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Title: Intermediate report for a pilot assessment for EU MSFD descriptor D4 food webs for Kattegat

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SUMMARY

This report presents a pilot assessment of the EU Marine Strategy Framework Directive (MSFD) Descriptor 4 (D4) – focusing on marine food webs – for the Kattegat region. The assessment employs the Ecopath with Ecosim (EwE) modelling framework, including its spatial component Ecospace, to analyze historical changes in the Kattegat ecosystem between 1982 and 2008. The objective is to evaluate the current state of the food web and provide a foundation for future operational food web assessments under the EU MSFD. Marine food webs are complex networks of trophic interactions that reflect ecological structure and ecosystem functioning. Understanding their dynamics is essential for assessing Good Environmental Status (GES) under Descriptor D4, which requires evaluating the diversity, abundance, size structure, and productivity of trophic guilds. Given the challenges of indicator development and data availability, the pilot utilizes a suite of ecological indicators derived from the EwE model and Ecological Network Analysis (ENA) to operationalize the D4 assessment criteria. Key findings show a regime shift in the Kattegat ecosystem from a pelagic-dominated to a benthic-dominated system, occurring between 1982 and 2008, in line with previous findings by Lindegren et al. (2012). This shift is reflected in changes to modelled biomass trends, spatial distributions, and multiple food web indicators. Important trends include a decline in cod and other pelagic species, a rise in plaice, seals, and benthic organisms, and alterations in trophic efficiency, biomass ratios, diversity indices, and system structure metrics such as Average Mutual Information (AMI) and Path Length. The spatial Ecospace component complements the temporal analysis by visualizing changes in biomass and indicator distribution across the Kattegat, although these outputs remain preliminary due to the model still being under development and validation.

In addressing the EU MSFD D4 criteria, the pilot proposes a set of indicators for each criterion, including:

- Diversity and abundance: Shannon Index, Kempton's Q, trophic levels.
- Trophic balance: Biomass ratios (e.g., demersal/pelagic), trophic efficiency.
- Size distribution: Mean length of fish, predatory biomass.
- Productivity: L index, AMI, primary production measures.

Despite being an initial effort, the study demonstrates the potential of the EwE modelling framework to support EU MSFD implementation by linking ecosystem structure, function, and resilience to food web indicators. The authors emphasize the need for further model refinement, threshold development, regional coordination, and uncertainty analysis to establish an operational assessment tool by 2024. Finally, the report provides a roadmap for future work, outlining key improvements needed to strengthen the model's robustness, expand the temporal scope, and support its application in management contexts, including alignment with HELCOM, OSPAR, and the ICES advisory processes.

1. INTRODUCTION

Background and Rationale

The EU Marine Strategy Framework Directive 2008/56/EC (MSFD) requires EU Member States to achieve Good Environmental Status (GES) in their marine waters by 2020, as measured through 11 Descriptors. Among these, Descriptor 4 (D4) focuses on marine food webs, with the goal that: "All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity."

Food webs are complex networks of trophic feeding interactions that span different levels of biological organization among species or populations. These networks characterize the structure and functioning of ecological communities and ecosystems. Marine food webs, in particular, are strongly size-structured (Sheldon et al., 1972; Kerr and Dickie, 2001). Recent research has highlighted the link between food web dynamics and ecosystem functioning by examining, for example, the energy transferred between trophic levels and the biomass consumption rates of species assemblages. This provides an energy budget representation of the food web. One effective method to analyse food web functioning is by aggregating species into functional groups based on shared ecological traits—such as habitat use, body size, feeding strategies, mobility, trophic level, and reproductive patterns. Trait-based aggregation enhances comparability across ecosystems and improves the understanding of how ecological communities respond to pressures. This approach is particularly useful when assessing the system's adaptability to various drivers, such as anthropogenic impacts (e.g., commercial fishing), bottom-up changes (e.g., variability in nutrient supply), and top-down controls (e.g., changes in predation pressure). The European Commission Decision 2010/477/EU, which was repealed and replaced by Decision (EU) 2017/848, defines four criteria for assessing food web structure and energy flow (see Table 1). However, these decisions do not provide explicit guidance on how to integrate these criteria into a comprehensive and holistic assessment. In response, the ICES WKGMSFDD4-II (Workshop on Guidance for the Review of MSFD Descriptor 4 – Food Webs, 2015) recommended shifting from species-specific assessments to a trophic guild-based approach. Trophic guilds are defined as groups of species that exploit the same resources in similar ways. This shift improves ecological relevance by emphasizing food web structure, function, and resilience. Guild-based assessments are more suitable for capturing emergent ecosystem properties such as trophic connectivity, redundancy, and energy transfer pathways. These advances have laid the foundation for using ecosystem modelling tools such as Ecopath with Ecosim (EwE), which simulate energy flows and trophic interactions among functional groups. This model enables the calculation of indicators aligned with MSFD D4 requirements and supports the development of operational frameworks for food web assessments. Although the revised Commission Decision outlines the criteria for D4, it does not specify how they should be synthesized into an integrated assessment. The MSFD Article 8 Assessment Guidance (EC, 2022) provides more detailed recommendations on this integration. The Kattegat pilot study will apply the EwE modelling framework in accordance with this guidance, using it to evaluate food web indicators that correspond with the D4 criteria. This effort will also contribute to refining future D4 assessments across European marine regions.

Table 1. The four criteria of the EU MSFD of descriptor D4 'food webs' in the revised Commission decision (EU) 2017/848 2017.

<table>
<tr><th>Criteria elements</th><th>Criteria</th><th>Methodological standards</th></tr>
<tr><td rowspan="4">Trophic guilds of an ecosystem.

Member States shall establish the list of trophic guilds through regional or subregional cooperation.</td><td>D4C1 – Primary:
The diversity (species composition and their relative abundance) of the trophic guild is not adversely affected due to anthropogenic pressures.
Member States shall establish threshold values through regional or subregional cooperation.</td><td rowspan="4">Scale of assessment:
Regional level for Baltic Sea and Black Sea; subregional level for North-East Atlantic and Mediterranean Sea.
Subdivisions may be used where appropriate.

Use of criteria:
Where values do not fall within the threshold values, this may trigger further research and investigation to understand the causes for the failure.</td></tr>
<tr><td>D4C2 – Primary:
The balance of total abundance between the trophic guilds is not adversely affected due to anthropogenic pressures.
Member States shall establish threshold values through regional or subregional cooperation.</td></tr>
<tr><td>D4C3 – Secondary:
The size distribution of individuals across the trophic guild is not adversely affected due to anthropogenic pressures.
Member States shall establish threshold values through regional or subregional cooperation.</td></tr>
<tr><td>D4C4 – Secondary (to be used in support of criterion D4C2, where necessary):
Productivity of the trophic guild is not adversely affected due to anthropogenic pressures.</td></tr>
</table>

2. POLICY AND MANAGEMENT NEEDS FOR FOOD WEB INDICATORS

EU MSFD Decision on D4 and Swedish national legislation
The implementation of the MSFD is governed by Commission Decision (EU) 2017/848. This decision, revised and published in May 2017, introduces the categorization of criteria as either primary (mandatory for reporting) or secondary (optional). The revised decision combines the assessment of ecosystems and food webs under Descriptor 4 (D4). According to this decision, D4 addresses the functional aspects of ecosystems, while Descriptor 1 (D1 – Biodiversity) focuses on the structural position of functional groups (e.g., pelagic feeders within bird populations) within the ecosystem.

Descriptor 4 consists of two primary and two secondary criteria (see Table 1). Each criterion, when reported, should cover at least three distinct trophic guilds, including at least one non-fish guild. Moreover, it is recommended that the selected trophic guilds represent the bottom, middle, and top levels of the food web. To ensure comparability between Member States, the definition of trophic guilds within a given region (e.g., the Greater North Sea, or the Baltic Sea) should ideally be determined through regional coordination. However, such coordination has not yet begun, and it is unlikely to be completed before the 2024 reporting deadline. As a result, assessments will need to proceed on a national basis. Under the revised decision, all criteria within D4 must be assessed against clearly defined thresholds. These thresholds are expected to be established at the regional level—covering either the entire Baltic Sea or specific sub-basins, where ecologically appropriate. The establishment of these thresholds again underscores the need for regional coordination and the development of surveillance indicators beyond 2018. If an indicator fails to meet its threshold, it should trigger further scientific investigation to identify the underlying causes. Currently, the indicators used for D4 assessments are still considered "surveillance indicators," reflecting their developmental status. D4 assessments are intended to be sensitive to broad ecosystem changes rather than to specific anthropogenic pressures. For the Baltic Sea, assessments are generally conducted at the regional scale (entire Baltic Sea) or sub-regional scale in the case of the Northeast Atlantic. Subdivisions (e.g., basins) may be applied if they are ecologically relevant. The spatial resolution of assessments may also be adjusted in response to the development of operational food web indicators and improvements in data availability beyond 2018.

3. A MODELLING APPROACH FOR THE ASSESSMENT OF THE EU MSFD DESCRIPTOR D4 ‘FOOD WEBS’

Food webs represent the networks of feeding interactions among species or populations that co-occur within ecological communities or ecosystems (Ulanowicz, 1980). These interactions are fundamental to the structure and functioning of ecosystems, as they determine how energy and nutrients flow through biological systems. Understanding food-web dynamics is essential to interpreting how ecosystems respond to biotic and abiotic changes, including anthropogenic pressures such as fishing. Disruptions to food webs can lead to significant structural and functional changes within ecosystems. Currently, there is limited information available on food web dynamics in the Kattegat region.

Moksnes et al. (2008) illustrated how trophic cascades influence eelgrass communities on the Swedish west coast. Their findings linked the effects of overfishing to increases in macroalgal blooms, which in turn impacted eelgrass beds and mesograzer populations. Similarly, Lindegren et al. (2012) described regulatory pathways in the Kattegat ecosystem, identifying a potential regime shift from pelagic to benthic dominance, driven in part by recovery from eutrophication and changes in environmental drivers.

Developing simple yet meaningful food web indicators that capture Good Environmental Status (GES) in the face of complex and dynamic ecosystem interactions is inherently challenging. However, the availability of ecosystem models has made it increasingly feasible to estimate food web indicators and evaluate their uncertainty. As noted by Korpinen et al. (2022), these models support the development of robust tools for ecosystem-based assessments. Ecosystem models enable the simulation of interactions within the food web and allow for scenario testing under varying pressures. This makes them valuable tools for assessing ecosystem responses and informing management decisions. Despite growing recognition of their utility, there remains a notable knowledge gap regarding the influence of food web dynamics on the structure and functioning of coastal ecosystems in the Kattegat. The EwE (Ecopath with Ecosim) modelling framework offers a promising approach to address this gap. EwE models food web interactions by simulating biomass flows and predator-prey dynamics. It provides a platform for deriving food web indicators that are directly relevant for management applications, particularly within the context of the MSFD Descriptor D4 (Bentley et al., 2019). EwE has proven especially useful for exploring ecosystem responses and quantifying indicators related to trophic structure, productivity, and resilience (Korpinen et al., 2022; Piroddi et al., 2021).

In this assessment, an EwE model previously developed for an adjacent area (Olsen et al., 2023) will be adapted for use in the Kattegat region. The model is designed to produce food web indicators at the level of trophic guilds, following the ICES (2015) recommendations and the GES criteria established under the MSFD. This approach will facilitate the integration of food web indicators into MSFD assessments, providing a scientifically grounded and policy-relevant basis for evaluating ecosystem status in the Kattegat.

4. PILOT ASSESSMENT OF THE EU MSFD DESCRIPTOR D4 ‘FOOD WEBS’ FOR KATTEGAT

Lindegren et al. (2012) documented key changes in the Kattegat ecosystem between 1982 and 2008, identifying a regime shift in trophic pathways. Their findings described a transition from a pelagic-dominated to a benthic-dominated system, driven by a combination of environmental and anthropogenic factors. Specifically, they outlined three distinct states in the system's development: a pelagic state (1982–1988), a transitional state (1989–1991), and a benthic state (1992–2008). These changes are reflected in alterations to biomass distribution, trophic structure, and food web stability.

To revisit and build upon these findings in alignment with the MSFD Descriptor D4, this project developed a pilot assessment using the EwE model tailored for the Kattegat ecosystem. The modelling approach enables the exploration of food web dynamics and ecosystem responses under varying conditions, offering quantitative indicators that can inform both national and regional assessments of GES.

This pilot assessment aims to address the following key objectives:

- To develop a strategic roadmap for improving future assessments of pelagic and benthic food webs in Swedish marine waters;
- To describe and assess the current state of the Kattegat food web, identifying structural and functional changes over time;
- To provide an initial set of food web and Ecological Network Analysis (ENA) indicators that are aligned with the MSFD D4 criteria;
- To support collaboration with the Swedish Agency for Marine and Water Management (SwAM) in advancing the integration of food web indicators into monitoring frameworks beyond 2023, with a focus on both temporal and spatial dynamics.

By addressing these objectives, the pilot assessment lays the groundwork for operationalizing ecosystem-based management tools in the Kattegat and contributes to the broader MSFD implementation across the Baltic Sea region.

5. METHODS

5.1 ECOPATH WITH ECOSIM (EWE) METHODOLOGY

Food webs represent the networks of feeding interactions among species or populations that co-occur within ecological communities or ecosystems (Ulanowicz, 1980). These interactions are fundamental to the structure and functioning of ecosystems, as they determine how energy and nutrients flow through biological systems. Understanding food-web dynamics is essential to interpreting how ecosystems respond to biotic and abiotic changes, including anthropogenic pressures such as fishing. Disruptions to food webs can lead to significant structural and functional changes within ecosystems. Currently, there is limited information available on food web dynamics in the Kattegat region.

Ecosystem models enable the simulation of interactions within the food web and allow for scenario testing under varying pressures. This makes them valuable tools for assessing ecosystem responses and informing management decisions. Despite growing recognition of their utility, there remains a notable knowledge gap regarding the influence of food web dynamics on the structure and functioning of coastal ecosystems in the Kattegat. The EwE (Ecopath with Ecosim) modelling framework offers a promising approach to address this gap.

We employed the Ecopath with Ecosim (EwE) approach as described by Christensen et al. (2005), comprising several components:

- **Ecopath**, a mass-balance static snapshot of the ecosystem,
- **Ecosim**, a dynamic module allowing temporal simulations and fitting to time series data,
- **Ecospace**, a spatial-temporal module for spatially explicit simulations (Stenback et al., 2013).

The core of Ecosim's dynamic modeling framework is the biomass dynamic equation, which describes the change in biomass of functional group over time as:

$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i$

Where:

- B_i – Biomass of functional group i
- g_i – Net growth efficiency of group i
- Q_{ji} – Consumption of group i by predator j
- Q_{ij} – Consumption by group i on its prey j
- I_i – Immigration into group i
- M_i – Natural mortality rate

- F_i – Fishing mortality rate
- e_i – Emigration rate

This formulation enables the simulation of time-dynamic responses of the ecosystem to changes in fishing pressure, environmental conditions, and species interactions.

Additionally, the ECOIND plug-in (Coll and Steenbeek, 2017) was used to extract ecological indicators from model outputs, helping to assess ecosystem status under different stressors. ECOIND calculates a range of ecological indicators relevant to ecosystem structure and function, including trophic level metrics, biomass ratios (e.g., pelagic to benthic), mean length of fish, and primary production required to sustain fisheries. These indicators are designed to track ecological responses to anthropogenic and environmental pressures and support the evaluation of MSFD D4 criteria.

The **Ecological Network Analysis (ENA)** plug-in was also employed to compute systemic properties of the food web based on network theory. ENA calculates indices such as system throughput, ascendency, redundancy, average mutual information (AMI), and Finn's cycling index. These indices offer insights into the stability, efficiency, and resilience of the ecosystem, and are particularly valuable for characterizing the overall health and structure of food webs. Results from ECOIND and ENA are explored further in later sections of this report.

5.2 KATTEGAT ECOPATH WITH ECOSIM (EWE) MODEL

The Kattegat food web model is composed of 29 biological groups that characterize the main ecological components and trophic flows within the region's marine ecosystem (see Figures 1 and 2). These groups are structured into a network of 39 nodes interconnected through 257 trophic links, representing feeding interactions.

The functional groups in the model include:

- **Primary producers**: phytoplankton, benthic microalgae, and perennial macroalgae (Fucus spp.),
- **Zooplankton**: two groups, namely gelatinous zooplankton and mesozooplankton,
- **Benthic invertebrates**: six groups comprising molluscs, Nephrops, polychaetes, echinoderms, and shrimp/mysis,
- **Fish**: 11 species, with three of them further divided into juvenile and adult life stages (e.g., cod, dab), covering both commercial and non-commercial species,
- **Top predators**: offshore fish-feeding birds, seals, and harbour porpoise.

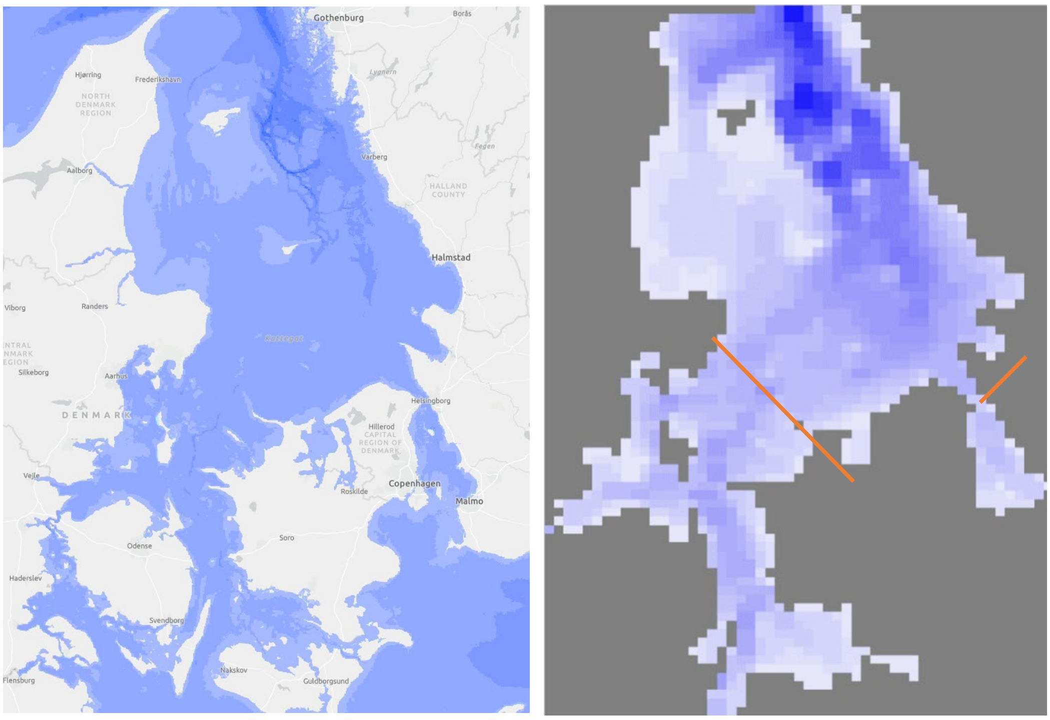


Figure 1. Study area (Kattegat) (left panel) and full Kattegat model domain (right panel). Please note that current analysis are restricted to Kattegat only - see orange lines.

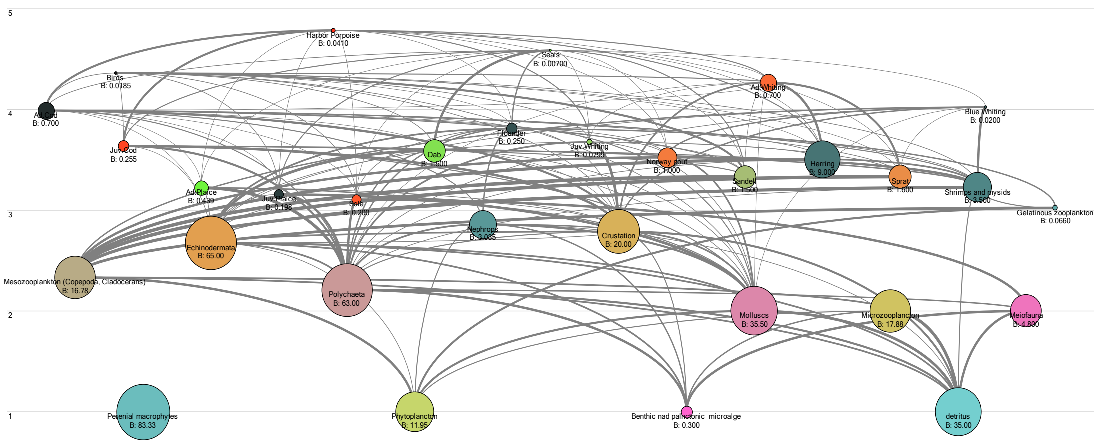


Figure 2. Kattegat Ecopath with Ecosim (EwE) model food-web structure. This figure illustrating the relationship between the trophic groups and shows the complexity of the topological position of the food web nodes. The model is composed of 29 biological groups, that characterize the main ecological components and trophic flows within the region's marine ecosystem, and are structured into a network of 39 nodes interconnected through 257 trophic links, representing feeding interactions (see Figures 1 and 2).

The initial Ecopath model was parameterized using data from the year 1982, which serves as the baseline for the ecosystem's structure and energy flow. This configuration reflects the state of the Kattegat food web prior to the observed regime shift and provides the foundation for the temporal simulations conducted with Ecosim.

The temporal Ecosim model for the Kattegat covers the period from 1982 to 2008 to capture the ecosystem regime shift described by Lindegren et al. (2012). This shift marks a transition from a pelagic-dominated to a benthic-regulated system. The model integrates a range of calibration data, including biomass estimates across nearly all trophic levels (sourced from field surveys and other ecosystem models), fishery catch and landing statistics, and environmental variables such as chlorophyll-a concentrations.

Model calibration was performed by fitting simulated outputs to observed time series data (Figure 3), ensuring ecological realism and consistency with known tropho-dynamic constraints, following the principles outlined by Link (2019) and Heymans et al. (2016). The dynamics of the system are driven by trophic interactions, fishing effort, and multiple environmental forcing functions. These include primary production, sea surface temperature (SST), and the extent of hypoxic bottom areas. Additionally, seal biomass was used as a proxy to represent top-down control by marine predators.

The calibrated Ecosim model reproduced observed biomass trends and variability reasonably well, capturing key patterns and fluctuations seen during the modelled period (Figure 3). Nevertheless, while the model's performance is satisfactory for qualitative and preliminary quantitative assessments, further validation is necessary. Future steps should include sensitivity testing and uncertainty analyses to better quantify the robustness of model predictions and improve confidence in its use for management applications.

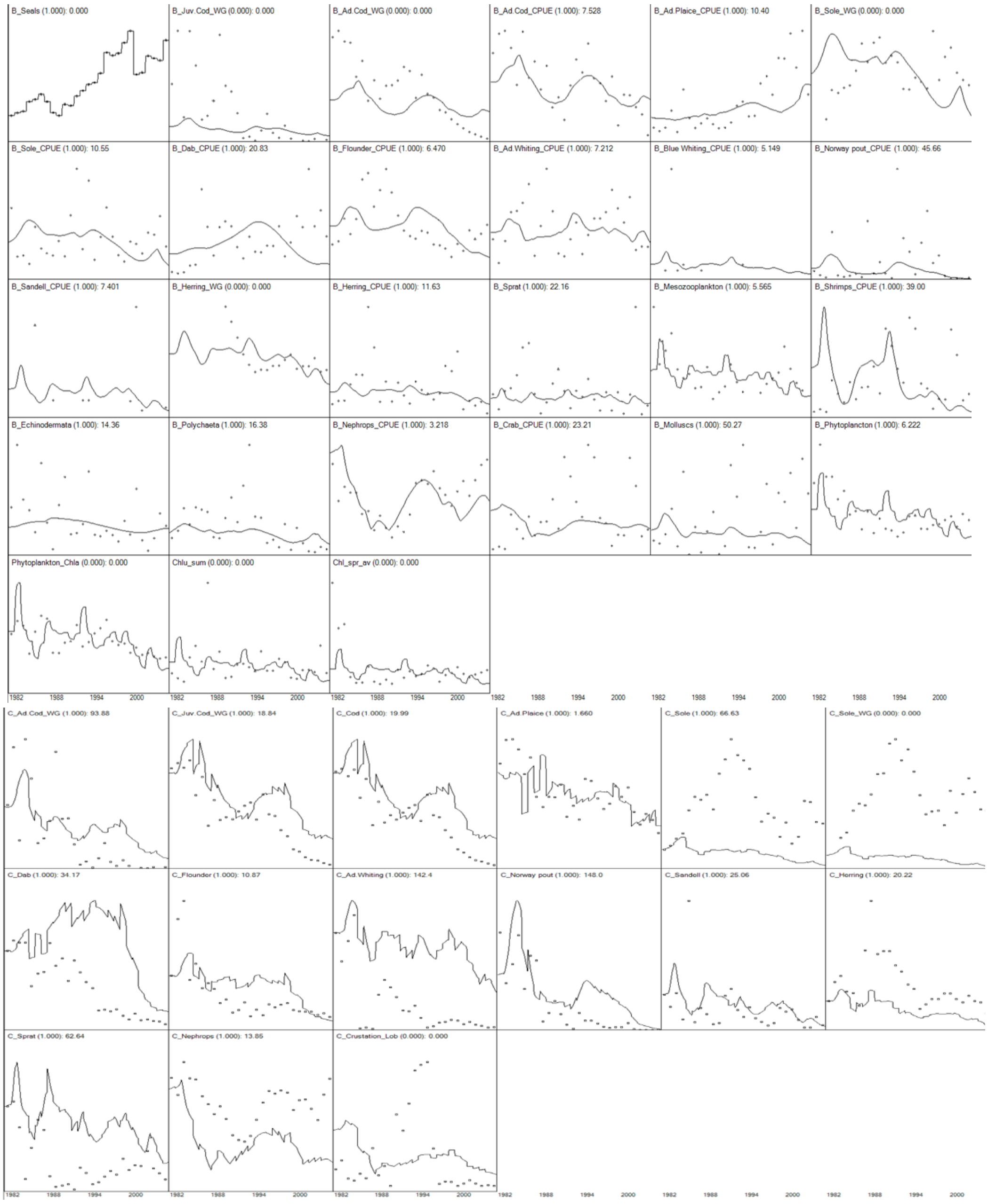


Figure 3. Kattegat Ecosim model fit. Lines are model estimates, dots are observations/input data. Upper panel fit for biomass and survey data, lower panel – fit to landings.

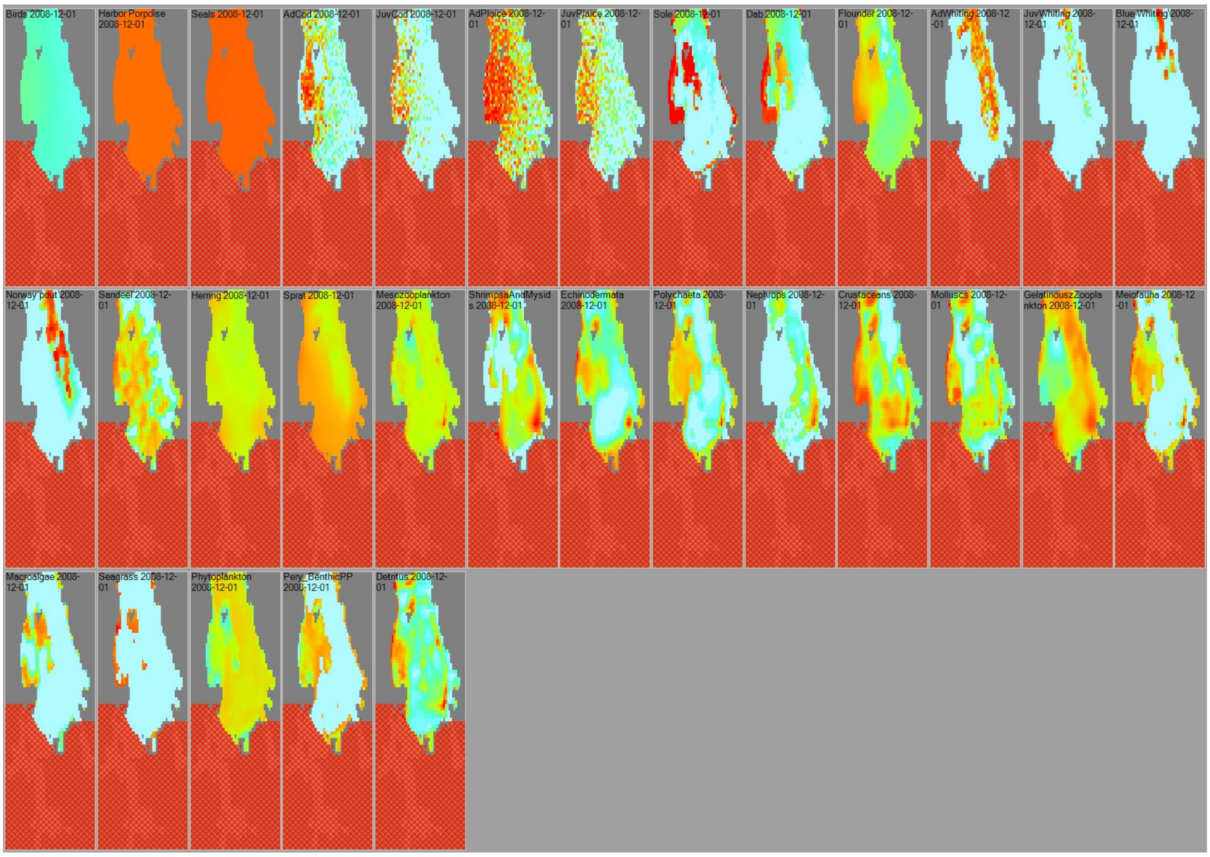


Figure 4. Example of model output. Spatial maps of biomass distributions. The figure shows Kattegat (see Figure 1)

Ecospace is the spatially explicit module of the Ecopath with Ecosim (EwE) modelling framework, designed to simulate ecological processes and food web interactions across a geospatial grid (Pauly et al., 2000; Christensen et al., 2014; Romagnoni et al., 2015). It extends the temporal dynamics of Ecosim by incorporating a spatial structure composed of land and water grid cells, also referred to as the basemap. In Ecospace, functional groups interact dynamically within water cells, and their distributions and interactions are governed by modified Ecosim equations.

One of the critical differences between Ecospace and Ecosim is the enhanced representation of species life histories and spatial behaviour (Walters et al., 2010). Ecospace introduces the concept of habitat capacity, which plays a central role in determining predator-prey interactions.

Habitat capacity in a grid cell is defined as the relative suitability of that cell to support a given functional group, depending on environmental conditions and the group's tolerance or preference for those conditions. Specifically, low habitat capacity for a consumer group results in reduced prey vulnerability within that cell—i.e., predators become less effective in low-quality habitats (Christensen et al., 2014).

Habitat capacity is determined by two main factors:

1. **Environmental suitability**, defined by a group's response functions to multiple environmental drivers (e.g., temperature, salinity, oxygen levels), and
2. **Biotic interactions**, including predation and fishing pressure in the cell.

Thus, habitat capacity reflects both the abiotic environment and local ecological dynamics. Cells with high capacity are more likely to retain biomass, while organisms are more likely to emigrate from cells with low capacity.

The Kattegat spatial domain is defined in Ecospace using 4 km × 4 km grid cells, covering the area north of the Danish Straits (Figures 1 and 4). At model initialization, biomasses of functional groups are spatially distributed according to their respective relative habitat capacities. These distributions evolve over time through trophic interactions, species dispersal, and fishing, eventually reaching a dynamic spatial equilibrium. Before applying any spatio-temporal forcing, the model undergoes a spin-up period under stable conditions to stabilize the biomass distributions.

Species dispersal is represented by the redistribution of biomass among adjacent grid cells based on each group's **basal migration rate**. Migration is inversely proportional to local habitat capacity: functional groups are more likely to remain in suitable habitats and leave cells with poor environmental or ecological conditions.

Fishing pressure in Ecospace is also spatially distributed. Fishing effort by each fleet is allocated to cells using a **gravity model**, where the attractiveness of a cell (based on expected catch and profitability) influences the distribution of fishing activity. The fishing mortality exerted by each fleet on target species in a specific cell is proportional to the fleet's allocated effort in that cell.

To configure Ecospace, spatially explicit **driver maps** were developed for a suite of environmental parameters, including:

- Bathymetry
- Sea Surface Salinity
- Bottom Salinity
- Annual mean Sea Surface Temperature (SST)
- Summer Sea Surface Temperature (SST_summer)
- Bottom Temperature
- Bottom Oxygen Concentration
- Bottom Oxygen Saturation

- Area with low oxygen concentrations (2–0.5 ml/l)
- Area with hypoxia (oxygen <0.5 ml/l)
- Mid-water temperature in spring (at 50m depth)
- Muddy bottom area
- Sandy bottom area

These driver maps were generated using output from the RCO-SCOBI model or obtained from the HELCOM Map and Data Service (www.helcom.fi). Additionally, we used the yearly production-to-biomass ratio of phytoplankton as a proxy for relative primary production to inform the spatial distribution of productivity.

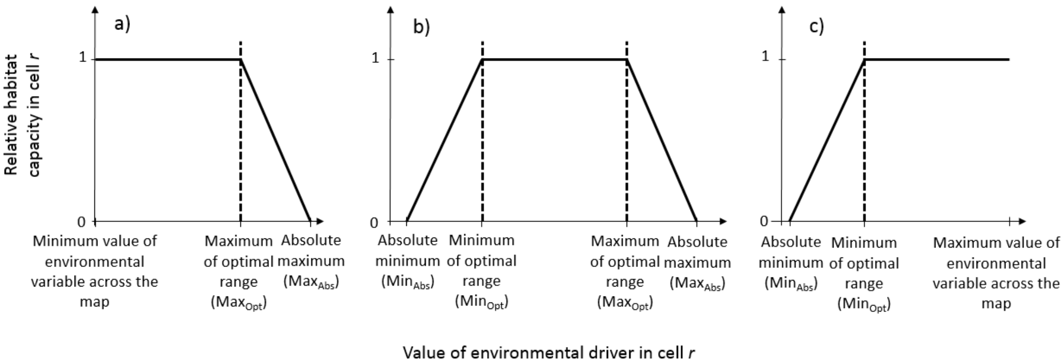


Figure 5. shapes and parameters of environmental response functions (ERF). Cells with environmental driver values lower than MinAbs or higher than MaxAbs are completely unsuitable for the functional group, while habitat capacity in relation to the given driver is maximal a) at values below MaxOpt (left-shoulder shaped ERFs), b) between MinOpt and MaxOpt (trapezoid shaped ERFs) and c) above MinOpt (right-shoulder shaped ERFs).

To parameterize environmental response functions (ERFs) in the Ecospace model, we collected information from species distribution modelling literature, particularly regarding how functional groups and species biomasses respond to abiotic factors (Clemmesen et al., 2016). These ERFs define how habitat capacity for a functional group varies across environmental gradients.

We applied three generic shapes of ERF:s to represent species–environment relationships:

- **Left-shoulder**: suitability declines when values are too high;
- **Right-shoulder**: suitability declines when values are too low;
- **Trapezoid**: suitability is optimal over a preferred range, with lower suitability at both extremes.

These function types are illustrated in Figure 5. The selection of a specific ERF shape for a group-environmental driver pair does not reflect inherent ecological traits of the group itself. Instead, it reflects the extent to which the environmental gradient in the Kattegat encompasses the group's optimal range. A trapezoid ERF implies that the full preference range is represented, while left- or right-shoulder ERF:s indicate that the group may only be constrained by high or low extremes of that variable in this ecosystem.

Habitat capacity is dynamically influenced by these ERFs during simulation. The values of environmental drivers in each grid cell are matched against species-specific ERFs to compute a cell-specific habitat suitability score. These scores then interact with food web processes, fishing pressure, and species movement to determine local biomass distributions.

It is important to note that the current Ecospace model is still under development and undergoing validation. As such, the outputs—including spatial patterns of biomass, catches, and spatial indicators—are considered preliminary. They are presented here to illustrate model progress and provide early insights into the spatial dynamics captured so far. Further model refinement, calibration, and validation will be necessary to improve reliability before applying the model in operational assessments.

5.3 DATA ANALYSIS; FOOD WEB INDICATORS, ENA INDICES

Following the methodologies outlined in Tomczak et al. (2013) and Heymans and Tomczak (2016), we performed a multi-tiered analysis of the Kattegat food web to explore changes in biomass, ecosystem properties, and food web dynamics, with a particular focus on evaluating the regime shift previously described by Lindegren et al. (2012). The work by Tomczak et al. (2013) and Heymans and Tomczak (2016) demonstrated how ecosystem modelling outputs—specifically from EwE—can be used to calculate food web indicators and Ecological Network Analysis (ENA) indices, and how these metrics can be interpreted over time to detect structural shifts in ecosystem function and trophic pathways.

In this study, we addressed the following key features:

- **Observed biomass trends**: Testing for significant changes in the input biomass data (based on surveys and observations) to evaluate consistency with the findings of Lindegren et al. (2012);
- **Modelled biomass trends**: Assessing the temporal dynamics of simulated biomass outputs to detect shifts from pelagic to benthic-dominated trophic pathways;
- **Food web and ecosystem indicators**: Analysing ENA indices and food web indicators derived from EwE model outputs in the context of MSFD Descriptor D4 requirements.

To identify regime shifts in the Kattegat ecosystem, we applied the Integrated Trend Assessment (ITA) method developed by Diekmann and Möllmann (2010). The ITA method was applied to both input (observed) and model-based variables, including environmental drivers, functional group biomasses, and ENA-derived indicators. The ITA comprises the following analytical steps:

- **Principal Component Analysis (PCA)** was conducted using the correlation matrix of log-transformed data (ln + 1) for the selected variables. PCA reduces multidimensional data to principal components that describe the main trends in the data.
- The **PC scores** for the first and second components were extracted and analysed to trace the temporal evolution of the system.

These trajectories were used to visualise and assess whether the system underwent a directional shift over time, consistent with a structural regime shift in the food web. This combined approach provides a robust framework to examine both observed and model-simulated changes, offering insight into whether the observed regime shift corresponds with changes in ecosystem structure and function across multiple trophic levels.

5.4 ECOLOGICAL NETWORK ALALYSIS (ENA) AND MODEL-BASED INDICES (ECOIND)

To evaluate the structural and functional dynamics of the Kattegat ecosystem, we extracted a suite of indicators from the Ecopath with Ecosim model using two complementary approaches: **Ecological Network Analysis (ENA)** and the **EcoInd plug-in**. These indicators help assess food web organization, biodiversity, trophic functioning, and resilience, and are particularly relevant for meeting MSFD Descriptor D4 requirements. A full list of definitions, units, and references for each indicator is available in Supplementary Tables S1 and S2.

Ecological Network Analysis (ENA) Indices

The ENA indices were derived from the **Ecosim** simulations using network-based methods described in Heymans et al. (2007). These indices quantify emergent properties of the ecosystem, including information flow, redundancy, and structural organization. The selected ENA indices include:

- **Primary Production (PrimProd)**: Total system primary production, an indicator of the base energy input.
- **Shannon Diversity**: Measures community complexity based on biomass distribution.
- **Kempton's Q-index**: Biodiversity index sensitive to changes in evenness and richness.
- **Trophic Level of the Catch (TLc)**: Mean trophic level of species caught by fisheries.
- **Community Trophic Levels**:
    - **TL ≥ 3.25**: Biomass-weighted trophic level for higher trophic species.
    - **TL ≥ 2**: Represents broader food web contributions.

- **Community TL**: Mean trophic level across all functional groups.

- **Total Trophic Efficiency (Total TE)**: Reflects energy transfer efficiency from lower to higher trophic levels.
- **Path Length**: Average number of trophic steps between primary producers and top predators.
- **Overflow**: Indicates recycling and redundancy in trophic pathways.
- **Average Mutual Information (AMI)**: Quantifies how structured and efficient the food web is; higher values indicate more specialized and predictable interactions.
- **L-index**: Integrates energy requirements of the fisheries relative to primary production, trophic level of catch, and transfer efficiency; higher values may indicate ecosystem stress (Ulanowicz, 2004; Libralato et al., 2008).

These ENA indices, computed from Ecosim, were used in time series analyses to evaluate system-level responses to pressures and changes over the study period.
EcoInd Indices
In parallel, we extracted a complementary set of ecological indicators using the **EcoInd plug-in** developed for EwE (Coll and Steenbeek, 2017). These indicators were derived from both **Ecosim** and **Ecospace** outputs to reflect spatial and temporal changes in community structure and function. Selected EcoInd indices include:

- **Mean Length of Fish in the Community (MLoffishcommunity)**: Proxy for size structure and fishing pressure.
- **Demersal-to-Pelagic Biomass Ratio (DemersalperPelagicB)**: Indicates changes in dominance between benthic and pelagic pathways.
- **Invertebrates-to-Fish Biomass Ratio (InvertebratesperFishB)**: Tracks bottom-up support relative to predatory pressure.
- **Commercial Biomass (CommercialB)**: Biomass of commercially important species.
- **Predatory Biomass (PredatoryB)**: Biomass of higher trophic level predators.

These EcoInd indicators provide additional insight into community structure, biodiversity, and potential shifts in ecological balance. Some were computed from Ecosim, while others—especially those involving spatial variation—were extracted from Ecospace. All indices were calculated for the period 1981–2008. Time series trends were analysed using Integrated Trend Assessment (ITA) to examine long-term dynamics. Selected indicators were mapped to illustrate spatial variability and emerging food web patterns. Together, the ENA and EcoInd indicators demonstrate the model's ability to describe not only biomass and catch dynamics, but also deeper aspects of ecosystem functioning, spatial reorganization, and resilience.

6. RESULTS

6.2 OBSERVED DATA (MODEL VALIDATION)

The observed data used for model validation are the same as those used during the calibration phase, providing a consistent baseline for evaluating model performance.

The observed data used as model calibration biomass, displayed in Fig. 6, clearly illustrate the main trends in the Kattegat ecosystem over the period from the 1980s to the early 2000s. These patterns confirm the regime shift described by Lindegren et al. (2012), highlighting a transition from a pelagic- to a benthic-dominated food web.

The figure reveals consistent declines in several pelagic indicators, including phytoplankton (both biomass and chl-a), mesozooplankton, herring, sprat, and cod (both juvenile and adult stages). In contrast, there is a clear increase in multiple benthic components such as shrimps, Nephrops, molluscs, and adult plaice. These trends are further supported by declines in trophically linked species like microzooplankton and polychaetes, and a general decrease in pelagic fish CPUE (e.g., whiting, Norway pout, juvenile cod).

Meanwhile, benthic species (e.g., dab, flounder, Nephrops) and demersal-feeding species show stable or increasing CPUE over time, aligning with the system's shift to a more benthic food web dynamic processes. Additionally, increases in top predators like seals are evident, suggesting changes in top-down control.

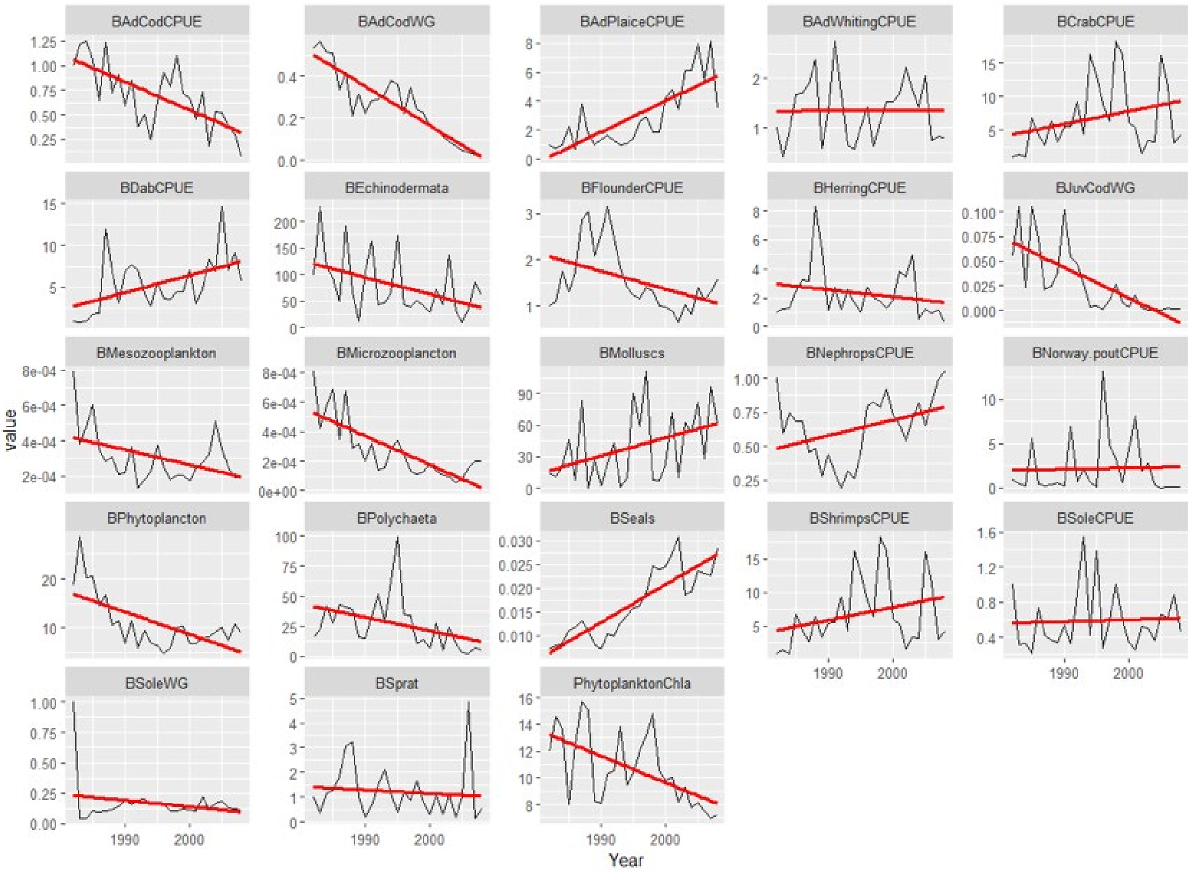


Figure 6. Displayed trend on model calibration biomass.

The Principal Component Analysis (PCA) performed on the observed dataset (Fig. 7 left panel) further highlights the dominant ecological gradients within the Kattegat ecosystem over time. The first principal component (PC1) captures a major trend characterized by a decline in cod, echinoderms, and planktonic groups, and a concurrent increase in benthic and demersal species such as seals, plaice, dab, and molluscs. This axis reflects the overall pelagic-to-benthic transition identified in the biomass data.The second component (PC2) represents a contrasting pattern, with a rise in Nephrops and sole and a decline in flounder, whiting, and herring, suggesting secondary ecological shifts within the benthic domain.

The temporal trajectory shown in Fig. 7 right panel, visualizes ecosystem dynamics along these principal components. The year 1982 is marked by high biomasses of phytoplankton, mesozooplankton, and adult cod, while the ecosystem state in 2008 reflects higher biomasses of seals and adult plaice. This shift in system structure is consistent with the observed reduction in cod biomass and the resulting changes in predator-prey relationships within the food web.

The PC1 scores (solid line) in Fig. 7 right panel, display a gradual and persistent upward trend from the early 1980s to 2008, reflecting a long-term directional shift in the ecosystem toward benthic dominance and increased biomass of top predators like seals. In contrast, the PC2 scores (dashed line) fluctuate more sharply over time, suggesting episodic or more variable shifts related to species such as Nephrops, sole, flounder, and whiting. This temporal PCA pattern highlights both a gradual transformation in ecosystem structure (PC1) and additional short-term variability (PC2), capturing the complex nature of food web reorganization in the Kattegat.

These PCA results complement the observed biomass trends and reinforce previous findings by Lindegren et al. (2012), offering a robust synthesis of how the Kattegat food web has evolved over recent decades.

In support of these patterns, the traffic-light plot for the modelled biomass (Fig. 8) provides a visual summary of the direction and magnitude of biomass changes between 1982 and 2008. The plot uses a color-coded system—green indicating increases, red indicating decreases, and yellow for stable or intermediate trends. Species and functional groups such as phytoplankton, zooplankton, cod, and herring show notable declines (highlighted in red), while increases (highlighted in green) are observed for benthic species such as shrimps, Nephrops, molluscs, and adult plaice, as well as seals.

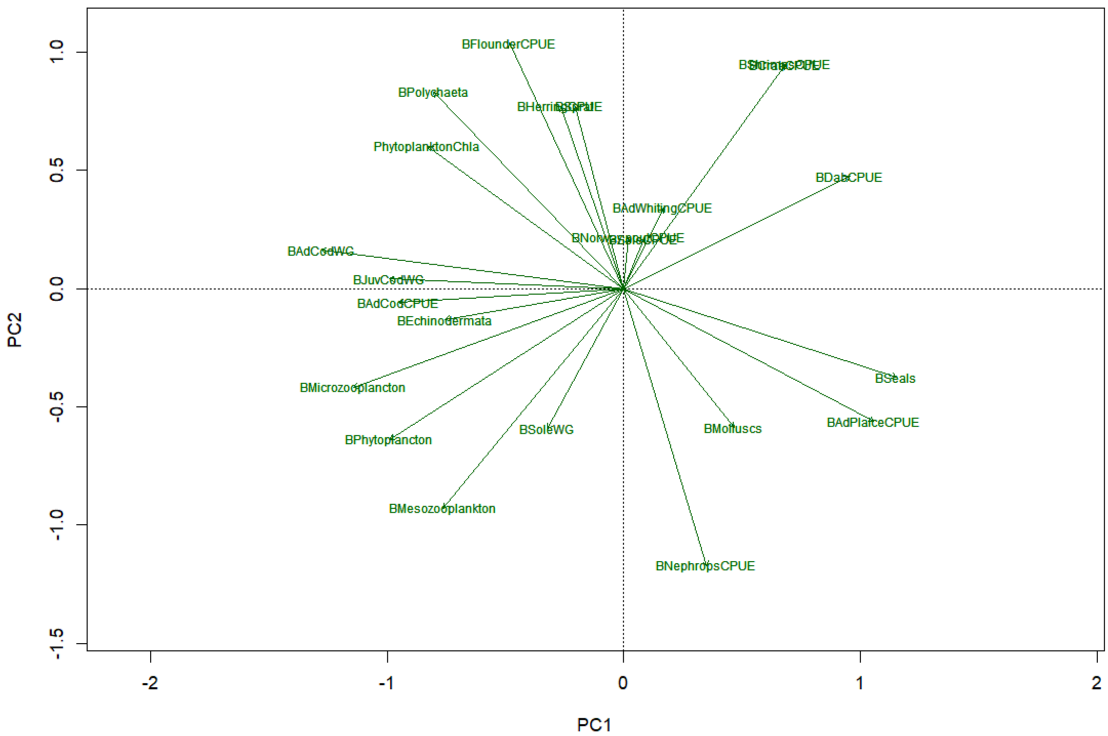


Figure 7. Principal Component Analysis (PCA) on observed biomass, left panel - PC loading, right panel PC scores over time

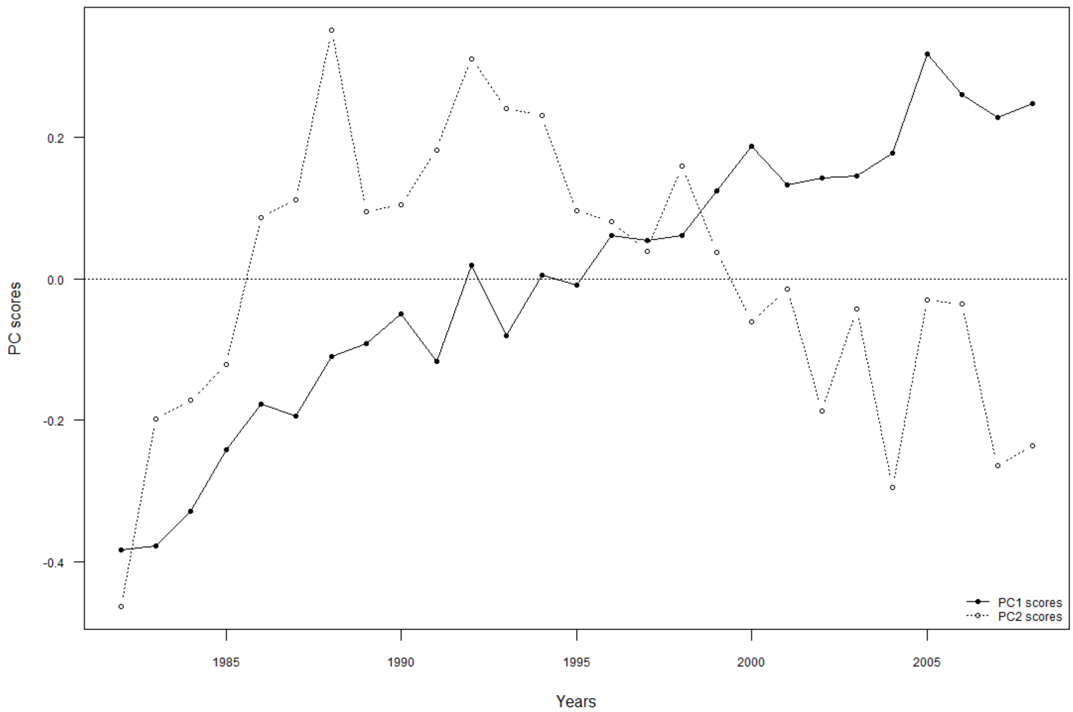


Figure 7. Principal Component Analysis (PCA) on observed biomass, left panel - PC loading, right panel PC scores over time

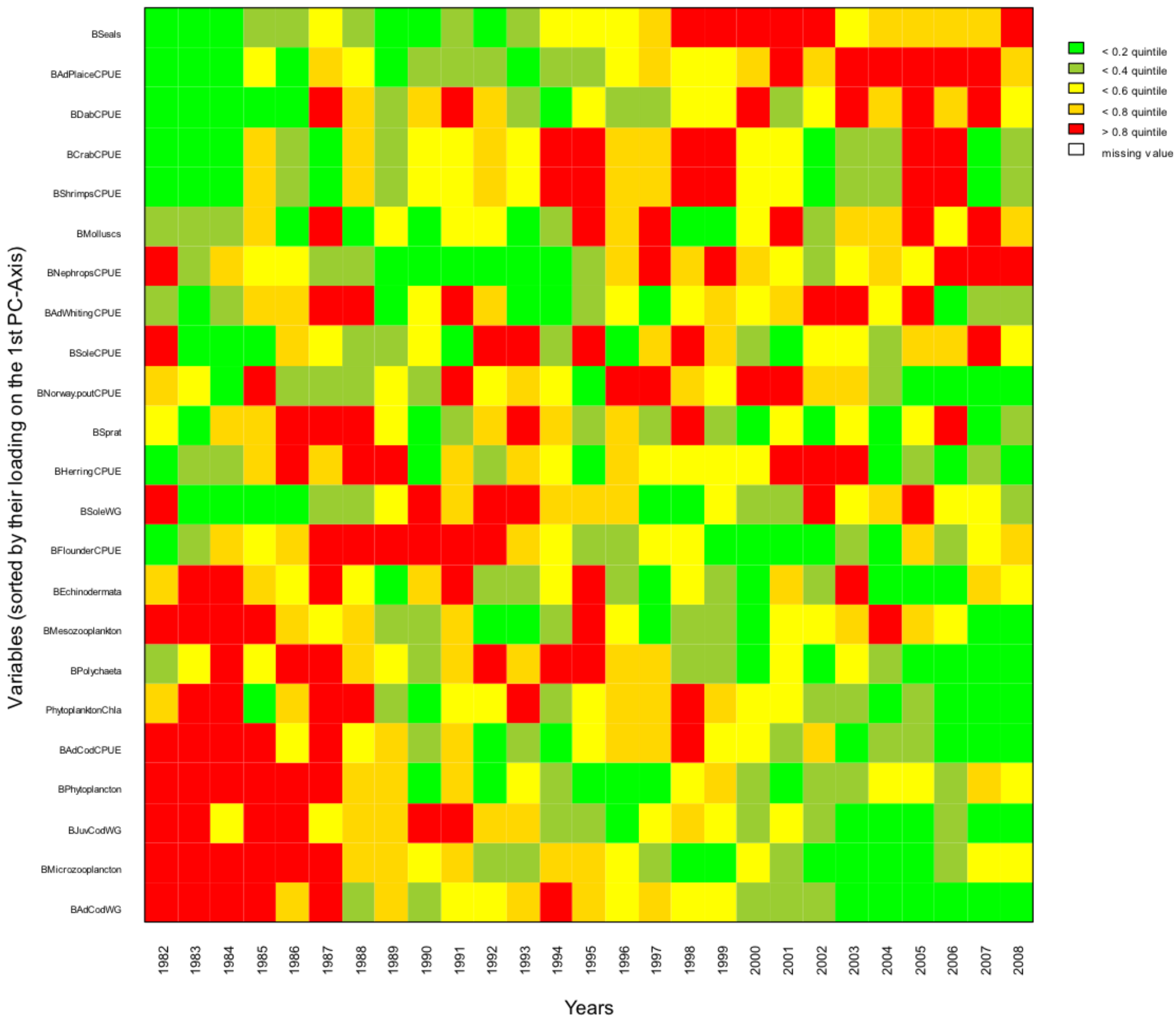


Figure 8. Traffic-light plot for the model calibrated biomass, showing their changes over time.

6.3 MODELLING BIOMASS (MODEL OUTPUT)

The trends in modelled biomass for the main functional groups, as shown in Fig. 9, reflect similar dynamics to those observed in the empirical data (Fig. 6), reinforcing the ecosystem's transition from a pelagic- to a benthic-dominated state. However, while general patterns are reproduced, the model does not fully capture the detailed temporal variability of all functional groups. The majority of functional groups demonstrate declining biomass trends over the period 1982–2008, particularly among pelagic and zooplanktonic species such as mesozooplankton, juvenile cod, juvenile plaice, herring, whiting, sandeel, and Norway pout. Likewise, planktonic producers like phytoplankton and detritus also show steady declines. Conversely, several benthic and demersal groups display increasing trends. Notable increases are observed in macroalgae, seagrass, and adult plaice, suggesting a shift in primary production and habitat complexity. The biomass of seals and other top predators such as harbor porpoise also increased, aligning with indications of top-down control intensifying over time. Some invertebrate groups, including molluscs and echinoderms, show decreasing trends, whereas Nephrops and shrimps/mysids remain relatively stable or slightly increase. These mixed results reflect the complexity of benthic responses, likely influenced by spatial and environmental heterogeneity. Overall, while the model accurately captures the general trajectory of benthification and predator recovery, it may underestimate temporal fluctuations in several mid-trophic level groups. Nonetheless, the consistent increase in key benthic indicators and top predators, together with widespread declines in pelagic biomass, supports the robustness of the model in describing long-term structural change in the Kattegat food web.

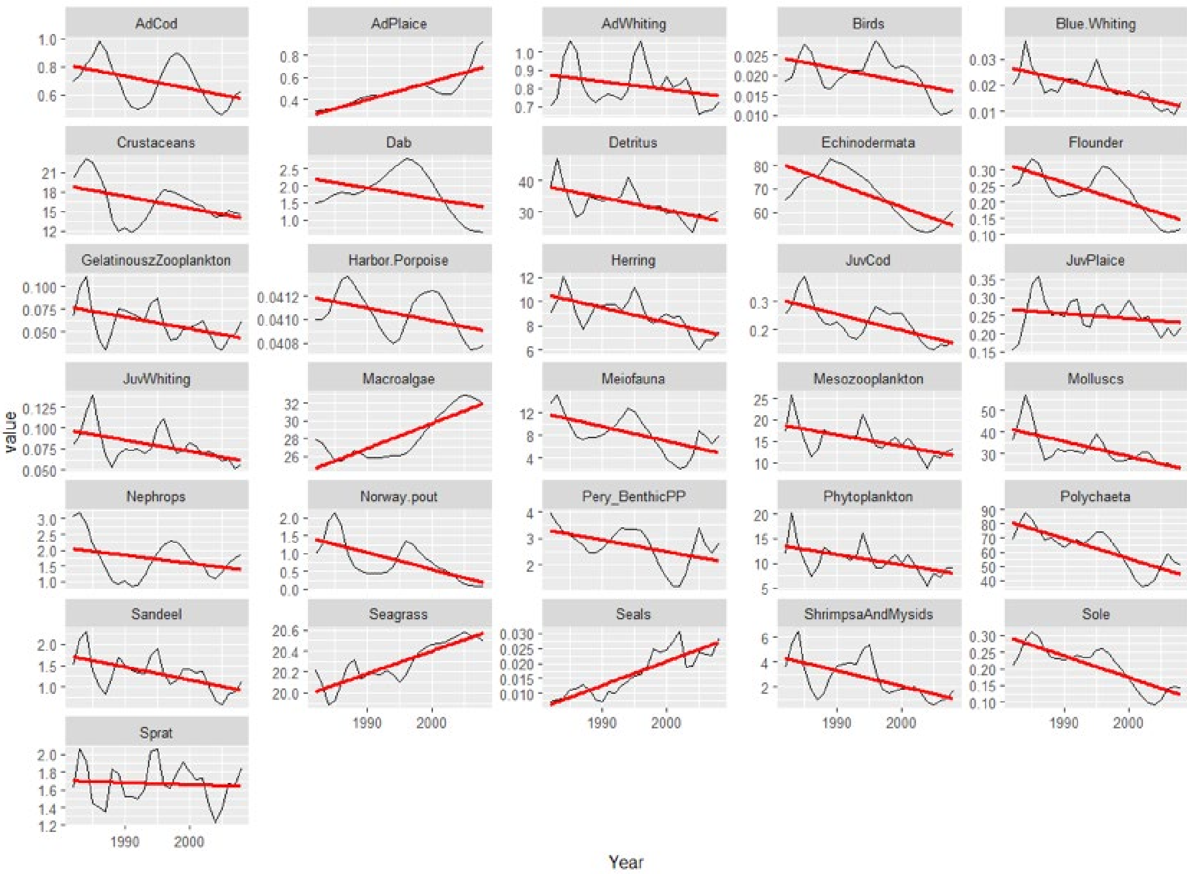


Figure 9. Modelled biomass and trends over time.

Despite some discrepancies in dynamic detail, the PCA on modelled biomass (Fig. 10 left panel) captures the underlying shift between benthic and pelagic domains within the ecosystem. The first principal component (PC1) is associated with increases in adult plaice, seals, macroalgae, and seagrass, and reflects a trend toward benthic biomass and habitat-forming species. Simultaneously, PC1 indicates declines in several pelagic species such as herring, blue whiting, and sole.

The second principal component (PC2) illustrates variability primarily among mid- and upper-trophic species, including sprat, harbour porpoise, cod, and whiting. These species may reflect more episodic fluctuations or responses to specific environmental conditions such as primary production.

Together, the PCA axes represent a combination of long-term structural change (PC1) and shorter-term dynamics (PC2). This is further emphasized in the temporal PCA plot (Fig. 10 right panel), where PC1 scores show a gradual decline beginning in the late 1990s, reflecting a shift in the system toward increased benthic biomass and habitat structure. In contrast, PC2 scores exhibit more frequent fluctuations, particularly evident during the mid-1980s and around 2000, suggesting that variability in mid-trophic species and primary production dynamics continues to shape the ecosystem. These patterns reinforce the interpretation that multiple processes—including both gradual ecosystem restructuring and episodic environmental changes—have contributed to the observed food web changes in the Kattegat. While the separation between benthic and pelagic signals is less pronounced than in the observed data PCA, the model still reasonably captures ecosystem-level directional change.

The traffic-light plot of modelled biomass changes (Fig. 11) reveals distinct temporal patterns in functional group responses across the Kattegat model domain. The green-dominated areas indicate consistent increases in biomass for key functional groups over the simulation period, particularly in benthic or demersal components and top predators. Red-dominated areas correspond to functional groups that experienced long-term declines, primarily among pelagic and lower trophic level species. The prevalence of yellow cells signals transitional states, where biomass remained relatively stable or underwent moderate fluctuations. These results indicate that while positive trends such as benthic expansion and top predator recovery are evident, many areas have experienced persistent or uneven declines, especially among pelagic species.

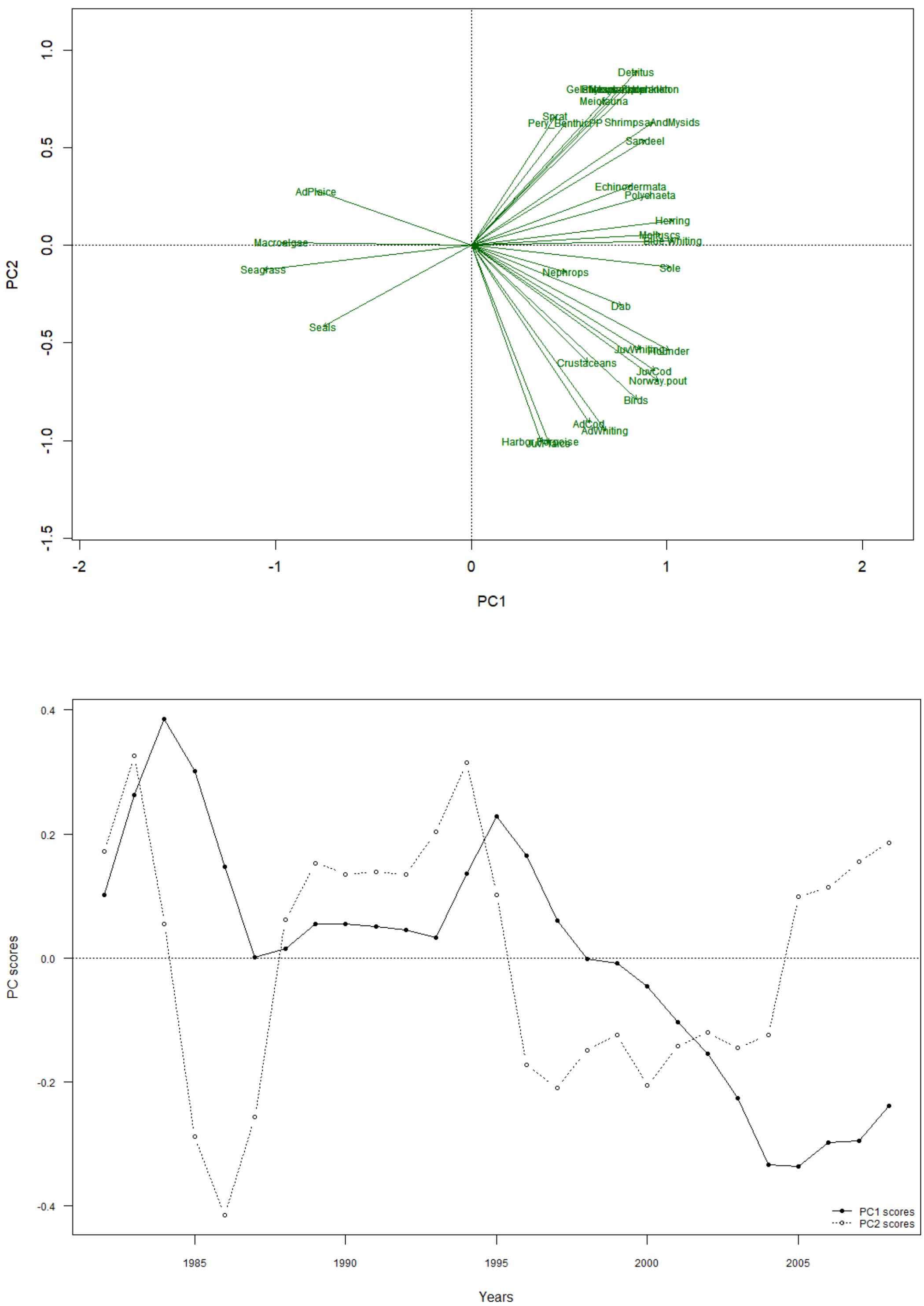


Figure 10. Principal Component Analysis (PCA) on modelled biomass left panel; and Principal Component Analysis (PCA), showing the PC1 and PC2 scores over time on modelled biomass, right panel.

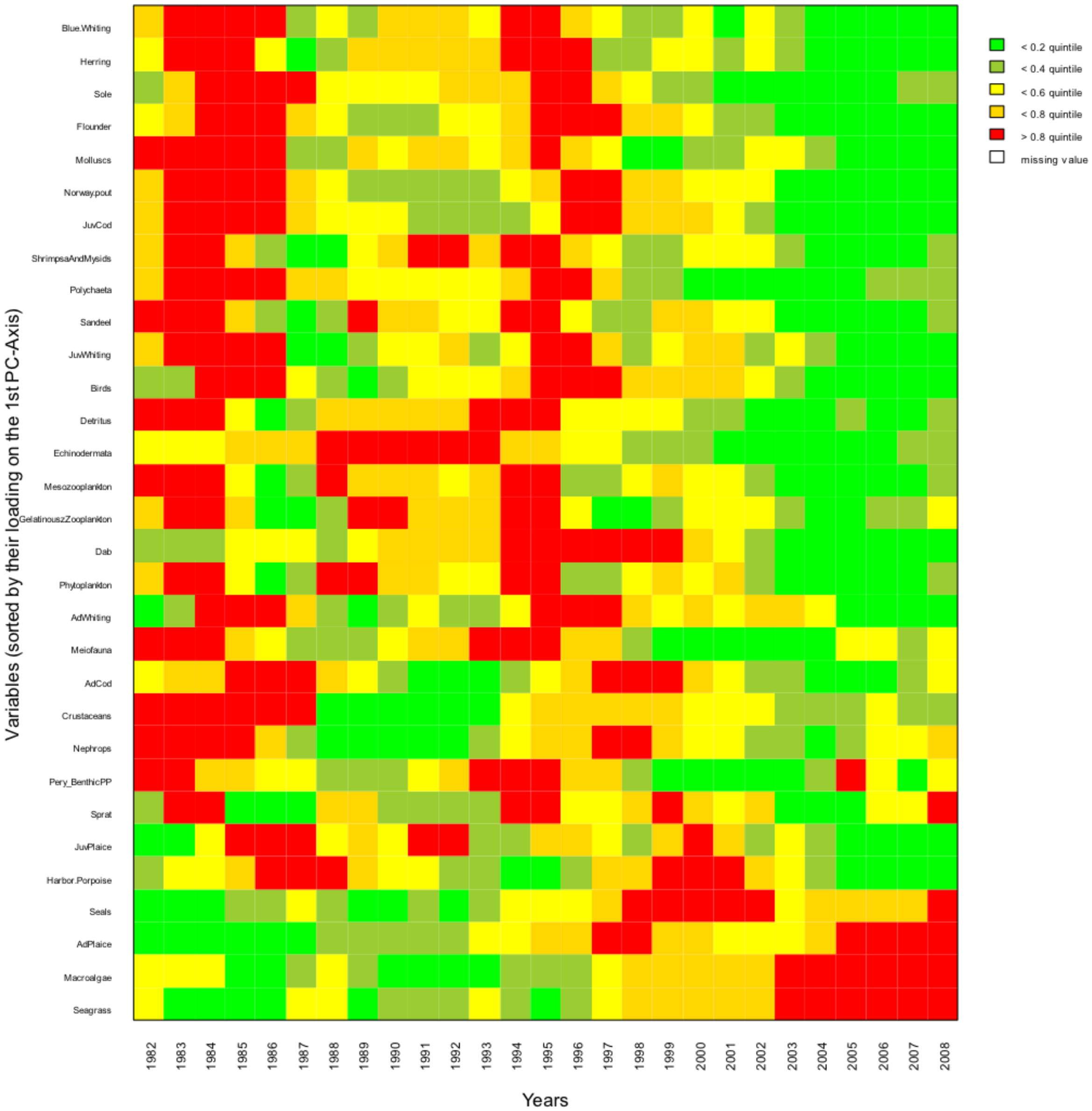


Figure 11. Traffic-light plot for the modelled biomass, showing their changes over time.

6.4 ECOLOGICAL NETWORK ANALYSIS (ENA) INDICES

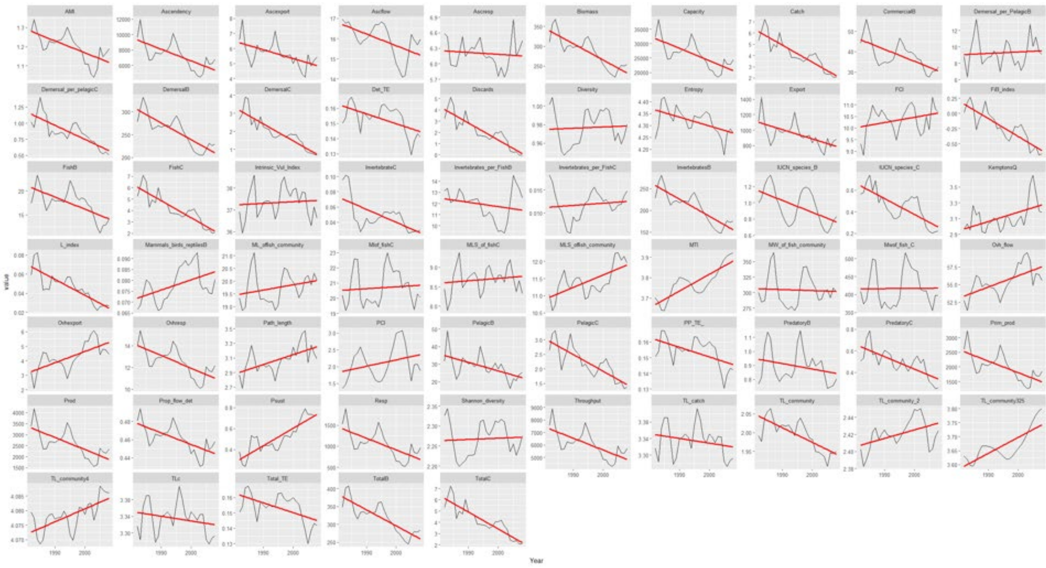


Figure 12. Modelled ENA Indices and trends over time.

The time series of ecosystem and food web indicators (Fig. 12) derived from the EwE model provides insights into the structural and functional changes in the Kattegat ecosystem between 1982 and 2008. Overall, the trends observed across these indicators are consistent with a long-term shift in ecosystem dynamics, particularly supporting the benthic food web re-organisation of the system and changes in energy transfer efficiency.

Key findings include:

- **Declining trends** in several structural and functional indicators, such as:
    - **Total System Throughput, Ascendency, and Overhead**: indicating a reduction in total system activity and potential structural simplification.
    - **Trophic Level of the Community (TL_community), TL_catch, and TL_community_3.25:** reflecting a decline in the relative abundance of higher trophic level species, consistent with a shift from pelagic to benthic dominance.
    - **Shannon Diversity, Finn's Cycling Index, and Kempton's Q index:** suggesting declining biodiversity and reduced system complexity.
    - **Indicators of fisheries output, including Catch, Commercial Biomass, and Fishing in Balance (FiB),** also exhibit downward trends, suggesting diminishing fisheries productivity or altered fishing patterns over time.

- **Increasing trends** were observed in:
    - **L-index and Primary Production Required (PPR):** reflecting increased pressure on lower trophic levels to sustain the catch, and potentially decreased energy transfer efficiency.

- o **Mean Length of Fish in the Community (ML_Fish) and Predatory Biomass:** indicating some recovery or stability among larger or top predator species (e.g., seals).
  - o **Seagrass and macroalgae indicators:** align with habitat recovery and expansion of benthic vegetation.

- **Mixed or fluctuating trends**:
  - o Indicators such as **AMI (Average Mutual Information), Asc/Cap ratio, and Resilience (Resip)** show non-linear patterns, possibly reflecting transitional stages in ecosystem re-organisation.

These trends collectively support the interpretation of a regime shift in the Kattegat ecosystem, moving away from pelagic-dominated pathways toward a more benthic-oriented structure. The consistent decline in trophic indicators, productivity metrics, and biodiversity indices, alongside increases in benthic biomass and habitat complexity, reinforce the robustness of the EwE model outputs and their relevance to MSFD Descriptor D4 assessments. in describing major ecosystem dynamics in the Kattegat and reflects key aspects of trophic restructuring relevant to Descriptor D4. that the EwE model is effective in describing major ecosystem dynamics in the Kattegat and reflects key aspects of trophic restructuring relevant to Descriptor D4.

The PCA of the selected food web and ecological indicators (Fig. 13 left panel) further supports the indicator-based assessment by revealing major gradients of change in ecosystem structure and function. The first principal component (PC1) captures the separation between trophic level-related indicators such as TL_community, TL_community_3.25, TL_catch, and Predatory Biomass (positively loaded), versus indicators of structural complexity and organization such as AMI, Ascendency, Lindex, and Invertebrates per Fish Biomass (negatively loaded). This suggests a trade-off between trophic structure and network complexity over time.

The second principal component (PC2) is more closely associated with increases in benthic-related indicators such as Demersal per Pelagic Biomass and Total Trophic Efficiency (TE), versus Shannon diversity and TL_community_2, suggesting contrasting dynamics between benthic expansion and biodiversity loss. The temporal PCA trajectory (Fig. 13 right panel) reveals an increasing trend in PC1 scores from the mid-1990s onward, indicating a progressive shift toward benthic-dominated and top predator-rich communities.

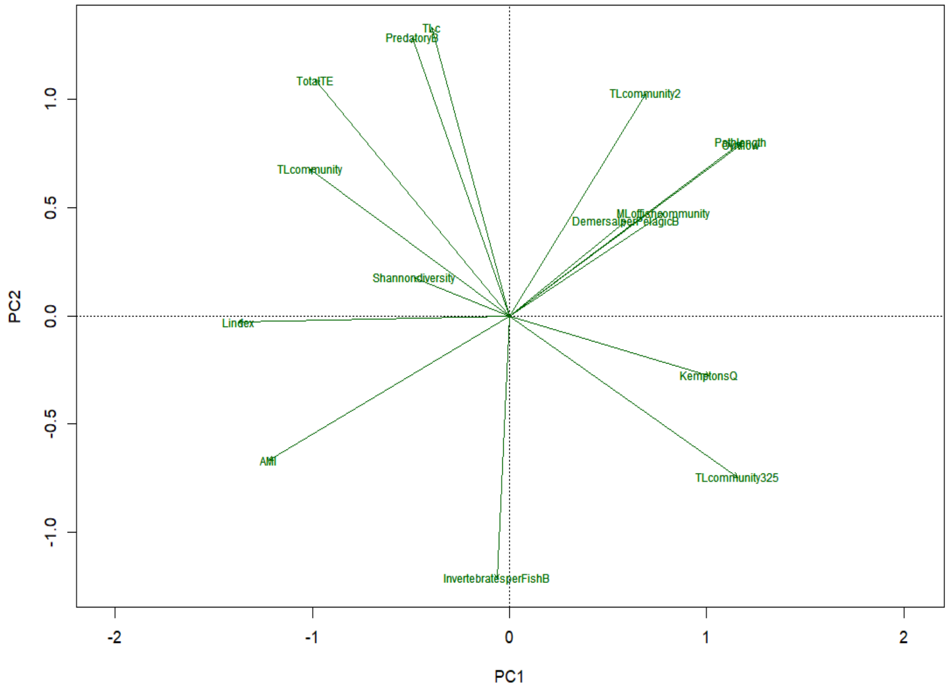
This trend supports the interpretation of long-term structural change within the Kattegat food web. PC2 scores fluctuate throughout the period, reflecting variable responses in mid-trophic indicators and diversity, likely linked to episodic environmental influences and primary production variability.

Overall, the PCA results confirm a shift in the Kattegat food web towards greater benthic and demersal dominance, a decline in trophic complexity and diversity, and increased pressure on lower trophic levels to sustain catches. These findings align with time series indicator trends and reinforce the model's capacity to diagnose long-term ecological change in line with MSFD Descriptor D4.

Additional insights into structural dynamics are provided by the Overhead Flow (Ovh_flow) indicator, which measures ecosystem redundancy and represents the system's degrees of freedom in response to perturbations (Ulanowicz, 2012). The increase in Ovh_flow observed in the model reflects growing resilience due to a more distributed and redundant energy transfer network—this is also supported by a longer path length from primary production to top predators and an increase in the demersal-to-pelagic biomass ratio. Indicators related to the size structure of the ecosystem, such as Kempton's Q index and Mean Length (ML) of the community, also increased, suggesting a shift toward dominance by larger-bodied organisms with lower production-to-biomass ratios. This transition is consistent with ecosystem maturation and reduced turnover rates. In contrast, the decline in the Average Mutual Information (AMI) indicates a reduction in the organization and predictability of trophic exchanges. This decline implies that while redundancy (and thus resilience) is increasing, the efficiency and specificity of interactions have diminished—likely due to redistribution of energy flow across more diffuse and variable pathways. Finally, the L-index, which integrates aspects of primary production required, transfer efficiency, and the trophic level of the catch, showed a decreasing trend—suggesting a movement toward higher sustainability and reduced exploitation pressure in the Kattegat ecosystem.

The temporal variation in ecosystem functioning is further highlighted by the indicator-based traffic-light plot (Fig. 14). This visualization captures temporal changes in ecosystem-level indicators—such as biodiversity, trophic structure, and energy efficiency—across the model domain. The prevalence of green cells indicates areas and periods where ecosystem functioning has improved, particularly through increases in indicators linked to benthic recovery, predator biomass, and structural redundancy. This suggests enhanced energy retention, greater stability, and more robust food web dynamics in those regions. Conversely, the red cells highlight areas of concern, where ecosystem functioning has deteriorated over time. These zones often correspond to declines in trophic level, efficiency, or biodiversity indicators—implying increased stress on ecosystem processes such as energy transfer, top-down control, and productivity. The persistence of red patches over time suggests that some functional impairments may be long-lasting or spatially localized. The yellow cells, representing moderate or stable dynamics, suggest transitional states or zones where indicators show limited directional change, possibly due to balancing effects between top-down and bottom-up processes or local resilience mechanisms.

In the context of ecosystem functioning, this pattern reflects a system undergoing reorganization—recovering structure in some components (e.g., benthic and predatory) while still experiencing degradation or instability in others (e.g., pelagic and mid-trophic interactions).



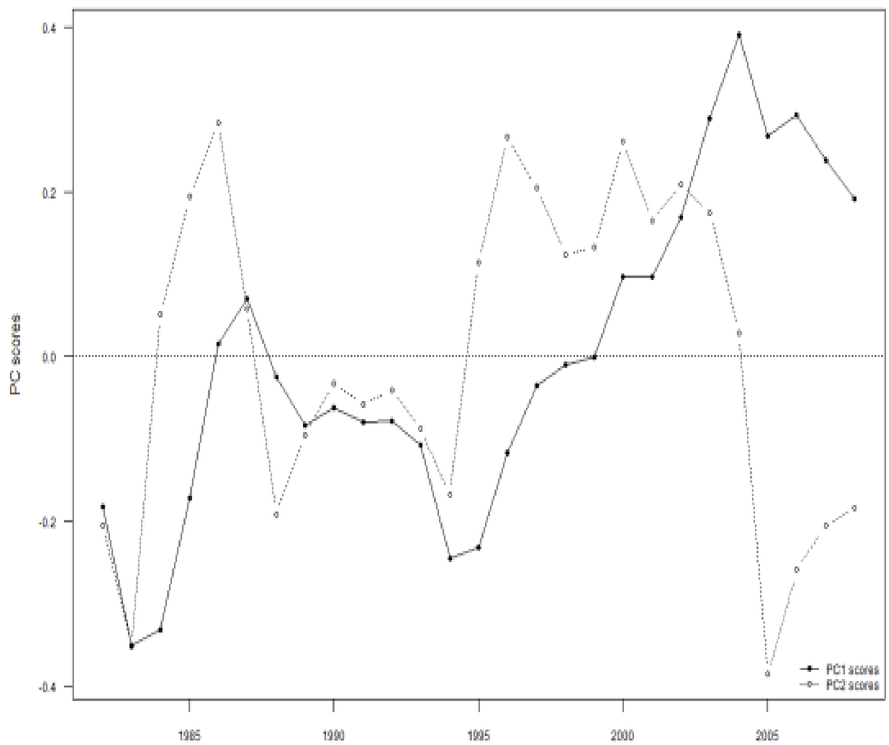


Figure 13. Principal Component Analysis (PCA) on the modelled ENA Indices left panel; and Principal Component Analysis (PCA), showing the PC1 and PC2 scores over time on the modelled ENA Indices, right panel.

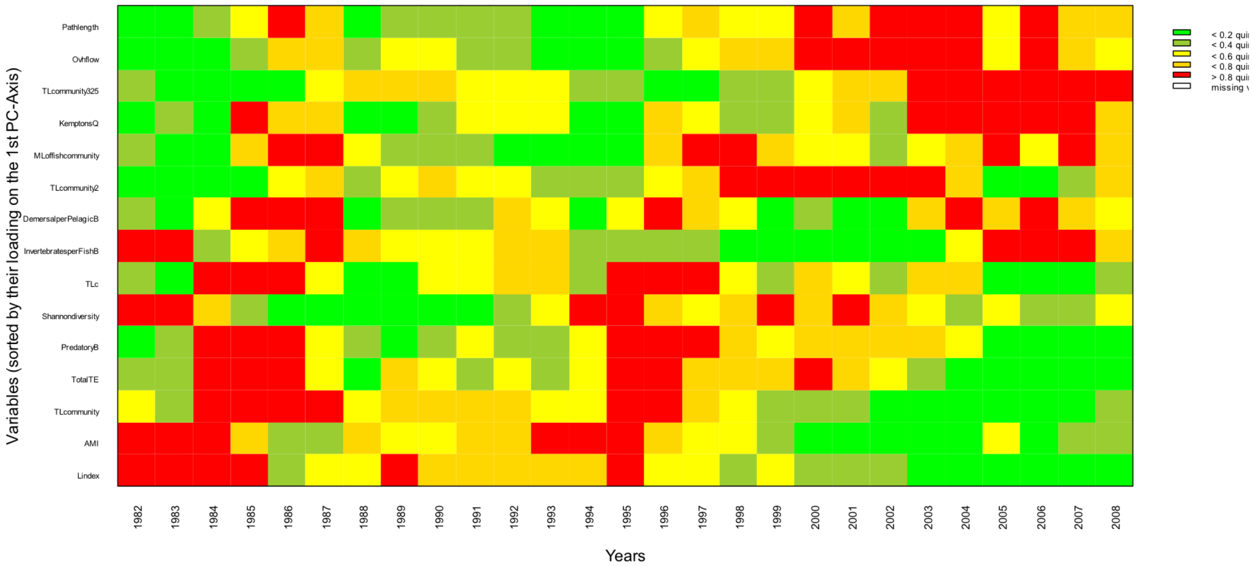


Figure 14. Traffic-light plot for the modelled ENA Indices, showing their changes over time.

6.5 SPATIAL ECOSYSTEM DESCRIPTION, BIOMASS DISTRIBUTION AND ENA INDICES

Please note that the Ecospace model is still under development. While the spatial results are displayed and interpreted in this section, they should be viewed as preliminary outputs that demonstrate the model's current capability. The findings presented here represent the state-of-the-art in spatial modelling for the Kattegat and serve as an illustration of the model’s potential to support ecosystem-scale assessments. Further refinement, validation, and calibration of the model are necessary to confirm the robustness of these patterns. Nonetheless, these results provide valuable insights into the ecosystem’s spatial dynamics and highlight the utility of Ecospace for evaluating trends in biomass, biodiversity, and ecosystem functioning in support of MSFD Descriptor D4 objectives.

The Ecospace model provides valuable insights into spatially explicit biomass distributions, offering a complementary layer of understanding to the temporal patterns discussed in previous sections. The spatial results for phytoplankton and herring (Fig. 15A–D) show clear changes in biomass distributions between 1982 and 2008. Phytoplankton biomass (Fig. 15A–B) was initially concentrated in the eastern and southern parts of the model domain in 1982, reflecting areas of relatively high productivity. By 2008, this distribution appears more uniform with a slight decrease in intensity, particularly in previously high-biomass areas. This spatial flattening may indicate reduced nutrient availability or altered mixing dynamics, consistent with observed declines in primary production.

Herring biomass (Fig. 15C–D) showed a notable contraction over the same period. In 1982, herring biomass was relatively widespread across the domain. However, by 2008, the distribution had become patchier and biomass levels were markedly lower. This reduction aligns with broader model results showing pelagic species decline and trophic shifts toward benthic-dominated dynamics.

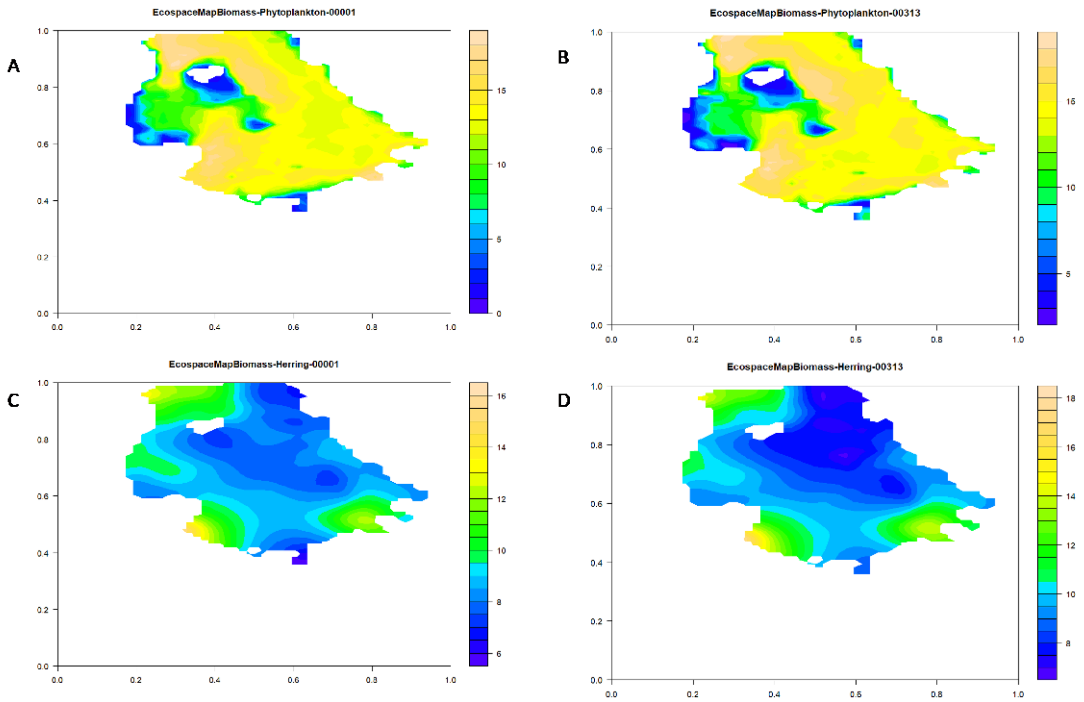


Figure 15. A – Phytoplankton biomass distribution 1982, B – Phytoplankton distribution 2008, C - Herring biomass distribution 1982, D- Herring biomass distribution 2008.

Additional spatial dynamics are illustrated in the distribution maps of adult plaice and adult whiting biomass (Fig. 16A–D). In 1982, adult plaice biomass (Fig. 16A) was generally low, with small patches of moderate concentrations. By 2008 (Fig. 16B), the biomass of adult plaice had increased noticeably, both in terms of intensity and spatial extent. This shift suggests favorable habitat conditions and a functional response to ecosystem changes favoring benthic species. In contrast, adult whiting biomass (Fig. 16C–D) demonstrates an opposite trend. In 1982 (Fig. 16C), biomass was more widely distributed, particularly in central and southern areas of the domain. However, by 2008 (Fig. 16D), the spatial coverage had diminished and biomass intensity declined substantially, indicating a contraction in population or a shift in spatial habitat use, potentially linked to broader pelagic declines and food web restructuring.

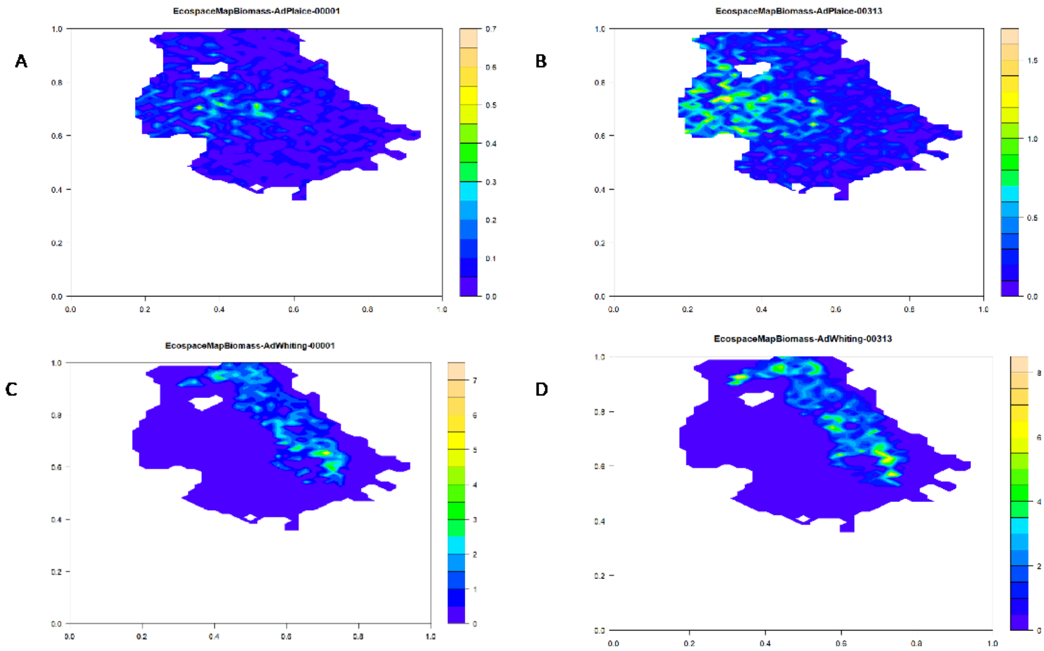


Figure 16. A – Adult Place biomass distribution 1982, B – Adult Place biomass distribution 2008, C – Adult Whiting biomass distribution 1982, D – Adult Whiting biomass distribution 2008.

Further spatial patterns are revealed through the distribution of ecological indicators and adult cod biomass shown in Fig. 17A–D. The top row illustrates the spatial distribution of the biodiversity index for trophic level >3.25 in 1982 and 2008 (Fig. 17A–B). In 1982, higher values of biodiversity were more evenly spread throughout the northern and eastern regions, while lower values were concentrated in the southwest. By 2008, the spatial extent of high biodiversity areas had declined slightly, with stronger gradients between northern and southern zones. This reflects a contraction of higher-trophic diversity, in line with the overall reduction in top predator abundance. The bottom row of Fig. 17 (C–D) shows the distribution of adult cod biomass. In 1982, cod biomass was concentrated in the central zone, with moderate intensity and spatial coverage. By 2008, the intensity in central areas had declined, and cod biomass became more fragmented and reduced in range, further confirming the weakening of top-down control within the food web. These spatial changes in both biodiversity and cod reinforce broader ecosystem restructuring observed in the Kattegat, especially the decline in key top predators and simplification of trophic dynamics.

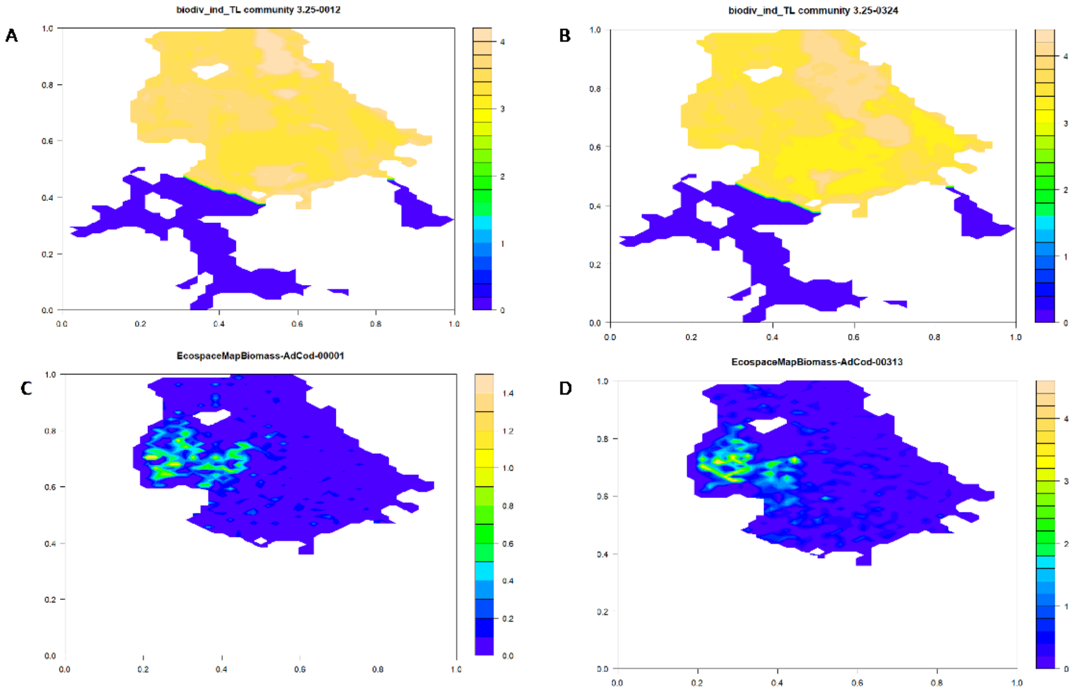


Figure 17. A – Trophic Level of the community 3.25 and above in 1982, B - Trophic Level of the community 3.25 and above in 2008, C -Adult Cod biomass distribution in 1982, D - Adult Cod biomass distribution in 2008.

Further insights into ecosystem structure are shown in Fig. 18A–D, which present the spatial distribution of two key biodiversity-related indicators: Kempton's Q index and the Mean Length (ML) of the fish community. In Fig. 18A–B, Kempton's Q index illustrates biodiversity patterns in 1982 and 2008, respectively. In 1982 (Fig. 18A), higher Kempton's Q values were observed across a broader part of the domain, particularly in the north and northeast. By 2008 (Fig. 18B), these values became more spatially fragmented and reduced in range, indicating a decline in community evenness and richness. This is consistent with findings of overall biodiversity decline and trophic simplification. Similarly, the spatial distribution of the Mean Length of the fish community (Fig. 18C–D) shows a clear shift. In 1982 (Fig. 18C), the ML index was lower across much of the domain, with only limited regions of larger individuals. By 2008 (Fig. 18D), the areas with higher average fish size had expanded, particularly in the northwestern part of the domain. This pattern suggests a shift toward a more size-structured community, potentially driven by reduced exploitation rates or selective fishing impacts that favoured larger-bodied species.

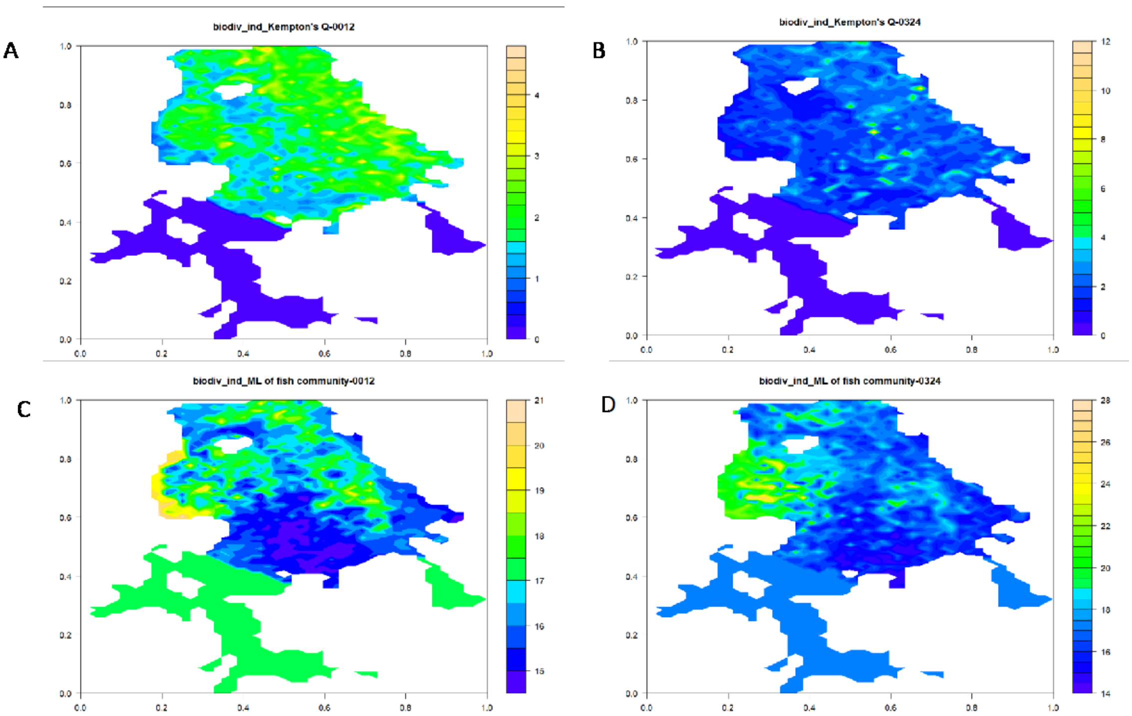


Figure 18. A - Kempton's Q ENA index in 1982, B - Kempton's Q ENA index in 2008, C-Mean Length of fish community distribution in 1982, D - Mean Length of fish community distribution in 2008.

These spatial patterns support temporal indicator trends, demonstrating both a decline in biodiversity and a simultaneous increase in community size structure. Together, they reflect structural reorganization in the Kattegat ecosystem consistent with Descriptor D4, where ecosystem functioning is increasingly supported by fewer but larger species under changing pressure and energy flow dynamics. The results in Fig. 19A–D offer additional insight into biodiversity and trophic structure. The top row (Fig. 19A–B) displays the spatial distribution of Shannon Diversity Index in 1982 and 2008, respectively. In 1982, Shannon diversity was more evenly distributed across much of the domain, while in 2008, the diversity appears slightly reduced, particularly in southern and southwestern areas. This trend reinforces previous findings of declining evenness and richness in community structure. The bottom row (Fig. 19C–D) presents the trophic level of the community (TL_community). In 1982, higher trophic level values were widely distributed, especially in northern areas. By 2008, TL_community values remained relatively stable in the north but declined elsewhere, reflecting a contraction of higher trophic interactions and a likely decline in top-down control. These spatial shifts support the conclusion that functional diversity and trophic complexity have decreased in certain areas of the Kattegat, in line with observed trends in predator biomass and trophic efficiency.

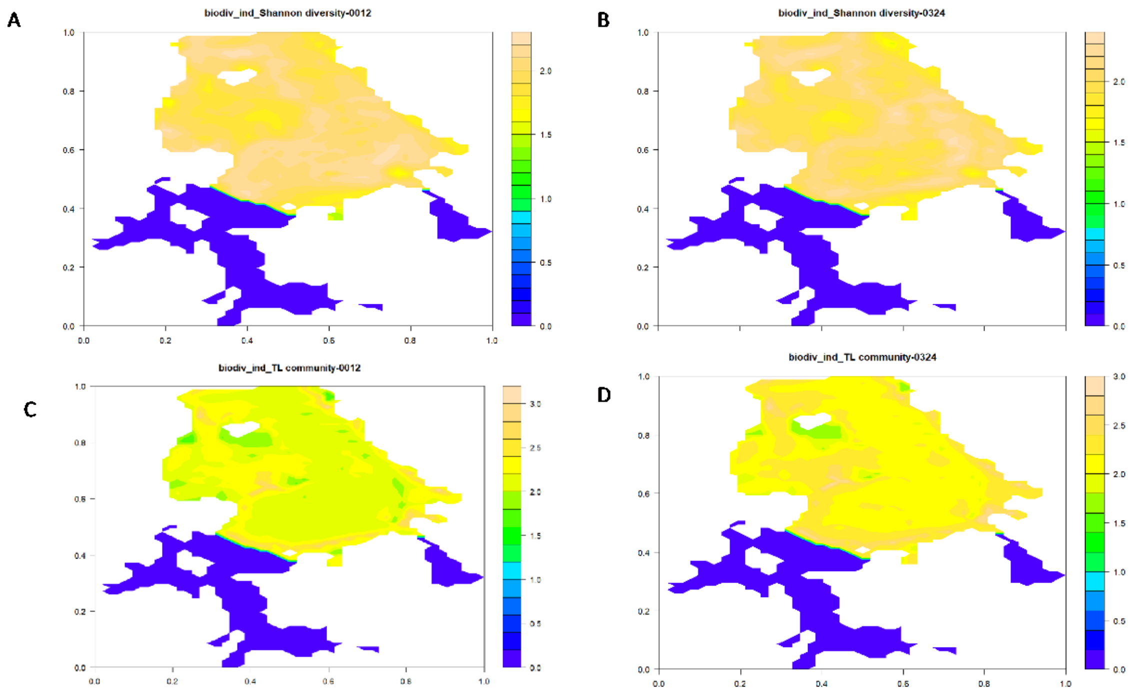


Figure 19. A – Shannon diversity in 1982, B - Shannon diversity in 2008, C- Trophic Level of the community (average) in 1982, D - Trophic Level of the community (average) in 2008.

7. DISCUSSION AND CONCLUSION

7.1 DESCRIPTION AND ASESSMENT OF THE STATE OF THE FOOD WEB FOR THE KATTEGAT ECOSYSTEM BASED ON THE EWE MODELLING APPROACH

This first pilot assessment of the Kattegat ecosystem food web using the Ecopath with Ecosim (EwE) model, including Ecospace, provided valuable insights into recent ecological changes. The EwE model successfully captured shifts in trophic pathways influenced by multiple drivers, indicating a transition in the Kattegat ecosystem from pelagic to benthic regulation. These findings align with the ecosystem dynamics described by Lindegren et al. (2012), which identified three distinct ecological states between 1982 and 2008: a pelagic-dominated period (1982–1998), a transitional phase (1989–1991), and a benthic-dominated state (1992–2008).

Throughout the modelled period, major shifts in the Kattegat food web were detected through a suite of model-derived indices. Declines in primary production, along with changes in trophic, biomass-based, biodiversity, and system-level indicators, consistently pointed to the ecosystem's reorganization. Notably, the decline in cod biomass and the concurrent rise in benthic species such as plaice and nephrops reflect alterations in predator-prey dynamics. Trophic-based indicators captured these shifts and also reflected changes in fishing pressures (e.g., Hornborg et al., 2013).

System-based indices, including the Average Mutual Information (AMI), revealed that the ecosystem may have become more constrained in recent years—indicative of a restructured network of energy exchanges. Over the nearly 30-year period, the Kattegat system demonstrated increased resilience, characterized by longer energy flow pathways, albeit with lower transfer efficiency between trophic levels (Fogarty et al., 2016). This work provides the first comprehensive model-based description of the Kattegat as a complex ecological system. While the model remains in development, and simplifications and assumptions introduce some uncertainties, the preliminary outputs have nonetheless succeeded in capturing key dynamics and trends.

Furthermore, this pilot assessment contributes to ongoing work by OSPAR and HELCOM on food web indicators and supports the efforts of ICES Working Group on Integrated Assessments of the North Sea (WGINOSE, ICES 2023).

7.2 INITIAL SET OF FOOD WEB INDICES TO ADDRESS THE EU MSFD DESCRIPTOR D4 REQUIREMENTS

The analysis of food web indicators derived from the EwE model provides a robust foundation for assessing the status of the Kattegat food web under the EU MSFD Descriptor D4. The preliminary results, summarized in Table 2, suggest candidate indices aligned with each D4 criterion.

Ecological Network Analysis (ENA) indices used in this assessment include:

- Trophic-based indicators: Trophic Level of the Catch (TL_c), TL_community, TL_community_2, TL_community_3.25
- System function and energy flow indicators: Total Trophic Efficiency (Total TE), Path Length, Overflow, AMI (Average Mutual Information), and the L index.

In addition, EcoInd-based indicators included:

- Biomass-based indicators: Demersal/Pelagic Biomass Ratio, Invertebrates per Fish Biomass, Commercial Biomass
- Biodiversity indicators: Shannon Diversity, Kempton's Q Index
- Size-based indicators: Mean Length (ML) of the Fish Community

This initial suite of indicators, though preliminary, demonstrates the applicability of the EwE modelling framework for MSFD Descriptor D4 assessments. It also highlights the potential for these tools to guide future integrated ecosystem assessments in the Kattegat and beyond.

Table 2. MSFD D4 Criteria and Pilot D4 Food Web indices for Kattegat

MSFD D4 CRITERIA	PILOT D4 FOOD WEB ENA INDICES KATTEGAT
D4C1 – Primary: The diversity (species composition and their relative abundance) of the trophic guild is not adversely affected due to anthropogenic pressures. Member States shall establish threshold values through regional or subregional cooperation.	Shannon diversity Kempton's Q-index (Biodiversity index) TL c – Trophic Level of the Catch TL community 3.25 – Trophic level 3.25 and above TL community 2 – Trophic level 2 and above TL community – Trophic Level of the community Path length
D4C2 – Primary: The balance of total abundance between the trophic guild is not adversely affected due to anthropogenic pressures. Member States shall establish threshold values through regional or subregional cooperation.	TL c – Trophic Level of the Catch TL community 3.25 – Trophic level 3.25 and above TL community 2 – Trophic level 2 and above TL community – Trophic Level of the community AMI - Average Mutual Information (AMI) Total TE – Total Trophic Efficiency Demersal Pelagic B – (B) indicates Biomass Invertebrates per Fish B – (B) indicates Biomass Commercial B – (B) indicates Biomass

D4C3 – Secondary: The size distribution of individuals across the trophic guild is not adversely affected due to anthropogenic pressures. Member States shall establish threshold values through regional or subregional cooperation.	Predatory B – (B) indicates Biomass Demersal B – (B) indicates Biomass ML of fish community – (ML) Mean Length Kempton's Q-index (Biodiversity index)
D4C4 – Secondary (to be used in support of Criterion D4C2 where necessary): Productivity of the trophic guild is not adversely affected due to anthropogenic pressures.	Average Mutual Information (AMI) L index – Integrates Primary Production Required/transfer efficiency/trophic level of the catches/primary production required) Path length Overflow Predatory B – (B) indicates Biomass Demersal B – (B) indicates Biomass Prim Prod – Primary Production

8. RECOMMENDATIONS

8.1 A ROADMAP AND FUTURE WORK NEEDED TO ASSESS FOOD WEBS BEYOND 2023, INCLUDING THE INTEGRATION OF FOOD WEB INDICATORS IN ORDER TO ASSESS TEMPORAL AND SPATIALCHANGES IN THE FOOD WEB DYNAMICS FOR THE KATTEGAT

The current Ecopath with Ecosim (EwE) model and Ecospace module require further development to extend the model timeframe to the present and enhance its readiness for providing management advice in support of the EU Marine Strategy Framework Directive (MSFD) and the EU Biodiversity Strategy for 2030.

To improve the accuracy and ecological representation of the Kattegat ecosystem model, the following key updates and actions are recommended:

- Revise the structure of primary producers to reflect more functional diversity.
- Update the fishing fleet structure to better align with data from the Data Collection Regulation (DCR).
- Incorporate spatially explicit fishing effort inputs.
- Extend and update forcing functions, validation time series, and spatial maps up to the present day.
- Validate the spatial component of the model using observed data from scientific surveys.
- Conduct uncertainty analysis using Monte Carlo Markov Chain (MCMC) simulations.
- Re-estimate Good Environmental Status (GES)-related indicators to align with current policy targets.
- Perform ICES key runs and apply model quality checks to support its use in formal advisory processes.

These improvements will require dedicated support and funding for the years 2024 and 2025. Strengthening the model in these areas will significantly enhance its utility for ecosystem-based management and ensure it meets the scientific standards required for regional and international marine policy frameworks.

8.2 ADDITIONAL RECOMMENDATIONS

- **Improve Data Integration and Availability**
  Enhance coordination with national monitoring programs to ensure regular updates of biological and environmental time series. This includes access to fishery-independent surveys, satellite remote sensing, and habitat mapping data.

- **Enhance Regional Collaboration**
  Coordinate modelling efforts with neighbouring countries and regional bodies (e.g., HELCOM, OSPAR, ICES) to develop harmonized models and indicators for better cross-border comparability and integration.
- **Develop a Stakeholder Engagement Framework**
  Engage stakeholders from fisheries, conservation, and policy sectors early in the modelling process to increase transparency and ensure models support relevant management questions.
- **Incorporate Climate Change Scenarios**
  Include projections of climate-driven variables (e.g., sea temperature, salinity, oxygen) to assess potential long-term impacts on food web dynamics and ecosystem functioning.
- **Develop Decision Support Tools**
  Translate model outputs into user-friendly dashboards or decision-support systems for managers and policymakers. This will facilitate the use of scientific results in environmental planning and adaptive management.
- **Improve Functional Group Resolution**
  Refine model resolution for key functional groups (e.g., seabirds, benthic invertebrates, mesopelagic fish) to better capture their roles in the food web and improve the accuracy of trophic interactions.
- **Train and Build Capacity**
  Invest in capacity building through training and workshops for model users, managers, and scientists, particularly in ecosystem-based management and food web modelling methods.

REFERENCES

Bentley, J. W., et al. 2019. Diet uncertainty analysis strengthens model-derived indicators of food web structure and function. Ecological Indicators, 98: 239-250.

Christensen, V., and C.I.J. Walters. 2004. Ecopath with Ecosim: Methods, capabilities and limitations. Ecological Modelling 172: 109–139.

Coll, M., Steenbeek, J. 2017. Standardized ecological indicators to assess aquatic fod webs: The ECOIND software plug-in for Ecopath with Ecosim models. Environmental Modelling & Software 89: 120-130.

Clemmesen, C., Behrens, J., Christensen, A., Christensen, E.A.F., Dutz, J., Jaspers, C., Flindt, E., Griniene, E., Günther, C., Herrmann, J.P. and Hinrichsen, H.H., 2016. Documentation on key drivers and physiological tolerance limits for resident and invasive species.

Ellingsen KE, Yoccoz NG, Tveraa T, et al. The rise of a marine generalist predator and the fall of beta diversity. Glob Change Biol. 2020;26:2897–2907. https://doi.org/10.1111/gcb.15027

EU, 2022. European Commission, 2022. MSFD CIS Guidance Document No. 19, Article 8 MSFD, May 2022.

EU. 2017. Commission Decision (EU) 2017/848 of 17 May 2017 laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardized methods for monitoring and assessment, and repealing Decision 2010/477/EU (Text with EEA relevance). Official Journal of the European Union, L 125: 43–74. http://data.europa.eu/eli/dec/2017/848/oj

Fogarty M. J, Gamble R and Perretti C. T. 2016. Dynamic Complexity in Exploited Marine Ecosystems. Front. Ecol. Evol. 4:68. doi: 10.3389/fevo.2016.00068.

Heymans, J. J., Tomczak, M. T. 2016. Regime shift in the Northern Benguela ecosystem: challanges for management. Ecological Modelling, 331: 151-159.

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V. (2017). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecological Modelling, 331:173-184.

Heymans, J. J., et al. 2016. Best practice in ecopath with ecosim food-web models for ecosystem-based management. Ecological Modelling, 331: 173-184.

Hornborg S, Belgrano A, Bartolino V, Valentinsson D, Ziegler F. 2013 Trophic indicators in fisheries: a call for re-evaluation. Biol Lett 9: 20121050. http://dx.doi.org/10.1098/rsbl.2012.1050

ICES. 2023. Working Group on Integrated Assessments of the North Sea (WGINOSE).

ICES Scientific Reports. 5:72. 95 pp. https://doi.org/10.17895/ices.pub.23592129

ICES 2015. (WKGMSFDD4-II). Report of the Workshop on guidance for the review of MSFD decision descriptor 4 – foodwebs II (WKGMSFDD4-II), 24-25 February 2015, ICES Headquarters, Denmark. ICES CM 2015\ACOM:49. 52 pp.

Kerr, S. R., and Dickie, L. M. 2001. The biomass spectrum: a predator prey theory of aquatic production. Columbia University Press, New York, USA.

Korpinen, S., Uusitalo, L., Nordström, M. C., Dierking, J., Tomczak, M. T., Haldin, J., Optiz, S., Bonsdorff, E., Neuenfeldt, S. 2022. Food web assessments in the Baltic Sea: models bridging the gap between indicators and policy needs. Ambio, https://doi.org/10.1007/s13280-021-01692-x

Libralato, S., Coll, M., Tudela, S., Palomera, I., Pranovi, F. 2008. Novel index for quantification of ecosystem effects of fishing as removal of secondary production. Mar. Eco. Prog. Ser., 355: 107-129, doi:10.3354/meps07224

Lindegren, M.., Blenckner, T., Stenseth, N. C. 2012. Nutrient reduction and climate change cause a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. Global Change Biology, 18, 3491–3503, doi: 10.1111/j.1365-2486.2012.02799.x

Link, J. S. 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. Ecological Modelling, 221: 1580-1591.

Moksnes, P.-O., Gullström, M., Tryman, K., Baden, S. (2008). Trophic cascades in a temperate seagrass community. Oikos 117:763-777.

Olsen, E., Tomczak, M. T., Lynam, C. P., Belgrano, A., Kenny, A. 2023. Testing management scenarios for the North Sea ecosystem using qualitative and quantitative models, ICES Journal of Marine Science, Volume 80, Issue 1, January 2023, Pages 218–234, https://doi.org/10.1093/icesjms/fsac231

Piroddi, C., Akoglu, E., Andonegi, E., Bentley, J.W., Celić, I., Coll, M., Dimarchopoulou, D., Friedland, R., De Mutsert, K., Girardin, R. and Garcia-Gorriz, E., 2021. Effects of nutrient management scenarios on marine food webs: a Pan-European Assessment in support of the Marine Strategy Framework Directive. Frontiers in Marine Science, 8, p.596797.

Rodionov, S. N. 2004. A sequential alogorithm for testing climate regime shifts. Geophys Res. Lett., 31: L09204.

Romagnoni, G., Mackinson, S., Hong, J., Eikeset, A. M. 2015. The Ecospace model applied to the North Sea: Evaluating spatial predictions with fish biomass and fishing effort data. Ecological Modelling, 30: 50-60.

Safi, G., et al. 2019. Vitamine ENA: a framework for the development of ecosystem-based indicators for decision makers. Ocean and Coastal Management, 174: 116-130.

Sheldon et al. 1972. The size distribution of particles in the ocean. Limnol. Oceanogr., 17: 327-340.

Steenbeek, J., Coll, M., Gurney, L., Melin, F., Hoepffner, N., Buszowski, J., Christensen, V., 2013. Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatiale-temporal data. Ecol. Model. 263, 139e151.

Tomczak MT, Heymans JJ, Yletyinen J, Niiranen S, Otto SA, et al. (2013) Ecological Network Indicators of Ecosystem Status and Change in the Baltic Sea. PLoS ONE 8(10): e75439. doi:10.1371/journal.pone.0075439.

Ulanowicz, R. E. (1980). An hypothesis on the development of natural communities. J-Theor. Biol. 85 (223-245): 0022-5193.

Ulanowicz, R.E., 2012. Growth and development: ecosystems phenomenology. Springer Science & Business Media.

SUPPLEMENTARY INFORMATION

Table S1. Extended information about the ecological indicators included in ECOIND plug-in. (Modified from Coll and Steenbeek 2017).

Table S2. ENA Indices, Formula and Definition.

Table S1.

Ecological Indicators	Definition	Description	Units	Reference
A. Biomass-based indicators				
Total B	Total biomass (B)	Sum of the biomass of all species in the ecosystem	t·km^{-2}	Hilborn and Walters, 1992; Rochet and Trenkel, 2003.
Commercial B	Biomass (B) of commercial species	Sum of the biomass of the species in the ecosystem that are landed	t·km^{-2}	
Fish B	Biomass (B) of fish species	Sum of the biomass of fish species	t·km^{-2}	
Invertebrates B	Biomass (B) of invertebrate species	Sum of the biomass of invertebrate species	t·km^{-2}	
Invertebrates / Fish B	Biomass (B) of invertebrates over fish	Sum of the biomass of invertebrate species / sum of the biomass of fish species		
Demersal B	Biomass (B) of demersal species	Sum of the biomass of all demersal species	t·km^{-2}	
Pelagic B	Biomass (B) of pelagic species	Sum of the biomass of all pelagic species	t·km^{-2}	
Demersal / Pelagic B	Biomass (B) of demersal over pelagic species	Sum of the biomass of demersal species / sum of the biomass of pelagic species		
Predatory B	Biomass (B) of predatory organisms with trophic level ≥ 4 (i)	Sum of the biomass of all species with a trophic level ≥ 4	t·km^{-2}	
Kempton's Q	Kempton's biodiversity index (Q) (i)	Inverse slope of the species-abundance curve		Ainsworth and Pitcher, 2006.
B. Catch-based indicators				
Total C	Total Catch (C)	Sum of the catch of all species in the ecosystem	t·km^{-2}·year^{-1}	Hilborn and Walters, 1992; Rochet
Fish C	Catch (C) of all fish species	Sum of the catch of all fish species	t·km^{-2}·year^{-1}	

Invertebrate C	Catch (C) of all invertebrate species	Sum of the catch of all invertebrate species	t·km^{-2}·year^{-1}	and Trenkel, 2003; Zeller and Pauly 2007.
Invertebrates/Fish C	Catch (C) of invertebrates over fish	Sum of the catch of all invertebrate species / sum of the catch of all fish species		
Demersal C	Catch (C) of demersal species	Sum of the catch of all demersal species	t·km^{-2}·year^{-1}	
Pelagic C	Catch (C) of pelagic species	Sum of the catch of all pelagic species	t·km^{-2}·year^{-1}	
Demersal / pelagic C	Catch (C) of demersal over pelagic species	Sum of the catch of all demersal species / sum of the catch of all pelagic species		
Predatory C	Catch (C) of predatory organisms with trophic level ≥ 4	Sum of the catch of all species with a trophic level ≥ 4	t·km^{-2}·year^{-1}	
Discards	Total discarded catch	Sum of the catch of all species that are discarded	t·km^{-2}·year^{-1}	
C. Trophic-based indicators				
TL catch	Tropic level (TL) of the catch	Weighted mean (catch) of the trophic level of species in the catch		Christensen 1996; Pauly et al., 1998.
MTI	Marine trophic index, trophic level (TL) of the catch (including organisms with TL ≥ 3.25)	Weighted mean (catch) of the trophic level of the species in the catch with a trophic level ≥ 3.25		Pauly and Watson, 2005.
TL co.	Trophic level (TL) of the community (including all organisms)	Weighted mean (biomass) of the trophic level of species in the ecosystem		Shannon et al., 2014
TL co. 2	Trophic level (TL) of the community (including organisms with TL ≥ 2)	Weighted mean (biomass) of the trophic level of species in the ecosystem with a trophic level ≥ 2		
TL co. 3.25	Trophic level (TL) of the community (including organisms with TL ≥ 3.25)	Weighted mean (biomass) of the trophic level of species in the ecosystem with a trophic level ≥ 3.25		
TL co. 4	Trophic level (TL) of the community (including organisms with TL ≥ 4)	Weighted mean (biomass) of the trophic level of species in the ecosystem with a trophic level ≥ 4		
D. Size-based indicators				

ML of fish co.	Mean length (ML) of fish in the community	Weighted mean (biomass) of the mean length of fish species in the ecosystem	cm	Rochet and Trenkel, 2003
ML of fish C	Mean length (ML) of fish in the catch (C)	Weighted mean (catch) of the mean length of fish species in the catch	cm	
MW of fish co.	Mean weight (MW) of the fish in the community	Weighted mean (biomass) of the mean weight of fish species in the ecosystem	kg	
MW of fish C	Mean weight (MW) of fish in the catch (C)	Weighted mean (catch) of the mean weight of fish species in the catch	kg	
MLS of fish co.	Mean life span (MLS) of fish in the community	Weighted mean (biomass) of the mean life span of fish species in the ecosystem	year	
MLS of fish C	Mean life span (MLS) of fish the catch (C)	Weighted mean (catch) of the mean life span of fish species in the catch	year	
E. Species-based indicators				
Intrinsic Vul. Index	Intrinsic Vulnerability Index of the catch	Weighted mean (catch) of the vulnerability index of fish species in the catch		Cheung et al., 2007
Endemics B	Biomass (B) of endemic species in the community	Sum of the biomass of endemic species in the ecosystem	t·km^{-2}	Rochet and Trenkel, 2003; Coll et al. 2012; 2015; 2016; IUCN, 2015
Endemics C	Endemic species in the catch (C)	Sum of endemic species in the catch	t·km^{-2}·year^{-1}	
IUCN species B	Biomass (B) of IUCN-endangered species in the community	Sum of the biomass of species listed in the IUCN red list as endangered	t·km^{-2}	
IUCN species C	IUCN-endangered species in the catch (C)	Sum of the catch of species listed in the IUCN red list as endangered	t·km^{-2}·year^{-1}	
Mammals, birds & reptiles B	Biomass (B) of marine mammals, seabirds and reptiles	Sum of the biomass of species of marine mammals, seabirds and reptiles in the community	t·km^{-2}	
Mammals, birds & reptiles C	Catch (C) of marine mammals, seabirds and reptiles	Sum of the catch of species of marine mammals, seabirds and reptiles	t·km^{-2}·year^{-1}	

Table S2.

Indices	Formula	Definition
TST	$TST = \sum_{ij} T_{ij}$	The total system throughput is defined as the sum of all flows (T_{ij} is the flow between two compartments) in a particular ecosystem. It represents the "size of the entire system in terms of flow" and its value is expected to decrease when a system becomes more degraded.
C	$C = \sum_{ij} T_{ij} \log\left(\frac{T_{ij}}{TST}\right)$	The development capacity (C) is a measure of potential of an ecosystem to develop and the theoretical maximum of the ascendency (A).
A	$A = \sum_{i,j} (T_{ij}) \cdot \log\left(\frac{T_{ij} \cdot TST}{T_j \cdot T_i}\right)$	The ascendency (A) is defined as where T_{ij} is the flow between two compartments and it includes all outflows from each compartment, T_i is the sum of all material leaving the ith compartment, and T_j is the sum of all flows entering the jth compartment [9]. A describes the growth and development of the system and it increases as a system matures.
A/C	A/C	Relative ascendency A/C is the fraction of a potential food-web organization that is actually realized and it is negatively related to maturity.
R	$R = -\sum_{i=1}^{n} \sum_{j=1}^{n} (T_{ij}) \cdot \log\left(\frac{T_{ij}^2}{\sum_{j=1}^{n} T_{ij} \cdot \sum_{i=1}^{n} T_{ij}}\right)$	The Redundancy (R): indicates the system's energy in reserve. R is the best indicator of a change in the degrees of freedom of the system, and describes the distribution of energy flow among the ecosystem pathways. Based on the description of R by Ulanowicz, who suggested that "it strongly ties to the effective multiplicity of parallel flows by which medium passes between

		any two arbitrary system components", Heymans et al. proposed R as an index of system resilience.
AMI	$$AMI = \sum_{i,j}\left(\frac{T_{ij}}{TST}\right) * \log\left(\frac{T_{ij} * TST}{T_j * T_i}\right)$$	Average Mutual Information (AMI) measures the organization of the exchanges among components. A rise in AMI signifies that the system is becoming more constrained and is channelling flows along more specific pathways. T_i is the sum of all material leaving the ith component and T_j is the sum of all flows entering the jth component .
H	$$H = -\sum_{ij}\frac{T_{ij}}{TST} * \log\left(\frac{T_{ij}}{TST}\right)$$	Entrophy - by Ulanowicz [2021], the diversity of flows or systems entropy (H) is an indication of the total uncertainty embodied in the given configuration of flows of the system, and represents the total number and diversity of flows in a system.
MPL	MPL = throughput/sum of exports + respiration	The mean path length (MPL), accounts for the number of functional groups involved in a flow of matter and represents the average number of groups that an inflow or outflow passes through. The MPL is expected to decrease with fishing.
Kempton's Q index	$$Q90 = \frac{0.8S}{log\ (\frac{R_2}{R_1})}$$	Where S is the total number of functional groups in the model; R1 and R2 are the representative biomass values of the 10th and 90th percentiles in the cumulative abundance distribution.

		Kempton's Q index - The Q-90 statistic, a variant on Kempton's Q index, is developed to measure the effects of mortality from fishing or climate on species diversity in whole ecosystem simulation models that group functionally similar organisms. The statistic represents the slope of the cumulative species abundance curve between the 10- and 90-percentiles.
FCI	$FCI = \frac{TST_c}{TST_{tot}}$	The Finn's cycling index (FCI) is the proportion of the total system throughput (TST) that is recycled in the system. According to Monaco and Ulanowicz , cycling is considered to be an important indicator of an ecosystem's ability to maintain its structure and integrity through positive feedback and is used as an indicator of stress and systems maturity. FCI is an indicator of the recovery time of an ecosystem through development of routes to conserve nutrients [50]. An increase in the FCI would mean the system would recover faster from a perturbation, whereas a system would be expected to take longer to recover (lower FCI) when it is in a more degraded state.
PCI	$PCI = \frac{TST_{no\ det}}{TST_{tot}}$	The Predatory Cycling Index (PCI) - is a slightly modified FCI. PCI is calculated by excluding the cycling through detritus. Disturbed systems are characterized by short and fast cycles while complex trophic structures have long and slow recycling of matter.
PFD	Proportion of total trophic flows that flow into the detritus box (t/km²/year).	The proportional flow to detritus (PFD) - it has

		been proposed that as fishing impact increases, this indicator increases due to disruption of energy paths in the food web.
mTLcPPR	$$mTLc = \frac{\sum_j Y_j \cdot TL_j}{\sum_j Y_j}$$	
Total Catch-mTLc	ΣYj $$mTLc = \frac{\sum_j Y_j \cdot TL_j}{\sum_j Y_j}$$	Sum of all fishery catches extracted from modelled ecosystem at given year.The Mean Trophic Level of Catch (mTLc) - Where mTLc is the mean trophic level of catch, TL_j - Trophic level of the caught species by their proportion in total landings ($Y_j/\sum Y_j$) instead of the catches. TL of catch captures 'fishing down marine food webs' (Pauly et al., 1998) as removal of top predatory fish results in catches dominated by small, lower TL species. It is expected to decrease with fishing.
L index-Total Catch	$$L = \int_{TL_c}^{\infty} \frac{PPR}{P_1} \cdot TE^{TL_c-1} \cdot TE^{\tau-TL_c} d\tau = -\frac{PPR \cdot TE^{TL_c-1}}{P_1 \cdot \ln TE}$$ ΣYj	L index – Integrates Primary Production Required/transfer efficiency/trophic level of the catches/primary production required). A lower L index indicates that the ecosystem is more sustainably fished (Libralato et al. 2008).
L index	$$L = \int_{TL_c}^{\infty} \frac{PPR}{P_1} \cdot TE^{TL_c-1} \cdot TE^{\tau-TL_c} d\tau = -\frac{PPR \cdot TE^{TL_c-1}}{P_1 \cdot \ln TE}$$	L index – Integrates Primary Production Required/transfer efficiency/trophic level of the catches/primary production required). A lower L index indicates that the ecosystem is more sustainably fished (Libralato et al. 2008).

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