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Contribution to the Theme Section 'Advancing dynamic modelling of marine populations and ecosystems'

Sensitivity of the fish community to different prey fields and importance of spatial–seasonal patterns

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ABSTRACT: Different fish species and life stages depend not only on food abundance, but also on the size of planktonic prey, and (mis-)matches in time and space with suitable prey may influence the growth and survival of fish during their lifetime. We explored the sensitivity of a fish community to spatial–temporal differences in plankton prey fields. Data from 5 different lower trophic level models in the North Sea (Delft3D-WAQ, ECOHAM, ECOSMO, HBM-ERGOM and NORWECOM) were used to force the food web model OSMOSE which simulates spatially and temporally explicit higher trophic level fish dynamics. The estimated fish biomass levels were clearly and positively linked to zooplankton biomass, and sensitivity studies varying zooplankton biomass revealed that spatial and temporal variation in zooplankton drives the differences in absolute fish biomass. More zooplankton size bins resulted in less fish biomass due to size-based foraging constraints (i.e. a smaller proportion of bins falls within the prey size range of a fish, resulting in a decrease in available food). Nevertheless, we found a consistent response across models in the relative biomass contribution and spatial patterns of selected fish groups, indicating low sensitivity of the composition of the simulated fish community to the zooplankton input. The robustness of the outcome will aid model acceptance and implementation into management action. Relative, not absolute, changes in primary and secondary production may therefore be used to study the effects of management scenarios on fish communities.

KEY WORDS: Trophic transfer · Lower trophic levels · Higher trophic levels · Modelling · North Sea · Food web

1. INTRODUCTION

As the food web or ecosystem approach becomes more widely used in fisheries management (Österblom et al. 2010, Möllmann et al. 2014), it is important to assess the various impacts of lower trophic levels (LTLs) on higher trophic level (HTL) model results and the uncertainties associated with it. HTL models are designed to describe and predict the effects of fishing, climate and other anthropogenic pressures on natural resources to provide decision support to nature management (Peck et al. 2018). The HTL models may include planktivorous fish, piscivorous fish and/or benthivorous fish, of which many undergo

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ontogenetic diet shifts depending on the choice of age-, stage- or size-structure in the models (Shin et al. 2010). Since different fish species and life stages rely on specific sections of the planktonic prey size-spectrum (Munk 1992), (mis-)matches in time and space with suitable prey may influence the growth and survival of fish during their lifetime (Frederiksen et al. 2007, Huebert et al. 2018). In addition, climate change and other natural and anthropogenic stressors have been shown to induce changes in the spatial–temporal dynamics of plankton (Li et al. 2009, Mackas et al. 2012, Maar et al. 2013, Holt et al. 2016). This further emphasizes the need to understand the uncertainties associated with the choice of the prey field on HTL models, especially as these types of models are likely to be used in scenario studies on climate change (Olsen et al. 2018).

Some of the most advanced spatially and temporally explicit HTL models consider several fish species and predation interactions (e.g. OSMOSE, Travers et al. 2009; NORWECOM.E2E, Hjøllo et al. 2012), but also require plankton input as a potential food source for these fish (Travers et al. 2007, Hjøllo et al. 2012, Utne et al. 2012, Daewel et al. 2014). This plankton input is mostly obtained from LTL models, often called 'Nutrient–Plankton–Zooplankton–Detritus' (NPZD) models or biophysical models, which typically include 3D hydrodynamics, temperature, nutrient fluxes and phyto- and zooplankton functional groups (Lenhart et al. 2010, Sailley et al. 2013, Maar et al. 2018). The phyto- and zooplankton fields calculated by these LTL models thus form the basic resources for the HTL food web (Travers et al. 2009, Gurkan et al. 2013, Radtke et al. 2013, Daewel et al. 2019). However, these fields can substantially differ from each other, and the spatially explicit HTL model might respond to the choice of the LTL forcing field. Still, the sensitivity of HTL models to different plankton prey fields obtained from various LTL models has, to our knowledge, not yet been investigated.

Effects of LTL dynamics on higher trophic food webs have been addressed in modelling studies, often with models integrating all levels including zooplankton. Some are spatially explicit (see Rose et al. 2010 for references); others are not (e.g. Araújo et al. 2008, Niiranen et al. 2013, Heneghan et al. 2020). While scenarios with varying levels of productivity show the importance of zooplankton for fish biomass, the variance in time and space does not change in these studies because the underlying assumptions or LTL models remain the same. However, earlier studies emphasized the specific relevance of spatio-temporal patterns in zooplankton prey fields especially for the survival of fish early life stages (e.g. Beaugrand & Kirby 2010, Daewel et al. 2011). Different LTL models covering the same region, even though they are validated for the same system, exhibit differences in spatio-temporal dynamics as well as absolute values of LTL production, as they presume different assumptions about the planktonic food web and the environmental forcing conditions (Maar et al. 2018). Plankton fields from different models represent a range of realistic outcomes in the respective ecosystem, but the variance may have consequences for subsequent estimates in higher trophic levels, which thus far has not been addressed. In the present study, we hypothesize that differences in LTL patterns and magnitude translate into differences in HTL biomass and spatial and temporal patterns. To test this hypothesis, we used prey fields received from 5 different LTL models (Delft3D-WAQ, ECOHAM, Pätsch & Kühn 2008; ECOSMO, Daewel & Schrum 2013; HBM-ERGOM, Maar et al. 2011, Maar et al. 2016; and NORWECOM, Skogen et al. 1995, Skogen & Søiland 1998) to force the temporally and spatially explicit HTL model OSMOSE in a setup for the North Sea (see Fig. 1). The plankton fields provided were divided into size bins and then used as time- and spatially explicit prey fields in the OSMOSE model. The HTL model was run with an invariant mode setup (domain, spatial resolution, year and time step) to allow a clear analysis of the forcing impacts of the different LTL models. The resultant HTL biomass and spatial distributions are analysed for each LTL model and compared for zooplanktivorous fish, flatfish and piscivorous/benthivorous fish (hereafter called predators). Sensitivity analyses were performed with the aim of understanding the role of zooplankton size categories and the magnitude of the zooplankton biomass, by varying size classes and total biomass in each LTL model while maintaining each model's unique spatial and temporal pattern.

2. MATERIALS AND METHODS

2.1. LTL models

Five different LTL models were chosen to provide prey fields for the HTL model (Delft3D-WAQ, ECOHAM, ECOSMO, HBM-ERGOM and NORWECOM; Fig. 1). While data from ECOHAM, HBM-ERGOM and NORWECOM were provided as 2 groups of phytoplankton and 2 groups of zooplankton, ECOSMO results were combined into one group of each, and Delft3D-WAQ provided 4 groups of phytoplankton

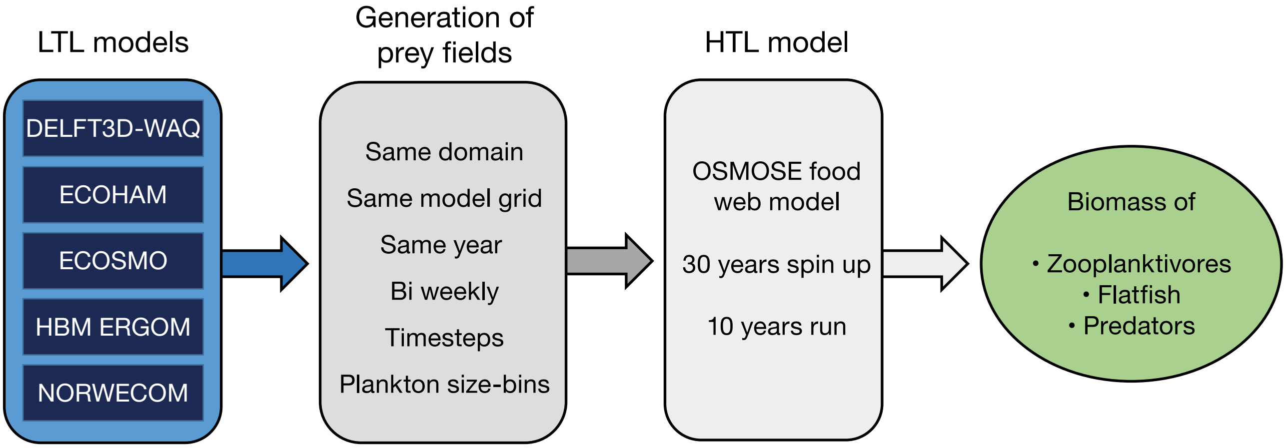

Fig. 1. Conceptual diagram of the model approach. Five lower trophic level (LTL) models are providing 3D plankton fields that are modified so that the spatial and temporal format of the prey fields is the same as that of the input to the higher trophic level (HTL) food web model OSMOSE. The HTL model estimates spatial-resolved biomass of zooplanktivores, flatfish and predators

Table 1. Lower trophic level models used and the available plankton functional groups

Model	Phytoplankton	Zooplankton
Delft3D-WAQ	Flagellates, diatoms, *Phaeocystis*, dinoflagellates	Bulk zooplankton
ECOHAM	Non-diatoms, diatoms	Microzooplankton and mesozooplankton
ECOSMO	Phytoplankton	Bulk zooplankton
HBM-ERGOM	Flagellates, diatoms	Microzooplankton and mesozooplankton
NORWECOM	Flagellates, diatoms	Microzooplankton and mesozooplankton

and one group of zooplankton (Table 1). A description of these models (except for ECOHAM), their setup configuration and their planktonic food web was provided in Maar et al. (2018) as well as in the associated references given in Section 1. ECOHAM is described in detail in Lorkowski et al. (2012). All LTL model results were provided as bi-weekly averages of the year 2004 to eliminate inter-annual variability. The reason for using 2004 is that at the time of this study, that was the only calendar year all 5 models had in common. Further, according to the annual North Atlantic Oscillation (NAO) index of 0.2, 2004 could be considered to be a normal year without extreme events (https://www.cpc.ncep.noaa.gov). Long-term differences in interannual variability of the LTL models were not considered. The LTL model results were interpolated to the OSMOSE model grid of 1/9 ICES grid cell (20 km longitude and 18.5 km latitude) and integrated with depth (0 m to bottom). The LTL fields were reduced to the largest spatial domain the LTL models had in common: the central to southern North Sea (Fig. 2).

Because foraging in the HTL model is based on relative size ranges of predator and prey, assumed size ranges of the plankton groups were included for the input to OSMOSE (Table 2). Non-diatoms from ECOHAM were given the same size range as flagellates. For the single groups of phyto- and zooplankton from ECOSMO, the minimum and maximum values from the other groups were used. Plankton biomass from the LTL models was provided in gram carbon (gC) converted to the standard unit of g wet-weight (gWW) required in OSMOSE, using the factors 6.625 molC molN^{-1} for phytoplankton, 5 molC molN^{-1} for zooplankton, 12 gC molC^{-1}, 0.45 gC (g dry-weight [gDW])$^{-1}$ and 5.38 gWW gDW^{-1} (Brey et al. 2010).

Biomass of macro-invertebrates (deposit feeders, meiofauna and suspension feeders) was obtained from a previous setup using results from the ERSEM model (Butenschön et al. 2016) and applied to all simulations because it was not a standard output in the considered LTL models (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m680p079_supp.pdf. For macro-invertebrates, conversions were made assuming mgC to correspond to ash-free dry weight, and assuming that the benthos groups defined in ERSEM consist of

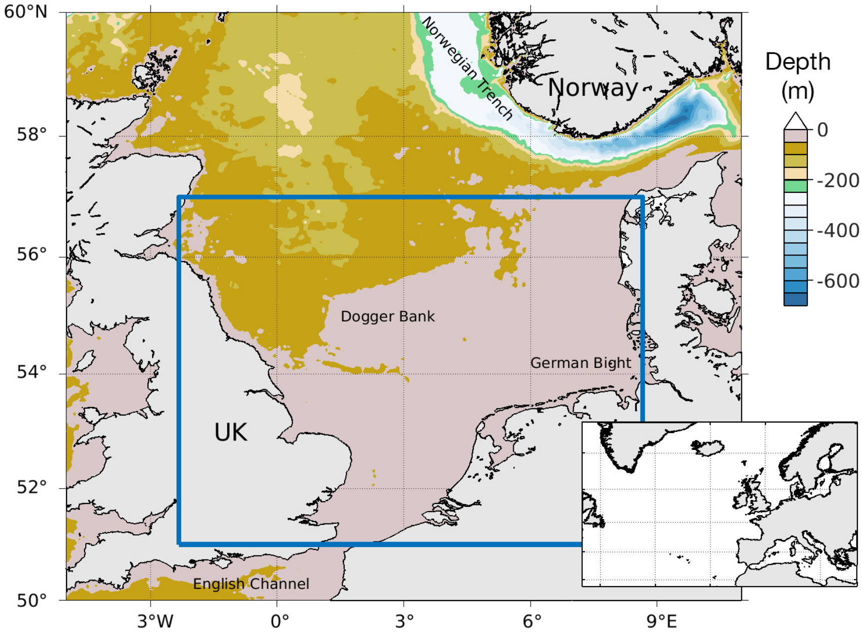

Fig. 2. North Sea bathymetry and its position within the North Atlantic Ocean (small insert). Blue rectangle: the domain common to all 5 LTL models, thus used for the OSMOSE simulations

Table 2. Size ranges per plankton group estimated as equivalent spherical diameter. The ranges are agreed upon by all authors and based on literature (Hansen et al. 1997, Tonnesson et al. 2005, Daewel et al. 2008). Because the classes of suspension feeders, deposit feeders and meiobenthos are based on their foraging mode in the ERSEM model and not on size, different size ranges were chosen arbitrarily to discriminate between benthic food sources allowing for size-dependent foraging in the HTL model

	Minimum size (µm)	Maximum size (µm)
Plankton		
Flagellates/non-diatoms	2	10
Diatoms	8	14
Microzooplankton	10	100
Mesozooplankton	125	1600
Phytoplankton bulk	2	14
Zooplankton bulk	10	1600
Macro-invertebrates		
Meiobenthos	1	5
Deposit feeders	1	10
Suspension feeders	1	30

equal percentages of polychaetes, crustaceans, gastropods and bivalves, we arrive at an average conversion of 10.5 gWW gC^{-1} (Ricciardi & Bourget 1998). Size ranges were assigned to allow for size-dependent predation (Table 2).

2.2. HTL model

The HTL model we used is OSMOSE, developed by e.g. Shin et al. (2004) and Travers et al. (2009) and here parameterized for the North Sea (Texts S1 & S2). A brief description of the OSMOSE model and the assumptions are given in the following sections. The model is size-based and spatially explicit, and multiple species can be incorporated (Tables S1 & S2). Each species consists of super-individuals, and within each super-individual all individuals are considered physically identical, of the same age and in the same spatial location.

For each time step, super-individuals move randomly on the grid with a distance of 1 grid cell per time step. However, movement is bounded by presence–absence maps that force size classes to specific regions, such as nursery areas. After reaching a size threshold, a super-individual is randomly placed on the appropriate map for its species and size, after which a random walk with one grid cell per time step starts again. The presence–absence maps were constructed using 20 yr International Bottom Trawl Survey (IBTS) and Beam Trawl Survey (BTS) data (obtained from the ICES Datras database, period 1985–2005) for the North Sea. Differences in distributions of size classes were visually assessed based on the present–absence maps. 'Present' was defined as more than 2 individuals of a size class present in an ICES rectangle during the 20 yr period. Spatial differences in abundance arise mechanistically through spatially explicit resource availability, predation by other fish and fishing mortality.

At each time step, grid cells are addressed in a random order and the super-individuals present are listed. These super-individuals are addressed randomly to prevent an *a priori* feeding order from affecting the results. Foraging is based on co-occurrence of predator and prey in time and space. Prey suitability is based on the relative sizes of predator and prey, bounded by a minimum and maximum ratio (Table S3). An accessibility matrix is used to exclude prey from the diet in case of unrealistic predator to prey size ratios; for example, to exclude herring consuming infauna (Table S4).

After consuming prey biomass upon satiation or until prey run out, the predation efficiency, ξ_i, is calculated as the amount of food eaten divided by the available food corresponding to predator satiety. If more than one prey type is available, predation is uniformly distributed according to relative abundance. Satiation is set to a maximum ingestion rate of 3.5 g of food g^{-1} predator body mass yr^{-1} (Shin et al. 2004, Travers et al. 2009). The total prey biomass consumed (*PB*) is used to assess the predation efficiency. Prey consists of fish (conspecifics or other species), which are dynamically modelled, and resources used as forcing function, namely phyto- and zooplankton and macro-invertebrates. Densities of the forced resources are spatially explicit and vary in time using time steps of 14 d and result from LTL models.

Based on the consumption efficiency, an individual may grow, maintain itself or starve. If predation is sufficient (i.e. $\xi_i > \xi_{\text{crit}}$), individuals grow. The value of ξ_{crit} represents a species-independent predation efficiency of $\xi_{\text{crit}} = 0.57$ (Shin & Cury 2004). The minimum growth is zero if no food is consumed. The realized growth is bounded by the maximum and minimum growth and is a function of food intake (following Travers et al. 2009) (Table 3). The maximum attainable growth increment per time step is based on the von Bertalanffy growth curve (von Bertalanffy 1957) and the individual's length. A hypothetical age is set based on the current individual length. The potential maximum length at the next time step is then the length at the hypothetical age + the time step. This assumption allows individuals that by chance move from a food-poor cell to a food-rich cell to catch up in size to individuals of similar age that by chance encountered more profitable circumstances.

If predation is insufficient (i.e. $\xi_i < \xi_{\text{crit}}$), individuals suffer from starvation mortality, which increases linearly with decreasing predation efficiency (Table 3). Besides starvation mortality, individuals suffer predation mortality from other model individuals, from additional background mortality and fishing mortality (Table S5). The additional background mortality is species-specific and includes mortality from other predators such as birds and mammals, diseases and parasites based on stock assessment (ICES 2002). Fishing mortality is species-specific and size-dependent and varies seasonally. Fishing pressure is modelled spatially explicitly, based on the effort distribution of the otter trawl, demersal fleet, industrial fleet and herring fleet (Jennings et al. 1999).

Species-specific maturation size, the size at which 50% of the population is mature, was based on IBTS

Table 3. OSMOSE model equations. A super-individual is indicated by *i* and its state at time *t*. Prey (super-individuals) are indicated by *j*. See also Travers et al. (2009)

Process	Equation	Details
Predation	$PB_{i,j,t} = B_{j,t} \cdot \frac{r \cdot B_{i,t}}{\sum B_{j,t}} \text{ if } \frac{L_i}{L_{\max}} < L_j < \frac{L_i}{L_{\min}}$	Predation (*P*) of biomass (*B*) per super-individual *i*, consuming prey *j*, per grid cell, depending on the species specific minimum ($L_{\min}$) and maximum ($L_{\max}$) size ratio. Maximum intake rate (r) = 3.5 g g^{-1} yr^{-1}
Growth	$\begin{cases} \Delta L_{i,t} = 0 & \text{if } \xi_{i,t} < \xi_{\text{crit}} \\ \Delta L_{i,t} = \frac{2\Delta L}{1-\xi_{\text{crit}}}(\xi_i - \xi_{\text{crit}}) & \text{if } \xi_{i,t} > \xi_{\text{crit}} \end{cases}$	Growth, ΔL $\xi_{i,t}$ is the consumption efficiency ξ_{crit} is the maintenance cost
Reproduction	$N_0 = \alpha \cdot \varphi \cdot \frac{1}{2} \cdot \sum_{L>Lmat} B_{L,t}$	Fecundity (*N*) per species summed over biomass (*B*) of mature individuals weighted by spawning seasonality (α) and sex ratio 1. φ is the fecundity parameter in eggs g^{-1}
Additional background mortality	$e^{-M_{\text{add}}}$	Species-specific constant; values provided in Table S1
Starvation mortality	$1 - e^{M_{i,t}}$ with $M_{i,t} = \frac{M_{\max}}{\xi_{\text{crit}}} \cdot \xi_{i,t} + M_{\max}$	$M_{\max} = 1$ $\xi_{i,t}$ is the consumption efficiency ξ_{crit} is the maintenance cost
Fishing mortality	$e^{\beta \cdot F} \text{ if } L > LF$	Species specific fishing mortality (*F*) weighted by seasonality (β)

and BTS data (Blanchard et al. 2014). Annual fecundity parameters are based on the literature, as is the species-specific spawning period. Spawning has a seasonal cycle, and hence the total annual fecundity is spread out over the year based on the spawning period (Table S2). Per time step, the biomass of mature individuals is multiplied with fecundity and seasonal scalar to obtain the total reproduction per species at time step t (N_0). These new individuals are split over a fixed number of 500 super-individuals per time step. Each super-individual is then randomly distributed onto the appropriate presence–absence map.

The focus of the present study was to investigate the effects on the OSMOSE HTL model fish biomass when using different LTL model results as input. The HTL model results will therefore be compared on a group level and not on a species level. We grouped the fish species into functional types: 'predators' (cod, grey gurnard, haddock, saithe and whiting), 'flatfish' (dab, plaice and sole) and 'zooplanktivores' (herring, sandeel, Norway pout and sprat). Further, it is beyond the scope of this study to validate the used HTL model against measured species biomasses, especially as data on fish biomass are sparse and do not cover the required temporal and spatial scale. However, OSMOSE has already been successfully applied in other regions (Travers et al. 2009, Halouani et al. 2016, Fu et al. 2017). Because we only have 1 calendar year of LTL input (2004), the prey input from that year was repeated 40 times to create a time series for OSMOSE. The first 30 yr are for spin-up and the following 10 yr were used to generate the results. This step is necessary due to differences in lifespan of the fish species modelled. We calculated the annual mean (±SD) of biomass over these 10 years. Biomass values were normalized using the mean of the specific model, so a value of 1 equals the mean.

2.3. Sensitivity study

The sensitivity of HTL biomass to the provided plankton prey fields was tested for (1) zooplankton size bins and (2) the amount of total zooplankton biomass. In the first sensitivity study, we evaluated the effect of different size classes on the HTL model results. To do this we first adjusted the annual average of zooplankton biomass to the same level (10 gWW m^{-2}) by multiplying biomass with a LTL model-specific conversion factor (conversion = 10 gWW m^{-2} / annual mean gWW m^{-2}) and then providing the prey fields as the original zooplankton groups or as 1 bulk zooplankton group for each of the LTL models. For the models with both micro- and mesozooplankton (ECOHAM, HBM-ERGOM and NORWECOM), the groups were pooled (but no change in total biomass) to obtain 1 bulk zooplankton group with the same size range for all models (Table 2). Of the results of this sensitivity study, we show only the zooplanktivores in the main document because that group has the strongest response to changes in zooplankton. The results for biomass of flatfish and predators can be found in the Supplement. This sensitivity analysis was also done with the original size bins, presented in the Supplement.

In the second set of sensitivity runs, we investigated the functional response of HTL to the amount of food in the different models. Accordingly, we changed the total amount of zooplankton by the respective factor to achieve a range from 2–18 gWW m^{-2} of the annual mean for each model. We used 1 zooplankton group for all models (sensitivity study no. 1) to remove potential effects from different size bins, while the phytoplankton biomass remained unchanged.

Finally, we wanted to explore whether the different HTL responses across the models could be explained by differences in spatial–seasonal patterns in zooplankton biomass. We therefore calculated the coefficient of variation (CV, %) of the spatial and seasonal means of zooplankton as:

$$\mathrm{CV} = \frac{\mathrm{SD}}{\mathrm{mean}} \times 100 \qquad (1)$$

The spatial CV was estimated from the annual mean and SD for the whole area. The seasonal CV was estimated from the mean and SD from the bi-weekly data averaged over the model domain. A low CV reflects a more evenly distributed zooplankton biomass in space or time and vice versa.

The seasonal correlation of zooplankton biomass (bi-weekly data averaged for the model domain) across models was evaluated using multiple linear regression analysis (Spearman) with a significance level of 0.05.

3. RESULTS

3.1. Prey fields

Fig. 3 a shows annual means of total plankton, phytoplankton and zooplankton biomass for the study area for the 5 different LTL models. The numbers include diatoms and autotrophic flagellates/non-diatoms or micro- and mesozooplankton (Table 1). The phyto-

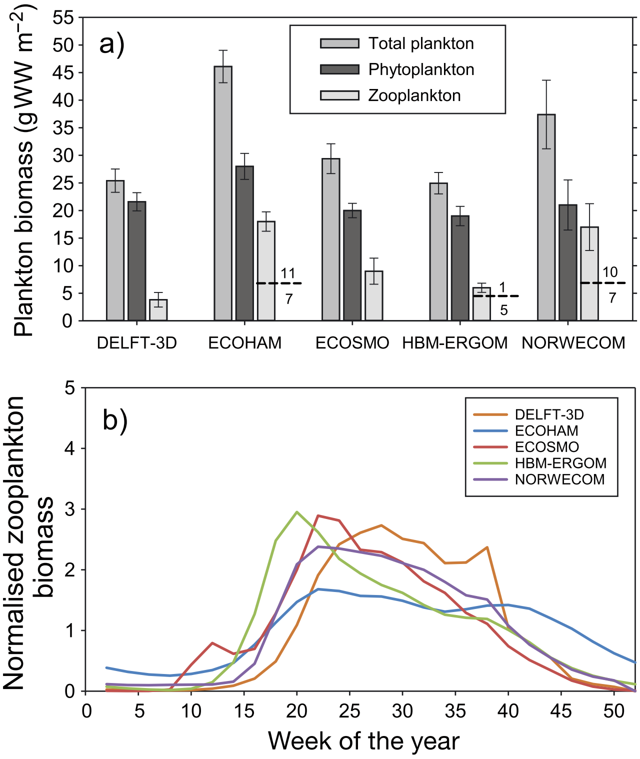

Fig. 3. (a) Annual means (±SD) of total plankton, phytoplankton and zooplankton biomass and (b) seasonal development of total zooplankton biomass (normalised by the mean of each model) for the 5 LTL models within the HTL model domain. The biomass of meso- and microzooplankton contributing to total zooplankton are given below and above the horizontal line, respectively, indicated in (a) for the 3 models with 2 zooplankton groups

plankton biomass across the models varied between 19 and 28 gWW m^{-2}, with the highest value for ECOHAM and similar values for the other models (Fig. 3a). Zooplankton biomass varied between 4 and 18 gWW m^{-2}, with NORWECOM and ECOHAM delivering 2–5 times higher input zooplankton biomass than the other models (Fig. 3a). Total plankton biomass was highest for ECOHAM and lowest for Delft3D-WAQ and HBM-ERGOM. The contribution of mesozooplankton to total zooplankton biomass was 38, 84 and 41 % for ECOHAM, HBM-ERGOM and NORWECOM, respectively (Fig. 3a). For the seasonal patterns, total zooplankton biomass was normalised by the annual mean for each model to allow more direct comparison across models (Fig. 3b). The timing of the spring bloom had a maximum around Week 20–22 for all models except Delft3D-WAQ, which had a later maximum in Week 28 and another in Week 38. ECOHAM also had a weak signal of a second maximum around Week 40. The seasonal patterns were significantly correlated across all models, with the highest correlations between ECOSMO and NORWECOM (R^2 = 0.91) and lowest between Delft3D-WAQ and HBM-ERGOM (R^2 = 0.48) (Table 4). The spatial pattern of annual zooplankton biomass (normalised) showed generally higher values in the southern part and along the coastline with the strongest spatial gradients for Delft3D-WAQ, ECOSMO and NORWECOM (Fig. 4). Macro-invertebrate data showed the highest biomass of deposition feeders along the eastern coastline and northern part of the model domain and the highest meiofauna biomass in the southern part, whereas suspension feeders had a patchier distribution (Fig. S1).

3.2. HTL model results

The input from the 5 different LTL models produced similar relative contributions of the 3 HTL groups to total biomass but more than 5-fold difference in total fish biomass (Fig. 5). Zooplanktivores were the dominant group for all LTL model inputs, with 75–82 % of total HTL biomass. The biomasses of predators and flatfish were on average 14–22 and 3–4 %, respectively, of total adult HTL biomass across LTL model inputs (Fig. 5). Hence, predator biomass was always higher than that of flatfish. Total adult biomass of HTL was highest for prey fields from ECOHAM (273 kt wet weight (ktWW) and lowest for prey fields from Delft3D-WAQ (50 ktWW), while prey fields from the 3 remaining models gave more similar results (153–205 ktWW). Both the total biomass and the individual biomass for each HTL group increased with increasing zooplankton biomass (Fig. 6). For ECOHAM and NORWECOM with similarly high levels of zooplankton biomass, the biomass of zooplanktivores was, nevertheless, 33 % higher in ECOHAM. Flatfish, which mainly feed on benthic prey items, showed a similar but weaker response with increasing zooplankton biomass due to

Table 4. Seasonal correlation of zooplankton patterns across lower trophic level models (Fig. 3b) showing R^2 values from regression statistics ($n = 26$, $p < 0.05$)

	ECOHAM	ECOSMO	HBM-ERGOM	NORWECOM
Delft3D-WAQ	0.73	0.74	0.48	0.87
ECOHAM		0.66	0.67	0.82
ECOSMO			0.78	0.91
HBM-ERGOM				0.79

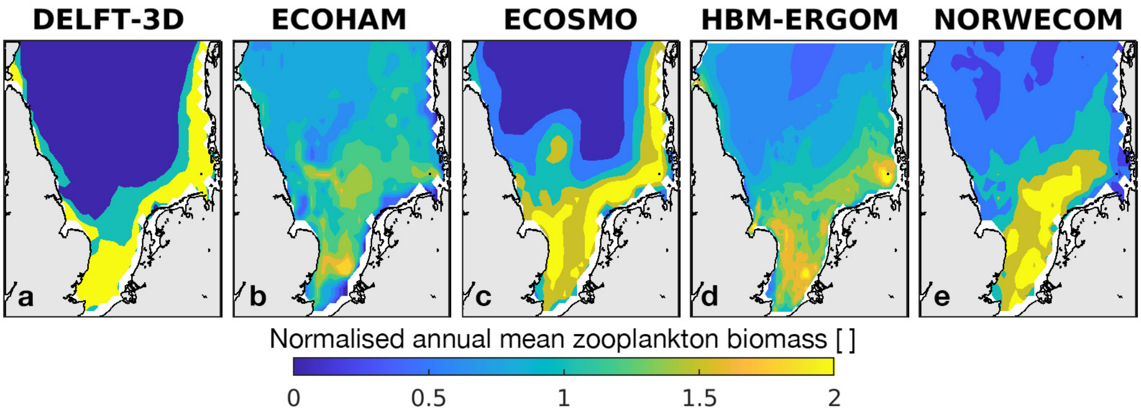

Fig. 4. Normalised annual means of total zooplankton biomass (normalised by the mean of each model) for the 5 LTL models (a) DELFT-3D, (b) ECOHAM, (c) ECOSMO, (d) HBM-ERGOM and (e) NORWECOM

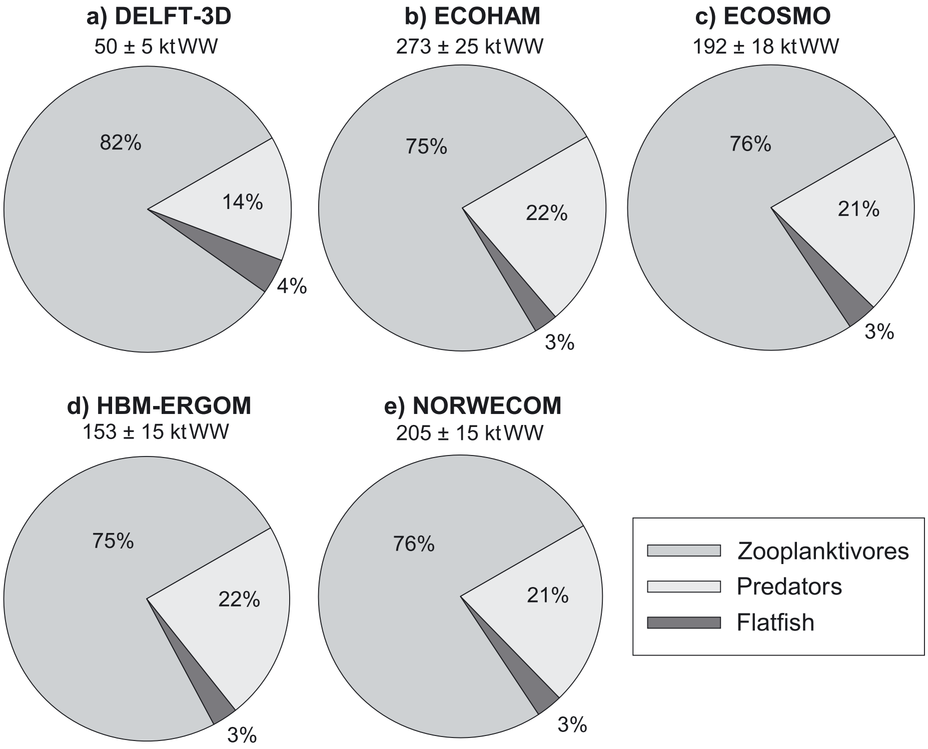

Fig. 5. Relative (%) adult HTL group biomass composition for each of the 5 LTL model inputs (a) Delft3D-WAQ, (b) ECOHAM, (c) ECOSMO, (d) HBM-ERGOM and (e) NORWECOM. Mean (±SD) total adult HTL biomass is indicated as ktWW for the last 10 yr (last time steps)

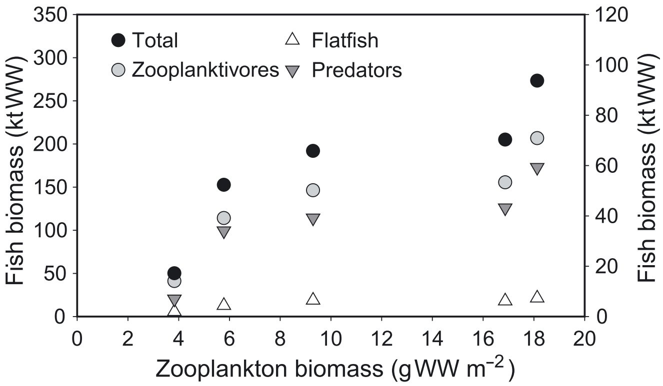

Fig. 6. Means (±SD) of the last 10 yr of the adult HTL biomass for total HTL and zooplanktivores (spheres, left axis), and flatfish and predators (triangles, right axis) versus annual mean zooplankton biomass from each LTL model. LTL model order from left to right based on mean zooplankton biomass: Delft3D-WAQ, HBM-ERGOM, ECOSMO, NORWECOM and ECOHAM

their short but crucial dependence on zooplankton during early life stages. There was also a positive linear correlation between predator biomass and its fish prey (zooplanktivores and flatfish) biomass across models ($n = 5$, $R^2 = 0.87$, $p < 0.05$).

The spatial distribution of simulated HTL adult biomass of the zooplanktivores, flatfish and predators showed overall similar patterns between the different LTL models (Fig. 7). Zooplanktivore biomass was concentrated in the southern areas and decreased northwards for all LTL model inputs. ECOHAM showed the highest total zooplanktivore biomass (Fig. 6), which reflected that the zooplankton was widely distributed throughout most of the study area (Fig. 4). Flatfish biomass produced from all the LTL model inputs had an even stronger south–northward gradient than zooplanktivores, with lowest biomass levels for Delft3D-WAQ and HBM-ERGOM (Fig. 7). Predators were distributed all over the study area for all LTL models, with core areas found either in the north-eastern part of the area or in the English Channel outlet.

3.3. Sensitivity study results

The first sensitivity study revealed that the zooplanktivores responded strongly to different prey sizes, i.e. whether the zooplankton prey fields were adjusted to the same annual mean of 10 gWW m^{-2} and provided as micro- and mesozooplankton or as 1 bulk group (Fig. 8a). Especially in ECOHAM and NORWECOM with a high share of microzooplankton, the resultant zooplanktivore biomass was substantially increased when the zooplankton was made available as 1 group with a wider size range. The second sensitivity study, using a single zooplankton size bin for all models, showed a positive, linear response of HTL biomass to increasing zooplankton biomass for all LTL models (Figs. 8b & S2). In ECOHAM, zooplanktivores exhibited the strongest response to increasing zooplankton biomass and was up to 3 times higher than for Delft3D-WAQ. The relative biomass contributions of the fish groups did not change with increasing zooplankton biomass (Fig. S3).

The spatial and seasonal variability of zooplankton biomass expressed as the CV (Eq. 1) was found to be important for the resultant zooplanktivore biomass (Fig. 8c) and fish biomass in general (data not shown). A low CV, reflecting a more even distribution of prey, was found to give a higher zooplanktivore biomass and vice versa, despite equal zooplankton biomass (using 1 size bin for each LTL model). The spatial and seasonal CV were lowest for ECOHAM (20 and 51%) and highest for Delft3D-WAQ (96 and 106%). The CV of the spatial and seasonal patterns were similar for Delft3D-WAQ and ECOSMO (92–106%), whereas NORWECOM showed lower spatial (38%) than seasonal (90%) variability. Zooplanktivore biomass did not differ much between NORWECOM and HBM-ERGOM, and seasonal CVs were alike (90%) while spatial CVs differed (38% NORWECOM and 70% HBM-ERGOM).

4. DISCUSSION

4.1. General findings

In the present study, we explored the sensitivity of a modelled fish community to spatially–temporally varying zooplankton prey fields provided by 5 LTL models. This is, to our knowledge, the first attempt to examine the relevance of differences in plankton dynamics for the performance of a spatially explicit fish model in an ensemble-like manner. We found that fish group composition was similar across zooplankton prey fields, despite spatial and temporal differences in zooplankton model input. There were large differences in absolute fish biomass corresponding to differences in zooplankton biomass input.

4.2. Characteristics of the LTL models

The zooplankton biomass provided to the HTL model varied by a factor of up to 5 between the models (Fig. 6). In addition, the applied LTL models showed differences in their spatial–seasonal patterns (Fig. 8c) that can affect the trophic match–mismatch and outcome of the HTL model. Delft3D-WAQ showed e.g. very strong spatial gradients, with highest values in the coastal waters, but with lower zooplankton biomass in the open waters compared to the other LTL models (Figs. 4 & 8c). ECOHAM and NORWECOM showed the overall highest zooplankton biomass, but their spatial–seasonal patterns were very different (Figs. 3b, 4 & 8c), with ECOHAM having a smoother spatial and seasonal variability (Figs. 3c & 8c). LTL models are often based on similar principles yet differ in model assumptions, the underlying hydrodynamics, their resolutions in space and time, the external forcing conditions and choices and description of functional groups, and hence they can lead to substantially different results (Skogen & Moll 2005, Lenhart et al. 2010, Sailley et al. 2013, Maar et al. 2018). Most stud-

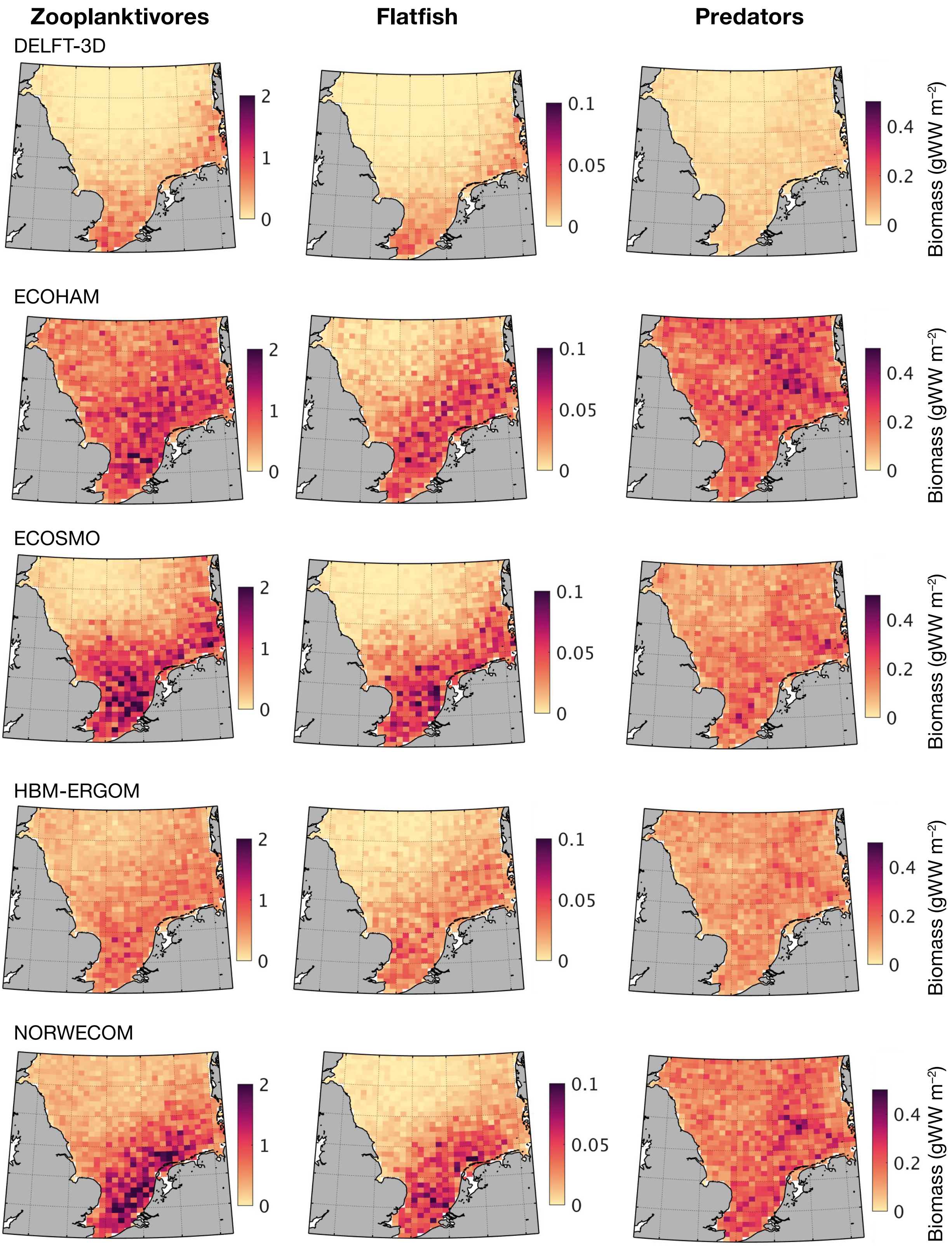

Fig. 7. Spatial distribution of annual means of HTL biomass (zooplanktivores, flatfish and predators; last time step) based on prey fields from 5 LTL models

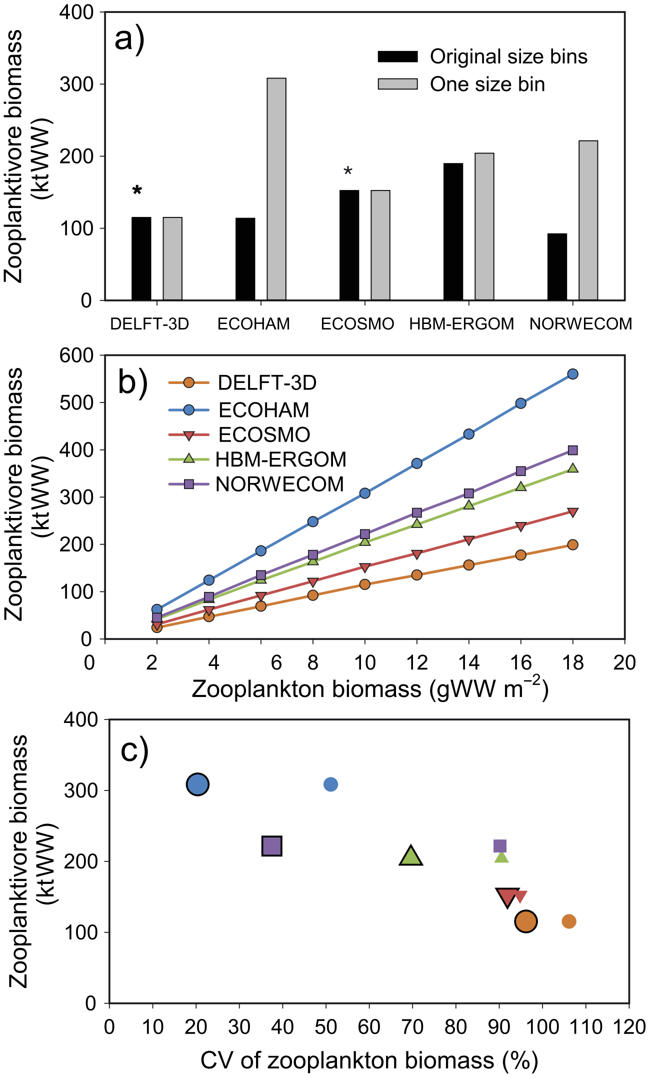

Fig. 8. Sensitivity studies of zooplanktivore biomass responses to (a) zooplankton biomass (adjusted to the same annual mean of 10 gWW m^{-2} for all LTL models) distributed across the original size bins (Table 2) or as 1 common size bin; * indicates the 2 models with a single zooplankton size bin; (b) zooplanktivore biomass as a function of increasing zooplankton biomass using 1 size bin for all LTL models; and (c) spatial variability (large symbols) and seasonal variability (small symbols) of zooplankton biomass expressed as the coefficient of variation (CV) using 1 zooplankton size bin adjusted to the same annual mean (10 gWW m^{-2}) for all 5 LTL models. Zooplanktivore biomass corresponds to the biomass indicated by the grey bars in (a)

ies found high variability across LTL model results but concluded that ensemble modelling can be used to reduce uncertainty in model projections and estimate a range of possible outcomes (Niiranen et al. 2013, Queirós et al. 2016, Maar et al. 2018).

Continuous Plankton Recorder (CPR) data from the period 1990–2000 showed a mesozooplankton biomass of 3–4 gWW m^{-2} (0–20 m) in the southern North Sea (Pitois & Fox 2006). Other reported values were 6 gWW m^{-2} from May–September in the central part (Fransz et al. 1991) and 16 gWW m^{-2} for the whole North Sea including the northern part (outside our model domain) with a high *Calanus finmarchicus* abundance (Fransz et al. 1991, Mackinson & Daskalov 2007). The reported range is similar to our model results of 4–9 gWW m^{-2} for the mesozooplankton biomass in the 3 models with 2 zooplankton groups and total zooplankton biomass in the models with 1 zooplankton group (Fig. 3a). CPR data show that zooplankton biomass generally starts to increase in March (Weeks 9–12) and peaks in May–August (Weeks 18–39), after which it gradually declines to winter values (Pitois et al. 2012). This pattern is consistent with the modelled seasonality of zooplankton biomass (Fig. 3b). It should be noted that it is difficult to directly compare modelled annual zooplankton biomass with (scarce) observations because sampling often occurs in peak biomass periods and at different years, locations and depths (Skogen et al. 2021, Hjøllo et al. 2021, both this Theme Section). Zooplankton biomass is most often calibrated against measured mesozooplankton biomass e.g. from CPR data and ICES data because there is no coherent data set for microzooplankton in the North Sea. Microzooplankton plays different roles (e.g. feeding mode, size range) in the models and can therefore have different biomasses relative to that of mesozooplankton (Maar et al. 2018). Hence, the highest uncertainty probably lies within the estimation of microzooplankton biomass, as previously highlighted (Sailley et al. 2013, Maar et al. 2018). However, the differences between the LTL models were suited to test a range of realistic prey patterns in the HTL sensitivity study.

4.3. Bottom-up control of HTL biomass

Total HTL biomass responded positively to increasing zooplankton biomass, indicating bottom-up control of the food web (Figs. 6 & 8b). This bottom-up regulation of plankton to fish biomass fits well within general food web theory (Ware & Thomson 2005, Wollrab et al. 2012, Heath et al. 2014), where changes in nutrient or food availability lead to similar responses for each trophic level, as observed for zooplanktivores, flatfish and predators (Fig. 6). Further, bottom-up control has previously been demonstrated for the North Sea (Heath 2005), although occasional top-down control may occur (Daewel et al. 2014).

Zooplanktivores showed the strongest response to increasing zooplankton biomass among the HTL

(Fig. 6), due to the lifetime dependence on zooplankton as food. The zooplankton biomass was similar for ECOHAM and NORWECOM, but the resultant biomass of zooplanktivores from ECOHAM was 33% higher than for NORWECOM. The 2 models had the same share of meso- and microzooplankton, so in this case different size bins could not be the reason for the difference in zooplanktivore biomass. Instead, the more evenly spatial–seasonal distribution of zooplankton in ECOHAM compared to NORWECOM could explain the observed difference (Fig. 8c). Zooplanktivore biomass appears to be sensitive to spatial and temporal variation in LTL input. A higher CV, i.e. greater spatial and temporal differences, resulted in lower biomass. Since the movement behaviour of HTL in the OSMOSE model is random, i.e. not influenced by food density, a wider distribution of food will increase the chances for a predator–prey match and cause a higher overall biomass of zooplanktivores in the modelled area (Fig. 7). However, the assumption of random migration might not be realistic for all HTL species and has been shown to result in comparably low fish biomass growth when directly compared to reactive movement strategies (Humston et al. 2004). The OSMOSE model could benefit from further investigations of this topic.

Flatfish biomass responded to a lesser extent to increasing zooplankton biomass, and its spatial distribution coincided mainly with that of its main prey, the macro-invertebrates and especially meiobenthos (Fig. S1). Since the macro-invertebrate field roughly matches that of the ICES fishmap data for sole/plaice/dab (https://data.ices.dk/), so does the flatfish biomass resulting from the various runs. Biomass of the predators increased with increasing prey biomass (zooplanktivores and flatfish) and was therefore also highest in ECOHAM relative to other LTL models (Fig. 6).

Overall zooplanktivore biomass was found to be sensitive to the provided zooplankton groups (meso-, micro- or bulk zooplankton) due to differences in the size range each group represents (Fig. 8a). The HTL will outgrow the smallest zooplankton first and then only rely on the mesozooplankton due to the predator/prey size-ratios applied in the model (Table S3). However, when the zooplankton are provided as 1 group with a wider size bin, the HTL can exploit them more efficiently, and especially over a longer time period, as differences in seasonality between the different zooplankton groups are levelled out. A sensitivity study with the original size bins (Figs. S4 & S5) shows the same pattern for each model compared to using a single size bin. Results differ in total fish biomass driven by differences in meso-zooplankton biomass, not total zooplankton biomass. Therefore, the present study suggests that it is important to consider size bins in the zooplankton field when coupling to HTL models (Daewel et al. 2008, Huebert et al. 2018). The use of a size-spectrum for zooplankton, instead of groups with a given size range, can further improve the assumption of size-based foraging and will affect the HTL results (Huebert et al. 2018). A size-spectrum approach or modelling specific zooplankton species may also allow inclusion of prey preference in ways other than size-based predation. For a more mechanistic approach, this could include species preference, caloric content or catchability differences. Overall, our findings confirm that zooplankton is an influential link in the trophic transfer between LTL and HTL (Munk 1997, Heath 2007, Daewel et al. 2014).

4.4. HTL group composition and spatial patterns are similar across models

The HTL group composition and overall spatial patterns (Figs. 5 & 7) were similar despite the spatial and temporal differences between the LTL model inputs and differences in absolute biomass (Figs. 3b, 4 & 8c). The dominance of zooplanktivores over predators and predators over flatfish is in agreement with previous studies in the North Sea (Greenstreet et al. 1997, Heath 2005). The efficient transfer of energy from zooplankton to zooplanktivores for all LTL inputs suggests that no strong phenological trophic mis-matches occur in our simulations. On the contrary, the differences in spatial and temporal scales between LTL models fade out at higher trophic levels when considering the relative group composition. A possible explanation for this may stem from the wider spatial and temporal scales relevant for HTL species when compared to the LTL food web, i.e. fish have longer longevity and swim longer distances than their plankton prey. Also, most fish species only rely on zooplankton for a relatively short period of time during their lifespan; thus, plankton is not the only food source even though it plays a crucial role during critical life stages of fish (Bochdansky et al. 2008). As the fish grow larger, they will start feeding on other resources, such as benthic organisms and other fish, which has a stronger effect on the overall stock biomass. Other compensatory mechanisms that dampen food web responses to differences in plankton prey fields include loss of energy due to respiration and metabolic costs, cannibalism, predation and other types of mortality (McCann et al. 1998b, Andersen &

Pedersen 2010), which are included in OSMOSE through the growth curve, feeding and use of background mortality. The observed dampening of the trophodynamics in relative group composition when using different prey fields is in agreement with previous findings of weak food web responses to changes in bottom-up or top-down forcing (McCann et al. 1998a, Pace et al. 1999, Shurin et al. 2002, Andersen & Pedersen 2010, Bossier et al. 2018). Overall, the similar responses of the HTL spatial biomass distribution and feeding group composition across LTL model inputs suggest high confidence in the fish community model results, which is important for model acceptance by stakeholders and for the implementation of model results into management actions (Niiranen et al. 2013, Peck et al. 2018).

4.5. Model caveats and experiences from this process

The present study offers a number of lessons on linking HTL food web models to LTL models. Our approach only considered 1-way coupling and not feedback processes from HTL to LTL. This lack of feedback could give a bias in the estimates of available food and hence growth of HTL (Travers et al. 2007). We found a linear food response of fish biomass to increasing zooplankton biomass in the sensitivity runs (Fig. 8b) because there is no feedback from HTL to planktonic prey (no food depletion) inhibiting top-down control. Although within a time step food availability decreases due to consumption, food is replenished in each time step as if no consumption occurred. Two-way coupling or intermediate solutions may alter the HTL response to increased prey fields (Rose et al. 2010). Food-based movement of the HTL in combination with a 2-way coupling of LTL and HTL could dampen the linear increase of HTL biomass with increasing zooplankton. Travers et al. (2009) compared 1-way and 2-way coupling for OSMOSE parameterized for the Benguela system and found changes in the food web pathways and relative contribution of fish groups. Directional movement to high-value food patches may lead to local food reduction, dampening spatial variation in prey fields. This in turn may lead to a more even distribution of fish. Even though all employed LTL models include a general zooplankton mortality component that implicitly takes predation from HTL into account, a more dynamic predation mortality element would result in differences in zooplankton seasonality and biomass composition (Travers et al. 2009, Maar et al. 2014, Daewel et al. 2019). We would recommend a 2-way coupling for ecosystems especially with clear top-down controls of HTLs on the zooplankton.

Another experience from the LTL and HTL coupling is related to the model domain. In a first set of experiments (results not shown), the LTL results from the model covering only the southern and central part of the North Sea (Delft3D-WAQ) were extrapolated to the larger spatial domains of the other models that include the northern part of the North Sea with the Norwegian Trench. However, this approach severely underestimated the biomass levels of both LTL and HTL compared to the results from the other LTL models (data not shown). In our final approach, therefore, we used the same smaller spatial domain of all LTL models, which must always match (or be greater than) the HTL domain. The drawback of this approach is that the HTL domain is now limited to the central-southern North Sea, which does not fully cover the biological domain of all the HTL species. This could have an impact on total biomass; for example of boreal round fish. This limitation has been one of the reasons why the model domain of the newer version of the Delft3D-WAQ North Sea model has been extended to include a much wider area (Zijl et al. 2018).

The presented approach of combining LTL models and an HTL model did not take into account differences in the macro-invertebrates between the applied models because this group is typically not considered in standard NPZD-type models. Instead, data on macro-invertebrates was delivered from the ERSEM model and is thus not consistent with the LTL plankton fields provided by the different models. Even though they are the main food source for flatfish and form a large part of the diet of predators, exploring the role of macro-invertebrates for HTL models was beyond the scope of this study. We used LTL from the same year as input to the HTL model although there is year-to-year variability in zooplankton biomass levels and distributions (Pitois & Fox 2006). However, this variability is in the same range as the high spatial–temporal variability in the LTL prey fields from the same year which we used (Fig. 8c); thus, we can assume that data from more years would likely not change the overall conclusions. The HTL model used a size-based approach for zooplankton predation because the LTL models simulate only plankton functional types and not species diversity. As it is well known that the predator–prey size ratio is very important for fish predation (Munk 1992, 1997, Daewel et al. 2008), we believe that this approach is valid. However, due to the missing information, other factors like prey quality and selectivity cannot be considered in our modelling approach, although they could influence the energy transfer into and within the food web (Mitra & Flynn 2006). Climate change effects were not considered in this paper. Previously performed climate scenarios for the North Sea ecosystem agree that the overall productivity of the ecosystem will be reduced under high-emission scenarios as a consequence of changed stratification and circulation and the associated reduction in nutrient inflow (Holt et al. 2016, Mathis et al. 2019). In addition, Villarino et al. (2015) showed that species may shift northward and that the spring bloom may advance under climate change conditions across the North Atlantic region, and such changes are likely to occur in the North Sea (Helaouët et al. 2011, Mackas et al. 2012, Maar et al. 2013). It depends on fish species' tolerance ranges and spatial and temporal overlap if and under which conditions changes in zooplankton may affect fish (Beaugrand et al. 2003). In addition, climate change will affect fish directly and indirectly through changes in temperature, depending on fish size and species (Wang et al. 2020), and for example through phenological changes in spawning place and timing as well as larval drift (Lacroix et al. 2018, van de Wolfshaar et al. 2021). Feeding an HTL model with LTL climate scenarios is not sufficient to study full system effects. Coupling of LTL and HTL models to study the effects of climate change must therefore encompass possible responses at lower as well as higher trophic levels. In addition, we did not vary fishing mortality in combination with the different zooplankton fields. Varying fishing pressure may lead to direct effects on target species and indirect effects on target and non-target species due to changes in competitive and predatory interactions (Travers et al. 2010), while climate change may affect long-lived species less than short-lived species (Field et al. 2006). To allow for cascading effects of top-down and bottom-up control would require a 2-way coupling of LTL and HTL. Further, non-linear effects are expected due to the complexity of the model, largely because the fish are modelled fully size-structured, allowing for (size-dependent) changes between predator–prey and competitive interactions. Varying both zooplankton biomass and anthropogenic pressures would be a logical next step to study the interplay between bottom-up and top-down effects on the food web.

4.6. Conclusions

This study demonstrated that, overall, the estimated fish biomass levels are clearly and positively linked to the provided zooplankton biomass, indicating bottom-up control of the North Sea food web. In addition, fish biomass also increased when the prey fields were more evenly distributed on spatial–seasonal scales. Surprisingly, the differences in spatial and seasonal patterns in the prey fields resulting from the various LTL models did not translate into corresponding differences in fish group composition or spatial patterns. This suggests that strong spatial or temporal mismatches between fish and their prey are less apparent in the modelled studied area, while minor differences in the general pattern of zooplankton dynamics fade out at higher trophic levels (acknowledging aforementioned assumptions and caveats). However, the sensitivity studies also highlighted the relevance of providing different zooplankton functional groups since fish depend on different prey sizes during their development. When using HTL models to address relative effects of, for example, management strategies such as large-scale windparks and mariculture, our results indicate that a high degree of similarity is expected when using inputs from different LTL models. However, absolute biomass values and spatial differences depend on the LTL model input field chosen, and therefore differences in absolute biomass are to be expected.

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