

TOWARD ASSESSING THE SPATIOTEMPORAL STRUCTURE OF MARINE FOOD WEBS FROM A MSFD DESCRIPTOR 4 PERSPECTIVE: A CASE STUDY IN DANISH KATTEGAT

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Data sheet

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Abstract:	Marine food webs are complex systems of trophic and non-trophic interactions influenced by temporal, spatial, and environmental variations. The Marine Strategy Framework Directive (MSFD) descriptor 4 requires European member states to assess these webs and evaluate the impacts of climate and anthropogenic stressors. This study examines data availability and modelling approaches for fulfilling these requirements in Danish waters. While existing data supports parts of the four MSFD criteria, gaps remain in areas like species ontogeny and trophic associations. Recommendations include improving data collection and advancing quantitative models to assess marine food web status comprehensively.
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Contents

Preface	5
Sammenfatning	6
Summary	7
1 Introduction	8
2 Present state and future potential of marine food web assessment in Denmark	10
3 What can current datasets potentially tackle within Descriptor 4	12
3.1 D4C1: diversity of trophic guilds	12
3.2 D4C2: balance of abundance between trophic guilds	13
3.3 D4C3: size distribution within guilds	14
3.4 D4C4: productivity of the trophic guild	14
4 Broader MSFD adherence of food web assessment	16
5 Potential models for food web assessment based on current datasets	19
5.1 StrathE2E2	19
5.2 Baltic Sea Atlantis	20
5.3 Ecopath with Ecosim Ecospace	20
5.4 Ecological networks	21
6 Potential for future assessments	23
7 References	26
8 Appendix	30

Preface

The overarching goal of this small project is to review data suitable for assessing the Marine Strategy Framework Descriptor (MSFD) food web descriptor FW4 in the Danish part of the Kattegat and the Skagerrak regions, determine, and explore how these data can be used to assess their status within the framework of Article 8 MSFD Assessment Guidance version 19.

In the review, we assess the extent to which the different Descriptor 4 criteria can be fulfilled by investigating the data available for food web analysis. Our evaluation is made for each of the MSFD trophic guilds. We then investigate the suitability of some ecosystem or food web models for assessing food web interactions between trophic levels and guilds. Following our assessment, we put forward some recommendations for work required to achieve the MSFD targets, both in the short and long term.

Sammenfatning

Marine fødenet er sammensat af et netværk komplekse trofiske interaktioner mellem arter. Disse interaktioner varierer i tid og rum, afhængigt af arternes udbredelse, livsstadier og miljøet. Under EU's marine havstrategi (MSFD) deskriptor 4, er det pålagt at de europæiske medlemsstater at foretage en grundig vurdering af marine fødenet og estimere effekten af klimatiske og menneskeskabte påvirkninger. Vurdering skal udføres i overensstemmelse med fire specifikke kriterier, der er designet til at forstå delelementer af fødenettet og evaluere dets tilstand.

Vurderingen af disse kriterier kræver store mængder data, som i nogle tilfælde skal være specifikke, f.eks. omkring arternes livsstadier, biomasse, habitat udbredelser, reproduktion eller tilknytning til trofiske grupper. Desuden kræver vurderingen af interaktionerne mellem trofiske niveauer eller trofiske grupper kan implementeres i modeller. Som en del af arbejdet, der er nødvendigt for at opfylde kravene i MSFD-deskriptor 4 for danske farvande, giver vi en vurdering af de tilgængelige nødvendige data til at arbejde med marine fødenet og identificerer, hvilke delkomponenter af hvert kriterium under MSFD-deskriptor 4, der kan løses ved hjælp af de eksisterende data.

Vi undersøger yderligere økosystem- eller fødenetsmodeller, der kan bidrage til at opnå en forståelse af tilstanden i forskellige trofiske grupper og især estimere interaktionerne mellem grupper. Vi finder, at der er muligheder for at imødekomme flere dele af hvert af de fire kriterier under MSFD-deskriptor 4, for de fleste trofiske grupper. Der er dog også behov for at indsamle yderligere data om specifikke elementer af arter (f.eks. ontogenese og trofisk tilknytning), og udvikle mere passende kvantitative metoder eller modeller, til at vurdere fødekædeinteraktionerne bredere. Vi giver anbefalinger om fem centrale udviklingsområder, der er nødvendige for at kunne levere en mere omfattende vurdering af tilstanden for marine fødenet i danske farvande under kravene i MSFD.

Summary

Marine food webs are composed of highly complex networks of trophic and non-trophic interactions between species. Such interactions can vary on temporal scales or across space, depending on species distribution, changes in species life stages, or the environment. Under the Marine Strategy Framework Directive (MSFD) descriptor 4, there is a requirement within the European member states to produce a thorough assessment of marine food webs and estimate the impact of climate or anthropogenic stressors on food webs. Such an assessment should follow four criteria designed to understand different aspects of the food web and evaluate its status. Nonetheless, assessing these criteria requires a large amount of data, which in some cases need to be quite specific about different aspects of species life stages, reproduction, or association to trophic guilds. Additionally, understanding the interactions between trophic levels or guilds require appropriate modelling. As part of an evaluation of the work required to fulfill the requirements of the MSFD descriptor 4 for Danish waters, we provide an assessment of the data that is available for food web assessment and which aspects of each criterion within descriptor 4 can be resolved using the current data available. We further delve into broader ecosystem or food web models that can help understand the state of different trophic guilds and, especially, estimate the interactions between guilds. We find that there are possibilities of fulfilling multiple parts of each of the four criteria for most trophic guilds. However, there is also a need to gather some data on specific aspects of species (e.g., ontogeny and trophic association) and develop more appropriate quantitative methods or models to assess broader interactions. Therefore, we provide recommendations on five key potential avenues that need development to provide a more comprehensive assessment of the status of marine food webs for Danish waters under the requirements of the MSFD.

1 Introduction

A resilient food web is key for ecosystem health and maintaining good environmental status. Highly complex interactions between trophic and non-trophic networks provide redundancy, and feedback mechanisms that enhance the ability of food webs to restore and be less vulnerable to disturbance (i.e., food web complexity can increase resilience; Sanders et al., 2018). On the other hand, food webs that have low complexity tend to lean heavily on few trophic interactions and are more susceptible to disturbances (Nagelkerken et al., 2020). Understanding the structure of the food web within a system is, therefore, critical for managing the system. Importantly, there is also a necessity to understand the spatial scale of feedback mechanisms that drive food webs within that system. Migration, transient species, environmental restrictions, or spatial connectivity can expand or compress food webs' spatial reach and feedback mechanisms (McCann et al. 2005) and drive the strength of species interactions. Therefore, species population dynamics, their spatial distribution, and the strength or complexity of their interactions are all important for assessing food web structure.

Under the Marine Strategy Framework Directive (MSFD) and MSFD Article 8 guidance document (European Commission 2022), there is a requirement of the European member states to produce a thorough assessment of marine food webs. Such an assessment requires an examination of the diversity and the population dynamics of species (through the use of indicators) composing different trophic guilds to understand the state of the trophic guilds themselves. Additionally, the state of spatial feedback mechanisms that support the different guilds is very important in order to estimate the potential resilience of the trophic guilds (i.e., when a population is sustained or revitalized after a stressful event by the influx of individuals from other populations, or a mobile predator species affects several spatially distant prey populations). For example, mobile consumers can be key stabilizers when there is high connectivity, but also have potent destabilizing potentials if connectivity is low (McCann et al., 2005). As per the MSFD, four criteria are important and need addressing for assessing food web status: (1) species diversity within trophic guilds, (2) guild biomass and balance between guilds, (3) size distribution within guilds, and (4) the productivity of the guilds. Addressing these criteria is a major undertaking, even if some criteria are of higher priority, and relies heavily on the type of data available, such as species biomass, trophic links between species, size categorization of biomass and trophic links, or species turnover rates and population dynamics. Such a resolution of data is not often available for all species but rather often mainly available for species of economic importance (e.g., fisheries species).

While large collections of monitoring data can be available either specifically for each member state (e.g., national or local monitoring programs) or across regional scales (ICES data, EMODNET), the suitability of the dataset to address these four food web criteria is yet unclear. For example, the resolution of data available may be far better for important fish stock species than other species, which favors information on some guilds (e.g., Planktivorous fish and invertebrates or sub-apex demersal predators) but make inferences of the state of other guilds unreliable or even unfeasible in some cases. In addition, some parameters, such as productivity or size composition, are only available for some guilds and a few species within that guild. The problem is that the need

for more homogeneous information on guilds can create an unbalanced estimation of food web properties, hence possible biased assessment of the whole food web. Another major drawback remains that currently, the assessment of the four MSFD food web criteria is focused on indicator-based research (e.g., population of specific species) that is not particularly fit for overall food web assessment because they do not incorporate interconnectivity, such as balance between guilds (Korpinen et al., 2022).

There are two pragmatic approaches to address the drawbacks above. Firstly, assessments can be based on the overall guilds, food web structure or complexity rather than on specific indicators, that is, population dynamics of trophic groups (see recommendation by Korpinen et al., 2022, based on the Baltic Sea). Secondly, data collection can target specific requirements of descriptors. For example, better coverage of species with each guild by increased resolution, better resolution of trophic linkages of species and their specific size fractions, or better estimation of population dynamics of all species within a guild can increase the potential to assess food webs more broadly and thoroughly. Here, we use Denmark as a case study to delve into some of the different types of data sets and methods available to address the MSFD food web criteria (Descriptor 4). This review aims to identify the gaps in data structure and methods available to assess marine food webs *per* the MSFD. Importantly, we strive to identify what aspects of these gaps can be addressed in the short and long term to improve our assessment of marine food webs under the MSFD auspice. We, therefore, undertake a review of the present state of marine food web research in Denmark and then apply some of the available data to directly examine the extent to which addressing the MSFD food web criteria is possible. We then provide some recommendations on what additional data or research would facilitate a better assessment of food webs based on the MSFD criteria.

2 Present state and future potential of marine food web assessment in Denmark

Denmark's coastal waters are highly dynamic and spatially heterogeneous. This heterogeneity is physically driven by complex estuarine circulation processes that occur in the transition zone between the North Sea, the Skagerrak, the Kattegat, and the Baltic Sea, and divide the area into basins with different physico-chemical properties (Gustafsson and Stigebrandt, 1996; Kristiansen and Aas, 2015). Such interacting basins mean that the marine food-webs surrounding Denmark can also be intricate and variable. The physical connectivity likely influences spatial interlinkages and feedback mechanisms between species distributed across the sea areas due to current systems (Bendtsen & Hansen 2013), but also acts as a restrictive barrier due to the gradients in physicochemical parameters (e.g., salinity, different water masses). In addition, the temporal variability (seasonal) and long-term trends (yearly) between species interactions and trophic interaction are key to understanding the state of marine food webs around Denmark. Evaluating the spatial and temporal aspects of changes in complexity and trophic interactions is essential in fulfilling the four assessment criteria for the MSFD Descriptor 4. Currently, the research on food web dynamics around the Danish coastal seas is limited, remains localized and thematically scattered, and is often related to fisheries management. There seems to be swaying towards examining fisheries species (Pecuchet et al., 2020), lower benthic/pelagic trophic levels (hormar et al., 2016; Petersen et al., 2017), and accumulation of contaminants (e.g., mercury, microplastics) along the trophic links (Strand et al., 2005; Stephansen et al., 2012) using food web analysis techniques that include trophic modelling or stable isotope (Hansen et al., 2012; Grønkjær et al., 2013; Lyngsgaard et al., 2017). Nonetheless, the number of studies determining the state of food webs in Danish coastal waters remains limited. Most importantly, there is no assessment of the interaction between different and separated food webs or food webs that cover large sea areas. On the other hand, several broad ecosystem functioning models have the potential to be applied more specifically to food web analysis and fulfil some MSFD criteria (e.g., Bossier et al., 2018; Fath et al., 2019; Heath et al., 2021). Nonetheless, in their current form, these models tend to be primarily designed to gain an understanding of broad ecological functioning for environmental management or swayed towards understanding fisheries impacts on ecosystems.

While there is currently a low number of in-depth studies on the food web structure and dynamics around Denmark, given the large collection of species distribution monitoring data available for the Seas surrounding Denmark through the ICES, EMODNET, or local monitoring programs, there is good potentials to examine food web dynamics through modelling trophic linkages. Even with the structure and resolution of the data currently available, there are some possibilities and drawbacks in fulfilling all the criteria within the MSFD Descriptor 4 (Figure 3.1). Table 8.1 shows an overview of the different species within each trophic guild of the food web in the Kattegat for which data is available. The table was developed by doing a literature search of the guild association of each species based on their food preferences. The trophic guilds presented in Table 8.1 and throughout this document match the structure of Article 8 MSFD assessment guidance (European Commission 2022) but also follow the ICES trophic guild structure. Phytoplankton and zooplankton data of species-specific abundance (individual/L) and biomass (mgC/m³) from the Kattegat are available from multiple stations (point data)

(NOVANA monitoring program). Data from some stations have very long temporal continuity (~30 years) and resolution (monthly sampling), while others provide more sporadically sampled data. Nonetheless, data coverage can be expanded through simple extrapolation, considering water mass distribution (Bendtsen et al., 2024). The data for both phytoplankton and zooplankton are available in abundance or biomass. Nekton and Elasmobranch data are available based on life-history specific distribution (adults, juveniles; see Screening and environmental mapping of offshore wind potential in Denmark" project, The Danish Energy Agency, 2022-2025) and are derived from the ICES DATRAS and Danish Fisheries Agency databases (Danish fishery catch and spatial distribution from the Danish fishery registration project). The data from these sources were extrapolated to provide a spatial estimation of fish densities using Kernel Density Estimation. The data from the ICES DATRAS had a long temporal continuity (23 years; 2000-2023), while that of the Danish Fisheries Agency covers 7 years (2017-2023). Benthic communities are covered by a large number of stations with long time series and provide species-specific abundance and biomass data (. Data on bird abundance and distributions were collected using standard transect surveys and modelled spatially using CReSS-based (Complex Region Spatial Smoother; Scott-Hayward, 2013) spatially adaptive generalized additive models (see Petersen et al., 2022). The data for seagrass and marine mammals come species distribution models based on the ECOMAR project (Andersen et al., 2020). Data for marine mammals also comes from the tracking data from the sensitivity mapping project (Iben et al., 2024).

3 What can current datasets potentially tackle within Descriptor 4

Based on the data available, we have assessed the feasibility of achieving the targets within each criterion of Descriptor 4, for the MSFD trophic guilds ((European Commission 2022) (Figure 3.1). The criteria were evaluated below to identify what is needed for a full assessment and what additional information or data may be required. For each criterion, we looked at what needs to be achieved, what type of data is needed, and whether that data is available. For example, for secondary production (zooplankton), long temporal point-based datasets cover many stations across the Kattegat, which can be modelled into spatial data through species distribution models. These datasets include detailed information on the species composition, biomass, size, and life stages. Additionally, information on the diet preferences of different zooplankton species and predators is largely available in the literature. Therefore, assessing all criteria for the secondary production guild is feasible (Figure 3.1). Similar evaluation was done for each of the trophic guilds of the MSFD, and indications of the feasibility of assessments are depicted in Figure 3.1.

3.1 D4C1: diversity of trophic guilds

Criterion 1 of the Descriptor 4 involves identifying the diversity of trophic guilds within the region, the diversity of organisms composing each trophic guild, their relative abundances, and any change in their abundances due to anthropogenic activities (European Commission 2022). Assessment of this criterion primarily depends on the accuracy and resolution of basic quantitative monitoring data (abundance, biomass) of species and environment over temporal and spatial scales. Data resolution depends on the accuracy of spatial coverage, temporal coverage (monthly, yearly, and total periods), information on trophic niche partitioning, and, importantly, the number of species and anthropogenic pressures for which data is available. Here, data can be split into MSFD guilds (European Commission 2022) or ICES trophic guilds (ICES 2015) based on taxonomy, size classification of species (see D4C3), age, or sex (Jones et al., 2020; Keppeler et al., 2020; Zango et al., 2020). It is important that these parameters are all considered when assigning species to guilds because if parameters such as shifts in trophic guild based on ontogeny, functional traits or population preferences are not accounted for, there may be major inaccuracies in the assessment of the food web. Then, species' diversity (e.g., Shannon diversity index) within each guild can be assessed, along with any spatial or temporal variation in diversity or species abundance/biomass. Additionally, the community structure, including all species, within the guild can be assessed, and any further information on guild stability or redundancy within the guild can be inferred in relation to anthropogenic pressures. The current data can provide a good assessment of criterion 1 and fulfil its aims. The assessments required in this criterion are feasible for all of the trophic guilds (Figure 3.1), even if, in some instances, the number of species included within some guilds may not be comprehensive.

3.2 D4C2: balance of abundance between trophic guilds

Criterion 2 is based on assessing the overall abundance or biomass within a guild and inferring how anthropogenic pressures impact the guild's interaction with other guilds (balance of guilds). Assessing the overall state of specific guilds based on abundance or biomass is relatively feasible, given the data available through various monitoring programs. Species can be classified into guilds based on taxonomy, size structure, age, or sex (e.g., ICES guilds), and the overall biomass of the guild modelled across space or time. The problem here is that assessing connectivity between guilds (balance of guilds) across space and time is challenging. In fact, the MSFD guidance document highlights the absence of an unexacting means of assessing connectivity between guilds. In addition, indicator-based research is unsuitable for assessing the balance between guilds (Korpinen et al., 2022). Nonetheless, some methods can assess connectivity and guild interaction (Parravicini et al., 2020; Garcia-Callejas et al., 2023). For example, by assessing diet information of species within and between trophic guilds and co-existence probability (e.g., competition, mutualism), it is possible to develop networks of non-random (to separate causation from correlation) interactions between species. Currently, several models may allow for the assessment of the connectivity of species or groups between and within the guild(s), such as StrathE2E2 (Heath et al., 2021), Baltic Sea Atlantis (Bossier et al., 2018), Ecological Network Analyses such as Causal Networks (based on Granger causality or convergent cross mapping; Barraquand et al., 2021), Bayesian Belief Networks (Eklöf et al., 2013), or Ecopath with Ecosim (EwE) (Vilasante et al., 2016). However, while these models may be applied to estimate the connections between trophic levels, they are not explicitly designed for examining trophic guilds interactions, most cannot include non-trophic interactions between species, and they have limited capacity to include multiple guilds within the analysis. Instead, they provide an overall assessment of the state of the ecosystem, species interaction networks, or modelling specific parameters. For examining how different guilds influence each other more specifically (balance between guilds), bipartite graph theory can be more suitable, such as weighted bipartite networks (Beckett, 2016) or weighted tripartite networks (Timóteo et al., 2022). These methods allow for a more robust assessment of interactions between species only present in different guilds and, therefore, can convey more accurate information on how one guild influences another (Rumeu et al., 2020; Tochigi et al., 2023). To build such bipartite/tripartite networks, it is important to have robust information on the interaction between species from each guild. For example, suppose the connectivity is based on predator-prey dynamics. In that case, it is a requirement to have robust information on which species from the predator guild is feeding on which species from the prey guild. Such information is often devised from stable isotope analyses, lipid characterization, or gut content analyses (Layman et al., 2012; Kelly and Scheibling, 2012; Thompson et al., 2020, Thibodeau et al., 2023). While the data available can allow for such an assessment of the relationship between pelagic primary producers and secondary producers, we find that to incorporate other trophic guilds, the parameters on species connectivity are not comprehensive enough. However, this can be fulfilled through literature review, gut content analysis, or stable isotope analysis. Secondly, we do not have a current fully functional EwE model, causal network model, Bayesian network model, or bipartite/tripartite model that can assess species' connectivity and interactions between guilds. Nonetheless, there is potential to develop interaction models (e.g., Parravicini et al., 2020; Garcia-Callejas et al., 2023) to address this criterion adequately.

3.3 D4C3: size distribution within guilds

Criterion 3 focuses on understanding the size distribution of species in each trophic guild and how the environment and anthropogenic pressures influence these. The central aspect of this criterion is to use size indicators (e.g., mean maximum length, 95th percentile of length) for different species to assess any changes in overall size and to use survey data rather than commercial catch data to avoid biases based on commercial equipment size selectivity. A comprehensive assessment would require an understanding of the ontogenetic influence of trophic guild structuring (Nakazawa, 2013), including trophic niche partitioning based on life-stage driving size (Egan et al., 2018; Campagna et al., 2021), then an assessment of the size indicator for each species within each guild. This criterion heavily depends on the detail of survey data, that is, details involving the size measurement of different species within different guilds. Currently, this information is mostly available for plankton and fish species. This means that the possibility of fulfilling this criterion for other trophic guilds is currently relatively low (Figure 3.1).

3.4 D4C4: productivity of the trophic guild

Criterion 4 focuses on the productivity of different guilds. For example, the guidance for assessing this criterion includes estimating primary productivity, recruitment, growth, or mortality. To assess criterion 4, there is a need to focus on specific aspects of population structure across spatial and temporal scales, especially with seasonality. These aspects can differ largely between trophic guilds, especially, between species within a guild. Additionally, one guild's productivity may influence another's productivity in two ways. First, based on predator-prey interactions, the availability of prey may influence the productivity of a predator. For example, pelagic primary production will drive secondary production. Second, the size structuring of some species may affect interactions between guild productivity whereby, for example, fish eggs may be planktonic, fish larvae may be primarily planktivorous, juvenile fish may be primarily benthic feeders, and adults may be primarily pelagic predators (Sanchez-Hernandez et al., 2022; Valentine and Whitley, 2024). Based on the data available, currently, such an assessment is likely mainly possible for pelagic primary producers, secondary producers, fisheries species and mammals (Figure 3.1), which have quite good models of population demographics, ontogeny, and population structuring processes (e.g., sub-apex pelagic predators, sub-apex demersal predators).

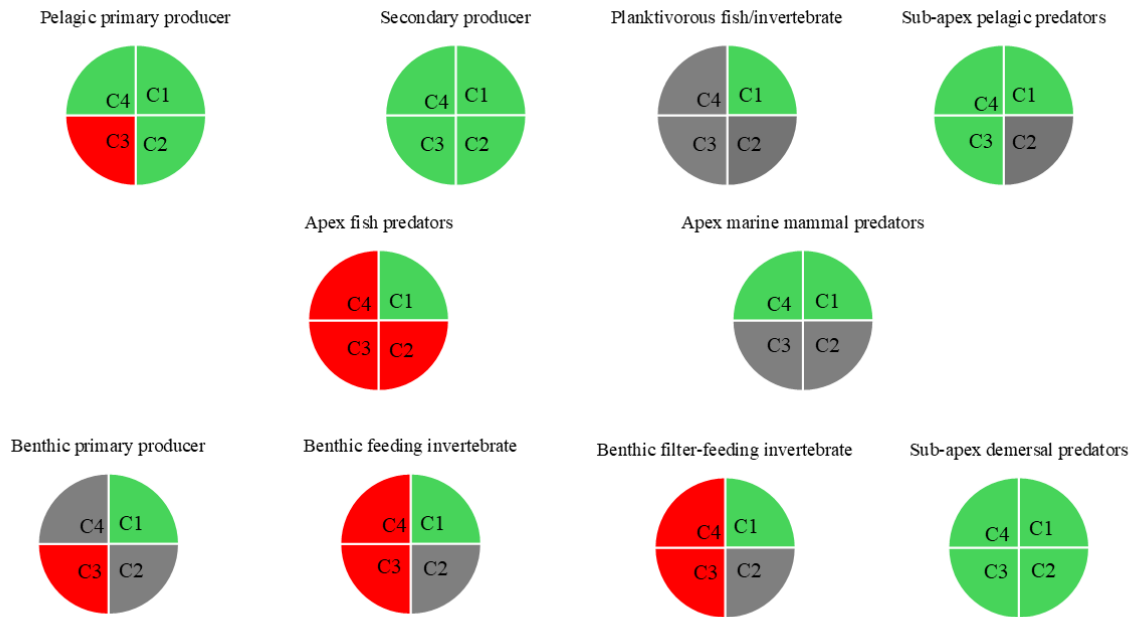


Figure 3.1. Evaluation of the feasibility of fulfilling each criterion of Descriptor 4 (C1, C2, C3, and C4) based on the data available for Kattegat, Denmark. The feasibility assessment is done for each trophic guild as per Article 8 of the MSFD guidance. Green indicates that, given the data at hand, assessing the criterion is feasible. Grey indicates that the relevant data for the parameters required for assessing the criteria are not readily available and may require some work to be put together. Red indicates that there needs to be more data to fulfil the criterion realistically. *Note: As opposed to Article 8, where the colors indicate the completion level of each criterion's assessment, here we are only indicating whether a reasonable assessment of each criterion is feasible given the data at hand. Additionally, Secondary producer refers to pelagic secondary producers only.*

4 Broader MSFD adherence of food web assessment

Following the MSFD guidelines, several factors must be incorporated to assess food webs. First, the assessment is expected to be based on at least three guilds, including those at the bottom, middle, and top of the food web. These should also comprise at least two non-fish guilds and one primary production guild. Second, the assessment is expected to be on a regional basis rather than a national basis. This also includes spatial connectivity assessments based on species distribution (both geographically and by water masses). Finally, the assessment period is expected to be within a relatively recent period, that is, within the last 6 years.

The available data covers all guilds defined in the MSFD guidance document (see Table 8.1) and can be further split to fit within the guilds defined by ICES, OSPAR, and HELCOM. The number of species included in each guild is also quite comprehensive. Therefore, it is possible to have an estimation of food web interactions using species from at least three or more trophic guilds, including primary and secondary producers (Figure 4.1), planktivorous and demersal sub-apex predators (Figure 4.2), and apex mammal predators (Figure 4.3). The exception is 'apex fish predators' whereby only one species (Porbeagle shark; *Lamna nasus*) is currently included, and the actual distribution and abundance of this species are not particularly well covered. Regarding the regional analysis and spatial distribution of species, there is a need to align clearly with the food web analysis undertaken under OSPAR and HELCOM. While the present study focuses on understanding the feasibility of assessments for the Kattegat in Denmark, the extent of the data set covers broader areas in the Baltic and North Seas. This means that regional analyses by merging datasets and efforts with the regional sea conventions (OSPAR and HELCOM) are feasible. Additionally, similar indicators (either species-based or network analysis-based) (Ojaveer et al., 2020) and methods can be used as per the work performed in the Working Group on Integrated Assessment of the Baltic Sea (joint ICES and HELCOM group) and the OSPAR Food Web Expert group which also feeds into the Intersessional Correspondence Group on Coordination of Biodiversity Monitoring and Assessment (ICG-COBAM).



Figure 4.1. Spatial distribution map of primary and secondary producer trophic guild components (excluding macroalgae) for which data is available. For eelgrass, the habitat suitability is mapped and not the actual spatial distribution. Data for phytoplankton and zooplankton are currently in point format and can be transformed to spatial scale through species distribution models. The spatial expanse shown here is based on an expected total coverage given the large number of sampling stations for phytoplankton and zooplankton and do not represent actual spatially modelled data. The current graph is based on the ECOMAR data (Andersen et al., 2020). More recent and comprehensive data is being compiled through the “Screening and environmental mapping of offshore wind potential in Denmark” project (The Danish Energy Agency, 2022-2025).

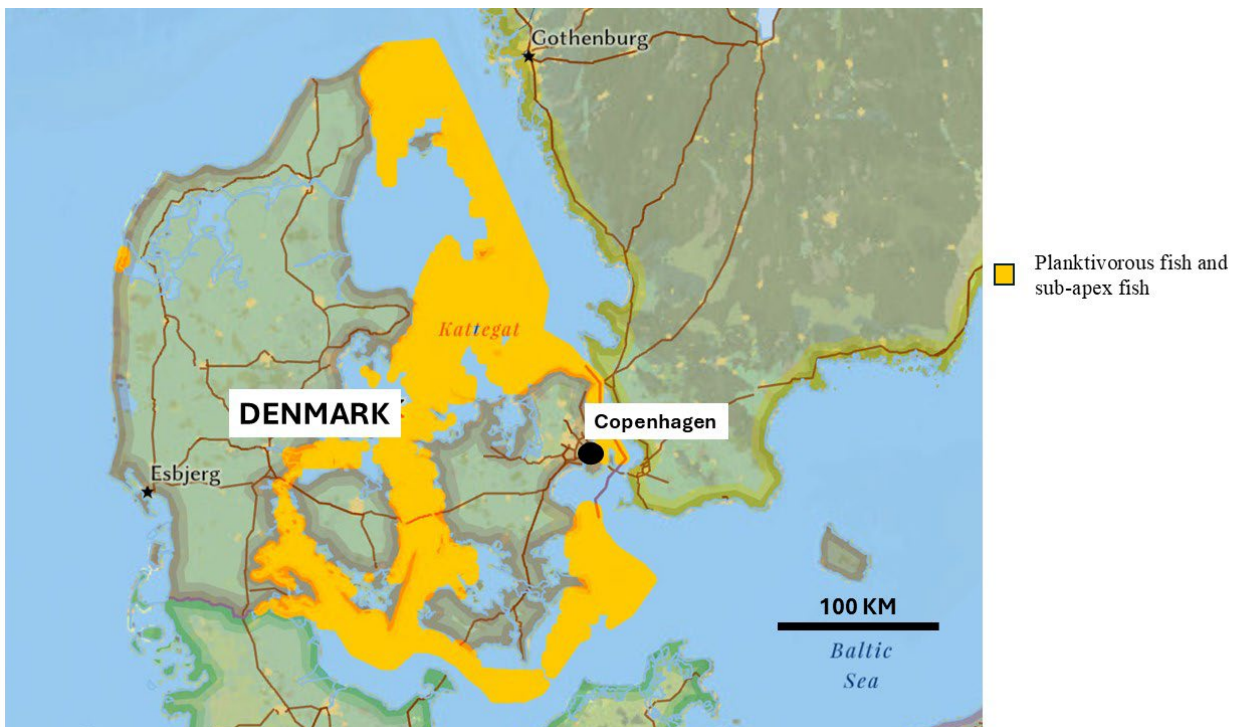


Figure 4.2. Distribution of fish trophic guilds based on modelled distribution. The data incorporated in the graph covers planktivorous fish and sub-apex fish predators. The current graph is based on the ECOMAR data (Andersen et al., 2020). More recent and comprehensive data is being compiled through the “Screening and environmental mapping of offshore wind potential in Denmark” project (The Danish Energy Agency, 2022-2025).

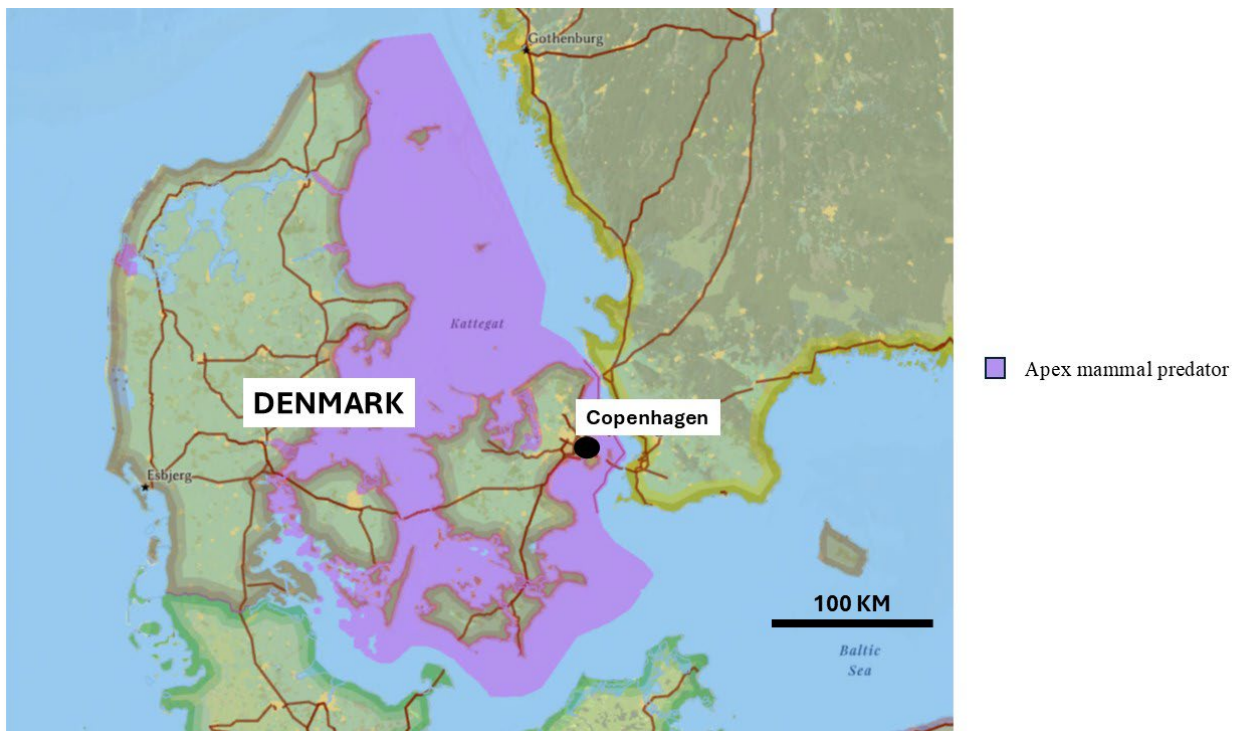


Figure 4.3. Spatial extent of apex mammal predators. Incorporated in the data layer are Harbour seals, Harbour porpoise, and Grey seals. The current graph is based on the ECOMAR data (Andersen et al., 2020). More recent and comprehensive data is being compiled through the “Screening and environmental mapping of offshore wind potential in Denmark” project (The Danish Energy Agency, 2022-2025).

A large proportion of the analyses required in D4C1 (diversity within guilds) and partly D4C2 (state of species biomass within each guild) are already incorporated and performed in other MSFD criteria (e.g., Descriptor 1 or Descriptor 6) even if these are not described per specific trophic guild. These assessments are based on the most recent datasets, meaning that a recent assessment specifically based on trophic guilds can be feasible. Additionally, the compilation of new data sets and analysis under the “Screening and environmental mapping of offshore wind potential in Denmark” project (The Danish Energy Agency, 2022-2025) means that data available for assessing food webs are comprehensive, recently quality assured and spatially interpreted. Therefore, the current major steps required towards fulfilling the MSFD involve more specific assessments under the different criteria of Descriptor 4. For example, food web structure (e.g., balance between guilds), detailed understanding of guilds based on size and ontogenetic niche partitioning, and specific productivity of species or guilds. Several models exist or can be developed to tackle part or most of the required assessments.

5 Potential models for food web assessment based on current datasets

Several food web models exist or can be developed to fulfil more specific aspects of the MSFD criteria. It is important to note that no single model can fulfill all criteria and even if a model can be particularly suited for one criterion, it may not assess all the specificities under that criterion. Additionally, there are certain aspects of criterion two (balance between guilds) and criterion three (assessing size distribution across trophic guilds) where guidance from the MSFD has not been developed yet (see Article 8). For example, there are no specific assessment protocols for understanding the interaction between different guilds within the food web or assessing how changes in the size of a species drive its association with different guilds (e.g., switching from one guild to another, or increased overlap between guilds). For these, it is important to develop appropriate models that align with the regional sea conventions. Therefore, below (Table 5.1), we describe a focused selection of models that have the potential to fulfil some of the MSFD criteria in their current state or have been given some modifications but could also be developed to assess criteria two and three more specifically.

5.1 StrathE2E2

The StrathE2E2 (Heath et al., 2021) is primarily a predictive model developed for merging top-down and bottom-up processes with fishing-based extractions to understand how cascading effects are attenuated or amplified along the food web. The model outputs include scenario-based changes in the nitrogen mass of different components and potential comparisons between different scenarios. To achieve this, the model uses two, quite comprehensive, sub-networks: (1) a nutrient recycling network and (2) a predator-prey network, both of which are expressed in terms of nitrogen mass transfer throughout the network (as opposed to carbon). The model can be developed for annual or monthly data. Based on the North Sea, the current version has only a coarse spatial component separating food webs based on bathymetry (threshold of 30m depth). Two different modes of benthic-pelagic coupling drive it. The input data for the model includes sedimentary and suspended nitrate and ammonia, sedimentary and suspended bacteria and detritus, phytoplankton, omnivorous and carnivorous zooplankton, suspension-feeding and scavenging benthic invertebrates (adult and larvae), planktivorous and demersal fish (adult and larvae), and apex vertebrates (birds, pinnipeds, and cetaceans). These categories of input data correspond broadly to the ICES guilds, but they are in terms of nitrogen mass and not abundance or biomass (although Redfield ratios can be applied for conversion). In addition, a fisheries component includes input data such as benthic and pelagic invertebrate landings, cetacean landings, and planktivorous and demersal fish landings. This fisheries component data is embedded in the ecological predator-prey network and, therefore, includes an estimation of total landings based on data on extracting of organisms and discards. Finally, the model also considers the potential resuspension of nutrients or detritus from fishing activities (e.g., abrasion by benthic trawling). The specific relationships between the model components are derived from the literature and represented in the model by differential equations (see Heath et al., 2021 Appendices for specific equations and literature references). While the StrathE2E2 is a comprehensive model and can be adapted to multiple ecosystems, given that the required information about the

ecosystem for the model is available, it needs to be revisited to understand multiple aspects of food webs. For example, the model is designed to estimate fisheries' impact on the change in nitrogen stoichiometric mass (productivity) of the different components (guilds). Therefore, it may be difficult to implement the potential impact of other anthropogenic pressures, especially given that the relationships between the components (guilds) are pre-established.

5.2 Baltic Sea Atlantis

The Baltic Sea Atlantis (Bossier et al., 2018) is another comprehensive model that integrates multiple ecosystem components (physical-chemical-biological) to provide a holistic overview of how human pressures influence the ecosystem. The model was developed based on datasets from the Baltic Sea with a focus on ecosystem-based management and, therefore, integrates detailed information from the system, including biogeochemistry and fisheries pressure. It also utilizes multiple vertical (depth) and horizontal spatial sub-areas to account for spatial differences in ecosystem functioning. In addition, the model incorporates 30 biological functional groups, although these are not specifically based on trophic guilds (e.g., those proposed by ICES). To do this, the Baltic Sea Atlantis merges three pre-existing models (HBM-ERGOM - Atlantis - FISHRENT), each feeding information into the next. First, it uses the HBM-ERGOM model to generate 3D information on ocean hydrodynamics. With the inclusion of biogeochemistry and plankton dynamics. This information is then fed into the Atlantis model which is an ecosystem-based fisheries management tool that includes food web dynamics (Fulton et al., 2011). Finally, the results are fed into a FISHRENT model, which is a multi-stock multi-fleet bio-economic fisheries model (Salz et al., 2011). The overall Baltic Sea Atlantis model outputs scenario-based (e.g., reduction of nitrogen) predictions of biogeochemistry, biomass of different functional groups, and net present value of total fisheries over a specified number of years (e.g., following 30 years). One of the major drawbacks with the Baltic Sea Atlantis (and the Atlantis component itself) is that although it potentially provides a comprehensive assessment of ecosystems, given the complex integration of different "sub-models", it can be highly complex to calibrate to the extent where it produces reliable outputs, especially when more specific food web questions or hypotheses need to be tested.

5.3 Ecopath with Ecosim Ecospace

The Ecopath with Ecosim model (EwE) is a trophic interaction model based on specific predator-prey interactions between individual species from different trophic levels. The model is based on two components; (1) Ecopath, which is a trophic mass balance component that is the transfer of biomass from one trophic level to another through predator-prey relationship, and (2) Ecosim which is a dynamic modelling component that allows for changes in variables such as fishing effort, climate change, or other environmental variables (Christensen and Walters, 2004). An additional module to EwE is Ecospace. Ecospace essentially adds a spatial component by allowing the modelling of the same food web to be repeated over space, such as in different grid cells. Therefore, EwE and Ecospace provide a highly versatile platform for analyzing changes in food web interactions based on different types of pressure on ecosystems. They are probably the most used models for this purpose and are used in further applications such as ecosystem-based management (Heymans et al., 2016), marine spatial planning (Dichmont et al., 2013; Ortega-Cisneros,

et al., 2022), fisheries impact and management (Serpetti et al., 2017), or cumulative impact assessment (Raoux et al., 2020). Although EwE and Ecospace are extremely applicable in different contexts, there remain certain ecological components that they cannot incorporate. For example, EwE is only based on predator-prey relationships and, therefore, cannot incorporate indirect food web driving relationships such as mutualism or competition. Additionally, it cannot integrate multiple sub-networks within the larger food web network that indirectly influence each other. For this one would require the development and addition of bipartite motifs (Simons et al., 2018) to EwE; something that may not be feasible currently. Finally, while Ecospace integrates a spatial component within the model, its resolution is relatively coarse and, more importantly, it cannot account for spatial feedback mechanisms (e.g., Pichon et al., 2024) that drive food web stability and resilience.

5.4 Ecological networks

Ecological network analysis (ENA) is likely among the most versatile models in terms of integrating large amounts of information on species interactions (Fath et al., 2007; Schückel et al., 2022). ENA can incorporate both direct and indirect interactions between as many species as one has data for, measure the strength of the relationship between different species, and use a variety of network assessment metrics to understand how the food web functions, what organisms have a vital role in the network, or how many organisms are directly or indirectly impacted based on changes in one species. This means that ENA can also provide a variety of information to different stakeholders for environmental status assessment (Fath et al., 2019), such as what extent of food web interaction shifts can be expected by some extraction of a species (fisheries applicability), what thresholds in species biomass will change resilience or stability in the food web (analysis of thresholds and food web dynamics shifts based), or how quickly disturbance or restoration effects spread through the food web (impact assessment). ENA can be built based on different means of linking species (nodes) to each other (Schückel et al., 2022). For instance, linkages can be based on correlation or similarity matrices (e.g., Hemraj et al., 2017), causal relationships (e.g., convergent cross mapping; Barraquand et al., 2021), or Bayesian belief, which is more probabilistic expert-based assessment of linkages between species (Lim et al., 2018). Additionally, ENA can be expanded to a spatial scale by computing the network by grid cell (similar to EwE) or by computing causal relations by leveraging spatial replication of species data (Clark et al., 2015). Finally, ENA can implement bipartite or tripartite graph analysis to look more specifically at the interactions between predefined groups of species (e.g., sub-networks, trophic guilds) (Parravicini et al., 2020; Garcia-Callejas et al., 2023). Given the possibility of making ENA very comprehensive and complex, this complexity can also come at a cost. Building a robust and informative ecological network (or food web network) requires a significant amount of data to reliably assess the strength of interactions between species (although this can also be supplemented by isotope or DNA analyses). Additionally, assessing long-term shifts in the food web may require developing individual networks by partitioning the data over multiple shorter time series (e.g., splitting a 20-year time series into four 5-year time series to assess changes in food web structure over four different time periods). Depending on the length of the time series, the number of individual data points, and the metric used to assess the strength of inter-species linkages (correlation, cross-mapping), splitting data into too short sections may reduce the reliability of the network.

Table 5.1. Key aspects of models that allow the assessment of food webs and can be applied for fulfilling different the criteria of the MSFD Descriptor four both locally for Denmark and that can align with the regional sea conventions. The last three columns denote whether the model is commonly used within the context of assessing ecosystems or food webs in these conventions. Note that there may be some studies as part of these conventions that have utilized one or more of these models, but the models do not seem to form the basis of ecosystem or food web assessment in the conventions.

Method	Data requirement	Food web currency	Horizontal spatial (area)	Vertical spatial (depth)	Spatial feedback	Direct food web interactions	Indirect food web interaction	Guild interaction	Complex to setup	Assessment of pressure impact	Used in OSPAR*	Used in HELCOM*	Used in ICES*	MSFD criteria applicable
<i>StrathE2E2</i>	High	Nitrogen biomass	No	No	No	High	No	No	Moderate	Low	No	No	Yes	1,2,3,4
<i>EwE</i>	High	Carbon biomass	No	No	No	High	No	No	Low	High	Yes	Yes	Yes	2
<i>Ecospace</i>	High	Carbon biomass	High	No	No	High	No	No	Low	High	Yes	No	Yes	2
<i>Baltic Sea Atlantis</i>	High	Carbon biomass	Moderate	High	No	High	No	No	High	Low	No	Yes	Yes	1,2,3,4
<i>Ecological Network (empirical or Bayesian belief network)</i>	High (except for Bayesian belief network)	Carbon biomass, Abundance	High	Moderate	High	High	High	High	Moderate	High	Yes	Yes	Yes	2

6 Potential for future assessments

Much of the work under ICES, OSPAR, and HELCOM currently involves developing and testing indicators to support ongoing food web assessment. Many of these indicators are based on individual species, trophic levels, or trophic guilds. On a short-term basis, such indicator-based work can be implemented in the assessment of trophic guilds for the Kattegat. For example, the diversity of guilds and diversity within guilds (D4C1), and the status of different trophic guilds based on abundances or biomass (D4C2) can be assessed in a relatively immediate term. These will also highlight exactly what gaps there may be in terms of monitoring data relevant to food web analyses in relation to fulfilling the MSFD. Additionally, using these assessments, there is potential to develop and test some indicators that can link directly with the current work from OSPAR and HELCOM. Nonetheless, it is important that indicators are not only based on specific guilds but also on the dynamics of food web interactions. Such work can be developed in the medium to long term (Table 6.1).

From a more short-term practical perspective, there are several avenues that can be delved into to make the assessment of Descriptor 4 more concrete. (1) The diversity of species within guilds can be assessed more concretely, both temporarily and spatially (D4C1). This can be based on the MSFD trophic guilds that are also used in OSPAR. Such a classification is already done here in the Appendix (Table 7.1) and can form the basis for evaluating diversity within guilds. (2) Spatial variations of the diversity of guilds can be assessed (D4C1). This can be based on combined biomass or abundances of species within a guild and then used to calculate alpha and beta diversity of guilds per grid cell to get a spatial overlay of diversity. (3) There is a need to extend the current databases to include information on the prey of different organisms, especially those that are not of major fisheries interest (D4C2). For example, such information can be very scarce for planktivorous fish and benthic species and would require analysis of gut contents. (4) There is a need to extend databases to include sizes of organisms to assess the changes in size distribution (temporally and spatially). This ideally should include individuals of different life stages. The potential for an adequate analysis of size distribution is currently fairly low for the majority of species (D4C3). (5) Key anthropogenic pressures affecting specific guilds or food web indicators such as those used in OSPAR or HELCOM. (6) Defining temporal patterns for species from specific guilds to define productivity (D4C4). For example, there is low information on the population demographics several species. This is especially required for benthic species.

Table 6.1. Five key medium- to long-term food web assessment avenues that will lead to a comprehensive understanding of the status of food webs in the Kattegat and help determine the environmental status from a food web perspective.

Major research opportunity (medium to long term)	Potential direction
Development of species interaction-based indicators using direct and indirect interspecific interactions.	Food web interaction-based indicators (e.g., connectedness, complexity, stability) are likely more relevant to assessing the state of the food web than species or guild specific indicators. Such interaction-based indicators should be derived from food web interaction networks developed through a suitable model. Here, EwE with Ecospace can be a good option because it is very widely used and thus allows for comparative assessment across regions. However, ENA-based analyses and indicators may provide an even more appropriate assessment, especially because of its versatility. ENA can incorporate both direct and indirect interactions between species and provide very detailed analyses of the food web network using a large variety of metrics (e.g., Hemraj et al., 2017, Lewis et al., 2022). This will also fit well with the current work undertaken in OSPAR and HELCOM, for example.
Trophic guild interactions (e.g., D4C2).	There is a need to develop a means of properly assessing the balance between guilds. Currently, this is difficult given the lack of interconnectivity analysis implemented in the MSFD. Nonetheless, techniques such as bipartite, or tripartite networks can provide an appropriate avenue to assessing interactions between guilds (e.g., Kondoh et al., 2010, Parravicini et al., 2020).
Spatial assessment of food web feedback (both geographically and by depth).	There are two spatial factors that are key to the assessment of the food webs. First is the geographical connectivity between multiple local food webs that form broader meta-web whereby spatial feedback (population sustained by migration) plays a very important role in influencing the stability, complexity, or resilience of the food web. Such broad scale connectivity is very important because it makes the assessment of the food web more relevant and informative on a broader ecosystem scale (e.g., across the whole Kattegat) compared to specific within a small system (e.g., only focusing of eelgrass supported food web). Second, depth categorization of food web interactions can be difficult, especially in deep waters, but also in shallow waters where strong pycnoclines and haloclines occur or other environmental factors drive depth partitioning of species distribution (e.g., light penetration). Here again, Ecospace and ENA seem more appropriate to implement spatial analyses into food web assessment (e.g., Fortin et al., 2021).
Species ontogeny-based niche and trophic segregation.	Most species can be associated with different trophic levels and guilds based on their developmental stages (e.g., Lorenzo et al., 2020). This means that there is a need to develop an assessment of trophic level or guild association of different species to address trophic guild status or productivity. Such assessments can be done through stable isotope or metabarcoding techniques.
Analysis of anthropogenic and climate change related impacts on food web structure.	A major part of Descriptor 4 includes a requirement to evaluate the impact of different pressures on driving changes in the food

web. Such an impact can be evaluated based on specific indicators and on broader food web dynamics. While it is of interest to evaluate the response specific trophic levels and guilds to pressures, a broader assessment of cumulative pressure impact on food web interconnectivity and dynamics would be ideal because of the comprehensiveness of such an assessment, and, importantly, it can help identify weak links and relevant thresholds within the food web (e.g., trophic guilds that are most under pressure, extent of pressure that drive key thresholds in specific species or guilds, and how such thresholds can disrupt the overall food web).

7 References

- Andersen, J.H., Bendtsen, J., Hammer, K.J., Harvey, T., Knudsen, S.W., Murray, C.J., Carstensen, J., Petersen, I.K., Sveegaard, S., Tougaard, J. and Edlevang, K., 2020. ECOMAR: A data-driven framework for ecosystem-based Maritime Spatial Planning in Danish marine waters. NIVA.
- Barraquand, F., Picoche, C., Detto, M. and Hartig, F., 2021. Inferring species interactions using Granger causality and convergent cross mapping. *Theoretical Ecology*, 14(1), pp.87-105.
- Beckett, S.J., 2016. Improved community detection in weighted bipartite networks. *Royal Society open science*, 3(1), p.140536.
- Bendtsen, J. and Hansen, J.L., 2013. Effects of global warming on hypoxia in the Baltic Sea–North Sea transition zone. *Ecological modelling*, 264, pp.17-26.
- Bendtsen, J., Daugbjerg, N., Jensen, R.S., Brady, M.C., Nielsen, M.H., Hansen, J.L. and Richardson, K., 2024. Phytoplankton community changes in relation to nutrient fluxes along a quasi-stationary front. *Marine Ecology Progress Series*, 727, pp.67-80.
- Bossier, S., Palacz, A.P., Nielsen, J.R., Christensen, A., Hoff, A., Maar, M., Gislason, H., Bastardie, F., Gorton, R. and Fulton, E.A., 2018. The Baltic Sea Atlantis: An integrated end-to-end modelling framework evaluating ecosystem-wide effects of human-induced pressures. *PLoS One*, 13(7), p.e0199168.
- Campagna, J., Lewis, M.N., González Carman, V., Campagna, C., Guinet, C., Johnson, M., Davis, R.W., Rodríguez, D.H. and Hindell, M.A., 2021. Ontogenetic niche partitioning in southern elephant seals from Argentine Patagonia. *Marine Mammal Science*, 37(2), pp.631-651.
- Clark, A.T., Ye, H., Isbell, F., Deyle, E.R., Cowles, J., Tilman, G.D. and Sugihara, G., 2015. Spatial convergent cross mapping to detect causal relationships from short time series. *Ecology*, 96(5), pp.1174-1181.
- Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A. and Claudet, J., 2020. Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish and Fisheries*, 21(5), pp.906-915.
- Donati, E., Fabbri, F., Russo, E., Pranovi, F., Ponti, M., Turicchia, E., Airoidi, L., Mazzotta, M. and Brigolin, D., 2022. Application of spatial food web simulations at a marine Natura 2000 site: analysis of vulnerability and management actions. In *ADATTAMENTI DEGLI ECOSISTEMI ALLE PRESSIONI DELL'ANTROPOCENE: 31. congresso S. It. E* (pp. 186-186). Università di Siena.
- Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de Sassi, C., Galetti, M., Guimarães, P.R. and Lomáscolo, S.B., 2013. The dimensionality of ecological networks. *Ecology letters*, 16(5), pp.577-583.
- European Commission, 2022. MSFD CIS Guidance Document No. 19, Article 8 MSFD, May 2022.

- Fath, B.D., Asmus, H., Asmus, R., Baird, D., Borrett, S.R., de Jonge, V.N., Ludovisi, A., Niquil, N., Scharler, U.M., Schückel, U. and Wolff, M., 2019. Ecological network analysis metrics: the need for an entire ecosystem approach in management and policy. *Ocean & Coastal Management*, 174, pp.1-14.
- Fortin, M.J., Dale, M.R. and Brimacombe, C., 2021. Network ecology in dynamic landscapes. *Proceedings of the Royal Society B*, 288(1949), p.20201889.
- García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J.B., Allen-Perkins, A. and Bartomeus, I., 2023. Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. *Ecology Letters*, 26(6), pp.831-842.
- Grønkjær, P., Pedersen, J.B., Ankjærø, T.T., Kjeldsen, H., Heinemeier, J., Steingrund, P., Nielsen, J.M. and Christensen, J.T., 2013. Stable N and C isotopes in the organic matrix of fish otoliths: validation of a new approach for studying spatial and temporal changes in the trophic structure of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(2), pp.143-146.
- Gustafsson, B. and Stigebrandt, A., 1996. Dynamics of the freshwater-influenced surface layers in the Skagerrak. *Journal of Sea Research*, 35(1-3), pp.39-53.
- Heath, M.R., Speirs, D.C., Thurlbeck, I. and Wilson, R.J., 2021. StrathE2E2: an R package for modelling the dynamics of marine food webs and fisheries. *Methods in Ecology and Evolution*, 12(2), pp.280-287.
- Hemraj, D.A., Hossain, A., Ye, Q., Qin, J.G. and Leterme, S.C., 2017. Anthropogenic shift of planktonic food web structure in a coastal lagoon by freshwater flow regulation. *Scientific Reports*, 7(1), p.44441.
- ICES. 2015. 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
- Jones, A.G., Quillien, N., Fabvre, A., Grall, J., Schaal, G. and Le Bris, H., 2020. Green macroalgae blooms (*Ulva* spp.) influence trophic ecology of juvenile flatfish differently in sandy beach nurseries. *Marine environmental research*, 154, p.104843.
- Kelly, J.R. and Scheibling, R.E., 2012. Fatty acids as dietary tracers in benthic food webs. *Marine Ecology Progress Series*, 446, pp.1-22.
- Keppeler, F.W., Montaña, C.G. and Winemiller, K.O., 2020. The relationship between trophic level and body size in fishes depends on functional traits. *Ecological Monographs*, 90(4), p.e01415.
- Kondoh, M., 2010. Linking learning adaptation to trophic interactions: a brain size-based approach. *Functional Ecology*, 24(1), pp.35-43.
- Korpinen, S., Uusitalo, L., Nordström, M.C., Dierking, J., Tomczak, M.T., Haldin, J., Opitz, S., Bonsdorff, E. and Neuenfeldt, S., 2022. Food web assessments in the Baltic Sea: Models bridging the gap between indicators and policy needs. *Ambio*, 51(7), pp.1687-1697.

- Kristiansen, T. and Aas, E., 2015. Water type quantification in the Skagerrak, the Kattegat and off the Jutland west coast. *Oceanologia*, 57(2), pp.177-195.
- Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A. and Post, D.M., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological reviews*, 87(3), pp.545-562.
- Lewis, K.A., Christian, R.R., Martin, C.W., Allen, K.L., McDonald, A.M., Roberts, V.M., Shaffer, M.N. and Valentine, J.F., 2022. Complexities of disturbance response in a marine food web. *Limnology and Oceanography*, 67, pp.S352-S364.
- Lim, R.B.H., Liew, J.H., Kwik, J.T.B. and Yeo, D.C.J., 2018. Predicting food web responses to biomanipulation using Bayesian Belief Network: Assessment of accuracy and applicability using in-situ enclosure experiments. *Ecological Modelling*, 384, pp.308-315.
- Lyngsgaard, M.M., Markager, S., Richardson, K., Møller, E.F. and Jakobsen, H.H., 2017. How well does chlorophyll explain the seasonal variation in phytoplankton activity? *Estuaries and Coasts*, 40, pp.1263-1275.
- McCann, K.S., Rasmussen, J.B. and Umbanhowar, J., 2005. The dynamics of spatially coupled food webs. *Ecology letters*, 8(5), pp.513-523.
- Nagelkerken, I., Goldenberg, S.U., Ferreira, C.M., Ullah, H. and Connell, S.D., 2020. Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. *Science*, 369(6505), pp.829-832.
- Nakazawa, T., 2015. Ontogenetic niche shifts matter in community ecology: a review and future perspectives. *Population Ecology*, 57, pp.347-354.
- Ojaveer, H., Neuenfeldt, S., Eero, M. and Uusitalo, L., 2020. Review of food web indicators for the Baltic Sea. BONUS XWEBS Deliverable, D3.1 . EU BONUS project XWEBS, 16 pp. DOI 10.3289/XWEBS_D3.1.
- Parravicini, V., Casey, J.M., Schiettekatte, N.M., Brandl, S.J., Pozas-Schacre, C., Carlot, J., Edgar, G.J., Graham, N.A., Harmelin-Vivien, M., Kulbicki, M. and Strona, G., 2020. Delineating reef fish trophic guilds with global gut content data synthesis and phylogeny. *PLoS Biology*, 18(12), p.e3000702.
- Petersen, M.E., Maar, M., Larsen, J., Møller, E.F. and Hansen, P.J., 2017. Trophic cascades of bottom-up and top-down forcing on nutrients and plankton in the Kattegat, evaluated by modelling. *Journal of Marine Systems*, 169, pp.25-39.
- Rumeu, B., Donoso, I., Rodríguez-Pérez, J. and García, D., 2020. Frugivore species maintain their structural role in the trophic and spatial networks of seed dispersal interactions. *Journal of Animal Ecology*, 89(9), pp.2168-2180.
- Sánchez-Hernández, J., Prati, S., Henriksen, E.H., Smalås, A., Knudsen, R., Klemetsen, A. and Amundsen, P.A., 2022. Exploring temporal patterns in fish feeding ecology: Are ontogenetic dietary shifts stable over time?. *Reviews in Fish Biology and Fisheries*, 32(4), pp.1141-1155.

Sanders, D., Thébault, E., Kehoe, R. and Frank van Veen, F.J., 2018. Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences*, 115(10), pp.2419-2424.

Schückel, U., Nogues, Q., Brito, J., Niquil, N., Blomqvist, M., Sköld, M., Hansen, J., Jakobsen, H. and Morato, T. 2022. Pilot Assessment of Ecological Network Analysis Indices. In: *OSPAR, 2023: The 2023 Quality Status Report for the North-East Atlantic*. OSPAR Commission, London. Available at: <https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/pilotassessment-ecological-network-analysis-indices/>

Scott-Hayward, L.A.S., 2013. Novel methods for species distribution mapping including spatial models in complex regions (Doctoral dissertation, University of St Andrews).

Stephansen, D.A., Svendsen, T.C., Vorkamp, K. and Frier, J.O., 2012. Changes in patterns of persistent halogenated compounds through a pelagic food web in the Baltic Sea. *Marine environmental research*, 73, pp.17-24.

Strand, J. and Jacobsen, J.A., 2005. Accumulation and trophic transfer of organotins in a marine food web from the Danish coastal waters. *Science of the Total Environment*, 350(1-3), pp.72-85.

Thibodeau, B., Allais, L., Agosto, L.E., So, M.W.K. and Cannicci, S., 2023. Isotopes of amino acids give novel insights on nitrogen sources partitioning and trophic position of invertebrates in a subtropical mangrove. *Ecological Indicators*, 150, p.110261.

Thompson, M.S., Pontalier, H., Spence, M.A., Pinnegar, J.K., Greenstreet, S.P., Moriarty, M., Hélaouët, P. and Lynam, C.P., 2020. A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning. *Journal of Applied Ecology*, 57(9), pp.1769-1781.

Thormar, J., Hasler-Sheetal, H., Baden, S., Boström, C., Clausen, K.K., Krause-Jensen, D., Olesen, B., Rasmussen, J.R., Svensson, C.J. and Holmer, M., 2016. Eelgrass (*Zostera marina*) food web structure in different environmental settings. *PLoS One*, 11(1), p.e0146479.

Timóteo, S., Albrecht, J., Rumeu, B., Norte, A.C., Traveset, A., Frost, C.M., Marchante, E., López-Núñez, F.A., Peralta, G., Memmott, J. and Olesen, J.M., 2023. Tripartite networks show that keystone species can multitask. *Functional Ecology*, 37(2), pp.274-286.

Tochigi, K., Steyaert, S.M., Naganuma, T., Yamazaki, K. and Koike, S., 2022. Differentiation and seasonality in suitable microsites of seed dispersal by an assemblage of omnivorous mammals. *Global Ecology and Conservation*, 40, p.e02335.

Valentine, S.A. and Whitledge, G.W., 2024. Spatial and Ontogenetic Patterns in the Trophic Ecology of Two Predatory Fishes in a Large River. *Ecology of Freshwater Fish*, p.e12814.

Villasante, S., Arreguín-Sánchez, F., Heymans, J.J., Libralato, S., Piroddi, C., Christensen, V. and Coll, M., 2016. Modelling marine ecosystems using the Ecopath with Ecosim food web approach: New insights to address complex dynamics after 30 years of developments. *Ecological Modelling*, 331, pp.1-4.

8 Appendix

Trophic Guild	Taxonomic group for which data is available
Pelagic primary producers	<p><u>Phytoplankton:</u></p> <ul style="list-style-type: none">• Picoplankton <p>Bacillariophyta:</p> <ul style="list-style-type: none">• Cyclotella• Hemiaulus• Phaeodactylum tricornutum <p>Charophyta:</p> <ul style="list-style-type: none">• Closterium• Staurastrum• Elakatothrix <p>Chlorophyta:</p> <ul style="list-style-type: none">• Pyramimonas/tetraselmis• Actinastrum hantzschii• Binuclearia lauterbornii• Binuclearia submarina• Chlamydomonas• Chlorococcales• Coelastrum microporum• Halosphaera• Kirchneriella• Koliella• Lobocystis planctonica• Lobocystis planctonica• Micromonas pusilla• Monoraphidium• Monoraphidium contortum• Monoraphidium komarkovae• Nephroselmis• Oocystis• Pachysphaera• Pediastrum• Pediastrum duplex• Planctonema

-
- Prasinophyceae
 - Pseudopediastrum kawraiskyi
 - Pseudopediastrum boryanum
 - Pseudoscourfieldia
 - Pterosperma
 - Pterosperma
 - Pyramimonas longicauda
 - Scenedesmus
 - Stichococcus minutissimus
 - Tetradron caudatum
 - Tetradron minimum
 - Tetrastrum

Choanozoa:

- Pleurasiga
- Stephanoeca

Ciliophora:

- Balanionidae
- Cyclidium
- Epistylis
- Euplotes
- Hypotrichia
- Laboea
- Mesodinium pulex
- Mesodinium rubrum
- Oxytricha
- Spirostrombidium sauerbreyae
- Strombidium ovale

Cryptophyta:

- Hemiselmis virescens
- Cryptophyceae
- Plagioselmis prolonga
- Teleaulax acuta
- Teleaulax amphioxeia
- Cryptomonas
- Cryptophyceae

Cyanobacteria:

-
- *Anabaena oscillarioides*
 - *Aphanizomenon flos-aquae*
 - *Aphanizomenon gracile*
 - Aphanothece
 - Calothrix
 - Chroococcales
 - *Coelomoron pusillum*
 - *Cyanodictyon planctonicum*
 - *Cyanodictyon reticulatum*
 - *Cyanonephron styloides*
 - Cyanophyceae
 - *Dolichospermum heterosporum*
 - *Dolichospermum lemmermannii*
 - *Dolichospermum spiroides*
 - Gloeotrichia
 - Lemmermanniella
 - *Lemmermanniella pallida*
 - Limnothrix
 - *Merismopedia tenuissima*
 - *Microcystis wesenbergii*
 - *Nodularia spumigena*
 - Nostocales
 - Oscillatoria
 - Picoplankton blågrøn
 - Planktolyngbya
 - Planktothrix
 - *Pseudanabaena acicularis*
 - *Pseudanabaena limnetica*
 - *Snowella litoralis*
 - Spirulina
 - Synechococcus
 - *Woronichinia compacta/coelomoron pusillum*
 - *Woronichinia/gomphosphaeria*

Dinophyta:

- *Akashiwo sanguinea*
- *Alexandrium margalefii*

-
- *Alexandrium minutum*
 - *Alexandrium ostenfeldii*
 - *Alexandrium tamarense*
 - *Amphidinium crassum*
 - *Amylax triacantha*
 - *Athekate furealger*
 - *Azadinium*
 - *Ceratium furcoides*
 - *Ceratium fusus*
 - *Ceratium hirundinella*
 - *Ceratium horridum*
 - *Ceratium lineatum*
 - *Ceratium lunula*
 - *Ceratium trichoceros*
 - *Ceratium tripos*
 - *Cochlodinium*
 - *Dinophysis acuminata*
 - *Dinophysis acuta*
 - *Dinophysis dens*
 - *Dinophysis fortii*
 - *Dinophysis norvegica*
 - *Dinophysis tripos*
 - *Diplopsalis/zygabikodinium*
 - *Ensiculifera carinata*
 - *Fragilidium subglobosum*
 - *Glenodinium*
 - *Gonyaulax digitale*
 - *Gonyaulax scrippsae*
 - *Gonyaulax spinifera*
 - *Gonyaulax verior*
 - *Gymnodinium aureolum*
 - *Gymnodinium simplex*
 - *Gyrodinium flagellare*
 - *Hemidinium ocharceum*
 - *Heterocapsa minima*
 - *Heterocapsa rotundata*

-
- *Heterocapsa triquetra*
 - *Karenia mikimotoi*
 - *Katodinium glaucum*
 - *Kryptoperidinium foliaceum*
 - *Lepidodinium chlorophorum*
 - *Lingulodinium polyedrum*
 - *Mesoporos perforatus*
 - *Oxytoxum*
 - *Peridiniella catenata*
 - *Peridinium aciculiferum*
 - *Peridinium quinquecorne*
 - *Peridinium willei*
 - Prorocentrales
 - *Prorocentrum balticum*
 - *Prorocentrum lima*
 - *Prorocentrum micans*
 - *Prorocentrum triestinum*
 - *Protoceratium reticulatum*
 - *Pyrophacus horologicum*
 - *Scrippsiella trochoidea*
 - *Sinophysis*
 - *Thekate furealger*
 - *Torodinium robustum*
 - *Tripos arietinus*
 - *Tripos furca*
 - *Tripos macroceros*
 - *Warnowia*

Euglenophyta:

- Euglenophyceae
- Eutreptia
- *Eutreptiella braarudii*
- *Eutreptiella gymnastica*
- *Trachelomonas*
- *Chrysochromulina*
- *Coccolithophora*
- *Phaeocystis globosa*

-
- *Prymnesium*
 - *Chrysochromulina polylepis*
 - *Phaeocystis globosa*

Haptophyta:

- *Chrysochromulina parkeae*
- *Chrysochromulina parva*
- *Chrysochromulina spinifera*
- *Coccolithophora*
- *Emiliana huxleyi*
- *Phaeocystis globosa*
- Prymnesiophyceae
- *Prymnesium radiatum*

Heterokontophyta:

- *Achnanthes armillaris*
- *Actinoptychus octonarius*
- *Actinoptychus senarius*
- *Actinoptychus splendens*
- *Amphiprora*
- *Amphora*
- *Apedinella radians*
- *Apedinella/pseudopedinella*
- *Asterionella formosa*
- *Asterionellopsis glacialis*
- *Asteroplanus karianus*
- *Attheya decora*
- *Attheya septentrionalis*
- *Aulacoseira italica*
- *Bacillaria paxillifera*
- Bacillariophyceae
- *Bacteriastrum hyalinum*
- *Biddulphia rhombus*
- Biddulphiales
- *Brockmanniella brockmannii*
- *Cerataulina pelagica*
- *Chaetoceros affinis*
- *Chaetoceros anastomosans*

-
- *Chaetoceros borealis*
 - *Chaetoceros brevis*
 - *Chaetoceros brevis/diadema*
 - *Chaetoceros castracanei*
 - *Chaetoceros ceratosporus*
 - *Chaetoceros circinalis*
 - *Chaetoceros concavicornis*
 - *Chaetoceros constrictus*
 - *Chaetoceros contortus*
 - *Chaetoceros convolutus*
 - *Chaetoceros crinitus*
 - *Chaetoceros curvisetus*
 - *Chaetoceros danicus*
 - *Chaetoceros debilis*
 - *Chaetoceros decipiens*
 - *Chaetoceros densus*
 - *Chaetoceros diadema*
 - *Chaetoceros didymus*
 - *Chaetoceros eibenii*
 - *Chaetoceros gracilis*
 - *Chaetoceros holsaticus*
 - *Chaetoceros lacinosus*
 - *Chaetoceros lauderi*
 - *Chaetoceros lorenzianus*
 - *Chaetoceros perpusillus*
 - *Chaetoceros peruvianus*
 - *Chaetoceros pseudocrinitus*
 - *Chaetoceros radicans*
 - *Chaetoceros seiracanthus*
 - *Chaetoceros similis*
 - *Chaetoceros simplex*
 - *Chaetoceros socialis*
 - *Chaetoceros subtilis*
 - *Chaetoceros tenuissimus*
 - *Chaetoceros thronsenii*
 - *Chaetoceros wighamii*

-
- *Chattonella*
 - *Chromulina*
 - *Chrysamoeba*
 - *Chrysococcus*
 - *Chrysophyceae*
 - *Cocconeis*
 - *Corethron hystrix*
 - *Coscinodiscophyceae*
 - *Coscinodiscus centralis*
 - *Coscinodiscus concinnus*
 - *Coscinodiscus granii*
 - *Coscinodiscus radiatus*
 - *Coscinodiscus wailesii*
 - *Cylindrotheca closterium*
 - *Cylindrotheca closterium*
 - *Cymbella*
 - *Dactyliosolen blavyanus*
 - *Dactyliosolen fragilissimus*
 - *Delphineis surirella*
 - *Detonula confervacea*
 - *Detonula pumila*
 - *Diatoma tenuis*
 - *Dinobryon acuminatum*
 - *Dinobryon balticum*
 - *Dinobryon divergens*
 - *Dinobryon faculiferum*
 - *Ditylum brightwellii*
 - *Entomoneis alata*
 - *Eucampia zodiacus*
 - *Fragilaria*
 - *Grammatophora marina*
 - *Guinardia delicatula*
 - *Guinardia flaccida*
 - *Guinardia striata*
 - *Gyrosigma*
 - *Heterosigma akashiwo*

-
- Kephyrion
 - Lauderia annulata
 - Leptocylindrus danicus
 - Leptocylindrus minimus
 - Licmophora
 - Lithodesmium undulatum
 - Mediopyxis helysia
 - Melosira arctica
 - Melosira moniliformis
 - Melosira nummuloides
 - Melosira varians
 - Meuniera membranaceae
 - Minutocellus polymorphus
 - Navicula transitans
 - Navicula vanhoeffenii
 - Neocalyptrella robusta
 - Nitzschia acicularis
 - Nitzschia closterium/longissima
 - Nitzschia frigida
 - Nitzschia longissima
 - Nitzschia pungens/seriata
 - Ochromonas
 - Odontella aurita
 - Odontella granulata
 - Odontella longicuris
 - Odontella mobiliensis
 - Odontella mobiliensis
 - Odontella regia
 - Odontella sinensis
 - Paralia sulcata
 - Paraphysomonas
 - Pauliella taeniata
 - Plagiogramma
 - Pleurosigma strigosum
 - Podosira stelliger
 - Porosira glacialis

-
- *Proboscia alata*
 - *Pseudochattonella farcimen*
 - *Pseudo-nitzschia delicatissima*
 - *Pseudo-nitzschia pseudodelicatissima*
 - *Pseudo-nitzschia pungens*
 - *Pseudo-nitzschia seriata*
 - *Pseudopedinella pyriformis*
 - *Pseudosolenia calcar-avis*
 - *Rhaphoneis*
 - *Rhizosolenia hebetata*
 - *Rhizosolenia hebetata* f. *semispina*
 - *Rhizosolenia imbricata*
 - *Rhizosolenia setigera*
 - *Rhizosolenia styliiformis*
 - *Schroederella/lauderia*
 - *Skeletonema costatum*
 - *Stephanodiscus hantzschii*
 - *Stephanopyxis turris*
 - *Streptotheca thamensis*
 - *Striatella unipunctata*
 - *Surirella*
 - *Synedra*
 - *Tabellaria*
 - *Thalassionema frauenfeldii*
 - *Thalassionema nitzschioides*
 - *Thalassiosira angulata*
 - *Thalassiosira eccentrica*
 - *Thalassiosira gravida*
 - *Thalassiosira gravida*
 - *Thalassiosira levanderi*
 - *Thalassiosira minima*
 - *Thalassiosira nordenskiöldii*
 - *Thalassiosira punctigera*
 - *Thalassiosira rotula*
 - *Triceratium favus*
 - *Trigonium alternans*

-
- Tryblionella compressa
 - Ulnaria acus
 - Ulnaria ulna

Ochrophyta:

- Dictyocha fibula
- Dictyocha speculum
- Octactis octonaria

Benthic primary producer

Macrophyte and Eelgrass:

- Ahnfeltia plicata
- Callithamnion corymbosum
- Carradoriella elongata
- Ceramium nodulosum
- Ceramium virgatum
- Chaetomorpha melagonium
- Chondrus crispus
- Chorda filum
- Chordaria flagelliformis
- Cladophora rupestris
- Coccotylus truncatus
- Coccotylus/Phyllophora
- Colaconema
- Corallina officinalis
- Cystoclonium purpureum
- Dasya baillouviana
- Dasysiphonia japonica
- Delesseria sanguinea
- Desmarestia aculeata
- Desmarestia viridis
- Dilsea carnosia
- Ectocarpus fasciculatus
- Ectocarpus siliculosus
- Ectocarpus/Pilayella
- Elachista fucicola
- Eudesme virescens
- Fucus serratus

- *Fucus vesiculosus*
- *Furcellaria lumbricalis*
- *Halidrys siliquosa*
- *Himanthalia elongata*
- *Leathesia marina*
- *Leptosiphonia fibrillosa*
- *Melobesia membranacea*
- *Membranoptera alata*
- *Osmundea truncata*
- *Palmaria palmata*
- *Phycodrys rubens*
- *Phyllophora pseudoceranoïdes*
- *Plumaria plumosa*
- *Polyides rotunda*
- *Polysiphonia*
- *Polysiphonia fucoides*
- *Polysiphonia stricta*
- *Ptilota gunneri*
- *Ptilothamnion sphaericum*
- *Pylaiella littoralis*
- *Rhodomela confervoides*
- *Saccharina latissima*
- *Spermothamnion repens*
- *Sphacelaria cirrosa*
- *Sphaerotrichia divaricata*
- *Zostera marina*

Secondary producers

Holozooplankton:

Copepoda

- *Acartia bifilosa*
- *Acartia discaudata*
- *Acartia tonsa*
- *Aetideopsis armatus*
- *Anomalocera patersoni*
- *Calanus finmarchicus*
- *Calanus helgolandicus*

- *Centropages hamatus*
- *Centropages typicus*
- *Eurytemora affinis*
- *Eurytemora hirundoides*
- *Euterpina acutifrons*
- Harpacticoida
- *Longipedia coronata*
- *Metridia longa*
- *Metridia lucens*
- *Microcalanus pusillus*
- *Microcalanus pygmaeus*
- *Microsetella norvegica*
- *Microsetella rosea*
- *Oithona atlantica*
- *Oithona nana*
- *Oithona plumifera*
- *Oithona similis*
- *Paracalanus parvus*
- *Pseudocalanus elongatus*
- *Pseudocalanus minutus*
- *Temora longicornis*
- *Tigriopus*

Cladocera

- *Bosmina coregoni*
- *Bosmina longirostris*
- *Chydorus sphaericus*
- *Daphnia*
- *Diaphanosoma brachyurum*
- *Evadne nordmanni*
- *Evadne spinifera*
- *Penilia avirostris*
- *Pleopsis polyphaemoides*
- *Podon intermedius*
- *Podon leuckartii*

Protists:

- *Acanthostomella norvegica*

- *Alexandrium pseudogoniaulax*
- *Amphidinium sphenoides*
- *Askenasia*
- *Balanion*
- *Calliacantha*
- *Choanoflagellida*
- *Ciliophora*
- *Diaphanoeca grandis*
- *Diaphanoeca sphaerica*
- *Didinium*
- *Dinobryon*
- *Diplopelta bomba*
- *Diplopelta pusilla*
- *Diplopsalis gruppen*
- *Diplopsalis lenticula*
- *Ebria tripartita*
- *Eutintinnus pectinis*
- *Favella ehrenbergii*
- *Favella serrata*
- *Gymnodinium litoralis*
- *Gyrodinium dominans*
- *Gyrodinium spirale*
- *Helicostomella*
- *Helicostomella subulata*
- *Katablepharis remigera*
- *Laboea strobila*
- *Leegaardiella sol*
- *Leprotintinnus pellucidus*
- *Leucocryptos marina*
- *Lohmanniella oviformis*
- *Mesodinium velox*
- *Miracanthodinium claytonii*
- *Nematodinium armatum*
- *Nematopsides vigilans*
- *Noctiluca scintillans*
- *Oblea rotunda*

- *Oligotrichida*
- *Oxyrrhis marina*
- *Parafavella denticulata*
- *Parvicorbicula socialis*
- *Pelagostrobilidium spirale*
- *Peridiniella danica*
- *Phalacroma rotundatum*
- *Polykrikos kofoidii*
- *Preperidinium meunieri*
- *Pronoctiluca pelagica*
- *Prorocentrum cordatum*
- *Protoperidinium bipes*
- *Protoperidinium brevipes*
- *Protoperidinium cerasus*
- *Protoperidinium claudicans*
- *Protoperidinium conicum*
- *Protoperidinium crassipes*
- *Protoperidinium deficiens*
- *Protoperidinium denticulatum*
- *Protoperidinium depressum*
- *Protoperidinium divergens*
- *Protoperidinium granii*
- *Protoperidinium mariebourae*
- *Protoperidinium oblongum*
- *Protoperidinium ovatum*
- *Protoperidinium pallidum*
- *Protoperidinium paulsenii*
- *Protoperidinium pellucidum*
- *Protoperidinium pentagonum*
- *Protoperidinium punctulatum*
- *Protoperidinium pyriforme*
- *Protoperidinium steinii*
- *Protoperidinium subinerme*
- *Protoperidinium thorianum*
- *Ptychocylis urnula*
- *Pyrocystis noctiluca*

- Salpingella
- Spatulodinium pseudonociluca
- Stenosemella ventricosa
- Strombidium conicum
- Strombidium cornucopiae
- Strombidium emergens
- Strombidium vestitum
- Tiarina fusus
- Tintinnopsis beroidea
- Tintinnopsis campanula
- Tintinnopsis fluviatile
- Tintinnopsis rapa
- Uronema/cyclidium
- Urotrichia

Merozooplankton:

Bryozoan larvae:

- Conopeum reticulum
- Conopeum seurati
- Einhornia crustulenta
- Electra monostachys
- Electra pilosa
- Membranipora membranacea

Annelida larvae:

- Alitta succinea
- Arenicola marina
- Autolytinae
- Dipolydora coeca
- Eteone longa
- Gattyana cirrhosa
- Glycera alba
- Harmothoe
- Harmothoe imbricata
- Harmothoe impar
- Lepidonotus squamatus
- Magelona
- Magelona mirabilis

- Malacoceros
- Myriochele danielsseni
- Mystides southerni
- Nephtys ciliata
- Nereididae
- Nereimyra punctata
- Nereis pelagica
- Orbiniidae
- Pectinaria
- Phyllodoce groenlandica
- Polydora ciliata
- Polydora cornuta
- Polydora flava
- Prionospio malmgreni
- Pygospio elegans
- Scolelepis foliosa
- Spionidae
- Tomopteris (Johnstonella) helgolandica
- Tomopteris septentrionalis
- Trochochaeta multisetosa

Bivalvia larvae:

- Mya arenaria
- Mytilus edulis

Gastropoda larvae:

- Aporrhais pespelecani
- Littorina littorea
- Peringia ulvae
- Philine aperta

Echinoderm larvae:

- Asteroidea
- Echinoidea
- Psammechinus miliaris
- Ophiothrix fragilis
- Ophiura albida

Arthropod larvae:

- Amphibalanus improvisus

- *Balanus balanus*
- *Balanus crenatus*
- *Cirripedia*
- *Verruca stroemia*
- *Bopyroidea*
- *Calocaris macandreae*
- *Cancer pagurus*
- *Caprella linearis*
- *Carcinus maenas*
- *Crangon allmanni*
- *Euphausiacea*
- *Galathea*
- *Hyas araneus*
- *Hyperia galba*
- *Liocarcinus holsatus*
- *Macropodia rostrata*
- *Pagurus bernhardus*
- *Palaemon adspersus*
- *Palaemon elegans*
- *Pandalina brevirostris*
- *Pisidia longicornis*
- *Themisto abyssorum*
- *Thysanoessa inermis*

Benthic filter-feeding invertebrate

Benthic filter-feeders:

Arthropoda:

- *Balanus crenatus*
- *Philomedes globosus*

Mollusca:

- *Kurtiella bidentata*
- *Fabulina fabula*
- *Nucula nitidosa*
- *Abra nitida*
- *Astarte montagui*
- *Abra alba*
- *Chamelea gallina*
- *Varicorbula gibba*

- *Ennucula tenuis*
- *Macoma calcarean*
- *Macoma balthica*
- *Cochlodesma praetenu*
- *Thyasira flexuosa*
- *Thracia phaseolina*
- *Mytilus edulis*
- *Phaxas pellucidus*
- *Astarte borealis*
- *Crenella decussata*
- *Astarte sulcata*
- *Donax vittatus*
- *Dosinia lupinus*

Benthic feeding invertebrate

Annelida:

- *Scoloplos armiger*
- *Rhodine gracilior*
- *Pholoe inornata*
- *Heteromastus filiformis*
- *Maldane sarsi*
- *Galathowenia oculata*
- *Spiophanes bombyx*
- *Terebellides stroemii*
- *Trochochaeta multisetosa*
- *Spio filicornis*
- *Ampharete baltica*
- *Harmothoe sp.*
- *Labidoplax buskii*
- *Scalibregma inflatum*
- *Anobothrus gracilis*
- *Ophelina acuminata*
- *Ampharete finmarchica*
- *Notomastus latericeus*
- *Goniada maculata*
- *Spiophanes kroyeri*
- *Lanice conchilega*
- *Levinsenia gracilis*

- *Magelona alleni*
- *Lagis koreni*
- *Trichobranchus roseus*
- *Prionospio steenstrupi*
- Enchytraeidae
- *Phyllodoce groenlandica*
- *Nephtys longosetosa*
- *Euchone papillosa*
- *Pherusa plumosa*
- *Polyphysia crassa*
- *Owenia fusiformis*
- *Oxydromus flexuosus*
- *Pseudopolydora pulchra*
- *Polydora ciliata*
- *Nephtys hombergii*
- *Apistobranchus tullbergi*
- *Prionospio cirrifera*
- *Scolelepis* sp.
- *Flabelligera affinis*
- *Glycera unicornis*
- *Nephtys ciliata*
- *Mediomastus fragilis*
- Nereididae
- *Chaetoderma nitidulum*

Arthropoda:

- *Diastylis rathkei*
- *Ampelisca brevicornis*
- *Ampelisca tenuicornis*
- *Hardametopa nasuta*
- *Harpinia pectinata*
- *Eudorella emarginata*
- *Eudorella truncatula*
- *Urothoe grimaldii*
- *Ampelisca macrocephala*
- *Protomedeia fasciata*
- *Bathyporeia guilliamsoniana*

- Bathyporeia elegans
- Diastylis laevis
- Photis reinhardi
- Pagurus cuanensis
- Harpinia antennaria
- Leucon (leucon) nasica
- Medicorophium affine
- Argissa hamatipes
- Synchelidium haplocheles

Mollusca:

- Turritellinella tricarinata

Echinodermmata:

- Amphiura chiajei
- Echinocyamus pusillus
- Echinocardium cordatum

Amphiura filiformis

Planktivorous fish or invertebrate

Nekton:

- Atlantic herring (*Clupea harengus*)
- European sprat (*Sprattus sprattus*)
- Sandeel (*Ammodytes* spp.)
- Twaite shad (*Alosa fallax*)
- Allis shad (*Alosa alosa*)

Houting (*Coregonus oxyrhynchus*)

Seabird:

Sub-apex pelagic predators

Nekton:

- Atlantic cod (*Gadus morhua*)
- Twaite shad (*Alosa fallax*)

Allis shad (*Alosa alosa*)

Elasmobranch:

- Blackmouth catshark (*Galeus melastomus*)
- Spiny dogfish (*Squalus acanthias*)
- Tope shark (*Galeorhinus galeus*)

Velvet belly lanternshark (*Etmopterus spinax*)

Seabird:

- Northern fulmar (*Fulmarus glacialis*)
- Northern gannet (*Morus bassanus*)

Great cormorant (*Phalacrocorax carbo*)

Sub-apex demersal predators

Nekton:

- Atlantic cod (*Gadus morhua*) juvenile
- Haddock (*Melanogrammus aeglefinus*)
- Common dab (*Limanda limanda*)
- European plaice (*Pleuronectes platessa*)
- European flounder (*Platichthys flesus*)
- Twaité shad (*Alosa fallax*)
- Allis shad (*Alosa alosa*)
- Houting (*Coregonus oxyrinchus*)
- Sturgeon (*Acipenser sturio*)

Seabird:

- Red-necked grebe (*Podiceps grisegena*)
- Red-throated diver (*Gavia stellata*)
- Black-throated diver (*Gavia arctica*)
- Diver sp. (*Gavia sp.*)
- Great cormorant (*Phalacrocorax carbo*)
- Velvet scoter (*Melanitta fusca*)
- Common scoter (*Melanitta nigra*)
- Common Eider (*Somateria mollissima*)
- Long-tailed duck (*Clangula hyemalis*)
- Long-tailed duck (*Clangula hyemalis*)
- Goldeneye (*Bucephala clangula*)

Elasmobranch:

- Blackmouth catshark (*Galeus melastomus*)
- Blonde ray (*Raja brachyura*)
- Blue skate (*Dipturus batis*)
- Longnosed skate (*Dipturus oxyrinchus*)
- Norwegian skate (*Dipturus nidarosiensis*)
- Spiny dogfish (*Squalus acanthias*)
- Sailray (*Rajella lintea*)
- Small-eyed ray (*Raja microocellata*)
- Small-spotted catshark (*Scyliorhinus canicularis*)
- Spotted ray (*Raja montagui*)
- Thornback ray (*Raja clavate*)
- White skate (*Bathyraja spinosissima*)
- Starry smooth-hound (*Mustelus asteria*)
- Common smooth-hound (*Mustelus mustelus*)

- common stingray (*Dasyatis Pastinaca*)
- Thorny skate (*Amblyraja radiata*)
- Shagreen ray (*Leucoraja fullonica*)
- Cuckoo ray (*Leucoraja naevus*)

Apex fish predator

Elasmobranch:

- Porbeagle shark (*Lamna nasus*)

Apex marine mammal predators

- Harbour seal (*Phoca vitulina*)
- Grey seal (*Halichoerus grypus*)
- Harbour porpoise (*Phocoena Phocoena*)

TOWARD ASSESSING THE SPATIOTEMPORAL STRUCTURE OF MARINE FOOD WEBS FROM A MSFD DESCRIPTOR 4 PERSPECTIVE: A CASE STUDY IN DANISH KATTEGAT

Marine food webs are complex systems of trophic and non-trophic interactions influenced by temporal, spatial, and environmental variations. The Marine Strategy Framework Directive (MSFD) descriptor 4 requires European member states to assess these webs and evaluate the impacts of climate and anthropogenic stressors. This study examines data availability and modelling approaches for fulfilling these requirements in Danish waters. While existing data supports parts of the four MSFD criteria, gaps remain in areas like species ontogeny and trophic associations. Recommendations include improving data collection and advancing quantitative models to assess marine food web status comprehensively.