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Ecopath with Ecosim for the Baltic Sea (ICES SD 22-32 excluding the Gulf of Riga)

Model description

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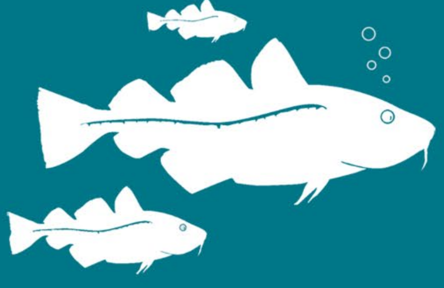

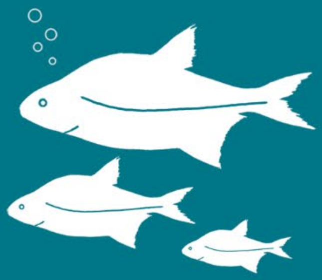

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Sammanfattning

Östersjön är ett ekologiskt unikt brackvattenekosystem med kraftiga salthalts- och temperaturgradienter, låg biodiversitet samt omfattande områden med syrebrist. Dessa naturliga begränsningar, i kombination med antropogena effekter såsom övergödning, föroreningar, överfiske och klimatförändringar, gör Östersjön till ett särskilt sårbart marint system.

För att bättre förstå och förvalta detta komplexa ekosystem utvecklade vi en omfattande Ecopath with Ecosim (EwE)-modell, som täcker nästan hela Östersjön (ICES delområden 22-32, exklusive Rigabukten). EwE är ett väletablerat verktyg som används för att simulera trofiska interaktioner, energiflöden och ekosystemets dynamik över tid under olika miljö- och förvaltningsscenarier.

Ecopath-komponenten ger en statisk, massbalanserad representation av ekosystemet för referensåret 2004 och omfattar 46 funktionella grupper som representerar primärproducenter, zooplankton, bentiska evertebrater, fisk (inklusive olika livsstadier), sjöfåglar och marina däggdjur. Tio fiskeflottor inkluderades för att spegla fiskets mångfald och dess påverkan. Ecosim-modulen utvidgar analysen över tid och simulerar ekosystemets respons på förändringar i fisketryck och produktivitet mellan 2004 och 2019.

Modellvalideringen visade att EwE effektivt återskapade historiska trender i biomassa och fångster för de flesta nyckelarter, särskilt sälar, torsk och sill. Vissa avvikelser, till exempel för skarpsill, nors och vikarsäl, belyser dock databegränsningar och behovet av förbättrad parameterisering eller inkludering av ytterligare ekologiska processer.

Den resulterande modellen representerar den första EwE-modellen som täcker hela Östersjöområdet och integrerar tidigare regionala modeller i en enhetlig rumslig och funktionell struktur. Modellen ger värdefulla insikter i ekosystemets funktion och trofiska samband och möjliggör en helhetsbedömning av kumulativa effekter från fiske och miljöförändringar.

Trots vissa begränsningar, såsom förenklad representation av lägre trofiska nivåer, brist på data för vissa grupper och dåliga passningar till observationer i vissa fall, utgör modellen en robust grund för ekosystembaserad fiskeriförvaltning (EBFM) och stödjer målen i havsmiljödirektivet (MSFD).

Framtida modellutveckling bör inkludera miljödrivande faktorer (salthalt, temperatur, näringsämnen), koppling till fysikalisk-biogeokemiska modeller, öka den rumsliga upplösningen (via Ecospace) samt integrera osäkerhetsanalyser och socioekonomiska dimensioner.

Summary

The Baltic Sea is an ecologically unique semi-enclosed brackish ecosystem, characterized by sharp salinity and temperature gradients, low biodiversity, and extensive hypoxic zones. These natural constraints, combined with human-induced pressures such as eutrophication, pollution, overfishing, and climate change, make it a particularly vulnerable marine system.

To better understand and manage this complex ecosystem, we have developed a comprehensive Ecopath with Ecosim (EwE) model covering nearly the entire Baltic Sea (ICES Subdivisions 22-32, excluding the Gulf of Riga). EwE is a well-established modelling framework used to simulate trophic interactions, energy flows, and temporal ecosystem dynamics under various environmental and management scenarios.

The Ecopath component provides a static, mass-balanced representation of the ecosystem for the reference year 2004, incorporating 46 functional groups representing primary producers, zooplankton, benthic invertebrates, fish (including multi-stanza life stages), seabirds, and marine mammals. Ten fishing fleets were included to reflect the diversity of fisheries and their impacts. The

Ecosim module extends the analysis temporally, simulating ecosystem responses to changing fishing pressure and productivity between 2004 and 2019.

Model validation showed that the EwE framework effectively reproduced historical biomass and catch trends for most key species, particularly seals, juvenile cod, and herring. However, discrepancies for some groups, such as sprat, smelt, and ringed seals; highlight data limitations and the need for refined parameterisation or inclusion of additional ecological processes.

The resulting model represents the first Baltic-wide EwE model, integrating previous regional efforts into a unified spatial and functional framework. It provides valuable insights into ecosystem functioning and trophic linkages, enabling holistic assessment of cumulative impacts from fishing and environmental change.

Despite certain limitations, such as simplified lower trophic level representation, missing data for some groups and misfit to some data, the model serves as a robust foundation for ecosystem-based fisheries management (EBFM) and supports Marine Strategy Framework Directive (MSFD) objectives.

Future model developments should integrate environmental forcing (salinity, temperature, nutrients), couple with physical-biogeochemical models, increase spatial resolution (via Ecospace), and incorporate uncertainty analyses and socio-economic dimensions.

Table of contents

1. Introduction

The Baltic Sea represents one of the most extreme environments for both marine and freshwater species due to its abiotic conditions. It is characterized by steep gradients in both temperature and salinity, creating a transitional zone that is challenging to many organisms adapted to either marine or freshwater environments (Ojaveer et al., 2010). The brackish nature of the sea limits the range of species able to thrive, resulting in naturally low biodiversity relative to other large marine ecosystems (Elmgren & Hill, 1997). Furthermore, extensive hypoxic and anoxic zones in deeper areas severely constrain benthic species and disrupt trophic linkages, as benthic invertebrates serve as critical prey for demersal fish and other predators (Conley et al., 2009).

This low biodiversity leads to a fragile food web structure in which species interactions are strong and functional redundancy is limited. Consequently, the removal or decline of a single species can disrupt ecosystem functioning due to the absence of other species capable of fulfilling similar ecological roles (Möllmann et al., 2009).

In addition to natural stressors, the Baltic Sea is subject to a multitude of anthropogenic pressures. These include eutrophication, introduction of pollutants and hazardous substances, overexploitation of commercial fish species, habitat degradation, and the overarching effects of climate change (HELCOM, 2023). The simultaneous occurrence of these stressors increases the risk of cumulative and potentially synergistic impacts on individuals, populations, and entire ecological communities (Crain et al., 2008; Griffiths et al., 2017).

To enhance our understanding of the structure, dynamics, and potential future vulnerabilities of the Baltic Sea ecosystem, we have developed a comprehensive Ecopath with Ecosim (EwE) model covering the entire region. EwE is a widely used modelling framework in marine ecology designed to simulate energy and biomass flows and to explore ecosystem responses under various management and environmental scenarios (Christensen & Pauly, 1992; Walters et al., 1997).

The Ecopath component of the model establishes a static, mass-balanced representation of the ecosystem, quantifying biomass and energy flows across trophic levels. Each functional group, ranging from primary producers to top predators, is parameterized by its biomass, production-to-biomass ratio (P/B), consumption-to-biomass ratio (Q/B), diet composition, and other ecologically relevant metrics. This mass-balance approach ensures that the energy gained and lost within the ecosystem remains consistent, allowing for the estimation of trophic efficiencies, predator-prey dependencies, and system-level indicators such as omnivory index and keystoneness (Christensen et al., 2005).

The Ecosim module extends this analysis by incorporating temporal dynamics into the model. It allows for simulation of how ecosystems evolve over time in response to internal ecological processes (e.g., reproduction, mortality, predation) and external drivers such as fishing pressure, nutrient loading, or climate variability. Ecosim enables scenario analysis, thereby supporting decision-making in ecosystem-based management by comparing the effects of alternative policy strategies and environmental change projections (Mackinson et al., 2009; Coll et al., 2015).

Through the EwE framework, our model offers a valuable tool for integrated assessments, facilitating the exploration of cumulative impacts and supporting adaptive management of the Baltic Sea ecosystem accounting for both natural and anthropogenic stressors.

This report presents progress in the Baltic Sea ecosystem modelling and introduces the first EwE model developed for the entire region. The model focuses on representing ecosystem dynamics, energy flows, and key ecological functions. A particular emphasis is placed on supporting ecosystem-based fisheries management, providing a scientific basis for sustainable exploitation and conservation strategies.

The model description is structured as follows: Chapter 2 presents descriptions of the functional groups, including their ecological roles, parameterization, and the species and components included in the Ecopath with Ecosim model. Chapter 3 describes the approach and the results of the Ecopath mass-balance model, providing insights into energy flows, trophic interactions, and ecosystem structure. Chapter 4 details the dynamic simulations from the Ecosim model, illustrating temporal changes in response to various natural and anthropogenic drivers. Finally, Chapter 5 offers a discussion of the strengths and limitations of the modelling approach and explores potential applications and future developments in light of current advances in ecosystem-based management and ecological modelling science.

1.1 Model domain

The model developed in this study builds upon experience of the previously published Ecopath with Ecosim (EwE) model for the Central Baltic Sea (Bauer et al., 2019). Spatial coverage is almost the entire Baltic Sea, described as ICES Sub-Divisions 22-32. This expanded model includes a broader range of environmental gradients and ecological conditions, excluding only the Gulf of Riga (Figure 1).

Such an extension allows for a more comprehensive investigation of ecosystem dynamics across diverse hydrographic regimes and species distributions.

By incorporating these additional areas, the model enhances the ability to address spatial variation in stock structures, trophic interactions, and ecosystem functioning. It provides an improved framework for exploring how differences in environmental conditions influence ecological processes and for assessing the potential implications for ecosystem-based fisheries management.

The Gulf of Riga was excluded from the model domain due to its distinct hydrological and ecological characteristics. This semi-enclosed sub-basin exhibits unique seasonal dynamics, stratification patterns, and species composition, which differ significantly from those observed in the broader Baltic Sea (Jansons et al., 2017; Strāķe et al., 2020). As such, it requires a separate, specifically tailored modelling approach to accurately represent its ecosystem functioning.

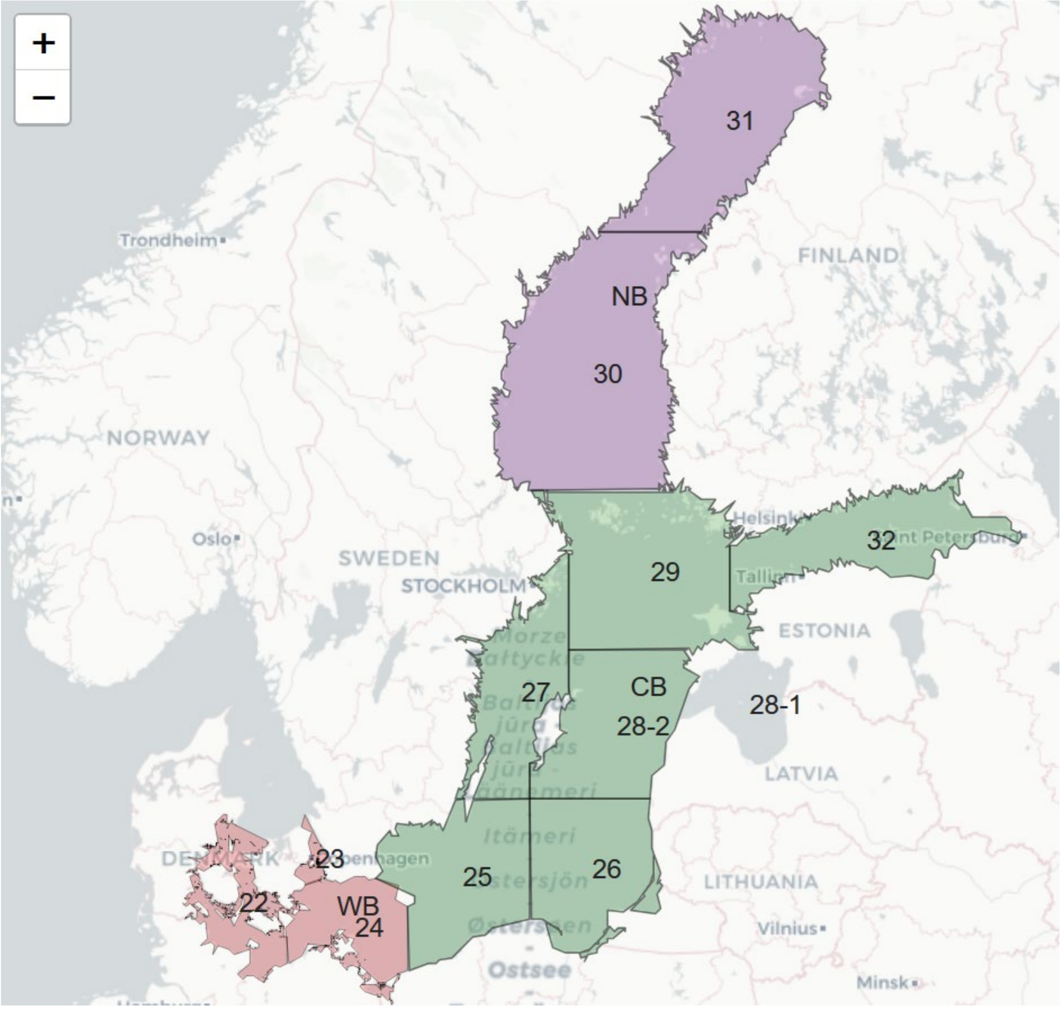

Figure 1.Map of the model area. Numbers correspond to the ICES Subdivisions (SDs). These are grouped into three parts based on similarity in environmental conditions and characteristic species, as noted by the colours: Western Baltic (WB, red), Central Baltic (CB, green), and Northern Baltic (NB, violet).

2. Functional groups description: ecology, parameters, components

In order to simplify complex food webs into manageable components, species in EwE models are organized into functional groups based on their ecological roles and trophic interactions. The functional groups incorporated in the present model (Figure 2) represent the most ecologically significant components of the open sea regions of the Baltic Sea.

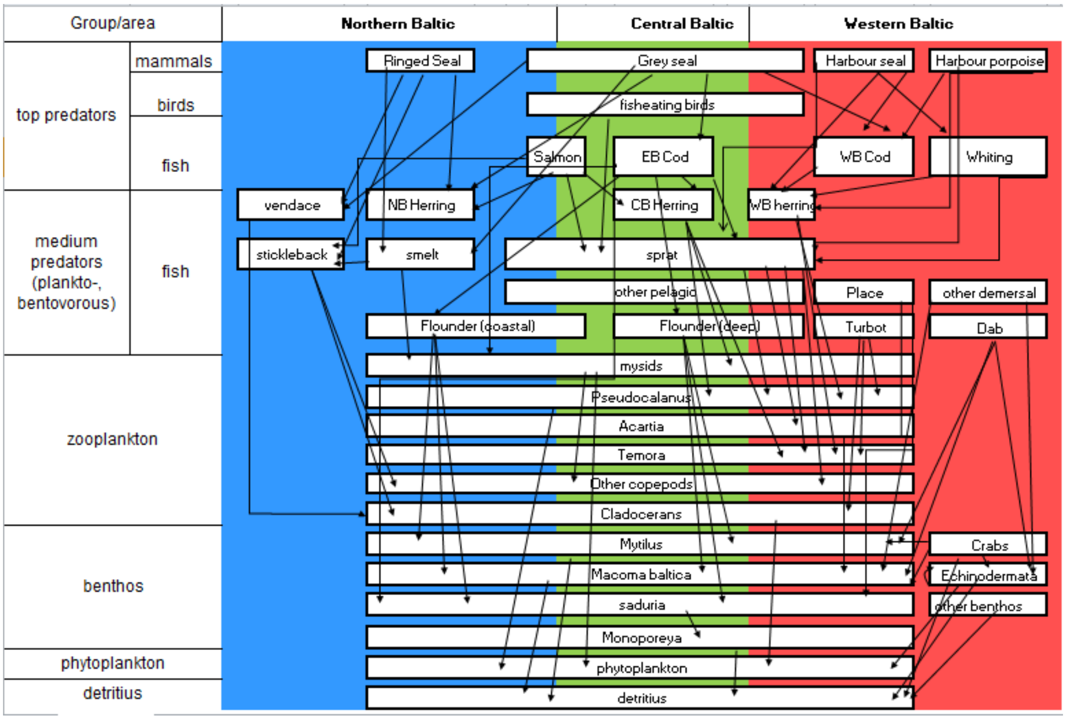

Figure 2. Conceptual food-web model of the entire Baltic Sea based on previously documented trophic relationships. Group areas are organized vertically by major ecological roles (e.g., predators, zooplankton, phytoplankton), and horizontally by subregions: Northern Baltic (blue), Central Baltic (green), and Western Baltic (red). Overlaps of functional groups with coloured sections denote their spatial distribution across different Baltic subregions. Arrows illustrate the direction of trophic linkages based on known diet compositions and regional prey availability. This structure enables the model to simulate energy flow, biomass cycling, and trophic interactions across spatially distinct, but ecologically connected sub-basins. Source: Wikström et al. 2024

The uppermost trophic level (Figure 2) consists of top predators, including marine mammals (ringed, grey, and harbour seals, and harbour porpoise), fish-eating birds (e.g., black guillemot), and piscivorous fish (e.g., cod and salmon). These apex predators exert top-down control on medium-sized planktivorous and benthivorous fish species. Region-specific fish stocks (e.g., Eastern Baltic Cod, Western Baltic Cod) are represented to capture differences in life history traits, prey availability, and spatial distribution.

Medium trophic levels include key forage fish such as herring, sprat, stickleback, vendace, and smelt, which act as both consumers of lower trophic level organisms (e.g., zooplankton) and prey for top predators.

Lower trophic levels include various zooplankton taxa (e.g., Temora, Acartia, Pseudocalanus, cladocerans) and benthic invertebrates (e.g., Mytilus, *Limecola balthica*, polychaetes, and echinoderms), which link primary production to higher trophic levels. Phytoplankton and detritus form the base of the food web, representing primary productivity and organic matter recycling, respectively.

Ringed seals (*Pusa hispida*) are predominantly distributed in ice-covered northern regions, especially the Gulf of Bothnia, which hosts approximately 90% of the population. Smaller southern populations inhabit the Archipelago Sea, the eastern Gulf of Finland, and the Gulf of Riga (Halkka and Tolvanen, 2017). Their diet is dominated by small to medium-sized fish species, such as three-spined stickleback, herring, and vendace (Scharff-Olsen et al. 2019).

The grey seal (*Halichoerus grypus*) is the largest predator in the Baltic Sea. They inhabit a diverse range of coastal environments: rocky islets, sandy shores, and ice-covered areas during winter months. Grey seals are opportunistic predators, with a diet varying based on prey availability, geographic location, and the age of the seal. Primary prey species across the Baltic Sea is herring, while sprat and cod are significant in the southern regions and vendace in the northern areas (Lundström, et al. 2007, 2010).

Harbour seals (*Phoca vitulina*) typically favour nearshore habitats such as rocky shores and sandbanks and tend to avoid areas with intense human activity. As other seals, they are opportunistic predators, feed on a variety of prey, but mainly herring, sprat, cod, flatfish and sandeel (Andersen, 2007). They typically hunt in shallow coastal waters but can dive deeper when necessary, using whiskers to detect prey movements.

The harbour porpoise (*Phocoena phocoena*) is a small cetacean found in the southwestern Baltic, Kattegat, and Belt Seas. The central Baltic subpopulation is critically endangered, with estimates indicating only a few hundred individuals remaining (Koschinski, 2001). Harbour porpoises prefer shallow coastal waters, but can also inhabit deeper offshore areas. They are often found in regions with strong currents and variable salinity levels, where prey is abundant. Harbour porpoises primarily feed on small, schooling fish, including herring, sprat, juvenile cod and gobies (Lindroth, 1962, Aarefjord, et al. 1995). Due to their high metabolic rate, they must eat frequently, consuming the equivalent of up to 10% of their body weight daily (Berggren and Petterson, 1990, Kastelein et al., 1997),

To adequately represent the ecological structure and trophic interactions at the mid trophic levels and of the fish community in the Baltic Sea, the model incorporates 18 distinct fish functional groups, as described in Table 1. These groups were defined based on multiple criteria, including their relative biomass, diet composition, and significance in both total ecosystem biomass and fishery landings. This functional classification ensures that ecologically and commercially important species are appropriately represented.

Moreover, the grouping strategy reflects a simplified approximation of the underlying stock structures. This allows the model to account for the ecological diversity and spatial heterogeneity of fish populations while maintaining a manageable level of complexity suitable for ecosystem-based modelling approaches (Christensen & Walters, 2004; Coll et al., 2008).

In the current EwE model, a multistanza approach was applied to key commercially important fish species to better represent ontogenetic shifts in diet composition and recruitment patterns. Multistanza groups allow for the division of a single species into multiple life-history stages (e.g., juvenile, subadult, adult), each with distinct trophic interactions, mortality rates, and ecological roles (Christensen & Walters, 2004). This method is particularly useful for species with complex life cycles and size-structured predation, such as cod (*Gadus morhua*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*), which play crucial roles in the Baltic Sea food web.

By using multistanza groups, the model can more accurately capture the variability in energy transfer across trophic levels and provide improved resolution of species-specific dynamics relevant to both ecosystem functioning and fisheries management. This technique also enhances the capacity of the model to simulate recruitment variability and size-dependent predator-prey relationships, which are essential for understanding population resilience and the effectiveness of different management strategies (Walters et al., 2010).

Table 1. Fish groups in the model. ICES SD is management sub-divisions used by ICES, multi-stanza is life-history stages.

Fish species or group	Stock	ICES SD	Multi-stanza
Atlantic cod (*Gadus morhua*)	Eastern Baltic	25-32	juveniles; adults
	Western Baltic	22-24	juveniles; adults
Atlantic salmon (*Salmo salar*)		25-32	no
Atlantic herring (*Clupea harengus*)	Northern Baltic	30-31	juveniles; adults

	Central Baltic	25-29;32 excluding Gulf of Riga (GoR)	juveniles; adults
	Western Baltic	22-24	juveniles; adults
European sprat (*Sprattus sprattus*)		25-32	juveniles; adults
Vendace (*Coregonus albula*)		30-31	no
Three-spined stickleback (*Gasterosteus aculeatus*)		22-32	no
European smelt (*Osmerus eperlanus*)		30-31	no
European flounder (*Platichthys flesus*)		22-26, 28	no
Baltic flounder (*Platichthys solemdali*)		27, 29-32	no
European plaice (*Pleuronectes platessa*)		22-29, 32	no
Turbot (*Scophthalmus maximus*)		22-24	no
Common dab (*Limanda limanda*)		22-24	no
Whiting (*Merlangius merlangus*)		22-24	no
Western Baltic flatfish (common sole (*Solea solea*), brill (*Scophthalmus rhombus*))		22-24	no
Western Baltic other fish (gobies, sandeel)		22-24	no

At the lower trophic level, the model includes 13 functional groups representing zooplankton and benthic invertebrates, which serve as critical components in energy transfer and nutrient cycling within the Baltic Sea ecosystem. These groups are central to mediating trophic interactions between primary producers and higher-level consumers, particularly fish.

Zooplankton groups are aggregated into taxonomic and functional categories based on their ecological roles and prey availability for fish. Key groups include mysids, *Pseudocalanus spp*, *Acartia spp*, *Temora spp*, all of which constitute major prey items for juvenile and planktivorous fish species such as herring and sprat (Möllmann and Köster, 2002). Remaining taxa are grouped into two broader categories: zooplankton copepods and zooplankton cladocerans, which collectively represent the bulk of micro- and mesozooplankton biomass in the system.

Benthic invertebrates are similarly grouped based on ecological function, feeding strategy, and taxonomic identity. Functionally significant taxa include the large omnivorous crustacean isopod *Saduria entomon* and dominant molluscs such as *Mytilus spp*. (blue mussels) and *Limecola balthica* (formerly *Macoma balthica*), which play important roles in benthic-pelagic coupling. Deposit-feeding macrofauna, such as *Monoporeia affinis* and *Pontoporeia femorata*, are essential for sediment bioturbation and organic matter processing.

Predatory and suspension-feeding benthos are grouped separately to reflect their different ecological roles. Predatory benthic invertebrates include polychaetes such as *Bylgides sarsi*, *Hediste diversicolor*, and the echinoderm *Henricia spinulosus*. Suspension feeders (*Astarte spp*., *Arctica islandica* and *Modiolus modiolus*) are included due to their filtering capacity and contribution to energy flow in benthic food webs. Additionally, crabs, echinoderms, and a residual “other benthos” group are included to account for less abundant but ecologically relevant taxa.

In the current model, primary production is represented by a single functional group: phytoplankton. Phytoplankton are the principal autotrophic organisms in the open waters of the Baltic Sea and form the base of the pelagic food web.

Given that the model domain primarily encompasses open sea areas, macroalgae and other benthic macrophytes (e.g., *Fucus spp*., *Zostera marina*) were not included. These groups are typically restricted to coastal and shallow benthic habitats, where light penetration allows for their growth and productivity. While benthic primary producers can be ecologically significant in nearshore ecosystems, their exclusion is justified by the spatial scale and focus of the model, which emphasizes pelagic processes and open-sea trophic dynamics.

Details of the parametrization are described in Tables 2-5.

Table 2. Ecopath input parameters and their sources for mammals and birds. All biomasses (B) are in units of t/km2. P/B is production/biomass, Q/B is consumption/biomass, UA is unassimilated consumption and Diet is diet composition. Number in brackets is initial value used in previous versions of the model and subsequently adjusted. All values are yearly.

Group name	Parameter	Value	Source
Ringed seal	*B*	0.00428	Number of individuals from Helcom (2018) were multiplied by average weight of 91 kg (Oksanen, 2015) and divided by size of Northen Baltic area to get density.
	P/B	0.1	Harvey *et al.*, 2003 in Bauer et al (2018)
	Q/B	8.79 (16.28)	adjusted, initially from Bauer et al (2018)
	Diet		Scharf 2018
Grey seal	*B*	0.0073	Number of individuals from censusing (Helcom, 2018) were divided by 0.7 (haul-out fraction during surveys is assumed 70% by HELCOM.), then multiplied by average weight of 100 kg (Tomczak, pers.comm.) and divided by size of Baltic area to get density
	P/B	0.1	Harvey *et al.*, 2003 in Bauer et al (2018)
	Q/B	7.5 (16.28)	adjusted, initially from Bauer et al (2018)
	Diet		Scharf 2018
Harbor seal	*B*	0.00113	Number of individuals from censusing (Helcom, 2018b) were devided by 0.7 (to bring censusing to population level, Harding), then multiplied by average weight of 70 kg (Härkönen and Heide-Jørgensen, 1990) and divided by size of Western Baltic area to get density
	P/B	0.1	Harvey *et al.*, 2003 in Bauer et al (2018)
	Q/B	21.85 (20)	adjusted, initially from WB EwE
	Diet		Scharf 2018
Harbour porpoise	*B*	0.0137	Number of individuals from Helcom (2018) were multiplied by average weight of 55 kg (https://www.ascobans.org/en/species/phocoena-phocoena) and divided by size of Western Baltic area to get density
	P/B	0.18	WB EwE
	Q/B	26.36 (28)	adjusted, initially from WB EwE
	Diet		Lundström et al. *in press*
	B	0.002	Bauer et al (2018)

Fish-feeding birds	*P/B*	0.1	Bauer et al (2018)
	Q/B	130	Bauer et al (2018)

Table 3. Ecopath input parameters and their sources for fish groups. All biomasses (B) are in units of t/km2. The 'Total mortality' parameter of multistanza groups is equivalent to the P/B (production/biomass) in other groups. 'Q/B' refers to consumption/biomass, 'UA' to unassimilated consumption and 'Diet' to diet composition. Number in brackets is initial value used in previous versions of the model and subsequently adjusted. All values are yearly.

Group name	Parameter	Value	Source
EB cod adults	*B*	0.5 (0.215)	Adjusted (initially SSB from WGBFAS, 2020 divided by Baltic area)
	Total mortality	0.9 (1.1)	adjusted (initially total mortality calculated as the sum of natural mortality M (WGBFAS, 2020) and ratio of catch (landings and discards) and SSB)
	Q/B	3.81	Witek, 1995
	UA	0.17	Harvey *et al.*, 2003
	Diet		stomach data (WKSPATIAL, 2017)
EB cod juveniles	*B*	0.619	calculated by EwE
	Total mortality	1.2	assumed to be 1.2 times adult mortality, as in Bauer et al (2018)
	Q/B	7.65	calculated by EwE
	Diet		stomach data (WKSPATIAL, 2017)
WB cod adults	*B*	0.15 (0.066)	Adjusted (initially SSB from WGBFAS, 2020 divided by Baltic area)
	Total mortality	0.9	sum of natural mortality M (WGBFAS, 2020) and ratio of catch (landings and discards) and SSB
	Q/B	3.81	Witek, 1995
	Diet		diet composition in 2007 (Huwer et al., 2014)
WB cod juveniles	*B*	0.354	calculated by EwE
	Total mortality	1	assumed to be 1.2 times adult mortality, as in Bauer et al (2018)
	Q/B	7.65	calculated by EwE

	Diet		diet composition in 2007 (Huwer *et al.*, 2014)
Salmon	*B*	0.024	number of smolt (WGBAST , 2020) multiplied by 5kg average weight divided by sum of Northern and Central Baltic areas
	Total mortality	0.7 (0.38)	Adjusted from mortality on FishBase
	Q/B	4 (7.14)	Adjusted (initially FishBase)
	UA	0.17	Harvey *et al.*, 2003
	Diet		Karlsson 1999 (used values for >60 cm, if less than 60 mostly eats sprat)
NB herring adults	*B*	0.964	SSB (WGBFAS, 2018) divided by Baltic area
	Total mortality	1 (0.296)	adjusted (initially total mortality calculated as the sum of natural mortality M (WGBFAS, 2018) and ratio of landings and SSB)
	Q/B	3	Witek, 1995
	Diet		Peltonen 2004; Parmanne 2004
NB herring juveniles	*B*	0.577	calculated by EwE
	Total mortality	1.25	assumed to be 1.2 times adult mortality, as in Bauer et al (2018)
	Q/B	5.811	calculated by EwE
	Diet		Parmanne 2004
CB herring adults	*B*	1.9	SSB (WGBFAS, 2020) divided by Baltic area
	Total mortality	1 (0.35)	adjusted (initially total mortality calculated as the sum of natural mortality M (WGBFAS, 2020) and ratio of landings and SSB)
	Q/B	3	Witek, 1995
	Diet		Casini & Cardinale, 2004; Möllmann *et al.*, 2004
CB herring juveniles	*B*	1.169	calculated by EwE
	Total mortality	1.2	assumed to be 1.2 times adult mortality, as in Bauer et al (2018)

	Q/B	5.811	calculated by EwE
	Diet		Casini & Cardinale, 2004
WB herring adults	*B*	1.66 (0.166)	Adjusted (initially SSB (HAWG, 2020) divided by Baltic area
	Total mortality	0.9 (0.768)	adjusted (initially total mortality calculated as the sum of natural mortality M (HAWG, 2020) and ratio of landings and SSB)
	Q/B	3	Witek, 1995
	Diet		
WB herring juveniles	*B*	0.773	calculated by EwE
	Total mortality	1	assumed to be 1.2 times adult mortality, as in Bauer et al (2018)
	Q/B	5.811	calculated by EwE
	Diet		Casini & Cardinale, 2004; Möllmann *et al.*, 2004; Tomczak *et al.*, 2012
Vendace	*B*	0.12	ssb (Bergenius, pers.comm) divided by Northern Baltic area
	Total mortality	0.74	Natural mortality from FishBase
	Q/B	4.4	FishBase
	Diet		ratios approximate, species from FishBase
Stickleback	*B*	0.328	Olsson 2019
	Total mortality	2.57	Natural mortality from FishBase
	Q/B	8.76	Rajasilta 1980
	Diet		Peltonen 2004
Sprat adults	*B*	3.017	SSB (WGBFAS, 2020) divided by Baltic area
	Total mortality	1.24 (0.474)	adjusted (initially total mortality calculated as the sum of natural

			mortality M (WGBFAS, 2020) and ratio of landings and SSB)
	Q/B	4.63	Witek, 1995
	Diet		Casini & Cardinale, 2004; Möllmann *et al.*, 2004
	B	5.623	calculated by EwE
Sprat juvenile	*Total mortality*	1.865	assumed to be 1.5 times adult mortality, as in Bauer et al (2018)
	Q/B	8.466	calculated by EwE
	Diet		Casini & Cardinale, 2004
Smelt	*B*		calculated by EwE
	Total mortality	0.66 (0.22)	Adjusted (initially natural mortality from FishBase)
	Q/B	2.7 (5.9)	Adjusted (initially from FishBase)
	Diet		FishBase
Whiting	*B*	0.1	DATRAS
	Total mortality	0.9 (0.47)	Adjusted (initially natural mortality from FishBase)
	Q/B	3.3	FishBase
	Diet		Ross, 2016
Northern and Central Baltic flounder	*B*	0.16	DATRAS
	Total mortality	0.6 (0.79)	Adjusted (initially total mortality from Bauer et al, 2018)
	Q/B	3.5 (4.2)	Adjusted (initially Bauer et al, 2018)
	Diet		Haase, 2020, Florin, 2010
Western and Central Baltic flounder	*B*	0.5	DATRAS
	Total mortality	0.6 (0.79)	Adjusted (initially total mortality from Bauer et al, 2018)
	Q/B	3.5 (4.2)	Adjusted (initially Bauer et al, 2018)
	Diet		Borg, 2014
Place: adult	*B*	0.45 (0.067)	Adjusted (initially ssb (WGBFAS, 2020) divided by Baltic area)
	Total mortality	0.5 (0.12)	Adjusted (initially natural mortality from FishBase)
	Q/B	3 (3.42)	Adjusted (initially from FishBase)
	Diet		Rijnsdorp and B. Vingerhoed 2011
Dab	*B*	0.25	DATRAS

	Total mortality	0.5	Same as place
	Q/B	3	Same as place
	Diet		FishBase
Turbot	*B*	0.035	DATRAS
	Total mortality	0.5	Same as place
	Q/B	3	Same as place
	Diet		ratios approximate, species from FishBase
Western Baltic flatfish	*B*	0.007	DATRAS
	Total mortality	0.7	Adjusted from place
	Q/B	3.257	Adjusted from place
	Diet		Fishbase

Table 4. Ecopath input parameters and their sources for lower links in trophic web (zooplankton, benthos, primary producers). All biomasses (B) are in units of t/km2. P/B is production/biomass. 'Q/B' refers to consumption/biomass, 'UA' unassimilated consumption. Number in brackets is initial value used in previous versions of the model and subsequently adjusted. All values are yearly.

Group name	parameter	Value	source
Mysids	*B*		calculated by EwE
	P/B	5 (3)	Adjusted (initialy Witek, 1995)
	Q/B	15	Witek, 1995
	Diet	yes	Bauer et al (2018)
Pseudocalanus sp	*B*	1.93	Bauer et al (2018)
	P/B	6.3 (6)	Adjusted (initialy Witek, 1995)
	Q/B	30	Witek, 1995
	Diet	yes	Bauer et al (2018)
Acartia sp	*B*	3.027	Bauer et al (2018)
	P/B	20 (16.8)	Adjusted (initialy Witek, 1995)
	Q/B	83	Witek, 1995
	Diet	yes	Bauer et al (2018)
Temora sp	*B*	2.271	Bauer et al (2018)
	P/B	20 (12)	Adjusted (initialy Witek, 1995)
	Q/B	83 (60)	Adjusted (initialy Witek, 1995)
	Diet	yes	Bauer et al (2018)
zooplankton copepods	*B*	5	
	P/B	10	Witek, 1995
	Q/B	57	Witek, 1995
	Diet	yes, but no ratios	havet.nu

zooplankton cladocerans	*B*	4.006	
	P/B	19.3	Witek, 1995
	Q/B	97	Witek, 1995
	Diet	yes, but no ratios	havet.nu
Saduria	*B*	2.4 (2)	Adjusted (initially Bauer et al (2018))
	P/B	1.3	Witek, 1995
	Q/B	6.51	Witek, 1995
	Diet	yes	Bauer et al (2018)
Mytilus sp	*B*	3.46 (10)	Adjusted (initially Bauer et al (2018))
	P/B	1.75	Witek, 1995
	Q/B	8.73	Witek, 1995
	Diet	yes	Bauer et al (2018)
Macoma baltica	*B*	54.01 (45)	Adjusted (initially Bauer et al (2018))
	P/B	0.4	Witek, 1995
	Q/B	2	Witek, 1995
	Diet	yes	Bauer et al (2018)
Deposit feeders	*B*	9	Sharkweb, Aranda survey
	P/B	2 (1.85)	Adjusted (initialy Witek, 1995)
	Q/B	10 (9.35)	Adjusted (initialy Witek, 1995)
	Diet	yes	
predatory benthos	*B*	0.86	Sharkweb, Aranda survey
	P/B	2.7	Witek, 1995
	Q/B	13.5	Witek, 1995
	Diet	yes, but no ratios	havet.nu
Crabs	*B*	4.5	Sharkweb
	P/B	0.9	Witek, 1995
	Q/B	5.22	Witek, 1995
	Diet	yes, but no ratios	havet.nu
Echinodermata	*B*	3	Sharkweb
	P/B	2	Witek, 1995
	Q/B	4	Witek, 1995

	Diet	yes, but no ratios	havet.nu
Suspension feeders	*B*	21.5	Sharkweb, Aranda survey
	P/B	4	Witek, 1995
	Q/B	10	Witek, 1995
	Diet		
other benthos	*B*	2.3	Sharkweb, Aranda survey
	P/B	3	Witek, 1995
	Q/B	10	Witek, 1995
	Diet		
Primary producers	*B*	7.05	

Table 5. Ecopath input (regular text) and output (bold text) parameters of the functional groups used in the model. Biomass (B) is in units of t/km2, production/biomass (P/B) and consumption/biomass (Q/B) ratios and total mortality (Z) are yearly rates. EE is ecotrophic efficiency. TL is trophic level.

Group name	B	Z	P/B	Q/B	EE	Unassim. consumption	TL
Ringed seal	0.004		0.1	8.79	**0.000**	0.2	**4.04**
Grey seal	0.007		0.1	17.5	**0.000**	0.2	**4.17**
Harbour seal	0.001		0.1	21.85	**0.000**	0.2	**4.54**
Harbour porpoise	0.014		0.18	26.36	**0.000**	0.2	**4.38**
Fisheating birds	0.002		0.1	130	**0.000**	0.2	**4.00**
EB Cod Juv	0.619	1.2		7.196	**0.127**	0.2	**3.82**
EB Cod Ad	0.500	0.9		3.5	**0.496**	0.17	**4.06**
WB Cod Juv	0.158	1		6.736	**0.967**	0.2	**3.99**
WB Cod Ad	0.150	0.9		3.5	**0.484**	0.2	**4.13**
Salmon	0.024		0.7	4	**0.556**	0.2	**4.02**
NB herring juv	0.577	1.25		5.764	**0.658**	0.2	**3.05**
NB herring ad	0.964	1		3	**0.230**	0.2	**3.16**
CB herring juv	1.169	1.2		6.550	**0.310**	0.2	**3.03**
CB herring ad	1.900	1		3.5	**0.753**	0.2	**3.09**
WB herring juv	0.773	1		6.478	**0.275**	0.2	**3.03**
WB herring ad	1.660	0.9		3.5	**0.163**	0.2	**3.08**
Sprat Juv	5.623	1.865		8.466	**0.233**	0.2	**3.00**
Sprat Ad	3.017	1.24		4.63	**0.634**	0.2	**3.00**
Vendace	0.120		0.74	4.4	**0.215**	0.2	**3.00**
Stickleback	0.328		2.57	8.76	**0.320**	0.2	**3.00**

Smelt	**0.184**	0.66	2.7	0.500	0.2	**3.25**
NCB Flounder ad	0.160	0.6	3.5	**0.313**	0.2	**3.12**
WCB Flounder ad	0.500	0.6	3.5	**0.702**	0.2	**3.41**
Plaice ad	0.450	0.5	3	**0.331**	0.2	**3.27**
Turbot	0.035	0.5	3	**0.740**	0.2	**3.94**
Dab	0.250	0.5	3	**0.848**	0.2	**3.23**
Whiting	0.100	0.9	3.3	**0.783**	0.2	**3.87**
WB flatfish	0.007	0.7	3.257	**0.525**	0.2	**3.31**
WB other fish	**3.741**	1.5	4.5	0.500	0.2	**2.72**
Mysids	**2.057**	5	15	0.750	0.2	**2.30**
Pseudocalanus sp	1.930	6.3	30	**0.981**	0.2	**2.00**
Acartia sp	3.027	20	83	**0.269**	0.2	**2.00**
Temora sp	2.271	20	83	**0.729**	0.2	**2.00**
zooplankton copepods	5.000	10	57	**0.252**	0.2	**2.00**
zooplankton cladocerans	4.006	19.3	97	**0.423**	0.2	**2.00**
Saduria	2.400	1.3	6.51	**0.507**	0.2	**3.01**
Mytilus sp	3.460	1.75	8.73	**0.454**	0.2	**2.00**
Limecola balthica (Macoma)	54.010	0.4	2	**0.192**	0.2	**2.00**
Deposit feeders	9.000	2	10	**0.653**	0.2	**2.00**
predatory benthos	0.860	2.7	13.5	**0.163**	0.2	**2.80**
crabs	4.500	0.9	5.22	**0.057**	0.2	**2.90**
echinodermata	3.000	2	4	**0.911**	0.2	**3.00**
suspention feeders	21.500	4	10	**0.070**	0.2	**2.00**
other benthos	2.300	3	10	**0.820**	0.2	**2.17**
Primary producers	7.050	200		**0.877**	0	**1.00**
Detritus	1645			**0.339**	0	**1.00**

3. Ecopath: method, results, diagnostics

Ecopath (see Box 1 for basic principles) integrates functional groups into a food-web structure under the principle of mass balance: the biomass available at each trophic level must be sufficient to support predation by higher trophic levels and fisheries catches, with energy supplied through primary production and trophic transfers. As a static model, Ecopath reconstructs a snapshot of the ecosystem that is internally balanced in terms of energy and biomass flows, representing conditions in a specific reference year. For this study, the year 2004 was selected as the base

Box1: Principles of Ecopath

The Ecopath modelling approach is founded on the principle of mass balance, which ensures that all energy and biomass entering a functional group within an ecosystem is fully accounted for through various loss processes. These include predation, respiration, unassimilated food, fishing mortality, and other forms of mortality. The Ecopath model provides a static, steady-state snapshot of ecosystem structure and function, typically representing average conditions over a defined temporal baseline (usually one year).

The model operates under the assumption that, for each functional group, inputs and outputs of energy (or biomass) are in balance. This is formalized through two primary master equations:

1. Energy Balance Equation**:**

Consumption=production+respiration+unassimilated food

This equation represents the partitioning of consumed energy. A portion is converted into biomass (production), some is used for metabolic maintenance (respiration), and the remainder is lost as unassimilated matter (e.g., feces or excreted waste).

2. Production Balance Equation:

Production=predation mortality+fishing mortality+biomass accumulation+net migration+other mortality

This equation describes the fate of the production within each group. Production may be removed via consumption by predators, harvested through fisheries, lost or gained through migration, or lost due to natural causes such as disease or senescence. In some cases, biomass may also accumulate if growth exceeds losses.

year, since it is the beginning of consistent fisheries effort data available for the Baltic Sea.

To achieve mass balance, Ecopath requires a set of key input parameters for each functional group:

- Biomass (in t/km²);
- Production rate, typically expressed as the production-to-biomass ratio (P/B);
- Consumption rate, expressed as the consumption-to-biomass ratio (Q/B);
- Diet composition, specifying trophic links among groups.

Where available, biomass values were sourced from stock assessment reports, scientific surveys, and official statistics. When such data were unavailable, values were derived from published literature or estimates from other ecosystem models. For three functional groups: smelt, mysids, and Western Baltic "other fish", biomass data were not available; therefore, Ecopath estimated their biomass as part of the balancing procedure.

Values for P/B and Q/B ratios were taken from empirical studies whenever possible. In the absence of specific empirical estimates, values were taken from Ecopath parameter databases, regional studies, or ecosystem modelling literature relevant to the Baltic Sea (e.g., Christensen et al., 2005; Coll et al., 2008).

Additionally, the model includes a habitat area parameter for each functional group, representing the proportion of the total Baltic Sea area inhabited by the group. For groups distributed across the entire sea, the habitat area value was set to 1. Value 1 was also assigned to functional groups defined using multistanza structure (i.e., with separate juvenile and adult stanzas), as Ecopath requires a value of 1 for each stanza group regardless of actual spatial restriction. For these groups biomass was divided by size of entire Baltic. For groups limited to specific subregions, habitat area values were assigned based on the relative size of each sub-basin: Northern Baltic (0.29), Western Baltic (0.127), Central Baltic (0.583).

However, the value for the Central Baltic was not directly used, since only multistanza-defined fish groups inhabit this region exclusively, and these require a habitat area value of 1 by default. For species with a distribution spanning multiple regions, the habitat area value was calculated as the sum of the proportions for the corresponding subregions. For example, Atlantic salmon (*Salmo salar*), which migrates between the Northern and Central Baltic, was assigned a habitat area of 0.873 (0.29 + 0.583). This spatial parameterization enables the model to approximate the ecological footprint of each functional group and ensures accurate scaling of biomass and energy flow across the Baltic Sea heterogeneous subregions.

The Ecopath model incorporates fishing pressure through the inclusion of 10 distinct fishing fleets (Table 6), each representing a specific aggregation of fishing activities. These fleets are defined based on combinations of gear type and vessel size category, following the classification system developed by the Scientific, Technical, and Economic Committee for Fisheries - STECF (STECF, 2006). This approach ensures that the diversity and specialization of the Baltic Sea fisheries are adequately captured, reflecting their impacts on ecosystem structure and function. Each fleet was characterized by its interaction with different functional groups and life stages (stanzas) of species within the model. The proportions of landings and discards for each functional group and stanza were assigned using STECF data for the year 2004, which corresponds to the base year of the model. These data provide detailed records of catch composition, fleet effort, and discard rates, enabling realistic parameterization of fishing mortality for both target and non-target species. This fleet-based representation is essential for simulating the difference in impact of fishing gears on various components of the ecosystem, including demersal versus pelagic species, juveniles versus adults, and retained versus discarded biomass. Moreover, it provides a structured foundation for exploring management scenarios, such as gear-selective regulations or fleet-specific effort reductions, within the dynamic Ecosim simulations.

Table 6. Ecopath model fleet groups based on type of operation (active or passive bottom, pelagic), type of gear used and size of vessel in STECF data.

Ecopath fleet	STECF gears	STECF size categories
ACT0018	'DEM_SEINE','OTTER','R-DEM_SEINE','R-OTTER'	'O10T12M','O8T10M','U8M','O12T18M','U10M'
ACT1824	'DEM_SEINE','OTTER','R-DEM_SEINE','R-OTTER'	'O18T24M'
ACT2440	'DEM_SEINE','OTTER', 'R-DEM_SEINE','R-OTTER'	'O24T40M'
PAS0012	'GILL','POTS','R-GILL','LONGLINE','R-LONGLINE','TRAMMEL','R-TRAMMEL'	'O10T12M','O8T10M','U8M','U10M'
PAS1218	'GILL','POTS','R-GILL','LONGLINE','R-LONGLINE','TRAMMEL','R-TRAMMEL'	'O12T18M'
PAS1840	'GILL','POTS','R-GILL','LONGLINE','R-LONGLINE','TRAMMEL','R-TRAMMEL'	'O18T24M', 'O24T40M'
PEL0018	'PEL_SEINE','PEL_TRAWL','R-PEL_TRAWL'	'O10T12M','O8T10M','U8M','O12T18M','U10M'
PEL1824	'PEL_SEINE','PEL_TRAWL','R-PEL_TRAWL'	'O18T24M'

PEL2440	'PEL_SEINE','PEL_TRAWL' ,'R-PEL_TRAWL'	'O24T40M'
PEL4000	'PEL_SEINE','PEL_TRAWL' ,'R-PEL_TRAWL'	'O40M'

To assess whether the Ecopath model output was both mass-balanced and ecologically realistic, we applied a Pre-balance (Prebal) analysis following the approach described by Link (2010) and further elaborated in Ecopath modelling guidelines (Heymans et al. 2016). This diagnostic tool helps verify that the modelled food web follows the general patterns observed in natural ecosystems. A key assumption in ecological theory is that biomass should decline with increasing trophic level, due to the cumulative energy loss associated with trophic transfers (typically 90% loss between levels). As such, the slope of a linear regression between the logarithm of biomass and trophic level should fall within a typical range of 5–10%. This slope serves as a proxy for trophic transfer efficiency and indicates whether energy flows through the food web in a biologically realistic manner. In our model, the estimated slope of this regression was 7.5% (Figure 3), which lies well within the expected theoretical range. This result suggests that the model adequately captures realistic energy loss patterns across the trophic hierarchy and meets key mass-balance criteria. Nevertheless, a few functional groups deviated from the expected biomass-trophic level trendline, including harbour seals, Western Baltic flatfish (sole and brill), EB cod (both juveniles and adults) and *Limecola balthica*. These deviations may reflect uncertainties in parameter estimation (e.g., biomass, diet composition), data limitations, or real-world ecological anomalies. These groups may require further review and potential refinement to improve overall model realism and predictive accuracy.

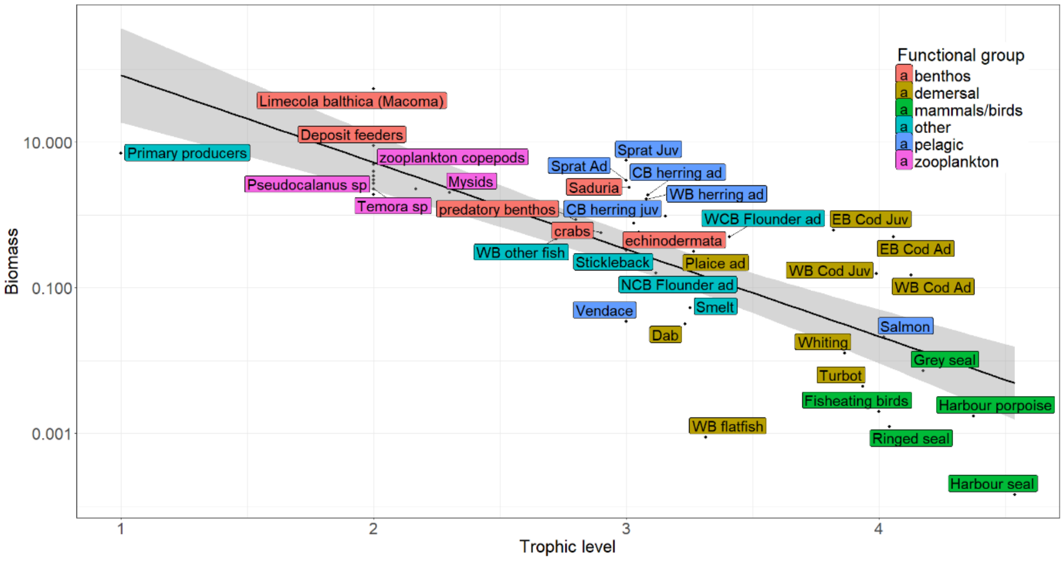

Figure 3. Declining biomass with increasing trophic level. Line: linear regression.

4. Ecosim: input and results

The static mass-balanced output from Ecopath served as the initial condition for the Ecosim dynamic simulations (see Box 2 for principles). Ecosim was used to simulate temporal changes in the Baltic Sea food web from the base year 2004 until 2019, providing insight into the ecosystem's responses to changing fishing pressure and environmental conditions over time. The simulations were driven by time series of fishing effort, fishing mortality rates and primary production (Figures 4-6).

Box2: Principles of Ecosim

Ecosim is the dynamic simulation module of the Ecopath with Ecosim (EwE) modelling framework. It extends the static, mass-balanced snapshot provided by Ecopath into a time-dynamic model that simulates changes in biomass, energy flow, and trophic interactions over time. Ecosim allows for the evaluation of ecosystem responses to external drivers such as fishing pressure, environmental variability, and species interactions.

The core of Ecosim is a set of differential equations that govern the biomass dynamics of each functional group based on ecological and anthropogenic processes.

The general form of the Ecosim master equation for each functional group *i* is:

growth rate = growth efficiency × total consumption by i on its prey - total consumption on i by its predators + immigration rate - (fishing mortality rate + other mortality + emigration rate) × biomass

To ensure the model realistically reflected observed historical ecosystem dynamics, it was fitted to a range of empirical time series (Table 7), including stock assessment results, scientific survey data, and fisheries catch statistics (Figures 7-11). This fitting process allowed for the adjustment of key parameters, such as vulnerability settings to optimize the model’s alignment with observed trends. The close match between model outputs and empirical data provides confidence in the model’s ability to reproduce historical ecosystem dynamics and its potential utility in forecasting future scenarios under alternative management and environmental conditions.

Table 7. Time series used in Ecosim

Name	Period	Source
Ringed seal_HELCOM	2004-2016	HELCOM
Grey seal_HELCOM	2004-2017	HELCOM
Harbour seal_HELCOM	2004-2017	HELCOM
Fisheating birds_Henth	2004-2014	HELCOM
EB Cod Juv_SS3	2004-2019	ICES WGBFAS 2020
EB Cod Juv_BITS1	2004-2019	DATRAS
EB Cod Ad_SS3	2004-2019	ICES WGBFAS 2020
EB Cod Ad_BITS1	2004-2019	ICES WGBFAS 2020
WB Cod Juv_SAM	2004-2019	ICES WGBFAS 2020
WB Cod Juv_BITS1	2004-2019	DATRAS
WB Cod Ad_SAM	2004-2019	ICES WGBFAS 2020
WB Cod Ad_BITS1	2004-2019	DATRAS
Salmon_smolt_as	2004-2019	ICES WGBAST 2021
NB herring ad_SS3	2004-2019	ICES WGBFAS 2020
NB herring ad_BIAS	2007-2017	BIAS
CB herring juv_as	2004-2019	ICES WGBFAS 2020
CB herring ad_as	2004-2019	ICES WGBFAS 2020
CB herring juv_sur	2004-2019	BIAS
CB herring ad_sur	2004-2019	BIAS
WB herring juv_sur	2004-2019	ICES WGBFAS 2020
WB herring ad_sur	2004-2019	BIAS
WB herring juv_as	2004-2019	ICES WGBFAS 2020
WB herring ad_as	2004-2019	ICES WGBFAS 2020
sprat Juv_sur	2004-2019	BIAS
Sprat Ad_sur	2004-2019	BIAS
sprat Juv_as	2004-2019	ICES WGBFAS 2020
Sprat Ad_as	2004-2019	ICES WGBFAS 2020
Vendace	2004-2019	M. Bergenius Nord
Stickleback	2004-2014	Olsson et. al., 2019
Smelt	2004-2017	DATRAS
NCB Flounder ad_BITS1	2004-2019	DATRAS
WCB Flounder ad	2004-2019	ICES WGBFAS 2020
Plaice ad_sur	2004-2019	DATRAS
Plaice ad_as	2004-2019	ICES WGBFAS 2020
Turbot	2004-2019	DATRAS
Dab	2004-2019	DATRAS
Whiting	2004-2019	DATRAS
WB flatfish	2004-2019	DATRAS
Pseudocalanus sp	2004-2019	SHARK/ICES WGIAB

Acartia sp	2004-2019	SHARK/ICES WGIAB
Temora sp	2004-2019	SHARK/ICES WGIAB
zooplankton copepods	2004-2019	SHARK/ICES WGIAB
zooplankton cladocerans	2004-2019	SHARK/ICES WGIAB
Saduria	2004-2019	SHARK/ICES WGIAB
Mytilus sp	2004-2019	SHARK/ICES WGIAB
Limecola balthica (Macoma)	2004-2019	SHARK/ICES WGIAB
Deposit feeders	2004-2019	SHARK/ICES WGIAB
predatory benthos	2004-2019	SHARK/ICES WGIAB
Crabs	2004-2019	SHARK/ICES WGIAB
echinodermata	2004-2019	SHARK/ICES WGIAB
suspention feeders	2004-2019	SHARK/ICES WGIAB
other benthos	2004-2019	SHARK/ICES WGIAB
PhytoC_spr_orig	2004-2019	BALTSEM
PhytoC_sum_orig	2004-2019	BALTSEM
EB Cod Juv_Catch	2004-2019	ICES WGBFAS 2020
EB Cod AD_Catch	2004-2019	ICES WGBFAS 2020
WB Cod Juv_Catch	2004-2019	ICES WGBFAS 2020
WB Cod Ad_Catch	2004-2019	ICES WGBFAS 2020
Salmon_Catch	2004-2019	STECF
NB herring juv_catch	2004-2019	ICES WGBFAS 2020
NB herring ad_catch	2004-2019	ICES WGBFAS 2020
CB herring juv_catch	2004-2019	ICES WGBFAS 2020
CB herring ad_catch	2004-2019	ICES WGBFAS 2020
WB herring juv_catch	2004-2019	ICES WGBFAS 2020
WB herring ad_catch	2004-2019	ICES WGBFAS 2020
Sprat Juv_catch	2004-2019	ICES WGBFAS 2020
Sprat Ad_catch	2004-2019	ICES WGBFAS 2020
Vendace_catch	2004-2019	STECF
Stickleback_catch	2014-2019	STECF
Smelt_catch	2004-2019	STECF
NCB Flounder ad_catch	2004-2019	ICES WGBFAS 2020
WCB Flounder ad_catch	2004-2019	ICES WGBFAS 2020
Plaice ad_catch	2004-2019	ICES WGBFAS 2020
Turbot_catch	2004-2019	ICES WGBFAS 2020
Dab_catch	2004-2019	ICES WGBFAS 2020
Whiting_catch	2004-2019	STECF
WB flatfish_catch	2004-2019	STECF
WB other fish_catch	2004-2019	STECF
EB Cod Juv_F	2004-2019	ICES WGBFAS 2020
EB Cod Ad_F	2004-2019	ICES WGBFAS 2020

WB Cod Juv_F	2004-2019	ICES WGBFAS 2020
WB Cod Ad_F	2004-2019	ICES WGBFAS 2020
NB herring ad_F	2004-2019	ICES WGBFAS 2020
CB herring juv_F	2004-2019	ICES WGBFAS 2020
CB herring ad_F	2004-2019	ICES WGBFAS 2020
WB herring juv_F	2004-2019	ICES WGBFAS 2020
WB herring ad_F	2004-2019	ICES WGBFAS 2020
Sprat Juv_F	2004-2019	ICES WGBFAS 2020
Sprat Ad_F	2004-2019	ICES WGBFAS 2020
Plaice ad_catch	2004-2019	STECF
effort_ACT0018	2004-2019	STECF
effort_ACT1824	2004-2019	STECF
effort_ACT2440	2004-2019	STECF
effort_PAS0012	2004-2019	STECF
effort_PAS1218	2004-2019	STECF
effort_PAS1840	2004-2019	STECF
effort_PEL0018	2004-2019	STECF
effort_PEL1824	2004-2019	STECF
effort_PEL2440	2004-2019	STECF
effort_PEL4000	2004-2019	STECF

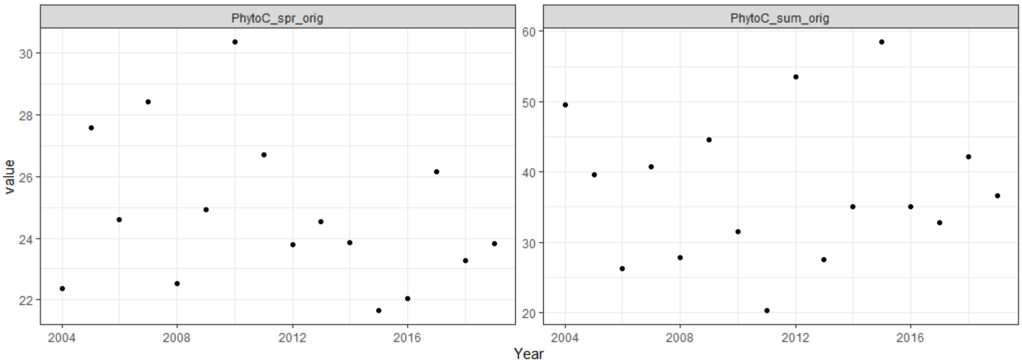

Figure 4. Time series of spring and summer biomasses of phytoplankton.

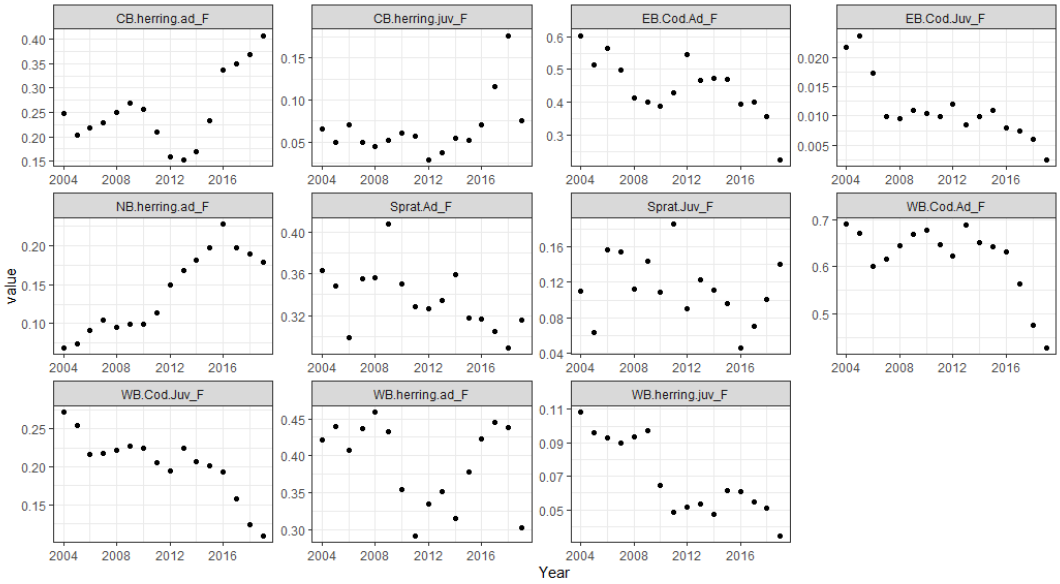

Figure 5. Time series of fish fishing mortalities estimated in stock assessments.

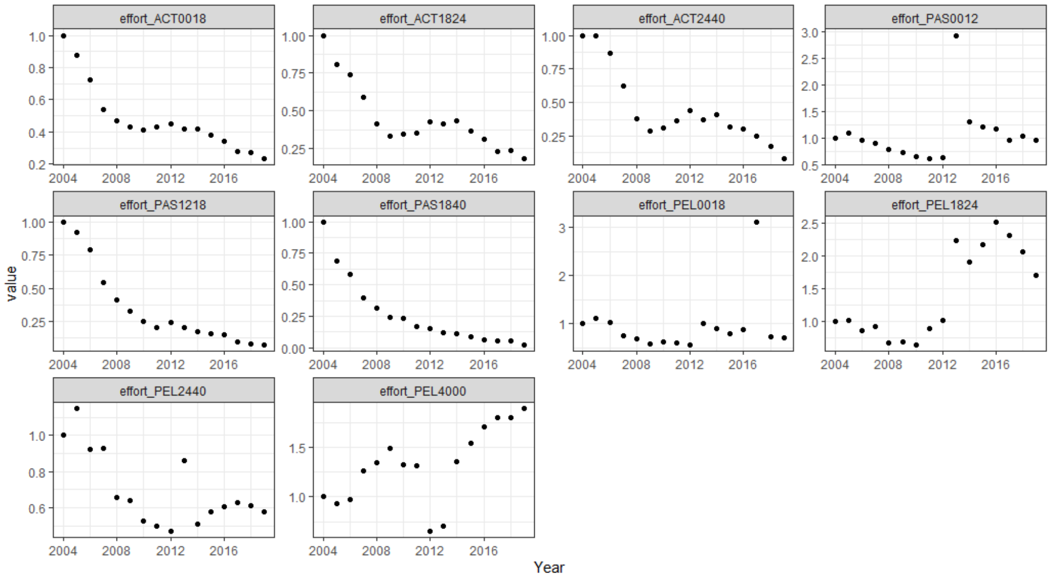

Figure 6. Time series of fisheries efforts for each fleet category (see table 6 for details).

The vulnerability parameters (Table A1 in Supplementary material) are central to the structure and behaviour of the Ecosim model representing predator-prey interactions. Vulnerability values quantify the susceptibility of prey populations to predation, reflecting the principles of the "foraging arena theory" implemented in Ecosim. According to this theory, prey populations are conceptually divided into vulnerable and invulnerable states, with predators having access primarily to the vulnerable fraction at any given moment (Walters et al., 1997; Christensen and Walters, 2004).

A low vulnerability parameter (close to 1 or 2, as observed for many predator-prey pairs in this table) implies strong prey refuge or limited accessibility of prey to predators, resulting in a bottom-up controlled food web. Conversely, very high vulnerability values (as noted for some predator-prey pairs, e.g., North Baltic herring juvenile predation on stickleback with a value of 1e+08) suggest a scenario with limited prey refuge, effectively representing a top-down control where predator biomass strongly influences prey biomass dynamics. Such high values, often deliberately extreme, are typically used to simulate specific predator-prey relationships where predation intensity and trophic cascades are hypothesized to be dominant ecological drivers. The current vulnerability settings suggest differing ecological assumptions across trophic interactions. For instance, several key fish groups, such as cod, herring and sprat (both juvenile and adult), exhibit substantial vulnerabilities (ranging from approximately 17.8 to 56.4). These indicate that these groups are susceptible to predation. Conversely, the relatively low vulnerability assigned to top predators (e.g., seals and harbour porpoises with values around 2) indicates these species are less vulnerable to predation, consistent with their ecological roles.

4.1.1 Model fit and validation (modelled vs data)

To evaluate the performance of the Ecosim model, outputs were compared against observed time series from scientific surveys, stock assessments, and fisheries catch statistics over the period 2004–2019. Figures 7-11 present visual comparisons between modelled trajectories (lines) and empirical data (points) for biomass and catch across multiple functional groups. Additionally, goodness of fit (Sum of Squared differences; SS) is presented. A lower SS indicate a better fit to specific dataset, while high value shows potential issues with fitting.

The model captured the overall trends in seal biomasses (Figure 7) reasonably well, with the exception of ringed seals, where a mismatch was observed toward the end of the time series, suggesting potential issues with overestimation in recent years.

For Eastern Baltic (EB) cod, the modelled biomass showed considerable fluctuations; however, these fluctuations corresponded well with the trends observed in survey indices (BITS1) for juvenile cod. In the case of Western Baltic (WB) cod, the model did not fit the stock assessment results (SAM) well during the early years of the time series, but the fit improved substantially from 2008 onward. However, when compared to survey data (BITS1), the model fit was better at the beginning of the time series and worsened slightly in later years.

From the group grey seals have the lowest SS value indicating good fit of model estimates to data, while WB cod the highest indicating the misfit especially at the beginning of time-series. However for fisheating birds SS value is low, visual inspection of fit suggest rather poor fit, especially in the second half of time-series.

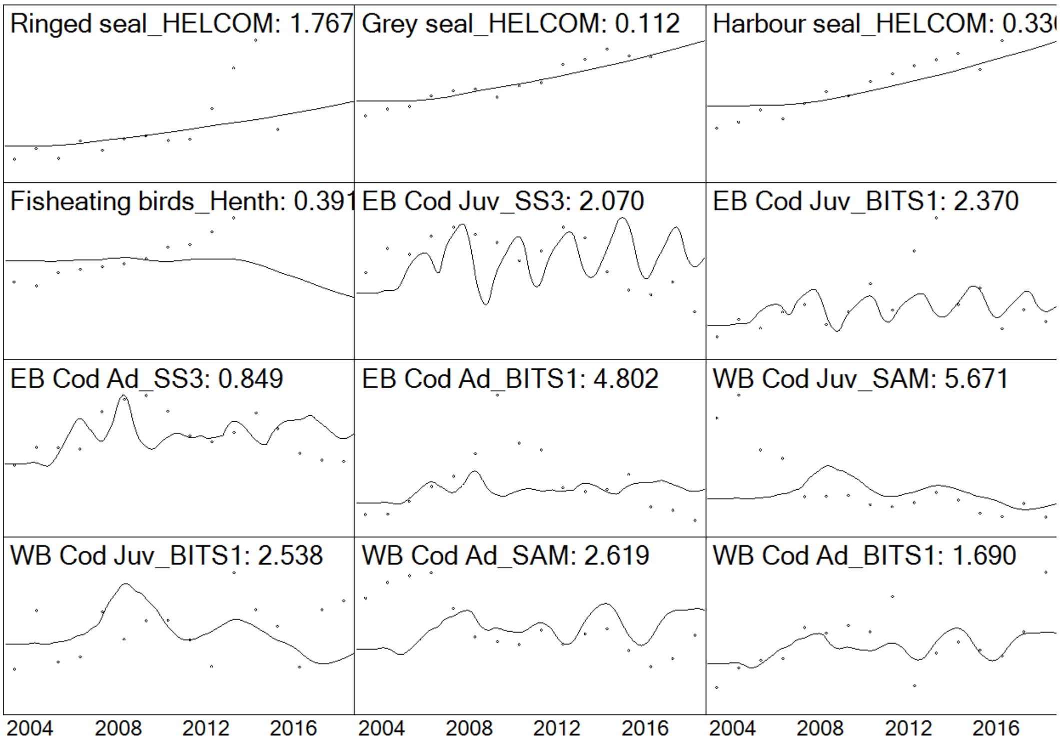

Figure 7. Fit of modelled biomasses (line) of higher trophic levels to survey or assessment (dots). Values indicate contribution of dataset to Sum of Squared differences (SS).

The model fit for Northern Baltic (NB) herring (Figure 8) was generally good, although the fit to the adult biomass from the stock assessment (SS3) was weaker, except during the middle of the time series where the model briefly captured observed trends. For Central Baltic (CB) herring the model showed reasonable agreement for adult survey-based indices (sur), though juvenile biomass exhibited excessive fluctuations not reflected in the data. For Western Baltic (WB) herring, the model provided its best performance (though fit to adult biomass from survey got the highest SS value), especially for adult biomass during 2010–2015. Juvenile WB herring fits were moderately accurate but failed to capture the highest peaks observed in survey data.

Among clupeids, the model fit for sprat biomass was the poorest. Adult sprat biomass from surveys was underestimated in both magnitude and variability, whereas the model fit for juvenile sprat was better aligned with observed patterns, particularly in the later part of the time series. Still, the model tended to overestimate biomass levels in years with known stock declines.

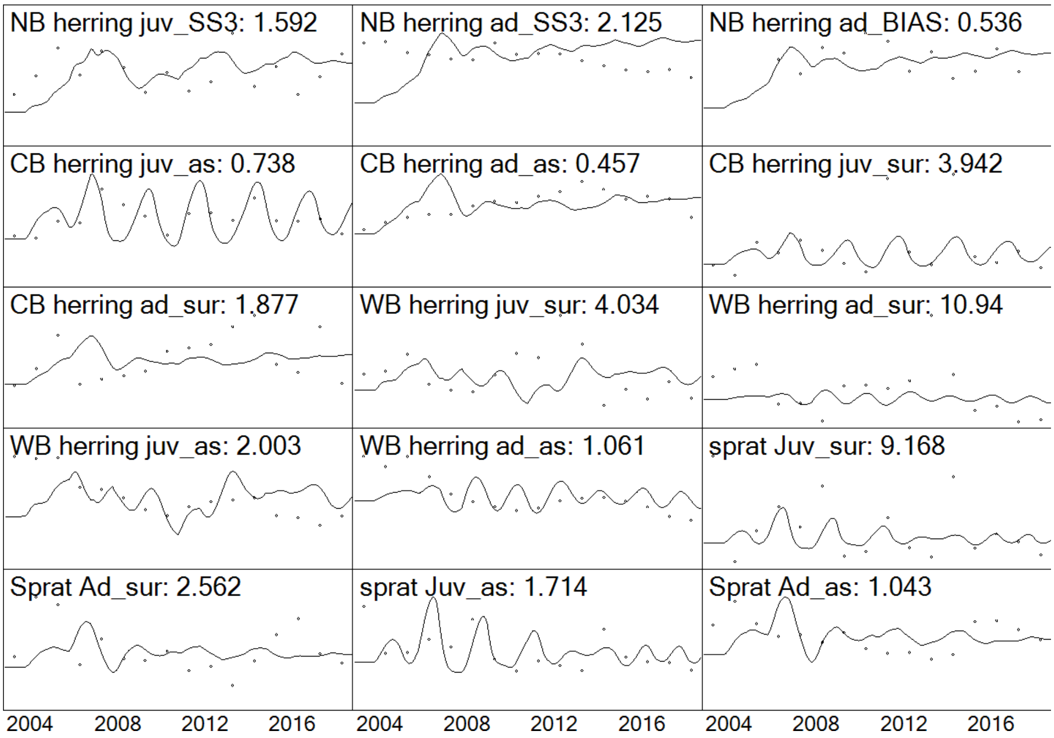

Figure 8. Fit of modelled biomasses (line) of clupeids to survey or assessment (dots). Values indicate contribution of dataset to Sum of Squared differences (SS).

The biomasses of other fish stocks (Figure 9) were generally well captured by the model, including vendace, stickleback, and flounder, with trajectories following the main patterns of survey data. However, some species, especially smelt and Northern and Central Baltic flounder, were modelled with high uncertainty.

Model fits for plaice, turbot, and dab were acceptable in early years but diverged from survey trends toward the end of the time series, with the model consistently underestimating observed biomasses. This discrepancy suggests either emerging ecological changes not accounted for in the model or limitations in survey catchability estimates.

Modelled salmon smolt biomass showed limited variation and underestimated the observed peaks, indicating potential issues in recruitment parameterisation.

Among zooplankton and bentic organisms (Figure 10) *Saduria, Acartia, Temora* and clasocerans had a good fit to data, while crabs and suspension feeders were completely and *Pseudocalanus* to a large extent misfitting data.

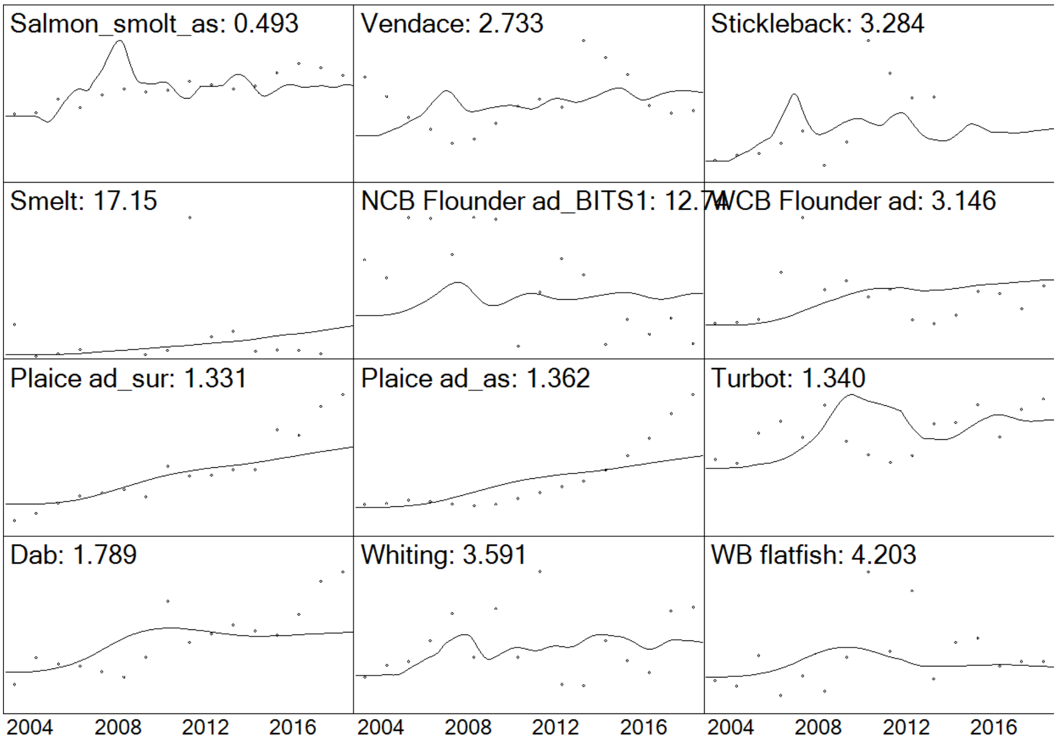

Figure 9. Fit of modelled biomasses (line) of other fish to survey or assessment (dots). Values indicate contribution of dataset to Sum of Squared differences (SS).

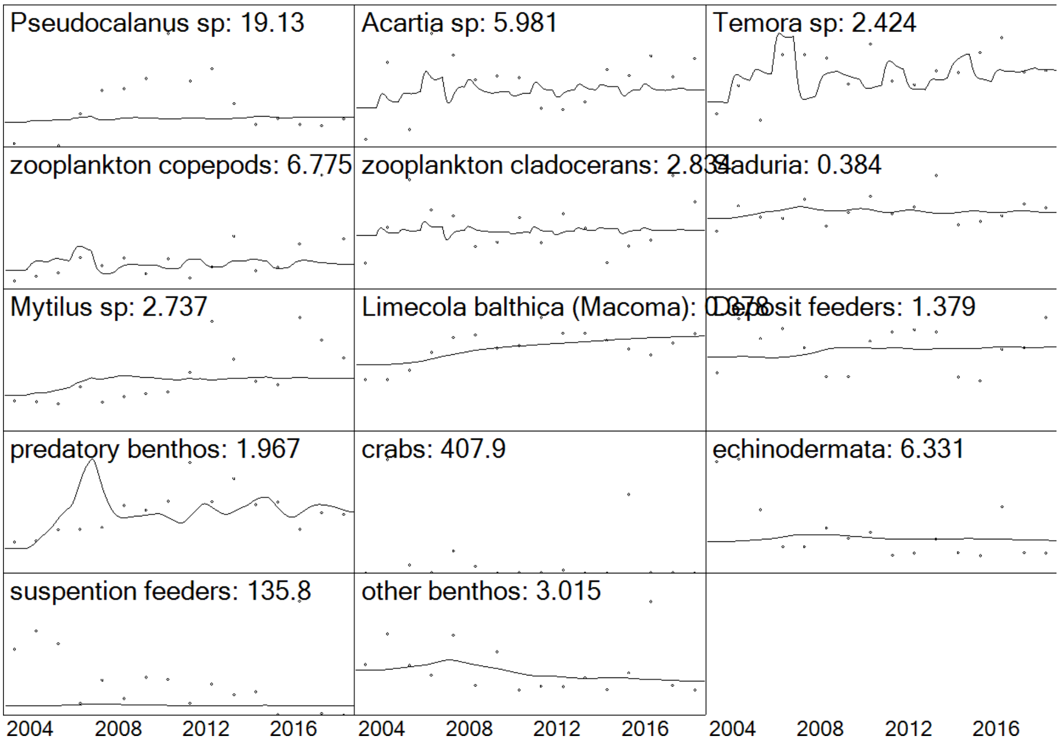

Figure 10. Fit of modelled biomasses (line) to zooplankton and benthos data (dots). Values indicate contribution of dataset to Sum of Squared differences (SS).

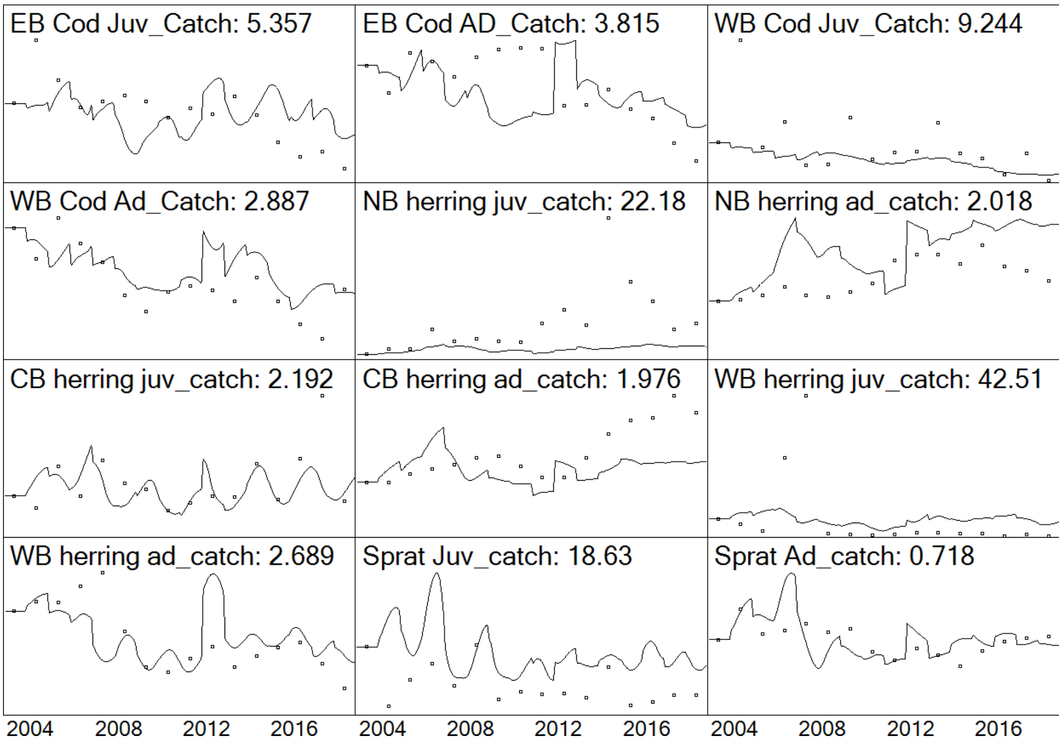

Figure 11. Fit of modelled catches (line) of cod and clupeids to data (dots). Values indicate contribution of dataset to Sum of Squared differences (SS).

Modelled catches of cod stocks and clupeids (Figure 11) show considerable temporal fluctuations, reflecting realistic dynamics in exploitation rates and stock variability. However, fit to observed catch data was weak overall, particularly for cod and juvenile herring.

For cod, juvenile catches in both the EB and WB regions were overestimated during several years, whereas adult catch trends were only moderately well captured. Fit to WB cod juvenile catch was relatively strong after 2008, consistent with biomass fit improvements (Figure 8).

For clupeids, Western Baltic herring adult catch aligned well with reported landings, while juvenile catches were overestimated resulting in largest SS value. Catch fits for sprat were more variable: adult sprat catch was reasonably represented, while juvenile sprat catch was notably overestimated, possibly due to overestimation of stock size or selectivity.

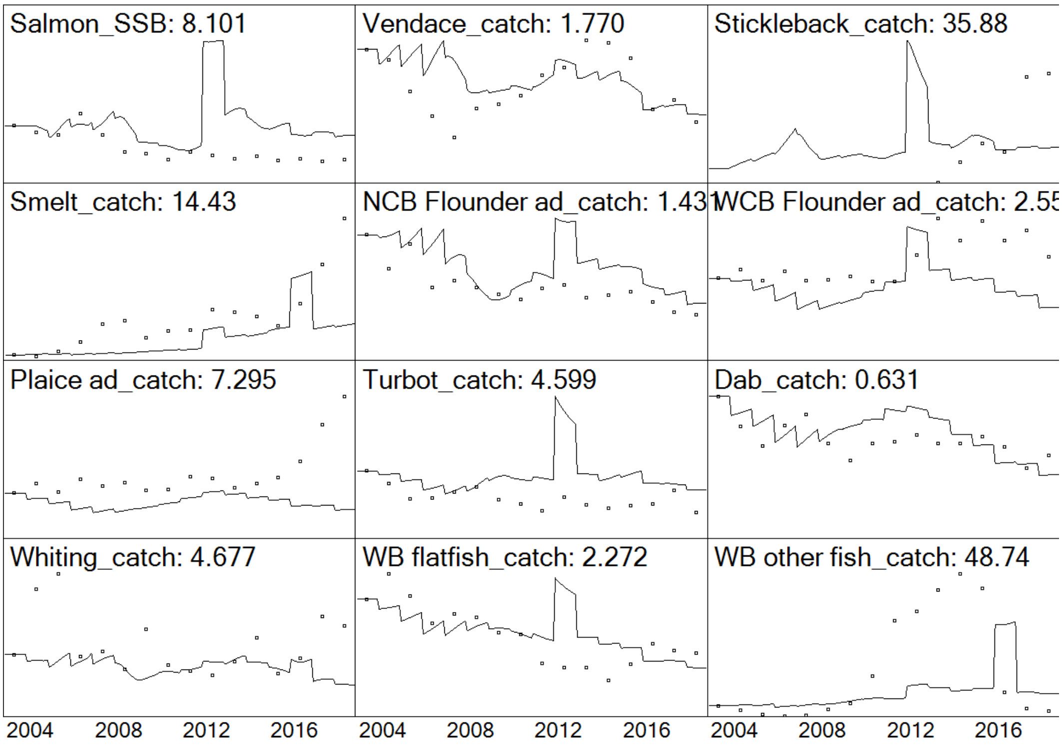

Figure 12. Fit of modelled catches (line) of other fish to data (dots). Values indicate contribution of dataset to Sum of Squared differences (SS).

Fit to catches of other fish groups (Figure 12) were generally good, except for WB other fish and stickleback (which got the highest SS values), however most of the groups reflect a strange artifact visible as a bump in the middle or end of the time-series.

Overall, the model reasonably reproduces observed trends in biomass and catches across major functional groups, especially for seals, herring, and juvenile cod. However, mismatches for some groups (e.g., smelt, sprat, ringed seals, flatfish) suggest areas, where further parameter refinement, improved environmental forcing, or consideration of additional ecological processes (e.g., migration, disease, unobserved predation) may enhance performance.

The model's ability to capture key interannual variability while maintaining ecological realism supports its utility for exploring ecosystem-based management scenarios. However, future refinements should focus on improving model-data fits for underperforming groups and validating assumptions about fishing selectivity, habitat use, and environmental sensitivity.

Evaluation of goodness of fit

To quantitatively evaluate the goodness-of-fit of the Ecosim model and provide an objective metric for comparing alternative parameterisations, Akaike's Information Criterion (AIC) and its small-sample correction (AICc) were calculated. These metrics balance model fit against complexity by penalising higher numbers of free parameters, making them particularly well suited for evaluating Ecosim calibration choices. For least-squares models such as Ecosim, AIC is computed as:

$$AIC = n \cdot \ln(RSS) + 2K,$$

where RSS is the residual sum of squares from the fitting procedure, *n* is the total number of empirical observations, and K is the number of estimated parameters (including one parameter representing residual variance). The corrected criterion AICc is defined as:

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$$

For the primary Ecosim calibration run, the model yielded a residual sum of squares of *RSS* = 985.6, based on *n* = 1421 observations and *K* = 44 fitted parameters. Substituting these into the equations gives:

$$RSS = 0.6936, \qquad \ln(RSS) = -0.3665,$$

$$AIC = -433.61, \ AIC_c = -430.73.$$

These strongly negative values indicate a comparatively good fit once model complexity is accounted for.

5. Discussion

The development of a full-scale Ecopath with Ecosim (EwE) model covering the majority of the Baltic Sea (ICES Subdivisions 22-32, excluding the Gulf of Riga) marks a significant step forward in holistic ecosystem modelling for this complex brackish water body. It provides a more integrated and ecologically coherent basis for understanding and managing the cumulative impacts of fisheries, eutrophication, and climate change under varying environmental regimes.

Previous EwE efforts in the Baltic Sea have been limited in spatial or functional scope. For instance, Bauer et al. (2019) constructed a well-resolved model for the Central Baltic Sea (ICES SDs 25-28), focusing primarily on mid-trophic level interactions and key pelagic species such as cod, herring, and sprat. Similarly, Western Baltic (Opitz & Froese, 2019), Finish Archipelago (Uusitalo et al. 2023), Gdansk Basin (Calkiewicz et al. 2019), Lithuanian coast, Gulf of Riga and Puck Bay (Tomczak et al. 2009) models have been developed, but these were largely confined to regional scale and national waters or focused on localized processes.

Compared to these regional models, the present Baltic-wide model provides a holistic spatial framework, capable of analysing cross-basin connectivity, regional productivity gradients, and the distributional dynamics of species that span multiple sub-basins. This spatial comprehensiveness is particularly important in the context of basin-specific hydrographic conditions (e.g. salinity, oxygen), which influence critical processes such as cod recruitment (Hinrichsen et al., 2011) and trophic interactions across benthic and pelagic subsystems.

A major strength of the model lies in its resolution of functional groups, particularly fish species structured by life stages (via multistanza groups), the inclusion of detailed zoobenthic and zooplankton taxa, and a top predator guild comprised of seals, seabirds, and harbour porpoise. These inclusions allow for realistic simulations of trophic dynamics and top-down controls, improving upon previous aggregated representations that could mask ontogenetic shifts and ecosystem feedbacks (Walters et al., 2008).

The model demonstrates generally good performance in reconstructing empirical time series for many functional groups (Figures 3-6). Biomass fits for top predators and juvenile cod are particularly strong, while adult clupeid dynamics are captured reasonably well. Nevertheless, biomass for some groups (e.g., smelt, mysids, ringed seals) and catch dynamics for sprat show room for improvement, indicating data limitations and the potential need for refined parameterisation or incorporation of ecological processes such as migration, density dependence, or disease.

As part of the evaluation of model performance, Akaike's Information Criterion (AIC) and its small-sample correction (AICc) were calculated to complement the visual assessment of model-data fit. These metrics provide an objective way to compare alternative calibration settings by balancing goodness-of-fit against the number of parameters estimated. For least-squares models such as Ecosim, AIC was calculated using the total number of observational data points (n), the residual sum of squares (RSS), and the number of fitted parameters (K). In the primary calibration run, the Ecosim model produced $RSS = 985.6$, based on $n = 1421$ observations and $K = 44$ fitted parameters. The resulting values (AIC = –433.61; AICc = –430.73) indicate a strong fit relative to the level of model complexity and provide a sound reference point for comparing future calibration variants. Incorporating AIC and AICc into the calibration workflow provides a transparent and reproducible basis for comparing alternative vulnerability patterns, forcing structures, or parameter sets, complementing visual inspection of model-data agreement. In interpreting these results, the AIC and AICc values support the conclusion that the current vulnerability structure and parameterisation achieve an efficient balance between explanatory power and parsimony. The negative values reflect a model that captures the main temporal dynamics of the Baltic Sea food web without excessive parameterisation. These criteria also establish a transparent basis for evaluating alternative Ecosim configurations, such as revised vulnerability patterns or forcing functions, ensuring that increases in complexity are accepted only when they result in demonstrably improved model performance.

The model is subject to several limitations. Some biomass inputs had to be estimated internally (e.g., for mysids and smelt) due to data unavailability, introducing parameter uncertainty. Catch fit performance is also variable, particularly in early years of the time series, possibly reflecting inconsistent fishing effort data or unreported discards. Additionally, the exclusion of the Gulf of Riga (due to its distinct hydrography and enclosed nature) means the model cannot account for ecological connectivity involving this sub-basin, including migration routes or larval dispersal. Another notable limitation is that the lower trophic levels, particularly microbial loops and phytoplankton phenology, are represented in a simplified manner. This may constrain the model's ability to fully capture bottom-up control mechanisms, which can be critical during periods of environmental perturbation or regime shifts.

The model provides a robust tool for informing ecosystem-based fisheries management (EBFM) and Marine Strategy Framework Directive (MSFD) implementation. Under MSFD, EU Member States are required to achieve Good Environmental Status (GES) across 11 descriptors, many of which are ecological (e.g., D1: Biodiversity, D4: Food webs, D3: Commercial fish and shellfish). EwE models directly contribute to Descriptors 3 and 4 by simulating trophic flows, biomass dynamics, and fisheries pressure. By integrating environmental drivers, this model also allows for scenario testing relevant to Descriptor 5 (Eutrophication) and Descriptor 7 (Hydrography). For instance, the model could be used to explore how nutrient reduction targets or salinity shifts due to climate change affect trophic transfer and stock productivity.

In the context of EBFM, the model supports:

- Multi-species harvest strategy evaluation, considering predator-prey feedbacks,
- Trade-off analysis between conservation goals (e.g., seal recovery) and fishing yields,
- Management Strategy Evaluation (MSE) to compare outcomes under different policy options, fishing effort allocations, or climate scenarios.

Furthermore, the model can help evaluate Good Environmental Status thresholds effects, for example, by simulating thresholds beyond which cod recruitment collapses due to hypoxia or low salinity (Lehmann et al., 2022).

To enhance model robustness and utility, several future developments are recommended:

- Adding environmental forcing variables (i.e. salinity, temperature, and nutrient concentrations) to link physical and biogeochemical processes to biological dynamics.
- Integration with coupled physical-biogeochemical models (e.g., ERGOM or GETM) to simulate fine-scale salinity and oxygen dynamics,
- Adding a spatial component of analysis (Ecospace)
- Bayesian parameter estimation or Monte Carlo simulation to incorporate uncertainty in key inputs,
- Inclusion of socio-economic layers (e.g., fleet dynamics, market responses) for full end-to-end modelling.

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Supplementary material

Table A1. Vulnerabilities of specific prey group to each of the predators.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1	Ringed seal																																												
2	Grey seal																																												
3	Harbour seal																																												
4	Harbour porpoise																																												
5	Fisheating birds																																												
6	EB Cod Juv		56.4					1																																					
7	EB Cod Ad	1E+08	56.4																																										
8	WB Cod Juv			23	2					1							1									1		1.4																	
9	WB Cod Ad			23	2																																								
10	Salmon	1E+08	56.4																																										
11	NB herring juv	1E+08	56.4								1		2.4																																
12	NB herring ad	1E+08	56.4								1																																		
13	CB herring juv		56.4				1.2	1			1				2									2.5																					
14	CB herring ad		56.4				1.2	1			1																																		
15	WB herring juv			23	2				17.8	1																1		1.4																	
16	WB herring ad			23	2				17.8	1																		1.4																	
17	Sprat Juv		56.4	23	2	1E+08	1.2	1	17.8	1	1						1							2.5		1		1.4																	
18	Sprat Ad		56.4	23	2	1E+08	1.2	1	17.8	1	1						1									1		1.4																	
19	Vendace	1E+08																																											
20	Stickleback	1E+08						1			1	1E+08	2.4											2.5																					
21	Smelt	1E+08	56.4					1																																					
22	NCB Flounder ad	1E+08	56.4																																										
23	WCB Flounder ad		56.4	23						1																																			
24	Plaice ad		56.4	23																								1.4																	
25	Turbot																																												
26	Dab			23																						1																			
27	Whiting				2																					1		1.4																	
28	WB flatfish			23																																									
29	WB other fish			23	2		1.2	1	17.8	1														2.5		1		1.4																	
30	Mysids						1.2	1	17.8	1		1E+08	2.4	1	2	2		1	1.1			1E+08		2.5				1.4									1								
31	Pseudocalanus sp											1E+08	2.4	1	2	2		1	1.1		1E+08																								
32	Acartia sp											1E+08	2.4	1	2	2		1	1.1		1E+08										2														
33	Temora sp											1E+08	2.4	1	2	2		1	1.1		1E+08										2														
34	zooplankton copepods																	1	1.1	2.8																					6.9				
35	zooplankton cladocerans											1E+08	2.4	1	2	2	1	1	1.1	2.8	1E+08										2										6.9				
36	Saduria						1.2	1	17.8	1													1	2.5		1																			
37	Mytilus sp																					1E+08	1	2.5													1					2	1		
38	Limecola balthica (Macoma)						1.2	1	17.8														1	2.5													1					2	1		
39	Deposit feeders						1.2	1							2																						1				6.9				
40	predatory benthos						1.2	1	17.8	1												1E+08	1	2.5				1.4																	
41	crabs																								1E+08				2.3																
42	echinodermata																								1E+08		2															2			
43	suspention feeders																						1	2.5						1E+08															
44	other benthos						1.2	1	17.8	1							1					1E+08	1	2.5	1E+08	1	2	1.4	2.3	1E+08															1
45	Primary producers											1E+08	2.4																		2	1	3.6	8.2	1E+08	1		3.7	2.4		6.9			1	
46	Detritus																													1E+08	2	1					1	3.7	2.4	1		2		1	1