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1 Sensitivity of the fish community to different prey fields and importance of spatial-seasonal
2 patterns

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18 Running page head with 3 to 6 words; 'Sensitivity of fish on prey'

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1 **Abstract**

2 Different fish species and life-stages not only depend on food abundance, but also on the size
3 of planktonic prey, and (mis-)matches in time and space with suitable prey may influence
4 growth and survival of fish during their life-time. This study explored the sensitivity of the fish
5 community to spatial-temporal differences in the plankton prey fields. Data from five different
6 lower trophic level models in the North Sea (Delft3D-WAQ, ECOHAM, ECOSMO, HBM-
7 ERGOM, and NORWECOM) were utilized to force the food web model OSMOSE that
8 simulates spatially and temporally explicit higher trophic level fish dynamics. The estimated
9 fish biomass levels were clearly and positively linked to the provided zooplankton biomass.
10 Sensitivity studies with varying zooplankton biomass revealed that spatial and temporal
11 variation in zooplankton drives differences in absolute fish biomass. More zooplankton size
12 bins resulted in less fish biomass due to size based foraging constraints. Nevertheless, we found
13 a consistent response between models in the relative biomass contribution and spatial patterns
14 of selected fish groups indicating a low sensitivity of the composition of the simulated fish
15 community to the zooplankton input. The robustness of the outcome will aid model acceptance
16 and implementation into management action. Relative, not absolute, changes may therefore be
17 used to study effects of management scenarios on the fish community.

18 Key words (3-8): trophic transfer, lower trophic levels, higher trophic levels, modelling, North
19 Sea, food web

1 **1. Introduction**

2 As the food web or ecosystem approach becomes more widely used in fisheries management
3 (Österblom et al. 2010, Möllmann et al. 2014), it is important to assess the various impacts of
4 lower trophic levels (LTL) on higher trophic level (HTL) model results and the uncertainties
5 associated with it. Higher trophic level models are designed to describe and predict the effects
6 of fishing, climate and other anthropogenic pressures on natural resources to provide decision
7 support to nature management (Peck et al. 2018). The HTL models may include planktivorous
8 fish, piscivorous fish and / or benthivorous fish, of which many undergo ontogenetic diet shifts
9 depending on the choice of age-, stage- or size-structure in the models (Shin et al. 2010). Since
10 different fish species and life-stages rely on specific sections of the planktonic prey size-
11 spectrum (Munk 1992), (mis-)matches in time and space with suitable prey may influence the
12 growth and survival of fish during their life-time (Frederiksen et al. 2007, Huebert et al. 2018).
13 In addition, climate change and other natural and anthropogenic stressors have been shown to
14 induce changes in the spatial-temporal dynamics of plankton (Li et al. 2009, Mackas et al.
15 2012, Maar et al. 2013, Holt et al. 2016). This further emphasizes the need to understand the
16 uncertainties associated with the choice of the prey field on HTL models, especially as these
17 types of models are likely to be used in scenario studies on climate change (Olsen et al. 2018).

18 Some of the most advanced spatially and temporally -explicit HTL models consider several
19 fish species and predation interactions (e.g. OSMOSE (Travers et al. 2009),
20 NORWECOM.E2E (Hjøllo et al. 2012)), but also require plankton input as a potential food
21 source for these fish (Travers et al. 2007, Hjøllo et al. 2012, Utne et al. 2012, Daewel et al.
22 2014). This plankton input is mostly obtained from lower trophic level (LTL) models, often
23 called ‘Nutrient-Plankton-Zooplankton-Detritus’ (NPZD) models or biophysical models,
24 which typically include 3D hydrodynamics, temperature, nutrient fluxes, and phyto- and
25 zooplankton functional groups (Lenhart et al. 2010, Sailley et al. 2013, Maar et al. 2018). The

1 phyto- and zooplankton fields calculated by these LTL models thus form the basic resources
2 for the HTL food web (Travers et al. 2009, Gurkan et al. 2013, Radtke et al. 2013, Daewel et
3 al. 2019). However, these fields can substantially differ from each other and the spatially
4 explicit HTL model might respond to the choice of the LTL forcing field. Still, the sensitivity
5 of HTL models to different plankton prey fields obtained from various LTL models has to our
6 knowledge not yet been investigated.

7

8 Effects of lower trophic level dynamics on higher trophic food webs have been addressed in
9 modeling studies, often with models integrating all levels including zooplankton. Some are
10 spatially explicit (see Rose et al. (2010) for references), others are not (e.g. Araujo et al. (2008),
11 Niiranen et al. (2013) and Heneghan et al. (2020)). While scenarios with varying levels of
12 productivity show the importance of zooplankton on fish biomass, the variance in time and
13 space does not change in these studies because the underlying assumptions or LTL models
14 remain the same. However, earlier studies emphasize the specific relevance of spatio-temporal
15 patterns in zooplankton prey fields especially for the survival of fish early life stages (e.g.
16 Beaugrand and Kirby (2010) and Daewel et al. (2011)). Different LTL models covering the
17 same region, even though they are validated for the same system, exhibit differences in spatio-
18 temporal dynamics as well as in absolute values of lower trophic level production as they
19 presume different assumptions about the planktonic food web and the environmental forcing
20 conditions (Maar et al. 2018). Plankton fields from different models represent a range of
21 realistic outcomes in the respective ecosystem, but the variance may have consequences for
22 subsequent estimates in higher trophic levels, which thus far has not been addressed. In the
23 present study we hypothesize that differences in LTL patterns and magnitude translate into
24 differences in HTL biomass and spatial and temporal patterns. To test this we use prey fields
25 received from five different LTL models (Delft3D-WAQ , ECOHAM (Pätsch & Kühn 2008),

1 ECOSMO (Daewel & Schrum 2013), HBM-ERGOM (Maar et al. 2011, Maar et al. 2016), and
2 NORWECOM (Skogen et al. 1995, Skogen & Sjøiland 1998)) to force the temporally and
3 spatially explicit HTL model OSMOSE in a setup for the North Sea (Figure 1). The provided
4 plankton fields were divided into size bins and then used as time- and spatially explicit prey
5 fields in the OSMOSE model. The HTL model was run with an invariant mode setup (domain,
6 spatial resolution, year and time-step) to allow a clear analysis of the forcing impacts of the
7 different LTL models. The resultant HTL biomass and spatial distributions are analysed for
8 each LTL model and compared for zooplanktivorous fish, flatfish and
9 piscivorous/benthivorous fish (hereafter called predators). Sensitivity analyses were performed
10 with the aim to understand the role of zooplankton size categories and the magnitude of the
11 zooplankton biomass, by changing both for each LTL model while maintaining its unique
12 spatial and temporal pattern.

13

14 **2. Methods and Materials**

15 **2.1. Lower trophic level models**

16 Five different LTL models were chosen to provide prey fields for the HTL model (Delft3D-
17 WAQ, ECOHAM, HBM-ERGOM and NORWECOM (Figure 1). While data from
18 ECOHAM, HBM-ERGOM and NORWECOM were provided as two groups of phytoplankton
19 and two groups of zooplankton, ECOSMO results were combined into one group of each, and
20 Delft3D-WAQ provided four groups of phytoplankton and one group of zooplankton (Table
21 1). A description of these models (except for ECOHAM), their setup configuration and their
22 planktonic food web was provided in Maar et al. (2018) as well as in the associated references
23 given above. ECOHAM is described in detail in Lorkowski et al. (2012). All LTL model results
24 were provided as bi-weekly averages of the year 2004 to eliminate inter-annual variability. The

1 reason for using 2004 is that at the time of this study this was the only calendar year all five
2 models had in common. Further, according to the annual North Atlantic Oscillation (NAO)
3 index of 0.2, 2004 could be considered as a normal year without extreme events
4 (<https://www.cpc.ncep.noaa.gov>). Long-term differences in interannual variability of the LTL
5 models is not considered. The LTL model results were interpolated to the OSMOSE model
6 grid of 1/9ICES grid cell (20 km longitude and 18.5 km latitude) and integrated with depth (0
7 m to bottom). For application by the HTL model, the LTL fields were reduced to the largest
8 spatial domain the LTL models had in common, the central to southern North Sea (Figure 2).

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

18 Biomass of macro-invertebrates (deposit feeders, meiofauna, and suspension feeders) was
19 obtained from a previous set-up using results from the ERSEM model (Butenschön et al. 2016)
20 and applied to all simulations, because it was not a standard output by the considered LTL
21 models (Supplementary Fig. S1). For macro-invertebrates, conversions were made assuming
22 mgC to correspond to ash free dry weight, and assuming that the benthos groups defined in
23 ERSEM consist of equal percentages of polychaetes, crustaceans, gastropods and bivalves, we
24 come to an average conversion of 10.5 gWW gC^{-1} (Ricciardi & Bourget 1998). Size ranges
25 were assigned to allow size-dependent predation (Table 2).

2.2.Higher trophic level model

The HTL model used is OSMOSE, developed by e.g. Shin et al. (2004) and Travers et al. (2009), and here parameterized for the North Sea (Supplementary Text S1 and Text S2). A brief description of the OSMOSE model and the assumptions are given in the following sections. The model is size-based, spatially explicit and multiple species can be incorporated (Supplementary Tables S1 and 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 one 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 year International Bottom Trawl Survey (IBTS) and Beam Trawl Survey (BTS) data (obtained from the ICES Datas database, period 1985-2005) for the North Sea. Differences in distributions of size classes were visually assessed on the basis of the present-absence maps. 'Present' was defined as more than 2 individuals of a size class present in an ICES rectangle during the 20 year 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

1 minimum and maximum ratio (Supplementary Table S3). An accessibility matrix is used to
2 exclude prey from the diet in case of unrealistic predator to prey size ratios, for example to
3 exclude herring consuming infauna (Supplementary Table S4).

4 After consuming prey biomass upon satiation or until prey run out, the predation efficiency, ξ_i ,
5 is calculated as the amount of food eaten divided by the available food corresponding to
6 predator satiety. If more than one prey type is available, predation is uniformly distributed
7 according to relative abundance. Satiation is set to be a maximum ingestion rate of 3.5 gram of
8 food per gram predator body mass per year (Shin et al., 2004; Travers et al., 2009). The total
9 prey biomass consumed (PB) is used to assess the predation efficiency. Prey consists of fish
10 (conspecifics or other species), which are dynamically modelled, and resources used as forcing
11 function, namely phyto- and zooplankton and macro-invertebrates. Densities of the forced
12 resources are spatially explicit and vary in time using biweekly time steps, and result from LTL
13 models.

14 Based on the consumption efficiency, an individual may grow, maintain itself or starve. If
15 predation is sufficient, $\xi_i > \xi_{crit}$, individuals grow. ξ_{crit} represents species independent predation
16 efficiency value of $\xi_{crit} = 0.57$ (Shin & Cury 2004) . The minimum growth is zero if no food is
17 consumed. The realized growth is bounded by the maximum and minimum growth and is a
18 function of food intake (following Travers et al. (2009)) (Table 3). The maximum attainable
19 growth increment per time step is based on the von Bertalanffy growth curve (Bertalanffy
20 1957) and the individual's length. A hypothetical age is set based on the current individual
21 length. The potential maximum length at the next time step is then the length at the hypothetical
22 age + the time step. This assumption allows individuals that by chance move from a food-poor
23 cell to a food-rich cell to catch-up in size with individuals of similar age that by chance
24 encountered more profitable circumstances.

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

10 Species-specific maturation size, the size at which 50% of the population is mature, was based
11 on IBTS and BTS data (Blanchard et al. 2014). Annual fecundity parameters are based on
12 literature, as is the species-specific spawning period. Spawning has a seasonal cycle, and hence
13 the total annual fecundity is spread out over the year based on the spawning period
14 (Supplementary Table S2). Per time step, the biomass of mature individuals is multiplied with
15 fecundity and seasonal scalar to obtain the total reproduction per species at time step t (N_0).
16 These new individuals are split over a fixed number of 500 super-individuals per time step.
17 Each super-individual is then randomly distributed on to the appropriate presence-absence
18 map.

19 The focus of the present study was to investigate the effects on the OSMOSE HTL model fish
20 biomass, when using different LTL model results as input. The HLT model results will
21 therefore be compared on group level and not on species level. We grouped the fish species
22 into functional types; ‘predators’ (cod, grey gurnard, haddock, saithe and whiting), ‘flatfish’
23 (dab, plaice and sole) and ‘zooplanktivores’ (herring, sandeel, Norway pout and sprat). Further,
24 it is out of scope for this study to validate the used HTL model against measured species
25 biomasses, especially as data on fish biomass are sparse and do not cover the required temporal

1 and spatial scale. However, OSMOSE has already been successfully applied in other regions
2 (Travers et al. 2009, Halouani et al. 2016, Fu et al. 2017). Because we only have one calendar
3 year of LTL input (2004), the prey input from this year was repeated 40 times to create a time
4 series for OSMOSE. The first 30 years are for spin-up and the following 10 years were used to
5 generate the results. This is needed due to differences in lifespan of the fish species modelled.
6 We calculated the annual mean and standard deviation of biomass over these 10 years . Biomass
7 values were normalized using the mean of the specific model, so a value of 1 equals the mean.

8

9 **2.3. Sensitivity study**

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

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

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

$$11 \quad CV = \frac{SD}{mean} \times 100\% \quad (\text{eq. 1})$$

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

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

19

20 **3. Results**

21 **3.1. Prey fields**

22 Figure 3a shows annual means of total plankton, phytoplankton and zooplankton biomass for
23 the study area for the five different LTL models. The numbers include diatoms and autotrophic

1 flagellates/non-diatoms or micro- and mesozooplankton (Table 1). The phytoplankton biomass
2 across the models varied between 19 and 28 gWW m⁻² with highest value for ECOHAM and
3 similar values for the other models (Figure 3a). Zooplankton biomass varied between 4 and 18
4 gWW m⁻², with NORWECOM and ECOHAM delivering 2–5 times higher input zooplankton
5 biomass than the other models (Figure 3a). Total plankton biomass was highest for ECOHAM
6 and lowest for Delft3D-WAQ and HBM-ERGOM. The contribution of mesozooplankton to
7 total zooplankton biomass was 38%, 84% and 41% for ECOHAM, HBM-ERGOM and
8 NORWECOM, respectively (Figure 3a). For the seasonal patterns, total zooplankton biomass
9 was normalised by the annual mean for each model to allow a more direct comparison across
10 models (Figure 3b). The timing of the spring bloom had a maximum around week 20 to 22 for
11 all models except Delft3D-WAQ, which had a later maximum in week 28 and another in week
12 38. ECOHAM also had a weak signal of a second maximum around week 40. The seasonal
13 patterns were significantly correlated across all models with the highest correlations between
14 ECOSMO and NORWECOM ($R^2 = 0.91$) and lowest between Delft3D-WAQ and HBM-
15 ERGOM ($R^2 = 0.48$) (Table 4). The spatial pattern of annual zooplankton biomass (normalised)
16 showed generally higher values in the southern part and along the coastline with strongest
17 spatial gradients for Delft3D-WAQ, ECOSMO and NORWECOM (Figure 4). Macro-
18 invertebrate data showed highest biomass of deposition feeders along the eastern coastline and
19 northern part of the model domain, highest meiofauna biomass in the southern part whereas
20 suspension feeders were patchier distributed (Supplementary Fig. S1).

21 **3.2. HTL model results**

22 The input from the five different LTL models produced similar relative contributions of the
23 three HTL groups to total biomass but more than five-fold difference in total fish biomass
24 (Figure 5). Zooplanktivores were the dominating group for all LTL model inputs with 75–82%
25 of total HTL biomass. The predator biomass and flatfish biomass were on average 14–22% and

1 3–4%, respectively, of total adult HTL biomass across LTL model inputs (Figure 5). Hence,
2 predator biomass was always higher than that of flatfish. Total adult biomass of HTL was
3 highest for prey fields from ECOHAM (273 kilo tonne wet weight (ktWW)), lowest for prey
4 fields from Delft3D-WAQ (50 ktWW), while prey fields from the three remaining models gave
5 more similar results (153–205 ktWW). Both, the total biomass and the individual biomass for
6 each HTL group increased with increasing zooplankton biomass (Figure 6). For ECOHAM and
7 NORWECOM with similar high levels of zooplankton biomass, the biomass of
8 zooplanktivores was nevertheless 33% higher in ECOHAM. Flatfish, which mainly feed on the
9 benthic prey items, showed a similar but less strong response with increasing zooplankton
10 biomass, due to their short but crucial dependence on zooplankton during early life stages.
11 There was also an overall linear positive correlation between predator biomass and its fish prey
12 (zooplanktivores and flatfish) biomass across models ($n=5$, $R^2=0.87$, $p<0.05$).

13 The spatial distribution of simulated HTL adult biomass of the zooplanktivores, flatfish and
14 predators showed overall similar patterns between the different LTL models (Figure 7).
15 Zooplanktivores biomass was concentrated in the southern areas and decreasing northwards
16 for all LTL model inputs. ECOHAM showed the highest total zooplanktivores biomass (Figure
17 6), which reflected that the zooplankton was widely distributed throughout most of the study
18 area (Figure 4). Flatfish biomass produced from all the LTL model inputs had an even more
19 strong south-northward gradient than zooplanktivores with lowest biomass levels for Delft3D-
20 WAQ and HBM-ERGOM (Figure 7). Predators were distributed all over the study area for all
21 LTL models, with core areas found either in the north-eastern part of the area or in the English
22 Channel outlet.

23 **3.3. Sensitivity study results**

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

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

1 **4. Discussion**

2 **4.1. General findings**

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

11 **4.2.Characteristics of the LTL models**

12 The provided zooplankton biomass to the HTL model varied by a factor up to five between the
13 models (Figure 6). In addition, the applied LTL models showed differences in their spatial-
14 seasonal patterns (Figure 8c) that can affect the trophic match-mismatch and outcome of the
15 HTL model. Delft3D-WAQ showed e.g. very strong spatial gradients, with highest values in
16 the coastal waters, but with lower zooplankton biomass in the open waters, compared to the
17 other LTL models (Figure 4, 8c). ECOHAM and NORWECOM showed the overall highest
18 zooplankton biomass, but their spatial-seasonal patterns were very different (Figures 3b, 4 &
19 8c), with ECOHAM having a smoother spatial and seasonal variability (Figures 3c and 8c).
20 LTL models are often based on similar principles yet differ in model assumptions, the
21 underlying hydrodynamics, their resolutions in space and time, the external forcing conditions
22 and choices and description of functional groups and hence, can lead to substantially different
23 results (Skogen & Moll 2005, Lenhart et al. 2010, Sailley et al. 2013, Maar et al. 2018). Most
24 studies found a high variability across LTL model results, but concluded that ensemble

1 modelling can be used to reduce uncertainty in model projections and estimate a range of
2 possible outcomes (Niiranen et al. 2013, Queiros et al. 2016, Maar et al. 2018).

3 Continuous plankton recorder (CPR) data from the period 1990-2000 showed a
4 mesozooplankton biomass of 3–4 gWW m⁻² (0-20 m) in the southern North Sea (Pitois & Fox
5 2006). Other reported values were 6 gWW m⁻² from May to September in the central part
6 (Fransz et al. 1991) and 16 gWW m⁻² for the whole North Sea including the northern part
7 (outside our model domain) with a high *Calanus finmarchicus* abundance (Fransz et al. 1991,
8 Mackinson & Daskalov 2007). The reported range is similar to our model results of 4–9 gWW
9 m⁻² for the mesozooplankton biomass in the three models with two zooplankton groups and
10 total zooplankton biomass in the models with one zooplankton group (Figure 3a). CPR data
11 shows that zooplankton biomass generally starts to increase in March (weeks 9-12), peaks in
12 May to August (weeks 18-39) where after it gradually declines to winter values (Pitois et al.
13 2012). This pattern is consistent with the modelled seasonality of zooplankton biomass (Figure
14 3b). It should be noted that it is difficult to directly compare modelled annual zooplankton
15 biomass with (scarce) observations, because sampling often occurs in peak biomass periods
16 and at different years, locations and depth (Skogen et al. 2021, Hjøllø et al. in press).
17 Zooplankton biomass is most often calibrated against measured mesozooplankton biomass e.g.
18 from CPR data and ICES data, because there is no coherent data set for microzooplankton in
19 the North Sea. Microzooplankton plays different roles (e.g. feeding mode, size range) in the
20 models and can therefore have different biomasses relative to that of mesozooplankton (Maar
21 et al. 2018). Hence, the highest uncertainty probably lies within the estimation of
22 microzooplankton biomass as previously highlighted (Sailley et al. 2013, Maar et al. 2018).
23 However, the differences between the LTL models were suited to test a range of realistic prey
24 patterns in the HTL sensitivity study.

25

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 (Figures 6 and 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 (Figure 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 (Figure 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 two models had the same share of meso- and microzooplankton, so in this case different size bins could not be the reason. Instead, the more evenly spatial-seasonal distribution of zooplankton in ECOHAM compared to NORWECOM could explain the observed difference (Figure 8c). Zooplanktivore biomass shows to be sensitive to spatial and temporal variation in LTL input. A higher coefficient of variation, 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 (Figure 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.

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

8 Overall zooplanktivore biomass was found to be sensitive to the provided zooplankton groups
9 (meso-, micro- or bulk zooplankton) due to differences in the size range each group represents
10 (Figure 8a). The HTL will outgrow the smallest zooplankton first and then only rely on the
11 mesozooplankton due to the applied predator/prey size-ratios in the model (Supplementary
12 Table S3). However, when the zooplankton is provided as one group with a wider size bin, the
13 HTL can exploit them more efficiently and especially over a longer time period, as differences
14 in seasonality between the different zooplankton groups are levelled out. A sensitivity study
15 with the original size bins (Supplementary Fig. S4 and Fig. S5) shows the same pattern for each
16 model compared to using a single size bin. Results differ in total fish biomass driven by
17 differences in meso-zooplankton biomass not total zooplankton biomass. The present study
18 therefore suggests that it is important to consider size bins in the zooplankton field when
19 coupling to HTL models (Daewel et al. 2008, Huebert et al. 2018). The use of a size-spectrum
20 for zooplankton, instead of groups with a given size range, can further improve the assumption
21 of size-based foraging and will affect the HTL results (Huebert et al. 2018). A size-spectrum
22 approach or modelling specific zooplankton species may also allow inclusion of prey
23 preference in ways other than size-based predation, such as inclusion of species preference or
24 caloric content or catchability differences for a more mechanistic approach. Overall, our

1 findings confirm that zooplankton is an influential link in the trophic transfer between LTL and
2 HTL (Munk 1997, Heath 2007, Daewel et al. 2014).

3 **4.4.HTL group compositions and spatial patterns are similar across models**

4 The HTL group composition and overall spatial patterns (Figures 5 & 7) were similar despite
5 the spatial and temporal differences between the LTL model inputs and differences in absolute
6 biomass (Figures 3b, 4 & 8c). The dominance of zooplanktivores over predators, and predators
7 over flatfish, are in agreement with previous studies in the North Sea (Greenstreet et al. 1997,
8 Heath 2005). The efficient transfer of energy from zooplankton to zooplanktivores for all LTL
9 inputs suggests that no strong phenological trophic mis-matches occur in our simulations. On
10 the contrary, the differences in spatial and temporal scales between LTL models fade out at
11 higher trophic levels when considering the relative group composition. A possible explanation
12 for this may stem from the wider spatial and temporal scales relevant for HTL species when
13 compared to the LTL food web: i.e. fish have a longer longevity and swim larger distances than
14 their plankton prey. Also, most fish species only rely on zooplankton for a relatively short
15 period of time during their lifespan, wherefore plankton is not the only food source even though
16 it plays a crucial role during critical life stages for fish (Bochdansky et al. 2008). As the fish
17 grow larger, they will start feeding on other resources, such as benthic organisms and other
18 fish, which has a stronger effect on the overall stock biomass. Other compensatory mechanisms
19 that dampen food web responses to differences in plankton prey fields include loss of energy
20 due to respiration and metabolic costs, cannibalism, predation and other types of mortality
21 (McCann et al. 1998b, Andersen & Pedersen 2010), which are included in OSMOSE through
22 the growth curve, feeding and use of background mortality. The observed dampening of the
23 trophodynamics in relative group composition when using different prey fields is in agreement
24 with previous findings of weak food web responses to changes in bottom-up or top-down
25 forcing (McCann et al. 1998a, Pace et al. 1999, Shurin et al. 2002, Andersen & Pedersen 2010,

1 Bossier et al. 2018). Overall, the similar responses of the HTL spatial biomass distribution and
2 feeding group composition across LTL model inputs suggest a high confidence of the fish
3 community model results, which is important for model acceptance by stakeholders and
4 implementation of model results into management actions (Niiranen et al. 2013, Peck et al.
5 2018).

6 **4.4. Model caveats and experiences from this process**

7 The provided study offers a number of lessons on linking HTL food web models to LTL
8 models. Our approach only considered one-way coupling and not feed-back processes from
9 HTL to LTL, which could give a bias in the estimates of available food and hence growth of
10 HTL (Travers et al. 2007). We found a linear food response of fish biomass to increasing
11 zooplankton biomass in the sensitivity runs (Figure 8b) because there is no feed-back from
12 HTL to planktonic prey (no food depletion) inhibiting top-down control. Although within a
13 time step food availability decreases due to consumption, each time step food is replenished as
14 if no consumption occurred. Two-way coupling or intermediate solutions may alter the HTL
15 response to increased prey fields (Rose et al. 2010). Food based movement of the HTL in
16 combination with a two-way coupling of LTL and HTL could dampen the linear increase of
17 HTL biomass with increasing zooplankton. Travers et al. (2009) compared one-way coupling
18 and two-way coupling for OSMOSE parameterized for the Benguela system and found changes
19 in the food web pathways and relative contribution of fish groups. Directional movement to
20 high value food patches may lead to local food reduction, dampening spatial variation in prey
21 fields. This in turn may lead to a more even distribution of fish. Even though all employed LTL
22 models include a general zooplankton mortality that implicitly takes predation from HTL into
23 account, a more dynamic predation mortality would result in differences in zooplankton
24 seasonality and biomass composition (Travers et al. 2009, Maar et al. 2014, Daewel et al.

1 2019). We would recommend a two-way coupling for ecosystems especially with clear top-
2 down controls of HTLs on the zooplankton.

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

16 The presented approach of combining LTL models and a HTL model did not take into account
17 differences in the macro-invertebrates between the applied models, because this group is
18 typically not considered in standard NPZD –type models. Instead, data on macro-invertebrates
19 was delivered from the ERSEM model and is thus not consistent with the LTL plankton fields
20 provided by the different models. Even though they are the main food source for flatfish and
21 form a large part of the diet of predators, exploring the role of macro-invertebrates for HTL
22 models was beyond the scope of this study. We used LTL from the same year as input to the
23 HTL model although there is a year-to-year variability in zooplankton biomass levels and
24 distributions (Pitois & Fox 2006) . However, this variability is in the same range of the high
25 spatial-temporal variability amongst the provided LTL prey fields from the same year (Figure

1 8c) , thus we can assume that data from more years would likely not change the overall
2 conclusions. The HTL model used a size-based approach for zooplankton predation because
3 the LTL models simulate only plankton functional types and not species diversity. As it is well
4 known that the predator-prey size ratio is very important for fish predation (Munk 1992, 1997,
5 Daewel et al. 2008) we believe that this approach is valid. However, due to the missing
6 information other factors like prey quality and selectivity cannot be considered in our
7 modelling approach, although they could influence the energy transfer into and within the
8 food web (Mitra & Flynn 2006). Climate change effects were not considered in this paper.
9 Previously performed climate scenarios for the North Sea ecosystem agree that the overall
10 productivity of the ecosystem will be reduced under high emission scenarios as a consequence
11 of changed stratification and circulation and the associated reduction in nutrient inflow (Holt
12 et al. 2016, Mathis et al. 2019). In addition, Villarino et al. (2015) show that species may shift
13 northward and that the spring bloom may advance under climate change conditions across the
14 North-Atlantic region and such changes are likely to occur in the North Sea (Helaouët et al.
15 2011, Mackas et al. 2012, Maar et al. 2013). It depends on fish species tolerance ranges and
16 spatial and temporal overlap if and under which conditions changes in zooplankton may affect
17 fish (Beaugrand et al. 2003). In addition, climate change will affect fish directly and indirectly
18 through changes in temperature depending on fish size and species (Wang et al. 2020), and for
19 example through phenological changes in spawning place and timing, and larval drift (Lacroix
20 et al. 2018, van de Wolfshaar et al. 2021). Feeding a HTL model with LTL climate scenarios
21 is not sufficient to study full system effects. Coupling of LTL and HTL models to study the
22 effects of climate change must therefore encompass possible responses at lower trophic levels
23 as well as higher trophic levels. In addition, we did not vary fishing mortality in combination
24 with the different zooplankton fields. Varying fishing pressure may lead to direct effects on
25 target species and indirect effects on target and non-target species due to changes in

1 competitive and predatory interactions (Travers et al. 2010), while climate change may affect
2 long lived species less than short lived species (Field et al. 2006). To allow for cascading effects
3 of top-down and bottom-up control would require a two-way coupling of LTL and HTL.
4 Further, non-linear effects are expected due to the complexity of the model, largely due to the
5 fact that the fish are modelled fully size-structured, allowing for (size-dependent) changes
6 between predator-prey and competitive interactions. Varying both zooplankton biomass and
7 anthropogenic pressures would be a logical next step to study the interplay between bottom-up
8 and top-down effects on the food web.

9 **4.5. Conclusions**

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

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8

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21

1 **Tables**

2 Table 1. LTL models used and the available plankton functional groups.

Model	Phytoplankton	Zooplankton
Delft3D-WAQ	Flagellates, diatoms, <i>Phaeocystis</i> , 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

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1 Table 2. Size ranges (μm) per plankton group estimated as the Equivalent Spherical Diameter
 2 (ESD). The ranges are agreed upon by all contact persons of the LTL models and based on
 3 literature (Hansen et al. 1997, Tonnesson et al. 2005, Daewel et al. 2008). Because the classes
 4 of suspension feeders, deposit feeders and meiobenthos are based on their feeding in the
 5 ERSEM model and not on size, different size ranges (cm) were chosen arbitrarily to
 6 discriminate between benthic food sources based on size.

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

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- 1 Table 3. OSMOSE model equations. A super individual is indicated by i and its state at time t .
- 2 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·yr.
Growth	$\begin{cases} \Delta L_{i,t} \\ = 0 & \text{if } \xi_{i,t} \\ < \xi_{crit} \\ = \frac{2\Delta L}{1 - \xi_{crit}} (\xi_i - \xi_{crit}) & \text{if } \xi_{i,t} \\ > \xi_{crit} \end{cases}$	Growth, ΔL . $\xi_{i,t}$ is the consumption efficiency ξ_{crit} is the maintenance cost
Reproduction	$N_0 = \alpha \cdot \varphi \cdot \frac{1}{2} \cdot \sum_{L > L_{mat}} B_{L,t}$	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 per gram.
Additional background mortality	$e^{-M_{add}}$	Species specific
Starvation mortality	$1 - e^{M_{i,t}}$ With $M_{i,t} = \frac{M_{max}}{\xi_{crit}} \cdot \xi_{i,t} + M_{max}$	$M_{max} = 1$ $\xi_{i,t}$ 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)

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- 1 Table 4. Seasonal correlation of zooplankton patterns across LTL models (Figure 3b) showing
- 2 R^2 values from regression statistics ($n=26, p<0.05$).

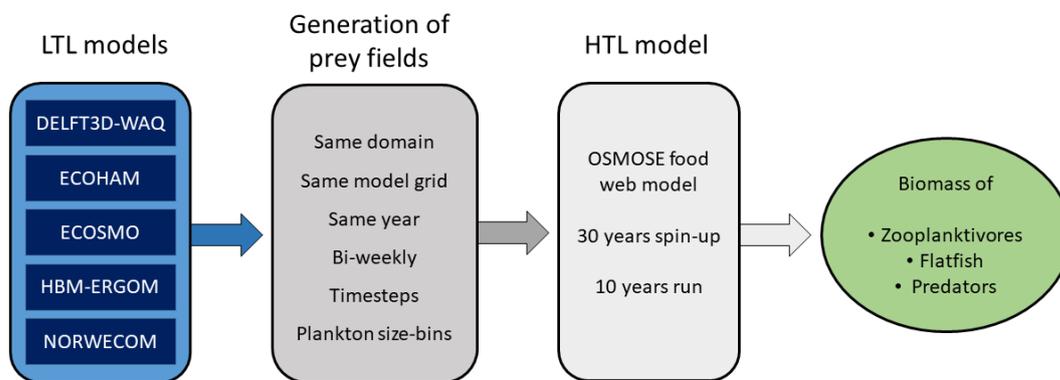
	ECOHAM	ECOSMO	HBM-ERGOM	NORWECOM
Delft3D-WAQ	0.73	0.74	0.48	0.87
ECOHAM		0.66	0.67	0.82
ECOSMO			0.78	0.91
HBM-ERGOM				0.79

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1 **Figures**

2 **Figure 1.** Conceptual diagram of the model approach. Five LTL models are providing 3D
3 plankton fields that are modified to have the same spatial and temporal format of the prey fields
4 as input to the HTL -food web model OSMOSE. The HTL model estimates spatial-resolved
5 biomass of zooplanktivores, flatfish and predators.



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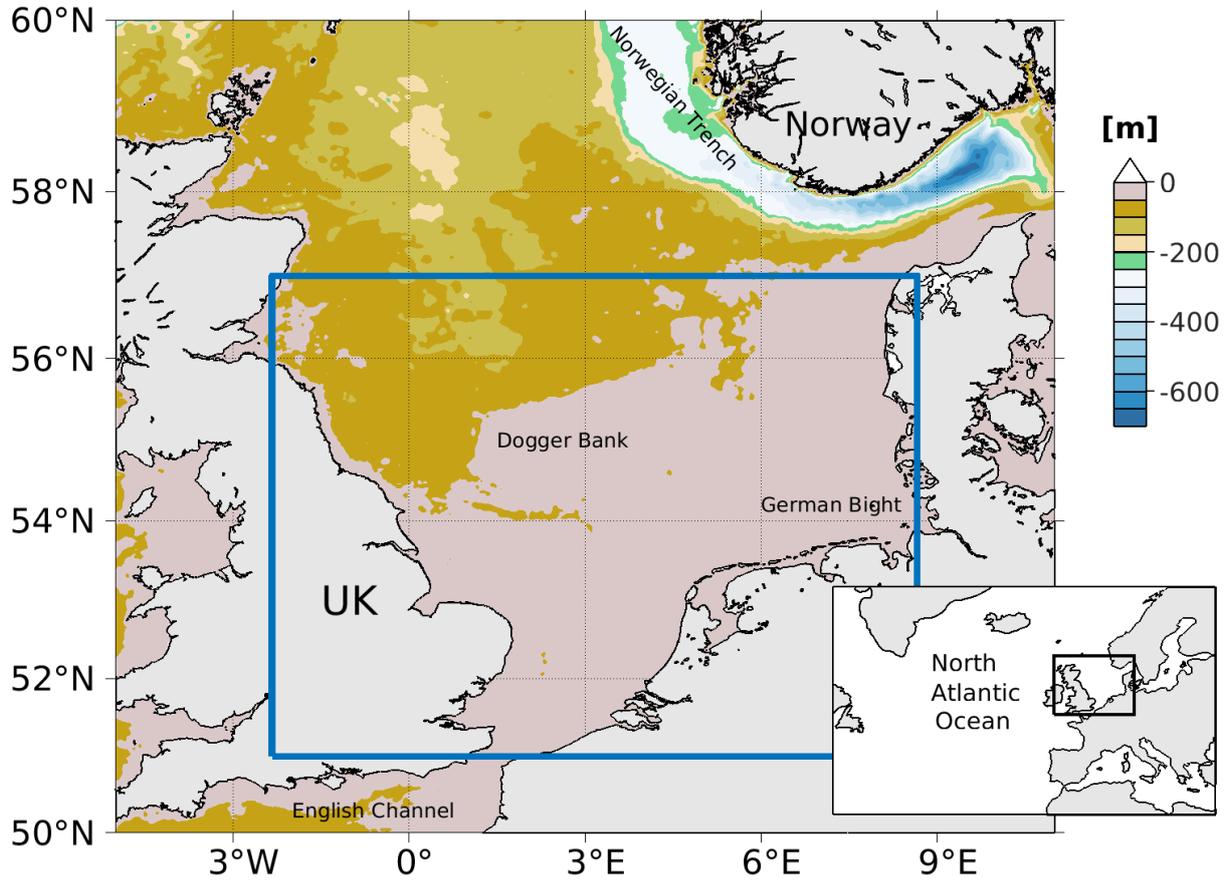
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1 **Figure 2.** North Sea bathymetry and its position within the North Atlantic Ocean (small insert).

2 The blue rectangle marks the domain common for all the 5 LTL models, and thus used for the

3 OSMOSE simulations

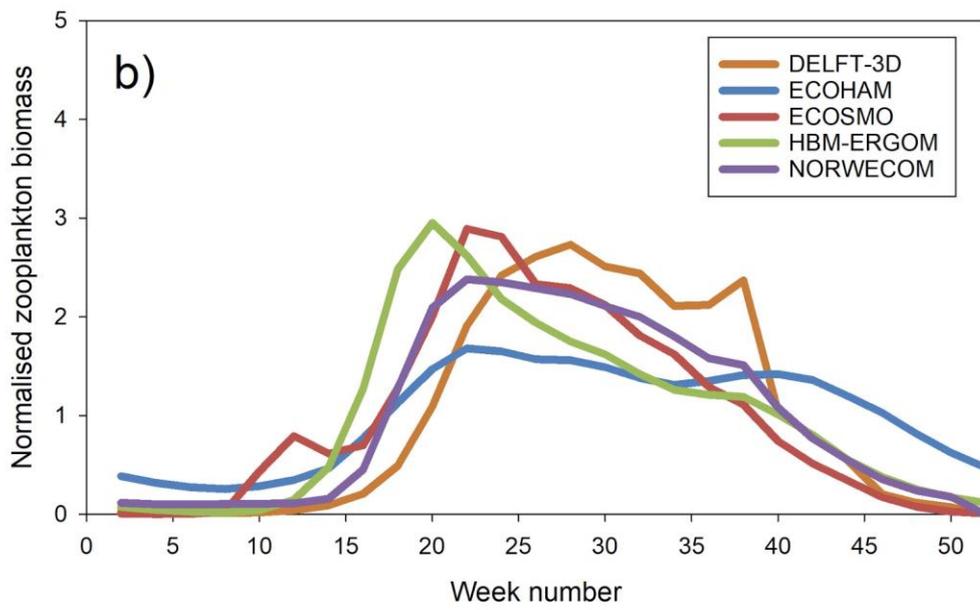
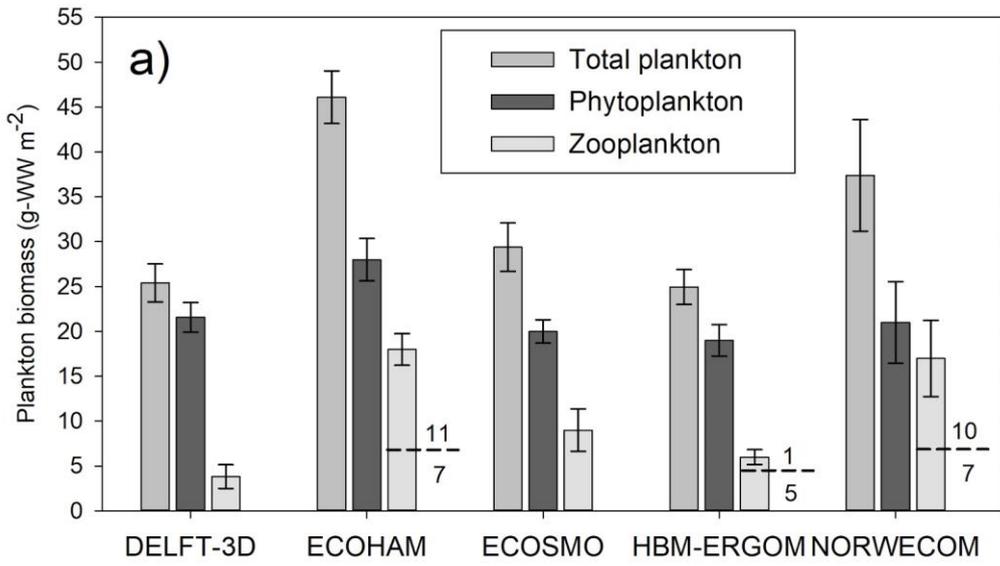
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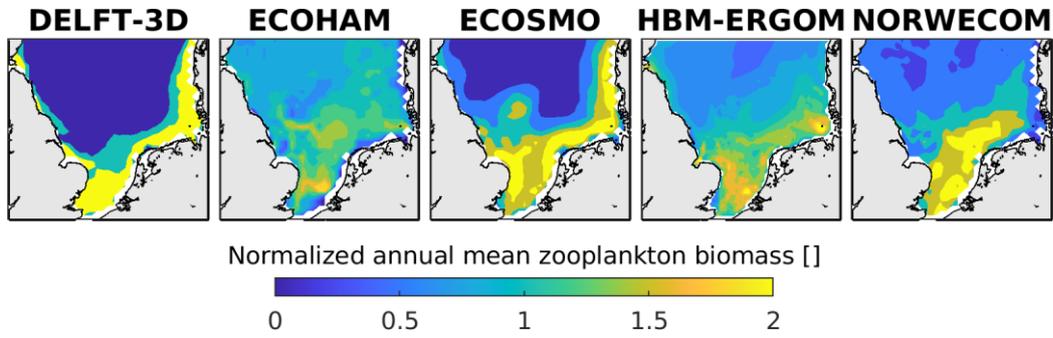
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1 **Figure 3:** a) Annual means (\pm SD) of total plankton, phytoplankton and zooplankton biomass
2 (gWW m⁻²) and b) seasonal development of total zooplankton biomass (normalised by the
3 mean of each model) for the five LTL models within the HTL model domain. The biomass of
4 meso- and microzooplankton contributing to total zooplankton are given below and above the
5 horizontal line, indicated in a) for the three models with two zooplankton groups.



1 **Figure 4.** Normalized annual means of total zooplankton biomass (normalised by the mean of
2 each model) for the five LTL models.

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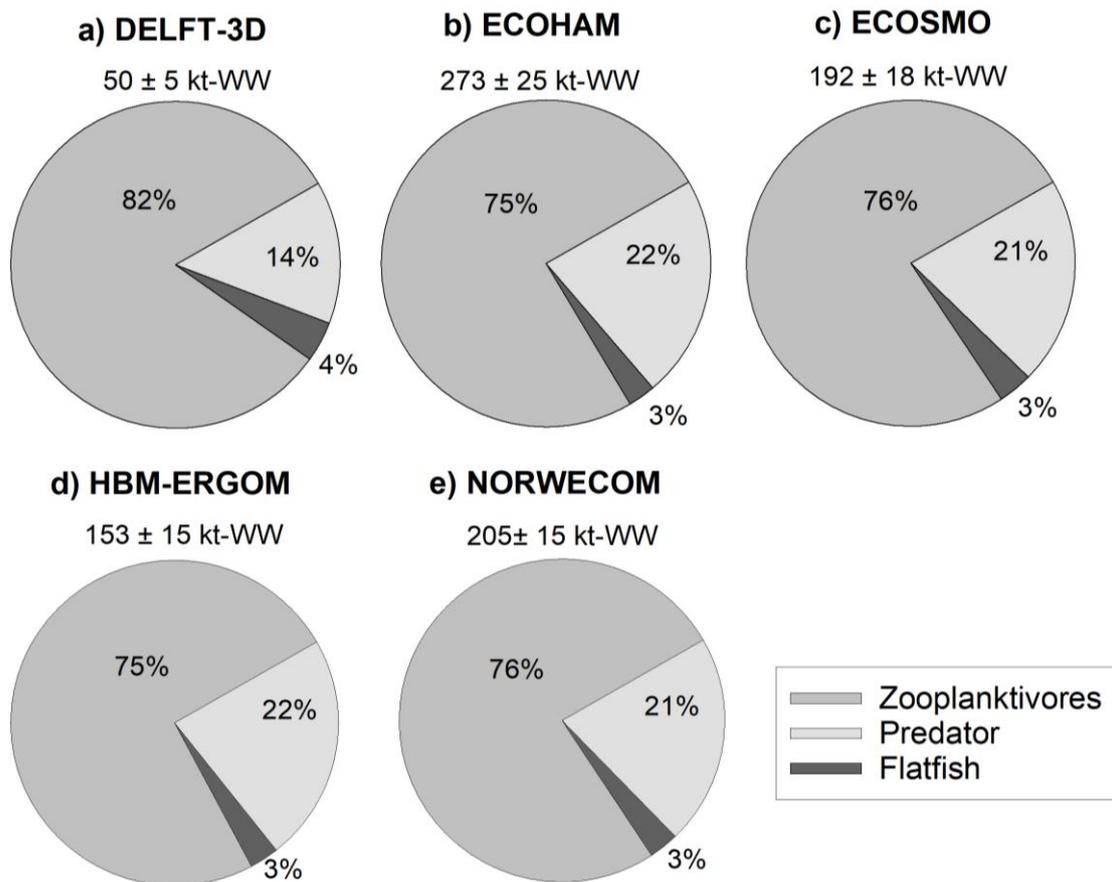
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- 1 **Figure 5.** Relative (%) adult HTL group biomass composition for each of the five LTL models
- 2 inputs a) Delft3D-WAQ, b) ECOHAM, c) ECOSMO, d) HBM-ERGOM and e) NORWECOM.
- 3 Mean total adult HTL biomass is indicated as ktWW \pm SD for the last 10 years (last time steps).

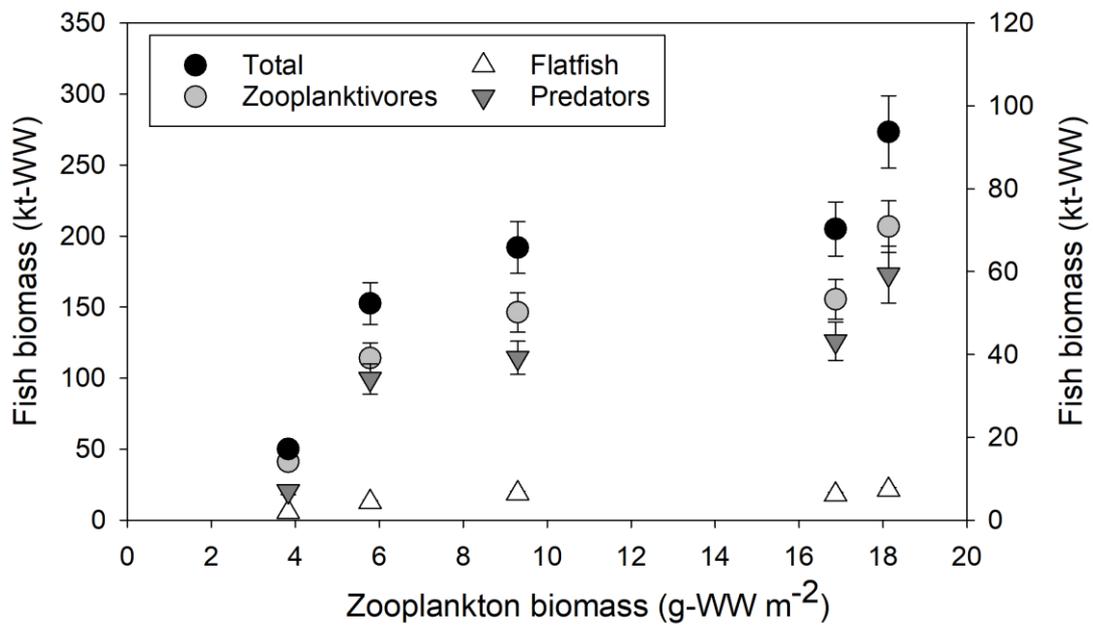


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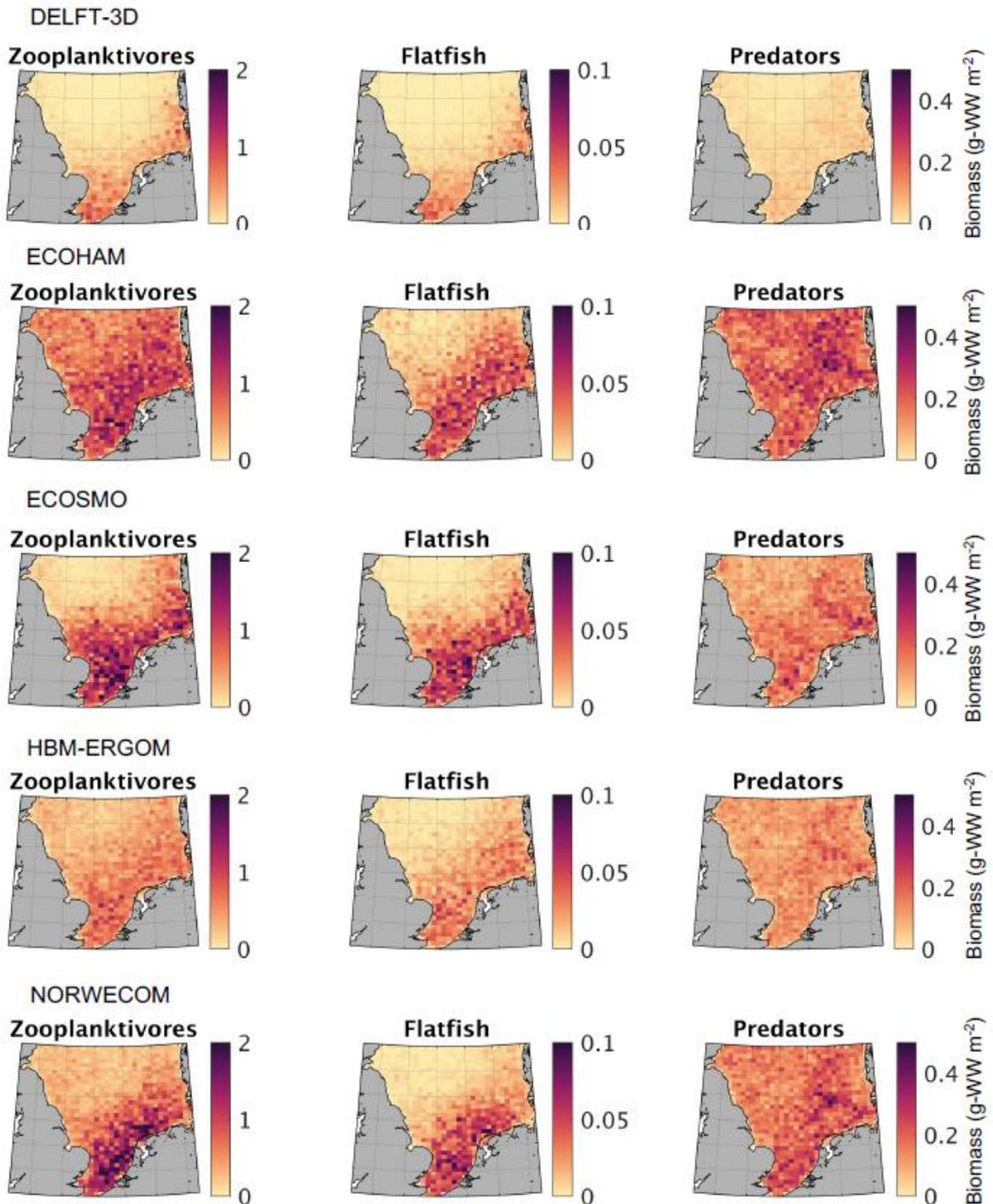
1 **Figure 6.** Means (\pm SD) of the last 10 years of the adult HTL biomass (ktWW) distributed on
 2 total HTL and zooplanktivores (spheres, left axis), and flatfish and predators (triangles, right
 3 axis) versus annual mean biomass (gWW m⁻²) of zooplankton biomass from each LTL model.
 4 LTL model order from left to right based on mean zooplankton biomass: Delft3D-WAQ, HBM-
 5 ERGOM, ECOSMO, NORWECOM and ECOHAM.



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1 **Figure 7.** Spatial distributed annual means of HTL biomass (gWW m⁻²) (zooplanktivores,
2 flatfish and predators; last time step) based on prey fields from five LTL models.

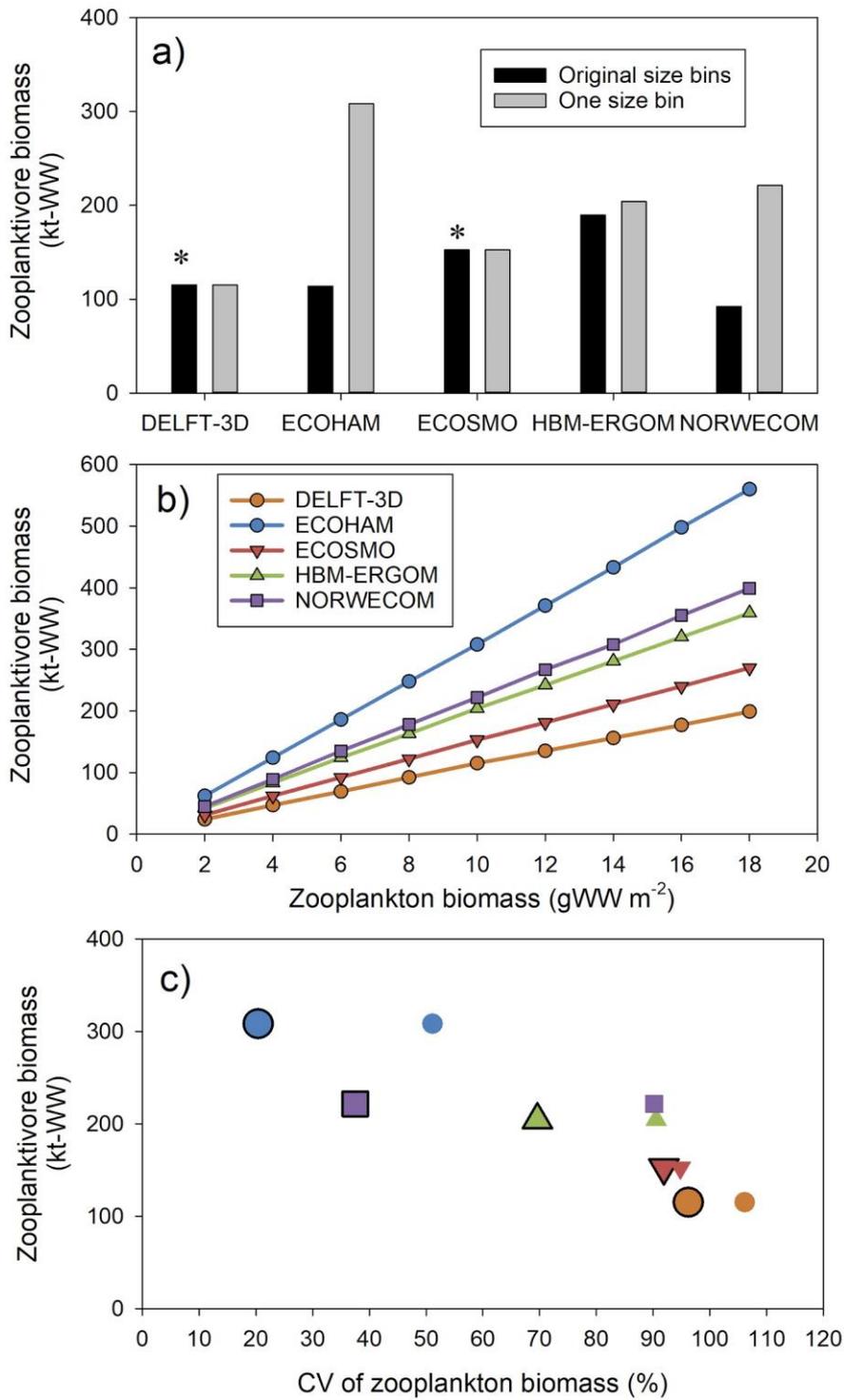
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1 **Figure 8.** Sensitivity studies of zooplanktivore biomass responses to a) zooplankton biomass
2 (adjusted to the same annual mean of 10 gWW m⁻² for all LTL models) distributed on the
3 original size bins (Table 2) or as one common size bin, b) zooplanktivore biomass as function
4 of increasing zooplankton biomass using one size bin for all LTL models and c) spatial
5 variability (large symbols) and seasonal variability (small symbols) of zooplankton biomass
6 expressed as the CV using one zooplankton size bin adjusted to the same annual mean (10 gWW
7 m⁻²) for all five LTL models. Zooplanktivore biomass corresponds to the biomass indicated by
8 the grey bars from panel a. * indicates the two models with a single zooplankton size bin.



Supplement.

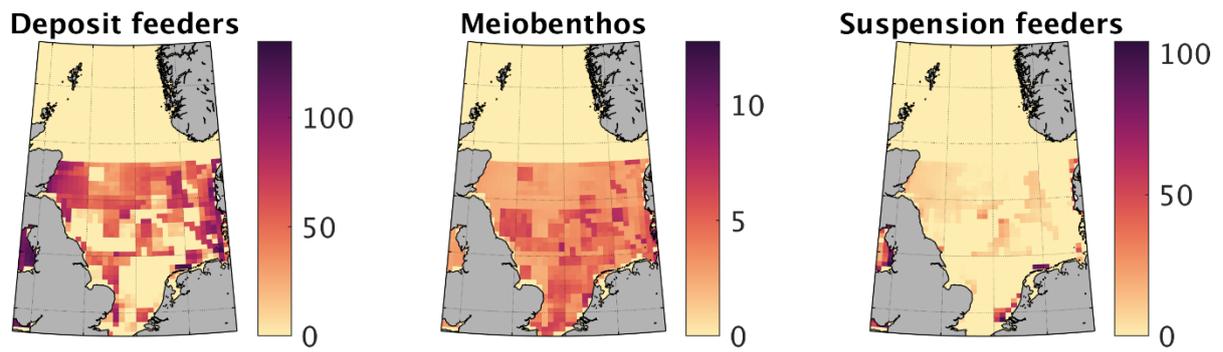


Fig. S1. Annual mean biomass (g-WW m⁻²) of the macro-invertebrate groups; deposit feeders, meiobenthos and suspension feeders from the ERSEM model for the used HTL model domain.

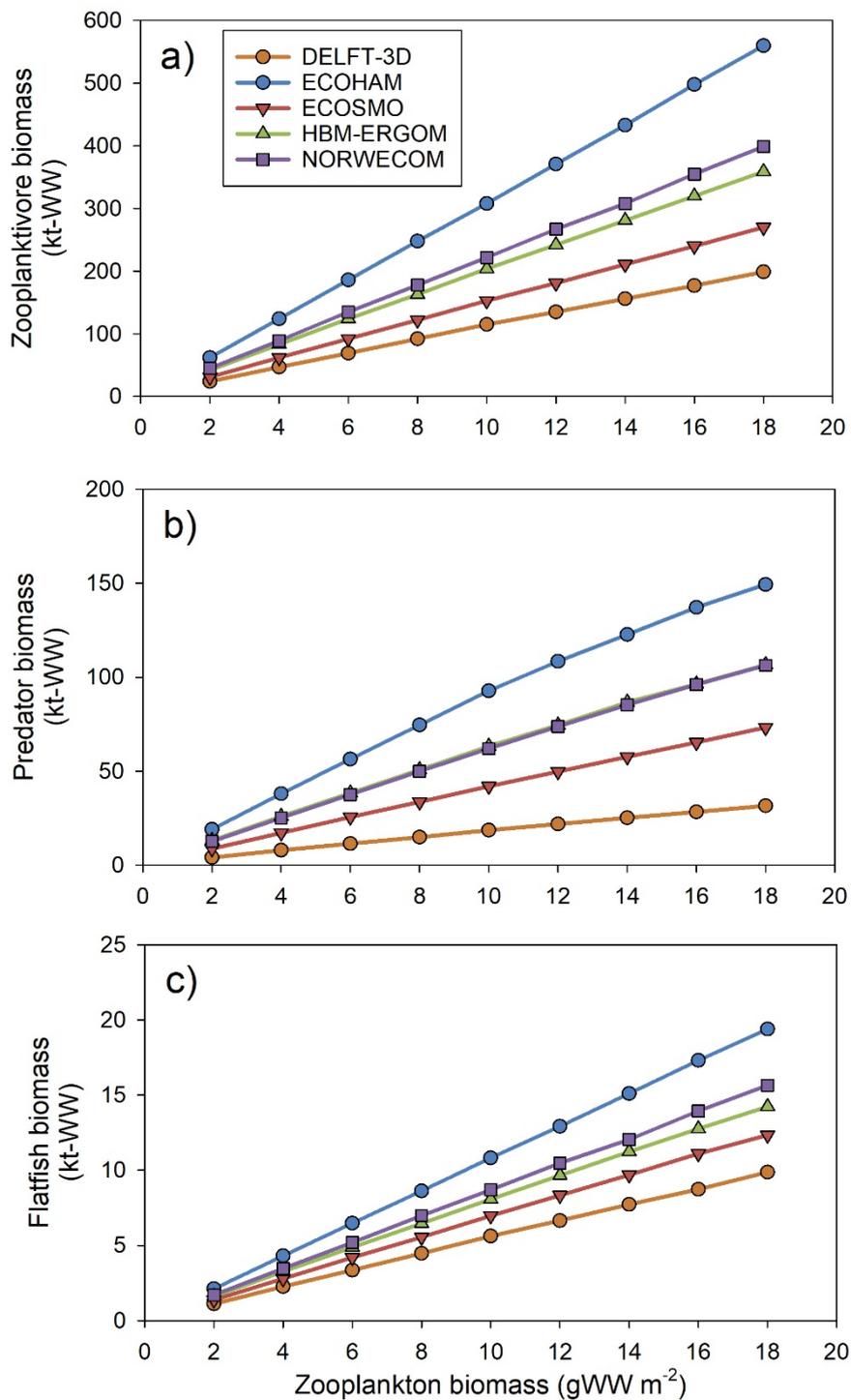


Fig. S2. Sensitivity study. Responses of zooplanktivore, predator and flatfish biomass versus increasing total zooplankton biomass, when using one bulk zooplankton size bin in all LTL models.

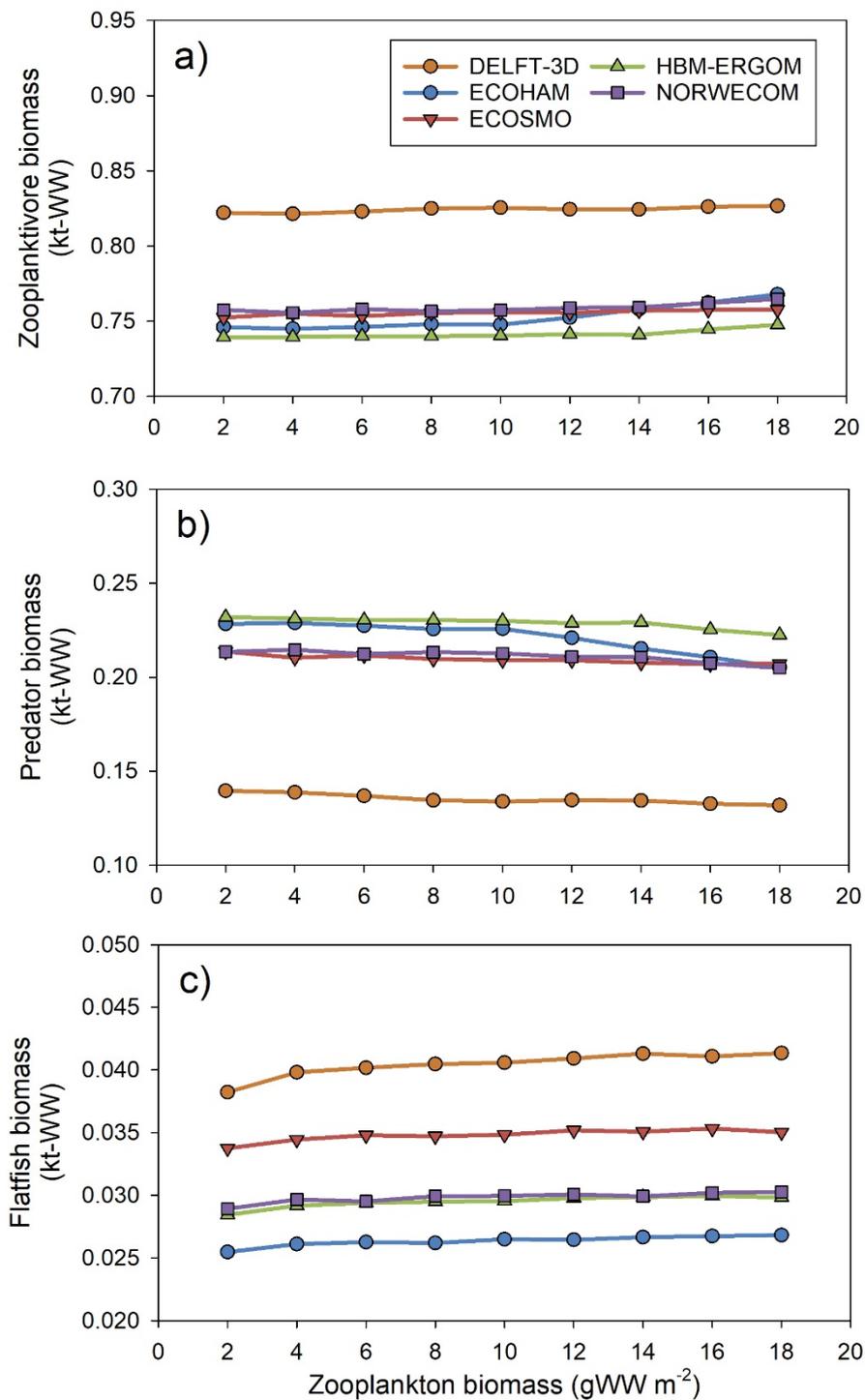


Fig. S3. Sensitivity study. Responses of zooplanktivore, predator and flatfish relative biomass contribution to total biomass versus increasing total zooplankton biomass, when using one bulk zooplankton size bin in all LTL models, see also Fig. S2.

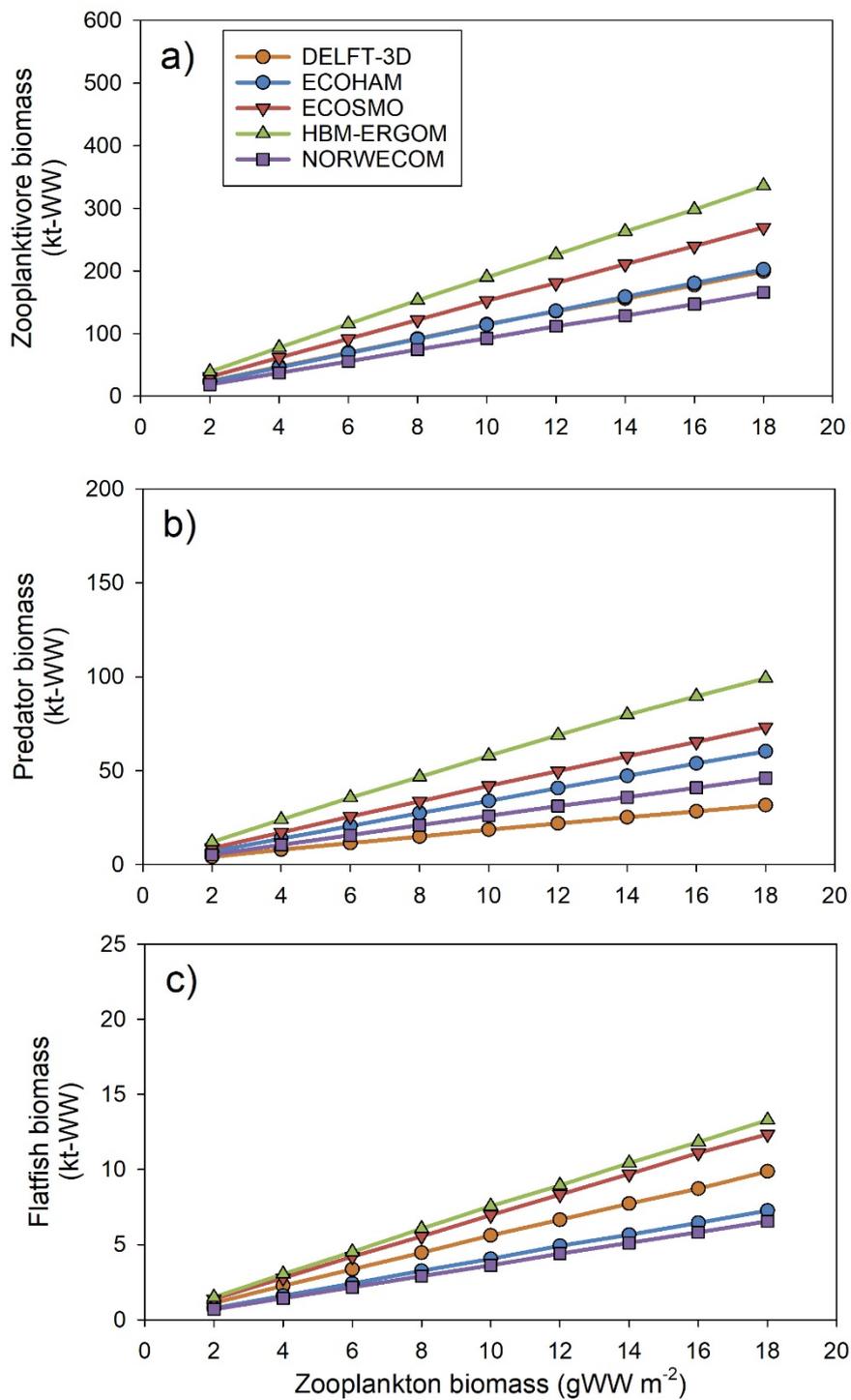


Fig. S4. Sensitivity study. Responses of zooplanktivore, predator and flatfish biomass versus increasing total zooplankton biomass, when using the original LTL model zooplankton size bins. Note that Delft3D-WAQ and ECOSMO have one size bin and ECOHAM, HBM-ERGOM and NORWECOM have two zooplankton size bins.

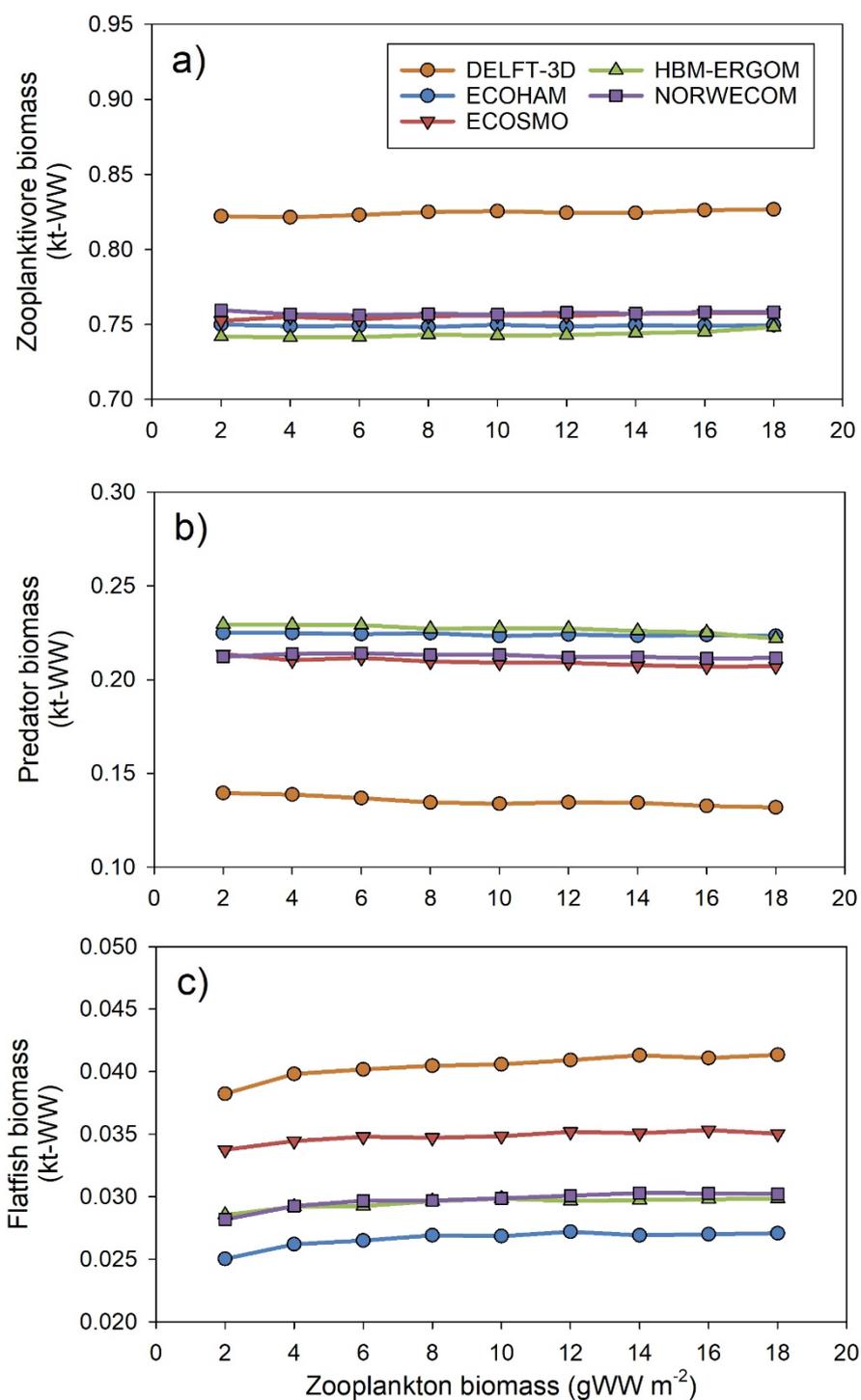


Fig. S5. Sensitivity study. Responses of zooplanktivore, predator and flatfish relative biomass contribution to total biomass versus increasing total zooplankton biomass, when using the original LTL model zooplankton size bins. Note that Delft3D-WAQ and ECOSMO have one size bin and ECOHAM, HBM-ERGOM and NORWECOM have two zooplankton size bins, see also Fig. S4.

Text S1. Fish life history

Life history parameter values on growth and maturation size were obtained from the ICES DATRAS database (accessed 24th of August 2012) for IBTS and BTS sex-maturity-age-length-weight data (SMALK). Only those 12 species present in the size spectrum model were selected (both Ammodytes and Ammodytidae for Sandeel were used) over the period 1983-2011 (1987 as starting year for BTS data). The Sex-Maturity ALK data was extracted for the North Sea IBTS and BTS data for all 4 quarters (noting that only quarters 1-3 are continued up till today for IBTS and quarter 3 is only present for BTS (in 2010 also in quarter 4 in area VIId)).

Estimating L_{inf} , K and t_0 was performed using a non-linear estimator using the Port algorithm following the equation $L = L_{inf}(1 - e^{-K(age-t_0)})$. As both the smallest as the largest fish are assumed to be underestimated in the survey due to catchability and measurement issues, additional weights are given to individual records to take this error into account. These sample weights are relative to the frequency of each length measurement. The most abundant length is assigned a weight 1, while each length measurement different from the most abundant one is given a weight equal to this difference in absolute length (in cm) and thereafter square root-transformed to not let weight scale linearly with the difference. As samples were taken from 4 different quarters, age were corrected for timing of the year by assuming that $age = age_{rings} + 0.125 + \frac{quarter-1}{4}$. The results are carefully scrutinized to ensure they are considered appropriate. Note that for some species, sexual dimorphism exists and hence L_{inf} growth is different for both sexes. In this study however, we have taken the average growth over both sexes together.

Also for the length-weight relationship a non-linear estimator, the Port algorithm, following the equation $W = \alpha L^\beta$ was used. As both the smallest as the largest fish are assumed to be underestimated in the survey due to catchability and measurement issues, additional weights are given to individual records to take this error into account, similar to the estimation of the growth parameters. The results are carefully scrutinized to ensure they are considered appropriate (and outlying values (input mistakes) that showed to be highly influential for the fit were removed).

Estimating size at maturity ($M50$) was performed again using a non-linear estimator using the Port algorithm following the equation $Mat = \frac{1}{1 + e^{S1 - S2 L}}$. To calculate proportion mature, all fish lengths were binned in centimetre classes and the ratio mature / immature was determined and treated as input value to the estimator algorithm. The results are carefully scrutinized to ensure they are considered appropriate (and outlying values (input mistakes) that showed to be highly influential for the fit were removed). The resulting estimates are presented in Table S1.

The seasonal cycle of spawning is based on literature (Table S2). Predation is based on the relative sizes of predator and prey. Based on literature and stomach content data the maximum and minimum predator-prey size ratios were estimated (Table S3). Besides size-based predation, an availability matrix was used to limit the diet of species when necessary. Limitations were based on benthic –pelagic foraging activity and a size-based scaling of the

grid cell area searched per time step. This scaling of ability of searching a grid cell per time-step is based on the assumption that larger species can cover a larger area than smaller species in search of food. For this we used the length at maturity (Table S1), assuming an average speed of 5 times this length and a search window of one square meter. Given the size of a grid cell and the time step this yields a fraction of the area covered per time step, for each species. As cod and haddock have a pelagic stage and diet until reaching 7 cm in length, we used two stages in the availability matrix for these two species, as this differentiation between benthic and pelagic prey is not covered by size-dependent predation (Table S4).

Table S1. Parameter values used for growth, reproduction and survival for each species. Growth parameters and size at maturity (L_{mat} , 50% mature) were estimated based on ICES data as described above (Text S1). Other references are given when used.

Species	Growth			Reproduction			Survival			
	L_{∞} (cm ⁻¹)	K (yr ⁻¹)	t0 (yr)	a (g cm ⁻³)	b	ϕ (eggs g ⁻¹)	Lmat (cm)	Egg size (cm)	Amax (yr)	Madd (yr ⁻¹)
Cod	137.95	0.183	0.519	0.005	3.173	492 ^g	54.39	0.153 ^h	25 ^c	0.1418 ^d
Dab	27.11	0.375	-0.206	0.01	2.986	3300 ^j	13	0.093 ^h	12 ^c	0.0736 ^k
Gr. gurnard	35.65	0.191	-1.261	0.004	3.198	339 ^a	17.69	0.14 ⁱ	9 ^c	0.141 ^k
Haddock	48.24	0.382	-0.051	0.005	3.16	480 ^g	26.91	0.145 ^h	20 ^c	0.1541 ^d
Herring	30.82	0.505	-0.193	0.002	3.429	247 ^g	23.36	0.12 ⁱ	10 ^c	0.1206 ^d
N. pout	21.78	0.606	-0.096	0.009	2.941	720 ^g	14.35	0.118	4 ^c	0.1877 ^d
Plaice	43.45	0.255	-0.473	0.007	3.101	343 ^g	22.19	0.195 ^h	50 ^c	0.1 ^f
Saithe	152.12	0.075	-0.939	0.007	3.075	750 ^c	48.62	0.112 ^h	25 ^c	0.179 ^f
Sandeel	18.61	0.758	-0.429	0.001	3.32	640 ^b	11	0.08 ⁱ	10	0.192 ^d
Sole	34.83	0.441	0.026	0.008	3.019	591 ^g	20.97	0.13 ⁱ	26 ^c	0.1 ^f
Sprat	16.17	0.469	-0.394	0.007	3.014	2250 ^c	12.01	0.1 ^g	5 ^c	0.1974 ^d
Whiting	38.88	0.457	-0.012	0.006	3.08	1382 ^g	21.40	0.115 ^g	20 ^c	0.1551 ^d

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h) Russell FS (1976) The eggs and planktonic stages of British marine fishes. Academic Press, London, UK. 524 p.

- i) Quéro J-C, Vayne JJ, Monod T (1984) Les poissons de mer de pêches francaises. Delachaux et Niestlé.
- j) Calculated using method Jennings et al. 1999
- k) Average of all other species

Table S2. Spawning seasonality (α) per species (Daan et al., 1990; ICES, 1993; Albert, 1994).

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cod	0.009	0.378	0.460	0.148	0.005	0	0	0	0	0	0	0
Dab	0.071	0.171	0.171	0.171	0.171	0.171	0.024	0.024	0.024	0	0	0
Grey gurnard	0.062	0.062	0.141	0.141	0.141	0.141	0.141	0.141	0.013	0.013	0	0
Haddock	0	0.055	0.332	0.332	0.221	0.055	0	0	0	0	0	0
Herring	0.077	0	0.068	0.068	0.068	0.055	0.055	0.132	0.132	0.132	0.132	0.077
Norway pout	0.074	0.145	0.257	0.222	0.151	0.038	0.038	0	0	0	0.036	0.036
Plaice	0.317	0.365	0.151	0.028	0.028	0.028	0	0	0	0	0.028	0.056
Saithe	0.224	0.224	0.224	0.224	0.100	0	0	0	0	0	0	0
Sandeel	0.042	0.042	0.113	0.113	0.042	0.042	0.042	0.042	0.077	0.077	0.113	0.255
Sole	0	0	0	0.415	0.415	0.166	0	0	0	0	0	0
Sprat	0	0	0	0.110	0.355	0.356	0.137	0.042	0	0	0	0
Whiting	0.093	0.148	0.194	0.223	0.135	0.097	0.037	0.037	0.037	0	0	0

Table S3. Maximum and minimum predator-prey size ratios and their references, either from literature or based on data available from ICES and/or WMR.

Species	Min ratio	Max ratio	References
Cod	0.022	0.44	(Scharf et al., 2000)
Dab	0.006	0.09	Based on BSIK stomach data; (Schuckel et al., 2012)
Grey gurnard	0.03	0.6	ICES stomach data 2010
Haddock	0.067	0.44	(Greenstreet et al., 1998)
Herring	0.0017	0.034	Based on minimum plankton sizes used in the model and foraging on 1 cm fish larvae at L_{inf} (ICES Fishmap report)
Norway pout	0.0018	0.087	Based on plankton sizes used in the model and 2 cm fish prey at L_{inf} (ICES Fishmap report on eating 'small' fish)
Plaice	0.008	0.06	Stomach data (Rijnsdorp and Vingerhoed, 2001)
Saithe	0.006	0.05	(Scharf et al., 2000); ICES stomach data 2010
Sandeel	0.0025	0.014	Based on minimum and maximum plankton sizes used in the model and including egg sizes of the species modelled.
Sole	0.005	0.06	Stomach data (Rijnsdorp and Vingerhoed, 2001)
Sprat	0.002	0.023	Based on minimum and maximum plankton sizes used in the model, includes eggs of all species modelled.
Whiting	0.005	0.69	(Greenstreet et al., 1998); ICES stomach data 2010

Table S4. Availability matrix for all predator (column) and prey (rows) combinations based on diet inclusion (generalist = 0.01, specialist = 0.5, not in diet = 0) multiplied by a relative measure on the fraction of a grid cell which can be searched within a time step of 14 days in order to maximize the search area. This was based on the size at maturity and assuming a speed of 1 body length per second and a search window of 1 body length. The values presented are used as a factor to scale the availability of a resource. Note that for the spatial extent used in this study limited to the southern North Sea values for plaice feeding on macro-invertebrates were raised in order to keep the species from going extinct. The values presented here were not validated in any way. Cod1 and had1 denote the stage of individuals smaller than 7 cm which are more pelagic than demersal. Cod: cod, cod1; Grey gurnard: gur; haddock: had, had1; herring: her; Norway pout: pout; plaice: plaice; saithe: sait; sandeel: sand; sole: sole; sprat: sprat; whiting: whit; diatoms: diat; flagellates: flag; micro-zooplankton: micro; meso-zooplankton: meso; deposit feeders: dep; suspension feeders: sus; meiobenthos: mei. The latter are the resources obtained from lower trophic level models. Values are multiplied by x1000 for readability purposes.

	cod	cod1	dab	Gur	had	had1	her	pout	plaice	sait	sand	sole	sprat	whit
cod	9.14	0	2.18	2.97	4.52	0	0	24.11	3.73	8.17	1.85	3.52	0	3.6
cod1	9.14	1.18	2.18	2.97	4.52	11.76	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
dab	9.14	0	2.18	2.97	4.52	0	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
gur	9.14	0	2.18	2.97	4.52	0	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
had1	9.14	0	2.18	2.97	4.52	0	0	24.11	3.73	8.17	1.85	3.52	0	3.6
had	9.14	1.18	2.18	2.97	4.52	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
her	9.14	1.18	2.18	2.97	4.52	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
pout	9.14	1.18	2.18	2.97	4.52	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
plaice	9.14	0	2.18	2.97	4.52	0	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
sait	9.14	1.18	2.18	2.97	45.21	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
sand	9.14	0	2.18	2.97	4.52	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6

sole	9.14	1.18	2.18	2.97	4.52	0	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
sprat	9.14	1.18	2.18	2.97	4.52	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
whit	9.14	1.18	2.18	2.97	4.52	1.18	39.24	24.11	3.73	8.17	1.85	3.52	20.18	3.6
diat	1.18	1.18	1.18	1.18	1.18	1.18	196.22	4.82	1.18	1.18	92.4	1.18	100.88	1.18
flag	1.18	1.18	1.18	1.18	1.18	1.18	196.22	4.82	1.18	1.18	92.4	1.18	100.88	1.18
micro	1.18	1.18	1.18	1.18	1.18	1.18	196.22	4.82	1.18	1.18	92.4	1.18	100.88	1.18
meso	1.18	1.18	1.18	1.18	1.18	1.18	196.22	4.82	1.18	1.18	92.4	1.18	100.88	1.18
dep	9.14	0	21.84	29.72	45.21	0	0	4.82	386.4	8.17	18.48	176.15	0	3.6
susf	9.14	0	21.84	29.72	45.21	0	0	4.82	386.4	8.17	18.48	176.15	0	3.6
mei	9.14	0	21.84	29.72	45.21	0	0	4.82	386.4	8.17	18.48	176.15	0	3.6

Text S2. Fishing

Fishing effort of each fleet was back-calculated with age dependent fishing mortality estimates from ICES. The annual effort for each species in a fleet was averaged to obtain the average effort per fleet, assuming that species are caught indiscriminately and based only on the abundance and selectivity. The stock assessment results of estimated F-at-age were extracted from the 2012 stock assessment reports to estimate L25 and L50 for the selectivity curve for each species. For most stocks, time series of F start before 1983 and extend up to 2011 (except for sprat which starts in 1991 and whiting which starts in 1990, no data for sab and gurnard are available).

The selection patterns as observed in the stock assessments are age based. To estimate L25 and L50 these need to be converted to length measures and they must be described by a sigmoid curve, instead of e.g. dome shaped curves. In many stock assessments, older ages are not targeted as well as the slightly younger, but fully selected, animals. This might be due to processes as out swimming the gear or a lack of spatio-temporal overlap. Given the size of older ages however, simple gear selection equations show that they are fully selected. Hence, we have to apply a correction to our data to adhere to this ‘assumption’. Therefore, per species by year, the selection pattern is rescaled to fit the interval [0,1]. Thereafter, the age at which selection equals one is determined and all older ages are assumed to have similar selection (equal 1). This results in approximations of sigmoid curves for all species-year combinations. The function fitted is described as: $Sel = \frac{1}{1+e^{S1-S2 \text{ age}}}$. The parameters are thereafter converted to lengths given the estimated growth parameters (Table S1) and are presented in Table S5.

Table S5. Species specific L25 and L50 values for the sigmoid selectivity curve. For dab, plaice values were used, for sprat Norway pout values were used and for Grey gurnard whiting values were used as sufficient information on these species is lacking.

Species	L25	L50
Cod	13.199	22.874
Dab	11.517	17.037
Gr. gurnard	19.813	29.019
Haddock	19.093	24.345
Herring	10.129	20.790
N. pout	8.694	12.236
Plaice	11.517	17.037
Saithe	35.317	43.551
Sandeel	9.832	11.824
Sole	16.401	25.800
Sprat	8.694	12.236
Whiting	19.813	29.019

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