice to quantify input uncertainty, a pedigree index was used to evaluate the data quality. The relatively low pedigree of the SOR is primarily due to limited empirical information available for benthic invertebrates (Table 5), particularly regarding Q/B ratios and diet composition, compared with better-studied fish and vertebrate groups. Nevertheless, it is noteworthy that the improved functional resolution of benthic compartments enhances the representation of ecosystem structure and trophic pathways, despite data limitations.

5. Conclusion

The German Marine Protected Area Sylt Outer Reef - Eastern German Bight (SOR) is a highly heterogeneous area, with different habitats and species with diverse feeding traits. Trophic flow analysis indicates that the SOR is dominated by low trophic levels and strong benthic recycling, with detritus playing a key role in supporting the system's productivity. The greater use of both dissolved organic matter (DOM) and particulate organic matter (POM) highlights the improved resolution and representation of low-trophic-level groups. Consequently, the food web of the SOR is primarily detritus-driven, making the ecosystem sensitive to bottom trawling and to long-term alterations in detrital input (Mutsert et al., 2012; Jorge-Romero et al., 2019; Pezy et al., 2018).

The comparison with the Southern Bight of the North Sea (SBNoS) and the Greater North Sea (GNS) indicates that the SOR has comparably high internal recycling and longer energy-flow pathways, which makes it a self-reliant system with robust matter recycling. The low relative ascendency and high relative overhead suggest that the ecosystem is potentially robust to disturbances, but lacking specialized pathways.

The SOR also showed a relatively higher omnivory index (SOI), suggesting greater feeding generalization and a complex trophic structure.

The keystone analysis identified both keystone groups and important key groups within the SOR food web. Diving-feeding birds and harbour porpoise were identified as keystone groups, whereas carnivourous polychaetes, phytoplankton, herbivorous zooplankton, and sandeels emerged as key structuring groups. The forage and benthivorous fish, such as sandeels, sprat, plaice, and brown shrimp, are highly targeted in the area. The Ecopath model presented in this study is the first trophic food web model developed for this marine protected area and incorporates the most complete biological dataset to date. Nonetheless, many uncertainties remain regarding the diet composition and life history of some functional groups. This model provides a baseline for understanding the structure and functioning of the SOR and will be used to assess the effectiveness of management measure through temporal simulations.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

The drafted paper was checked using Grammarly Pro (Grammarly Inc., 2025) to check readability, spelling, and grammar. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Chaimae Slila: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sabine Horn:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Miriam Püts:** Writing – review & editing, Validation, Supervision, Methodology, Formal analysis, Conceptualization. **Holger Haslob:** Writing – review & editing, Resources. **Jan Beermann:** Writing – review & editing, Resources. **Marie-Catherine Riekhof:** Writing – review & editing, Supervision. **Lars Gutow:** Writing – review & editing, Resources. **Karen Helen Wiltshire:** Writing – review & editing, Validation, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2026.102724.

Data availability

The authors do not have permission to share data.

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