BONUS XWEBS – Taking stock of Baltic Sea food webs: synthesis for sustainable use of ecosystem goods and services

Deliverable No: 3.2		Work package number and leader: WP 3, UTARTU	
Date:	31.03.2020	Delivery due date: March 2020	Project month: 15
Title:	Review of trophic models for the Baltic Sea		
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Citation: Neuenfeldt, S., Ojaveer, H., Opitz, S., Tomczak, M., Dierking, J. (2020) Review of trophic models for the Baltic Sea. BONUS XWEBS Deliverable D3.2. 22 pp. DOI 10.3289/XWEBS_D3.2			
Dissemination level		PU	
Nature of the Deliverable		RE	

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BONUS XWEBS overview

Food webs are essential for ecosystem functioning, yet resource management rarely incorporates food web knowledge, in part due to the complexity of food webs and the heterogeneous knowledge base. The overarching aims of BONUS XWEBS are to synthesize available knowledge on food webs in the Baltic Sea, to assess how food web knowledge is used in management, and to outline a future vision for this field. At the core of the XWEBS approach is a series of writing workshops, in which we link the expertise from our core consortium (four partner institutes from four Baltic nations, coordinated by the GEOMAR Helmholtz Centre for Ocean Research Kiel) with that of experts as well as stakeholders from around the Baltic Sea.

Why are food webs important?

Food webs are the backbones of healthy ecosystems providing sustainable goods and services to humans. Their function is essential for energy and matter cycling and for healthy populations and interactions of fish, seabirds and marine mammals. Food webs also play an important role in the buffering of global and regional anthropogenic impacts resulting from e.g., human exploitation, eutrophication, hypoxia, climate change, and the introduction of non-indigenous species. Understanding of the complex food web processes in the Baltic Sea will therefore be key to predict futures states of Baltic ecosystems and to manage resources sustainably, now and in the future.

The problem

While information about Baltic Sea food webs has grown strongly over the past decade, the synthesis of this knowledge and its transfer and integration into management strategies is lagging. Also, a number of crucial knowledge gaps remain, including insufficient abilities to forecast future states of food webs. Baltic food web science thus stands at a crossroad: synthesis is needed, and decisions need to be taken on where to direct future research efforts and on how to best apply the new wealth of information in practical management to benefit society.

XWEBS and Baltic Sea food webs

BONUS XWEBS has the objective to address these pressing needs, by

- Synthesizing what we know and need to know about Baltic food webs, their temporal and spatial dynamics, the impacts of bottom-up (e.g., nutrient availability) and top-down (i.e., grazing, predation, harvesting) forces under changing anthropogenic drivers, and their past, present and future states. In these efforts, we are taking stock and synthesizing the wealth of new information available from completed and running BONUS food web projects as well as from outside BONUS.
- Assessing the bottlenecks in the application of this knowledge in assessment and management.
- Providing a future vision for Baltic food web science, including the identification of the methods, tools and concepts required for the incorporation of knowledge into management.

The ultimate goal of these efforts is to guide Baltic food web science in the direction needed to support the sustainable use of ecosystem goods and services in the future.

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Executive Summary

This review aims to be a representative overview over the available types of trophic models in order to investigate, if their output can be used to quantify existing food-web indicators for the EU Marine Strategy Framework Directive (MSFD) . The goal is to obtain a comprehensive picture of the applicability of various model approaches to contribute to achieving MSFD objectives. The work will feed into XWEBS Task 3.3 on ' Evaluation of the model application potential'.

In total we have identified 27 food-web related models with different application areas in the Baltic Sea. We highlight the specific purpose for which each model was designed and the key assumptions underlying each model. The assessment of model applicability here is focused on strengths and gaps of the models to realistically depict size and dynamics of functional groups in the Baltic Sea food web. Based on the latter, we illustrate existing gaps in the models, and assess the extent to which the models can be applied to represent status and dynamics of the Baltic Sea food webs.

For the future, we recommend to use an ensemble approach where possible to determine guild biomasses as indicators for food web status. Spatial heterogeneity should be accounted for. This issue should be initiated by collecting all relevant processes in the Baltic Sea, such as source-sinks or coastal-offshore connectivity. The spatial and temporal scale of ecosystem models and potential food web indicators should be aligned as far as possible, and following functional criteria, such as topographic differences and known separated community structures. This way, one can avoid erroneous conclusions that are based on limited data projected over the whole Baltic.

Progress and deviations from the original workplan

No deviations from the workplan.

Introduction

Objectives of the workpackage 3 on 'Integration and transformation' is to: 1) contribute to meeting the objectives of the MSFD (essentially Descriptor 4), and implementation of the Common Fisheries Policy (CFP), and 2) evaluate the applicability of existing food web models in GES-assessments.

This workpackage first reviews the food web indicators proposed under the EU MSFD (essentially under Descriptor 4 (food webs), but also other Descriptors) and their suggested threshold values, together with associated uncertainties and gaps (Task „Review of indicators" with corresponding deliverable D3.1). Second, we perform a comprehensive review of existing food web models in the Baltic Sea, and select those potentially suited for testing indicators and their threshold values (Task 3.2 „Review of existing food web models", with corresponding deliverable D3.2 submitted here). Third, we work further with the sub-set of the selected models and assess their applicability to D4 and the implementation of the EU CFP.

Task 3.2 provides synthesis of existing Baltic foodweb models, and evaluation of the associated uncertainty and assessment of gaps in relation to MSFD. The focus has been put on trophic models that entail more than one trophic level. To this end, the term 'food web

models' might be misleading, because traditonally, food web models focus on the network structure, nodal point, species diversity and their impact on the functioning of food webs. However, since the MSFD D4 focus in on trophic guilds and their temporal development in terms of biomass or abundance and interactions, trophic models are more suited to deliver indicators that cannot just be measured in the field.

The review includes several types of published models of lower, intermediate and upper trophic levels. While we aimed at listing all published trophic models for the Baltic Sea, main focus has been put upon presenting a representative overview over the available types of models in order to investigate their applicability for MSFD indicators, focusing on indicators proposed under Descriptor 4 (food webs) but also relevant indicators suggested under other Descriptors (such as D3 – commercial fish species). This allows us to obtain a comprehensive picture of the need under MSFD, and to better investigate the applicability of various model approaches to contribute to achieving MSFD objectives. The combined work from Task 3.1 and 3.2 feeds into Task 3.3 on ' Evaluation of the model application potential'.

Methods

This is a desk study, based on the published evidences from multiple sources including research papers published in scientific journals, project reports and online publications. The consulted sources include those created only by international organisations, EU-funded projects and international research groups. First, we compiled a list of all published trophic model types for the Baltic. This list is not necessarily comprehensive, but covers all different applicaitons of trophich models in the Baltic. We characterized the main objectives of the models studies and chracterized their potential to quantify trophic guild biomasses.

Results

In total we have identified 28 published food-web related models with different application areas in the Baltic Sea. In the following, we first provide an overview over the identified models (Table 1 and Figure 1), and then briefly describe the single studies conducted since the mid-1980s. Subsequently, we describe the model types' applicability to quantify the biomass of trophic guilds and characterize major gaps and abstractions of the models, which might lead to some structural bias.
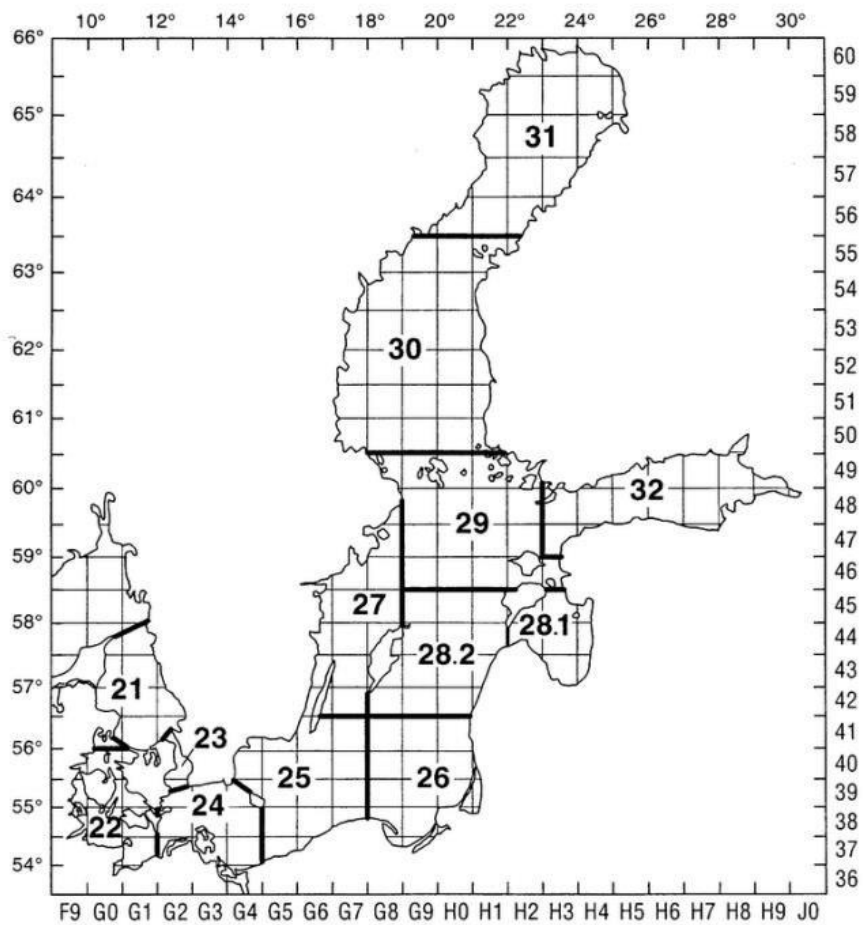
Figure 1: ICES subdivisions and statistical rectangles in the Baltic Sea

Table 1: Model applications by ICES subdivisions and purpose of the models (according to Opitz, 2014).

#	Authors	Year	Subdivisions														Purpose
			21	22	23	24	25	26	27	28.1	28.2	29	30	31	32	
1	Elmgren	1984														Overview over main carbon flows
2	Wulff & Ulanowicz	1989														Comparison of structure and function Baltic/Chesapeake Bay
3	Rudstam et al.	1995														Top-down control in the pelagic ecosystem
4	Jarre-Teichmann	1995														Seasonal energy flows
5	Horbowy	1996														Production model for commercial fish stocks
6	Sandberg et al.	2000														Updated carbon flows
7	Harvey et al.	2003														Interactions between fisheries and food web
8	Sandberg et al.	2004														Terrigene dissolved organic carbon as structuring factor for secondary production
9	Sandberg	2007														Comparison of pelagic food web structures in three main basins

No.	Author	Year												Description
10	Hansson et al.	2007												Management scenarios
11	Van Leeuwen et al.	2008												Apparent Allee effect
12	Tomczak et al.	2009				Coastal systems								Compared Carbon flows in five south-eastern Baltic coastal ecosystems
13	Lindegren et al.	2009												Demonstrate that in hindsight the cod collapse could only have been avoidable by adapting fishing pressure to environmental conditions and food-web interactions
14	Teschner et al.	2010												Impact of hypoxia on pelagic commercial fishes predation rates
15	Tomczak et al.	2013												Simulated the regime shift in the Central Baltic Sea of the 1980s
16	Gårdmark et al	2013												Biological ensemble model
17	Lindegren et al.	2014												Meta-commnity model for source-sink dynamics
18	Gårdmark et al.	2015												Detecting mechanisms underlying alternative table states
19	Norrström et al.	2017												Nash equilibrium for multispecies fisheries management reference points
20	Jacobsen et al.	2017												Ecosystem-level efficiency of fisheries in five large marine ecosystems
21	Bauer et al.	2018												Simulating reduced eutrophication
22	Bossier et al.	2018												End-to-end model implementation
23	Uusitalo et al.	2018												Dynamic Bayes-Network Implementation
24	Bauer et al.	2019												Food web and fisheries in the future Baltic
25	Bauer et al.	2019												Model uncertainty and simulated fisheries advice
26	Kulatska et al.	2019												Implementing GADGET multispecies model for commercial fish species
27	Maldonado et al.	2019												Analyze the Baltic Sea food web in order to examine potential unobserved processes
28	Karlson et al.	2020												Linking consumer physiological status to food web structure and prey food value

Elmgren (1984) was the first to model Baltic **energy flows** using a mass-balance model. He showed pelagic primary production to be the primary energy source with river input and benthic primary production to be important locally. Direct waste discharge of organic matter was only of minor importance. The paper suggests that most of the energy was utilized within the pelagic system, where the 'exudate-bacteria-microzooplankton-pelagic fish' food chain seemed to be more important, in terms of carbon transport, than the classic 'phytoplankton-mesoozooplankton-pelagic fish food chain. Energy reached the benthos passively by sedimentation and actively through suspension feeding by the macrofauna. Besides this first prioritization of carbon pathways, Elmgren (1984) stressed the sensitivity of the Baltic Sea to anthopogenic impacts.

Wulff and Ulanowicz (1989) concluded in their comparison of mass-balanced models of the Baltic Sea to Chesapeake Bay, that there appears to be a real biological difference between

the feeding habits of the planktivorous fishes in the two systems. In the Chesapeake the menhaden (*Brevoortia tyrannus*) acted in large part as herbivores consuming phytoplankton, whereas Baltic herring and sprat fed exclusively on trophically higher zooplankton during the warm months and on benthic invertebrates during the winter. The Baltic Sea, in spite of its lower species diversity compared to the Chesapeake Bay, had furthermore a higher relative **diversity of flows**.

Rudstam et al. (1995) review evidenced for and possible consequences of **top-down control** in the pelagic Baltic Sea ecosystem using partially a statistical approach. Two top-down control processes, cod predation on clupeids and clupeid predation on cod eggs, were considered important and tended to produce either a cod-dominated or a clupeid-dominated system. Several counteracting forces could prevent this from happening, including the side-effects of eutrophication, variable hydrographic conditions, cannibalism within species, the fishery, and separate spawning and nursing areas for herring. Top-down control of zooplankton was likely to be intense but variable with season. Zooplanktivores (primarily herring, sprat and mysids) were selective and consume a large proportion of the estimated zooplankton production (50-93%). In addition, zooplanktivory was at a peak in late summer and early autumn when zooplankton populations decline. Therefore, a negative correlation was expected between clupeid and zooplankton biomass although this was not found in available data sets (1974-1988). The lack of correlation could be due to relatively small changes (by a factor 2) in planktivore biomass over this time period and compensatory increases in other zooplanktivores (e.g. mysids and juvenile clupeids). Less was known about the top-down control of primary production in the Baltic Sea. Available information suggested that grazing rates on algae is maintained as metazooplankton decrease by compensatory responses of protozooplankton.

Jarre-Teichmann (1995) presented four preliminary mass-balance models of **carbon flow by season**, based on estimates of standing stock and energy flow from the late 1980s and early 1990s. The construction of the models emphasized on the commercially most important fish species, herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and cod (*Gadus morhua*). Further included were primary producers, several groups of planktonic invertebrates and benthos, as well as commercially less important fish. The models were analyzed and compared by means of network analysis.

Horbowy (1996) developed a **multispecies stock-production** model and used it to estimate the dynamics of cod, herring, and sprat stocks from 1982 to 1992. Inputs to the model were estimates of the fishing effort, recruitment indices, mean individual weight of fish in the stock, von Bertalanffy's growth parameters, and residual natural mortality. The model's parameters that were not known in advance (e.g., food preference parameters, catchabilities, calibration coefficient for recruitment indices) were estimated by minimizing the deviations of observed catches and food composition of cod from the values arrived at from the model. The standard errors of the fitted parameters of the model were evaluated using a bootstrap procedure. Sensitivity analyses showed that growth parameters had the largest influence on the model outcome. The model produced estimates of the population dynamics of Baltic fish stocks consistent with the estimates from age-structured models. In the period analyzed, the biomass of cod decreased by about 80%, the biomass of herring was stable, and sprat biomass fluctuated, increasing finally to a record high level. The estimated decrease of cod biomass is reflected in a decreasing predation mortality of herring and sprat.

Sandberg et al. (2000) used the EcopathII software (ver 3.1) to analyse models of **carbon flow through the food webs in the three main areas of the Baltic Sea**; the Baltic proper, Bothnian Sea and Bothnian Bay. Elmgren (1984) was complemented with the data on respiration and flow to detritus from Wulff and Ulnowicz (1989) in order to present complete mass balance models of carbon. The purpose of re-evaluating previous models with new analytic tools was to check how well their carbon flows balance, and to provide a basis for improved mass balance models using more recent data, including nutrients other than carbon. The resulting mass balance networks for the Baltic proper, Bothnian Sea and the Bothnian Bay were shown to deviate from steady state. There was an organic carbon surplus of 45, 25 and 18 g C m-2 year-1 in the pelagic zones of the Baltic proper, Bothnian Sea and Bothnian Bay, respectively. The Ecopath network analysis confirmed that the overall carbon flow was highest in the Baltic proper, somewhat lower in the Bothnian Sea and much lower in the Bothnian Bay. The only clear differences in food web structure between the basins was that the average trophic level was lower for demersal fish in the Bothnian Sea and higher for macrofauna in the Bothnian Bay, compared to the other basins.

Harvey et al. (2003) created a food web model for the Baltic proper, using the Ecopath with Ecosim software, to evaluate **interactions between fisheries and the food web from 1974 to 2000**. The model was based largely on values generated by multispecies virtual population analysis (MSVPA), an earlier commercial fish centered model. Ecosim outputs closely reproduced MSVPA biomass estimates and catch data for sprat, herring, and cod, but only after making adjustments to cod recruitment, to vulnerability to predation of specific species, and to foraging times. Among the necessary adjustments were divergent trophic relationships between cod and clupeids: cod exhibited top-down control on sprat biomass, but had little influence on herring. Fishing, the chief source of mortality for cod and herring, and cod reproduction, as driven by oceanographic conditions as well as unexplained variability, were also key structuring forces. The model generated many hypotheses about relationships between key biota in the Baltic Sea food web and may ultimately provide a basis for estimating community responses to management actions.

Sandberg et al. (2004) quantitatively assessed the **relative importance of terrigenous dissolved organic material** (TDOC) as a carbon source for secondary producers (e.g. bacteria) and as a structuring factor for the pelagic food web in the Gulf of Bothnia, northern Baltic Sea. The 3 study sites, situated in Bothnian Bay (BB), the Öre Estuary (ÖE) and the Bothnian Sea (BS), had markedly different freshwater loads and water-residence times. In Bothnian Bay, bacterial biomass and production were higher than expected from the levels of phytoplankton biomass and productivity there, suggesting an uncoupling of bacterial productivity from phytoplankton production. Phytoplankton size structure and size-fractionated production were, however, relatively similar among areas. A simplified carbon budget model suggested that bacterioplankton dominated organic carbon consumption in all of the food webs studied, but was most marked in BB. The model showed that the available autochthonous primary production could not alone support the heterotrophic carbon demand in BB. The most likely explanation of this discrepancy was that the total annual input of terrigenous dissolved organic carbon was bioavailable, resulting in a budget closer to balance with the heterotrophic carbon demand. BB, receiving 38% of the carbon input from land, was consequently a net heterotrophic ecosystem. A sensitivity analysis showed that the bacterial carbon demand, and growth efficiency in particular, had the greatest influence on the resulting budget. TDOC was the dominant carbon source in ÖE, but the losses of carbon through advection to offshore areas and sedimentation was high. The evidence of net heterotrophy in ÖE was therefore

weaker than in BB. In BS the input of TDOC was less important, and the carbon used for secondary production originated mainly from autochthonous primary production. The results suggested that the supply of TDOC is of great importance for the abundance of plankton and as a structuring factor for the aquatic food webs in the Gulf of Bothnia.

Sandberg (2007) compared Ecopath models of mass flow of carbon through pelagic food webs in the three major basins of the Baltic Sea: Bothnian Bay (BB), Bothnian Sea (BS) and the Baltic proper (BP) including the Gulfs of Finland and Riga. The carbon flows in the models were estimated indirectly based on monitoring data of bacterial and primary productivity as well as on literature data on predator's diets and size-fractionated primary production. Analysis of the carbon flows suggested that in order to present a good balance between inputs and losses of carbon to each system, the most sensitive factor in the models, e.g. averaged monitoring data on bacterial productivity had to be lowered for the BB and BS, whereas it was raised for the BP basin. The final model configuration resulted in fairly realistic productivity estimates and carbon demands for individual compartments in each area. The supply of carbon via autochthonous primary production was highest in the Baltic proper (192 g C m-2 year-1), whereas it was estimated 3 and 11 times lower in the BS and the BB, respectively. The input of allochthonous sources, via terrigenous dissolved organic carbon as well as advection between basins was relatively higher towards the north, being 7.4, 11.6, and 22 g C m-2 year-1 in the BP, BS, and BB, respectively. Along with the higher allochthonous supply there was a gradual increase in bacterial production relative to particulate primary production since that ratio was 20%, 60% and 160% in the BP, BS and BB, respectively. The relatively higher bacterial production as compared to primary production towards the north of the Baltic Sea resulted in systematic differences in carbon flow between basins. The flow from particulate primary production to the classic food chain (zooplankton and Mysids) and the microbial food web was fairly similar between areas. However, the demand for particulate primary production by the microbial food web was 79%, 54% and 29% in the BP, BS and BB, respectively. The study thus gave further indirect support to the view that **the carbon flow through the microbial food web** is enhanced in less productive aquatic systems with relatively high input of allochthonous carbon such as the Bothnian Sea and the Bothnian Bay.

Hansson et al. (2007) explored possible effects of different **management scenarios** for the Baltic Sea, based on an earlier published ecosystem model. (Harvey et al., 2003) The scenarios include an oligotrophication of the system, a drastic increase in the number of seals, and changes in the fishery management. From these simulations they concluded that fisheries, seals, and eutrophication all have strong and interacting impacts on the ecosystem. These interactions call for integrated management. The modeling highlighted the potential for conflicts among management mandates such as flourishing fisheries, rebuilt seal populations, and substantially reduced eutrophication. The results also suggested that fisheries management reference points have to be adjusted in response to changes in the presence of natural predators or ecosystem productivity.

Van Leeuwen et al. (2008) explored whether the lack of cod recovery can be ascribed to an emergent Allee effect, which is a mechanism intrinsic to the community in contrast to explanations involving environmental factors. They formulated a **stage-structured biomass model** for the cod-sprat interaction in the Baltic Sea, paying special attention to the size-dependent prey preference of differently sized cod. The model predicted that alternative community states can occur under the same environmental conditions, in which cod is either present or absent. In a stable equilibrium with its main prey cod has a strong effect on the

prey size distribution, resulting in larger densities of preferred prey sizes for cod than in the absence of any predation. Cod thus shapes its food environment to its own benefit. Furthermore, in response to increased exploitation cod biomass and yield tended to increase unless a stock collapse is imminent. After a cod stock collapse and the consequent drop in predation the prey size distribution becomes stunted and offers insufficient food for cod to grow and recover. These results were consequences of the indirect effects of predation and harvesting, whereby increased mortality relaxed competition among surviving individuals, leading to an increase in food intake and hence increased somatic growth and reproduction. The paper observed community changes following the collapse of the cod stocks in the North West Atlantic and the Baltic Sea in the light of model predictions. In line with the model predictions growth in body size of cod had slowed down after the collapse, despite high densities of prey biomass. Furthermore, estimates of total prey population fecundity in the Baltic Sea identified the emergent Allee effect as a potentially important mechanism contributing to the lack of cod recovery.

Tomczak et al. (2009) **compared carbon flows in five south-eastern Baltic coastal ecosystems** (Puck Bay, Curonian Lagoon, Lithuanian coast, Gulf of Riga coast and Pärnu Bay) on the basis of **ECOPATH models** using 12 common functional groups. The studied systems ranged from the hypertrophic Curonian Lagoon to the mesotrophic Gulf of Riga coast. Interestingly, they found that macrophytes were not consumed by grazers, but rather channeled into the detritus food chain. In all ecosystems fisheries had far reaching impacts on their target species and on the food-web in general. In particular, benthic food-webs were partly affected by indirect fisheries effects. For example, fisheries tended to change the biomass of piscivorous fish, causing a cascading effect on benthivorous fish and macrozoobenthos. These cascades were ecosystem specific and needed to be considered when using benthic invertebrates as productivity and eutrophication indicators. Odum's maturity attributes allowed a ranking of costal ecosystems according to their maturity. Namely, the community development decreased in the following order: Pärnu Bay > Gulf of Riga coast > Lithuanian coast > Puck Bay > Curonian Lagoon.

Developing ecosystem-based fisheries management (EBFM) to prevent catastrophic fisheries collapses in the future requires ecological models incorporating both internal food web dynamics and external drivers such as fishing and climate. Using a **stochastic food-web model** for the Baltic Sea, Lindegren et al. (2009) were able to reconstruct the history of the Eastern Baltic cod stock. Moreover, they demonstrated that in hindsight the collapse could only have been avoidable by adapting fishing pressure to environmental conditions and food-web interactions.

Teschner et al. (2010) investigated the **effects of oxygen deficiency on** cod consumption rates and how these translate to stock size estimates in multi-species models. Based on results from laboratory experiments, a statistical model was fitted to evacuation rates at different oxygen levels and integrated into the existing consumption rates for Baltic cod within a multispecies model. Individual mean oxygen corrected consumption rates were 0.1-10.9% lower than the uncorrected ones.

Tomczak et al. (2013) **simulated the regime shift in the Central Baltic Sea** of the 1980s that has been associated with food-web reorganization and redirection of energy flow pathways. The long-term dynamics from 1974 to 2006 have been simulated here using a **food-web model forced by climate and fishing. Ecological network analysis** was performed to calculate

indices of ecosystem change. The model replicated the regime shift. The analyses of indicators suggested that the system's resilience was higher prior to 1988 and lower thereafter. The ecosystem topology also changed from a web-like structure to a linearized food-web.

Natural resource management requires approaches to understand and handle sources of uncertainty in future responses of complex systems to human activities. Gårdmark et al. (2013) presented one such approach, the "**biological ensemble modeling approach**," using the Eastern Baltic cod as an example. The core of the approach was to expose an ensemble of models with different ecological assumptions to climate forcing, using multiple realizations of each climate scenario. They simulated the long-term response of cod to future fishing and climate change in seven ecological models ranging from single-species to food web models. These models were analyzed using the "biological ensemble modeling approach" by which they (1) identified a key ecological mechanism explaining the differences in simulated cod responses between models, (2) disentangled the uncertainty caused by differences in ecological model assumptions from the statistical uncertainty of future climate, and (3) identified results common for the whole model ensemble. Species interactions greatly influenced the simulated response of cod to fishing and climate, as well as the degree to which the statistical uncertainty of climate trajectories carried through to uncertainty of cod responses. Models ignoring the feedback from prey on cod showed large inter-annual fluctuations in cod dynamics and were more sensitive to the underlying uncertainty of climate forcing than models accounting for such stabilizing predator-prey feedbacks. Yet in all models, intense fishing prevented recovery, and climate change further decreased the cod population.

The degree to which metapopulation processes influence fish stock dynamics is a largely unresolved issue in marine science and management, especially for highly mobile species such as Atlantic cod and herring. The Baltic Sea comprises a heterogeneous oceanographic environment that structures the spatial and temporal distribution of the dominant species cod, herring, and sprat. Despite local differences, the stocks are traditionally managed as homogeneous units. Lindegren et al. (2014) presented a **metacommunity-perspective on source-sink dynamics of Baltic Sea fish stocks** by using a **spatially disaggregated statistical food web model.** The model was fitted to area-specific time series of multiple abiotic and biotic variables using state-space methods. Their analysis revealed pronounced net fluxes between areas, indicative of source-sink dynamics, as well as area-specific differences in species interactions (i.e., density dependence, competition, and predator-prey) and the degree of fishing and climate impact on survival and recruitment. Furthermore, model simulations showed that decreasing exploitation pressure in the source area for cod (without reallocating fishing effort) produces an increase in neighboring sink habitats, but a decline of prey species in response to increased predation.

Many marine ecosystems have undergone 'regime shifts', i.e. abrupt reorganizations across trophic levels. Establishing whether these constitute shifts between alternative stable states is of key importance for the prospects of ecosystem recovery and for management. Gårdmark et al. (2015) showed how **mechanisms underlying alternative stable states caused by predator-prey interactions** can be revealed in field data, using analyses guided by theory on size-structured community dynamics. This was done by combining data on individual performance (such as growth and fecundity) with information on population size and prey availability. They discussed and distinguished two types of mechanisms, 'cultivation depensation' and 'overcompensation', that can cause alternative stable states preventing the recovery of overexploited piscivorous fish populations. Importantly, the type of mechanism

can be inferred already from changes in the predators' body growth in different life stages. Their approach aimed to be applied to monitored stocks of piscivorous fish species, for which this information often can be assembled. However, these findings are only valid, if environmental impact can be assumed constant.

Norrström et al. (2017) stated that the current fisheries management goals set by the European Commission to deliver maximum sustainable yields (MSY) and simultaneously take ecosystem considerations into account creates unsolved trade-offs for the management of the stocks. They suggested a definition of a multi-species-MSY (MS-MSY) where no alternative fishing mortality (F) can increase yield (long term) for any ecologically interacting stock, given that the other stocks are fished at constant efforts (Fs). Such a MS-MSY can be solved through the **game theoretic concept of a Nash equilibrium** and they explored two solutions to this conflict in the Baltic Sea. They maximized the sustainable yield of each stock under two constraints: first, to harvest the other stocks at a fixed F (FNE); second, to keep the spawning stock biomasses of the other stocks fixed [biomass Nash equilibrium (BNE)]. As a case study, they have developed a multi-species interaction stochastic operative model (MSI-SOM), which contains a SOM for each of the three dominant species of the Baltic Sea, the predator cod, and its prey herring, and sprat. For the Baltic Sea case, MS-MSYs existed under both the FNE and the BNE, but there was no guarantee that point solutions exist. They found that the prey species' spawning stock biomasses are additive in the cod growth function, which allowed for a point solution in BNE. In the FNE, the herring MSY was found to be relatively insensitive to the other species' fishing mortalities (F), which facilitated a point solution. The MSY targets of the BNE and the FNE differed slightly where the BNE gave higher predator yields and lower prey yields.

Weighing objectives becomes increasingly challenging when managers have to consider opposing objectives from different stakeholders. Jacobsen et al. (2017) offered an alternative view on dealing with trade-offs: An alternative to weighing incomparable and conflicting objectives was to focus on win–wins until Pareto efficiency is achieved: a state from which it is impossible to improve with respect to any objective without regressing at least one other. They investigated the ecosystem-level efficiency of fisheries in five large marine ecosystems (LMEs), including the Baltic, with respect to yield and an aggregate measure of ecosystem impact using a **novel calibration of size-based ecosystem models**. They estimated that fishing patterns in three LMEs (North Sea, Barents Sea and Benguela Current) were nearly efficient with respect to long-term yield and ecosystem impact and that efficiency has improved over the last 30 years. In two LMEs (Baltic Sea and North East US Continental Shelf), fishing was inefficient and win–wins remained available. They additionally examined the efficiency of North Sea and Baltic Sea fisheries with respect to economic rent and ecosystem impact, finding both to be inefficient but steadily improving. Their results suggest the following: (i) a broad and encouraging trend towards ecosystem-level efficiency of fisheries; (ii) that ecosystem-scale win–wins, especially with respect to conservation and profits, may still be common; and (iii) single-species assessment approaches may overestimate the availability of win–wins by failing to account for trade-offs across interacting species.

Bauer et al. (2018) investigated, if eutrophication management has the potential to substantially affect which areas are going to be most suitable for commercial fishing in the future. They used a **spatial ecosystem model (ecospace)**, forced by a coupled physical-biogeochemical model, to simulate the spatial distribution of functional groups within a marine ecosystem, which depends on their respective tolerances to abiotic factors, trophic

interactions, and fishing. They simulated the future long-term spatial developments of the community composition and their potential implications for fisheries under three different nutrient management scenarios and changing climate. The three nutrient management scenarios resulted in contrasting developments of bottom oxygen concentrations and phytoplankton abundance, with substantial effects on fish production. Nutrient load reduction increases the spatial extent of the areas suitable for the commercially most valuable demersal fish predator and all types of fisheries.

Achieving good environmental status in the Baltic Sea region requires decision support tools which are based on scientific knowledge across multiple disciplines. Such tools should integrate the complexity of the ecosystem and enable exploration of different natural and anthropogenic pressures such as climate change, eutrophication and fishing pressures in order to compare alternative management strategies. Bossier et al. (2018) presented a new framework, with a **Baltic implementation of the spatially-explicit end-to-end Atlantis ecosystem model** linked to two external models, to explore the different pressures on the marine ecosystem. The HBM-ERGOM initializes the Atlantis model with high-resolution physical-chemical-biological and hydrodynamic information while the FISHRENT model analyses the fisheries economics of the output of commercial fish biomass for the Atlantis terminal projection year. The Baltic Atlantis model composes 29 subareas, 9 vertical layers and 30 biological functional groups. The balanced calibration provides realistic levels of biomass for, among others, known stock sizes of top predators and of key fish species. Furthermore, it gives realistic levels of phytoplankton biomass and shows reasonable diet compositions and geographical distribution patterns for the functional groups. By simulating several scenarios of nutrient load reductions on the ecosystem and testing sensitivity to different fishing pressures, they showed that the model is sensitive to those changes and capable of evaluating the impacts on different trophic levels, fish stocks, and fisheries associated with changed benthic oxygen conditions.

Ecosystems are known to change in terms of their structure and functioning over time. Modelling this change is a challenge, however, as data are scarce, and models often assume that the relationships between ecosystem components are invariable over time. **Dynamic Bayesian Networks** (DBN) with hidden variables have been proposed as a method to overcome this challenge, as the hidden variables can capture the unobserved processes. In Uusitalo et al. (2018), a series of DBNs with different hidden variable structures was fit to the Baltic Sea food web. The exact setup of the hidden variables did not considerably affect the result, and the hidden variables picked up a pattern that agrees with previous research on the system dynamics.

Bauer et al. (2019a) developed numerical simulations of potential future ecological states of the Baltic Sea ecosystem at the end of century under five scenarios. They used a **spatial food web (ecospace) model, forced by a physical–biogeochemical model**. The scenarios were built on consistent storylines that describe plausible developments of climatic and socioeconomic factors in the Baltic Sea region. Modelled species diversity and fish catches were driven by climate- and nutrient load-related changes in habitat quality and by fisheries management strategies. Their results suggest that a scenario including low greenhouse gas concentrations and nutrient pollution and ecologically focused fisheries management results in high biodiversity and catch value. On the other hand, scenarios envisioning increasing societal inequality or economic growth based on fossil fuels, high greenhouse gas emissions and high

nutrient loads result in decreased habitat quality and diminished biodiversity. Under the latter scenarios catches are high but they predominantly consist of lower-valued fish.

Different ecosystem models often provide contrasting predictions (model uncertainty), which is perceived to be a major challenge impeding their use to support ecosystem-based fisheries management (EBFM). The focus of Bauer et al. (2019b) was to examine the extent of model disagreements which could impact management advice for EBFM in the central Baltic Sea. They **compareed how much three models (EwE, Gadget and a multispecies stock production model) differ** in 1) their estimates of fishing mortality rates (Fs) satisfying alternative hypothetical management scenario objectives and 2) the outcomes of those scenarios in terms of performance indicators (spawning stock biomasses, catches, profits). Uncertainty in future environmental conditions affecting fish was taken into account by considering two seal population growth scenarios and two nutrient load scenarios. Differences in the development of the stocks, yields and profits existed among the models but the general patterns were also sufficiently similar to appear promising in the context of strategic fishery advice. Thus, they suggested that disagreements among the ecosystem models will not impede their use for providing strategic advice on how to reach management objectives that go beyond the traditional maximum yield targets and for informing on the potential consequences of pursuing such objectives. This was especially true for scenarios aiming at exploiting forage fish sprat and herring, for which the agreement was the largest among our models. However, the quantitative response to altering fishing pressure differed among models. This was due to the diverse environmental covariates and the different number of trophic relationships and their functional forms considered in the models. This suggested that ecosystem models can be used to provide quantitative advice only after more targeted research is conducted to gain a deeper understanding into the relationship between trophic links and fish population dynamics in the Baltic Sea.

Size of predator and prey determines, to a large extent, predator-prey interactions in aquatic systems. **Understanding the relationship between predator and prey size** in the individual predator's food selection process is a cornerstone of ecological modelling. Stomach content data are used to inform such models, as they provide prey species specific information about the predator diet in the wild. These data are strongly relevant as direct observations of species trophic interactions, but they have limitations, and are costly. Kulatska et al. (2019) developed and tested a model which is able to predict changes in the Baltic cod diet by reconstructing the dynamics of cod and its prey, herring and sprat, populations, their length distributions, and parametrizing trophic interactions between them. They analysed time-series of cod stomach data and built an **age-length structured multispecies model using Gadget**. Both observed and predicted diets of smaller (juvenile) cod consisted mainly of benthos, while larger cod fed mostly on fishes (herring and sprat). Their model could predict the main patterns in species and length composition of cod diet. They also identified important knowledge gaps, especially on benthos dynamics and processes affecting prey availability and predator preference.

Maldonado et al. (2019) analyzed the Baltic Sea food web in order to examine potential unobserved processes that could affect the ecosystem and make predictions on some variables of interest. To do so, **dynamic Bayesian networks** with different setups of hidden variables (HVs) were built and validated applying two techniques: rolling-origin and rolling-window. Moreover, two statistical inference approaches were compared at regime shift detection: fully Bayesian and Maximum Likelihood Estimation. Their results confirmed that,

from the predictive accuracy point of view, more data help to improve the predictions whereas the different setups of HVs did not make a critical difference in the predictions. Finally, the different HVs picked up patterns in the data, which revealed changes in different parts of the ecosystem.

Karlson et al. (2020) investigated changes in the physiological status and population/community traits of six consumer species/groups in the Baltic Sea (1993–2014), spanning four trophic levels and using metrics currently operational or proposed as indicators of food-web status. They asked whether the physiological status of consumers can be explained by food-web structure and prey food value. This was tested using **partial least square regressions** with status metrics for grey seal, cod, herring, sprat and the benthic predatory isopod *Saduria entomon* as response variables, and abundance and food value of their prey, abundance of competitors and predators as predictors. They found correlations implying that the physiological status of cod, herring and sprat is influenced by competition, predation, and prey availability; herring and sprat status also by prey size.

Model applicability for indicating food web status and model gaps in relation to this application

The trophic models represent a wide range of applications in the Baltic Sea. Each model has been designed for a specific purpose, and contains some key assumptions (Table 2). The key assumptions displayed in Table 2 are selected in relation to determine the extent to which the models can be applied to represent status and dynamics of the Baltic Sea food webs. Each model has hence certainly more assumptions which are not listed here. These include for example assumption on the statistical distributions of the parameters (multivariate statistics), deterministic process models (end-to-end), or simplifications in order to keep the models analytically tractable (size-spectra and theoretical models).

Table 2: Model applications by model type and basic assumptions

# in Table 1	Model type	Key assumptions
13,17,18,19, 28	Multivariate statistics	Stable relationship between variables also on the non-sampled future
5,16, 26,14	Commercial fish species multispecies	Food selection according to constant size preference and predator-prey overlap
1, 2, 3, 4,6, 7,8,9, 10,12, 15,16,21, 24, 25	Mass-balance	Mass has to be scaled up/down using a vulnerability parameter to reach mass balance. This parameter is not measurable
22	End-to-end	Many untested, deterministic sub-models
20	Size spectra	Size is the only parameter determining species interactions
11,18,	Theoretical (check refs for proper name)	Several model specific assumptions; in general difficult to falsify
23,27	Dynamic Bayesian Network	Graphical formalism for representing joint probability distributions, causality is not investigated

Classical food web metrics include for example **link density** (the Number of trophic interactions (links) per species), **connectance** (the proportion of directed links realized out of

the maximum number of possible links), **modularity** (describes how densely sub-groups of species interact with one another compared to species from other sub-groups), or **clustering** (describes the probability that two taxa that are linked to the same taxon are also linked together). For a more exhaustive list see Kortsch et al. (2019).

These food web metrics are not especially well represented in any ecosystem model, because the selection of species in all mentioned models, and the subsequent aggregation into guilds or functional groups, is not emerging from the models, but has to be given as input. Hence, these types of metric cannot be considered well-represented since they are input rather than output of the models.

On the other hand, all models represent the dynamics of species or functional groups (guilds). To that end, they can not only be used to show food web status in terms of guild biomasses, but also allow to infer about the dynamics between functional groups and hence good environmental status (GES). GES is poorly defined, but assuming that some sort of ecosystem stability, or 'minimizing the probability that something bad will happen' are to its core, then the dynamics of functional groups certainly are a good starting point.

For this reason, the assessment of model applicability here is focused on strengths and gaps of the model to realistically depict size and dynamics of functional groups in the Baltic Sea food web. The projection of the functional groups assessed by trophic model on trophic guilds, both in relation to species composition and spatio-temporal scale of models compared to spatio-temporal scales of indicators, will be focus in deliverable 3.3.

The kernel of consumer-resource interactions is the predator-prey encounter. How many prey does an individual predator encounter per unit of time? How can an individual predator maximize this rate? Would it be worth-while for a predator to cooperate with other predators? And the prey individuals, what do they do to minimize encounters?

The current paradigm is that per predator encounter rate is proportional to prey biomass (mass interaction, following the principles of gas kinetics). However, most recent research has shown that the predators of schooling fish might only have a distinct time window during school formation and deformation. Furthermore, if predators cooperate, where is the threshold in local predator abundance between cooperation and competition?

All models in this review that are not purely correlation-based use to some extent a functional response (Solomon 1949, Holing 1959). It describes, how many prey items a predator consumes per unit of time, dependent on the number of available prey individuals. This concept contains the tacit assumption that predator-prey encounter rate is directly proportional to prey number (Paloheimo 1979), or prey density (number per volume) in a three-dimensional context in the ocean. The Ecopath/Ecosim-type mass balance models (containing all mass balance models in this review) somehow try to circumvent this tacit assumption by introducing a vulnerability parameter, expressing the fraction of a functional group that is available for species interactions (Walters and Christensen, 2007). Yet, the vulnerability parameter allows to fit almost any mass balance and is very difficult to falsify.

All other model type in this review either implicitly contain some form of spatial overlap assumption that is not violated as long as spatial overlap can be considered constant over time (multivariate, multispecies, end-to-end, size-spectra, dynamic Bayesian), which is usually not the case in nature, or simply do not consider this aspect at all (other theoretical models).

Spatial aspects beyond predator-prey overlap are getting increasingly important in marine management, including conservation issues, which are becoming an integral part of the overall spatial planning. Especially in a multispecies and food web context, when several species interact in a system, it is of fundamental importance to describe the spatial patterns of different species and understand the causes and consequences of their distribution changes. Within species, information on the spatial population structure is pivotal for sustainable management.

The match and mis-match of natural populations with their management units, the existence of source-sink systems, local density dependence and migrations interact and affect estimates of natural and fisheries-induced vital rates, such as somatic growth and mortality. One mass balance model (Ecospace) and the end-to-end model Atlantis (Table 1) have been applied, both of which are potentially able to account for such issues. However, both the implementation of spatial heterogeneity and the model setup have to be carefully considered before they are applied for management decisions. Such considerations include the spatial units in the modes, re-distribution mechanisms at each model iteration as well as the representation of biomass or biomass-equivalent (e.g. nitrogen) flows between model compartments.

The most reliable data source for guild biomasses is the multispecies model type. Data on cod, herring and sprat biomasses are based on scientific surveys, conducted under the coordination of the International Council for the Exploration of the Seas (ICES). Together with data on commercial catches, weight and maturity at age and the model-derived estimates of natural mortality (Gårdmark et al., 2015) due to predation, these data are oftentimes used as first element in mass-balance (e.g. Harvey et al., 2003; Tomczak et al., 2009) and end-to-end models (Bossier et al. 2018). The term 'first element' in this case means, that the multi-species model derived fish biomass is assumed known in the mass-balance and end-to-end models, and the other guilds such as zooplankton or apex predators are then 'balanced' so that they fit the fish biomass. This procedure implies that any structural misconception of fish consumption and predation behavior is propagated in the models and leads to possibly erroneous estimates for the biomasses of non-fish trophic guilds. However, in the absence of reliable, Baltic-wide estimates of other guilds' biomasses, this is probably the only option.

Recommendations

We recommend to use an ensemble approach as in Gårdmark et al. (2015) where possible to determine guild biomasses as indicators for food web status. Using an ensemble will give an overview over the structural uncertainty resulting from different model assumptions and setups. To this end, the input data should be unified, limiting model discrepancies to the models and not the data.

Spatial heterogeneity should be accounted for. This issue should be initiated by collecting all relevant processes in the Baltic Sea, such as source-sinks or coastal-offshore connectivity. These issues are not necessarily represented in a model, because spatial population dynamics are still poorly understood (Turchin, 2003).

The spatial and temporal scale of ecosystem models and potential food web indicators should be aligned as far as possible, and following functional criteria, such as topographic differences, known separated community structures and so further. This way, one can avoid erroneous conclusions that are based on limited data projected over the whole Baltic.

Acknowledgements

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