Position Paper

Model-derived causal explanations are inherently constrained by hidden assumptions and context: The example of Baltic cod dynamics

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ABSTRACT

Models are widely used for investigating cause-effect relationships in complex systems. However, often different models yield diverging causal claims about specific phenomena. Therefore, critical reflection is needed on causal insights derived from modeling. As an example, we here compare ecological models dealing with the dynamics and collapse of cod in the Baltic Sea. The models addressed different specific questions, but also vary widely in system conceptualization and complexity. With each model, certain ecological factors and mechanisms were analyzed in detail, while others were included but remained unchanged, or were excluded. Model-based causal analyses of the same system are thus inherently constrained by diverse implicit assumptions about possible determinants of causation. In developing recommendations for human action, awareness is needed of this strong context dependence of causal claims, which is often not entirely clear. Model comparisons can be supplemented by integrating findings from multiple models and confronting models with multiple observed patterns.

1. Introduction

Ecosystem functions and services are at risk because of over-exploitation, habitat and biodiversity loss, pollution, and, in general, unsustainable management. Transformation to sustainability is therefore mandatory, as summarized in the UN Sustainable Development Goals (Messerli et al., 2019). However, due to the complexity of many ecosystems or social-ecological systems, clear cause-effect relationships are hard to identify. Often we do not know the causes of a certain feature or behavior of a system, and usually we cannot fully foresee the effects of certain interventions (e.g. policy, management, harvesting), be they desired or undesired effects. However, without understanding at least the most important causes underlying ecosystem dynamics, successful transformation to sustainability will be hard, if not impossible.

Traditionally, observation and experiments are used to discover causal relationships. If sufficient data are available, correlations can be identified and suggest certain causal pathways, which then can be tested in targeted experiments. With many ecological and especially social-ecological systems, though, data never can be comprehensive, as those systems are too complex and large. Likewise, experiments under controlled conditions are not possible. Modeling is therefore widely used to study such systems. Assuming that a model despite its simplifications reflects reality sufficiently well for its purpose, models seem to be an ideal tool for understanding causation: they can be complex and cover large scales, one can collect various virtual 'data' of the modeled system, and perform any kind of controlled experiments to identify causes.

Still, modeling of complex systems has its own challenges. Whether or not a model is realistic enough for its purpose often remains uncertain, also because usually there are not enough actual data to reduce uncertainty. Moreover, even for realistic and robust models, fully understanding cause-effect relationships is hard to achieve, for the same reasons that real systems are hard to understand: the large number of direct and indirect effects, nonlinearities, delayed effects, complex and nested networks of interactions, and the heterogeneity of the actors and factors involved in system dynamics. Nevertheless, inferences are made from models, but often the justifications and constraints of claimed cause-effect relationships are implicit and therefore not transparent and clear.

Most puzzling, though, is that different models addressing the same system and similar questions, often vary widely in their structure, the way they are analyzed and, hence, the respective conclusions. This variation is partly inevitable, as scientific explanations always depend on presuppositions of those seeking explanations (e.g. van Fraassen, 1980), and it also has benefits, as it means to look at the same problem from different angles. However, the diversity of models complicates establishing a generally accepted level of understanding of cause-effect relationships that could support successful interventions and transformation.

While numerous reviews of models of certain ecological or social-ecological systems exist, so far there seems to be no attempt to review models with a focus on their causal claims and how those might be constrained, not only explicitly, as stated by their developers, but also implicitly by decisions and presuppositions underlying the models' design. We therefore reviewed ecological models addressing the collapse of the Baltic cod, or its general population dynamics with a focus on collapse or recovery. We chose this subject mainly because the number of such models is limited so that we had the chance to zoom into details of the causal claims, but also because understanding collapses in general, and of the Baltic cod in particular, is of high general interest.

Cod is ecologically important as a top predator in a food web including its main prey species sprat and herring as well as benthic, zooplankton and phytoplankton species. This means that changes in cod abundance can cause, and be caused by, considerable changes in the abundance of other species in the food web. Moreover, the species populations respond to environmental conditions such as water temperature, salinity and oxygen content (e.g. Lindegren et al., 2009).

From an anthropocentric perspective, cod is economically important as a fishing resource. In the Baltic Sea, cod used to be harvested in large amounts especially during periods of consistently high abundance throughout the 20th century (e.g. Österblom et al., 2007). Starting in the 1980s, however, the cod populations severely declined (e.g. Casini et al., 2008; Möllmann et al., 2009) and have so far not recovered to consistently high abundance. The Baltic cod consist of two main populations, the Eastern and the Western Baltic cod stocks. While there have been slight indications of recovery for both stocks in the recent decade (Eero et al., 2012a, 2014; Hüssy et al., 2016; Sguotti et al., 2019), both stocks still have critically low abundances today (ICES, 2021a, 2021b). Additionally, the Baltic cod average body size has decreased, which is considered a further hindrance to recovery (Eero et al., 2019; Niiranen et al., 2019).

We found 15 relevant models and analyzed their corresponding publications as to which causal explanations of Baltic cod dynamics were derived. After inspecting the studies with respect to criteria such as the addressed research questions, the model types, system conceptualizations and additional assumptions, we focused on the question: Which causal claims were made, how were the claims derived and justified, and how were they shaped and constrained by the model assumptions? We show that multiple explicit and implicit choices are part of the context of

Table 1

List of models and studies, with the main cod-related research questions addressed. The questions are classified to the categories of causal inquiry: C – Causes of cod dynamics, M – Mechanisms driving cod dynamics, P – Predictions of cod dynamics. Certain questions cover elements of two categories. With respect to a category put in brackets, the question is answered indirectly in terms of discussing and interpreting model results. The models are classified as statistical (S) or dynamic simulation (D) models.

Model, Reference	Research questions	Question category	Model type
01a BALMAR, (Lindegren et al., 2009)	Which model can reconstruct the historical time series?	C	S, D
	Which management could have prevented the cod collapse?	P	
01b BALMAR, (Lindegren et al., 2010)	How would the Baltic cod stock develop under different climate and management scenarios through the 21st century?	P	S, D
	Which fisheries management would be sustainable?	P	
02 Baltic cod GAM, (Casini et al., 2016)	Which factors affect cod body condition before and after regime shift?	C, (M)	S
03 Baltic cod GAM, (Möllmann et al., 2008)	Is there a trophic cascade from cod to sprat to the zooplankton species *P. acuspes*?	C, (M)	S
	Which are the best explanatory variables for different biotic variables (e.g. cod recruitment)?	C	
	Which conceptual model explains the detected relations?	C, (M)	
04 Baltic cod state-space model, (Wikström et al., 2016)	What are the effects of harvesting and environmental variation on cod stock fluctuations?	C, (M)	D
	What is the future cod stock development under different harvesting and hydrographic scenarios?	P	
05 Baltic ecosystem state GAM, (Möllmann et al., 2009)	Which abiotic variables explain the biotic regime shift of the Baltic sea ecosystem?	C, (M)	S
06 Baltic Sea cod-sprat model, (van Leeuwen et al., 2013)	Which mechanisms explain the lack of recovery of top predator (cod) populations when including an intermediate life-stage feeding on benthos?	M	D
07 CHS model, (Heikinheimo, 2011)	Can the cod, herring and sprat stock dynamics for 1974–2004 be reproduced with the minimum realistic dynamic model?	M	D
	What are cod dynamics under different fishing scenarios?	P	
08a EwE – BaltProWeb, (Tomczak et al., 2012)	What type of trophic interactions and external multiple drivers (fisheries, environmental factors) are needed to reasonably simulate the observed dynamics and reorganizations of the food web flows between 1974 and 2006?	C, M	D
08b EwE – BaltProWeb, (Niiranen et al., 2012)	How sensitive are projected dynamics to variations in input data and environmental forcing?	M, P	D
09 Empirical Baltic Sea model, (Lade et al., 2015)	Have social processes contributed to the cod collapse and if so, how?	C, M	D
10 FishANN, (Krekoukiotis et al., 2016)	Which factors drive Baltic cod recruitment?	C	S
11a Gadget, (Kulatska et al., 2019)	What explains ontogenetic and temporal changes of the Eastern Baltic cod diet?	C	D
11b Gadget, (Bauer et al., 2019)	What is the respective management advice based on projections for 2014–2032 for different goals?	P	D
12 MSPM, (Horbowy, 2005)	Can the simpler and less data-demanding multispecies stock production model estimate Baltic fish stock dynamics and species interactions similarly to MSVPA?	C	D
13a MSVPA, (Sparholt, 1991)	How to use the MSVPA approach to the Baltic fish stocks?	-[a]	D
13b MSVPA, (Sparholt, 1994)	How will the cod stock behave under different fisheries scenarios?	P	D
14 Single species model, (Jonzén et al., 2002)	Which Eastern Baltic cod exploitation level can rebuild the cod population and sustain future fishery?	P	D
15 Stock recruitment model, (Margonski et al., 2010)	Is (cod) recruitment significantly related to spawning stock biomass, climatic forcing, feeding conditions?	C	S
	Can acknowledging these drivers improve management decisions?	(P)	

[a] – Model presentation and justification only.

causal claims derived from ecological models, which is crucial for fully comprehending the meaning and scope of these claims.

2. Methods

We selected 15 ecological models from 19 published studies (Table 1) to represent how Baltic cod dynamics have been studied with a particular focus on ecological aspects involved. All these models were used for studying causes of Baltic cod dynamics. They either represented a period including the collapse in the late 1980s and early 1990s or they were used to generally investigate the possibilities of cod collapse or recovery. We did not take into account studies in which the modeling primarily focused not on the causes, but on the consequences of the Baltic cod collapse (e.g. Casini et al., 2008, 2009).

To analyze how the ecological models were used to develop causal knowledge about cod dynamics, we assessed the following criteria. (1) Which main research questions were addressed? We distinguish between questions aiming at (a certain degree of) explanatory understanding (Kuorikoski and Ylikoski, 2015) and questions aiming at predictions. This criterion is of utmost importance because models do not represent systems per se, but systems with respect to a specific question. Understanding, evaluating, and comparing models thus requires awareness of the specific questions and the overall purposes of the models (Grimm et al., 2020a). (2) Which model type was used? Various categorizations of ecological models exist (e.g. Hilborn and Mangel, 1997; Otto and Day, 2007; Evans et al., 2013; DeAngelis and Grimm, 2014). We distinguished between statistical models and dynamic simulation models. As the boundaries between these types are blurred (e.g. Dormann et al., 2012; Oberpriller et al., 2021), we interpreted them broadly. For instance, we considered an artificial neural network belonging to the statistical models and any model representing system dynamics through state variables and processes that change them as dynamic simulation models. (3) How was the (social)-ecological system conceptualized in the models? This comprises which entities and which relationships between them were represented in a model and how, and whether entities were exogenous (i.e. only affecting other entities) or endogenous (i.e. also being affected by other entities). (4) Which additional assumptions were made to define the model, and how were they justified? (5) Which data were incorporated and how? (6) Which answers to the research questions were given? We reviewed the causal claims that were made, and differences among claims on similar subjects from the different modeling studies. In particular, we examined how the
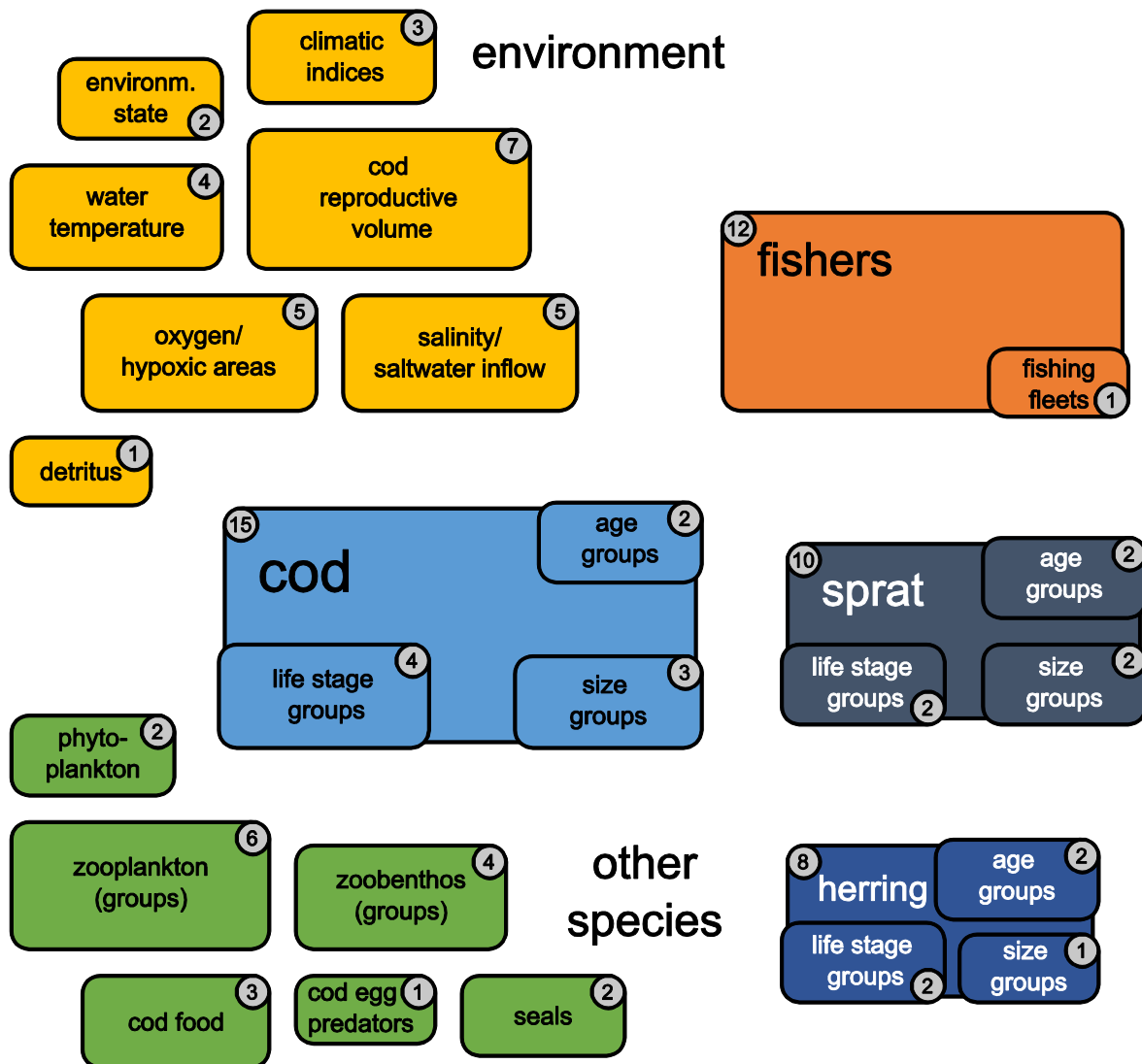
Fig. 1. Overview of entities taken into account in the 15 models. They are grouped into cod, sprat, herring and other species populations, the environment (represented by different factors), and fishers. Box sizes and grey numbers show the number of models in which the entity was included (out of 15 models in total). The additional boxes within larger ones show the separation of cod, sprat or herring populations into age groups, size groups or life stage groups, and the separation of fishers into multiple fleets.
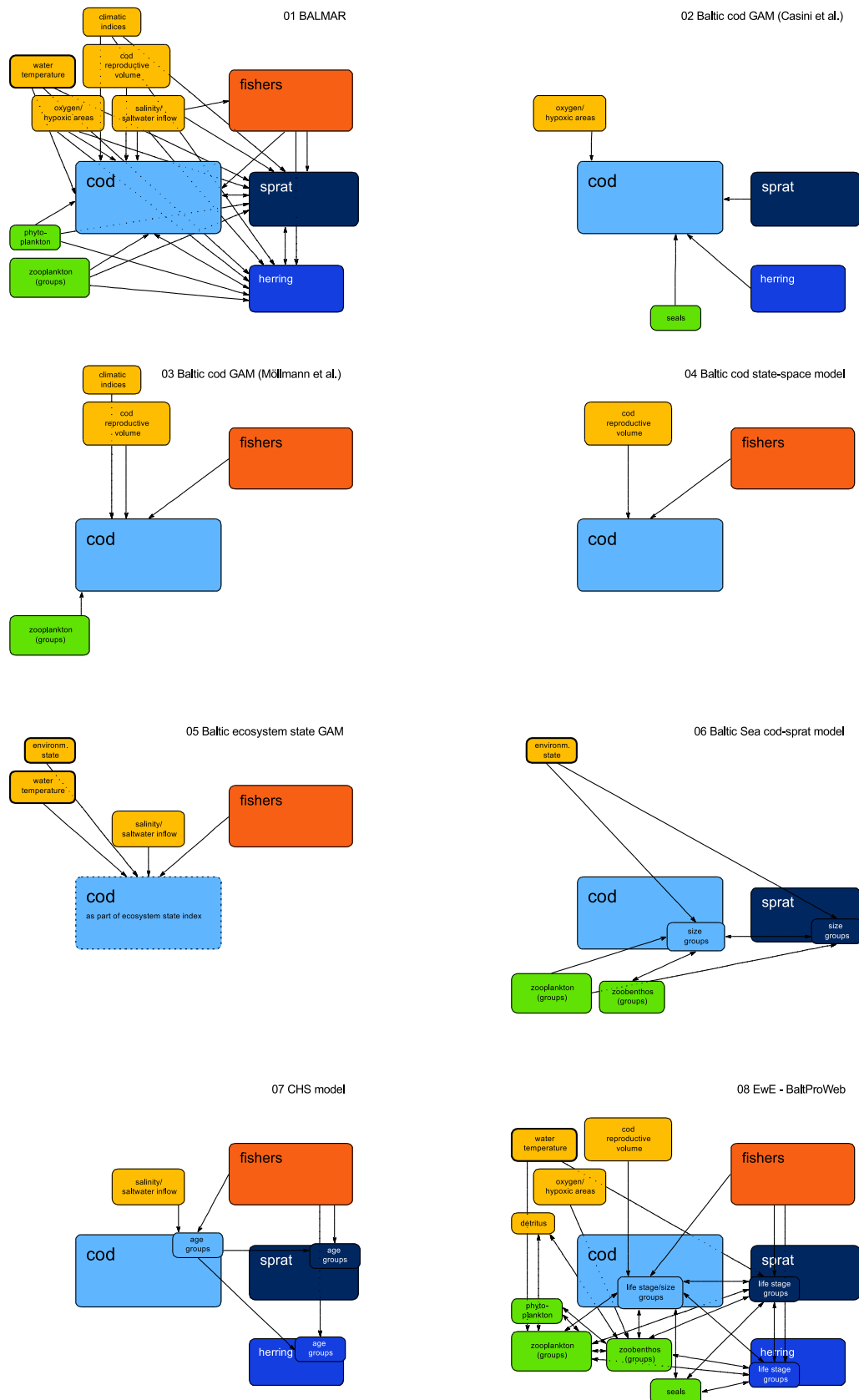
Fig. 2. System conceptualization for each of the models 01–15 (subplot titles, cf. Fig. 1). Boxes show entities included, arrows show relationships between them. Dashed boxes indicate that the entity 'cod' was represented as part of an ecosystem state index (model 05) or that the entity 'fishers' was part of a fishery submodel (model 09). See Table 1 for relating each model's system conceptualization to the main research question(s) addressed.
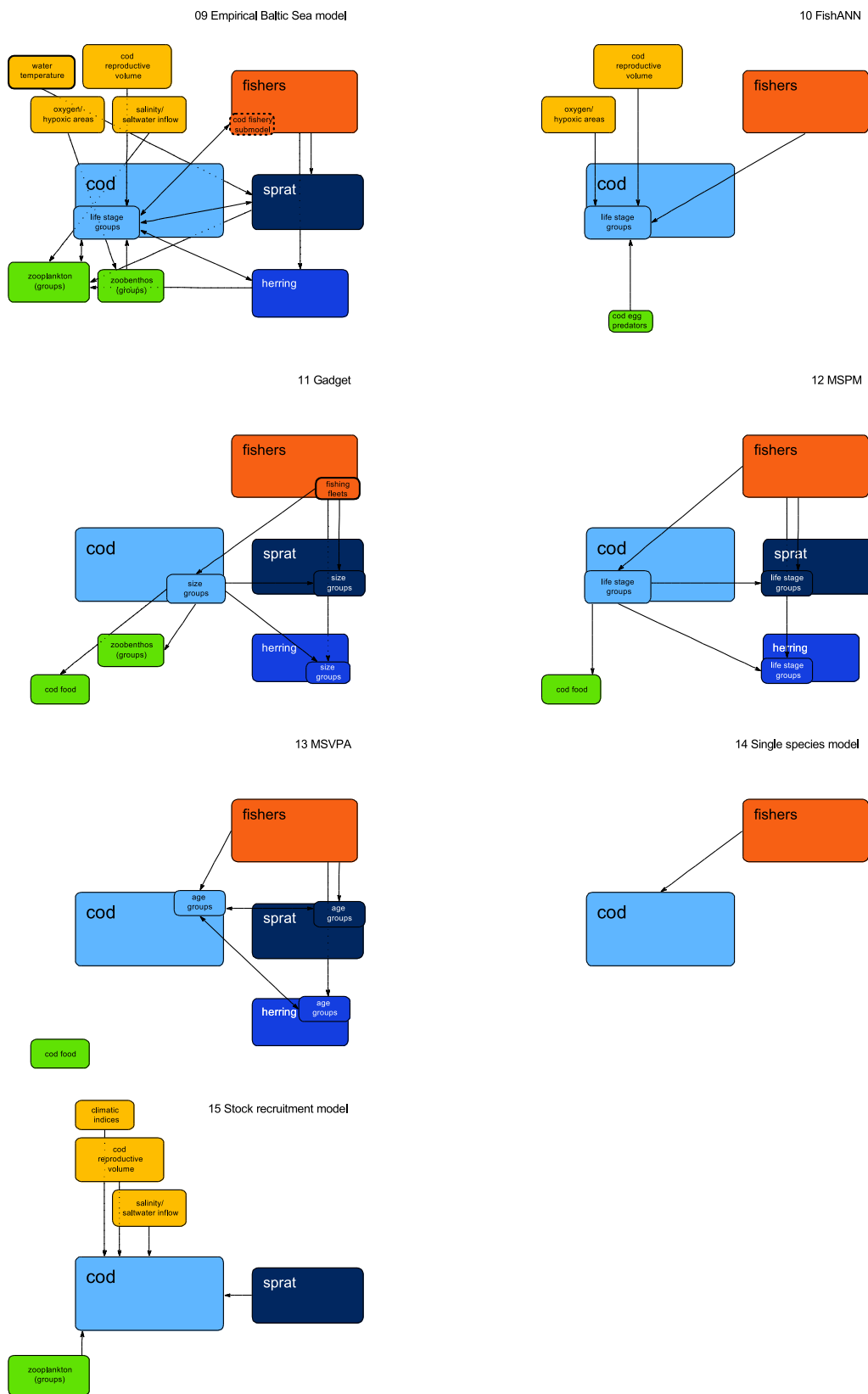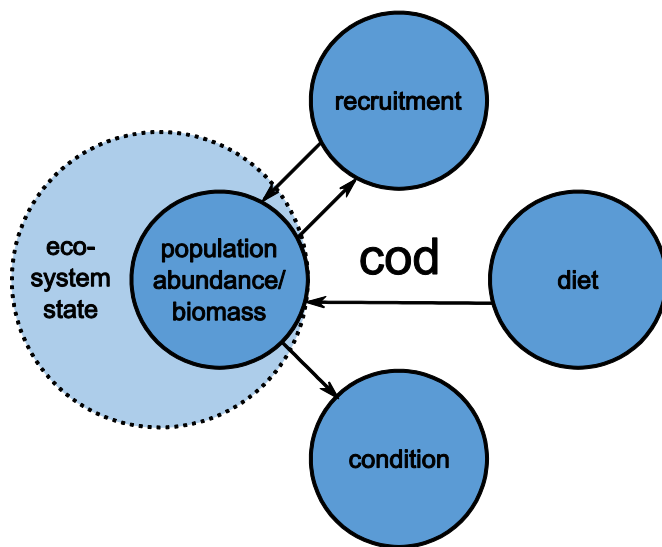
Fig. 2. (*continued*).

Fig. 3. Characteristics of cod dynamics (blue circles) that were used as outcomes of the models. Apart from the variety in variables to be explained or predicted, some measures used as output variables in certain models were also used as explanatory variables in others (visualized by arrows pointing from explanatory to output characteristics). Note that the manifold additional explanatory variables used in the models are not shown here (cf. Fig. 2). Cod abundance/biomass was either represented explicitly or implicitly as part of the Baltic ecosystem state. Cod recruitment was typically expressed by number or biomass of recruits, or by a recruitment index. Cod diet refers to food composition or food consumption rate. Cod condition refers to the mean body condition of individuals (measured by Fulton's K = weight/length^3 * 100, Casini et al., 2016).

models were used to derive and support these causal claims.

We stress that all our assessments of the model characteristics and analyses were done to the best of our understanding of the publications, but may be not fully precise and correct in all details. Unambiguously obtaining the specific information for a review of, for example, fish and fisheries models is not always possible (cf. Nielsen et al., 2018).

3. Results

3.1. Research questions

We found that the causal analyses based on the models always met at least one of the general research purposes of explanatory understanding or prediction (cf. 2 Methods). The identified key research questions related to (some measure of) cod dynamics (one to three questions per study) broadly fall in the following three categories of causal inquiry: C – Causes: which factors affect cod dynamics? M – Mechanisms: which mechanisms drive cod dynamics? P – Predictions: which consequences would certain environmental or management scenarios have for cod dynamics? Categories C and M aim at explanatory understanding, but the studies varied in terms of what exactly was intended to be explained (cf. Kuorikoski and Ylikoski, 2015). In category M not only the causes but also the underlying mechanisms shall be uncovered. We understand a mechanism as a causal explanation that explicitly (often stepwise) links cause(s) and effect(s). Mechanisms comprise processes that involve certain entities and that together bring about the phenomena of interest (cf. e.g. Hedström and Ylikoski, 2010; Cabral et al., 2017; Connolly et al., 2017; Heger, 2022 for alternatives and discussions on the definition of mechanisms in ecology and sociology). Category P aims at prediction of the effects of environmental change or management decisions. We rephrased the research questions to keep them brief and facilitate comparison (see Table 1 for all questions and their categorization).

For the 19 studies reviewed, we found 11 posing a research question of category C – Causes, 9 posing a question of category M – Mechanisms, and 9 posing a question of category P – Predictions. Some questions had overlaps, so they were assigned to two categories (Table 1). In several cases, mechanisms were asked for and also provided in the studies, but mainly through interpretation of the causal factors identified with the models rather than through dynamic simulations (Table 1; see also *3.6 Causal Claims*, Table 4). It also occurred that one model was used to address several questions of different categories, either in one or in different studies. For example, the model Gadget was developed and used to detect causes of cod diet dynamics by Kulatska et al. (2019) and used to predict cod fishery profits under various scenarios by Bauer et al. (2019).

Although the question categories are general, the particular research questions in each study often focused on specific elements of the ecological system, for example: 'Which factors drive Baltic cod recruitment?' (Category C, Krekoukiotis et al., 2016), 'Which mechanisms explain the lack of recovery of top predator (cod) populations when including an intermediate life-stage feeding on benthos?' (Category M, van Leeuwen et al., 2013), 'Which Eastern Baltic cod exploitation level can rebuild the cod population and sustain future fishery?' (Category P, Jonzén et al., 2002). These clear foci of analyses do not reveal which additional elements of the complex ecosystem were included in the models, and if so how. However, such system conceptualizations provided decisive context for answering the questions and may have considerably influenced the research findings. We therefore examined which entities were taken into account and linked in each of the models (cf. *3.3 System Conceptualizations*).

3.2. Model types

Given our broad categorization (cf. 2 Methods), most models could be assigned to either statistical or dynamic simulation models (Table 1). The model BALMAR (Lindegren et al., 2009, 2010) was assigned to both types, since a statistical multivariate autoregressive model was fitted to time series data, and the obtained food web model was then used for stochastic simulations of cod population dynamics under different scenarios. All statistical models were used to answer a research question of category C – Causes (Table 1). If they were used to address additional questions of another category, this happened through discussion and mechanistic interpretation of the statistical model results. By contrast, the dynamical models were used to answer questions of all three categories C, M and P (Table 1).

The multispecies virtual population analysis (MSVPA, e.g. Sparholt, 1991, 1994) is a very prominent dynamic model, used as a standard by the International Council for the Exploration of the Sea (ICES). This model provides time series of interacting Baltic fish stocks, separately for the Western (ICES subdivisions 22–24) and Eastern (ICES subdivisions 25–32) Baltic Sea. It is established to use these MSVPA output time series like input 'data' in other models, as it was done in several of the reviewed studies (cf. *3.5 Data Use*).

3.3. System conceptualizations

We observed that a large number of different species, several environmental factors and fishing were taken into account in the 15 different models (Fig. 1). This led to a huge variety of conceptualizations of the ecological or social-ecological system among the models, even more so as not only the entities considered vary, but also which of them were related and how (Fig. 2). In addition, different (sets of) variables have been used to characterize the entities. On top of these differences, relationships between the same entities and in the same direction have been defined and parameterized differently in the different models.

While the cod population was included in all 15 models, the models differ as to which characteristic of the cod population was the outcome of interest, that is, the measure of the 'cod dynamics' for which causes

should be investigated (Fig. 3). For instance, cod recruitment could be the outcome of interest and thus to be explained by a model, which then also included cod abundance as one explanatory variable (e.g. Baltic cod GAM, Möllmann et al., 2008; FishANN, Krekoukiotis et al., 2016). But in other models cod abundance was to be explained and a measure of cod recruitment used as an explanatory variable instead (e.g. MSVPA, Sparholt, 1994; MSPM, Horbowy, 2005).

The cod's main prey species sprat and herring were considered in several but not all models (10 models for sprat, 8 for herring). In several models the fish populations were divided into age groups (e.g. CHS model, Heikinheimo, 2011), size groups (e.g. Gadget, Bauer et al., 2019; Kulatska et al., 2019) or life stage groups (e.g. MSPM, Horbowy, 2005). Also here it became obvious that, even when considering the same entities, models may have incorporated different state variables and different relationships between them. One typical example relationship is sprat predation by cod. In some models, its effect on the sprat population was considered, but no effect on the cod population (e.g. CHS model, Heikinheimo, 2011). Other modelers did the opposite, taking into account the effect of the sprat population on the cod population but not vice versa (e.g. Margonski et al., 2010 in their stock recruitment model). In yet other models, both directions of this causal relationship were included (e.g. empirical Baltic Sea model, Lade et al., 2015). Additional biotic populations such as zooplankton, zoobenthos and other species were generally considered in fewer models (Fig. 1).

For specifying species interactions in dynamic simulation models, the parameter values for functional relationships representing interactions were often determined by fitting model output to data (e.g. Sparholt, 1991; Tomczak et al., 2012). Thereby, invariable functional relationships were commonly assumed. However, interactions do vary in reality, for example, when abundances of preferred or non-preferred prey species vary (Niiranen et al., 2019) or in response to varying abiotic conditions (Köster et al., 2005). Hence, more complex functional relationships reflecting these variations would be desirable for realistically representing actual causal relationships between species (sub)populations. Correctly defining and parametrizing such functional relationships remains a challenge (Plagányi et al., 2014; Peck et al., 2018). Generally, unavailable or incomplete data on relevant species precluded taking into account complex species interactions in some of the models (e.g. mentioned by Möllmann et al., 2008; Tomczak et al., 2012; Wikström et al., 2016).

The Baltic Sea environment was conceptualized in the models through including various abiotic factors. Cod reproductive volume (RV) was the most common abiotic factor (included in 7 models). RV is a standard measure of the suitable water volume for cod egg development, defined as the water volume with a suitable combination of salinity (>11 psµ) and oxygen (>2 ml^{-1}) conditions (MacKenzie et al., 2000). Other factors such as salinity or oxygen alone, temperature or climatic indices were included in several models, but less often (Fig. 1). The environmental factors were generally considered as exogenous entities without feedback in the models. They had an effect on, but were not affected by other entities. Here, an exception is detritus in the Ecopath with Ecosim (EwE) – BaltProWeb model, where this dead organic material was affected by zooplankton and zoobenthos populations (Niiranen et al., 2012; Tomczak et al., 2012).

In most but not all models (12 out of 15) was fishing explicitly considered. The reasons for the three exceptions are as follows: The Baltic cod GAM by Casini et al. (2016) aimed at explaining cod condition, the stock recruitment model by Margonski et al. (2010) at explaining cod recruitment. In both models, cod population abundance was used as one explanatory variable (cf. Fig. 3), which obviously was affected by fishing and, thus, fishing was implicitly taken into account. The Baltic Sea cod-sprat model (van Leeuwen et al., 2013) was used to mechanistically study the effects of cod prey-switching on cod abundance (cf. Fig. 3) and on food web dynamics in general. Thus, this model had a purely ecological focus disregarding fishing.

For the purpose of this analysis, we have taken explicit inclusion of

fishing in the models as fishers (or other fishing-related actors) being conceptualized as an entity (Fig. 1). This was usually an exogenous entity affecting ecological dynamics without feedback (apart from sometimes monitoring catch/profit as an output variable). Fishing was applied to cod, and sometimes also to sprat and herring. One model (Gadget) had separate fishing fleets, but this was not much discussed in the respective studies (Bauer et al., 2019; Kulatska et al., 2019). BAL-MAR had a simple bioeconomic submodel with different (incl. one adaptive) management strategies (Lindegren et al., 2009). The empirical Baltic Sea model had a sophisticated social submodel and also other social-ecological relationships than fishers affecting fish populations, namely perceptions and regulations depending on cod abundance and catches (Lade et al., 2015). However, we included it in our selection of ecological models because Lade et al. (2015) also analyzed an ecological model version in which the ecological subsystem was decoupled from social processes (i.e. with constant fishing effort).

With respect to how space and spatial heterogeneity were conceptualized, it was common in the modeling studies to assume that certain areas or locations can be regarded as representative or most important for environmental effects on cod dynamics, that mobile species are generally able to follow favorable conditions or prey species, that fishers follow the target species, or that species distributions and spatial overlap do not change and can therefore be captured by modeling invariant interactions of whole populations. However, it was also commonly mentioned that such assumptions were a potential limitation for correctly identifying complex causal relationships. To name just a few examples, Tomczak et al. (2012) wrote *"EwE models have a problem with highly migratory species or stocks patchiness (Christensen and Walters, 2004), in our case herring and sprat. According to one hypothesis, sprat aggregations could migrate (Stepputtis, 2006) dependent on the cod biomass or temperature at a certain habitat. Also herring shows high intra-species differences, local spawning groups and spawning migration to coastal areas and it is difficult to apply a single environmental factor that determines herring recruitment"*; Krekoukiotis et al. (2016) wrote *"we assumed for our data that mechanisms across Baltic subdivisions are roughly the same, since the integrated abundance of all spawning areas should be unaffected by transport between spawning areas (Köster et al., 2005). We kept this spatial homogeneity within the Central Baltic, similar to studies by Sparholt (1996) and Jarre-Teichmann et al. (2000). We can't be sure to what extent this decision affects the interpretations of complex non-linear relationships for recruitment."*; Kulatska et al. (2019) wrote *"'Negative switching' is when the proportion of a prey type in a predator's diet decreases slower than its proportion in total prey abundance. This has been suggested to cause destabilization of prey populations, as the impact of a predator on a prey with decreasing abundance is over-proportionally high (Chesson, 1984). However, this phenomenon can also be observed as an artifact of variable predator-prey spatial overlap (Neuenfeldt and Beyer, 2006), which was not accounted for in this study."*

Regarding the alternative option of spatially explicit models, a critical issue would be the use of appropriate data to define and fit a model (cf. *3.5 Data Use*). Some of the reviewed studies show that spatially resolved data (e.g. at the resolution of ICES subdivisions) would be available for several environmental factors and fish populations (Margonski et al., 2010; Casini et al., 2016, see also Casini et al., 2011). The two respective models did not explicitly include fishing (cf. Figs. 1, 2). However, also fishing data can be obtained at the resolution of ICES subdivisions (Eero et al., 2012b). Hence, it seems that data availability was not the major limitation preventing spatially explicit modeling, at least at a low resolution. Casini et al. (2016) did initially account for spatial heterogeneity at the resolution of ICES subdivisions 25–28, but then decided to use averages over this whole area of the Central Baltic Sea instead, because they did not observe significant variation among the subdivisions. The study by Margonski et al. (2010) is an example where an environmental factor (cod RV) from different spatial locations was initially taken into account (Bornholm Basin, Gdańsk Basin, Gotland Basin; the three main cod spawning areas in the Central Baltic Sea).

Table 2

Overview of strategies used in the modelling studies for deriving causal claims, and examples. Strategies are classified to the categories of causal inquiry: C – Causes of cod dynamics, M – Mechanisms driving cod dynamics, P – Predictions of cod dynamics. The strategies often overlapped and were closely interrelated such that clearly defined disjunctive categories could not be assigned.

Strategy for deriving causal claims	Example studies
Category C – Causes of cod dynamics	
Rely on published studies and expert knowledge for finding potential factors affecting cod dynamics to be included in the models	08a EwE – BaltProWeb (Tomczak et al., 2012), 09 Empirical Baltic Sea model (Lade et al., 2015), 15 Stock recruitment model (Margonski et al., 2010)
Test for statistical relationships between potential causes and cod output variables (cf. Fig. 3)	01a BALMAR (Lindegren et al., 2009), 02 Baltic cod GAM (Casini et al., 2016)
Compare agreement to data (sometimes based on multiple patterns) for different candidate models (both statistical and dynamic models)	10 FishANN (Krekoukiotis et al., 2016), 11a Gadget (Kulatska et al., 2019)
Aggregate output from multiple model fits to account for stochasticity	10 FishANN (Krekoukiotis et al., 2016),
Analyze temporal order of changes in variables to attribute cause and effect (e.g. changes in cod recruitment, biomass, fishing and environmental conditions)	03 Baltic cod GAM (Möllmann et al., 2008)
Analyze correlation between multiple potential causes to avoid redundant explanations	15 Stock recruitment model (Margonski et al., 2010)
Reflect on ecological soundness of detected causal factors	05 Baltic ecosystem state GAM (Möllmann et al., 2009), 15 Stock recruitment model (Margonski et al., 2010)
Category M – Mechanisms driving cod dynamics	
Observe effects of manipulating potential causal factors and functional relationships (i.e. sensitivity to choices and values for input data and parameters) in dynamic models	08b EwE – BaltProWeb (Niiranen et al., 2012), 09 Empirical Baltic Sea model (Lade et al., 2015), 12 MSPM (Horbowy 2005)
Translate structures or mathematical relationships from successfully fitted models into mechanisms	04 Baltic cod state-space model (Wikström et al., 2016)
Analyze simulated dynamics in detailed, model-specific manner (e.g. stability and feedback loops, differences between invasion and persistence conditions, energy flows through food web)	06 Baltic Sea cod-sprat model (van Leeuwen et al., 2013), 08a EwE – BaltProWeb (Tomczak et al., 2012), 09 Empirical Baltic Sea model (Lade et al., 2015)
Interpret detected potential causes mechanistically and discuss their feasibility, dependence on model assumptions, occurrence in published studies	07 CHS model (Heikinheimo 2011), 10 FishANN (Krekoukiotis et al., 2016), 13b MSVPA (Sparholt 1994)
Category P – Predictions of cod dynamics	
Simulate cod dynamics for different environmental or fishing scenarios	04 Baltic cod state-space model (Wikström et al., 2016), 11b Gadget (Bauer et al., 2019)
Aggregate multiple simulations for the same scenarios to account for stochasticity (e.g. when assessing extinction risks)	01b BALMAR (Lindegren et al., 2010), 14 Single species model (Jonzén et al., 2002)

Eventually, one best-fitting location was selected for the final statistical model.

3.4. Further model assumptions

The system conceptualizations include the tacit assumption that the entities and relationships considered in each model are the (most) relevant for the specific aspect of cod dynamics to be modeled, that is, for answering the research questions (cf. Table 1). Similarly, the selected model type and the particular definition of relationships (e.g. functional forms, parameter values) include the tacit assumption that these choices are (the most) appropriate to adequately represent the actual ecological dynamics. In addition, a variety of specific assumptions have been made and stated in the studies presenting the models.

We commonly observed that model assumptions were explicitly based on previously published literature. For example, candidate causal variables of the cod dynamics in statistical models were often selected, defined and justified in this way, for example *"We used 1 ml/l as threshold for hypoxia because the Baltic cod has been shown to avoid oxygen concentrations below this value [46]."* (Casini et al., 2016), *"we consider habitat driven variables, proposed by Köster et al. (2005), that potentially explain changes in recruitment regimes"* (Krekoukiotis et al., 2016). Also assumptions on specific forms of causal relationships in dynamic simulation models were obtained from earlier studies. For instance, the cod stock-recruitment equation in the CHS model (Heikinheimo, 2011) was taken from Heikinheimo (2008), the threshold cod lengths for ontogenetic shifts in the Baltic Sea cod-sprat model (van Leeuwen et al., 2013) were obtained from Hüssy et al. (1997), the assumption of multiple age groups to represent ontogenetic shifts in EwE – BaltProWeb (Tomczak et al., 2012) was made according to another EwE version for a different ecosystem (Walters et al., 2008).

We also found model assumptions based on prior knowledge that were not directly related to literature, for example *"In the 1980s and 1990s, a marked decline in the growth rate of Baltic herring was observed. This phenomenon was simulated in the model by presenting the anabolism coefficient h as a function of time linearly decreasing until 1998."* (MSPM, Horbowy, 2005). Such assumptions were apparently justified through presupposing sufficient expertise. In other cases, expert knowledge was explicitly referred to, for example *"a team of Baltic Sea experts from the natural and social sciences collaboratively developed a conceptual model of the key ecological and social quantities and processes that contributed to cod stock dynamics"* (empirical Baltic Sea model, Lade et al., 2015).

Other assumptions were not made to fully reflect the knowledge of the complex ecosystem, but to keep the model simple. This simplification could occur implicitly through stating assumptions that obviously simplify the actual ecological setting, such as *"The model is based on the assumptions that the distribution of predators and prey is spatially uniform; predator and prey populations are each made up of identical individuals with identical life-history parameters; and the growth and reproductive rates of cod do not depend on consumption rates."* (CHS model, Heikinheimo, 2011). Or it was made explicit, like *"we have made fewer assumptions and used a simple model structure, and this should enhance the robustness of our conclusions"* (single species model, Jonzén et al., 2002). We also found simplifying assumptions that were based on the model's lack of sensitivity to changes in these assumptions. For the CHS model, *"sensitivity analysis did not indicate any marked effect of an age-based preference coefficient, and for simplicity this was not taken into account"* (Heikinheimo, 2011). For EwE – BaltProWeb, of many vulnerability parameters that define predator-prey interactions, only those that the modeled dynamics were known to be most sensitive to were included in the calibration to data, while a default value was assumed for others (Niiranen et al., 2012; Tomczak et al., 2012).

Available data have often influenced and constrained model assumptions. This was explicitly stated in many studies, for example *"All in all, deep-water salinity data was not included due to lack of sufficient availability of the data set."* (FishANN, Krekoukiotis et al., 2016), *"Due to available data, we based our model on the Swedish cod fishery."* (empirical Baltic Sea model, Lade et al., 2015), *"The human impact was indicated by using one fishing fleet for each fish species due to the lack of historical fleet structure and effort data."* (EwE – BaltProWeb, Tomczak et al., 2012), *"The production models presented here are developed in such a way that the demand for age-based data is reduced to a minimum."* (MSPM, Horbowy, 2005), *"Because of limitations in the availability of the best data, we used time-series covering the period 1974–2005 in our analyses."* (Baltic cod GAM, Möllmann et al., 2008).

Table 3

Major causal claims derived with the models (literal quotes with clarifying additions in square brackets). Claims belong to the category of causal inquiry C – Causes of cod dynamics, and are grouped according to which measure of cod population (or ecosystem) dynamics is explained (highlighted in bold, cf. table section titles). Entries in the third column denote if and how the claims relate to fishing (F) and environmental conditions (E) as causes of cod population dynamics: F > E – fishing is more important than environmental conditions, E > F – environmental conditions are more important than fishing, R – recruitment is main cause of cod population dynamics, R(E) – recruitment is main cause of cod population dynamics and depends on environmental conditions.

Causal claim	Model	F or E?
Claims on cod population dynamics, general		
"the selected model [included] species interactions within the food web and the effects of fishing, zooplankton, and environmental variability [for **cod stock**: summer salinity (80–100 m) at the Gotland Basin]"	01a	F, E
"**fluctuations of [the Eastern Baltic cod] stock** are mainly driven by exploitation"	04	F
"fishing rate is approximately three times more important than RV in explaining the **[cod] population dynamics**. […] salinity and dissolved oxygen [separately] did not have any predictive power in our dataset"	04	F > E
"**predator population dynamics** are governed by a bottleneck in individual growth occurring in the intermediate life stage"	06	–
"[the] model reproduced well the **historical spawning stock biomasses of cod** […] from 1974 to 2004 [the model incorporates fishing mortality and] the recruitment of cod […] incorporates an environmental [salinity] index"	07	F, R (E)
"even when the cod catches collapsed, […] fisheries still have a main impact on the **cod biomass** in relation to natural mortality [here: predation by seals]"	08a	–
"[the multispecies stock production model including interactions between cod, herring, sprat, 'other food' and fishing] can provide estimates of **stock dynamics** and species interactions that are largely consistent with those estimated by MSVPA"	12	–
"reliable recruitment and fishing-effort (fishing mortality) indices are crucial for the successful application of the model [to estimate **stock dynamics**]"	12	F, R
"reducing fishing mortality to 40% of the 1992 level will […] mean a significant higher **spawning-stock biomass**"	13b	F
Claims on cod population dynamics, collapse		
"decreasing salinities combined with high fishing pressure explain the dramatic decline and **collapse of the cod stock** in the early 1990s"	01a	F, E
"cod fishing amplified, but did not initiate, the **collapse of the [cod] stock**, because fishing mortalities increased only after the decline in biomass had already occurred"	03	E > F
"**cod biomass** has decreased […] largely attributable to fluctuations in recruitment, since fishing mortality in cod has not varied much during the last 20 years"	13a	R, not F
Claims on Baltic ecosystem dynamics		
"a sequence of events has caused the observed **ecosystem regime shift** in the Central Baltic Sea, starting with a climate-induced salinity and temperature change and amplified by cod overfishing, cascading down to the zooplankton trophic level"	03	E > F
"our 'key species and driver analysis' displayed the primary importance of changes in the abiotic environment for triggering the **Baltic regime shift**. We showed deepwater salinity and oxygen conditions […] and the Baltic Sea Index (indicating thermal conditions) to be the primary agents of the change"	05	E
"the finally selected models explaining a large proportion of the **variance in the ecosystem state index** included salinity, temperature, nutrient conditions and cod fishing mortality, all being significant predictors"	05	F, E
"in addition to the physical and chemical conditions, unsustainable fishing pressure might have contributed to the **ecosystem changes**"	05	F, E
"[the interplay of fishery and environmental factors] may cause **regime shifts/reorganizations**"	08a	F, E
"fishing and environmental drivers, seem to **shape the Baltic Proper food web** as they both affect the food web dynamics, i.	08a	F, E

Table 3 (*continued*)

Causal claim	Model	F or E?
e. both explain a similar percentage (between 20% and 30%) of the variability in the food web dynamics"		
"limitations to fisher adaptability […] meant that ecosystem nonlinearities, strengthened by environmental changes, eventually led to a **regime shift**"[a]	09	F, E
Claims on cod recruitment dynamics		
"the best model explained >80% of the variance [in **cod recruitment**] and included, in addition to the spawning stock biomass […] RV and *P. acuspes* biomass"	03	–
"natural mortality and egg predation were ranked as the most important variables [for **Baltic cod recruitment dynamics**] with larval abundance and spawning stock biomass values also reaching above 10% on average across all ensemble members"[b]	10	–
"natural mortality and RV in May were […] the most influential variables for [**Baltic cod recruitment dynamics** followed by RV in August and spawning stock biomass]"[b]	10	–
"fishing mortality showed no consistent direction of influence on the model output [**cod recruitment**] and displayed the weakest average connection with the output"	10	–
"the **survival of cod eggs and larvae** until the 0-group stage […] appears to be negatively correlated to the spawning-stock biomass of sprat. Caution is, however, needed when interpreting the correlation because [it] might not be causal"	13b	–
"**recruitment of Eastern Baltic cod** was significantly related to spawning stock biomass, the winter North Atlantic Oscillation index, and the RV in the Gotland Basin in May […] none of the zooplankton explanatory variables stayed in the final models"	15	–
Claims on cod condition dynamics		
"the drastic variations in **cod condition** during the past 40 years are associated with a combination of an increased extent of hypoxic areas, density-dependence and pelagic fish prey (sprat) availability"	02	–
"[in] the final model of **cod condition** for the period 1976–1993 […] cod abundance was the only predictor of cod condition (negative effect)"	02	–
"[in] the final model for the period 1994–2014 […] sprat biomass (positive effect) and hypoxic areas (negative effect) were the predictors of **cod condition**"	02	–
Claims on cod diet dynamics		
"**diets of** smaller (juvenile) **cod** consisted mainly of benthos, while larger cod fed mostly on fishes (herring and sprat)"	11a	–
"changes in prey abundances alone are insufficient to explain the complex **temporal patterns observed in the cod stomachs**"	11a	–

[a] – Claim pertains to the coupled social-ecological model version.
[b] – Two different model versions were considered as showing comparable performance.

3.5. Data use

Almost all reviewed modeling studies referred to time series data of some of the variables representing biotic or abiotic entities or fishing (cf. Figs. 1, 2). There was also considerable overlap in the actual datasets used among the studies (cf. Gårdmark et al., 2013). These observational data were used directly to define the temporal dynamics of exogenous entities, or indirectly to fit modeled time series to the data. Common biotic time series data were the abundance or biomass of cod, sprat, herring and other species populations. Sometimes these time series were stratified by age. Particularly for cod, additional attributes (e.g. length, weight, age), life history events (e.g. mortalities, recruitment) or diet compositions (stomach contents) were used too. Typical fishing data were time series of fishing mortality or catch amounts, sometimes including age stratification (e.g. MSVPA, Sparholt, 1991, 1994). In some studies, the (fish and/or fishing) time series data used as model input were output data produced with the MSVPA model (e.g. Horbowy, 2005; Möllmann et al., 2008; Heikinheimo, 2011). Such MSVPA output data were obtained from reports of different Baltic Sea working groups of the

ICES. Abiotic time series data used in the models either covered single environmental factors (e.g. salinity, oxygen, water temperature) or specific measures obtained from these factors (e.g. cod RV (combining oxygen and salinity, cf. *3.3 System Conceptualizations*), Baltic Sea Index, Winter North Atlantic Index).

We also found cases where abiotic or biotic data used represent only specific times (e.g. cod RV in August, FishANN, Krekoukiotis et al., 2016) or specific locations (e.g. multiple locations in ICES subdivisions (25–32) which were then combined to represent the whole Baltic Sea as a single area, Kulatska et al., 2019) or specific times and locations in the study area (e.g. cod RV in May in the Gotland Basin, stock recruitment model, Margonski et al., 2010; summer temperature at 0–10m depth in the Bornholm Basin, spring abundance of zooplankton species in the Gotland Basin, BALMAR, Lindegren et al., 2009). Such specific constraints and decisions on data were presumably based on prior knowledge, which was sometimes directly stated. For instance, in EwE – BaltProWeb (Tomczak et al., 2012), sea surface temperature at 0–10 m depth in August was used because it had been found to be clearly and significantly related with sprat recruitment in published studies. In several models, abiotic time series data were used with a specific delay (lagged time series) as input data. This was done, for example, to take into account that once recruitment began under certain abiotic conditions, the cod had to reach a certain age, which was considered to be decisive (e.g. BALMAR, Lindegren et al., 2009; FishANN, Krekoukiotis et al., 2016).

Beyond time series, examples of additional quantitative or qualitative data used were information on species characteristics, such as on their diet (e.g. food selection, consumption rates, Baltic cod GAM, Möllmann et al., 2008), development (e.g. maturation time, empirical Baltic Sea model, Lade et al., 2015; diet shifts throughout the life-history, Baltic-Sea cod-sprat model, van Leeuwen et al., 2013) or mortality (e.g. natural and fishing mortality, CHS model, Heikinheimo, 2011). These data were typically taken from previously published studies. For the empirical Baltic Sea model, Lade et al. (2015) also used data on the social subsystem, such as on fishing fleet composition, cod supply from outside the study region or subsidy policy. These data were obtained from literature or from expert knowledge (fisher interviews).

3.6. Causal claims

The models were used to derive and support a huge variety of explicit claims on the causes of Baltic cod dynamics. This variety is partly due to the heterogeneity among the studies' different specific research questions (cf. Table 1). We therefore identified and grouped the causal claims according to the same three categories of causal inquiry as the research questions: C – Causes of cod dynamics (Table 3), M – Mechanisms driving cod dynamics (Table 4), and P – Predictions of cod dynamics (Table 5). In addition to claims that directly addressed the main research questions (cf. Table 1), we found many more causal claims that fit into the same categories and added several examples to the overviews (Tables 3–5). These claims did not always relate to the main focus of the respective studies, but they were based on the models presented and illustrate the overall diversity of the types of causal claims. By and large, the strategies for deriving causal claims were very diverse and hard to categorize (Table 2).

Inspecting the causal claims reveals that summarizing them and formulating claims that are supported by several modeling studies is only possible at a very broad level, like *"Unfavorable conditions and fishing pressure caused the Baltic cod collapse."* However, whether really both these factors caused the collapse and if so, which was more important, is already much more ambiguous. Some of the claims even seem conflicting, making the formulation of generalizations challenging. Examining the claims more specifically shows that they are often highly context-dependent. This was partly acknowledged together with the claims directly. More important, a lot of context dependence stemmed from the respective choices of model type, system

conceptualization and further assumptions (cf. above), and how the model was analyzed. We illustrate this high degree of context dependence by three example topics (one from each category of causal inquiry C, M and P, cf. above), on which we found various causal claims in the modeling studies.

3.6.1. C – Causes: fishing and/or environmental conditions as causes of cod population dynamics

Several of the causal claims of category C identified either fishing pressure (F) or environmental conditions (E) or both as main causes of cod population dynamics. In particular, too high fishing pressure and/or periods of unfavorable environmental conditions (and sometimes specifically their interplay) were claimed as causes of the cod collapse and remaining low abundance (Table 3). Of the claims that include both causes F and E, some explicitly ranked one cause as more important (F > E or E > F, Table 3). One broadly shared causal finding among the studies is that when E were claimed as a main cause of cod population dynamics, the specific environmental conditions considered in the model did include water salinity (either salinity directly or via the cod RV, which combines salinity and oxygen, cf. above). By contrast, several other claims did not explicitly mention E. However, some of those referred to recruitment (R) as another important cause of cod dynamics. Of course, this R can depend on E and thus mediate effects of E. This was explicitly mentioned in one causal claim (cf. Table 3). But also when these potential causal relationships from E to R were not mentioned, perhaps also not considered in the model, they may still have been present in the recruitment data and affected the cod dynamics. Thus, the modelers' selected focus – for formulating a claim as well as for designing a model – strongly shaped the causal findings. Apparent differences get less conflicting upon closer examination, and the causal claims should be considered in parallel rather than in opposition to each other. However, this makes it a big challenge to adequately summarize them into specific statements, except at a very general level.

3.6.2. M – Mechanisms: the cultivation/depensation hypothesis

This example topic concerns mechanistic explanations for why in many marine ecosystems (such as the Baltic Sea) either large predatory fish species (such as cod) or their prey species (such as sprat) tend to be highly abundant, but not both species together. The hypothesis is that there are two stable states (e.g. cod dominance or sprat dominance) and each state reinforces itself, either by cultivation or depensation (Walters and Kitchell, 2001).

The cultivation mechanism is supposed to operate when cod is abundant. Many adult cods that feed on sprats keep sprat abundance low. Thus, the cod adults reinforce favorable survival conditions for cod juveniles, because sprats have a negative effect on cod juveniles' survival: Sprats compete with cod larvae for zooplankton (mainly *Pseudocalanus acuspes*) and sprats feed on cod eggs (Walters and Kitchell, 2001; Möllmann et al., 2009).

By contrast, the depensation mechanism is supposed to operate when cod abundance is low. Then, sprats experience much less predation pressure and can achieve high abundance. It follows that their negative effects on cod juveniles' survival increase and, thus, reinforce unfavorable cod recruitment conditions. The latter means low reproductive success due to reduced fitness at low density for cod, also known as Allee effect (Allee et al., 1949; Stephens et al., 1999; Roos and Persson, 2002).

As a result from the mechanisms of cultivation and depensation, cod and sprat could not simultaneously be highly abundant and a shift from high to low cod abundance (irrespective of what has caused it) would mean that a new and self-reinforcing state of sprat dominance could establish and prevent the shift back to cod dominance. Therefore, these mechanisms have been suggested as causal explanations of the 1980s Baltic cod collapse and poor recovery (e.g. Möllmann et al., 2008; Casini et al., 2009).

While the suggested mechanisms are intuitive and appealing, there are several complications for confirming (or rejecting) that they underlie

Table 4

Major causal claims derived with the models (literal quotes with clarifying additions in square brackets). Claims belong to the category of causal inquiry M – Mechanisms driving cod dynamics, and are grouped according to which measure of cod population (or ecosystem) dynamics is explained (highlighted in bold, cf. table section titles). Entries in the third column denote if and how the claim relates to the cultivation/depensation hypothesis (CDH), mostly to the depensation mechanism (DM) in particular.

Causal claim	Model	CDH
Claims on cod population dynamics, general		
"characteristics of the [fitted] model are: density dependence in the **growth of the cod population**"	04	–
"fishing can either reduce or increase **temporal oscillations of the cod stock** depending on whether the dynamics is over- or undercompensatory"	04	–
"for small catches and high RV […] the oscillation effect is dominating over the increase in the median, which decreases the **probability that [the cod index in the year 2030 is high]**"	04	–
"when reproductive success declined and the **[cod] stock size decreased**, fishing effort has not been reduced. Hence, fishing mortality on cod was especially in the transition period too high for the level of reproductive success"	05	–
"simulations with rather similar model fits (max. 29% deviation from the original), but differences in trophic control, can lead to very different **biomass projections**"	08b	–
"the success of regulation [high **cod stocks** and high catches] would still have been strongly dependent on the type of regulatory goal and limited by the speed of fisher decision making and by the underlying ecological instabilities"[a]	09	–
"the magnitude of cannibalism suggest[s] a rather strong self-regulatory mechanism of the **cod stock**"	13b	–
Claims on cod population dynamics, collapse		
"conventional discounting may have fueled overfishing and caused the **collapse of Baltic cod**"	01a	–
"increase in environmental autocorrelation amplifies the probability of **collapse** owing to an elevated risk of prolonged periods of poor salinity conditions for spawning and recruitment **of Baltic cod**"	01b	–
"changes were initiated by the decreasing salinity (path 1), causing the **decline of** *P. acuspes* and **cod**. Increased temperature (path 2) resulted in the increase in *Acartia* spp. and sprat. In addition, high fishing pressure on cod contributed to its decline and cascaded down to *P. acuspes*. Both pathways have established the current regime of *Acartia* spp. and **sprat dominance**"	03	–
"different fluxes dominated the clupeids community: in the cod dominating regime the natural (predatory) flows prevail over the anthropogenic (fisheries) fluxes, while in the second regime an increasing **competition for resources between the human and natural predators** is present"	08a	–
Claims on Baltic ecosystem dynamics, stability		
"we demonstrate another [stabilizing] **prey-to-predator loop** in the ecosystem: the low cod stock caused the sprat stock to increase, now limiting the main food for cod larvae, i.e. *P. acuspes*"	03	DM, in line
"regardless of the degree of competition and feedback on the intermediate resource, the persistence boundaries always exactly coincide with the invasion boundaries. This means that irrespective of the level of competition experienced in the first life stage of the predator, there is no bistability between **stable community states with and without the predator**"	06	CDH, not in line
"we quantified both possible **predator-to-prey loops** in the food web model showing that the amount of energy transfer through these links, i.e., *P. acuspes* to cod larvae and cod larvae to sprat, are 10–100 times lower compared to the remaining flows"	08a	DM, not import.
"during the boom, the **dominant destabilizing feedback** loop in the decoupled ecological system may actually have been the risk of depensatory collapse in the cod	09	DM, in line

Table 4 (*continued*)

Causal claim	Model	CDH
stock, in which a population becomes unable to sustain itself"[b]		
"a prey-to-predator loop, in which sprat when present in large numbers can outcompete larval cod for its zooplankton prey, is likely to have been the **dominant destabilizing feedback** in the coupled social–ecological system, both during the boom and at the onset of the collapse. This feedback loop strengthened significantly between the boom and the onset of the collapse"[a]	09	DM, in line
"the **ecological system** under assumption of constant fishing effort, thus decoupled from social processes, may in fact have been **unstable** during the cod boom"[b]	09	–
"social feedbacks involving adaptive fisher decision making may have **stabilized an otherwise unstable ecosystem** during the boom, ensuring that the cod boom persisted at least temporarily"[a]	09	–
"the largest individual contribution [to **uncertainty in the model stability** estimates] was the degree of nonlinearity (elasticity) of cod catch with respect to cod biomass"[a]	09	–
Claims on cod recruitment dynamics		
"[**cod recruitment** is explained by] in addition to the spawning stock biomass, variables influencing egg and larval survival, respectively, i.e. RV and *P. acuspes* biomass"	03	–
"when feedback from predators foraging on the intermediate resource is present, **recruitment to the adult predator stage** is limited by a developmental bottleneck in the intermediate predator life stage. This bottleneck is induced by intraspecific competition among predators for the intermediate resource, in contrast to the juvenile bottleneck in predator development that may be imposed by competition with prey for the shared resource"	06	DM, not in line
"the average deepwater salinity […] index also acts as a proxy for other potential variables that change in synchrony with salinity and is assumed to reflect the state of the ecosystem, affecting the **recruitment success of cod** via both the survival of eggs and the availability of food resources for the early phases"	07	–
"an increase in the cod stock will mean an increase in cod cannibalism and thus fewer **cod will reach the commercial size**. However, in order to minimize cannibalism, the stock of large cod has to be exploited to a low stock level and the spawning-stock biomass will then be very small and probably not able to produce year classes of average size"	13b	–
"[the stock-recruitment] relationship for cod is not mainly causal but due to autocorrelation in recruitment between years. This can be deduced from [the fact] that the **recruitment** decreased before the spawning-stock biomass decreased. Thus, a more probable hypothesis is that recruitment is more related to some unknown environmental factors"	13b	–
"our results do not […] support the idea that predation [on cod eggs] from sprat influences **cod recruitment** significantly"	15	DM, not import.
"food availability for young fish could constitute such a limitation [of **cod recruitment**], but we found no indication of that in our analyses"	15	DM, not import.
"cannibalism was less important [for **cod recruitment**] than the other factors included in the analysis"	15	–
Claims on cod diet dynamics		
"changes in the proportions of flows [supporting the cod biomass] originating from different sources indicate a switch in the **diet composition** of predators due to resource availability, e.g. macrozoobenthos and sprat"	08a	–
"the **amount of herring and sprat eaten by cod** shows large variation between 1.63 (1982) and 0.33 million tonnes (1987). These fluctuations are much larger than the variations in cod biomass due to changes in the age structure of the cod stock, because during the years with high cod biomass the stock was dominated by juveniles, which are characterized by higher consumption rates relative to their weight than older cod"	13a	–

[a] – Claim pertains to the coupled social-ecological model version.
[b] – Claim pertains to the decoupled ecological model version.

Table 5

Major causal claims derived with the models (literal quotes with clarifying additions in square brackets). Claims belong to the category of causal inquiry P – Predictions of cod dynamics, and are grouped according to which measure of cod population (or ecosystem) dynamics is predicted (highlighted in bold, cf. table section titles). In the table section relating to cod recovery, the whole key statement on recovery is highlighted in bold in each row, and the entries in the third column show the main cause denoted in these claims (F – fishing, E – environmental conditions).

Causal claim	Model	Recovery
Claims on cod population dynamics, general		
"a strategy for adapting fishing mortalities to climate-driven stock production is necessary to ensure the **persistence of Baltic cod**"	01b	–
"whether fishing causes under- or overcompensatory **[cod] dynamics** depends on the size of catches and RV"	04	–
"the median value of the predicted **[cod population] index** is increasing with higher RV and lower catch"	04	–
"future **biomass estimates of cod** increased as a response to the decreased fishing pressure"	08b	–
"the total range of **biomass estimates** was rather large across all [...] scenarios being particularly high when future climate change was accounted for"	08b	–
"strong regulation might have been able to maintain both high **cod stocks and** high **catches** provided [...] that regulations could be rapidly updated to reflect the state of the fishery and [...] fisher compliance was sufficiently strong"[a]	09	–
"with low [or unknown] recruitment, the recommendation of fishing mortality being 40% of the 1992 level would be necessary to keep the **spawning stock biomass** high and safeguard the **recruitment**"	13b	–
Claims on cod population dynamics, stability		
"the sustainable level of fishing rate is [...] dependent on RV. Our model predicts a dual role of fishing rate, **stabilizing [the cod stock]** when RV is high and destabilizing when it is low"	04	–
"a hypothetical **Baltic cod fishery** without subsidies or with fixed regulations, such as catch quotas or fishing effort regulations, but with similar average effort levels as during the boom, was according to our model unlikely to have had a substantially different **stability**"[a]	09	–
"if regulations adapt to changes in fish stock [...] the **stability of a fishery** can be expected to substantially improve"[a]	09	–
Claims on cod population dynamics, collapse		
"precautionary management strategy, by adapting fishing pressure to environmental conditions and food web interactions, could significantly have prevented the **cod stock** from **collapsing**"	01a	–
"only the adaptive management approach may prevent future **stock collapses** and maintain the stock stably above ecologically sustainable levels"	01a	–
Claims on cod population dynamics, extinction		
"even if the mean climate does not change, current fishing mortality must be kept low in order to reduce the **risk of extinction**"	01b	–
"if fishing is reduced according to previously recommended precautionary reference levels then **extinction** may be postponed"	01b	–
"the **cod stock** may not remain above ecologically safe levels during the coming 100 years"	01b	–
"the average fishing mortality in the last 2 decades (0.9) is indeed very likely to push the **population** below [the quasi-**extinction** threshold] within 10 years"	14	–
Claims on cod population dynamics, recovery		
"a combination of long-term change in sea surface temperature and salinity with mean fishing mortality levels results in a forecast of **initial [cod] stock recovery** followed by a gradual decrease and probable extinction"	01b	F, E
"fishing pressure on cod is still high, **preventing recovery of the stock**"	03	F
"in contrast to explanations involving alternative stable community states, this study therefore points at changes in	06	E

Table 5 (*continued*)

Causal claim	Model	Recovery
relative habitat profitability of the benthic and pelagic resources as the major cause for **delayed [cod] stock recovery**"		
"the **cod stock would recover** if the recommended reduction of fishing mortality to 0.3 (ICES Advice, 2008) were to be realized, even if the environmental circumstances remain unchanged"	07	F
"a positive change in the environment **could lead to a recovery in the cod stock** even if the fishing effort is high. However, this scenario is uncertain"	07	E
"even in the low fishing pressure scenario, the **future cod biomasses were as high as in the 1980s** only in [one of 11 model versions]"	08b	E
"**[cod recovery was] achieved** by low overall fishing levels of cod and increased fishing on clupeids"	11b	F
"exploitation according to [...] the fishing mortality [...] at 0.6 is **very unlikely to let the [cod] stock recover**"	14	F
"our results reinforce the conclusions [...] to reduce fishing mortality considerably to **rebuild the [cod] stock**"	14	F
Claims on cod recruitment dynamics		
"unfavorable environmental conditions [...] mean that a higher spawning stock biomass is needed to maintain **[cod] recruitment** at a required level"	15	–
"managers can aim for maintaining higher SSB under unfavorable environmental conditions or, in contrary, be less restrictive if reproduction conditions are expected to be good [to achieve a desired level of **cod recruitment**]"	15	–
Claims on Baltic fishery profits		
"to maximize **profits of the cod fishery** [...] cod fishing needs to be decreased"	11b	–
"[to maximize **profits of the sprat and herring fisheries**] all stocks were fished at high levels [...] reducing the piscivore predator, cod, is necessary"	11b	–
"to maximize **total fishery profits**, [sprat and herring stock were fished at high levels and] fishing on cod [kept around the current level]"	11b	–
"the **optimal [cod] exploitation** level can be found as the point giving the maximum yield [...] there is no MSFOR maximum F [fishing mortality], i.e. the steady-state yield will increase with an increase in F even at very high F values"	13b	–
Claims on Baltic ecosystem dynamics, general		
"our results highlight the importance of regulating anthropogenic nutrient inputs, to dampen eutrophication and thus combat oxygen depletion also for **fish populations** and the future of the fisheries in the Baltic Sea."	02	–
"we consider a substantial reduction of the fishing mortality to be the only way of avoiding the far-reaching **ecological and socio-economic consequences** of continued exploitation at current levels"	14	–

[a] – Claim pertains to the coupled social-ecological model version.

cod dynamics in the Baltic Sea. Assuming that they are true, only one of the two mechanisms would operate at a time (either cultivation for cod dominance or depensation for sprat dominance). The spatial areas occupied by both species can differ and their spatial (geographical and vertical) overlap vary. The depensation mechanism with its negative effect of sprat on cod juveniles contains two pathways (predation as well as competition for food). Depensation of cod can be difficult to attribute to high sprat abundance or unfavorable environmental conditions or fishing (cf. claims on fishing and/or environmental conditions as causes of cod population dynamics above) or interactions of these potential causes, if they were simultaneously present. Also herring, the second important prey species for cod, feeds on cod eggs and zooplankton (e.g. Köster and Möllmann, 2000). Since all three species are subject to fishing, this certainly had considerable effects on their abundance apart from cultivation and depensation effects. Finally, showing that model results are in line with the cultivation/depensation hypothesis (CDH) does not necessarily show that the mechanisms operate.

The modeling studies we analyzed include diverse findings on the validity and importance of the CDH, particularly of the depensation mechanism, for the Baltic cod collapse or poor recovery. Among the mechanistic claims on cod dynamics, we found relations to the CDH in five studies, three using dynamic models and two using statistical models (Table 4). For the latter, the claims were located in the discussion section. The statistically detected findings were mechanistically interpreted as confirming that the depensation mechanism operates (Möllmann et al., 2008) or not (Margonski et al., 2010, cf. Table 4).

Using a dynamic model, van Leeuwen et al. (2013) explicitly focused on whether alternative stable states of either cod or sprat dominance in the Baltic Sea emerge when accounting for realistic diet shifts throughout cod life history. The model included an intermediate cod life stage, during which cods exclusively consume benthic organisms, and the (feedback) effect that consumption has on the benthic organisms' availability. They showed that this causes cod growth to the adult stage being limited by intraspecific resource competition in this intermediate life stage, instead of by interspecific competition with sprats in the juvenile life stage (i.e. not limited by depensation, section *Claims on cod recruitment dynamics* in Table 4). The model did not include cod egg predation by sprats. Strict criteria were applied for testing bistability under equal conditions (*"Differences between the persistence and invasion boundaries indicate a region of bistability where persistence is possible for combinations of resource productivity that do not allow for invasion."*, van Leeuwen et al., 2013). Hence, model analyses led to claims that the complex yet purely ecological dynamics (without fishing, Fig. 2) were not in full agreement with the CDH (section *Claims on Baltic ecosystem dynamics, stability* in Table 4).

In the empirical Baltic Sea model by Lade et al. (2015), an intermediate cod life stage was included too. Both the intermediate and the adult cod life stage feed on benthic organisms, but not exclusively as both feed on sprat and herring as well. Thus, the food web interactions of both life stages were fundamentally the same. In this *"generalized model, a dynamical systems model in which processes are represented only with abstract 'placeholder functions'"* (Lade et al., 2015), herring, several environmental factors, and fishers were included (in the full version with a complex social submodel, but also in the decoupled ecological version, cf. *3.3 System Conceptualizations*, Fig. 2). A specific feedback loop analysis was applied to detect main causes of cod collapse. The identified destabilizing feedback loops were found to be in line with the depensation mechanism (Table 4, claims for the decoupled ecological and for the full model version).

For EwE – BaltProWeb, after fitting the dynamic model to empirical time series, Tomczak et al. (2012) investigated how much the different interactions in the complex food web were realized in the actual simulations and over time (quantifying energy flows through pathways in the food web). The model included many species, environmental factors and fishing (Fig. 2). Pathways that would represent depensation were found to be not intensely used (from zooplankton to cod larvae, from cod larvae to sprats (cod larvae used as a proxy for cod eggs which were not modeled separately)). This led to a claim suggesting that depensation was not important for sprat dominance (Table 4). Whether the low flow of energy from zooplankton to cod larvae could be an effect of the competition with sprat for this resource was not explicitly discussed. It was mentioned that food web interactions with benthic organisms and herring could also play a significant role for shifts between different ecosystem states (Tomczak et al., 2012). However, in line with not claiming that the CDH prevents a shift back to high cod abundance, in one of several other studies applying the EwE model to the Baltic Sea, Österblom et al. (2007) found no indication that sprat and herring predation of cod eggs and larvae, and competition for zooplankton, are the mechanisms behind poor cod recovery.

Noteworthy, the model analyses and claims by Lade et al. (2015) and Tomczak et al. (2012) refer to empirical sets of population dynamics, environmental conditions and fishing for periods including the Baltic cod collapse. The claims relate to the depensation mechanism. With

these empirical approaches, it was not tested whether alternative (counterfactual) system states (e.g. cod instead of sprat dominance) for selected time points and under exactly the same conditions would have been possible. Such strict testing of bistability was done with the more theoretical and purely ecological model by van Leeuwen et al. (2013). Hence, the considerable differences with regard to system conceptualizations (Fig. 2), model assumptions and analyses can (partly) explain the apparently controversial claims regarding the CDH that were derived with the three dynamic models (Table 4). Similar explanations likely apply to statements in additional modeling studies that relate to the CDH, but not directly to causes of cod dynamics, and were therefore not included in Table 4 (e.g. *"The simulation results indicate that predation by cod is able to control the abundance of sprat and depress the stock to a low level"*, in line with the cultivation mechanism, Heikinheimo, 2011).

3.6.3. P – Predictions: cod recovery

The predictive claims on cod recovery were all derived from dynamic models, except for the Baltic cod GAM by Möllmann et al. (2008). In this study, the causal claim was formulated in the discussion of statistical model results. The claims show considerable variation and some appear controversial (section *Claims on cod population dynamics, recovery* in Table 5). This can partly be explained by different time frames and criteria for recovery. Moreover, the simulated scenarios varied, induced by the different research questions addressed (Table 1). Thus, in each of the studies, environmental conditions, fishing or both were varied and explicitly denoted in the claims as causes behind the predictions (Table 5). And the claims were influenced by the underlying system conceptualizations, assumptions and methods for analysis as well. For these reasons, the predictions derived are especially context-dependent and should be regarded together with all these influences.

4. Discussion

4.1. An analysis of causal explanations derived with ecological models

Models are an established means for studying causation in complex ecological systems. Yet it is well-known, not only in ecology, that for any system usually a multitude of models exist, often leading to diverging explanations about the causes of certain phenomena or dynamics (Spence et al., 2018; Shea et al., 2020). While many useful reviews of ecological models for certain systems and questions exist, they mostly focus on differences in model structure and model output, but not specifically on the corresponding causal claims, how those claims were derived and justified, and how they were constrained by model design and assumptions. We thus reviewed models from the perspective of the causal claims made. As a case, we used models addressing the dynamics of the Baltic cod, with a focus on the collapse around the late 1980s or the general potential for cod collapse or recovery.

4.2. Model-based causal claims are highly context-dependent

A variety of models have been applied to find causal explanations for Baltic cod dynamics over recent decades, including its 1980s collapse. Comparing these models, we found broad agreement on very general causal explanations, such as that intense fishing and unfavorable environmental conditions have been causes of the collapse and poor recovery since. However, regarding more nuanced claims, for example on the relative importance or interactions of different causes, less agreement can be found (Tables 3–5). Most importantly, our review shows that ecological models for the same system were developed and analyzed in quite different ways, which may reflect different research questions (Table 1), data availability, but also, for example, differences in knowledge and opinion of experts (Krueger et al., 2012). Consequently, the causal claims derived are highly context-dependent. Thus, the scope of these claims can be more specific than it seems, and certain claims that may appear conflicting should rather be regarded as

complementary. While most researchers are in principle aware of such context dependence, its critical impact on causal insights derived from specific models can easily be underestimated.

It is important to note that two different kinds of context can be distinguished. First, there are the explicit circumstances under which a certain causal claim holds. Once a model is created and specified, the interdependencies and the complexity of the virtual system as it is represented by the model often necessitate formulating context-dependent causation. These are claims of the kind 'for favorable environmental conditions, the cod stock would recover irrespective of fishing pressure, but for unfavorable conditions, only low fishing pressure would allow recovery'. The causal relationship from fishing pressure to cod recovery depends on the environmental context. Similarly, when comparing studies, different contexts applied in the different models (e. g. different environmental conditions or fishing scenarios) need to be considered and can clarify why causal claims diverge. Such dependence on the context that is explicitly represented in the models is often in the focus of causal explanations, which is natural, as it corresponds to how we also think about and try to find causal explanations for complex phenomena in the real world.

4.3. Another kind of context: the system conceptualization and further model assumptions

Second, the model-based causal findings depend on a lot of additional context, which is usually less explicit but at least as important. It can be summarized as 'what goes in a model, and how it is analyzed, predefine what can come out'. This second kind of context includes the chosen focal elements of a modeling study, for example the dynamics or phenomenon that shall be the model output (Fig. 3), the candidate causes for this output, or the processes and relationships that shall be varied to investigate their impact on the output. It goes on with all further elements included in the system conceptualization and the relationships between them, which we found differ considerably among models addressing similar questions (Figs. 1, 2). Moreover, the context comprises implicit assumptions, for example, global interactions implying that populations can always meet and interact in the same way, or the omission of certain aspects in the system conceptualization implying that these are not considered relevant for causation of the studied phenomenon (or perhaps simply not known).

A key advantage of modeling is that the second kind of context, determined by the system conceptualization and additional assumptions, need not be fixed, but can also be systematically varied to understand its role for causation. The sensitivity and robustness of causal findings in response to this context can be thoroughly tested (Saltelli, 2004; Thiele et al., 2014; Grimm and Berger, 2016; Peck et al., 2018; Drechsler et al., 2022). This means analyzing different model versions that exclude or include certain entities, follow different assumptions on causal relationships between them, or different definitions and parameterizations of processes representing these relationships. Such analyses can add to the insights gained from showing that a certain version of a dynamic model satisfactorily reproduces the data and inspecting the mechanisms at work in this specific model. Particularly very complex models, aimed to reflect the complexity of the real ecosystem, tend to have many degrees of freedom for adjusting them to data. This bears the risk that different model versions can reproduce a phenomenon similarly well, but the underlying causal relationships and mechanisms that lead to the phenomenon in the model differ strongly (equifinality). This was shown in a comparison of many versions of the same model EwE – BaltProWeb with similar goodness of fit to the data by Niiranen et al. (2012, cf. Table 4). It might apply also to other studies, such that alternative, equifinal model versions would exist that perform similarly well, but differ in terms of the explanations and predictions they provide. Hence, model equifinality may have contributed to the heterogeneity of causal claims that we observed (Tables 3–5).

4.4. Key ecosystem features when studying causation with models: species interactions and spatial heterogeneity

One example belonging to the second kind of context that can considerably affect model results and, thus, causal findings is how species interactions were represented. Although the marine food web in the Baltic Sea comprises comparably few species (e.g. Bagge and Thurow, 1994; Österblom et al., 2007), a variety of (potential) interactions are known. This required modelers' choices about which species and which relationships among them to include in the system conceptualizations, and these choices varied widely (cf. *3.3 System Conceptualizations*). For instance, separating species into subpopulations (age, size, or life stage groups) with different inter- and intraspecific interactions can be decisive for emergent cod dynamics (e.g. van Leeuwen et al., 2013). In addition, even when modeling the same biotic entities and the same interactions between them, the actual types and parametrization of functional relationships can still vary and strongly affect the overall simulation dynamics (Gårdmark et al., 2013; Möllmann et al., 2014; Muelder and Filatova, 2018).

Another aspect was treated similarly in all models, but is an important part of the second kind of context the causal claims depend on: spatial heterogeneity was rarely explicitly represented (cf. *3.3 System Conceptualizations*). Populations of fish and other species in the Baltic Sea are not homogeneously distributed and are highly mobile, and environmental factors and also fishing vary in space (and time). Obviously, this heterogeneity has high potential for affecting the causal relationships between these entities, and the resulting overall model output (e.g. Fulton et al., 2004; Travers et al., 2007). For example, varying spatial overlap between species (both horizontal and/or vertical, e.g. Köster et al., 2005) should lead to variation in the strengths of their interactions. Moreover, spatial variation in environmental factors means spatial variation in their impact on species and this, in turn, may change their overall impact. Things get more complex as such causal relationships modified by spatial heterogeneity are often interdependent. One example are areas with low oxygen concentration, which do not only hamper cod egg development, but also reduce the productivity of benthic species and thus the food availability for cod. However, benthic organisms can also tolerate low oxygen concentrations better than cod and therefore partly escape the cod predators in these areas. This reduction in spatial overlap additionally reduces the availability of benthic organisms as a resource for cod and modifies their interaction (Casini et al., 2016).

While in principle spatially explicit models could better account for the additional complexities that emerge from spatial heterogeneity (Filatova et al., 2013), there are also reasons for the non-spatial approach favored by most of the modeling studies. Spatially explicit models of Baltic cod dynamics are certainly much more complicated to develop and analyze. Studies that explored taking spatial heterogeneity explicitly into account used ICES subdivisions or the main cod spawning areas as spatial units (Margonski et al., 2010; Casini et al., 2016). These rather large areas might not be an adequate resolution for capturing the spatial variation in 'local' interactions between environmental factors, fish stocks and fishers. Further difficult questions would remain, such as how movement of entities should be correctly represented in spatially explicit models. Here, scarcity of data for assessing fish movement has been identified as a major hindrance of spatially explicit models (Plagányi et al., 2014). Nonetheless, addressing the complexity of spatial heterogeneity in the Baltic Sea at smaller scales is possible with models and may become more frequent. Recent examples include a spatially explicit version of the EwE model with a grid cell side length of 0.25° (Bauer et al., 2018) and an individual-based Baltic cod model with (time-varying) vertical layers of the represented water volume (Pierce et al., 2017).

4.5. From ecological to social-ecological models

Modeling cultures within a discipline, such as ecology, can tend to simplify or ignore important components of studied phenomena because these components include entities and processes belonging to other scientific domains. Ecological dynamics in the Baltic Sea are not isolated, but connected to human action, especially through fishing. Fishers were considered as an exogenous driver in most of the models (cf. *3.3 System Conceptualizations*). However, fishery comprises social and economic processes, individual, collective and political decisions, which are causally related to each other and to ecological factors in various ways (e.g. Österblom et al., 2007; Nielsen et al., 2018). For taking these manifold interactions into account, just linking two independent models, one social and one ecological, would be insufficient. Rather, they should be represented in one combined social-ecological system including the various strongly intertwined feedbacks between social and ecological processes (Folke et al., 2016; Preiser et al., 2021).

This shift from ecological to social-ecological models will often add complexity and make developing models and understanding the causes of modeled phenomena particularly challenging (Filatova et al., 2016; Will et al., 2021). For instance, selecting the entities and relationships to include in the system conceptualization, or obtaining and incorporating adequate data, is more difficult than for each subsystem separately. Lacking empirical information has been identified as a reason for not including social or economic processes in fisheries ecosystem models (Plagányi et al., 2014). Yet, models are an indispensable tool for determining causal relationships also in complex, intertwined social-ecological systems (Schulze et al., 2017; Schlüter et al., 2019). The coupled social-ecological version of the empirical Baltic Sea model (Lade et al., 2015) is one example. Several others have been developed for marine social-ecological systems, some of them also for the Baltic Sea (Plagányi, 2007; Nielsen et al., 2018). In general, we think that our observations for ecological models apply to social-ecological models too. Given the complexity and more ambiguous boundaries of the actual systems to be represented, a high diversity of models for similar phenomena can be expected, as well as a high dependence of causal findings on constraints that follow from various explicit and implicit assumptions in these models.

4.6. Future directions for using models to understand causes of ecosystem dynamics

Aside from social-ecological modeling, we see also other ways for making future models more useful for understanding causal relationships and supporting successful policy and management towards sustainability. Incorporating essential ecological system features, such as spatial heterogeneity or multiple and changing species interactions, and investigating their effects on the dynamics of interest is possible. In addition, comprehensive communication of models and their context is required (Grimm et al., 2014, 2020b). This should make models more user-friendly and the causal claims understandable to persons who have not developed them, especially the stakeholders who have to make decisions (Grimm et al., 2020a; Nielsen et al., 2018; Will et al., 2021).

A recommendable option to decrease the uncertainty in causal explanations is to apply ensembles of different models to the same system and questions (e.g. Jones and Cheung, 2015; Anderson et al., 2017; Carlson et al., 2018). However, this needs to be taken with care, since different models have rarely been developed to address exactly the same question (Table 1). Given the models' substantial differences at various levels, modifying them to serve as consistent members of an ensemble will often be very laborious, perhaps almost impossible without involving experts for each model included (Gårdmark et al., 2013; Bauer et al., 2019). A suggested solution is to use a statistical framework to combine information from ecological models that differ in system conceptualization, further assumptions and the kind of model output they provide (Spence et al., 2018). Still, different models contributing to outcomes of ensemble analyses may show substantial variation in their results, or may yield similar results but via different underlying mechanisms due to model equifinality. Both can be problematic for deriving precise but generally valid causal claims. Therefore, another recent recommendation is to complement the use of multiple models with a formal and structured discussion among the modelers (Shea et al., 2020). This shall elicit the models' similarities and differences, allow assessment why models disagree, and thus enhance the causal insights on the dynamics addressed.

Another strategy, dubbed 'pattern-oriented modeling' (Grimm, 2005; Grimm and Railsback, 2012), could be used for scrutinizing causal explanations and also predictions derived from models. The strategy is to confront model results with observed patterns, ideally characterizing the system at different scales and organizational levels. While it can be relatively easy to make a model reproduce a single observed pattern, for example cyclic population dynamics or certain ranges of abundance, reproducing multiple patterns simultaneously is more challenging. Each pattern serves as a filter to reject unrealistic parameter values or functional relationships. Regarding ensembles, the different models could be ranked by their ability to reproduce multiple patterns or even predict new patterns not used for model development and calibration. For example, Heine et al. (2005) used this approach to evaluate and rank the realism of different economic models representing the same phenomenon. So far it has to our knowledge not been tried to systematically relate the factors and processes represented in models to their potential of reproducing patterns, but this might be a promising quantitative complement to the structured discourse on multiple models (Shea et al., 2020, cf. above). The outcome could be an integrated model that incorporates all relevant factors, also those that become relevant only under certain circumstances, or an evaluation under which conditions each of the models evaluated is considered relevant enough for its purpose, if at all.

5. Conclusion

Models are indeed an indispensable tool for exploring causal relationships in complex systems. However, the causal findings coming out of modeling studies are to a considerable degree determined, or at least constrained, by what has been put in the models and how they were analyzed. This means that, in addition to the explicit scope of causal claims, various other aspects belong to the context of model-based causal explanations. This context is not always entirely clear, but it is a strong source for heterogeneity in causal claims derived, especially with regard to diverse specific statements on similar subjects made in different modeling studies. The multi-faceted context dependence needs to be considered when generalizing findings on the causes and potential manipulations of ecosystem dynamics, as a basis for policy and management decisions that enhance sustainability.

Software availability

Not applicable.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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