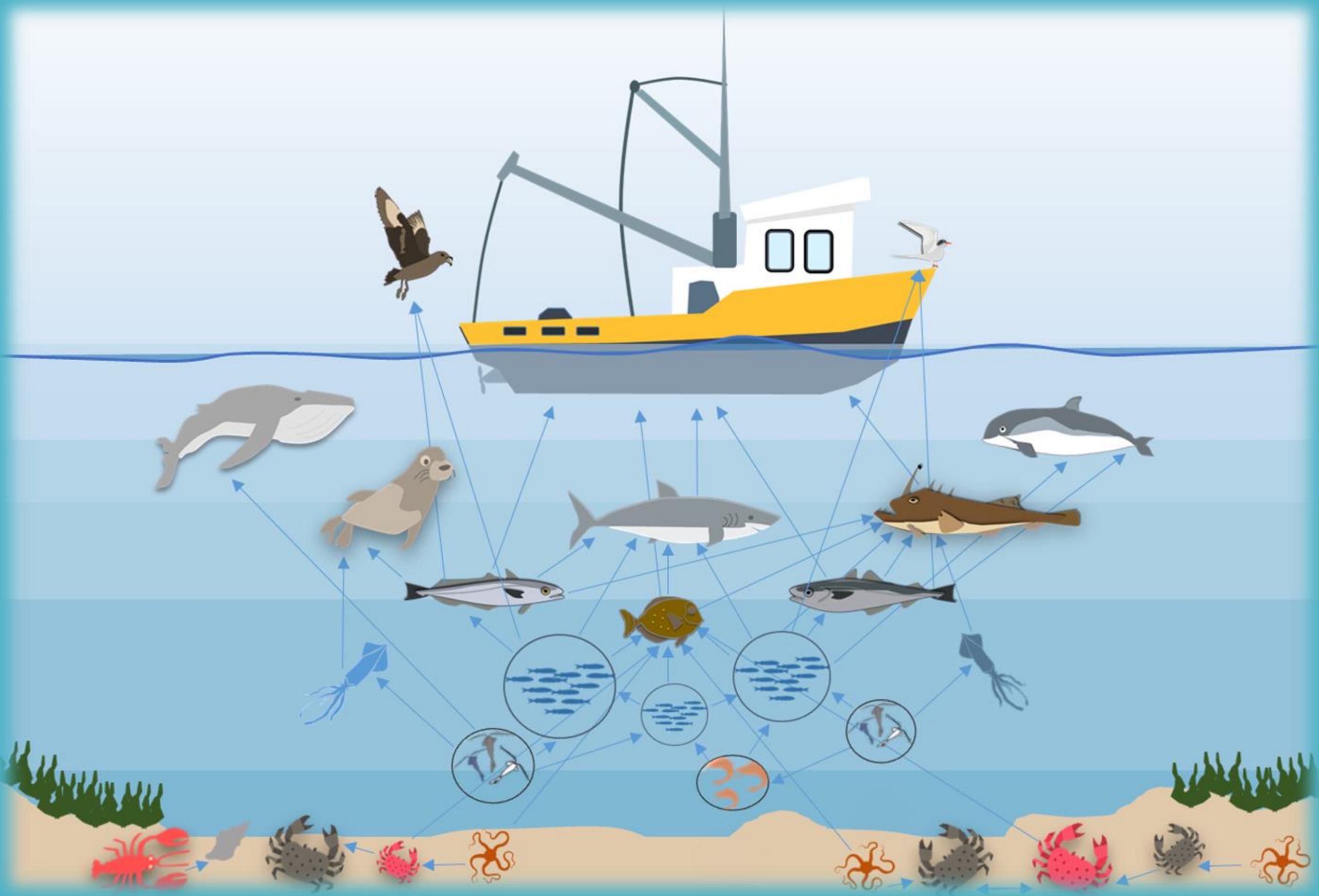
Modelling the trophic interaction, structure, and function of the northern North Sea food web.

Ecopath Technical Report



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EUROPE & SCOTLAND
European Regional Development Fund
Investing in a Smart, Sustainable and Inclusive Future

Modelling the trophic interaction, structure, and function of the northern North Sea food web.

Ecopath Technical Report

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Preface

This report outlines the model topology, describing in detail the methods used to create an ecologically balanced Ecopath model of the northern North Sea. This model builds upon previous research by Dr Steven Mackinson and others at the Centre for Environment Fisheries and Aquaculture Science (Cefas). The construction of their North Sea model (Mackinson and Daskalov, 2007), North Sea ICES Key run (ICES, 2016), and evaluation of fisheries management strategies (Platts and Mackinson, 2017; Mackinson *et al.*, 2018) inspired the creation and design of our northern North Sea model. The model of Mackinson and Daskalov (2007) treated the whole North Sea as a single unit, however the oceanographic and biological characteristics of the northern and southern North Sea are distinct. This suggests value in constructing a separate northern North Sea model, as has already been done for the southern North Sea (Stäbler *et al.*, 2018).

Commercial fishing in the Shetland Islands is a highly important economic and cultural activity. In 2019, 50,000 t of fish and shellfish, worth £81 million were landed in Shetland (Napier, 2019). This hub of fishing activity is driven by aggregations of demersal cod, monkfish and haddock, alongside large volumes of pelagic mackerel, herring, and blue whiting which are caught seasonally. It is hoped that this northern North Sea ecosystem model can be used to test future fisheries management scenarios of relevance to both Shetland and the wider Scottish and UK fishing industry.

Section 1: Basic input parameters

1.1 An introduction to the northern North Sea model

Ecopath with Ecosim (EwE) celebrated its 35th birthday in 2019, and since its invention by Polovina (1984) and subsequent updates by Christian and Pauly (1992) and Walters *et al.* (1997), has been used to address a long list of ecological questions. These range from evaluating environmental impacts of climate change, marine protected areas (MPAs), and the impacts to ecosystems of changing fishing methods and intensities. EwE is comprised of three different component elements: Ecopath (a mass balanced snap-shot of a food web), which is then used as a baseline for Ecosim (model fitting and temporal simulations) and, Ecospace (simultaneous spatial and temporal simulations) (https://ecopath.org/) (Christensen and Walters, 2000, 2004). In this report we describe the construction of the Ecopath model for the northern North Sea.

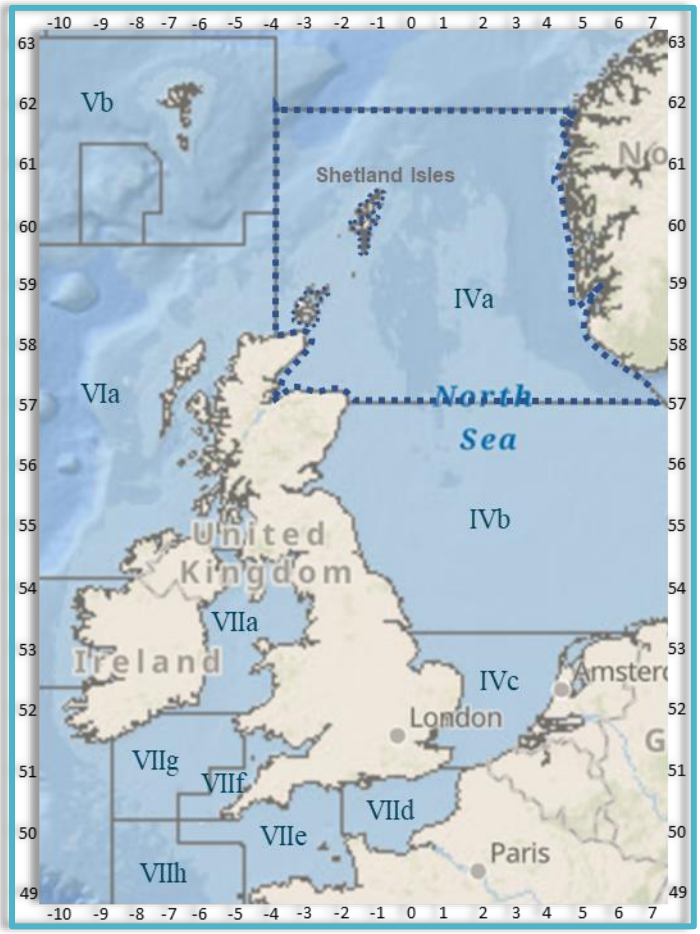


Figure 1 *Map of ICES divisions surrounding the United Kingdom Map background layer ERSI Ocean Basemap for ArcGIS (arcgis.com) with ICES area reference layer. The extent of the model area is outlined with a dark blue dashed line.*

For management purposes the International Council for the Exploration of the Seas (ICES), divides the North Sea (Area IV) into three divisions (IVa, IVb and IVc).

This northern North Sea Ecopath model focuses on division IVa which covers approximately 264,343 km^2 (Figure 1). The average depth of the North Sea is approximately 90 m (Mackinson and Daskalov, 2007) but the southern North Sea is relatively shallow with maximum depths of 125 m. The southern North Sea seabed is comprised of mainly terrigenous sediments (derived from the erosion of rock). In contrast, the northern North Sea is deeper with an average depth below 100 m and maximum depths down to 400 m within the Norwegian trench (Mackinson and Daskalov, 2007; Stäbler *et al.*, 2018).

Two major currents influence the northern North Sea bringing with them high salinity waters from the Atlantic Ocean (ICES, 2019f). One major inflow travels through the Fair Isle Channel whilst the second is a more substantial inflow along the western slope of the Norwegian trench. The northern North Sea also seasonally stratifies, which influences nutrient dispersion within the water column (ICES, 2019f).

The northern North Sea Ecopath model is a steady-state representation of the whole trophic food web from the lowest level primary consumers (zooplankton, and benthic invertebrates) to the highest level predators (marine mammals, seabirds and sharks) for the year 1991. This year was chosen to make the best use of the detailed information on fish diets from the "1991 and 1992 Year of the stomach" program co-ordinated by ICES, and to make direct comparisons to the North Sea EwE model (Mackinson and Daskalov, 2007), updated North Sea WGSAM ICES Key run (ICES, 2016), and southern North Sea EwE model (Stäbler *et al.*, 2018).

The Northern North Sea model is focussed on commercial fish and invertebrate species with some of the important commercial species being split into multi-stanza groups to represent juveniles and adults separately. Fishing activities are represented in the model as seven fleets by gear type (beam trawl, otter trawl, *Nephrops* trawl, pelagic (trawl and seine), dredge, gill/trammel nets, and pots).

1.2 An introduction to Ecopath

To construct an Ecopath model the food-web is firstly broken up into functional groups – each group (i) may represent an individual species, or a group of species which are assumed to have a similar ecological function. Diets (proportions) and catch data (where appropriate) are required for each functional group. An Ecopath model functions under two main structural master equations. The first of these equations (Equation 1) describes the total production rate (P_i) for each functional group (i) with the assumption that there is a mass balance within the system in a fixed time period. Since our Ecopath model represents the steady-state of the food-web in a specific year, rates are expressed in annual terms (Christensen and Walters, 2000, 2004).

$$\mathrm{P_i = Y_i + M2_i * B_i + E_i + BA_i + P_i(1 - EE_i)}$$

Equation 1

Y_i represents the total fishery catch rate of group (i), $M2_i$ is the instantaneous predation rate, B_i is biomass of group i, E_i is the net migration rate (emigration minus immigration), and BA_i is the biomass accumulation rate of the group (i) (Christensen *et al.*, 2008). EE_i is the ecotrophic efficiency of the group (i). Ecotrophic efficiency is a value that represents the proportion of the production of group (i) which is transferred within the model through predation, fishing, migration and/or biomass accumulation. Altogether, $\mathrm{P}(1{-}EE_i)$ represents the remaining unexplained mortality (or "other mortality" rate). Following on from Equation 1, Ecopath applies a loop of parameterisation algorithms in order to estimate 'missing' parameters before ensuring mass balance between the groups (Christensen and Walters, 2000, 2004). The loop helps to reduce the number of computations associated with establishing mass balance (for more information on the algorithms used within the loop see Christensen and Walters, 2004). After the 'missing' parameters have been estimated the energy balance is then ensured for each functional group using the second master equation Equation 2).

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

Equation 2

This equation is based on Winberg's formula (Winberg, 1956) which sums production, respiration (metabolic costs) and unassimilated food (waste products).

Each group in the model is represented by these two linear equations, each of which must be balanced, and requires six input parameters. Diet composition is compulsory and catch (export) is compulsory for groups where there is a catch. The other four basic parameters for each functional group are Biomass (B), Production/Biomass (P/B), Consumption/Biomass (Q/B), and Ecotrophic Efficiency (EE). The most robust approach is to enter values for B, P/B, and Q/B and allow the model to estimate EE (where this is possible with available data). With the linear equations solved this provides an immediate check for mass balance because EE cannot be greater than 1. Sometimes due to a lack of data it is necessary to instead enter a value for EE, in which case often a default value of 0.95 is used (Christensen and Pauly, 1992). A value of 0.95 thus assumes that 95% of the energy produced by this functional group is described/utilized in the model.

1.3 Determination of functional groups

Species present in the northern North Sea were initially determined from available fisheries survey data and ICES landings data (DATRAS; https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx). Species considered important were assigned their own functional groups but other species were combined on the basis of their diet, ecology and behavioural similarities e.g. "small demersal fish". The aim was to generate a characterisation of the northern North Sea food-web, which was representative, but not overly complex.

One of our aims was to build a model to address research questions on the fishery and ecological consequences of implementing the EU Landings Obligation (LO). This was considered during the designation of species and life stages to functional groups. Multi-stanza groups were created for the important commercial species cod (*Gadus morhua)*, whiting (*Merlangius merlangus*) and haddock (*Melanogrammus aeglefinus*). These groups were split into adults and juveniles as represented by their stock assessment maturity ogive. Single stanza functional groups were created for saithe (*Pollachius virens*), hake (*Merluccius merluccius*), ling (*Molva molva*) and plaice (*Pleuronectes platessa*).

Separate functional groups were also allocated to important forage fish including: Norway pout (*Trisopterus esmarkii*), herring (*Clupea harengus*), and sandeels (*Ammodytes marinus, Hyperoplus lanceolatus, A. tobianus*), and for commercially valuable shellfish and crustaceans such as: Norway lobster (*Nephrops norvegicus*), scallops (*Pecten maximus*), velvet crab (*Necora puber*), and edible crab (*Cancer pagurus*).

Where available, species biomass estimates for the year 1991 were taken from ICES stock assessments (ICES, 2018d, 2018c, 2019h, 2019b, 2019i). Stock assessments covered the whole North Sea so total stock biomasses (for single stanza groups) or total stock biomasses split by immature and mature (for multi-stanza groups) from the assessments were adjusted to be equivalent to area IVa. This was achieved through visual inspection of the spatial distribution of the stocks in the IBTS survey for the early 1990s. Where there was an even stock distribution the total biomass was dived by the whole North Sea stock area, giving an area–based biomass estimate. For stocks that resided mainly (above 90%) within area IVa, the total stock biomass was divided by the model area. For stocks that were unevenly distributed, a percentage was derived of the probable total stock biomass residing within the model area, achieved through visual inspection of the stock IBTS survey data. This percentage stock biomass was then divided by the model area to achieve an area–based biomass estimate.

Biomass estimates for un-assessed species were estimated from survey data available from the ICES Database of Trawl Surveys (DATRAS; https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx ,accessed 07/01/2019, (ICES, 2019j)). We used DATRAS data from the North Sea International Bottom Trawl Surveys (IBTS) (all available data for 1991 in Q1, Q2, Q3, Q4) to calculate relative swept area biomass for each species within the model area following methods in Greenstreet *et al.* (2007). For the North Sea IBTS in the 1990s the survey gear used was predominantly the Grande Ouverture Verticale (GOV) trawl.

To obtain area-based biomass estimates (t.km^{-2}), we calculated the swept area for each individual haul based on the towing speed, depth, and distance. However, tow distances were frequently not available. Missing tow distances were estimated from a regression of all the known data for wingspread (WS) and door spread (DS) against tow depth (Equation 3 and Figure 2).

$$\text{DS or WS} = \text{regression coefficient a (slope)} * \log \text{D} + \text{regression coefficient b (intercept)}$$

Equation 3

The estimated area swept by the gear for each haul was combined with count and length data for each species. The DATRAS database for 1991 provides length measurements of most species caught but not total weight which only became recorded as a standard in later years. Lengths were converted to weights using North Sea specific length to weight conversion factors from Silva *et al.* (2013). Estimated catch weights were then converted by dividing by the swept area.

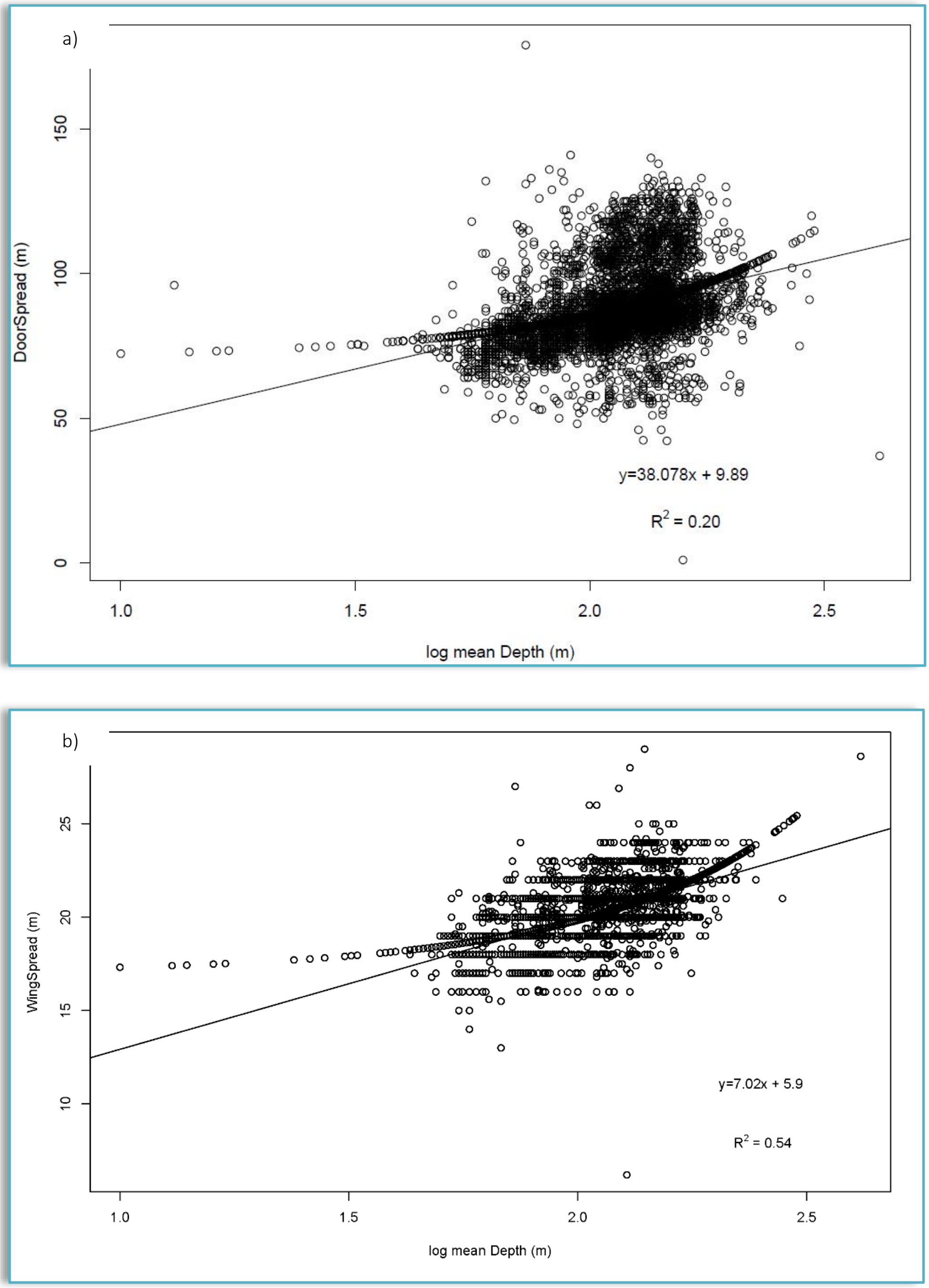


Figure 2 *a) Regression analysis performed on the relationship between door-spread and depth within each haul. b) Regression analysis performed on the relationship between wing-spread and depth within each haul.*

The North Sea IBTS only samples a range of statistical rectangles within ICES area IVa (Figure 3). Therefore, we applied a raising factor to calculate area-based biomass estimates for the whole model area. This raises our estimates equivalent to the expected numbers of each species caught had all of IVa been surveyed (Greenstreet *et al.*, 2007). A raising factor of 1.42 was calculated as the model area of division IVa; 264,343 km^2 divided by the area covered by the IBTS survey; 185,969 km^2. For input into the model the geometric mean of the individual area-swept biomass estimates were used for each species. This method assumes that the density of fish was the same on average across the whole model area as surveyed. Greenstreet *et al.* (2007) verified this method by examining landings data to check whether estimates of the numbers of fish within ICES areas, based on the stock assessments, would have altered radically if the stocks had been allocated both inside and out of the surveyed area. Both methods arrived at very similar allocations, justifying the use of a raising factor for our model biomass estimates for species which did not have specific stock assessments.

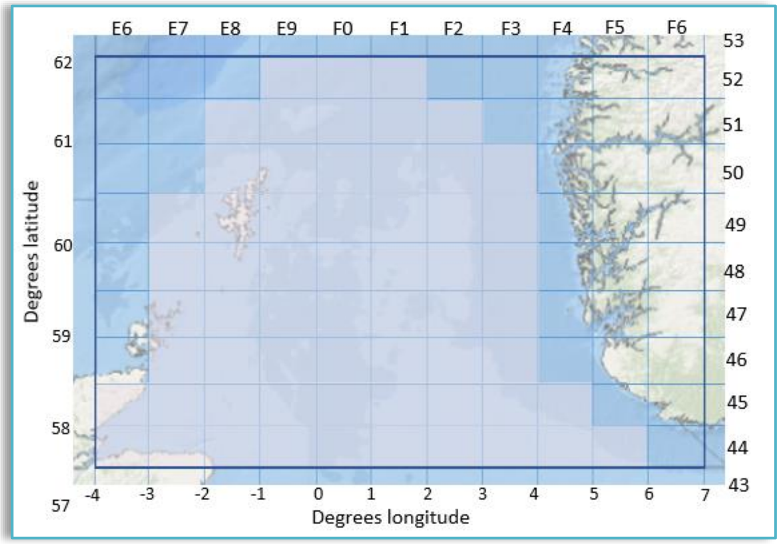


Figure 3 *Areas shaded pink are parts of ICES area IVa which are included within the IBTS area coverage for 1991. Dark blue outline indicates the total ICES area IVa (land areas excluded from calculations). Map background layer ERSI Ocean Basemap for ArcGIS (arcgis.com).*

For groups such as marine mammals, seabirds, and invertebrates biomass estimates were taken from (or calculated using) available literature. This process is described below for each functional group. Within the model 62% of the total biomass was based on stock assessments, 22% was estimated from the IBTS data and 16% estimated from literature sources.

The final model has 43 functional groups including discards and detritus, primary producers, secondary producers, commercial and non-commercial fish, commercial invertebrates, elasmobranchs, seabirds, and marine mammals (Table 1).

Table 1 *Structure of the 42 functional groups in the northern North Sea Ecopath model*

	Functional group	Species included in the functional group
1	Minke whale	Minke whale (*Balaenoptera acutorostrata*)
2	Toothed whales	Harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*), white beaked dolphin (*Lagenorhynchus albirostris*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*)
3	Seals	Grey seal (*Halichoerus grypus*), harbour seals (*Phoca vitulina*)
4	Seabirds (high discard diet)	Fulmar (*Fulmarus glacialis*), gannet (*Morus bassanus*), herring gull (*Larus argentatus*), lesser black backed gull (*Larus fuscus*),great skua (*Stercorarius skua*), Arctic skua (*Stercorarius parasiticus*), black-headed gull (*Chroicocephalus ridibundus*), cormorant (*Phalacrocorax carbo*), greater black backed gull (*Larus marinus*)
5	Seabirds (low discard diet)	Puffin (*Fratucula arctica*), kittiwake (*Larus tridactyla*), guillemot (*Uria aalge*), shag (*Phalacrocorax aristotelis*), razorbill (*Alca torda*), storm petrel (*Hydrobates pelagicus*), Arctic tern (*Sterna paradisaea*), Manx shearwater (*Puffinus puffinus*)
6	Sharks	Spotted catshark (*Scyliorhinus canicula),* common smooth hound *(Mustelus mustelus),* starry smooth hound *(Mustelus asterias),* spurdog *(Squalus acanthias),* tope *(Galeorhinus galeus),* blackmouth catshark *(Galeus melastomus),* porbeagle shark *(Lamna nasus),* lantern shark *(Etmopterus spinax)*
7	Skates & Rays	Cuckoo ray (*Leucoraja naevus*), thornback ray (*Raja clavata*), *Dipturus batis* complex (*Dipturus batis*), starry ray (*Amblyraja radiata*), sandy skate (*Leucoraja circularis*)
8	Atlantic cod (juvenile)	Atlantic cod (*Gadus morhua) 0-36 months*
9	Atlantic cod (adult)	Atlantic cod *(Gadus morhua) 36+ months*
10	Whiting (juvenile)	Whiting *(Merlangius merlangus) 0-24 months*
11	Whiting (adult)	Whiting *(Merlangius merlangus) 24+ months*
12	Haddock (juvenile)	Haddock *(Melanogrammus aeglefinus) 0-36 months*
13	Haddock (adult)	Haddock (*Melanogrammus aeglefinus) 36+ months*
14	Saithe	Saithe *(Pollachius virens)*
15	Hake	Hake *(Merluccius merluccius)*
16	Common ling	Common ling *(Molva molva)*
17	Norway pout	Norway pout (*Trisopterus esmarkii*)
18	Monkfish	White-bellied monkfish *(Lophius piscatorius),* black-bellied monkfish *(Lophius budegassa)*
19	Atlantic herring	Atlantic herring *(Clupea harengus)*
20	Small pelagic fish	European sprat *(Sprattus sprattus),* anchovy *(Engraulis encrasicolus),* argentines *(Argentina sp.),* silvery lightfish *(Maurolicus muelleri)*
21	Other pelagic fish	Atlantic mackerel *(Scomber scombrus),* Atlantic horse mackerel *(Trachurus trachurus),* blue whiting *(Micromesistius poutassou)*
22	Sandeels	Lesser sandeel (*Ammodytes marinus*), greater sandeel (*Hyperoplus lanceolatus*), small sandeel (*Ammodytes tobianus*)
23	European plaice	European plaice *(Pleuronectes platessa)*
24	Turbot	Turbot (*Scophthalmus maximus)*
25	Flatfish	Brill *(Scophthalmus rhombus),* halibut *(Hippoglossus hippoglossus),* megrim *(Lepidorhombus whiffiagonis),* lemon sole *(Microstomus kitt),* European flounder *(Platichthys flesus),* witch flounder *(Glyptocephalus cynoglossus),* long rough dab *(Hippoglossoides platessoides),* Norwegian topknot *(Phrynorhombus norvegicus),* common dab *(Limanda limanda),* solenette *(Buglossidium luteum),* common sole *(Solea solea)*
26	Small demersal fish	Bib (pouting) (*Trisopterus luscus*), lesser weaver (*Echiichthys vipera*), reticulated dragonet (*Callionymus reticulatus*), poor cod (*Trisopterus minutus*), common dragonet (*Callionymus lyra*), silvery pout (*Gadiculus argenteus*), spotted dragonet (*Callionymus maculatus*), snake blenny (*Lumpenus lampretaeformis*), Vahl's eelpout (*Lycodes vahlii*), gobies (*Gobiidae*)
27	Large demersal fish	Pollock *(Pollachius pollachius),* Northern wolffish *(Anarhichas lupus),* lumpfish *(Cyclopterus lumpus),* shorthorn sculpin *(Myoxocephalus scorpius),* cusk *(Brosme brosme),* Norway haddock *(Sebastes norvegicus),* red gurnard *(Chelidonichthys cuculus),* greater forkbeard *(Phycis blennoides),* John Dory *(Zeus faber),* grey gurnard *(Eutrigla gurnardus),* fourbeard rockling *(Enchelyopus cimbrius),* boarfish *(Capros aper),* hooknose *(Agonus cataphractus),* blackbelly rosefish *(Helicolenus dactylopterus),* three-beard rockling *(Gaidropsarus vulgaris),* red mullet *(Mullus surmuletus)*
28	Squid & Octopus	Common squid (*Loligo forbesii*), ringed octopus (*Eledone cirrhosea*), lesser flying squid (*Todaropsis eblanae*), shortfin squid (*Illex coindetii*), whale squid (*Walvisteuthis virilis*), European flying squid (*Todarodes sagittatus*), stout bobtail (*Rossia macrosoma*), common cuttlefish (*Sepia officinalis*), European common squid (*Allotheuthis subulate*), common octopus (Octopus *vulgaris*)
29	Large zooplankton	Zooplankton species >2mm in length
30	Small zooplankton	Zooplankton species <2mm in length
31	Gelatinous zooplankton	Moon jellyfish (*Aurelia aurita*), lion's mane jellyfish (*Cyanea capillata*), blue jellyfish (*Cyanea lamarckii*)
32	Edible crab	Edible crab (*Cancer pagurus*)
33	Velvet crab	Velvet swimming crab (*Necora puber*)
34	Crabs & lobsters	Flying crab (*Liocarcinus holsatus*), lyre crab (*Hyas coarctatus*), marbled swimming crab (*Liocarcinus marmoreus*), long clawed porcelain crab (*Pisidia longicornis*), northern stone crab (*Lithodes maia*)
35	Norway lobster	Norway lobster (*Nephrops norvegicus*)

36	Shrimp	*Pandalus (Pandalus montagui, Processa nouveli, Pandalus borealis)* and *Crangon (Crangon crangon, Crangon allamani)*
37	Scallops	Great scallop (*Pecten maximus*)
38	Epifauna	Brittle stars (*Amphiura filiformis, Ophiura albida, Ophiura affinis*), common starfish (*Asterias rubens*), common whelk (*Bussinum undatum*), mussels (*Mytilus edulis, Modiolus modiolus, Modiolus barbatus, Musculus niger*), hermit crabs (*Paguroidea*), sea urchin (*Echinus esculentus*), chiton (*Leptochiton asellus*), sea snails (*Euspira montagui, Hyala vitrea*), sea potato (*Echinocardium flavescens, E. cordatum*), oysters (*Anomia ephippium*, *Pododesmus patelliformis*)
39	Infauna	Polychaete worms (*Polychaeta*), razor clams (*Ensis ensis, Phaxas pellucidus*), Faroe sunset shell (*Gari fervensis*), burrowing bivalves (*Cochlodesma praetenue, Myrtea spinifera, Thyasira spp.*)
40	Seaweed	Kelp (*Laminaria hyperborea, Saccharina latissima, Saccorhiza polyschides, laminaria digitate*), bladder wrack (*Fucus vesiculosus*), toothed wrack (*Fucus serratus*), knotted wrack (*Ascophyllum nodosum*)
41	Phytoplankton	-
42	Discards	-
43	Detritus	-

1.4 Functional group input parameters

Equations for fish and mammal functional group input parameters are provided below. Explanation of each equation is provided within the functional group description for which they are first used.

$$R = 0.1W^{0.8}$$

Equation 4

$$Log_{10}(R) = - 0.293 + 0.85 * Log_{10}W$$

Equation 5

Where R is the daily ration of fish consumed and W is body weight in Equation 4 and Equation 5.

$$W = a * L^{b}$$

Equation 6

Where W is body weight, L is length, and a and b are estimated length to weight coefficients.

$$P/B = Z = M + F$$

Equation 7

Where P/B is production/biomass ratio, Z is the instantaneous total mortality for fish, M is natural mortality, and F is fishing mortality when expressed as instantaneous rates.

$$F=catch/biomass$$

Equation 8

$$log_{10}M = -0.2107 - 0.0824 log_{10}W_{\infty} + 0.675 log_{10}k + 0.4687 log_{10}T$$

Equation 9

Where W_{∞} is the species asymptotic weight, k is the curvature parameter of the von Bertalanffy growth function and T is the average annual sea surface temperature.

$$Log\ Q/B = 6.37 - 1.5045\ T' - 0.168 log W_{\infty} + 1.399 Pf + 0.2765 Hd$$

Equation 10

Where Q/B is consumption/biomass ratio, T' is the mean annual temperature in Kelvin, Pf is chosen depending on feeding behaviour; for apex predators, pelagic predators, and zooplankton feeders Pf =

1 and for other feeding types = 0. Hd characterises the food type; for herbivores Hd = 1 and for predators = 0.

Multi-stanza group input parameters for the population model are included in Table 2 with sources references.

Table 2 *Multi-stanza parameters based on reported values for the North Sea.*

	Biological parameters	Value	Source
Cod	Age at recruitment	36 months	(ICES, 2018d)
	Biomass accumulation/ biomass (BA/B)	0	-
	W maturity (W_{mat}) (g)	3971	(Armstrong *et al.*, 2004)
	Length at maturity (L_{mat}) (cm)	40	(Armstrong *et al.*, 2004)
	Weight at infinity (W_{∞}) (g)	19725	(Speirs *et al.*, 2010)
	Length at infinity (L_{∞}) (cm)	123	(Speirs *et al.*, 2010)
	W_{mat} / W_{∞}	0.201	-
	Biomass adult (t.km^{-2})	0.160	(ICES, 2018d)
	Total mortality (Z) adult (/year)	0.774	(ICES, 2018d)
	Z juvenile (/year)	1.732	(ICES, 2018d)
	Q/B adult (/year)	2.927	-
	K of the von Bertalanffy growth function (VBGF) (/year)	0.17	(Speirs *et al.*, 2010)
	a	0.0106	(Silva *et al.*, 2013)
	b	3.00	(Silva *et al.*, 2013)
Whiting	Age at recruitment	24 months	(ICES, 2018d)
	Biomass accumulation/ biomass (BA/B)	0	-
	W maturity (W_{mat}) (g)	125	(ICES, 2018d)
	Length at maturity (L_{mat}) (cm)	24	(ICES, 2018d)
	Weight at infinity (W_{∞}) (g)	578	(Speirs *et al.*, 2010)
	Length at infinity (L_{∞}) (cm)	42.70	(Speirs *et al.*, 2010)
	W_{mat} / W_{∞}	0.291	-
	Biomass adult (t.km^{-2})	0.154	(ICES, 2019l)
	Total mortality (Z) adult (/year)	0.961	(ICES, 2019l)
	Z juvenile (/year)	1.606	(ICES, 2019l)
	Q/B adult (/year)	5.297	-
	K of the von Bertalanffy growth function (VBGF) (/year)	0.34	(Pauly, 1978)
	a	0.0116	(Silva *et al.*, 2013)
	b	2.881	(Silva *et al.*, 2013)
Haddock	Age at recruitment	36 months	(ICES, 2018d)
	Biomass accumulation/ biomass (BA/B)	0	-
	W maturity (W_{mat}) (g)	454	(Jones, 1983)
	Length at maturity (L_{mat}) (cm)	40	(Jones, 1983)
	Weight at infinity (W_{∞}) (g)	2626	(Speirs *et al.*, 2010)
	Length at infinity (L_{∞}) (cm)	65	(Speirs *et al.*, 2010)
	W_{mat} / W_{∞}	0.173	-
	Biomass adult (t.km^{-2})	0.197	(ICES, 2019b)
	Total mortality (Z) adult (/year)	0.770	(ICES, 2019l)
	Z juvenile (/year)	1.743	(ICES, 2019l)
	Q/B adult (/year)	4.107	-
	K of the von Bertalanffy growth function (VBGF) (/year)	0.20	(Jones, 1983)
	a	0.0113	(Silva *et al.*, 2013)
	b	2.96	(Silva *et al.*, 2013)

1.4.1 Marine mammals

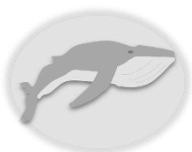
Seven marine mammal species occur regularly in the northern North Sea: harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncates*), minke whale (*Balenoptera acutorostrata*), white beaked dolphin (*Lagenorhynchus albirostris*), Atlantic white-sided dolphin (*Lagenorhynchus actus*), harbour seal (*Phoca vitulina*), and grey seal (*Halichoerus grypus*).

The abundance of cetaceans is not available for the model area for 1991, therefore data from SCANS III in 2016 were used to estimate their abundance under an assumption of minimal population change (Hammond *et al.*, 2016). SCANS I survey data were collected in 1994 but the survey area coverage of the northern North Sea and methods for data collection (on vessel versus aerial surveillance) were improved for SCANS III. This method for estimating cetacean abundance follows advice within the Joint Nature Conservation Committee (JNCC) Report No. 517 (2016).

Other species which have been reported from the northern North Sea include humpback whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), and Risso's dolphin (*Grampus griseus*). The presence of these latter species is uncommon and there are limited data describing their abundance and diets in the northern North Sea, so they were not included in the model.

In the last few years killer whale (*Orchinus orca*) sightings have greatly increased in places such as Shetland, but abundance data are not available for the early 1990's. As killer whales migrate and hunt over large areas of the North East Atlantic and there are limited data regarding their abundance and diet in the northern North Sea, for the purposes of the model it was assumed that they do not stay in the area for a significant period, and were therefore excluded.

1.4.1.1 FG1: Minke whales



a) Biomass, P/B, Q/B, bycatch (pre-balanced model)

Minke whales are the most common and regularly occurring baleen whales in the northern North Sea (ICES WGMME, 2004). During the SCANS III survey, a population of 4,212 minke whales were estimated to be present in the northern North Sea giving a density of 0.017 individuals per km^{-2} (Hammond *et al.*, 2016; Paxton *et al.*, 2016). The average weight of minke whale is stated by Bjorge and Tolly (2009) to be 5.25 t so that the biomass of minke whales was estimated as 0.089 t.km^{-2}. The maximum rate of population increase for whales is approximately 4% (Reilly and Barlow, 1986). Therefore, the P/B ratio for minke whales was set at half of the maximum rate at 2% or 0.02 yr^{-1} (Trites *et al.*, 1999). Q/B was estimated to be 6.58 yr^{-1} using Equation 4 (Trites *et al.*, 1999) with mean daily ration (R) as a function of individual weight (W).

Limited data was available to quantify the proportion of minke whale mortality attributable to bycatch in the northern North Sea. Perrin *et al*. (1994) estimated that in USA waters 0.3% of minke whale mortality was due to bycatch. Therefore, we assumed two minke whale mortalities per year due to fishing gear interactions in the model area which equates to 0.00004 t.km^{-2}.

b) Diet (pre-balanced model)

The modelled diet of minke whales was based upon a study by Olsen and Holst (2001), describing 15 minke whale stomach samples taken in 1999 from the central North Sea.

Table 3 *Diet of minke whales in the northern North Sea EwE model.*

Prey	Diet proportion	
	Pre-balanced	Balanced
Juvenile cod	-	0.016
Juvenile whiting	0.024	0.014
Juvenile haddock	-	0.010
Norway pout	0.005	0.005
Herring	0.010	0.016
Small pelagic fish	0.020	0.029
Other pelagic fish	0.060	0.060
Sandeels	0.600	0.500
Squid & Octopus	0.020	0.020
Large zooplankton	0.261	0.220
Small zooplankton	-	0.110

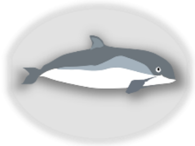
Although, their samples came from the central North Sea, they were from close to the southern border of the model area. Their diet was further adjusted to consider the likely greater importance of krill in more northern waters (Folkow *et al.*, 2000). This was achieved by decreasing the percentage of sandeels in the diet from 86.1% (Olsen and Holst, 2001) to 60% and attributing the remaining percentage to the large zooplankton functional group (Table 3).

c) Balancing changes

In the Norwegian Sea and adjacent waters, minke whales have a higher variety of prey than in the central North Sea (Folkow *et al.*, 2000). Folkow *et al.* (2000) studied minke whales in Norwegian and adjacent waters during their feeding period (180 days) in 1995 and estimated that they consumed 33% krill, 35% herring, 14% cod, 8% capelin, 7% haddock and 3% other fish by weight. The model was adapted to reflect this with the addition of juvenile cod and juvenile haddock for a wider variety of gadoid consumption in the balanced model (Table 3).The proportion of zooplankton in minke whale diet was also adapted to include both large and small zooplankton (Table 3). This adjustment was made to reflect different krill species and life stages included in zooplankton Continuous Plankton Recorder (CPR) sample data.

The final balanced EE for minke whales was 0.022. This low EE signifies that there is a large amount of unexplained mortality in the model (or outward migration). However, as this is a top predator, with very few predators in real life or the model, the only mortality that there could be is bycatch and without further information on bycatch of this species, or other sources of mortality, this value was not further adjusted.

1.4.1.2 FG2: Toothed whales



a) Biomass, P/B, Q/B, bycatch (pre-balanced model)

Harbour porpoise, bottlenose dolphin, white beaked dolphin, and Atlantic white-sided dolphin are grouped within the toothed whale functional group. For these species we obtained population density from SCANS III survey (Hammond *et al.*, 2016; Paxton *et al.*, 2016), average weight for harbour porpoise from Bjorge and Tolly (2009), and Trites and Pauly (1998) for other species. The number of individuals km^{-2} for each survey block located within the model area was used to give a mean density for each species (Table 4). The combined biomass estimate for other toothed whales in the model was estimated to have been 0.026 $t.km^{-2}$.

Table 4 *Toothed whale biological parameters for SCANS III survey blocks within northern North Sea.*

Species	Parameter	Value
Harbour porpoise	SCANS III survey blocks	S, T, U, V
	Population (no. of individuals)	56,965
	Average individual weight (t)	0.055
	Density (average no. of individuals per km^{-2})	0.253
	Biomass ($t.km^{-2}$)	0.014
Bottlenose dolphin	SCANS III survey blocks	S
	Population (no. of individuals)	151
	Average individual weight (t)	0.203
	Density (no. of individuals per km^{-2})	0.04
	Biomass ($t.km^{-2}$)	0.008
White beaked dolphin	SCANS III survey blocks	S, T, V
	Population (no. of individuals)	3,546
	Average individual weight (t)	0.147
	Density (no. of individuals per km^{-2})	0.022
	Biomass ($t.km^{-2}$)	0.003
Atlantic white-sided dolphin	SCANS III survey blocks	T, U
	Population (no. of individuals)	1,543
	Average individual weight (t)	0.105
	Density (no. of individuals per km^{-2})	0.012
	Biomass ($t.km^{-2}$)	0.001

The maximum rate of population increase for whales is approximately 4% (Reilly and Barlow, 1986). Following the methodology of Mackinson & Daskalov (2008) the P/B ratio for toothed whales was set at half of the maximum, i.e. 0.02 yr^{-1} (A. W. Trites *et al.*, 1999). Q/B was estimated for each species using Equation 4 at 16.38 yr^{-1} for harbour porpoise, 12.61 yr^{-1} for bottlenose dolphin, 13.45 yr^{-1} for white beaked dolphin, and 14.39 yr^{-1} for Atlantic white-sided dolphin. Prorating these species estimates by biomass provides a group Q/B estimate of 14.78 yr^{-1} for the other toothed whale functional group.

Harbour porpoise bycatch is evident from gill net use in the North Sea (ICES-WGBYC, 2015). The estimated total harbour porpoise bycatch from 2006 – 2013 in the North Sea was 1,235 – 1,990 individuals yr^{-1} (OSPAR Commission, 2010). The mean abundance of harbour porpoise across the whole

North Sea has been estimated as 345,400 individuals of which 56,965, or about 16% were in the northern North Sea (Hammond *et al.*, 2016). Therefore, the annual bycatch of harbour porpoise in the northern North Sea was estimated to be between 198 and 318 individuals (assuming that bycatch rates are spatially similar across the North Sea). An annual average bycatch of 258 porpoise yr^{-1}, or 0.000056 $t.km^{-2}$ was assumed for the northern North Sea model.

Bycatch of Atlantic white-sided and white beaked dolphins have also been reported in the North Sea but only on rare occasions. Bottlenose dolphins are reported to be taken as bycatch in gillnet and pelagic trawl gears (ICES-WGBYC, 2015). A mean bycatch rate of 0.4% yr^{-1} for North Sea gillnet and pelagic trawl (ICES-WGBYC, 2015), equates to 0.6 individuals yr^{-1} and a bycatch of 0.0000005 $t.km^{-2}$. Therefore, the overall estimated yearly bycatch for the toothed whale functional group was 0.0000565 $t.km^{-2}$ (0.000056 $t.km^{-2}$ gillnet bycatch and 0.0000005 $t.km^{-2}$ pelagic bycatch).

b) Diet (pre-balanced model)

The diet of toothed whales is based on the reported diet composition of harbour porpoise from 1992-2002 in Scottish waters (Santos *et al.*, 2004) where a total of 188 stomachs were sampled. In the absence of data for other species, this was assumed to represent the diet of the toothed whales group as a whole (MacLeod *et al.*, 2003; Mahfouz *et al.*, 2017; Isabel *et al.*, 2018) (Table 5).

Table 5 *Diet of toothed whales in the northern North Sea EwE model.*

Prey	Diet proportion	
	Pre-balanced	Balanced
Sharks	-	0.040
Juvenile cod	0.005	0.005
Adult cod	0.0006	0.003
Juvenile whiting	0.330	0.120
Adult whiting	0.184	0.130
Juvenile haddock	0.026	0.050
Adult haddock	0.003	0.023
Saithe	0.010	0.133
Hake	0.004	0.003
Ling	-	0.002
Norway pout	0.038	0.058
Herring	0.013	0.070
Small pelagic fish	0.082	0.004
Other pelagic fish	0.014	0.014
Sandeels	0.290	0.300
Small demersal fish	0.0003	0.0003
Large demersal fish	0.0003	0.010
Squid & octopus	-	0.036

c) Balancing changes

The toothed whale group was balanced in the model with an EE of 0.107. This relatively low EE signifies that there may be a large amount of unexplained mortality in the model. This is common for marine mammal parameter estimation as they are often an apex predator in the system, and information available on bycatch, or other sources of mortality is often scarce.

In the pre-balanced model 51% of toothed whale diet consisted of whiting. Brown and Pierce (1997) found that harbour porpoise populations surrounding the Shetland Isles have a greater dietary preference for haddock, saithe and pollack compared with other areas of the North Sea. Therefore, the percentage of whiting in the diet of toothed whales was reduced by 21% and allocated to haddock, saithe and pollock (within large demersal fish) (Table 5) (Brown and Pierce, 1997).

Bottlenose dolphins are known to predate upon sharks (spurdog and various shark eggs) in the Irish Sea (Hernandez-Milian and Rogan, 2010; Hernandez-Milian *et al.*, 2015). Within the Irish Sea EwE model (Bentley *et al.*, 2018), 4% of toothed whale diet is obtained from sharks. Using this as a guide, the diet proportion of sharks within the toothed whale diet was set at 4% in the balanced model by removing this proportion from whiting. Further information on the changes to balance these prey species in the model can be found below within their functional group description.

1.4.1.3 FG3: Seals

a) Biomass, P/B, Q/B, bycatch (pre-balanced model)

The seals functional group consists of grey seals and harbour seals. The total population size of grey seals in the North Sea from 1984 to 2010 was estimated by Thomas *et. al.* (2019) to be 28,000 individuals in the northern North Sea. Using an average individual weight of 160 kg (Trites and Pauly, 1998), the biomass of grey seals was an estimated 4,480 t, or 0.017 t.km^{-2}. The average population of harbour seals in the northern North Sea was estimated to be 16,190 individuals (Thompson *et al.*, 2019). Using an average weight of 63.6 kg (Trites and Pauly, 1998), the biomass of harbour seals was estimated at 1,030 t, or 0.004 t.km^{-2}. The overall biomass of the seals functional group is therefore 0.021 t.km^{-2}. The maximum growth rate for seals is approximately 12% per year (Small and DeMaster, 1995). The $\mathrm{P/B}$ ratio was assumed to be half of the maximum rate i.e. 0.06 yr^{-1} (Trites *et al.*, 1999). Estimation for seal $\mathrm{Q/B}$ was calculated using Equation 4 with an individual weight (W) for grey seal of 152 kg and harbour seal of 58.4 kg (Trites et al., 1999). $\mathrm{Q/B}$ was estimated to be 11.46 yr^{-1} for grey seals and 15.69 yr^{-1} for harbour seals, with a group estimate of 14.39 yr^{-1}.

Hall *et al.* (2001) used the SMRU seal tagging database to estimate that a minimum of 2% of the tagged seals were killed within gill and tangle nets (Hall *et al.*, 2001). In 2015 the ICES working group on bycatch estimated a total of 469 predominantly grey seals were caught in static net fisheries across the UK fisheries as bycatch (ICES-WGBYC, 2015). Due to a lack of species specific information in the study area we applied the estimate of 2% bycatch to the northern North Sea (ICES-WGBYC, 2015) as an estimate for the whole seal functional group. Applying this to the northern North Sea grey seal abundance, the bycatch for this group is 0.00034 t.km^{-2} yr^{-1}.

b) Diet

Grey seal diet in the North Sea varies with season and region but mainly comprises sandeels (*Ammodytes marinus, Hyperoplus lanceolatus, Ammodytes tobianus*), gadoids (*Gadus morhua, Melanogrammus aeglefinus, Molva molva*) and flatfish (*Limanda limanda, Platichthys flesus*,

Table 6 *Seal diet in the northern North Sea model.*		
Prey	Diet proportion	
	Pre-balanced	Balanced
Skates & rays		0.020
Juvenile cod	0.085	0.184
Adult cod	0.161	0.020
Juvenile whiting	0.037	0.014
Adult whiting	0.020	0.020
Juvenile haddock	0.006	0.002
Adult haddock	0.011	0.001
Saithe	0.031	0.305
Hake	-	0.001
Ling	0.001	0.008
Norway pout	0.018	0.018
Monkfish	-	0.010
Herring	0.021	0.021
Small pelagic fish	0.003	0.020
Sandeels	0.413	0.237
Plaice	0.058	0.008
Turbot	-	0.001
Other flatfish	0.041	0.021
Small demersal fish	0.015	0.015
Large demersal fish	0.079	0.055
Squid & Octopus	-	0.006
Edible crab	-	0.001
Crabs & lobsters	-	0.001
Shrimp	-	0.001
Discards	-	0.009

Pleuronectes platessa) (Boyd, 2002). For the northern North Sea, grey seal diet proportions have been estimated from scat samples from Shetland and Orkney in 1985, 2000 and 2010 (Hammond and Wilson, 2016). Daily food requirements vary depending on grey seal size and the oil level within prey type but the average is approximately 7 kg of cod (or other whitefish) in comparison to 4 kg of sandeels day^{-1} (Boyd, 2002). Harbour seals consume a wide variety of prey including sandeels, whitefish, herring (*Clupea harengus*), sprat (*Sprattus sprattus*), flatfish, squid and octopus (Hall *et al*., 1998; Boyd, 2002). Harbour seal diet is taken from Hall *et al.* (1998) study of 12,444 otoliths from 708 scat samples from haul out sites in the North Sea. Due to their smaller size in comparison to grey seals, harbour seals require only approximately 3–5 kg of prey day^{-1} (dependent upon the particular prey species consumed) (Boyd, 2002). The diet preferences for each seal species were pro – rated by their respective biomass in the northern North Sea to give an overall diet preference for the seals functional group (Table 6).

c) Balancing changes

To balance top-down predation within the model, the proportion of sandeels, cod and whiting in the diet of seals was reduced, and the diet proportion of saithe and discards increased (Hammond and Wilson, 2016) (Table 6). Brown & Pierce (1994) also found otoliths of monkfish within Scottish grey seal faecal matter so 1% of seal diet was attributed to monkfish by removing this amount from whiting (Table 6).

An examination of the trophic level (TL) of seals and hake showed that the TL of hake was higher, which is unrealistic for a species that would be eaten by seals. Hammond and Wilson (2016) reported that North Sea seal scat samples included hake otoliths. Hake was added to the seal diet in the model at 0.1%, which was removed from sandeels. Seals are also known to predate upon skates off the North coast of Scotland. *Raja sp.* comprised 2% of grey seal diet over the period 1967-1971 according to Rae (1973). This predator-prey relationship was included within the model by removing 2% from the juvenile haddock prey and adding it to skates & rays (Rae, 1973). Both seal species are known to predate upon octopus (*Eladone spp)* and squid (*Loligo spp*) in the waters surrounding Shetland and Orkney (Brown and Pierce, 1997; Hammond and Wilson, 2016). The original seal diet did not include these prey species, but they were included in the balanced model. Harbour seals also predate upon a small amount of crustaceans (edible crab, hermit crab and shrimp) which were also included within the model diet at 0.1% (Rae, 1973). Turbot was added to seal diet at 0.1% following results in Arnett and Whelan (2001). (More information on the balancing of prey functional groups can be found within their functional group description below). After balancing, the EE for the seals functional group was 0.018.

1.4.2 Seabirds

Seabirds were split into two separate functional groups: those with a high proportion of fisheries discards in their diet ('high discard diet') and those with a 'low discard diet'. Seabirds with a 'high discard diet' in the northern North Sea include fulmar (*Fulmaris glacialis*), gannet (*Moras bassanus*), herring gull (*Larus argentatus*), lesser black backed gull (*Larus fuscus*), greater black-backed gull (*Larus marinus*), great skua (*Stercorarius skua*), black headed gull (*Chroicocephalus ridibundus*), Arctic skua (*Stercorarius parasiticus*) and cormorant (*Phalacrocorax carbo*) (Bicknell *et al.*, 2013). The non-discard dependent functional group includes puffin (*Fratucula arctica*), kittiwake (*Larus tridactyla*), guillemot (*Uria aalge*), shag (*Phalacrocorax aristotelis*), razorbill (*Alca torda*), storm petrel (*Hydrobates pelagicus*), Arctic tern (*Sterna paradisaea*) and Manx shearwater (*Puffinus puffinus*) (Bicknell *et al.*, 2013). Allocating seabirds to these two functional groups was designed to allow for subsequent investigation into the potential impacts of the Landings Obligation.

1.4.2.1 FG4: Seabirds (high discard diet)

a) Biomass, P/B, Q/B, bycatch (pre-balanced model)

Biomass for this group was estimated as the number of counts for each species (averaged across 1985-1987 and 1999-2001) in ICES area IVa, multiplied by their body weight (Table 7). The total biomass of seabirds with 'high discard diet' was estimated to be 417 t, or 0.0016 t.km^{-2}.

Q/B was estimated for each species by dividing R in Equation 5 by the estimated biomass (Nilsson and Nilsson, 1976) (Table 7). Individual body weights for each seabird species are

Table 7 *Biomass, daily ration and Q/B estimates for seabirds (high discard diet). Counts from ICES (1996) Seabird/fish interactions, with reference to seabirds in the northern North Sea.*

Seabird	Weight (kg)	Number of counts	Biomass (t)	Daily ration	Q/B (yr^{-1})
Northern fulmar	0.90	316 000	284	0.18	67
Northern gannet	3.00	19 500	59	0.60	56
Herring gull	1.08	32 500	35	0.22	65
Lesser black backed gull	0.83	9 300	8	0.17	68
Great skua	1.40	8 750	12	0.28	63
Arctic skua	1.40	3 000	4	0.28	63
Black-headed gull	1.10	5 250	6	0.22	65
Cormorant	1.90	1 200	2	0.38	60
Greater black backed gull	1.24	5 500	7	0.25	64

given in Table 7. Since Q/B is an annual measure it was derived as $R * 365/W$ and group Q/B was pro-rated by species biomass giving an estimate of 65.04 yr^{-1}. Seabird P/B was estimated to be 0.4 yr^{-1}, taken from estimates for seabirds from Trites *et al*. (1999).

b) Diet (pre-balanced model)

Diet proportions were collected from multiple references (Table 8) and pro-rated by species biomass for proportional input into the model diet matrix. Due to the low biomass of arctic skua, black headed gull, cormorant, and greater black-backed gull, these species were not included within the group diet.

Table 8 *Diet composition and references for seabirds (high discard diet) in the northern North Sea*

Seabird	Prey species	Diet reference
Northern fulmar	Sandeel (20%), gadoid discards (30%), offal discards 30%, 20% large zooplankton	Furness (2002), ICES (1996)
Northern gannet	Sandeel (30%), herring (30%), mackerel (30%), discards (10%)	Furness (2002), ICES (1996)
Herring gull	Invertebrates (91%), discards (9%)	ICES (1996)
Lesser black backed gull	Gadoid discards(60%), sandeel (20%), gadoids (20%)	Furness (2002), ICES (1996)
Great skua	Sandeel (45%), discards (whitefish) (53%), seabirds (2%)	Hamer *et al.* (1991) Furness (2002)

c) Balancing changes

Table 9 *Seabirds high discard diet proportions.*

Prey group	Pre-balanced	Balanced
Seabirds (HDD)	0.0002	0.0002
Seabirds (LDD)	0.0002	0.0002
Norway pout	0.006	0.006
Herring	0.072	0.072
Other pelagic fish	0.072	0.072
Sandeels	0.221	0.221
Large zooplankton	0.134	0.133
Small zooplankton	0.0364	0.095
Velvet crab	0.00001	0.001
Discards	0.450	0.400

Seabirds (high discard diet) was balanced in the initial model with an EE of 0.033. Diet proportions were adjusted to include preferences of the new species added to the group (Furness, 2002) and pro-rated by biomass. To balance the discards functional group, the proportion of discards in the diet of seabirds with 'high discard diet' was reduced from 45% to 40% with the remaining 5% added to small zooplankton (Table 9).

1.4.2.2 FG5: Seabirds (low discard diet)

a) Biomass, P/B, Q/B, bycatch (pre-balanced model)

Biomass was estimated as the number of counts for each species (averaged across 1985-1987 and 1999-2001) in ICES area IVa (ICES, 1996), multiplied by their average body weight (Table 10). Biomass estimates for storm petrel (0.00001 $t.km^{-2}$) and Manx shearwater (0.00002 $t.km^{-2}$) were provided by Waggitt *et al*. (2019) for the model area (Waggitt *et al.*, 2019). Total biomass for seabirds with 'low discard diet' was estimated to have been 705 t, or 0.003 $t.km^{-2}$ in 1991.

Table 10 *Biomass, daily ration and Q/B estimates for seabirds (low discard diet). Counts from ICES (1996) Seabird/fish interactions, with reference to seabirds in the North Sea.*

Seabird	Weight (kg)	Number (thousand) counts	Biomass (t)	Daily ration	Q/B (yr^{-1})
Puffin	0.40	101.0	40.40	0.08	75.68
Kittiwake	0.41	176.0	72.16	0.08	75.40
Guillemot	0.95	570.0	539.90	0.19	66.50
Shag	1.90	11.4	21.66	0.38	59.94
Razorbill	0.71	43.3	30.74	0.14	69.44
Storm petrel	0.03	-	-	0.01	113.39
Manx shearwater	0.42	-	-	0.08	75.12

Q/B was estimated for each species by dividing R in Equation 5 by the estimated biomass (Nilsson and Nilsson, 1976) (Table 10). Individual body weights for each seabird species are given in Table 10. Since Q/B is an annual measure it was derived as R *365/W and group Q/B was pro-rated by species biomass giving an estimate of 67.87 yr^{-1}. Seabird P/B was estimated to be 0.4 yr^{-1}, taken from estimates for seabirds from Trites *et al.* (1999).

b) Diet (pre-balanced model)

Diet proportions were collected from multiple scientific references (Table 11) and pro-rated by species biomass for proportional input into the model diet matrix.

Table 11 *Diet composition and references for seabirds (low discard diet) in the northern North Sea*

Seabird	Prey species	Diet reference
Puffin	Sandeels (60%), gadoids (15%), sprat (15%), rockling (5%), large zooplankton (5%)	Furness (1991), ICES (1996)
Kittiwake	Sandeels (55%), sprat (25%), zooplankton (15%), discards (5%)	ICES (1996)
Guillemot	Sandeels (60%), sprat (25%), gadoids (15%)	Furness (2002)
Shag	Sandeels (100%)	Furness & Barret (1991), ICES (1996)
Razorbill	Sandeels (80%), sprat (20%)	Hamer *et al.* (1991) Furness (2002)
Storm petrel	Sprat (50%), sandeels (30%), zooplankton (20%).	ICES (1996)
Manx shearwater	Sprat (50%), sandeels (30%), zooplankton (15%), offal discards (5%).	ICES (1996)

c) Balancing changes

Seabirds (low discard diet) was balanced in the model with an EE of 0.020. Prior to balancing, the diet proportion attributed to Norway pout was 2.8%. This fraction was the unknown 'gadoids' within the diet studies used (ICES, 1996; Furness, 2002). During balancing 2.8% of the diet was removed from Norway pout and added as the proportion of saithe in the diet, to account for saithe being a known prey species of puffins breeding in the Shetland Isles (Martin, 1989).

1.4.3 Fish

The main reasons behind the creation of this model were to explore the drivers of historical biomass and catch trends for the commercial fish species in the northern North Sea, and the impacts of management upon these trends, particularly for the fisheries of the Shetland Islands. Fish are consequently represented within the model in detail and account for 22 out of the total 43 functional groups. The empirical equations and data sources which apply to fish functional groups are outlined below.

Average weights at length (kg) were needed for each fish species for the transformation of count to weighted data in setting up the diet preferences and for parameter calculations such as natural mortality (M) and consumption over biomass (Q/B). Mean weights at length were estimated using Equation 6 (Ricker, 1973, 1975): where W is the weight (kg), L is the length (cm), a and b are estimated coefficients. Estimates for a and b were mainly sourced from Silva *et al.* (2013). Where needed, maximum length (L_{max}) was converted to maximum weight (W_{max}), length at maturity (L_{mat}) into weights at maturity (W_{mat}), and length at infinity (L_{∞}) into Weight at infinity (W_{∞}) using the inverse relationship.

Under steady state conditions, it is assumed that the Production/Biomass ratio (P/B) is equivalent to the instantaneous total mortality (Z) for fish (Equation 7). Z is the sum of natural mortality (M) and fishing mortality (F) when expressed as instantaneous rates (Allen, 1971). Estimates for fish P/B ratios, biomass, catch, M and F can be found in Table 12. Fishing mortality (F) in equilibrium states can be estimated as catch yr^{-1} ($t.km^{-2}.yr^{-1}$) (landings plus discards) divided by the biomass ($t.km^{-2}$) for that year (Equation 8). Natural mortality (M) for fish was estimated using Pauly's (1980) empirical model (Equation 9), where W_{∞} is the species asymptotic weight, k is the curvature parameter of the von Bertalanffy growth function and T is the average annual sea surface temperature (SST) (°C) for northern North Sea in 1991 (Rayner *et al.*, 2003) (Table 12).

Consumption/Biomass (Q/B) values for fish groups were calculated using the empirical formula of Pauly *et al.* (1990) and Christensen and Pauly (1992) (Equation 10). Where T' is the mean annual SST for the northern North Sea in 1991 (Rayner *et al.*, 2003) in Kelvin, Pf is chosen depending on feeding behaviour; for apex predators, pelagic predators, and zooplankton feeders Pf = 1 and for other feeding types = 0. Hd characterises the food type; for herbivores Hd = 1 and for predators = 0; (estimates of Q/B, k, length, and weight parameters can be found in (Table 13).

Table 12 *Parameter estimates for fish functional groups. Estimates of M for functional groups with multiple species were derived pro-rated by biomass (shown with an asterisk) . F = fishing mortality, M = natural mortality, P/B = Production to Biomass ratio.*

Functional group	Biomass			Catch				
	t.km-2	FG prop.	Source	t.km-2	Source	F	M	P/B
6. Sharks	0.277	-	-	0.021		0.076	0.202*	0.278
Spotted catshark	0.090	0.325	DATRAS:IBTS-IVa	-	(Heath and	-	0.219	-
Common smooth hound	0.070	0.255	DATRAS:IBTS-IVa	-	Cook, 2015;	-	0.197	-
Starry smooth hound	0.053	0.191	DATRAS:IBTS-IVa	-	ICES, 2019k)	-	0.239	-
Spurdog	0.046	0.166	DATRAS:IBTS-IVa	-	-	-	0.242	-
Tope	0.012	0.042	DATRAS:IBTS-IVa	-	-	-	0.180	-
Blackmouth catshark	0.004	0.015	DATRAS:IBTS-IVa	-	-	-	0.160	-
Porbeagle shark	0.001	0.004	DATRAS:IBTS-IVa	-	-	-	0.089	-
Lantern shark	0.001	0.003	DATRAS:IBTS-IVa	-		-	0.309	-
7. Skates and Rays	0.230	-	-	0.007	-	0.034	0.233*	0.239
Cuckoo ray	0.086	0.372	DATRAS:IBTS-IVa	-	(Heath and	-	0.300	-
Thornback ray	0.064	0.277	DATRAS:IBTS-IVa	-	Cook, 2015;	-	0.140	-
Common skate	0.053	0.229	DATRAS:IBTS-IVa	-	ICES, 2019k)	-	0.023	-
Starry ray	0.017	0.074	DATRAS:IBTS-IVa	-	-	-	0.300	-
Sandy skate	0.011	0.048	DATRAS:IBTS-IVa	-	-	-	0.195	-
8. Cod (juvenile)	0.247	-	(ICES, 2018d)	0.067	(ICES, 2018d)	0.270	1.462	1.732
9. Cod (adult)	0.160	-	(ICES, 2018d)	0.087	(ICES, 2018d)	0.542	0.234	0.776
10. Whiting (juvenile)	0.098	-	(ICES, 2019e)	0.025	(ICES, 2019l)	0.293	1.313	1.606
11. Whiting (adult)	0.154	-	(ICES, 2019e)	0.071	(ICES, 2019l)	0.461	0.500	0.961
12. Haddock (juvenile)	0.342	-	(ICES, 2019b)	0.198	(ICES, 2019l)	0.579	1.264	1.743
13. Haddock (adult)	0.197	-	(ICES, 2019b)	0.091	(ICES, 2019l)	0.462	0.308	0.770
14. Saithe	1.213	-	(ICES, 2018d)	0.495	(ICES, 2018d)	0.408	0.277	0.685
15. Hake	0.052	-	(ICES, 2019c)	0.0466	(Heath and Cook, 2015; ICES, 2019c)	0.897	0.246	1.143
16. Ling	0.064	-	DATRAS:IBTS-IVa	0.049	(Cook and Heath, 2018; ICES, 2019k)	0.766	0.201	0.967
17. Norway pout	1.566	-	(ICES, 2018d)	0.258	(ICES, 2018d) No reported discards	0.165	0.776	0.941
18. Monkfish	0.085	-	-	0.038	-	0.447	0.092*	0.539*
White-bellied	0.065	0.762	DATRAS:IBTS-IVa		(Heath and		0.034	
Black-bellied	0.020	0.238	DATRAS:IBTS-IVa		Cook, 2015; ICES, 2019k)		0.143	
19. Herring	2.580	-	(ICES, 2018c)	1.08	(ICES, 2018c)	0.420	0.630	1.050
20. Small pelagic fish	1.726	-	-	0.019		0.011	0.613*	0.624
Sprat	1.714	0.993	(ICES, 2018c)	-	(ICES, 2018c)	-	0.612	-
European anchovy	0.007	0.004	DATRAS:IBTS-IVa	-	-	-	0.678	-
Argentines	0.004	0.002	DATRAS:IBTS-IVa	-	-	-	1.861	-
Silvery lightfish	0.001	0.001	DATRAS:IBTS-IVa	-	-	-	0.587	-
21. Other pelagic fish	1.816	-	-	0.311	-	0.171	0.368	0.539*
Atlantic mackerel	1.739	-	(ICES, 2019i)	-	(ICES, 2019i)	-	0.397	-
Horse mackerel	0.057	-	(ICES, 2019d)	-	(ICES, 2019d)	-	0.263	-
Blue whiting	0.020	-	(ICES, 2019a)	-	(ICES, 2019a)	-	0.473	-
22. Sandeels	2.801	-	-	0.340	-	0.121	1.031	1.152*
Raitt's sandeel	2.413	0.861	(ICES, 2018c)	-	(ICES, 2018c)	-	1.089	-
Greater sandeel	0.382	0.137	DATRAS:IBTS-IVa	-	-	-	0.669	-
Lesser sandeel	0.006	0.002	DATRAS:IBTS-IVa	-	-	-	0.735	-
23. Plaice	0.140	-	(ICES, 2018d)	0.066	(ICES, 2018d)	0.471	0.130	0.601
24. Turbot	0.024	-	(ICES, 2018d)	0.009	(ICES, 2018d)	0.375	0.426	0.801
25. Flatfish	0.201	-	-	0.064	-	0.318	0.398	0.717

Brill	0.085	0.421	DATRAS:IBTS-IVa	-	(Heath and Cook, 2015; Cook and Heath, 2018; ICES, 2019k)		0.615	
Halibut	0.041	0.202	DATRAS:IBTS-IVa	-			0.055	
Megrim	0.018	0.088	DATRAS:IBTS-IVa	-			0.225	
Lemon sole	0.016	0.077	DATRAS:IBTS-IVa	-			0.280	
European flounder	0.013	0.063	DATRAS:IBTS-IVa	-			0.368	
Witch flounder	0.007	0.036	DATRAS:IBTS-IVa	-	-		0.200	
Long rough dab	0.005	0.026	DATRAS:IBTS-IVa	-	-		0.176	
Norwegian topknot	0.005	0.025	DATRAS:IBTS-IVa	-	-		0.601	
Common dab	0.005	0.024	DATRAS:IBTS-IVa	-	-		0.440	
Solenette	0.004	0.022	DATRAS:IBTS-IVa	-	-		0.819	
Common sole	0.003	0.014	DATRAS:IBTS-IVa	-	-		0.528	
26. Small demersal fish	0.037	-	-	0.0004	(ICES, 2019k)	0.011	0.772	0.782*
Bib	0.014	0.371	DATRAS:IBTS-IVa	-	-		0.711	
Lesser weaver	0.006	0.161	DATRAS:IBTS-IVa	-	-		0.899	
Reticulate dragonet	0.006	0.156	DATRAS:IBTS-IVa	-	-		0.849	
Poor cod	0.003	0.086	DATRAS:IBTS-IVa	-	-		0.769	
Common dragonet	0.003	0.077	DATRAS:IBTS-IVa	-	-		0.669	
Silvery pout	0.003	0.074	DATRAS:IBTS-IVa	-	-		0.814	
Spotted dragonet	0.002	0.050	DATRAS:IBTS-IVa	-	-		0.932	
Snake blenny	0.001	0.016	DATRAS:IBTS-IVa	-	-		-	
Vahl's eelpout	0.0003	0.008	DATRAS:IBTS-IVa	-	-		-	
Gobies	0.0001	0.001	DATRAS:IBTS-IVa	-	-		-	
27. Large demersal fish	0.316			0.052	(Heath and Cook, 2015; ICES, 2019k)	0.165	0.287	0.452
Pollack	0.115	0.364	DATRAS:IBTS-IVa	-	-		0.286	
Northern wolffish	0.074	0.234	DATRAS:IBTS-IVa	-	-		0.188	
Lumpfish	0.043	0.136	DATRAS:IBTS-IVa	-	-		0.328	
Shorthorn sculpin	0.027	0.086	DATRAS:IBTS-IVa	-	-		0.430	
Cusk	0.018	0.058	DATRAS:IBTS-IVa	-	-		0.243	
Norway haddock	0.007	0.021	DATRAS:IBTS-IVa	-	-		0.126	
Red gurnard	0.006	0.020	DATRAS:IBTS-IVa	-	-		0.396	
Greater forkbeard	0.006	0.019	DATRAS:IBTS-IVa	-	-		0.344	
John Dory	0.006	0.019	DATRAS:IBTS-IVa	-	-		0.242	
Grey gurnard	0.004	0.014	DATRAS:IBTS-IVa	-	-		0.647	
Four-bearded rockling	0.004	0.011	DATRAS:IBTS-IVa	-	-		0.380	
Boarfish	0.003	0.009	DATRAS:IBTS-IVa	-	-		0.336	
Hooknose	0.002	0.005	DATRAS:IBTS-IVa	-	-		0.826	
Blackbelly rosefish	0.001	0.004	DATRAS:IBTS-IVa	-	-		0.118	
Three-bearded rockling	0.0002	0.001	DATRAS:IBTS-IVa	-	-		0.564	
Red mullet	0.0001	0.0003	DATRAS:IBTS-IVa	-	-		0.412	

Table 13 *Parameter estimates for fish functional groups. Q/B (consumption/biomass) estimates for functional groups with multiple species were pro-rated by species biomass (shown with an asterisk). Length coefficients unless otherwise stated are sourced from the North Sea specific findings of Cefas study on the length-weight relationships of marine fish collected from around the British Isles (Silva et al., 2013).*

Functional group	*a*	*b*	*a* & *b* reference	L_∞	W_∞	K	Q/B	K source
6. Sharks	-	-		-	-	-	3.77*	
Spotted catshark	0.002	3.119	(Silva *et al.*, 2013)	87.4	2505	0.12	4.14	(Ivory *et al.*, 2005)
Common smooth hound	0.003	2.979	(Silva *et al.*, 2013)	145	9332	0.12	3.32	(Ivory *et al.*, 2005)
Starry smooth hound	0.002	3.079	(Silva *et al.*, 2013) (Pallaoro *et al.*, 2005)	124	5512	0.15	3.63	(Farrell *et al.*, 2010)
Spurdog	0.002	3.208	(Silva *et al.*, 2013)	85.4	2670	0.14	4.10	(Orlov *et al.*, 2011)
Tope	0.004	3.033	(Silva *et al.*, 2013)	183	27625	0.12	2.77	(Moulton *et al.*, 1992)
Blackmouth catshark	0.002	3.063	(Silva *et al.*, 2013)	77.5	1409	0.07	4.56	(Froese *et al.*, 2014)
Porbeagle shark	0.040	2.777	(Hennache and Jung, 2010)	349	459963	0.06	1.73	(Natanson *et al.*, 2002)
Lantern shark	0.004	3.063	(Torres *et al.*, 2012)	45.0	417	0.16	5.60	(Gennari and Scacco, 2007)
7. Skates and Rays	-	-	-	-	-	-	3.24*	
Cuckoo ray	0.0036	3.140	(Silva *et al.*, 2013)	79.2	3297	0.24	3.95	(Farias *et al.*, 2005)
Thornback ray	0.0045	3.096	(Silva *et al.*, 2013)	139	19418	0.09	2.93	(Ryland and Ajayi, 1984)
Dipturus batis complex	0.0038	3.120	(Silva *et al.*, 2013)	254	121089	0.06	2.16	(Du Buit, 1977) (Vinther, 1989)
Starry ray	0.0107	2.940	(Silva *et al.*, 2013)	66.0	2392	0.23	4.17	(Froese *et al.*, 2014)
Sandy skate	0.0039	3.080	(Froese *et al.*, 2014)	123	10692	0.12	3.24	
8. Cod (juvenile)	-	-	-	-	-	-	-	-
9. Cod (adult)	0.0106	3.000	(Silva *et al.*, 2013)	123	19725	0.17	2.93	(Speirs *et al.*, 2010)
10. Whiting (juvenile)	-	-	-	-	-	-	-	-
11. Whiting (adult)	0.0116	2.881	(Silva *et al.*, 2013)	24.0	125	0.34	5.30	(Pauly, 1978)
12. Haddock (juvenile)	-	-	-	-	-	-	-	-
13. Haddock (adult)	0.0113	2.960	(Silva *et al.*, 2013)	65.0	2626	0.20	3.290	(Jones, 1983)
14. Saithe	0.0085	3.024	(Silva *et al.*, 2013)	101	9792	0.20	3.290	(Magnussen, 2007)
15. Hake	0.0076	2.972	(Silva *et al.*, 2013)	83.0	3843	0.13	3.853	(Ungaro *et al.*, 1993)
16. Ling	0.0039	3.074	(Silva *et al.*, 2013)	124	1062	0.163	3.248	(Magnussen, 2007)
17. Norway pout	0.0075	3.024	(Silva *et al.*, 2013)	22.6	78.5	0.51	7.407	(Jennings *et al.*, 1998)
18. Monkfish	-	-	-	-	-	-	2.476*	
White-bellied	0.0297	2.841	(Silva *et al.*, 2013)	511	147	0.166	1.412	(Macdonald *et al.*, 2017)
Black-bellied	0.0203	2.930	(Silva *et al.*, 2013) (Silva *et al.*, 2013)	102	156	0.080	3.044	(Macdonald *et al.*, 2017)
19. Herring	0.0037	3.198		28.3	73.40	0.41	3.77	(Kienzle, 2005)
20. Small pelagic fish	-	-	-	-	-	-	9.486*	
Sprat	0.006	3.109	(Silva *et al.*, 2013)	13.2	17.968	0.300	9.490	(Froese *et al.*, 2014)
European anchovy	0.005	3.107	(Silva *et al.*, 2013)	20.0	55.148	0.400	7.860	(Pauly, 1978)
Argentines	0.006	3.031	(Silva *et al.*, 2013)	4.90	0.717	1.050	16.305	(Pauly, 1978)
Silvery lightfish	0.115	1.607	(Silva *et al.*, 2013)	22.3	16.841	0.280	9.593	(Gjøsæter, 1981)
21. Other pelagic fish	-	-	-	-	-	-	4.832*	
Atlantic mackerel	0.0052	3.167	(Silva *et al.*, 2013)	47.3	1049	0.26	4.792	(Pauly, 1978)
Horse mackerel	0.0316	2.652	(Silva *et al.*, 2013)	49.1	9645	0.14	4.860	(Cubillos and Arancibia, 1995)
Blue whiting	0.0038	3.185	(Silva *et al.*, 2013)	31.8	231	0.28	6.177	(Bailey, 1982)
22. Sandeels	-	-	-	-	-	-	8.805*	

Lesser sandeel	0.0049	2.786	(Silva *et al.*, 2013)	21.4	24.82	0.36	8.989	(MacDonald *et al.*, 2019)
Greater sandeel	0.0087	2.626	(Silva *et al.*, 2013)	29.8	64.73	0.40	7.651	(Kändler, 1941)
Small sandeel	0.0049	2.786	(Silva *et al.*, 2013)	23.4	31.99	0.72	8.613	(Reay, 1970)
23. Plaice	0.0125	2.943	(Silva *et al.*, 2013)	81.6	5.73	0.060	3.653	(Chuenpagdee, 1990)
24. Turbot	0.0149	3.079	(Silva *et al.*, 2013)	54.6	3.286	0.310	3.947	(van der Hammen and Poos, 2012)
25. Flatfish	-	-	-	-	-	-	4.333*	
Brill	0.0140	3.009	(Silva *et al.*, 2013)	40.2	942	0.49	4.880	(Arneri *et al.*, 2001)
Halibut	0.0023	3.379	(Silva *et al.*, 2013)	303	559772	0.03	1.669	(Matiiisen and Olen, 1968)
Mergim	0.0022	3.343	(Silva *et al.*, 2013)	59.0	1832	0.12	4.364	(Landa *et al.*, 1996)
Lemon sole	0.0123	2.971	(Silva *et al.*, 2013)	50.0	1374	0.16	4.580	(Magnussen, 2007)
European flounder	0.0244	2.785	(Silva *et al.*, 2013)	44.9	975	0.23	4.851	(van der Hammen and Poos, 2012)
Witch flounder	0.0033	3.205	(Silva *et al.*, 2013)	60.5	1693	0.10	4.422	(Bowering, 1978)
Long rough dab	0.0053	3.143	(Silva *et al.*, 2013)	70.4	3404	0.09	3.932	(Pitt, 1975)
Norwegian topknot	0.0262	2.751	(Silva *et al.*, 2013)	12.8	29.08	0.31	8.752	(Pauly, 1978)
Common dab	0.0159	2.864	(Silva *et al.*, 2013)	35.0	420	0.27	5.588	(Albert *et al.*, 1998)
Solenette	0.0145	2.872	(Silva *et al.*, 2013)	13.3	24.51	0.48	9.007	(Ilkyaz *et al.*, 2010)
Common sole	0.0089	3.017	(Silva *et al.*, 2013)	36.9	475	0.36	5.473	(de Veen, 1976)
26. Small demersal fish	-	-	-	-	-	-	6.747*	
Bib (pouting)	0.0305	2.7204	(Silva *et al.*, 2013)	41.0	744.24	0.59	5.076	(Merayo and Villegas, 1994)
Lesser weaver	0.0070	3.2073	(Silva *et al.*, 2013)	15.9	49.927	0.60	7.993	(Hureau and Monod, 1973)
Reticulate dragonet	0.0296	2.3367	(Silva *et al.*, 2013)	19.5	30.600	0.52	8.678	(Froese *et al.*, 2014)
Poor cod	0.0103	3.0187	(Silva *et al.*, 2013)	20.0	87.148	0.51	7.278	(Jennings *et al.*, 1999)
Common dragonet	0.0187	2.7169	(Silva *et al.*, 2013)	25.0	117.46	0.43	6.922	(Chang, 1951)
Silvery pout	0.0200	2.7052	(Silva *et al.*, 2013)	16.2	37.412	0.50	8.390	(Albert, 1993)
Spotted dragonet	0.0369	2.2653	(Silva *et al.*, 2013)	17.5	24.148	0.58	9.030	(Froese *et al.*, 2014)
27. Large demersal fish	-	-	-	-	-	-	3.622*	
Pollack	0.0076	3.0686	(Silva *et al.*, 2013)	85.6	6468.49	0.20	3.530	(Moreau, 1964)
Northern wolffish	0.0046	3.180	(Silva *et al.*, 2013)	115	16435.27	0.12	3.018	(Liao and Lucas, 2000)
Lumpfish	0.088	2.8751	(Silva *et al.*, 2013)	52.7	7849.83	0.25	3.417	(Kasper *et al.*, 2014)
Shorthorn sculpin	0.0273	2.8524	(Silva *et al.*, 2013)	62.3	3585.60	0.34	3.898	(Froese *et al.*, 2014)
Cusk	0.0051	3.189	(Silva *et al.*, 2013)	73.0	4498.83	0.15	3.752	(Bergstad and Hareide, 1996)
Norway haddock	0.0178	2.9724	(Silva *et al.*, 2013)	75.6	6825.56	0.06	3.498	(Samdeman, 1964)
Red gurnard	0.0156	2.8276	(Silva *et al.*, 2013)	40.9	562.90	0.24	5.320	(Marriott *et al.*, 2010)
Greater forkbeard	0.0051	3.1469	(Silva *et al.*, 2013)	54.9	1519.95	0.22	4.503	(Casas and Piñeiro, 2000)
John Dory	0.0399	2.7536	(Silva *et al.*, 2013)	69.3	4673.22	0.15	3.728	(Moutopoulos and Stergiou, 2002)
Grey gurnard	0.0091	2.9772	(Silva *et al.*, 2013)	35.0	359.78	0.47	5.736	(Magnussen, 2007)
Four-beard rockling	0.008	2.8377	(Silva *et al.*, 2013)	36.0	208.65	0.20	6.286	(Albert, 1993)
Boarfish	0.0549	2.6322	(Silva *et al.*, 2013)	16.5	87.95	0.15	7.267	(Hüssy *et al.*, 2012)
Hooknose	0.0372	2.3604	(Silva *et al.*, 2013)	15.0	22.21	0.48	9.158	(Gall, 1969)
Blackbelly rosefish	0.0113	3.128	(Silva *et al.*, 2013)	57.1	3530.50	0.05	3.908	(Abecasis *et al.*, 2006)
Three beard rockling	0.0051	3.1481	(Silva *et al.*, 2013)	62.2	2262.57	0.48	4.211	(Albert, 1993)
Red mullet	0.0092	3.1048	(Silva *et al.*, 2013)	29.8	347.48	0.24	5.764	(Mahé *et al.*, 2013)

Table 14 *Catch estimates for multi-species functional groups with discard and landing sources. A dash represents that there was no available data for landing and/or discards for that species.*

Functional group	Catch			
	Landings t.km^{-2}	Source	Discards t.km^{-2}	Source
6. Sharks	0.021	-	0.0003	-
Spotted catshark	0.0001	(ICES, 2019k)	-	-
Common smooth hound	0.0024	(ICES, 2019k)	-	-
Starry smooth hound	0.0000	(ICES, 2019k)	-	-
Spurdog	0.0000	(ICES, 2019k)	0.0003	(Heath and Cook, 2015)
Tope	0.0000	(ICES, 2019k)	-	-
Blackmouth catshark	0.0184	(ICES, 2019k)	-	-
Porbeagle shark	0.0000	(ICES, 2019k)	-	-
Lantern shark	0.0002	(ICES, 2019k)	-	-
7. Skates and Rays	0.005		0.002	-
Cuckoo ray	0.002	(ICES, 2019k)	0.0007	(Heath and Cook, 2015)
Thornback ray	0.002	(ICES, 2019k)	0.0006	(Heath and Cook, 2015)
Common skate	0.001	(ICES, 2019k)	0.0005	(Heath and Cook, 2015)
Starry ray	0.0004	(ICES, 2019k)	0.0001	(Heath and Cook, 2015)
Sandy skate	0.0003	(ICES, 2019k)	0.0001	(Heath and Cook, 2015)
18. Monkfish	0.034		0.004	-
White-bellied	0.026	(ICES, 2019k)	0.003	(Heath and Cook, 2015)
Black-bellied	0.008	(ICES, 2019k)	0.001	(Heath and Cook, 2015)
20. Small pelagic fish	0.018	-	0.001	-
Sprat	0.018	(ICES, 2018c)	0.001	(ICES, 2018c)
European anchovy	0.0001	(ICES, 2019k)	-	-
Argentines	0.0001	(ICES, 2019k)	-	-
Silvery lightfish	0.0000	(ICES, 2019k)	-	-
21. Other pelagic fish	0.260	-	0.052	-
Atlantic mackerel	0.190	(ICES, 2019i)	0.012	slipping rate 0.045
Horse mackerel	0.021	(ICES, 2019d)	0.011	slipping rate 0.52
Blue whiting	0.049	(ICES, 2019a)	0.029	slipping rate 0.59
25. Flatfish	0.043		0.021	
Brill	0.016	(ICES, 2019k)	0.00001	(Heath and Cook, 2015)
Halibut	0.005	(ICES, 2019k)	0.0001	(Heath and Cook, 2015)
Me~~r~~gRim	0.004	(ICES, 2019k)	0.0007	(Heath and Cook, 2015)
Lemon sole	0.007	(ICES, 2019k)	0.0012	(Heath and Cook, 2015)
European flounder	0.000	(ICES, 2019k)	0.00003	(Heath and Cook, 2015)
Witch flounder	0.010	(ICES, 2019k)	0.0012	(Heath and Cook, 2015)
Long rough dab	0.000	(ICES, 2019k)	-	-
Norwegian topknot	0.000	(ICES, 2019k)	-	-
Common dab	0.001	(ICES, 2019k)	0.0107	(Cook and Heath, 2018)
Solenette	0.000	(ICES, 2019k)	-	-
Common sole	0.000	(ICES, 2019k)	0.00001	(Heath and Cook, 2015)
26. Small demersal fish	0.00008	(ICES, 2019k) Gadiformes n.e.i	0.0003	(STECF, 2015)
Bib	-	-	-	-
Lesser weaver	-	-	-	-
Reticulate dragonet	-	-	-	-
Poor cod	-	-	-	-
Common dragonet	-	-	-	-
Silvery pout	-	-	-	-
Spotted dragonet	-	-	-	-
Snake blenny	-	-	-	-
Vahl's eelpout	-	-	-	-
Gobies	-	-	-	
27. Large demersal fish	0.044		0.008	
Pollack	0.006	(ICES, 2019k)	0.0005	(Heath and Cook, 2015)
Northern wolffish	0.009		0.0004	(Heath and Cook, 2015)
Lumpfish	0.00004		-	-

Shorthorn sculpin	0.005		-	-
Cusk	0.017		0.0028	(Heath and Cook, 2015)
Norway haddock	0.007		-	-
Red gurnard	0.00003		-	-
Greater forkbeard	0.0001		-	-
John Dory	-		-	-
Grey gurnard	0.00004		0.0003	(Heath and Cook, 2015)
Four-bearded rockling	-		-	-
Boarfish	-		-	-
Hooknose	-		-	-
Blackbelly rosefish	0.00002		-	-
Three-bearded rockling	-		-	-
Red mullet	-		0.004	(Heath and Cook, 2015)

1.4.3.6 Fisheries landings and discards

Official landings data for 1970s onwards for ICES area IVa were obtained from ICES (https://www.ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx) and the 1991 data used for the Ecopath model construction. Landings were converted into t.km^{-2} by dividing by the total modelled area i.e. 264,343 km^2.

Where available, discard estimates from the ICES Working Group Report were used (ICES, 2018d). For discards of species not under assessment, or where the Working Group does not report a discard estimate, an alternative method was adopted. Heath and Cook (2015) developed a model to estimate quantities of fish discarded by the commercial fisheries in the North Sea. Their discard model was based on utilising additional information from scientific trawl surveys alongside existing landings and discard data for the five main species targeted by the fisheries (cod, haddock, whiting, plaice and sole) in the North Sea (Heath and Cook, 2015; Cook and Heath, 2018). Discard estimates for the northern North Sea were calculated by partitioning the discard values estimated for the total North Sea (Heath and Cook, 2015; Cook and Heath, 2018) by the ratio of landings in IVa verses the whole North Sea (ICES, 2019k) for each species. This approximation assumes that the discard rates were homogeneous across the whole North Sea area.

1.4.3.7 Diets

The diets for fish groups were estimated using data from the Database of Stomach Records (DAPSTOM) maintained by CEFAS (https://www.cefas.co.uk/data-and-publications/fish-stomach-records/) (Pinnegar, 2014). All available data from the 1800s to 2016 for ICES area IVa were downloaded (specific area assignment provided through personal communication with John Pinnegar). The DAPSTOM dataset was then filtered to only include records from 1970 onwards and supplemented with additional records from the NAFC Marine Centre in Shetland (Figure 4).

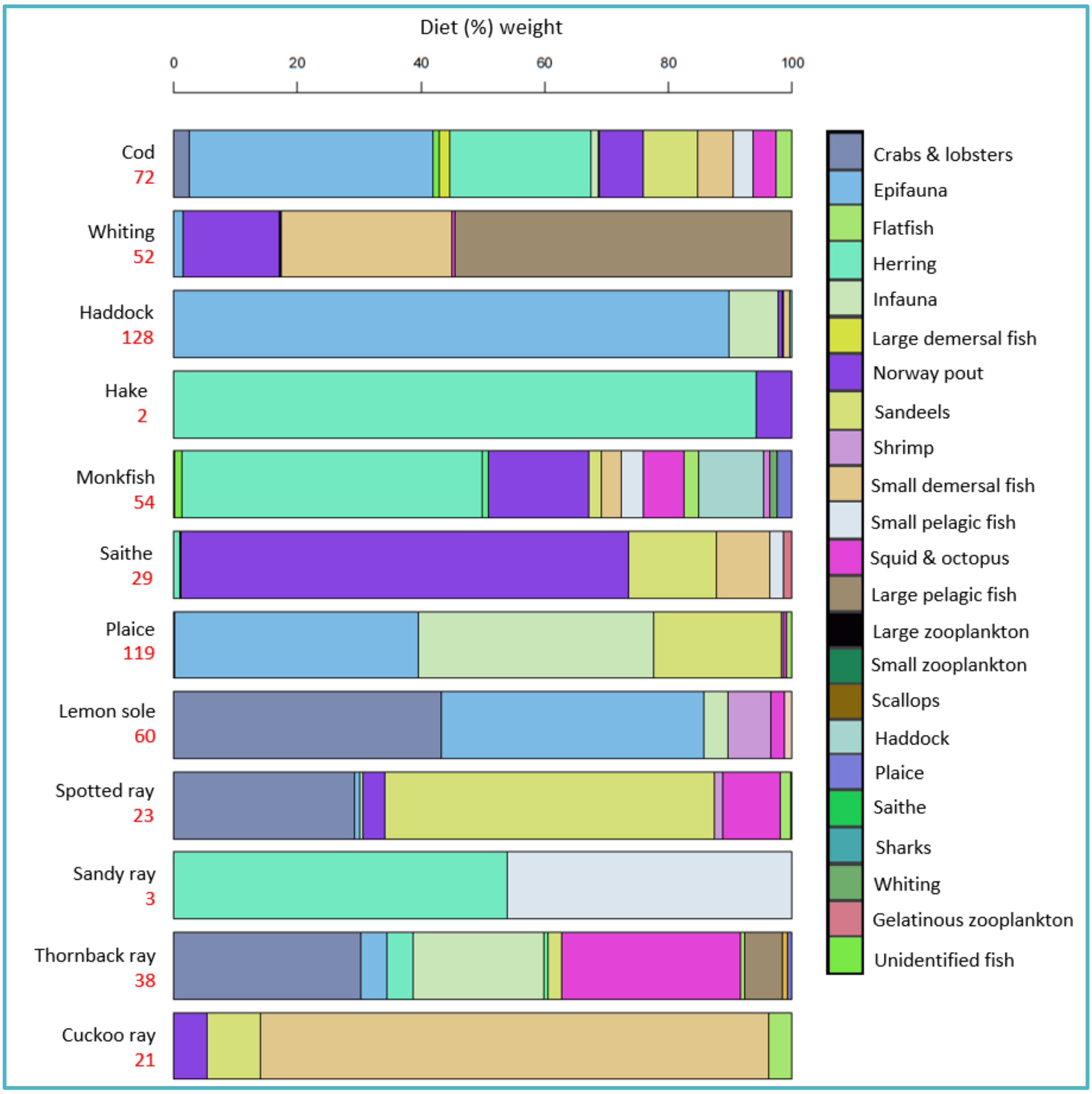


Figure 4 *Percentage predator diet by weight. Data collected during NAFC Marine Centre's 'Shetland food-web biodiversity and trophic interactions project 2017'. Stomachs sampled from demersal mixed fishery trawls. Prey species grouped into model functional groups. Red numbers next to each bar indicate the number of stomachs sampled.*

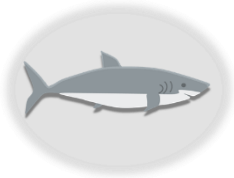
DAPSTOM generally records stomach contents as counts of prey within each sampled stomach because weighing digested and semi-digested prey items can be unreliable. Counts of prey items within each predator stomach therefore had to be converted into weight estimates of each prey species. For fish prey, weights were obtained by converting length to weights. Length information for each fish species specific to the North Sea was obtained from Silva *et al.* (2013) (Table 13). Length information from the NS IBTS was used to reference conversions from count to average length and weight for prey species in predator diets relative to the North Sea (ICES, 2019j). Although this method will overestimate the number of large prey items as fish are more likely to consume a smaller prey than itself, it is the only method currently available to get weighted diet estimates after the fact. For invertebrate prey, species average weight data were acquired from Robinson *et al*. (2010) and SeaLifeBase (Palomares and Pauly, 2017). These weighted diets were then transformed into proportional diets as required for the EwE diet matrix.

Where there was a large sample size of diet data for 1991 and/or 1992, these data were used for group diet proportions in the model. For groups with a large sample size for 1991 and/or 1992, plus supplementary 2017 data (juvenile and adult cod, adult whiting, adult haddock, and saithe) mean weighted proportional diets across these surveys were used within the model diet matrix. For these groups, the larger sample size for 1991/92 data allows the diet to better reflect the year of the model, but including a wider range of prey species (if supplementary 2017 data introduces a new prey species, not included within the DAPSTOM data) will allow for predator consumption to change dynamically in response to changes in prey biomass, under future Ecosim analysis.

For predators where there were no available stomach samples from 1991/92, the mean weighted proportional diets from 1970–2017 were used to parameterise the model diet matrix. Diets of functional groups consisting of multiple predator species were pro-rated by the biomass proportion that each species contributes towards the functional group.

The standard deviation of each mean diet proportion and the minimum and maximum percentile values allowed for a range of diet proportions within predator diet. For balancing, these ranges allowed for the diets of predators to be adjusted within sensible ranges (see model balancing sections of this report for each fish functional group for more information). For groups with large sample size for 1991 and/or 1992, plus supplementary 2017 data where a mean weighted proportional diets across these surveys were constructed (juvenile and adult cod, adult whiting, adult haddock, and saithe), the percentile ranges allowed for the diets of these predators to be adjusted to reflect the model year, if required for balancing. Visualisations of functional group diets derived from DAPSTOM and NAFC stomach records are provided for each fish functional group in the sections below.

1.4.3.8 FG6: Sharks



a) Biomass, P/B, Q/B, catch (pre-balanced model)

Shark species found in the northern North Sea include spotted catshark, common smooth hound, starry smooth hound, spurdog, hound shark (tope), black-mouth catshark, porbeagle shark, and lantern shark. The geometric mean area-swept biomass estimates for these species (Table 12) were generated using IBTS-IVa data for 1991, giving a combined biomass of 0.277 t.km^{-2}. Estimates for F and M for each species (Table 12) were used to calculate a group P/B of 0.278 yr^{-1} and group Q/B was estimated as 3.77 yr^{-1} (Table 13). Landings for sharks were estimated from ICES catch statistics in 1991 as 0.021 t.km^{-2} (ICES, 2019k). Shark discards were estimated as 0.0003 t.km^{-2} for the northern North Sea using North Sea discard estimates from Heath & Cook (2015), to give a total catch for sharks of 0.021 t.km^{-2} in 1991 (Table 14).

b) Diet (pre-balanced model)

For shark diets DAPSTOM only recorded empty spurdog stomachs in 1964. No other diet data was available. Therefore, diet proportions are from studies by Ellis *et al*. (1996) of elasmobranch stomach contents collected from 1981 to 1985 during ground-fish surveys in the north-eastern Atlantic (most sampled from the Irish Sea) (Table 15).

Table 15 *Diet of sharks in the pre-balanced and balanced northern North Sea EwE model.*

Prey	Diet proportion	
	Pre-balanced	Balanced
Skates & rays	0.003	0.027
Cod juvenile	-	0.021
Cod adult	0.016	0.008
Hake	0.016	0.004
Ling	0.021	0.006
Norway pout	0.015	0.017
Monkfish	0.007	0.001
Herring	0.045	0.045
Small pelagic fish	-	0.050
Other pelagic fish	0.065	0.065
Plaice	0.107	0.010
Other flatfish	0.179	0.046
Small demersal fish	0.107	0.107
Large demersal fish	0.088	0.010
Squid and Octopus	0.081	0.081
Large zoo.	0.003	0.003
Gelatinous zoo.	-	0.012
Edible crab	0.011	0.015
Velvet crab	0.000	0.0003
Crabs & lobsters	0.218	0.193
Norway lobster	-	0.001
Shrimp	0.006	0.006
Epifauna	0.006	0.169
Infauna	0.005	0.102

c) Balancing changes

Sharks were balanced in the pre-balance model with an EE of 0.306 but given that these shark species are unlikely to be top predators in the model and there is a fishery catch, EE should probably be higher for this group. Using the calculated P/B and Q/B ranges, the P/Q for sharks is slightly underestimated at 0.089. Due to the slower reproduction rate of cartilaginous fish, sharks should ecologically fall at the lower end of the 0.1 – 0.3 P/Q range for finfish (Link, 2016).

To balance sharks, we allowed the model to estimate P/B with an allocated P/Q of 0.1 yr^{-1}. P/B was originally 0.267 yr^{-1} but was re-estimated by the model as 0.377 yr^{-1} which is closer to estimates from other existing models for the Irish Sea (Bentley *et al.*, 2018) and West Coast of Scotland (Serpetti *et al.*, 2017).

Shark predation upon plaice was considered too high in the pre-balanced model (plaice EE 2.68). The proportion of plaice in the diet of sharks was therefore reduced to 1% with the remaining 10% added to epifauna (for more information see the plaice functional group description).

The proportion of edible crab, Norway lobster, epifauna and infauna in the shark diet were raised due to these shark species consuming large amounts of crustaceans and benthos (Ellis *et al.*, 1996), reducing the proportion of other flatfish in shark diet. The proportion of epifauna was also increased by reducing large demersal fish from 8.8% to 1%. The predation mortality of sharks upon adult cod was too high in the pre-balanced model with no predation on the juvenile stages. The diet proportion was therefore pro-rated by the relative biomass of each cod stanza (Table 15). The final balanced diet for sharks is shown in Table 15 and with these changes the shark group EE was increased to 0.363.

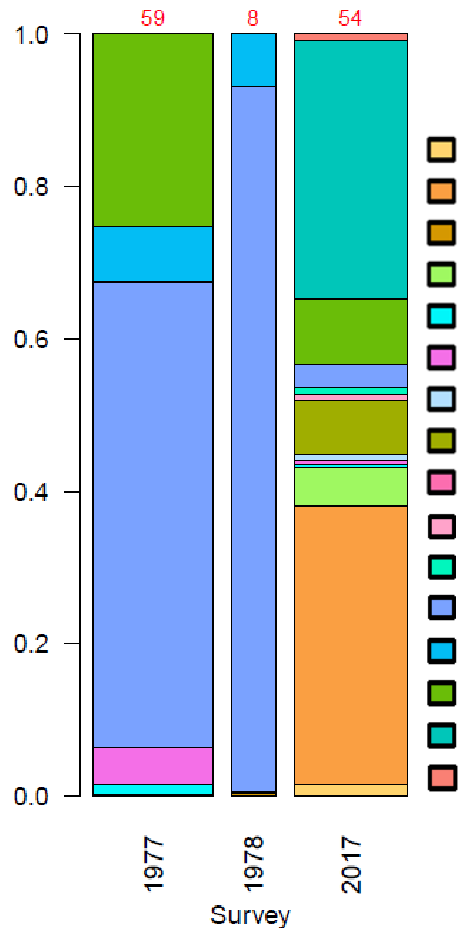
1.4.3.9 FG7: Skates & rays

a) Biomass, P/B, Q/B, catch (pre-balanced model)

Skate and ray species in this group include cuckoo ray, thornback ray, *Dipturus batis* complex, starry ray and sandy skate. The geometric mean area-swept biomass estimates for these species (Table 12) gave a combined skates and rays group biomass of 0.230 $t.km^{-2}$. Estimates for F and M for each species (Table 12) were used to calculate a group P/B of 0.239 yr^{-1} and group Q/B was estimated as 3.241 yr^{-1} (Table 13). Landings for skates and rays of 0.005 $t.km^{-2}$ were estimated from ICES catch statistics in 1991 (ICES, 2019k). Discards of skates and rays of 0.002 $t.km^{-2}$ were calculated for the northern North Sea from Heath & Cook (2015), giving a total catch for skates and rays of 0.007 $t.km^{-2}$ (Table 14).

b) Diet (pre-balanced model)

DAPSTOM data for this group was only available for the 1970's within ICES division IVa. Diet for skates and rays was thus estimated using available DAPSTOM data combined with the NAFC Marine Centre dataset (Figure 5). DAPSTOM samples from the 1970's for this predator contained mainly sandeels, whilst NAFC samples from 2017 contained predominantly epifauna and squid, and low amounts of sandeels. With no available data closer to the early 1990's for the study area this diet estimate was used for the skates and rays functional group (Figure 5).



	Mean prop.	SD	Min	Max
Bony fish	0.006	0.008	0	0.016
Epifauna	0.122	0.211	0	0.365
Flatfish	0.001	0.002	0	0.004
Herring	0.017	0.029	0	0.051
Infauna	0.006	0.006	0	0.013
Crabs & lobsters	0.018	0.027	0	0.049
Large demersal fish	0.002	0.004	0	0.006
Other pelagic fish	0.024	0.042	0	0.072
Large zooplankton	0.0007	0.001	0	0.001
Norway pout	0.002	0.004	0	0.006
Plaice	0.003	0.005	0	0.009
Sandeels	0.522	0.454	0.031	0.926
Shrimp	0.048	0.041	0	0.074
Small demersal fish	0.112	0.128	0	0.251
Squid	0.113	0.196	0	0.339
Whiting	0.003	0.005	0	0.009

Figure 5 *Bar plot of the total biomass weighted proportion of prey species found in skate & ray stomachs during each survey year sampled, in Area IVa . Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate an average diet shown in the table (above) by combining the data from DAPSTOM and NAFC Marine Centre .*

d) Balancing changes

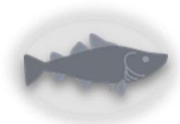
In the pre-balanced model, the skates & rays group was balanced with an EE of 0.214. The calculated P/Q for this group was underestimated by the model at 0.07 yr^{-1}. Cartilaginous fish, as explained above should ecologically fall at the lower end of the 0.1 – 0.3 P/Q range for finfish (Link, 2016). Therefore, a P/Q of 0.15 yr^{-1} was put in for this group and the model allowed to estimate P/B. The original P/B value of 0.262 yr^{-1} was thus re-estimated at 0.489 yr^{-1}. This P/B estimate is closer to estimates used within other existing Ecopath models; Irish Sea (Bentley *et al.*, 2018) and West Coast of Scotland (Serpetti *et al.*, 2017). With these changes EE for the skates and ray group is now 0.384.

Table 16 *Diet of skates & rays in the northern North Sea EwE model, estimated within DAPSTOM and NAFC mean data ranges.*

Prey	Diet proportion	
	Pre-balanced	Balanced
Whiting juvenile	0.002	0.002
Whiting adult	0.001	0.001
Norway pout	0.002	0.002
Herring	0.017	0.010
Small pelagic fish	-	0.009
Other pelagic fish	0.024	0.024
Sandeels	0.527	0.527
Plaice	0.003	0.003
Other flatfish	0.001	0.001
Small demersal fish	0.113	0.050
Large demersal fish	0.002	0.002
Squid and Octopus	0.113	0.104
Large zoo.	0.001	0.001
Velvet crab	0.0001	0.0001
Crabs & lobsters	0.018	0.018
Shrimp	0.048	0.048
Epifauna	0.122	0.182
Infauna	0.006	0.006
Discards	-	0.010

This group of ray species are known for their scavenging behaviour (Navarro *et al.*, 2016; Depestele *et al.*, 2019). The proportion of herring in their diet was therefore reduced from 1.7% to 1% with the remaining 0.7% being allocated to the discards. To include sprat within the diet of this group, a proportion of small pelagic fish was added at 0.9% (Ellis *et al.*, 1996). This amount was removed from squid & octopus, reducing their proportion in the diet from 11.3% down to 10.4%. Small demersal fish were also reduced in the diet from 11.3% to 5%, with the remaining 6.3% added to the epifauna (6%) and discards (0.3%) (Table 16).

1.4.3.10 FG8: Atlantic cod juvenile (0-36 months) and FG9: Atlantic cod adult (36+ months)



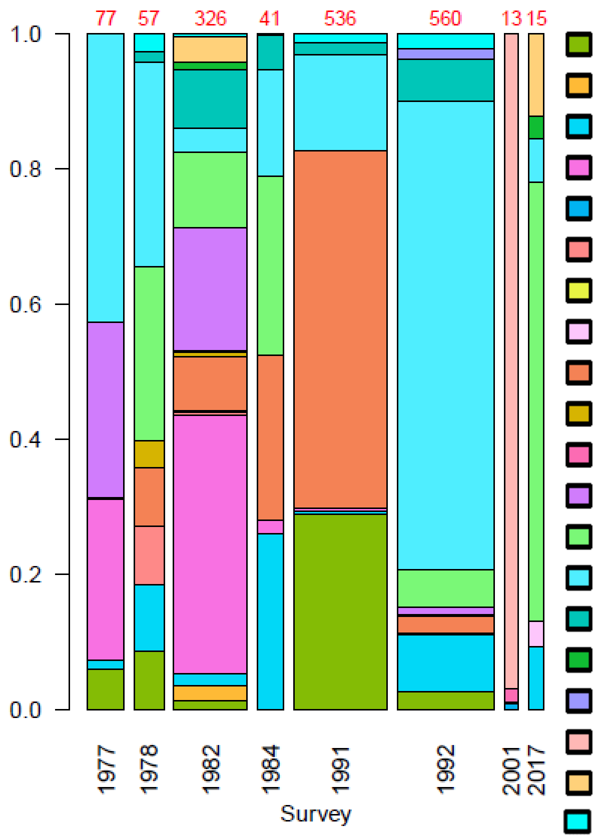
a) Biomass, P/B, Q/B, catch (pre-balanced model)

The Atlantic cod group was split into 2 stanzas: juvenile cod up to 36 months old and adult cod aged 36 months and above (ICES, 2018d). For 1991, the spawning stock biomass was estimated as 124,755 t across the whole North Sea (777,661 km^2) (ICES, 2018d). Based on visual inspection of the spatial distribution in the IBTS survey (see figure 2 in Engelhard *et al.* (2014)) a uniform distribution of abundance was assumed across the whole stock area in 1991. Therefore, the area-based biomass for the northern North Sea was estimated as 0.16 $t.km^{-2}$. M and F estimates in Table 12 was used to calculate a $\mathrm{P/B}$ of 0.774 yr^{-1} and the $\mathrm{Q/B}$ was estimated at 2.927 yr^{-1} (Equation **10**,Table 13). The population model for this group was parameterised using information within Table 2.

Juvenile cod biomass and $\mathrm{Q/B}$ ratios were estimated by the model as 0.247 $t.km^{-2}$ and 7.642 yr^{-1}, respectively. When constructing stanzas in Ecopath, the $\mathrm{Q/B}$ and biomass of the leading stanza (in this instance adult cod) determines the $\mathrm{Q/B}$ of the non-leading stanza. This is an assumption by the von Bertalanffy growth model that feeding rates vary with age as 2/3 the power of body weight. For multi-stanza groups within Ecopath the juvenile group also includes fish eggs and larvae so the juvenile Z required for the population model to function is always much greater than the Z calculated across the immature age classes in the stock assessment. Due to this and a lack of information on cod juvenile total mortality we assumed that the total mortality ($Z=P/B$) is double that of the adult P/B giving a value of 1.732 yr^{-1}.

Landings for juvenile cod were estimated using catch and numbers at age (ICES, 2018d) as 33,853 t, equivalent to 0.044 $t.km^{-2}$. Discards for juvenile cod in 1991 were estimated as 18,022 t (ICES, 2018d), equivalent to 0.023 $t.km^{-2}$. Adult cod landings were estimated as 67,437 t (ICES, 2018d), or 0.087 $t.km^{-2}$, with discards of 177 t and 0.0002 $t.km^{-2}$ (ICES, 2018).

b) Diet (pre-balanced model)



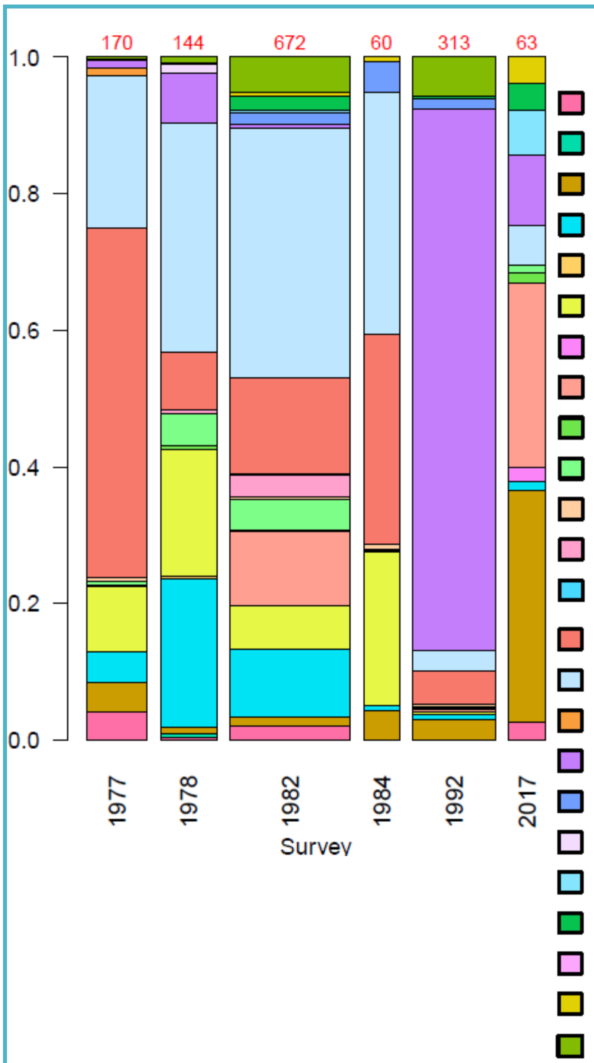
	Mean	SD	min	max
Bony fish	0.060	0.098	0	0.289
Edible crab	0.003	0.008	0	0.023
Epifauna	0.071	0.087	0	0.260
Flatfish	0.081	0.147	0	0.383
Gelatinous zoo.	0.001	0.003	0	0.010
Haddock	0.011	0.031	0	0.087
Herring	0.0002	0.001	0	0.002
Infauna	0.005	0.013	0	0.037
Crabs & lobsters	0.120	0.184	0	0.528
Lrg. demersal fish	0.006	0.014	0	0.039
Lrg. Zooplankton	0.003	0.008	0	0.022
Norway lobster	0.057	0.103	0	0.260
Norway pout	0.168	0.224	0	0.650
Sandeels	0.227	0.236	0	0.691
Shrimp	0.029	0.033	0	0.087
Sm. demersal fish	0.006	0.012	0	0.034
Sm. pelagic fish	0.002	0.005	0	0.016
Small zooplankton	0.122	0.342	0	0.968
Squid	0.020	0.044	0	0.123
Whiting	0.008	0.011	0	0.026

Figure 6 *Bar plot of the total biomass weighted proportion of prey species found in juvenile cod (<40 cm) during each survey year in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean diet across 1970-2017 shown in the table (above) by combining across these surveys.*

Using DAPSTOM and NAFC records for the northern North Sea the diet of cod was partitioned into juvenile and mature components using an L_{mat} value of 40 cm (Armstrong *et al.*, 2004). The mean diet proportion by weight for available surveys across 1970-2017 was used as the basis for the diet of mature and immature cod in the model (Figure 6 and Figure 7). There was a large sample size of diet data for cod in 1991 and 1992, plus supplementary 2017 data was available. Mean weighted proportional diets across these surveys were used within the model diet matrix. Larger sample size for 1991/92 data allows the diet to better reflect the year of the model, whilst including a wider range of known prey species. Average diets for cod with plausible minimum, maximum and percentile values, provided a range of proportions which allowed for the diets to be adjusted to reflect the model year, if required for model balancing. The consensus diet of juvenile cod consists primarily of sandeels, Norway pout and small zooplankton. Whilst the diet of mature cod consists primarily of Norway pout, Norway lobster and sandeels.

d) Balancing changes

Cod was unbalanced in the initial model with mature cod having an EE of 2.05 and immature cod an EE of 0.319. An EE of 0.319 for juvenile cod represents that nearly 70% of this groups' mortality is unexplained by the model. To resolve this, the predation mortality for this group was increased in the model by introducing saithe, sharks and monkfish as new predators. The proportion of juvenile cod in the diet of monkfish was also increased (more information on balancing changes to saithe, shark, ling and monkfish diet see their functional group descriptions).



	Mean	SD	min	max
Bony fish	0.016	0.017	0	0.042
Cod	0.001	0.002	0	0.004
Epifauna	0.079	0.128	0.008	0.340
Flatfish	0.065	0.083	0	0.219
Gelatinous zoo.	0.001	0.001	0	0.003
Haddock	0.096	0.094	0	0.226
Hake	0.003	0.008	0	0.020
Herring	0.064	0.110	0	0.270
Infauna	0.004	0.006	0	0.015
Crabs & lobsters	0.018	0.021	0.002	0.045
Lrg. demersal fish	0.004	0.003	0	0.008
Lrg pelagic fish	0.006	0.013	0	0.032
Lrg. zooplankton	0.0002	0.001	0	0.001
Norway lobster	0.183	0.193	0	0.512
Norway pout	0.228	0.151	0.029	0.365
Plaice	0.002	0.005	0	0.011
Sandeels	0.164	0.311	0	0.793
Shrimp	0.013	0.017	0	0.044
Skates & Rays	0.002	0.005	0	0.013
Sm. demersal fish	0.011	0.026	0	0.065
Sm. pelagic fish	0.011	0.016	0	0.039
Sm. zooplankton	0.0001	0.0002	0	0.001
Squid	0.009	0.015	0	0.038
Whiting	0.020	0.027	0	0.057

Figure 7: *Bar plot of the total biomass weighted proportion of prey species found in adult cod (>40cm) stomachs during each survey year in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean diet across 1970-2017 shown in the table (above).*

For the juvenile cod diet, the proportion of juvenile haddock was increased from 1% to 8% and consumption of small zooplankton reduced by the same amount. The relatively large proportion of small zooplankton within juvenile cod diet came from their dominance in the 2001 DAPSTOM data but was only based on 13 stomach samples.

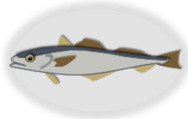
Seals, ling, monkfish, and sharks exert the highest predation mortality upon adult cod in the model. The proportion of adult cod in the diet these top predators was reduced to balance the model (more information on balancing changes to seals, ling and monkfish diet see their functional group descriptions). Cannibalism of adult cod was reduced by 0.02% with this portion added to juvenile cod instead).

Table 17 *Cod juvenile and adult diet before and after balancing*

Prey	Juvenile diet proportion		Adult diet proportion	
	Pre-balanced	Balanced	Pre-balanced	Balanced
Skates & rays	-	-	0.002	0.002
Juvenile cod	-	-	0.0003	0.001
Adult cod	-	-	0.001	0.0003
Juvenile whiting	0.009	0.004	0.013	0.012
Adult whiting	-	-	0.007	0.001
Juvenile haddock	0.013	0.080	0.033	0.030
Adult haddock	-	-	0.065	0.020
Hake	-	-	0.003	0.003
Norway pout	0.187	0.104	0.233	0.213
Herring	0.0003	0.0003	0.065	0.084
Small pelagic fish	0.002	0.002	0.011	0.025
Other pelagic fish	-	-	0.006	0.006
Sandeels	0.254	0.221	0.168	0.196
Plaice	-	-	0.002	0.002
Turbot	-	-	0.000	0.005
Flatfish	0.090	0.093	0.067	0.000
Small demersal fish	0.006	0.006	0.012	0.065
Large demersal fish	0.007	0.007	0.004	0.003
Squid & Octopus	0.020	0.021	0.009	0.008
Large zooplankton	0.002	0.207	0.0002	0.0002
Small zooplankton	0.123	0.067	0.0001	0.0001
Gelatinous zooplankton	0.001	0.001	0.001	0.0005
Edible crab	0.003	0.003	-	-
Velvet crab	-	-	0.0005	0.001
Crabs & lobsters	0.120	0.001	0.018	0.016
Norway lobster	0.057	0.059	0.183	0.216
Shrimp	0.029	0.030	0.013	0.012
Epifauna	0.071	0.087	0.079	0.074
Infauna	0.005	0.005	0.004	0.004

Diet of adult cod was adapted to increase the proportion of Norway lobster and sandeels (Holt *et al.*, 2019). The proportion of Norway lobster was increased from 18% to 21%, and sandeels from 17% to 20%. This amount was removed from the flatfish component reducing it from 6.7% to 0.7%. The remaining 7% was reassigned by adding 0.45% to turbot, 0.35% to herring and 0.35% to small pelagic fish. Adult haddock was reduced in the diet by 4.5% and Norway pout reduced by 2% (Table 17). With these changes, juvenile cod has an EE of 0.766 and adult cod an EE of 0.934 in the balanced model.

1.4.3.11 FG10: Whiting juvenile (0-24 months) and FG11: Whiting adult (24+ months)

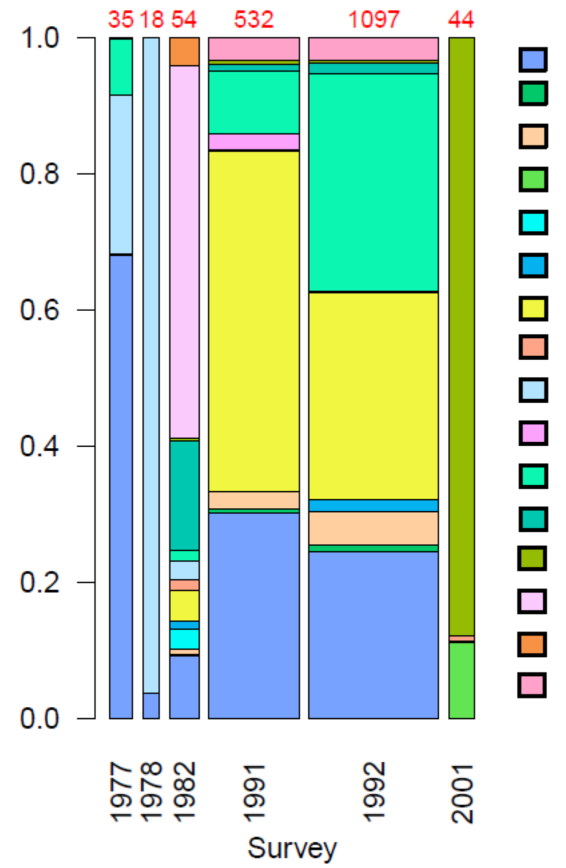


a) Biomass, P/B, Q/B, catch (pre-balanced model)

Whiting were split into two stanzas: juvenile whiting less than 24 months old (ICES, 2018c) and adult whiting aged above 24 months (ICES, 2018d). Based on visual inspection of the spatial distribution in the IBTS survey (see figure 3.1.3.3 Greenstreet *et al*. (2007) and figure 5 in Kerby *et al.* (2013)) it was assumed that approximately 20% of the whiting stock resides in the model area. The whiting spawning stock biomass (SSB) was estimated at 203,119 t in 1991 for the whole North Sea (ICES, 2019e), so that 40,624 t assumed to be within the model area, generating an area-based biomass estimate of 0.154 $t.km^{-2}$. The M and F estimates in Table 12 was used to calculate a $\mathrm{P/B}$ of 0.96 yr^{-1} and the $\mathrm{Q/B}$ for adult whiting was estimated at 5.297 yr^{-1} (Table13). The population model for this group was parameterised using information within Table 2.

With adult whiting as the leading stanza for this group, juvenile biomass and $\mathrm{Q/B}$ ratios were estimated by the model as 0.098 $t.km^{-2}$ and 11.29 y^{-1}, respectively. Juvenile whiting F was estimated as 0.256 yr^{-1} (Equation 8) using a catch of 0.025 $t.km^{-2}$ (ICES, 2019g) and an estimated area-based biomass of 0.128 $t.km^{-2}$ (ICES, 2019g) and a M of 1.350 yr^{-1} (mean natural mortality at age zero and 1 (ICES, 2018d)). This generated a $\mathrm{P/B}$ estimate of 1.606 yr^{-1} (Equation 8). The total North Sea landings (reduced to 20% to reflect the spatial distribution of whiting) were 0.019 $t.km^{-2}$ for juvenile and 0.050 $t.km^{-2}$ for adult whiting (catch at age weight * number at age (ICES, 2019g)). Discards for whiting were estimated as 0.006 $t.km^{-2}$ for juvenile and 0.021 $t.km^{-2}$ for adult whiting (discards weight at age * numbers at age (ICES, 2019g)).

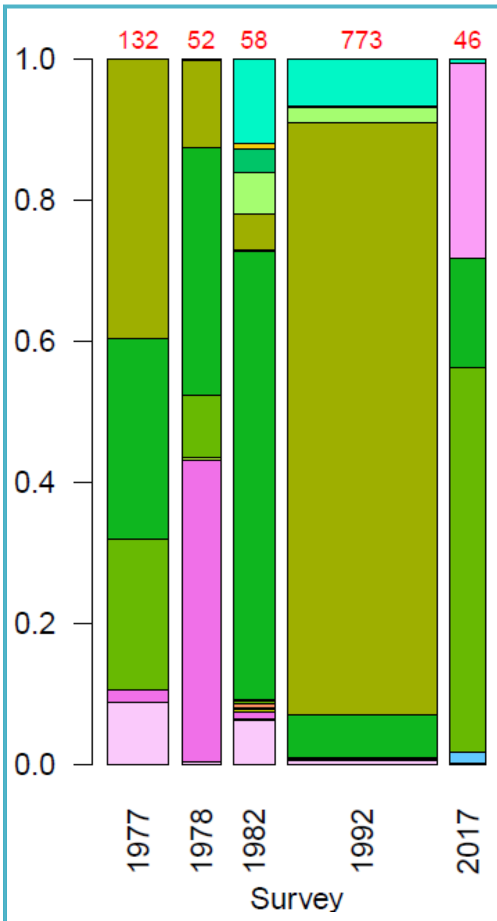
b) Diet (pre-balanced model)



	Mean	SD	min	max
Bony fish	0.227	0.252	0	0.681
Epifauna	0.002	0.004	0	0.009
Flatfish	0.014	0.020	0	0.048
Gelatinous zoo.	0.019	0.045	0	0.111
Herring	0.005	0.012	0	0.029
Infauna	0.006	0.008	0	0.018
Crabs & lobsters	0.141	0.212	0	0.499
Lrg. zooplankton	0.005	0.007	0	0.017
Norway pout	0.204	0.383	0	0.962
Saithe	0.004	0.010	0	0.025
Sandeels	0.085	0.123	0	0.321
Shrimp	0.031	0.064	0	0.160
Sm. zooplankton	0.149	0.357	0	0.878
Squid	0.091	0.223	0	0.546
Turbot	0.007	0.017	0	0.042
Whiting	0.011	0.017	0	0.034

Figure 8 *Bar plot of the total biomass weighted proportion of prey species found in juvenile whiting (<24cm) stomachs during each survey year in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean diet across 1970-2017 shown in the table (above) by combining the data across these surveys.*

The diet of whiting was partitioned into juvenile and mature components using an L_{mat} value of 24 cm (Table 2) and the mean diet proportion by prey weight derived from DAPSTOM and supplemented by NAFC stomach data (Figure 8 and Figure 9). The diet of adult whiting consists primarily of Norway pout and sandeels although the diet of immature whiting also includes Norway pout, crustaceans, and zooplankton.



	Mean	SD	min	max
Bony fish	0.032	0.040	0	0.087
Epifauna	0.003	0.007	0	0.015
Flatfish	0.0001	0.0001	0	0.0003
Haddock	0.091	0.189	0	0.429
Herring	0.001	0.001	0	0.003
Infauna	0.001	0.001	0	0.003
Crabs & lobsters	0.001	0.003	0	0.007
Lrg.demersal fish	0.0004	0.001	0	0.002
Lrg. pelagic fish	0.170	0.227	0	0.544
Lrg. zooplankton	0.001	0.001	0	0.002
Norway lobster	0.00002	0.0001	0	0.0001
Norway pout	0.297	0.220	0	0.636
Plaice	0.0003	0.001	0	0.001
Sandeels	0.282	0.347	0	0.840
Shrimp	0.016	0.025	0	0.058
Sm.demersal fish	0.055	0.123	0	0.275
Sm.pelagic fish	0.007	0.015	0	0.033
Sm.zooplankton	0.002	0.004	0	0.008
Squid	0.038	0.053	0	0.119
Whiting	0.0002	0.001	0	0.001

Figure 9 *Bar plot of the total biomass weighted proportion of prey species found in adult whiting (>24cm) stomachs during each survey year in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean diet across 1970-2017 shown in the table (above) by combining the data across these surveys.*

d) Balancing changes

Whiting was unbalanced in the model with immature whiting an EE of 2.17 and mature whiting having an EE of 1.31 and. To balance juvenile whiting their proportion in the diet of their predators were reduced – see section 1.4.1.2 on other toothed whales, 1.4.1.3 on seals, 1.4.2.2 on seabirds (low discard diet), 1.4.3.12 on haddock, 1.4.1.1 on minke whale, and 1.4.3.10 on cod. The cannibalism within this group was reduced in accordance with the minimum estimated mean diet proportions (Figure 8). The proportion of adult whiting in the diet of other toothed whale and saithe was also reduced (see section 1.4.1.2 and 1.4.3.13).This proportion was instead assigned to small zooplankton. With these changes juvenile whiting has an EE of 0.915 and adult whiting an EE of 0.898 in the balanced model.

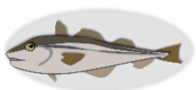
The proportion of Norway pout in juvenile whiting diet was also reduced from 35% to 10%. The remainder was added as 10% herring and 15% small pelagic fish. Predation mortality upon haddock was also unbalanced (adult haddock; EE 4.195, juvenile haddock; 0.319) so the proportion of adult haddock in the adult whiting diet was reduced by 5% (from 0.06 to 0.01), with the remainder added to small pelagic fish. Juvenile haddock was also removed from the diet of adult whiting (3%) and moved instead to epifauna, small pelagic fish and herring. Stomach sampling can underestimate the zooplankton present in fish stomachs due to their size and quick digestion times (Holt *et al.*, 2019). The proportion of small zooplankton in the juvenile whiting diet was therefore increased from 15% to 17% by lowering the proportion of turbot and small demersal fish in keeping with the maximum estimated mean diet proportions (Figure 9).

Norway pout was unbalanced in the model due to predation of adult whiting (Norway pout EE: 8.117). Therefore, the proportion of Norway pout in the diet of adult whiting was reduced by 10% (from 31% to 21%). The remainder was reallocated as 16% to herring, and 5% to small pelagic fish. Further changes to adult whiting diet included increasing the proportion of infauna by 0.14%, (from 0.12% to 0.26%), and of large zooplankton by 0.17% (0.06% to 0.23%), and the addition of gelatinous zooplankton (0.001%). The proportion of small demersal fish was reduced by 0.01% (from 0.0571 to 0.057) and that of sandeels reduced by 0.1% (from 29.3% to 29.2%) and plaice increased from 0.026% to 0.126%). The final diets for juvenile and adult whiting are shown in Table 18.

Table 18 *Whiting juvenile and adult diet before and after balancing.*

Prey	Juvenile diet proportion		Adult diet proportion	
	Pre-balanced	Balanced	Pre-balanced	Balanced
Juvenile whiting	0.019	0.009	0.0002	0.0002
Adult whiting	-	-	0.0001	0.0001
Juvenile haddock	-	-	0.032	-
Adult haddock	-	-	0.063	0.010
Saithe	0.007	0.007	-	-
Norway pout	0.345	0.100	0.308	0.100
Herring	0.008	0.100	0.001	0.159
Small pelagic fish	-	0.153	0.007	0.117
Other pelagic fish	-	-	0.176	0.176
Sandeels	0.143	0.143	0.293	0.292
Plaice	-	-	0.0003	0.001
Turbot	0.012	0.001	-	-
Flatfish	0.024	0.024	0.0001	0.0001
Small demersal fish	0.00003	-	0.057	0.057
Large demersal fish	-	-	0.0004	0.0004
Squid & Octopus	0.091	0.091	0.038	0.048
Large zooplankton	0.005	0.005	0.001	0.002
Small zooplankton	0.149	0.169	0.002	0.002
Gelatinous zooplankton	0.019	0.019	-	0.000001
Crabs & lobsters	0.141	0.141	0.001	0.0001
Velvet crab	-	-	0.000003	0.000003
Norway lobster	-	-	0.00002	0.00002
Shrimp	0.031	0.031	0.016	0.016
Epifauna	0.002	0.002	0.003	0.015
Infauna	0.006	0.006	0.001	0.003

1.4.3.12 FG12: Haddock juvenile (0-36 months) and FG13: Haddock adult (36+ months)



a) Biomass, P/B, Q/B, catch (pre-balanced model)

Haddock were split into two stanzas: juvenile haddock less than 36 months old, and adult haddock as those aged over 36 months (ICES, 2018c). For 1991, the spawning stock biomass was estimated as 52,110 t across the whole North Sea (ICES, 2019b). Based on visual inspection of the spatial distribution in the IBTS survey (see figure 4 in Hedger *et al.* (2004)) it was assumed that approximately 83% of the haddock stock resides in the model area. Therefore, the area-based biomass for the northern North Sea was estimated as 43,251 t or 0.197 $t.km^{-2}$. M and F estimates in Table 12 were used to calculate a P/B of 0.770 yr^{-1} and the Q/B was estimated at 4.107 $year^{-1}$ (Table 13). The population model for this group was parameterised using information within Table 2. Juvenile haddock fishing mortality was estimated as 0.579 yr^{-1}. This was estimated using a catch of 0.198 $t.km^{-2}$, and biomass of 0.342 $t.km^{-2}$. Juvenile biomass was calculated from total stock biomass (TSB) of 801,090 t minus SSB (ICES, 2019b) with 83% residing in the model area. Natural mortality at age 0-3 years of 1.64 yr^{-1} (ICES, 2018d) was used to give a total mortality of 1.743 yr^{-1} for juvenile haddock.

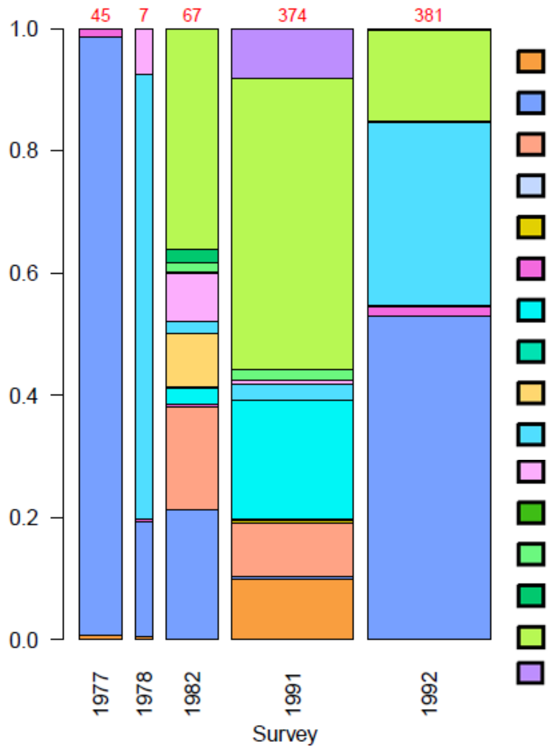
Following the same 83% distribution of stock within the model area; landings of juvenile haddock were estimated as 22,204 t (weight at age * numbers at age (ICES, 2019b)) with an area-based estimate of 0.084 $t.km^{-2}$, and discards of 30,135 t and 0.114 $t.km^{-2}$ (discard weight at age * numbers at age (ICES, 2019b)). Landings for adult haddock were estimated as 23,791 t (landings weight at age * numbers at age (ICES, 2019b)) with an area-based estimate of 0.09 $t.km^{-2}$, and discards of 264 t (discards weight at age * numbers at age (ICES, 2019b)) and 0.001 $t.km^{-2}$.

b) Diet (pre-balanced model)

The diet of haddock was partitioned into juvenile and mature components using an L_{mat} value of 40 cm (Jones, 1983). The mean diet prey proportions by weight from DAPSTOM were used as the basis for the diets of immature haddock in the model (Figure 10). The mean diet prey proportions by weight from DAPSTOM and NAFC samples for adult haddock.

d) Balancing changes

Haddock was unbalanced with mature haddock having an EE of 4.46 and immature haddock an EE of 0.97. Juvenile haddock was increased in the diet of juvenile cod (see section 1.4.3.10) and in other pelagic fish (see section 1.4.3.20). Minke whales were added as a predator to juvenile haddock (at 1% of minke whale diet) (Folkow *et al.*, 2000), to include all predator prey interactions within the model.

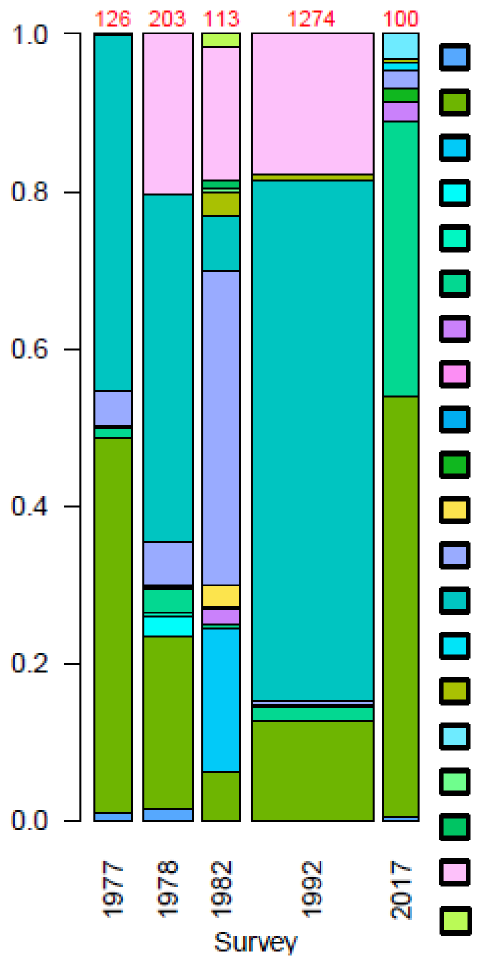


	Mean	SD	min	max
Bony fish	0.02	0.043	0.0005	0.099
Epifauna	0.383	0.383	0.004	0.979
Flatfish	0.051	0.076	0	0.169
Gelatinous zoo.	0.0001	0.0002	0	0.0004
Haddock	0.001	0.001	0	0.003
Infauna	0.008	0.005	0.002	0.014
Crabs & lobsters	0.045	0.085	0	0.195
Large zooplankton	0.001	0.001	0	0.002
Norway pout	0.017	0.040	0	0.087
Sandeels	0.214	0.312	0	0.728
Shrimp	0.032	0.040	0	0.079
Small demersal fish	0.0002	0.001	0	0.001
Small pelagic fish	0.007	0.009	0	0.018
Small zooplankton	0.004	0.010	0	0.022
Squid	0.197	0.215	0	0.476
Whiting	0.017	0.036	0	0.082

Figure 10 *Bar plot of the total biomass weighted proportion of prey species found in juvenile haddock (<40cm) stomachs during each survey year in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean diet across 1970-2017 shown in the table (above) by combining the data across these surveys.*

Due to their size, the lack of hard parts, and quick digestion times, zooplankton may be under-recorded in the stomach samples of immature haddock. The proportions of zooplankton in the diet of juvenile haddock diet were therefore increased. The proportion of sandeels was reduced by 16% (from 23% to 7%) and assigned to small (5.2%), large (10%), and gelatinous zooplankton (0.8%). Small amounts of the diet allocated to juvenile whiting and Norway pout were also transferred to small zooplankton. Predation upon crustaceans was reduced with edible crab and shrimp diet proportions reduced by approximately 1% and moved to large zooplankton (Table 19).

Overall, these changes reflect the less piscivorous diet of immature haddock in comparison to the adult life stage (Table 19). The proportion of adult haddock in the diet of saithe, large demersal fish, flatfish, cod and whiting was reduced – see sections 1.4.1.2, 1.4.3.26, 1.4.3.24, 1.4.3.10 and 1.4.3.11. Adult and juvenile haddock was then balanced with EE values of 0.851 and 0.882.



	Mean	SD	min	max
Bony fish	0.006	0.006	0	0.015
Epifauna	0.284	0.211	0.062	0.534
Flatfish	0.036	0.081	0	0.182
Gelatinous zoo.	0.005	0.011	0	0.024
Haddock	0.001	0.002	0	0.005
Infauna	0.083	0.150	0.005	0.351
Crabs & lobsters	0.010	0.011	0.001	0.025
Large demersal fish	0.0003	0.001	0	0.002
Other pelagic fish	0.0004	0.001	0	0.002
Large zooplankton	0.004	0.007	0	0.016
Norway lobster	0.006	0.013	0	0.028
Norway pout	0.106	0.165	0.005	0.399
Sandeels	0.325	0.281	0	0.663
Scallop	0.002	0.005	0	0.011
Shrimp	0.009	0.012	0.001	0.031
Small demersal fish	0.006	0.014	0	0.031
Small pelagic fish	0.001	0.003	0	0.006
Small zooplankton	0.002	0.004	0	0.008
Squid	0.110	0.101	0	0.203
Whiting	0.003	0.007	0	0.016

Figure 11 *Bar plot of the total biomass weighted proportion of prey species found in adult haddock (>40cm) stomachs during each survey year in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean diet across 1970-2017 shown in the table (above) by combining the data across these surveys.*

Table 19 *Haddock juvenile and adult diet before and after balancing.*

Prey	Juvenile diet proportion		Adult diet proportion	
	Pre-balanced	Balanced	Pre-balanced	Balanced
Juvenile whiting	0.018	0.001	0.002	0.002
Adult whiting	-	-	0.001	0.001
Juvenile haddock	0.001	0.001	0.0003	0.0003
Adult haddock	-	-	0.001	0.001
Norway pout	0.019	0.017	0.107	0.107
Small pelagic fish	0.007	0.007	0.001	0.001
Other pelagic fish	-	-	0.0004	0.0004
Sandeels	0.230	0.070	0.329	0.329
Flatfish	0.055	0.050	0.037	0.037
Small demersal fish	0.0002	0.0002	0.0063	0.0063
Large demersal fish	-	-	0.0004	0.0004
Squid & Octopus	0.197	0.179	0.110	0.110
Large zooplankton	0.001	0.116	0.004	0.004
Small zooplankton	0.005	0.090	0.002	0.002
Gelatinous zooplankton	0.0001	0.009	0.005	0.005
Crabs & lobsters	-	-	0.010	0.010
Edible crab	0.0446	0.031	-	-
Norway lobster	-	-	0.006	0.006
Shrimp	0.032	0.020	0.009	0.009
Scallops	-	-	0.002	0.002
Epifauna	0.383	0.380	0.284	0.284
Infauna	0.008	0.029	0.083	0.083

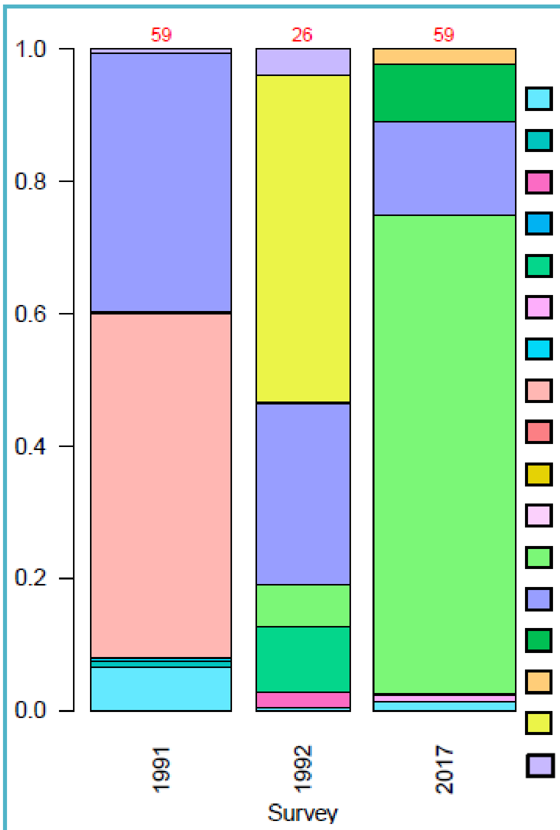
1.4.3.13 FG14: Saithe

a) Biomass, P/B, Q/B, catch (pre-balanced model)

For 1991, the total stock biomass for saithe was estimated as 320,648 t in the whole North Sea (ICES, 2018d). Based on the spatial distribution (see figure 3 in Cormon *et al.* (2014)) it was assumed that the TSB for saithe resides within the model area. Therefore, the area-based biomass for the northern North Sea was estimated as 1.213 t.km^{-2}. The M and F estimates in Table 12 was used to calculate a $\mathrm{P/B}$ of 0.685 yr^{-1} and the $\mathrm{Q/B}$ was estimated at 3.29 yr^{-1} (Table 13). Landings for saithe in 1991 were 108,058 t (ICES, 2018d), generating an area-based estimate of 0.409 t.km^{-2}. Discards for saithe were 22,886 t (ICES, 2018d), with an area-based estimate of 0.086 t.km^{-2}.

b) Diet (pre-balanced model)

Saithe diet was estimated using Cefas stomach records from 1991 and 1992 surveys for saithe in the northern North Sea, alongside data from NAFC Marine Centre for Shetland food-web biodiversity and trophic interactions project. The mean diet proportion by weight across these surveys was used as the basis for saithe diet in the model (Figure 12). Larger sample size for 1991/92 data allows the diet to better reflect the year of the model, whilst including a wider range of known prey species. Average diets for saithe with plausible minimum, maximum and percentile values, provided a range of proportions which allowed for the diets to be adjusted to reflect the model year, if required for model balancing. Saithe diet consists primarily of Norway pout, sandeels, other pelagic fish and crustaceans.



	Mean	SD	Min	Max
Bony fish	0.018	0.027	0	0.065
Epifauna	0.002	0.004	0	0.008
Flatfish	0.005	0.009	0	0.022
Gelatinous zoo.	0.0001	0.0001	0	0.0003
Haddock	0.084	0.086	0	0.204
Herring	0.002	0.004	0	0.009
Infauna	0.001	0.002	0	0.005
Crabs & lobsters	0.104	0.3233	0	0.522
Lrg. demersal fish	0.0001	0.0003	0	0.001
Lrg. pelagic fish	0.129	0.179	0	0.366
Large zoo	0.001	0.001	0	0.003
Norway pout	0.2328	0.299	0	0.724
Sandeels	0.162	0.171	0.14	0.392
Sm. demersal fish	0.022	0.038	0	0.087
Sm. pelagic fish	0.031	0.057	0	0.131
Squid	0.099	0.221	0	0.495
Whiting	0.013	0.016	0	0.039

Figure 12 *Bar plot of the total biomass weighted proportion of prey species found in saithe stomachs during each survey year, in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate an average diet shown in the table (above) by combining the data across these surveys.*

c) Balancing changes

Saithe was balanced in the model with an EE of 0.632. Saithe is one of the top predators in the northern North Sea as evidenced by its high trophic level (TL) in the model (TL 4.6). However, there is a relatively high amount of unexplained mortality for saithe (36.8%). To reduce this unexplained mortality, the consumption of saithe by its top predators was increased; toothed whale (from 1% of toothed whale diet to 13.3%), seal (from 3% of seal diet to 30.5%) and monkfish (from 0.5% of monkfish diet to 0.9%). Ling was also introduced as a predator (Rae and Shelton, 1982; Bergstad, 1991), with 10% of ling diet now attributed to saithe. Seabirds (low discard diet) were also added as a predator (2.8% of their diet), due to saithe being a known prey species of puffins breeding in the Shetland Isles (Martin, 1989) (more information on changes to seabird diet is in their functional group description).

Saithe diet was originally estimated using their mean values from 1991, 1992 and 2017 surveys. When examining the model, it was clear that the inclusion of 2017 NAFC survey data increased their predation of Norway pout compared to its available biomass. Saithe diet was thus updated to only reflect the data from 1991 and 1992 surveys (Figure 12, Table 20). This was achieved by reducing the proportion of

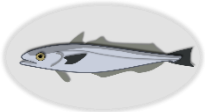
Norway pout by 31%, increasing crabs & lobsters by 9.6%, epifauna by 6.7%, small pelagic fish by 4%, sandeels by 3%, gelatinous zooplankton by 3%, small demersal fish by 2.7%, squid by 2%, and infauna by 0.1% (Table 20). Saithe predates heavily upon herring eggs within their spawning grounds in the northern North Sea, off the Norwegian coast (Høines and Bergstad, 1999). To reflect this, the proportion of herring in the diet was increased by 14.8% by decreasing other pelagic fish by 11.5%, adult haddock by 2.2%, adult whiting by 0.8% and juvenile whiting by 0.3%. We further reduced adult haddock in the diet by 2.9%, increasing both flatfish and large zooplankton by 0.6%. This increase in zooplankton proportion better reflects saithe feeding patterns in the early 1990s (Bromley *et al.*, 1997).

Table 20 *Saithe diet before and after balancing*

Prey	Saithe diet proportion	
	Pre-balanced	Balanced
Juvenile cod	-	0.032
Juvenile whiting	0.004	0.001
Adult whiting	0.008	0.0002
Juvenile haddock	0.032	0.003
Adult haddock	0.052	0.001
Norway pout	0.339	0.029
Herring	0.002	0.150
Small pelagic fish	0.032	0.073
Other pelagic fish	0.129	0.014
Sandeels	0.167	0.200
Flatfish	0.005	0.011
Small demersal fish	0.023	0.050
Large demersal fish	0.0001	0.0001
Squid & Octopus	0.099	0.120
Large zooplankton	0.001	0.007
Gelatinous zooplankton	0.0001	0.030
Crabs & lobsters	0.104	0.200
Epifauna	0.002	0.069
Infauna	0.001	0.002
Detritus	-	0.008

Juvenile cod EE in the pre-balanced model was 0.319 indicating that its predation was underestimated by the model. To address this, juvenile cod was added to the diet of saithe at 3%. This portion was removed from juvenile haddock (from 3% to 0.3%) (Table 20). Overall, with these changes, saithe was balanced with an EE of 0.811 and a slightly lowered trophic level of 4.1.

1.4.3.14 FG15: European Hake



a) Biomass, P/B, Q/B, catch (pre-balanced model)

Hake biomass was estimated using the TSB from ICES stock assessment (2019) of 65,975 t (ICES, 2019c). A uniform distribution was assumed across the whole stock area (stock area is ICES 27.3a46-8abd; Greater Northern Sea, Celtic Seas, and Bay of Biscay and Iberian Coast ecoregions) of 1,274,361 km^2 (ICES, 2018b), yielding an area-based biomass of 0.052 t.km^{-2}. The M and F estimates in Table 12 was used to calculate a $\mathrm{P/B}$ 1.143 yr^{-1} and a $\mathrm{Q/B}$ of 3.85 yr^{-1}. Landings for hake in 1991 were estimated as 58,129 t (ICES, 2019c) with an area-based estimate of 0.046 t.km^{-2}, and discards of 0.001 t.km^{-2} (Heath and Cook, 2015).

b) Diet (pre-balanced model)

Table 21 *Hake mean diet proportions from species weight provided within Du Buit (1996) for Celtic Sea Hake, in the pre-balanced and balanced model.*

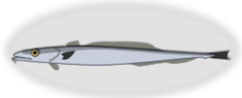
	total weight (g.)	Pre-balanced	Balanced
Other pelagic fish	63730	0.777	0.760
Herring	1246	0.015	0.015
Hake	393	0.005	0.001
Small demersal fish	7578	0.092	0.092
Large demersal fish	204	0.002	0.002
Flatfish	154	0.002	0.002
Epifauna	75	0.001	0.001
Crabs & lobsters	4	0.0001	0.0001
Norway pout	1296	0.016	0.016
Sandeels	65	0.001	0.001
Shrimp	3	0.00004	0.00004
Small pelagic fish	5550	0.068	0.068
Squids & Octopus	63	0.001	0.001
Juvenile whiting	1093	0.013	0.013
Adult whiting	590	0.007	0.007
Large zooplankton	-	-	0.017
Small zooplankton	-	-	0.0002
Gelatinous zooplankton	-	-	0.004

Due to a very low number of hake stomach samples for the northern North Sea between 1970-2017 in the DAPSTOM database (n=2), hake diet proportions were instead obtained from Du Buit (1996). That study examined 922 hake stomachs from the Celtic Sea between 1983 and 1985, throughout all seasons (Table 21).

d) Balancing changes

Hake diet was altered by reducing predation upon fish species (other pelagic fish reduced by 1.7%), and adding this to large zooplankton. Due to their size, lack of hard parts and their quick digestion zooplankton are often under-recorded in stomach samples. Cannibalism was reduced by 0.004, adding this portion to gelatinous zooplankton (Eriksen *et al.*, 2012) (Table 21). By reducing hake consumption of high tropic level pelagic fish (mackerel, horse mackerel, blue whiting), the trophic level of hake in the balanced model reduced from 5.63 to 4.60. Hake was balanced in the model with an EE of 0.907 and a $\mathrm{P/Q}$ of 0.297.

1.4.3.15 FG16: Ling



a) Biomass, P/B, Q/B, catch (pre-balanced model)

Ling is a substantial bycatch in mixed fisheries targeting cod and other gadoids of high commercial value in the North Sea. The geometric mean area-swept biomass estimate for ling was 0.064 t.km^{-2}. Estimates of F and M (Table 12) were used to calculate a $\mathrm{P/B}$ for ling of 0.967 yr^{-1} and $\mathrm{Q/B}$ was estimated as 3.248 yr^{-1} (Table 13). Landings for ling in 1991 were reported as 12,160 t (ICES, 2019k) giving an area-based estimate of 0.037 t.km^{-2}, and discards of 0.012 t.km^{-2} (Cook and Heath, 2018).

Table 22 *Ling diet proportions in the model.*

	Pre-Balanced	Balanced
Juvenile cod	-	0.096
Adult cod	0.166	0.020
Saithe	-	0.100
Herring	0.145	0.145
Other pelagic fish	0.099	0.099
Sandeels	0.036	0.02
Flatfish	0.007	0.007
Small demersal fish	0.085	0.085
Large demersal fish	0.225	0.050
Squid & octopus	0.084	0.084
Large zooplankton	0.001	0.001
Small zooplankton	0.0001	0.0001
Edible crab	-	0.010
Crabs & lobsters	0.0001	0.05
Shrimp	0.0002	0.0002
Epifauna	0.149	0.230
Infauna	0.003	0.003

b) Diet (pre-balanced model)

Due to a very low number of ling stomachs sampled in DAPSTOM (only three ling stomachs sampled in 1978), we used ling diet proportions from Muus & Nielsen (1999). Ling feeds upon cod, herring, flatfish, crabs, lobsters, cephalopods and starfishes. Sandeels, other pelagic fish, small demersal fish, large demersal fish, shrimp, zooplankton and infauna were also included in the ling diet according to the diet of other large gadoids in the Mackinson & Daslakov (2007) North Sea model. These additional amounts were added and the diet proportions summed to one within the model (Table 22).

d) Balancing changes

Ling was unbalanced in the model with an EE of 1.19 and $\mathrm{P/Q}$ of 0.298. To balance the model the proportion of ling in the diet of sharks was reduced by 1.5% (from 2.1% to 0.6%). Most of the mortality for this group is explained in the model by fishing, with only a small amount accounted for by predation mortality. This is due to ling having a biomass of 0.064 t.km^{-2} and a catch of 0.049 t.km^{-2} in the balanced model. Ling is a data limited species; and therefore, there are few examples of their predation within diet literature. Toothed whales were added as a possible predator, with 0.2% of their diet attributed to ling. The proportion of ling in seal diet was also increased from 0.1% to 0.2%.

The diet of ling was based on diet studies by Rae & Shelton (1982) (which examined 45 ling stomachs collected between 1951-59 by Scottish fisheries research vessels in the North Sea off the West coast of Scotland and Rockall Bank) and Bergstad (1991) who studied the diet of several gadoid species (including ling) in the Norwegian deep (with data collected on trawl surveys in winter, summer, and autumn of the years from 1984 to 1987). Using information from these studies saithe was added into the diet of ling at 10% (Rae and Shelton, 1982; Bergstad, 1991) by reducing the portion of large demersal fish from 22% down to 12%. Epifauna was increased in the diet of ling from 15% to 22% by further reducing large demersal fish by 7%. Sandeels in the diet were reduced by 2% by adding a further 1% to epifauna and 1% to edible crab (Bergstad, 1991) (Table 22). Also, in order to balance cod, we reduced the proportion of adult cod in the diet of ling from 17% down to 2%; placing the remaining 9.6% on to juvenile cod, and 5% on to crabs & lobsters (Bergstad, 1991) (Table 22). With these changes to input parameters and predation mortality ling was balanced in the model with an EE of 0.952.

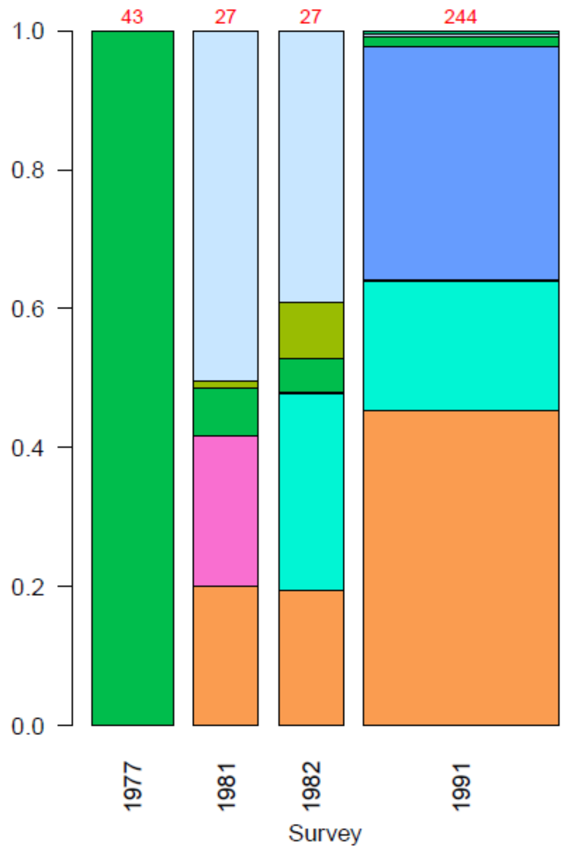
1.4.3.16 FG17: Norway Pout

a) Biomass, P/B, Q/B, catch (pre-balanced model)

Norway pout biomass was calculated using stock biomass from each quarter of IBTS 1991 survey totalling 1,529,804 t (ICES, 2018d). This stock assessment covers the northern North Sea (>57°N) and Skagerrak at depths between 50 and 300 m (ICES, 2018d). The mean total stock biomass for 1991 was calculated as 382,451 t (the mean across all quarters) and divided by the whole stock area (721,605 km North Sea Skagerrak and Kattegat), with an area-based biomass estimate of 0.530 t.km^{-2}. During model balancing, this resulted in too low a biomass and so the area-based estimate was adjusted, as described below (Section 1.4.3.16.c), to better reflect the spatial distribution of this species. $\mathrm{P/B}$ was calculated as 0.838 yr^{-1}, using Equation 8 with a F of 0.487 yr^{-1} (Equation 9, catch of 0.258 t.km^{-2} (ICES, 2018d)) plus a M of 0.351 yr^{-1}. $\mathrm{Q/B}$ for Norway pout was calculated as 7.407 yr^{-1}, using Equation **10** with a K of 0.51, L_∞ of 22.6cm generating a W_∞ of 785 grams (Equation 6) (using length to weight coefficients *a*: 0.0075 and *b*: 3.024 (Silva *et al.*, 2013)) (Table 13).

b) Diet (pre-balanced model)

Figure 13 shows the total biomass weighted proportion of prey species found in Norway pout stomachs during each survey year for the northern North Sea. In the 1991 stomach sampling project many of the fish prey of the pelagic 0-group gadoids (which includes Norway pout) could not be identified to species level (often it was only possible for them to be identified as "fish"). Hislop *et al.* (1997) showed the stomach contents (percentage by weight) of 0-group Norway pout to be nearly 80% copepods, with the remaining proportion being crustaceans and a very small amount attributed to whiting. It was also reported that larger Norway pout (above 3cm) continued to feed almost entirely upon copepods, in comparison to other gadoids which become more piscivorous (Bromley *et al.*, 1997). Therefore, the unknown "bony fish" proportion of Norway pout diet in the model (**Figure 13**) was re-allocated to copepods (across large and small zooplankton) and crustaceans (increasing crabs, shrimp and epifauna) (Table 23).



	Mean diet	SD	Min	Max
Bony fish	0.212	0.186	0	0.452
Epifauna	0.118	0.142	0	0.284
Gelatinous zoo.	0.0005	0.001	0	0.002
Infauna	0.054	0.109	0	0.218
Crabs & lobsters	0.084	0.168	0	0.336
Large zoo.	0.283	0.478	0	0.999
Shrimp	0.023	0.040	0	0.082
Small zoo.	0.225	0.264	0	0.504
Whiting	0.001	0.002	0	0.004

Figure 13 *Bar plot of the total biomass weighted proportion of prey species found in Norway pout stomachs during each survey year available, in Area IVa. Red numbers above each bar show the number of stomachs sampled, also illustrated by bar width. These data have been used to generate a mean diet 1977-1991 for Norway pout in the northern North Sea shown in the bar plot (left) table (above).*

c) Balancing changes

Norway pout was unbalanced in the model with an EE of 8.113 and a low P/Q of 0.113 yr^{-1}. Norway pout acts as a forage fish species for many predators in the model therefore the low P/Q may suggest that there is not a high enough biomass of this group to meet consumer demand. This likely reflected the fact that the starting area-based biomass was calculated using the area of the whole North Sea and Skagerrak but the highest densities of all age groups of Norway pout are found within the northern North Sea (ICES, 2018d), with spawning mainly taking place in the area between Shetland and Norway (Huse *et al.*, 2008; Lambert *et al.*, 2009; Nash *et al.*, 2012). Therefore, the biomass of Norway pout was re-calculated to reflect the stock abundance residing within the model area. Total stock biomass of Norway pout in 1991 was 414,022 t (ICES, 2018d) across the model area giving a new area-based biomass estimate of 1.566 $t.km^{-2}$.

This re-estimation of biomass gives a new P/B of 0.941 yr^{-1} for this group (Table 12). These changes reduced the EE for Norway pout to 2.445 and increased the P/Q to 0.127 yr^{-1}. The group remained unbalanced and P/Q estimated by the model was still too low to represent this productive forage fish species. Therefore, a P/Q of 0.2 was input directly for this group and a P/B of 1.481 yr^{-1} estimated by the model, lowering EE to 1.553.

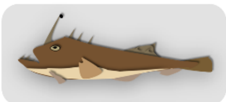
These parameter modifications gave an improved ecological representation of the Norway pout group in the model. Incrementally adjusting the proportions of this group in predator diets further lowered its EE, to balance the model. Norway pout in the diet of its top predator saithe was reduced from 33.9% down to 2.9% (Table 20), in the diet of juvenile whiting by 24% (from 34% to 10%), adult whiting by 21% (from 31% to 10%) Table 18), large demersal fish by 18% (from 29% to 11%) (Table 34); juvenile cod by 8% (from 19% to 10%) adult cod by 2% (from 23% to 21%) (Table 17), and flatfish by 2% (from 9% to 7%) (Table 32). These are substantial decreases in the predator diet proportions of Norway pout. For balancing, these average predator diets were kept within the bounds of their plausible minimum, maximum and percentile value ranges.

Table 23 *Norway pout diet proportions used in northern North Sea EwE 1991. Diet proportions from DAPSTOM and adapted with information from the ICES Database report of the stomach sampling project, 1991.*

Prey group	Pre-balanced	Balanced
Juvenile whiting	0.001	0.001
Large zooplankton	0.359	0.359
Small zooplankton	0.285	0.304
Gelatinous zooplankton	0.001	0.001
Crabs & lobsters	0.107	0.025
Shrimp	0.029	0.010
Epifauna	0.149	0.231
Infauna	0.069	0.069

Norway pout in the diets of seal and shark was increased by 2% (seal from 2.3% to 5.8%, shark from 1.5% to 1.7%) (Table 6 & Table 15). Norway pout diet was also adapted for the balanced model, with increased proportions of small zooplankton (by 1.9% removing this amount from shrimp) and epifauna (by 8.2% removing this amount from crabs) (Table 23) to further reflect the importance of copepods and epifauna in Norway pout diet. These changes balanced Norway pout in the model with an EE of 0.926.

1.4.3.17 FG18: Monkfish

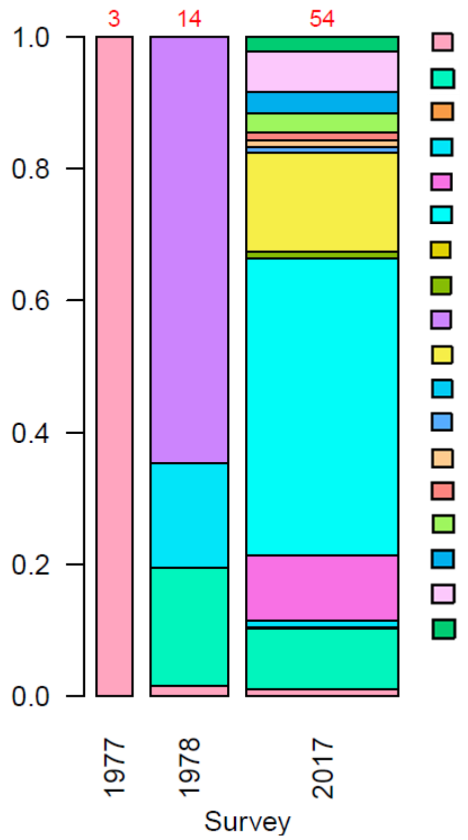


a) Biomass, P/B, Q/B, catch (pre-balanced model)

The monkfish group consists of white-bellied and black-bellied monkfish. The geometric mean area-swept biomass estimates for these species were generated using IBTS-IVa data for 1991 giving a combined biomass of 0.085 t.km^{-2} (Table 12). P/B was calculated as 0.539 yr^{-1} (Table 12), and Q/B was calculated as 2.476 yr^{-1} (Table 13). Landings for monkfish in 1991 were estimated as 8,988 t (ICES, 2019k) with an area-based estimate of 0.034 t.km^{-2}, and discards of 0.004 t.km^{-2} (Heath and Cook, 2015) (Table 14).

b) Diet (pre-balanced model)

The DAPSTOM database contained no monkfish records for 1991 so the mean diet proportions by weight were calculated across DAPSTOM diet surveys for 1977, 1978 and the Shetland stomach sampling project in 2017 (Figure 14). The 'bony fish' proportion of diet (34.2%) was split evenly between the other fish groups present in the diet.



	Mean	SD	Min	Max
Bony fish	0.342	0.570	0	1.000
Cod	0.091	0.089	0	0.178
Epifauna	0.0002	0.0003	0	0.0005
Flatfish	0.057	0.089	0	0.159
Haddock	0.033	0.057	0	0.098
Herring	0.150	0.261	0	0.451
Infauna	0.0001	0.0002	0	0.0003
Large demersal fish	0.003	0.006	0	0.010
Other pelagic fish	0.216	0.374	0	0.647
Norway pout	0.050	0.086	0	0.150
Plaice	0.00002	0.00003	0	0.0001
Saithe	0.003	0.005	0	0.009
Sandeels	0.003	0.006	0	0.010
Sharks	0.004	0.006	0	0.011
Small demersal fish	0.010	0.017	0	0.029
Small pelagic fish	0.011	0.019	0	0.033
Squid	0.020	0.035	0	0.061
Whiting	0.007	0.013	0	0.022

Figure 14 *Bar plot of the total biomass weighted proportion of prey species found in monkfish stomachs during each survey year, in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate an average diet shown in the table (above) by combining the data across these surveys.*

c) Balancing changes

Monkfish was balanced in the model with an EE of 0.776 and a P/Q of 0.218 yr^{-1}. An EE of 0.776 suggested that perhaps predation mortality should be higher for this group due to the remaining large amount of unexplained mortality. Thererfore, seals were added as a predator of of this group, with 1% of seal diet attributed to monkfish. Monkfish in the diet of sharks was reduced by 0.6%, from 0.7% down to 0.1% to better reflect shark diet. These changes increased monkfish EE to 0.912 and lowered the group TL from 5.213 down to 4.604.

Monkfish diet was estimated as a mean across all available survey years. However, in the 1977 and 1978 surveys only 17 stomachs were found to have prey, in comparison the NAFC survey contained 54 stomachs with prey (Figure 14). Therefore, the monkfish diet proportions were adapted in the model to reflect the mean prey proportions from the NAFC 2017 survey data (Table 24).

Table 24 *Monkfish diet proportions used in northern North Sea EwE model.*

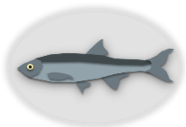
	Pre-balanced	Balanced
Sharks	0.006	0.007
Juvenile cod	0.046	0.090

Adult cod	0.091	0.046
Juvenile Whiting	0.007	0.007
Adult Whiting	0.004	0.004
Juvenile Haddock	0.017	0.017
Adult Haddock	0.033	0.034
Saithe	0.005	0.009
Norway pout	0.078	0.077
Herring	0.231	0.227
Small pelagic fish	0.017	0.017
Other pelagic fish	0.332	0.332
Sandeels	0.005	0.005
Plaice	0.000	0.000
Other flatfish	0.087	0.087
Small demersal fish	0.015	0.015
Large demersal fish	0.005	0.005
Squid & Octopus	0.020	0.020
Shrimp	0.000	0.000
Epifauna	0.001	0.001
Infauna	0.000	0.000

Although pelagic fish (other than herring) were not found within monkfish stomachs in the 2017 survey, "other pelagic fish" were retained as a major proportion within the diet (33%). This functional group includes mackerel, which is often found in the stomachs of white-bellied monkfish (Laurenson and Priede, 2005) and horse mackerel which is often found in black-bellied monkfish stomachs sampled from the waters surrounding Shetland (Preciado *et al.*, 2006). 4.5% of adult cod was removed from the diet with 4.4% of this added to juvenile cod and 0.1% moved on to sharks. 0.05% was removed from herring and 0.04% of this moved on to saithe and 0.01% on to adult haddock (Table 24).

1.4.3.18 FG19: Herring

a) Biomass, P/B, Q/B, catch (pre-balanced model)



Herring biomass was estimated using the total stock biomass estimate from ICES (ICES, 2018c). Herring are not resident in the northern North Sea throughout the year but seasonally migrate between Shetland and Fladen to the southern North Sea (East Anglia and the channel), Skagerrak and Kattegat, between feeding, spawning and nursey grounds (Petitgas, 2010). We therefore assumed that 50% of the TSB would, on average, be in the modelled area during the year. Thus, herring biomass was estimated as 2.58 t.km^{-2} using a TSB for the greater North Sea (721,925 km^{2}) of 3,731,640 t (ICES, 2018c). P/B for this group was calculated as 1.05 yr^{-1} (Table 12) and Q/B as 3.77 yr^{-1} (Table 13). Landings for herring in 1991 were estimated as 0.952 t.km^{-2} with discards of 0.171 t.km^{-2} (ICES, 2019k).

b) Diet (pre-balanced model)

Table 25 *Herring diet from DAPSTOM 1922-1934 data (only data available).*

	Mean	SD	Min	Max
Bony fish	0.342	0.570	0	1.000
Cod	0.091	0.089	0	0.178
Epifauna	0.0002	0.0003	0	0.0005
Flatfish	0.057	0.089	0	0.159
Haddock	0.033	0.057	0	0.098
Herring	0.150	0.261	0	0.451
Infauna	0.0001	0.0002	0	0.0003

For herring Cefas DAPSTOM diet data for the Northern North Sea was only available from 31 stomachs sampled between 1922–1934 ((Table 25). Therefore, the diet was adapted to also include sandeels and zooplankton (Eigaard *et al*., 2014). Herring diet was estimated to consist of sandeels (5%), large zooplankton (75.5%), small zooplankton (14.8%), epifauna (4.7%), and gelatinous zooplankton (0.0001%) (Table 26).

c) Balancing changes

The herring group was balanced in the model with an EE of 0.911 and P/Q of 0.16 yr^{-1}. A P/Q of 0.16 was not high enough to represent this highly productive fish and was estimated by the model from a P/B of 1.05 yr^{-1}. Therefore, the P/Q ratio of herring was adjusted to 0.2 and the model then estimated a more realistic P/B of 1.311 yr^{-1}.

Table 26 *Herring diet proportions used in the model.*

Prey group	Proportion
Sandeels	0.050
Large zooplankton	0.755
Small zooplankton	0.148
Gelatinous zooplankton	0.0001
Epifauna	0.047

No changes were made to herring diets during the balancing stages (Table 26). Predators added to herring included minke whale (herring 1.6% of their diet), mackerel (3.6% of other pelagic fish diet) and pollack (22.4% of large demersal fish diet as herring). Herring in the diet of adult whiting was increased by 15.8% (from 0.1% to 15.9%), saithe by 14.8% (from 0.2 to 15%), adult cod by 1.9% (from 6.5% to 8.4%), juvenile whiting by 9.2% (from 0.8% to 10%), and toothed whales by 5.7% (from 1.3% to 7%). Herring in the diet of skates & rays was decreased by 0.7% (from 1.7% to 1%), squid & octopus by 0.7% (from 2.2% to 1.5%), and monkfish by 0.5% (from 23.1% to 22.7%). Overall, these changes produced an EE for herring of 0.983 in the balanced model and is considered more representative of this important prey species.

1.4.3.19 FG20: Small pelagic fish

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The small pelagic fish functional group consists of sprat *(Sprattus sprattus*), anchovy (*Engraulis encrasicolus*), argentines (*Argentina sp.*) and silvery lightfish (*Maurolicus mueller*). Sprat are not resident in the northern North Sea throughout the year but seasonally migrate within the North Sea Skagerrak and Kattegat (ICES, 2018c). We therefore assumed that 25% of the TSB would, on average, be in the modelled area during the year. Thus, sprat biomass was estimated as 1.714 $t.km^{-2}$ using a TSB for the whole North Sea of 1,812,180 tonnes (ICES, 2018c). The geometric mean area-swept biomass estimates for anchovy, argentines and silvery lightfish using IBTS-IVa data for 1991 increased the overall biomass for small pelagic fish to 1.726 $t.km^{-2}$ (Table 12).

P/B was calculated as 0.624 yr^{-1} (Table 12) and QB as 9.486 yr^{-1} (Table 13). Landings of 4,500 t for sprat plus 332 t of argentines (ICES, 2019k) were used to give an area-based landing estimate of 0.018 $t.km^{-2}$. Landings for sprat of 4758 t, plus discards of 264 t at 0.001 $t.km^{-2}$ gave a catch estimate of 0.019 $t.km^{-2}$ (Table 14).

b) Diet (pre-balanced model)

Table 27 *Small pelagic fish diet proportions used in northern North Sea EwE.*

Prey group	Pre-balanced	Balanced
Large zooplankton	0.835	0.750
Small zooplankton	0.118	0.203
Gelatinous zooplankton	0.0001	0.0001
Epifauna	0.047	0.047

Small pelagic fish diet was based on diet studies of sprat and herring in the North Sea and the West coast of Scotland (De Silva, 1973; Mackinson and Daskalov, 2007), to include large zooplankton (83.5%), small zooplankton (11.8%), epifauna (4.68%), and gelatinous zooplankton (0.0001%) (Table 27).

d) Balancing changes

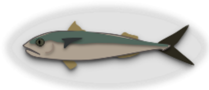
The small pelagic fish group was unbalanced in the model with an EE of 1.75 and a P/Q of 0.065 yr^{-1}. As sprat, anchovy and argentines are short lived, highly productive forage fish species the P/Q ratio for this group should be higher. Therefore, P/Q for this group was set at 0.2 and the model estimated a P/B of 1.897 yr^{-1}.

The EE was reduced by decreasing the proportions of small pelagic fish in the diets of its top predators in the model. Small pelagic fish in the diet of toothed whales was reduced by 8%, alongside seabirds (with low discard diet) by 2%, other pelagic fish by 1%, and squid & octopus by 1%. The proportion of small pelagic fish in whiting diet was increased by 15% for juvenile, and 11% for adults. In addition, the proportion of small pelagic fish in the diet of saithe was increased by 4%, seals by 2%, and adult cod by 1% (see predator group sections for further information).

As an important forage fish group in the model, it was important to ensure all possible predator interactions were included. In the whole North Sea EwE model (Mackinson and Daskalov, 2007), both spurdog (as 5% of their diet) and thornback ray (as 0.09% of their diet) predate on sprat. In the Irish Sea, predators of sprat also include spurdog (2.44% of their diet), thornback ray (8% of their diet) lesser spotted dogfish (*Scyliorhinus canicula*) (0.27% of diet) and argentines (0.25% of diet) (Ellis *et al.*, 1996). This information was used in the model to increase small pelagic fish in the diet of sharks by 5% and skates & rays by 1%.

Small pelagic fish diet was updated to include an increased proportion of small zooplankton by 8.5%, removing this amount from large zooplankton (Table 27). This change was to ensure all species and life stages of copepod under 2mm were included within the small zooplankton portion of the diet. With these changes the small pelagic fish group was balanced in the model with an EE of 0.984.

1.4.3.20 FG21: Other pelagic fish



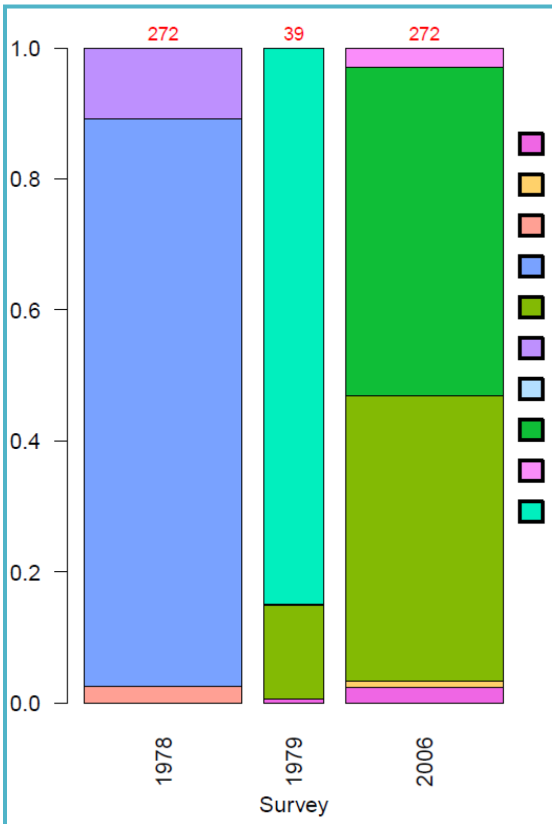
a) Biomass, P/B, Q/B, catch (pre-balanced model)

Species included within the other pelagic fish group are mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*). Biomass for mackerel was estimated as 1.739 $t.km^{-2}$ using 33% of the TSB (3204802 t) to account for extensive migration across the North East Atlantic (stock area 608,198 km^{-2}) (ICES, 2019i). Horse mackerel and blue whiting biomass was estimated as 0.057 $t.km^{-2}$ and 0.020 $t.km^{-2}$ respectively (ICES, 2018a, 2019d) (Table 12). Using these sources an overall group biomass of 1.816 $t.km^{-2}$ was used in the model. $\mathrm{P/B}$ was calculated as 0.539 yr^{-1} (Table 12) and $\mathrm{Q/B}$ was as 4.832 yr^{-1} (Table 13).

Landings for mackerel, horse mackerel and blue whiting in 1991 were estimated as 0.260 $t.km^{-2}$ (ICES, 2019k). The discard rate of mackerel in 1991 for northern North Sea was based on estimates of discards and slipping rates for mackerel for the whole North East Atlantic (ICES, 2018c). Slipping is the release of unwanted fish from purse seines whilst the gear is still in the water. Using estimated discards and slipping of 30,700 t and ICES catch of 675,665 t of mackerel in the North East Atlantic gives a discard rate of 4.5% for 1991. This discard rate was applied to the landings for mackerel giving discards of 0.012 $t.km^{-2}$ for mackerel in the model year. Discards for horse mackerel (stock area 608,198 km^{-2}) and blue whiting (stock area 3,040,990 km^{-2}) for 1991 were estimated using these same methods (Table 14). Therefore, overall group discards for other pelagic fish in the model were estimated as 0.052 $t.km^{-2}$.

b) Diet (pre-balanced model)

The diet for other pelagic fish was adapted from DAPSTOM data using the geometric mean diet proportions across surveys from 1978, 1979 and 2006 (Figure 15).



	Mean	SD	Min	Max
Bony fish	0.010	0.013	0	0.024
Epifauna	0.003	0.005	0	0.009
Haddock	0.008	0.014	0	0.025
Lrg. pelagic fish	0.289	0.501	0	0.867
Lrg. zooplankton	0.189	0.216	0	0.425
Norway pout	0.036	0.062	0	0.108
Shrimp	0.0003	0.0005	0	0.001
Sm. pelagic fish	0.167	0.290	0	0.502
Sm. zooplankton	0.013	0.022	0	0.039
Squid	0.283	0.491	0	0.850

Figure 15 *Bar plot of the total biomass weighted proportion of prey species found in other pelagic fish stomachs during each survey year, in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate an average diet shown in the table (above) by combining the data across these surveys.*

d) Balancing changes

The other pelagic fish group was unbalanced in the model with an EE of 4.205. This high EE was due to the biomass of other pelagic fish being too low in the model. To balance the model an EE of 0.9 was input for this group generating a higher model estimated biomass for this group of 2.545 $t.km^{-2}$. The need to re-estimate the biomass for the modelled area may reflect the migratory nature of the species in this group and thus the difficulty in establishing a biomass for the northern North Sea area when the stock assessments cover much larger areas.

There was a high proportion (29.5%) of cannibalism within the diet of other pelagic fish, which was also affecting the balance of the model. This cannibalism was within DAPSTOM diet data records for the northern North Sea, and may be ecologically realistic for schooling pelagic fish. However, EwE models are known to have difficulties if there are high levels of cannibalism within a functional group. Cannibalism above 5% within the diet matrix can cause large cascading effects on biomass, predation, and consumption within the model. Taking this into account, cannibalism was reduced in the other pelagic fish diet with that portion of the diet reallocated across the remaining prey groups (Table 28). On inspection of the diet it was seen that both herring and sandeels were not included (although it is clear from other studies that these species are eaten (Greenstreet, 1996) thus they were added to the diet (Table 28). To lower the model estimated biomass for squid & octopus, which was causing high consumption mortality on their prey, the portion of squid in the diet of other pelagic fish was reduced from 28% to 5% (Table 28). The large proportion of squid in the 1979 diet survey was most likely due to seasonal availability of squid causing large amounts of biomass to be present in some diet survey years, but not others. This 23% of squid was re-allocated to large zooplankton (Table 28), as zooplankton is often under recorded in stomach surveys due to their high digestibility.

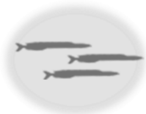
Table 28 *Other pelagic fish diet proportions used in northern North Sea EwE 1991.*

	Pre-balanced	Balanced
Juvenile haddock	0.008	0.009
Norway pout	0.037	0.036
Herring	0.000	0.036
Small pelagic fish	0.171	0.165
Other pelagic fish	0.295	0.000
Sandeels	0.000	0.040
Squid & Octopus	0.283	0.050
Large zooplankton	0.189	0.488
Small zooplankton	0.013	0.084
Shrimp	0.0003	0.0005
Epifauna	0.003	0.091

Norway pout and small pelagic fish were reduced a little in the diet to decrease the overall predation mortality of these groups (Table 28). Minke whale were added as a predator of other pelagic fish (other pelagic fish included as 6% of their diet), alongside seabirds with high discard diet (7%), turbot (3%), flatfish (3%) and small demersal fish (1%). The portion of other pelagic fish was also increased in the diets of hake (up to 76%), monkfish (33%), adult whiting (18%), skates and rays (2%) and saithe (1%). The portion of other pelagic fish in the diet was reduced for ling and large demersal fish to 9.9% for both predators. These changes increased the estimated biomass of other pelagic fish from 1.816 $t.km^{-2}$ in pre-balance to 2.554 $t.km^{-2}$ in the balanced model.

1.4.3.21 FG22: Sandeels

a) Biomass, P/B, Q/B, catch (pre-balanced model)



The sandeels functional group consists of Raitt's sandeel (*Ammodytes marinus*), greater sandeel (Hyperoplus *lanceolatus*) and lesser sandeel (*Ammodytes tobianus*). Biomass for Raitt's sandeel in the northern North Sea was estimated as 3.122 $t.km^{-2}$, using the total stock biomass estimate from MSVPA (ICES, 2002) (TSB 1,779,540 t), and assuming an even distribution across the North Sea (Mackinson and Daskalov, 2007). The geometric mean area-swept biomass estimates for greater and lesser sandeel were generated using IBTS-IVa data for 1991 and were estimated as 1.439 $t.km^{-2}$ and 0.006 $t.km^{-2}$, respectively. Overall, the total group biomass estimate for the sandeels group was 4.567 $t.km^{-2}$. P/B was calculated as 1.03 yr^{-1} and Q/B was calculated as 8.83 yr^{-1}.

b) Diet (pre-balanced model)

As the northern North Sea sandeels diet data in DAPSTOM only included small zooplankton (at 54%) and large zooplankton (46%), data for the whole North Sea from Hislop *et al*. (1997) was used to augment this. The whole North Sea data for 1991 had proportions of small zooplankton 65.6%, infauna

19.2%, phytoplankton 6.8%, large zooplankton 6.3%, epifauna 1.6% and fish larvae 0.5% (Hislop *et al.*, 1997).

Table 29 *Diet proportions for sandeels in the pre-balanced and balanced model.*

	Pre-balance diet	Balanced diet
Sandeels	0.000	0.010
Large zooplankton	0.068	0.163
Small zooplankton	0.656	0.667
Epifauna	0.016	0.015
Infauna	0.192	0.077
Phytoplankton	0.068	0.068

These values were used in the North Sea EwE model of (Mackinson and Daskalov, 2007). For our model as there is no fish larvae functional group, thus we combined this with the large zooplankton diet proportion (Table 29).

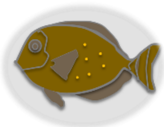
c) Balancing changes

The sandeels group was unbalanced in the model with an EE of 1.18 and a low $\mathrm{P/Q}$ of 0.117 yr^{-1}. To balance the model, the biomass for Raitt's sandeel was re-estimated using acoustic data from HAWG (2019) for survey areas only within the model area. This survey estimated a total stock biomass for *A. marinus* of 637,809 t, generating a new area-based biomass of 2.413 t.km^{-2}. This estimate increased the group biomass to 2.801 t.km^{-2}, changed the group's $\mathrm{P/B}$ to 1.152 yr^{-1}, and the group's $\mathrm{Q/B}$ of 8.805 yr^{-1}. This new $\mathrm{P/B}$ was too low to be viable for these highly productive pelagic fish, thus a $\mathrm{P/Q}$ ratio of 0.25 yr^{-1} was used allowing the model to estimate $\mathrm{P/B}$ at 2.201 yr^{-1}. This new $\mathrm{P/B}$ estimate is close to the North Sea EwE ICES Key run (ICES, 2015b) estimate of 2.28 yr^{-1}. $\mathrm{P/Q}$ for the sandeels group was set higher than the $\mathrm{P/Q}$ of 0.2 yr^{-1} for small pelagic fish (which are mainly sprat). This assumption was made due to sandeels having a faster growth rate than sprat (NSme MacDonald, Marine Scotland, pers. comms. 2019). With these changes the EE of sandeels was relatively low at 0.732 indicating that the predation mortality for this group might be too low. As mackerel are known predators of sandeels in the North Sea (MacDonald *et al*., 2019), the proportion of sandeels in the diet of mackerel was raised to 4% (by reducing cannibalism in the mackerel diet).

A sandeel stomach sampling study by Eigaard *et al.* (2014) sampled 748 sandeels from 36 different commercial hauls in the North Sea in 2012 and 2013 and found high levels of cannibalism (67 of these sandeel stomachs contained late stage sandeel larvae). This study also found that cannibalism was very high in the North Sea, although the stomachs sampled were those of swimming animals and these fish spend a large amount of time buried. In EwE models cannibalism within functional groups above 5% causes large cascading effects on biomass, predation, and consumption within the model. In the Irish Sea EwE model the original diet of sandeels included 57% cannibalism in the group (Bentley *et al.*, 2018), but this was reduced to 5% in the balanced and fitted Irish Sea model (Bentley *et al.*, 2019). The 1991 North Sea DAPSTOM data had 0.5% fish larvae in sandeel diet (Hislop *et al.*, 1997; Mackinson and Daskalov, 2007), which is most likely to be larval stages. Taking these findings into account, sandeel cannibalism was added into the model at 1% of the diet by removing this amount from infauna (Table 29).

Sandeels diet was further adapted by increasing the portion of large zooplankton by 9.5% (from 6.8% to 16.3%) and small zooplankton by 1%, and reducing infauna by 10.5% (Eigaard *et al.*, 2014) and epifauna by 1% (Table 29). These changes amounted to a balanced EE for sandeels of 0.983.

1.4.3.22 FG23: European Plaice



a) Biomass, P/B, Q/B, catch (pre-balanced model)

Plaice TSB for the whole North Sea, Skagerrak, and Kattegat (721, 925 km^{-2}) was estimated as 504,316 t using numbers at age and weight at age (ICES, 2018d). Engelhard *et al.*, (2011) indicates that only approximately 20% of plaice in the North Sea is present within the model area. Therefore, plaice biomass was estimated as 100,863 t, giving an area-based biomass estimate of 0.140 $t.km^{-2}$ for the model area.

Plaice $\mathrm{P/B}$ was estimated as 0.601 yr^{-1} (Table 12) and $\mathrm{Q/B}$ at 3.653 yr^{-1} (Table 13). Landings for plaice were and calculated as 0.044 $t.km^{-2}$ (ICES, 2018d), discards for plaice were calculated as 0.022 $t.km^{-2}$ (ICES, 2018d).

b) Diet (pre-balanced model)

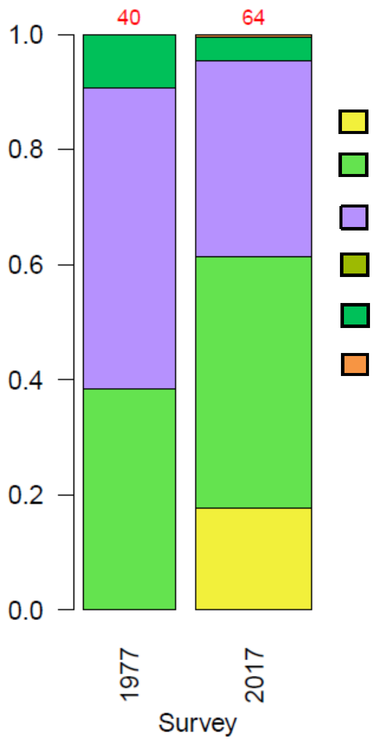
Table 30 *Diet proportions for plaice in the model.*

	Pre-balance and balanced diet.
Epifauna	0.451
Infauna	0.473
Large zooplankton	0.00001
Squid & octopus	0.003
Sandeels	0.073

Mean diet proportions by weight for plaice were calculated across DAPSTOM surveys for 1977and the Shetland stomach sampling project in 2017 (Table 30, Figure 16). Although 8.8% of the diet was allocated to bony fish, it is known that plaice mainly consume polychaete worms, small crustaceans (such as amphipods and mysids), bivalves and brittle stars (De Clerck and Buseyne, 1989; Rijnsdorp and Vingerhoed, 2001). Thus, the 8.8% bony fish was split between infauna (4.2%) and epifauna (4%) with a small amount of sandeels (0.6%) also included (Figure16).

d) Balancing changes

Plaice was unbalanced in the model with an EE of 2.6 and a $\mathrm{P/Q}$ of 0.165 yr^{-1}. To balance the model, predation mortality of this group was reduced. The top predators of plaice in the model are sharks, seals, skates & rays, adult cod, and monkfish. The proportion of plaice in the diet of sharks was reduced by 9.7% (from 10.7% to 1%), seals by 5% (from 5.8% to 0.8%) (Hall *et al.*, 1998; Arnett and Whelan, 2001), and adult cod by 0.01% (from 0.19% to 0.18%) (Arnett and Whelan, 2001).



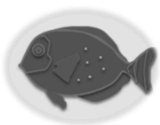
a)	Mean	SD	Min	Max
Bony fish	0.088	0.124	0	0.176
Epifauna	0.411	0.038	0.385	0.438
Infauna	0.431	0.128	0.341	0.521
Large zooplankton	0.00001	0.00002	0	0.00003
Sandeels	0.067	0.038	0.040	0.094
Squid & octopus	0.003	0.004	0	0.005

Figure 16 *Bar plot of the total biomass weighted proportion of prey species found in predator stomachs during each survey year, in Area IVa. Red numbers above each bar show the number of stomachs sampled which is also illustrated by bar width. These data have been used to generate a mean average diet proportion shown in table a (top) by combining the data across these surveys. Table b (below) shows the diet proportions used within the model diet matrix in both the pre-balanced and balanced model versions.*

These changes to predator diets balanced the plaice group in the model with an EE of 0.988.

1.4.3.23 FG24: Turbot

a) Biomass, P/B, Q/B, catch (pre-balanced model)



Although turbot has a low abundance within the model area, it is a species with high economic value it was therefore designated as a single species functional group in the model. Total Stock Biomass in 1991 was estimated to be 14,315 t (ICES, 2018d). An even distribution of turbot across the assessment area was assumed, generating an area-based biomass of 0.024 t.km^{-2}. Turbot $\mathrm{P/B}$ was estimated as 0.525 yr^{-1} (Equation **9**) and $\mathrm{Q/B}$ as 3.956 yr^{-1} (Equation **10**). Landings for turbot from ICES IVa were 132 t (ICES, 2019k) or 0.0005 t.km^{-2}. Discards for turbot were calculated as 0.0001 t.km^{-2} (Heath and Cook, 2015).

b) Diet (pre-balanced model)

Table 31 *Turbot diet using DAPSTOM data for flatfish and turbot diet information from ICES (2018d).*

	Pre-balanced & balanced
Norway pout	0.094
Small pelagic fish	0.028
Sandeels	0.055
Flatfish	0.010
Small demersal fish	0.009
Squid & octopus	0.008
Large zooplankton	0.006
Small zooplankton	0.005
Crabs & lobsters	0.082
Shrimp	0.172
Epifauna	0.270
Infauna	0.182
Discards	0.079

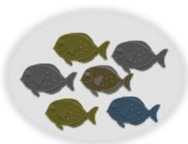
Turbot is a top predator and a typical visual feeder on benthic fish (including small gadoids such as Norway pout, sandeels, gobies, flatfish, dragonets and seabreams), pelagic fish (herring, sprat sardine), crustaceans and bivalves (ICES, 2018d) (Table 31).

d) Balancing changes

Turbot was unbalanced in the model with an EE of 1.459 and $\mathrm{P/Q}$ of 0.132. Turbot catch for the northern North Sea was re-calculated as 0.009 t.km^{-2} based on a catch of 5,605 t across the whole of the North Sea (ICES, 2018d). A limitation of this new catch estimate is that it is over 10 times greater than the original estimate, and more representative of southern North Sea turbot catch in 1991. Since the biomass estimate for turbot was derived from the whole North Sea TSB in 1991, the new catch estimate was the best option available to balance this group. With this new catch estimate the F was re-calculated as 0.375 yr^{-1} and a M as 0.426 yr^{-1} using Equation 10 and the same parameters as before (Table 12). This gives a new $\mathrm{P/B}$ of 0.801 yr^{-1}, and a new $\mathrm{Q/B}$ of 3.947 yr^{-1} for this group (Table 13). With these changes a new $\mathrm{P/Q}$ of 0.203 yr^{-1} was estimated by the model. However, the group was still unbalanced with an EE of 2.093.

To balance turbot, we reduced the predation mortality on turbot by decreasing their proportion in the diet of its top predators, juvenile whiting, flatfish squid and octopus. Turbot was reduced in the diet of juvenile whiting by 1.1% (from 1.2% to 0.1%), flatfish by 0.9% (from 1% to 0.1%), and squid & octopus by 0.4% (0.5% to 0.1%). In the North Sea EwE (Mackinson and Daskalov, 2007), predators of turbot include seals (1% of diet) and squid (0.5% of diet). In the southern North Sea EwE (Stäbler *et al.*, 2018b), the only predator for turbot are seals (0.91% of diet). Arnett & Whelan (2001) found turbot to be a component of the diets of cod and grey seals in the North Sea. Therefore, seals (0.1% of their diet) and cod (0.45% of adult cod diet) were included as predators of turbot. These percentages were removed from the Norway pout portion for each predator (Arnett and Whelan, 2001). This allowed turbot to be balanced with and EE of 0.984.

1.4.3.24 FG25: Flatfish



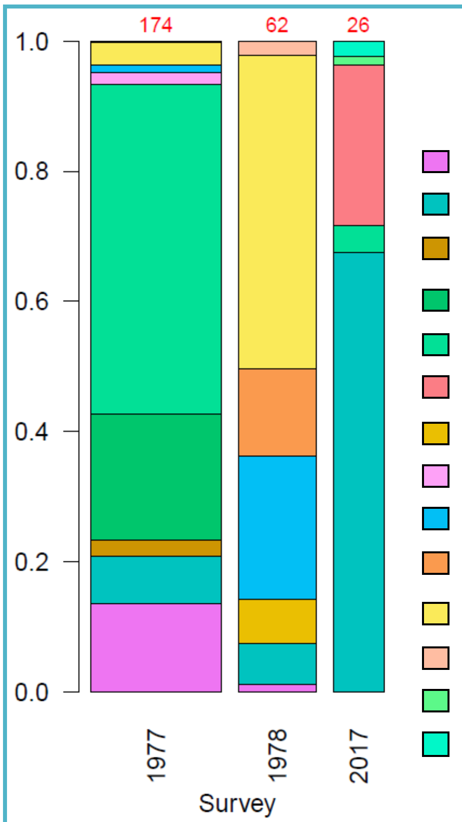
a) Biomass, P/B, Q/B, catch (pre-balanced model)

The flatfish group consists of brill (*Scophthalmus rhombus*), halibut (*Hippoglossus hippoglossus*), megrim (*Lepidorhombus whiffiagonis*), lemon sole (*Microstomus kitt*), European flounder (*Platichthys flesus*), witch flounder (*Glyptocephalus cynoglossus*), long rough dab (*Hippoglossoides platessoides*), Norwegian topknot (*Phrynorhombus norvegicus*), dab (*Limanda limanda*), solenette (*Buglossidium luteum*), and common sole (*Solea solea*). Megrim and halibut are commercially important species but due to a paucity of diet and biomass data available for the model area in 1991 were placed within a multi-species functional group. Common sole is a more important commercial species in the southern North Sea, and the other flatfish included in this group are mainly by-catch species of the mixed fishery. The geometric mean area-swept biomass estimates for flatfish were generated using IBTS-IVa data for 1991 giving a total group biomass of 0.201 $t.km^{-2}$ for flatfish (Table 12).

The pro-rated P/B of the flatfish group was calculated as 0.717 yr^{-1} and the group Q/B was calculated as 4.333 yr^{-1} (Table 12 and Table 13). Combined landings for flatfish were calculated as 0.037 $t.km^{-2}$ (ICES, 2019k), and discards of 0.027 $t.km^{-2}$ (Heath and Cook, 2015; Cook and Heath, 2018) (Table 14).

b) Diet (pre-balanced model)

Fish stomach records from DAPSTOM (in 1977 and 1978) and the 2017 Shetland stomach sampling project were used to generate a biomass weighted diet for this group (Figure 17). Flatfish take a wide variety of prey with preference for benthic invertebrates (shrimp, infauna, and epifauna) (Mackinson and Daskalov, 2007). The 'bony fish' portion of the diet was split between the other fish species found in the diet. Turbot was assigned as the prey for the flatfish proportion of the diet (Table 32).



	Mean diet	SD	Min	Max
Bony fish	0.049	0.076	0	0.136
Epifauna	0.270	0.350	0.063	0.674
Flatfish	0.008	0.014	0	0.024
Haddock	0.065	0.112	0	0.194
Infauna	0.182	0.281	0	0.506
Crabs & lobsters	0.082	0.142	0	0.247
Other pelagic fish	0.023	0.040	0	0.068
Large zoo.	0.006	0.011	0	0.019
Norway pout	0.077	0.123	0	0.219
Sandeels	0.045	0.078	0	0.135
Shrimp	0.172	0.268	0	0.481
Small demersal fish	0.007	0.013	0	0.022
Small zoo.	0.005	0.008	0	0.014
Squid	0.008	0.014	0	0.024

Figure 17 *Bar plot of the total biomass weighted proportion of prey species found in flatfish stomachs during each survey year available, in Area IVa. Red numbers above each bar show the number of stomachs sampled, also illustrated by bar width. These data have been used to generate a biomass weighted mean diet for flatfish in the northern North Sea shown in the table (above).*

d) Balancing changes

Table 32 *Flatfish diet proportions used in the model.*

	Pre-balanced	Balanced
Juvenile haddock	0.027	0
Adult haddock	0.053	0
Norway pout	0.094	0.074
Other pelagic fish	0.028	0.028
Sandeels	0.055	0.020
Turbot	0.010	0.001
Small demersal fish	0.009	0.009
Squid & Octopus	0.008	0.008
Large zooplankton	0.006	0.006
Small zooplankton	0.005	0.009
Gelatinous zooplankton	-	0.020
Crabs & lobsters	0.082	0.052
Shrimp	0.172	0.150
Epifauna	0.270	0.355
Infauna	0.182	0.192
Discards	-	0.001
Detritus	-	0.075

The flatfish group was unbalanced in the model with an EE of 6.523. This indicated that predation pressure upon flatfish in the model is too high for the available biomass. Catchability of GOV gear for flatfish is known to be low, and the survey data within NS IBTS may underestimate the total stock biomass of these species in the northern North Sea. To balance flatfish an EE of 0.9 was used, allowing the model to estimate a higher biomass for flatfish of 1.519 $\mathrm{t.km^{-2}}$. In addition, flatfish proportions in the diet of their predator species were reduced: for sharks by 13.4% (from 17.9% to 4.6%), squid & octopus by 6.3% (from 8.3 to 2%), seals by 2% (from 4.1 to 2.1%) and juvenile haddock by 0.5% (from 5.5% to 5%). The proportion of flatfish in the diet of saithe was increased by 0.6% (from 0.5 to 1.1%) and juvenile cod increased by 0.3% (from 9% to 9.3%). Flatfish are known to consume discarded fish and other detritus (Depestele *et al.*, 2019). Discards were added to the diet at 0.01% and detritus at 7.5% (Table 32). This amount was removed from haddock with the remaning 0.04% placed on to small zooplankton. Norway pout, sandeels and turbot were reduced in the model by 2%, 3.5% and 0.9% respectively and added to epifauna.

Gelatinous zooplankton were added to flatfish diet at 2%. This was to include all trophic interactions with jellyfish (Lamb *et al.*, 2019) and better explain their mortality in the model. This 2% plus a further 0.2% was removed from the shrimp proportion and added to epifauna. Crabs & lobster were also decreased in the diet by 3% and increased the infauna proportion by 1% (Table 32). Flatfish was then balanced in the model with an EE of 0.90 and a $\mathrm{P/Q}$ of 0.165 $\mathrm{yr^{-1}}$.

1.4.3.25 FG26: Small demersal fish

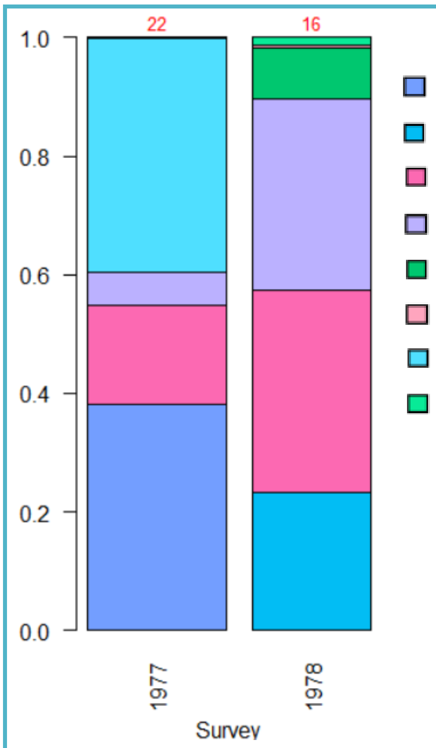
a) Biomass, P/B, Q/B, catch (pre-balanced model)

The small demersal fish group consists of bib (pouting) (*Trisopterus luscus*), lesser weaver (*Echiichthys vipera*), reticulate dragonet (*Callionymus reticulatus*), poor cod (*Trisopterus minutus*), common dragonet (*Callionymus lyra*), silvery pout (*Gadiculus argenteus*), and spotted dragonet (*Callionymus* *maculatus*). The combined 1991 biomass for this group was calculated as 0.037 $t.km^{-2}$ using IBTS-IVa data and the methods in Greenstreet *et. al* (2007) (Table 12).

The group P/B was pro-rated by biomass and calculated as 0.782 yr^{-1} (Table 12) and the group Q/B was pro-rated by biomass as 6.75 yr^{-1}. Landings were calculated as 0.00008 $t.km^{-2}$ (ICES, 2019k), with discards of 0.0007 $t.km^{-2}$ (Heath and Cook, 2015) (Table 14).

b) Diet (pre-balanced model)

Bib and poor cod were the only species in the group with diet data available within DAPSTOM for the northern North Sea. Fish stomach records for these species in DAPSTOM (in 1977 and 1978) were used to generate a biomass weighted diet for this group (Figure 18). The 'bony fish' portion of the diet (19%) was split between sandeels and other pelagic fish in the diet (15.6% added to sandeels and 3.4% added to other pelagic fish) (Table 33).



	Mean	SD	Min	Max
Bony fish	0.190	0.269	0	0.380
Epifauna	0.117	0.163	0.001	0.232
Infauna	0.255	0.124	0.167	0.342
Crabs & lobsters	0.189	0.188	0.056	0.322
Other pelagic fish	0.042	0.060	0.010	0.084
Large zooplankton	0.003	0.004	0	0.006
Sandeels	0.197	0.279	0	0.394
Shrimp	0.007	0.008	0.001	0.013

Figure 18 *Bar plot of the total biomass weighted proportion of prey species found in small demersal fish stomachs during each survey year available, in Area IVa. Red numbers above each bar show the number of stomachs sampled, also illustrated by bar width. These data have been used to generate a biomass weighted mean diet for small demersal fish in the northern North Sea shown in the table (above).*

d) Balancing changes

The small demersal fish group was unbalanced in the model with an EE of 17.918 and a P/Q of 0.112 yr^{-1}. This high EE indicated that the predation pressure upon small demersal fish in the model was too high for the available biomass. Therefore, an EE of 0.9 was inserted, allowing the model to generate a biomass of 0.809 $t.km^{-2}$. The model estimated P/Q of 0.112 was low for this productive group of species. Therefore, a P/Q of 0.15 yr^{-1} was then put in for this group, allowing the model to estimate a P/B of 1.012 yr^{-1}.

Although the inclusion of an EE would create a balanced functional group, the biomass estimated was still quite high in comparison to other forage fish prey groups in the model. Therefore, the proportion of small demersal fish was reduced in the diet of skates & rays by 6% (from 11% down to 5%), in the diet of large demersal fish by 8% (from 8.5% to 16.5%), adult cod by 5.3% (from 1.2% to 6.5%) and saithe by 2.7% (from 2.3% to 5%) (more information on changes to predator diets in their functional group descriptions).

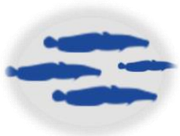
The small demersal fish group should act in the model as a forage fish prey group. However, a proportion of their diet consisting of other pelagic fish raises their trophic level within the model to an un-realistic level. The original proportion of other pelagic fish within the small demersal fish diet may be due to the bathypelagic species of the group predating on blue whiting juveniles. However, in the food web dynamics of the model this would not be obvious, and these small fish species eating mackerel is highly unlikely.

Table 33 *Small demersal fish diet in the model*

	Pre-balanced	Balanced
Herring	-	0.040
Other pelagic fish	0.076	0.010
Sandeels	0.354	0.050
Large zooplankton	0.003	0.003
Small zooplankton	-	0.021
Crabs & lobsters	0.189	0.050
Shrimp	0.007	0.007
Epifauna	0.117	0.389
Infauna	0.255	0.430

The proportion of other pelagic fish in the diet was therefore reduced to the estimated minimum of 1% (Figure 18) and the difference added to herring (4%), small zooplankton (2.1%) and epifauna (0.5%) (Table 33). The proportion of sandeels in the diet was also reduced by 30.4% (from 35.4% to 5%) with the difference transferred to epifauna and infauna (Table 33). In addition, the crabs & lobster proportion of the diet was reduced by 13.9% (from 18.9% down to 5%) with the difference transferred to epifauna. These changes lowered the trophic level of small pelagic fish in the model from 3.8 down to 3.4 and gave a final estimated biomass for small demersal fish of 0.809 $t.km^{-2}$.

1.4.3.26 FG27: Large demersal fish



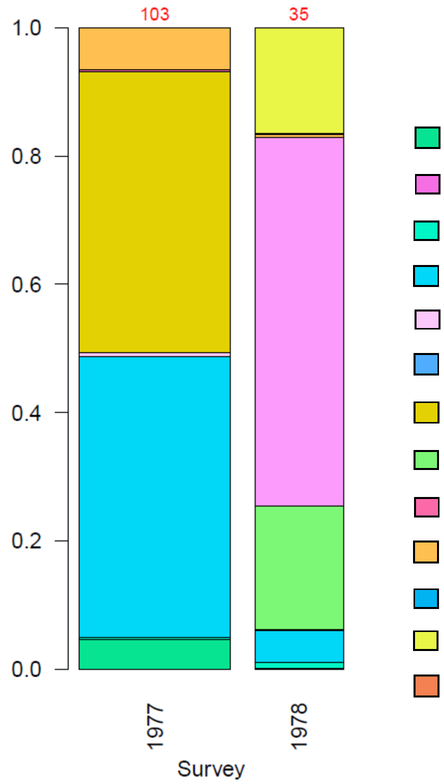
a) Biomass, P/B, Q/B, catch (pre-balanced model)

The large demersal fish group consists of pollock (*Pollachius pollachius*), Northern wolffish (*Anarhichas lupus*), lumpfish (*Cyclopterus lumpus*), shorthorn sculpin (*Myoxocephalus scorpius*), cusk (tusk or torsk) (*Brosme brosme*), Norway haddock (*Sebastes norvegicus*), red gurnard (*Chelidonichthys cuculus*), greater forkbeard (*Phycis blennoides*), John Dory (*Zeus faber*), grey gurnard (*Eutrigla gurnardus*), fourbeard rockling (*Enchelyopus cimbrius*), boarfish (*Capros aper*), hooknose (*Agonus cataphractus*), blackbelly rosefish (*Helicolenus dactylopterus*), and three-beard rockling (*Gaidropsarus vulgaris*). Most of these species are not of great commercial value or when landed mainly from by-catch. The biomass for large demersal fish was calculated using IBTS-IVa and the method of Greenstreet *et al.* (2007) (Table 12).

The pro-rated group $\mathrm{P/B}$ was calculated as 0.452 yr^{-1} (Table 12). The group $\mathrm{Q/B}$ of 3.622 yr^{-1} was calculated using species $\mathrm{Q/B}$ (Table 13) and pro-rated by biomass. Landings of 0.044 $t.km^{-2}$ (ICES, 2019k), with estimated discards for pollack, cusk and wolfish of 0.008 $t.km^{-2}$ (Heath and Cook, 2015) (Table 14).

b) Diet (pre-balanced model)

Fish stomach records from DAPSTOM (in 1977 and 1978) were used to generate a biomass weighted diet for this group (Figure 19). Large demersal fish have a largely piscivorous diet with preference for haddock, other pelagic fish, small demersal fish, and a high level of cannibalism . The 'bony fish' portion of the diet was split between the other fish groups present in the diet (Figure 19).



	Mean diet	SD	Min	Max
Bony fish	0.023	0.033	0.000	0.046
Epifauna	0.001	0.001	0	0.002
Flatfish	0.013	0.015	0.003	0.024
Haddock	0.278	0.227	0.117	0.439
Infauna	0.003	0.004	0.000	0.005
Crabs & lobsters	0.0003	0.0004	0	0.001
Large demersal fish	0.219	0.310	0	0.439
Other pelagic fish	0.228	0.322	0.001	0.455
Large zooplankton	0.001	0.002	0	0.002
Sandeels	0.038	0.038	0.011	0.065
Shrimp	0.0004	0.0002	0.0002	0.001
Small demersal fish	0.195	0.275	0.000	0.389
Small zooplankton	0.0001	0.0002	0	0.0003

Figure 19 *Bar plot of the total biomass weighted proportion of prey species found in large demersal fish stomachs during each survey year available, in Area IVa. Red numbers above each bar show the number of stomachs sampled, also illustrated by bar width. These data have been used to generate a biomass weighted mean diet for small demersal fish in the northern North Sea shown in the table (above).*

d) Balancing changes

The large demersal fish group was unbalanced in the model with an EE of 3.616 and a $\mathrm{P/Q}$ of 0.125 yr^{-1}. It was evident from the high EE that predation pressure upon large demersal fish in the model was too high for the available biomass. Therefore, to balance the model the proportion of large demersal fish in the diet of various species were lowered: for common ling by 17.5% (from 22.5% to 5%), sharks by 7.8% (from 8.8% to 1%) and seals by 2.4% (from 7.9 to 5.5%). Cannibalism in the group was also reduced by 21.5% to 1% (Figure 19) (Table 34). With these changes large demersal fish was balanced in the model with an EE of 0.893. The diet proportions of haddock were reduced (juvenile haddock by 8.2%, adult haddock by 16.5%) (Table 34) alongside Norway pout (by 18.2% with these portions added to sandeels (2.4% increase), small demersal fish (8% increase) and epifauna.

Table 34 *Large demersal fish diet proportions used in northern North Sea EwE 1991.*

	Pre-balanced	Balanced
Juvenile haddock	0.084	0.001
Adult haddock	0.166	0.001
Norway pout	0.294	0.112
Herring	-	0.224
Other pelagic fish	0.099	0.099
Sandeels	0.036	0.060
Flatfish	0.007	0.007
Small demersal fish	0.085	0.165
Large demersal fish	0.225	0.010
Large zooplankton	0.001	0.001
Small zooplankton	0.0001	0.0001
Crabs & lobsters	0.0001	0.0001
Shrimp	0.0002	0.0002
Epifauna	0.0004	0.290
Infauna	0.003	0.029

1.4.4 Invertebrates

A total of 10 invertebrate groups were included within the northern North Sea model (Table 34). These include squid and octopi, gelatinous zooplankton, edible crab, velvet crab, crabs & lobsters, Norway lobster, shrimp, scallops, epifauna and infauna groups. Table 35 provides a list of species included within each invertebrate group in the model, their biomass estimates and data sources.

The P/B ratio for invertebrate groups was estimated using an empirical model for marine benthos (Tumbiolo and Downing, 1994) (Equation **11**).

$$LogP = 0.24 + 0.96LogB - 0.21LogW_m + 0.03T - 0.16Log(D+1)$$

Equation 11

Where P is production, B is the biomass of the functional group, W_m is the maximum body mass, D is depth, and T is the sea surface temperature. Annual average sea surface temperature used for the northern North Sea in 1991 was 9.6°C (Rayner *et al.*, 2003), and an average shelf depth 150 m.

Table 35 *Biomass estimates for invertebrate functional groups in the EwE model of the northern North Sea.*

Functional group		t.km^{-2}	Source
Squid & Octopus		0.0879	(ICES, 2019j)
Common squid	*Loligo forbesii*	0.047	-
Ringed octopus	*Eledone cirrhosa*	0.009	-
Lesser flying squid	*Todaropsis eblanae*	0.007	-
Shortfin squid	*Illex coindetii*	0.006	-
Whale squid	*Walvisteuthis virilis*	0.005	-
European flying squid	*Todarodes sagittatus*	0.005	-
Stout bobtail	*Rossia macrosoma*	0.003	-
Bobtail squid	*Sepiola rondeletii*	0.002	-
Common cuttlefish	*Sepia officinalis*	0.001	-
European common squid	*Alloteuthis subulata*	0.001	-
Common octopus	*Octopus vulgaris*	0.001	-
Elegant cuttlefish	*Sepia elegans*	0.0004	-
Warty bobtail squid	*Rossia palpebrosa*	0.0003	-
Cuttlefish sp.	*Sepietta neglecta*	0.0002	-
Gelatinous zooplankton		0.780	
Moon jellyfish	*Aurelia aurita*	0.523	(Eriksen *et al.*, 2012)
Lion's mane jellyfish	*Cyanea capillata*	0.222	(Hay *et al.*, 1990)
Blue jellyfish	*Cyanea lamarckii*	0.036	(Hay *et al.*, 1990)
Edible crab	*Cancer pagurus*	0.125	(Zuhlke *et al.*, 2001; Callaway *et al.*, 2002)
Velvet crab	*Necora puber*	0.001	(Zuhlke *et al.*, 2001; Callaway *et al.*, 2002)
Crabs & lobsters		1.098	(Zuhlke *et al.*, 2001; Callaway *et al.*, 2002)
Flying crab	*Liocarcinus holsatus*	0.667	-
Lyre crab	*Hyas coarctatus*	0.221	-
Marbled swimming crab	*Liocarcinus marmoreus*	0.085	-
Squat lobster	*Pisidia longicornis*	0.064	-
Northern stone crab	*Lithodes maia,*	0.061	-
Norway lobster	*Nephrops norvegicus*	0.450	(ICES, 2018d)
Shrimp		0.093	
Pandalus	*Pandalus montagui*	0.071	(ICES, 2006)
-	*Processa nouveli*		(ICES, 2006)
-	*Pandalus borealis*		(ICES, 2006)
Crangon	*Crangon crangon*	0.022	(Tulp *et al.*, 2016)
-	*Crangon allamani*		(Tulp *et al.*, 2016)
Scallops	*Pecten maximus*	0.160	(Dobby *et al.*, 2017)
Epifauna	-	21.776	
Brittle stars	*Amphiura filiformis,*	10.401	(Zuhlke *et al.*, 2001; Callaway *et al.*, 2002; Mackinson and Daskalov, 2007) Species presence northern North Sea, NS IBTS DATRAS 1990-2018 (ICES, 2019j).
-	*Ophiura albida,*	1.388	
-	*Ophiura affinis*	0.493	
Common starfish	*Asterias rubens*	0.233	
Common whelk	*Bussinum undatum*	0.388	
Queen scallop	*Aequipecten opercularis*	0.097	-
Mussels	*Mytilus edulis*	0.242	-
-	*Modiolus modiolus*	2.716	-
-	*Modiolus barbatus*	0.103	-
-	*Musculus niger*	0.296	-
Hermit crabs	*Paguroidea*	0.305	-
Sea urchin	*Echinus esculentus*	0.289	-
Chiton	*Leptochiton asellus*	2.322	-
Sea snails	*Euspira montagui*	0.851	-
-	*Hyala vitrea*	0.574	-
Sea potato	*Echinocardium flavescens*	0.406	-

-	*E. cordatum*	0.304	-
Oysters	*Anomia ephippium*	0.288	-
-	*Pododesmus patelliformis*	0.070	-
Infauna	-	20.510	
Polychaete worms	*Polychaeta*	18.779	(Zuhlke *et al.*, 2001; Callaway *et al.*, 2002; Mackinson and Daskalov, 2007) Species presence northern North Sea, NS IBTS DATRAS 1990-2018 (ICES, 2019j).
Razor clams	*Ensis ensis*	0.510	
-	*Phaxas pellucidus*	0.240	
Faroe sunset shell	*Gari fervensis*	0.460	
Burrowing bivalves	*Cochlodesma praetenue*	0.261	
-	*Myrtea spinifera*	0.180	-
-	*Thyasira spp.*	0.080	-

1.4.4.1 FG28: Squid & octopus

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The squid & octopus functional group is composed of common squid (*Loligo forbesii*), ringed octopus (*Eledone cirrhosa*), lesser flying squid (*Todaropsis eblanae*), shortfin squid (*Illex coindetii*), whale squid (*Walvisteuthis virilis*), European squid (*Todarodes sagittatus*), and other cephalopods present in the northern North Sea. The total estimated biomass of this group was calculated using North Sea IBTS estimates, at 0.0879 t.km^{-2} (Table 35). The group P/B was estimated as 1.2 yr^{-1} using an empirical model for marine benthos (Tumbiolo and Downing, 1994) (Equation 11), with maximum body mass 286 g (Robinson *et al.*, 2010), a dry weight to wet weight ratio of 1:21, annual mean surface temperature as 9.6°C (Rayner *et al.*, 2003) for the northern North Sea in 1991, and an average shelf depth 150 m..

P/B estimated at 1.2 yr^{-1} was low for this group in comparison to other EwE models (Mackinson and Daskalov, 2007; Serpetti *et al.*, 2017; Bentley *et al.*, 2018). Therefore, a much higher P/B estimate of 4.5 yr^{-1}, taken from the NS EwE model (Mackinson and Daskalov, 2007) was used for this group.

There are a wide range of estimates for the daily food consumption of *L. forbessii* in the North Sea, of between 0.14 - 5.6% of its body weight (Pierce *et al.*, 1994; Young *et al.*, 2004). However, for the other species in this group few consumption estimates exist. Parameter estimates for the squid and octopus group are thus only based on *L. forbessii.* Assuming the weight of stomachs as roughly equal to the weight of prey ingested provided an annual Q/B of between 0.5-20 yr^{-1}. However, 2.5% daily food consumption from mean weight of stomach contents was recorded by Howard *et al*. (1987) who calculated a Q/B of 9 yr^{-1} (Howard *et al.*, 1987; Pierce *et al.*, 1994). Daily consumption of *L. forbessii* has also been estimated as approximately 14% for the North Sea which would have instead yielded a higher Q/B of 51 yr^{-1} (Segawa, 1990; Pierce *et al.*, 1994). Mackinson & Daskalov (2007) used a conservative estimate of 20 yr^{-1}, which was also adopted for the Q/B of the squid & octopus group in the northern North Sea model. The official catch statistics (ICES, 2019k) reported landings for cephalopods in 1991 of 793 t, giving an area-based catch estimate of 0.003 t.km^{-2}.

b) Diet (pre-balanced model)

Diet for this group was constructed using data collected from *L. forbessii* stomachs in the North Sea in 1990-1993 (Pierce *et al.*, 1994). This study found these squid to have a preference for fishes (mainly whiting, Norway pout and other *Trisopterus* species), crustaceans and cephalopods. *Todaropsis eblanae* are also mainly piscivorous consuming both gadoids and pelagic fish (Hastie *et al.*, 2009), with *Alloteuthis subulate* preferring sandeels, sprat and crustaceans (Nyegaard, 2001). Cuttlefish have a wider range of prey including small pelagic fish, flatfish, crustacean and cephalopod species (Hastie *et al.*, 2009), while bobtail squid consume mainly mysids, decapod shrimps and zooplankton (Hastie *et al.*, 2009). Ringed octopus feeds on a diet of decapod crustaceans, cephalopod eggs and other molluscs, whilst common octopus feed upon a wide variety of fish crustaceans, polychaetes and cephalopods (Hastie *et al.*, 2009). Larvae stages of these squid and octopus feed heavily upon zooplankton, their abundance being a limiting factor of stock recruitment success (Hastie *et al.*, 2009).

Using this information for each species (Pierce *et al.*, 1994; Nyegaard, 2001; Hastie *et al.*, 2009), diet proportions for squid and octopus were split between fish (Norway pout 3.6%, herring 2.2%, small pelagic fish 3%, turbot 0.5% and other flatfish 8.3%) shrimp (2%), scallops (0.1%), zooplankton (large 21.3% and small 35.6%), epifauna (15.6%), infauna (2.1%), phytoplankton (5.2%) and cannibalism (0.5%)(Table 36).

d) Balancing changes

The squid & octopus group was unbalanced in the model with an EE of 10.382 and a $\mathrm{P/Q}$ of 0.225 yr^{-1}. Predation pressure upon this group was reduced by lowering their proportion in the diet of other pelagic fish by 23% (from 28% to 5%), juvenile haddock by 2% (from 20% to 18%), skates & rays by 1% (from 11% to 10%) and adult cod by 0.1% (from 0.9% to 0.8%). Squid & octopus proportions in the diet of saithe were increased by 2% (from 10% to 12%) and adult whiting by 1% (from 4% to 5%). To ensure all trophic interactions were included squid & octopus was added to the diet of toothed whales (at 4% of their diet) and seals (at 0.6% of their diet).

The $\mathrm{Q/B}$ calculation was revised for this group to balance the model. EwE models of the Irish Sea (Bentley *et al.*, 2018), West coast of Scotland (Serpetti *et al.*, 2017), and North Sea ICES key run (ICES, 2016) used a lower $\mathrm{Q/B}$ estimate of 15 yr^{-1} for cephalopods. Due to scarce empirical information available for cephalopod consumption rates in the North Sea, a $\mathrm{Q/B}$ value of 15 yr^{-1} was also used in the northern North Sea model.

The $\mathrm{P/B}$ for this group was found to be very high. A high $\mathrm{P/B}$ ratio increases the production of a species, and often creates high predation pressure on its prey species. In this model this high $\mathrm{P/B}$ had an impact on multiple prey species including Norway pout, herring, and small pelagic fish.

In the North Sea EwE model (Mackinson and Daskalov, 2007) the high predation mortality inflicted by squid was resolved by the construction of a fish larvae functional group to act as a fish prey group for invertebrates. In doing so, the North Sea model kept a low biomass of 0.06 t.km^{-2}, and the high productivity of 4.5 yr^{-1} (ICES, 2016). For the northern North Sea model a compromise was made by constraining P/B for this group to 2 yr^{-1} (similar to the P/B used for this group in Irish Sea EwE of 1.98 yr^{-1} (Bentley *et al.*, 2018)).

Table 36 *Diet proportions in the model for squid & octopus.*

	Pre-balanced	Balanced
Norway pout	0.036	-
Herring	0.022	0.015
Small pelagic fish	0.030	0.020
Sandeels	-	0.010
Turbot	0.005	0.0001
Flatfish	0.083	0.020
Squid & octopus	0.005	0.005
Large zooplankton	0.213	0.227
Small zooplankton	0.356	0.397
Shrimp	0.020	0.030
Scallops	0.001	0.006
Epifauna	0.156	0.196
Infauna	0.021	0.022
Phytoplankton	0.052	0.052

To balance the model, certain prey portions in the diet of this group were reduced including: flatfish (by 6.3%), Norway pout (3.6%), small pelagic fish (1%), herring (0.7%) and turbot (0.5%) (Table 36) (further explanations see prey functional group descriptions). The remainder was split between epifauna (4.1%), small zooplankton (3.2%), large zooplankton (1.4%), shrimp (1%), scallops (0.5%) and infauna (0.1). Sandeels were added to the diet (at 1%) to include all known trophic interactions. These changes in combination with the new P/B and Q/B ratios and the adoption of an EE of 0.95 balanced the group with an estimated biomass of 1.264 t.km^{-2} and a P/Q of 0.133 yr^{-1}.

1.4.4.2 FG31: Gelatinous zooplankton

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The gelatinous zooplankton group includes moon jellyfish (*Aurelia aurita)*, lion's mane jellyfish *(Cyanea capillata)* and blue jellyfish (*Cyanea lamarckii)*. Due to limited data for these taxa, biomass for this group was taken from Eriksen *et al.* (2012) jellyfish biomass estimates in the Barents Sea of 0.78 t.km^{-2} (moon 67%, lion's mane 28%, blue 5%).

For the northern North Sea model we used Q/B estimates for each species from the North Sea EwE model (Mackinson and Daskalov, 2007) of 6.48 yr^{-1} for *A. aurita* and 6.12 yr^{-1} for *Cyanea spp.* giving an average Q/B of 1.79 yr^{-1} for this group, pro-rated by biomass. These estimates were based upon carbon food ration in the North Sea for *A. aurita* which ranged between 0.018–0.38 (average of 0.199) (g.C medusa^{-1} day^{-1}) and between 0.017–0.26 (average of 0.139) (g. C/medusa/day) for *Cyanea spp.* (Martinussen and Bamstedt, 1995). The P/B was estimated by the model as 0.537 yr^{-1}, using a P/Q of 0.30 yr^{-1}. This P/Q was used for gelatinous zooplankton in the Irish Sea (Lees and Mackinson, 2007; Bentley *et al.*, 2019) and North Sea (Mackinson and Daskalov, 2007) fitted EwE models.

b) Diet (pre-balanced model)

Diet for gelatinous zooplankton was taken from the North Sea EwE model (Mackinson and Daskalov, 2007) which was constructed using diets reported by Martinussen and Bamstedt (1995). The diet consisted of 90% zooplankton (45% large and 45% small zooplankton), 5% phytoplankton and 5% cannibalism.

d) Balancing changes

Gelatinous zooplankton was balanced in the model with an EE of 0.157. This low EE implied that the jellyfish group was under-utilized in the model. A recent review of over 30 years of EwE models by Lamb *et al.* (2019) revealed that although an increasing number of ecosystem models are including jellyfish, their EE is often at low levels, highlighting that jellyfish trophic interactions within ecosystems are possibly being under-valued (Lamb *et al.,* 2019). Sampling difficulties with gelatinous zooplankton often lead to them being under-sampled in diet studies, perhaps explaining the low predation mortality of gelatinous zooplankton in the model. Predators of gelatinous zooplankton in the model included cod, whiting, haddock, saithe, Norway pout, herring, small pelagic fish, squid & octopus, and cannibalism (Lynam *et al*., 2005; Oken *et al*., 2018). The proportion of gelatinous zooplankton in the diet of haddock was increased by 0.9% (juvenile haddock increased from 0.01% to 0.901%), and saithe by 3% (from 0.01% to 3.01%) (Oken *et al.*, 2018). In addition to these predators, some others were included in the model including sharks (at 1.2% of their diet), hake (at 0.4%), flatfish (at 2%), and squid & octopus (at 1%) based on Lynam et a. (2005). These changes resulted in an increase in the EE of gelatinous zooplankton to 0.957.

1.4.4.3 FG32: Edible crab

a) Biomass, P/B, Q/B, catch (pre-balanced model)

Biomass for edible crab was estimated as 0.125 t.km^{-2} using data from benthic surveys conducted in the North Sea during 1999 and 2000 (Zuhlke *et al.*, 2001; Callaway *et al.*, 2002). These surveys sampled a total of 511 stations across the North Sea. The numbers and weights of each species were recorded at each station allowing for the mean weight of each species, and therefore biomass density to be estimated at each station. Area average biomass was obtained based on arithmetic mean across all stations for the North Sea. This method assumes abundance and distribution for edible crab to be the same across the whole North Sea area.

The $\mathrm{P/B}$ ratio for edible crab was estimated to be 1.25 yr^{-1}, using an empirical model for the $\mathrm{P/B}$ of marine benthos (Tumbiolo and Downing, 1994) (Equation 11). P was calculated using a $\mathrm{W_m}$ of 150 g with a dry weight to wet weight ratio of 1:26 (Robinson *et al.*, 2010), surface temperature 9.6°C (Rayner *et al.*, 2003), and average shelf depth of 150m. The $\mathrm{Q/B}$ was estimated by the model as 8.302 yr^{-1}, using a $\mathrm{P/Q}$ of 0.15 yr^{-1}. Landings for edible crab were 1,586 t in 1991 (ICES, 2019k) giving an area-based estimate of 0.006 t.km^{-2}. Discards were estimated as 264 t (ICES, 2019k) for 1991, giving area-based estimate of 0.001 t.km^{-2}.

b) Diet (pre-balanced model)

Table 37 *Diet proportions in the model for edible crab.*

	Pre-balanced	Balanced
Norway lobster	0.020	0.020
Shrimp	0.001	0.001
Crabs & lobsters	0.001	0.001
Epifauna	0.355	0.355
Infauna	0.394	0.394
Detritus	0.100	0.198
Discards	0.128	0.030
Seaweed	-	0.010

Edible crab forage on a range of benthos including bivalves, polychaetes and crustaceans, as well as being important scavengers of discarded fish (Sherley *et al.*, 2020). For the diet of edible crab in the model, proportions were taken from the North Sea EwE model (Mackinson and Daskalov, 2007) of 39.4% infauna, 35.5% epifauna, 12.8% discards, 10% detritus, 2% Norway lobster, 0.1% shrimp and 0.1% crabs & lobsters (Table 37).

d) Balancing changes

Edible crab was unbalanced in the initial model with an EE of 1.177. To balance the model the proportion of edible crab in the diet of its predator, juvenile haddock, was lowered by 1.4% (from 4.5 to 3.1%). To include all known predators of edible crab in the model they were added to the diet of common ling (1%), and seals (0.1%) and the proportion of edible crab in the diet of sharks was increased by 0.4% (Hammond *et al.*, 1994; Ellis *et al.*, 1996). The discard functional group was unbalanced in the initial model. To balance discards the diet of edible crab was altered by lowering the proportion of discards in the diet by 9.8%, the remainder added to general detritus. Seaweed was added as 1% of the diet by reducing the Norway lobster. With these changes the edible crab group was balanced in the model with an EE of 0.899.

1.4.4.4 FG33: Velvet crab

a) Biomass, P/B, Q/B, catch (pre-balanced model)

Velvet crab are an important commercial catch in the northern North Sea, and included as a separate functional group in the model. Biomass for velvet crab was estimated using the same survey data as used for FG 32, edible crab (Zuhlke *et al.*, 2001; Callaway *et al.*, 2002). Area average biomass was obtained based on arithmetic mean across all stations for the North Sea, it was assumed that abundance and distribution for velvet crab was the same across the whole North Sea area. For velvet crab the total biomass in the northern North Sea was estimated at 359 t giving 0.001 t.km^{-2} (Table 35). The $\mathrm{P/B}$ ratio for velvet crab was estimated to be 1.58 yr^{-1}. This was calculated using Equation **11** with a $\mathrm{W_m}$ of 80 g. (Robinson *et al.*, 2010) with a dry weight to wet weight ratio of 1:24, surface temperature of 9.6°C (Rayner *et al.*, 2003), and average shelf depth of 150m. The $\mathrm{Q/B}$ was taken from the North Sea EwE model large crab group of which velvet crab is a component species as 5.64 yr^{-1} (Mackinson and Daskalov, 2007).

Landings for velvet crab in 1991 were reported as 237 t (ICES, 2019k), giving an area-based estimate of 0.0009 $t.km^{-2}$. Predators of velvet crabs in the North Sea include squid & octopus, seabirds, cod, skates & rays (thornback ray, cuckoo ray, shagreen ray, spotted ray), sharks (spurdog, smooth hound, starry smooth hound), haddock, whiting, flatfish (megrim), saithe and large demersal fish (scaldfish, red, grey and tub gurnards) (Pinnegar, 2014).

b) Diet (pre-balanced model)

The diet for velvet crabs was taken from Norman & Jones (1992) and include 70.4% seaweed (consisting of brown, green, red algae), 10.4% epifauna (bivalves, gastropods, echinoderms), 9.4% detritus, 6.7% crabs & lobsters (unidentified crustaceans), and 3.1% infauna (polychaetes).

d) Balancing changes

Velvet crab was balanced in the model with an EE of 0.829 and $\mathrm{P/Q}$ of 0.28 yr^{-1}. The estimated $\mathrm{Q/B}$ for this species was erroneously calculated using a formula for fish, and the $\mathrm{P/Q}$ estimate was slightly too high in the model compared to other crustacean functional groups (edible crab and Norway lobster have a $\mathrm{P/Q}$ of 0.15 yr^{-1}). Therefore, a P/Q of 0.15 yr^{-1} was inserted into the model instead, which generated a new model estimate a new $\mathrm{Q/B}$ of 10.5 yr^{-1}.

The fishing mortality for velvet crab was high in the model at 0.9 yr^{-1}. This was due to the relatively low biomass estimate (0.001 $t.km^{-2}$) with the catch (0.0009 $t.km^{-2}$) being almost as high for this group in the model. As velvet crab is a relatively new fishery to Scotland estimating biomass using benthic survey data was currently the best option available. The landings for 1992 are reported to be much lower than the model year as 63 t for ICES area IVa (ICES, 2019k). Using these reported landings for 1992, the area-based estimate for catch is 0.0002 $t.km^{-2}$ with a fishing mortality of 0.2 yr^{-1}. This catch was therefore assumed to be more correct and included in the model giving an EE of 0.474. This did however indicate that the predation upon velvet crab was too low in the model. Therefore, velvet crab proportion in the diet of cod was raised to 0.1% (from 0.05%), with 0.1% removed from the crab & lobster group. Velvet crab in the diet of seabirds (high discard diet) was also raised to 0.1% (from 0.001%), with 0.1% removed from large zooplankton. A final increase of velvet crab proportion in the diet of sharks to 0.025% (from 0.0025%), removing 0.01% from the crabs & lobster group, gave an EE of 0.836 for this group in the balanced model.

1.4.4.5 FG34: Crabs & lobsters

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The crabs & lobsters group consists of flying crab (*Liocarcinus holsatus*), lyre crab (*Hyas coarctatus*), marbled swimming crab (*Liocarcinus marmoreus*), squat lobster (*Munida rugosa*), and Northern stone crab (*Lithodes maia*). Biomass for crabs & lobsters across the whole North Sea was estimated as 1.097 t.km^{-2}, using benthic surveys in the North Sea during 1999 and 2000 (Zuhlke *et al.*, 2001; Callaway *et al.*, 2002) (Table 35). This whole North Sea biomass estimate was used in the model. The $\mathrm{P/B}$ ratio for crabs & lobsters was estimated to be 2.14 yr^{-1}, using an empirical model for the $\mathrm{P/B}$ of marine benthos (Tumbiolo and Downing, 1994) (Equation **11**). This was calculated using Equation **11** with a $\mathrm{W_m}$ of 10 g. (Robinson *et al.*, 2010) with a dry weight to wet weight ratio of 1:26, surface temperature of 9.6°C (Rayner *et al.*, 2003), and average shelf depth of 150m. The $\mathrm{Q/B}$ was estimated by the model as 10.7 yr^{-1}, using a $\mathrm{P/Q}$ of 0.2 yr^{-1}.

b) Diet (pre-balanced model)

Crabs and lobsters forage mainly on a range of benthos including bivalves, polychaetes, crustaceans, and also exhibit cannibalism (Mackinson and Daskalov, 2007). Crabs and lobster species included in this group are also important scavengers of discarded fish and shellfish (Depestele *et al.*, 2019; Sherley *et al.*, 2020). For the diet of crabs & lobsters in this model, diet proportions from the large crab group in the North Sea EwE model were used (Mackinson and Daskalov, 2007) giving a diet of 39.4% infauna, 35.5% epifauna, 12.8% discards, 10% detritus, 2% Norway lobster, 1% shrimp, and 1% cannibalism (Table 38).

c) Balancing changes

Table 38 *Crab & lobster diet proportions used in northern North Sea EwE 1991.*

	Pre-balanced	Balanced
Epifauna	0.355	0.355
Infauna	0.394	0.395
Norway lobster	0.020	0.015
Shrimp	0.010	0.010
Crabs & lobsters	0.010	0.010
Seaweed	-	0.023
Scallops	-	0.0006
Discards	0.128	0.0015
Detritus	0.100	0.208

Crabs & lobsters were balanced in the model with an EE of 0.70. As seaweed is much more prevalent in the northern North Sea than in the south, and seaweed was not a specific functional group in the Mackinson and Daskalov (2007) model, it was added here at 2.3% of the diet, removing this amount from discards (12.8% down to 10.5%) (Table 38). To balance discards in the model, the proportion of discards reduced to 0.15%, with the difference transferred to detritus (Table 38). The proportion of Norway lobster was also reduced by 0.5%, with this amount added to detritus (now 20.8% of the diet). Scallops were added to the diet of crabs & lobsters at 0.06% (Paul, 1987; Barbeau and Scheibling, 1994).

1.4.4.6 FG35: Norway lobster

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The biomass of Norway lobster (*Nephrops norvegicus*) was estimated to be 0.450 t.km^{-2}. This was calculated from underwater TV surveys in 1993 (ICES, 2018d) for the Fladen Grounds (4,450 million individuals with an average weight of 25.38 g), and the Moray Firth (345 million individuals with an average weight of 17.34) (Table 32). The P/B was estimated as 1.13 yr^{-1}, using an empirical model for the P/B of benthos (Tumbiolo and Downing, 1994) (Equation **11**). This was calculated using Equation 11 with a Wm of 250 g. (Robinson *et al.*, 2010) with a dry weight to wet weight ratio of 1:26, surface temperature of 9.6°C (Rayner *et al.*, 2003), and average shelf depth of 150m. The Q/B ratio was estimated by the model as 5.65 yr^{-1}, using a P/Q of 0.2 yr^{-1}. The same P/Q estimate was used in North Sea EwE model (Mackinson and Daskalov, 2007). Landings of Norway lobster were reported as 5,301 t in 1991, giving an area-based estimate of 0.02 t.km^{-2}. Reported discards of Norway lobster were 214 t, giving an area-based estimate of 0.001 t.km^{-2} for discards in the model.

b) Diet (pre-balanced model)

Norway lobster diet was taken from Cristo & Cartes (1998) as infauna (42%), epifauna (35%), phytoplankton (15%), detritus (5%)., squid (1%), shrimp (1%), and discards (1%) (Table 39).

c) Balancing changes

Norway lobster was unbalanced in the model with an EE of 1.076. To balance the model a P/Q estimate for this group of 0.15 yr^{-1} (Christensen, 1995) was used, in order to generate a model estimated Q/B of 7.53 yr^{-1}. This balanced the group giving an EE of 0.924. In addition, Norway lobster in the diet of edible crab and the crabs & lobster group was lowered by 1% and 0.5% respectively further lowering the EE for Norway lobster to 0.793. Norway lobster in the diet of juvenile and adult cod was increased by 0.2% and 3.3%, respectively and a new predator of sharks was added with 0.1% of diet attributed to Norway lobster (see predator group description for more information). To balance discards in the model the proportion of discards in the diet of Norway lobster was reduced from 1% to 0.1% with the remaining 0.9% added to infauna (Table 39). With these changes the Norway lobster functional group was balanced in the model with an EE of 0.835.

Table 39 *Norway lobster diet proportions used in northern North Sea EwE 1991.*

	Pre-balanced	Balanced
Shrimp	0.01	0.01
Squid	0.01	0.01
Epifauna	0.35	0.35
Infauna	0.42	0.429
Discards	0.01	0.001
Detritus	0.05	0.05
Phytoplankton	0.15	0.15

1.4.4.7 FG36: Shrimp

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The shrimp group in the model contains *Pandalus* spp. (*P. montagui, nouveli and borealis*) and *Crangon spp.* (*C. crangon and allmani*). Biomass for this group was estimated as 0.093 t.km^{-2} using biomass estimates for *Pandalus* shrimp from ICES (2006), and Crangon estimates from Tulp *et al.* (2016). Pandalus shrimp biomass in 1991 was estimated to be 18821 t (ICES, 2006). This gave an area-based biomass of 0.071 t.km^{-2} for *Pandalus* shrimp in the model. (An even distribution across the stock area of 265,085 km; northern North Sea and Skagerrak was assumed) (ICES, 2006)). *Crangon* shrimp biomass estimates for 1991 of 5,810 t was estimated which gave an area-based biomass estimate of 0.022 t.km^{-2} (survey area 264,091 km^{2}) (Tulp *et al.*, 2016). The P/B ratio for shrimp was calculated using Equation 8 as 3.30 yr^{-1}, with a F for shrimp of 0.140 yr^{-1} (Equation 9), plus a group M of 3.16 yr^{-1} (*Crangon* M 3.6 yr^{-1} (Oh *et al.*, 2001) and *Pandalus* M of 3.02 yr^{-1} (ICES, 2006) pro-rated by biomass). The Q/B ratio was estimated by the model as 22 yr^{-1}, using a P/Q of 0.15 yr^{-1}. Reported landings for this group were 3,444 t (ICES, 2019k) in 1991, giving an area-based estimate of 0.013 t.km^{-2}.

b) Diet (pre-balanced model)

Table 40 *Diet proportions in the model for shrimp.*

	Pre-balanced	Balanced
Shrimp	0.010	0.010
Small zooplankton	0.500	0.500
Large zooplankton	0.090	0.090
Epifauna	0.150	0.155
Detritus	0.200	0.240
Discards	0.050	0.005

Shrimp diet was taken from diet studies of *Pandalus borealis* (Shumway *et al.*, 1985; Hopkins *et al.*, 1993) to include proportions of small (50%) and large (9%) zooplankton, detritus (20%), epifauna (15%), discards (5%), and cannibalism (1%) (Oh *et al.*, 2001) in the model (Table 40).

c) Balancing changes

The shrimp group was unbalanced in the model with an EE of 2.178. This group was unbalanced due to their predation mortality being too high for the available biomass in the model. Therefore, using a biomass estimate of 0.093 t.km^{-2} for this group was insufficient for the consumption needs of its predators. The initial biomass estimate of *Pandalus* shrimp from WGPAND 2006 was calculated with an assumed catch efficiency of 1.0 – which might be too high. Therefore, to balance the model the shrimp group biomass was estimated by the model using an EE of 0.9. This gave a new higher shrimp biomass estimate of 0.735 t.km^{-2} in the balanced model. Shrimp diet was also adjusted in order to balance the discards functional group in the model by lowering the proportion of discards from to 0.5% and with 4% re-assigned to detritus, and 0.5% to epifauna (Table 40).

1.4.4.8 FG37: Scallops

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The scallop group is a single species functional group containing great scallops (*Pecten maximus)*. The biomass for scallops in 1991 was estimated as 0.16 t.km^{-2} by combining the spawning stock biomass estimates of 8,976 t for North East Scotland, 3,017 t for Orkney, and 3,090 t for Shetland (Dobby *et al.*, 2017), divided by the total stock area of 93,912 km^{2} (Cappel *et al.*, 2018). It is acknowledged that this will be an under-estimate of the total stock biomass because it does not include immature scallops.

Using an empirical model for the P/B of marine benthos (Tumbiolo and Downing, 1994)(Equation **11**) with an individual weight for great scallops of 220 grams (average weight from NS IBTS survey), sea surface temperature of 9.6 °C and an average depth of 140 m, P/B of scallops was estimated to be 0.14 yr^{-1}. The Q/B was estimated by the model using a P/Q of 0.15. Landings for scallops were calculated as 0.004 t.km^{-2} (ICES, 2019k).

b) Diet (pre-balanced model)

The diet for scallops was taken from the North Sea EwE model (Mackinson and Daskalov, 2007) as 35% detritus, 35% phytoplankton, 25% small zooplankton and 5% detritus.

c) Balancing changes

The scallop group was balanced in the model with an EE of 0.53, and a model estimated Q/B of 7.60 yr^{-1}. Scallops were increased in the diet of octopus by 0.5% (from 0.1 to 0.6%), decreasing their consumption of epifauna. To balance the discards functional group, the proportion of discards in the diet of scallop was reduced by 4% (from 5% to 1%), with the remainder added to detritus (increase from 35% to 39%). With these changes EE for scallops was 0.69 in the balanced model.

1.4.4.9 FG38: Epifauna

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The key epifauna species included within this group are brittle stars, common starfish, common whelk, queen scallops, mussels, hermit crabs, sea urchins, chitons, sea snails, sea potatoes and oysters (Table 35). Species presence for epifauna in the northern North Sea was determined using NS IBTS data for 1991 (ICES, 2019j) and surveys of epibenthic distribution in the North Sea (Callaway *et al.*, 2002). Biomass estimates for these species were extracted from Mackinson and Daskalov (2007) giving an epifaunal group biomass of 21.77 t.km^{-2} (Table 34). The P/B was estimated to be 1.01 yr^{-1}, using the empirical model for the P/B of marine benthos (Equation **11**), and the Q/B was estimated by the model using a P/Q 0.2 yr^{-1}, which was also the estimate used in the North

Sea EwE model (Mackinson and Daskalov, 2007). In 1991 the landings reported for this group were 5,023 t (ICES, 2019k), giving an area-based estimate of 0.019 $t.km^{-2}$.

b) Diet (pre-balanced model)

The diet for epifauna was taken from the North Sea EwE model (Mackinson and Daskalov 2007) macrobenthos groups due to a lack of more recent dietary information in the literature for these species. The diet for epifauna in the model was 35% infauna, 20% seaweed, 15% phytoplankton, 15% detritus, 9.5% small zooplankton, 5% discards, 0.5% cannibalism (Table 41).

c) Balancing changes

Epifauna in the model was balanced with an EE of 0.597 and a low model estimated $\mathrm{Q/B}$ of 5.050 yr^{-1}. Given the fact that the catchability of epifauna in benthic surveys are not well known, the biomass estimate was likely to be inaccurate with a high level of associated uncertainty. Therefore, an EE of 0.9 was set and the model allowed to estimate a biomass of 1.429 $t.km^{-2}$. These biomass values were considered to be more reasonable biomass estimates for the northern North Sea epibenthos (Reiss *et al.*, 2011). The estimated $\mathrm{P/B}$ for this group was low in comparison to other EwE models. Therefore a $\mathrm{P/B}$ estimate of 20 yr^{-1} was used, as also in the West Coast of Scotland models (Haggan and Pitcher, 2005; Serpetti *et al.*, 2017) and the North Sea 2001 model (Mackinson, 2001). The $\mathrm{Q/B}$ was then re-estimated by the model as 80 yr^{-1}, using a $\mathrm{P/Q}$ of 0.25 yr^{-1}.

Table 41 *Diet proportions in the model for epifauna.*

	Pre-balanced	Balanced
Small zooplankton	0.095	0.095
Epifauna	0.005	0.005
Infauna	0.35	0.35
Seaweed	0.20	0.10
Phytoplankton	0.15	0.25
Detritus	0.15	0.199
Discards	0.05	0.001

Changes to the diet of this group included removing 10% from seaweed and re-allocating it to phytoplankton (Table 41). This may be justified as toxins in kelp mean that the source of carbon consumed by epibenthos is more likely settling phytoplankton which reach the seabed (Norderhaug and Christie, 2009). To balance the discards functional group, 4.9% of epifauna diet was moved from discards to detritus (Table 41). The main predators of epifauna were crustaceans, flatfish, gadoids, large and small demersal fish. To balance the model the proportion of epifauna was raised in the diet of large (29%) and small (27%) demersal fish and sharks (16%) (for descriptions of why epifauna proportions were raised in the diets of predators see skates & rays, cod, whiting, saithe, ling, Norway pout, other pelagic fish, other flatfish, squid & octopus and shrimp group descriptions). The epifauna proportion was lowered in the diets of sandeels by 11.5% (from 19.2 to 7.7%) and cannibalism was lowered by 4.9% from 5 to 0.1%). This balanced the model with an epifaunal biomass estimated at 1.43 $t.km^{-2}$.

1.4.4.10 FG39: Infauna

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The key species included in this group are polychaetes, razor clams (*Ensis spp.*) and other burrowing bivalves (*Gari fervensis*, *Cochlodesma praetenue*, *Myrtea spinifera*, *Phaxas pellucidus, Thyasira spp.*). Infauna species are even more likely to be under-represented in survey and catch data than epifauna, as they spend a large proportion of their time burrowing underground and evading capture. They also evade capture due to their small size and many of these species only being found in intertidal zones (Kunitzer *et al.*, 1992). Biomass estimates for these species were extracted from Mackinson and Daskalov (2007) giving an infauna group biomass of 20.51 t.km^{-2} (Table 35). A $\mathrm{P/B}$ of 0.699 yr^{-1} was estimated using an empirical model for the $\mathrm{P/B}$ of marine benthos (Equation **11**), and the $\mathrm{Q/B}$ was estimated by the model using a $\mathrm{P/Q}$ of 0.2 yr^{-1}. In 1991, the landings reported for species in this group were 53 t giving an area-based estimate of 0.0002 t.km^{-2}.

b) Diet (pre-balanced model)

The diet for infauna was taken from the North Sea EwE model (Mackinson and Daskalov, 2007) macrobenthos groups due to a lack of more recent dietary information in the literature for these species. The diet was 60% detritus, 25% phytoplankton, 10% discards and 5% infauna/cannibalism (Table 42).

c) Balancing changes

Infauna was unbalanced in the model with an EE of 4.065. As the northern North Sea is less productive than the southern North Sea, an infauna biomass of 20.51 t.km^{-2} seems too high. But even with that value the model was unbalanced which pointed to problems with other parameters for this group. The estimated $\mathrm{P/B}$ of 1.01 yr^{-1} was also very different to the values used for other EwE models. The $\mathrm{P/B}$ was therefore increased to 20 yr^{-1}, similar to that estimated for the North Sea 2001 EwE model (Mackinson, 2001) the West Coast of Scotland (Haggan and Pitcher, 2005; Serpetti *et al.*, 2017), and. In keeping with the methods used in those models the $\mathrm{P/Q}$ for infauna was raised from 0.2 to 0.25 per yr^{-1}. This change increased the $\mathrm{Q/B}$ from 3.495 yr^{-1} to 80 yr^{-1} and decreased the biomass from 20.51 t.km^{-2} to 3.24 t.km^{-2} (with an input EE of 0.9). These values were considered to be more reasonable estimates for the benthic infauna.

Table 42 *Diet proportions in the model for infauna.*

	Pre-balanced	Balanced
Infauna	0.05	0.001
Phytoplankton	0.25	0.298
Detritus	0.60	0.70
Discards	0.10	0.001

The diet of the infauna was changed to 70% detritus, with discards lowered by 9.9% (Table 42). Cannibalism was also reduced by 4.9% and this amount added to phytoplankton (Table 42). Infauna was raised in the diet of small demersal fish by 17.5% , sharks by 9.7%, juvenile haddock by 2.1%, large demersal fish raised by 2.6%, and Norway lobster by 0.9%. After these changes the infauna was balanced with an estimated biomass of 3.001 t.km^{-2}, using an EE of 0.9.

1.4.5 Zooplankton

Zooplankton in the northern North Sea were split into two functional groups: large (> 2mm body length) and small (<=2 mm). The species and relative biomass trends (1991-2017) included in these groups were gathered from Continuous plankton Recorder (CPR) surveys provided by the Marine Biological Association Sir Alister Hardy Foundation for Ocean Science (MBA SAHFOS; P. Helaouët, pers. comm., 2017). Compared with the southern North Sea, CPR coverage of the northern North Sea in 1991 was quite limited (Figure 20). This limited coverage did not facilitate the estimation of total biomass (t.km^{-2}).

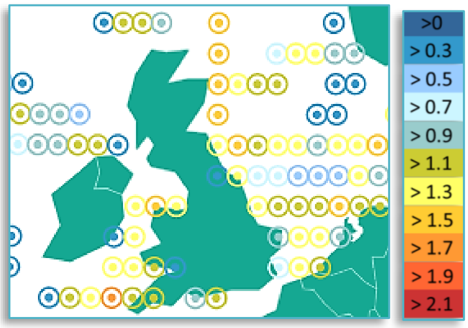


Figure 20 *Representation of the CPR data based on 1° by 1° squares for CPR sampling effort (number of samples in 1991) (Java Script map by amCharts cprsurvey.org).*

The zooplankton species list associated with this dataset verified species presence within the model area and designated species and life stages by size into 'large' and 'small' zooplankton (as explained within their functional group descriptions). This designation was used in our estimation of predator diets, and zooplankton group input parameters. The CPR dataset also provided a relative biomass trend for both phytoplankton, and large/small zooplankton groups which will be used later during model fitting with the Ecosim module.

1.4.5.1 FG29: Large zooplankton

a) Biomass, P/B, Q/B, catch (pre-balanced model)

Large zooplankton includes species and life stages above 2 mm in length. These include the fully-grown life stages of *Calanus finmarchicus* and *C. glacialis*, and the three dominant krill species within the North Sea: *Thysanoessa inermis*, *T. raschi* and *Meganyctiphanes norvegica*. The biomass and P/B ratio of large zooplankton was assumed to be similar to that used in the North Sea EwE model (Mackinson and Daskalov, 2007) carnivorous zooplankton group, 3.345 t.km^{-2} and 4 yr^{-1} respectively. The Q/B ratio was estimated by the model as 12.5 yr^{-1}, using a P/Q of 0.32 yr^{-1} (Mackinson and Daskalov, 2007).

b) Diet (pre-balanced model)

The diet of large zooplankton is assumed to include 73.5% small zooplankton, 14.3% phytoplankton, 7.2% large zooplankton, and 5% detritus (Mackinson and Daskalov, 2007).

c) Balancing changes

Large zooplankton was unbalanced in the model with an EE of 2.744. Using the biomass estimate from the North Sea EwE carnivorous zooplankton group neglects the planktivorous and omnivorous species of zooplankton above 2 mm in length. An example was *Euphausiid* krill species included within northern North Sea specific CPR data (MBA SAHFOS, 2017). Therefore, the biomass for this group is an underestimation. To balance this group, the biomass was therefore estimated by the model as 15.633 $t.km^{-2}$, using an EE of 0.9. The diet of this group was also modified to include increased proportions of phytoplankton (52.8%) and decreased proportions of small zooplankton (30%), detritus (12.2%) and cannibalism (5%).

1.4.5.2 FG30: Small zooplankton

a) Biomass, P/B, Q/B, catch (pre-balanced model)

Even the larger zooplankton have early life stages which would be smaller than 2 mm in length. The small zooplankton group therefore includes species such as *Calanus finmarchicus* but also smaller species such as *Psedocalanus elongates, Paracalanus parvus, Microcalanus pusillus, Acatia spp.* and *Temora longicornis* (Krause and Trahms, 1982). In the northern North Sea, production is dominated by *Calanus finmarchicus* (Williams and Lindley, 1980), although its dominance has gradually declined probably due to climate effects. The biomass, $\mathrm{P/B}$ and $\mathrm{Q/B}$ of small zooplankton was assumed to be similar to that of the North Sea EwE (Mackinson and Daskalov, 2007) herbivorous and omnivorous zooplankton groups at 16 $t.km^{-2}$, 9.167 yr^{-1} and 30 yr^{-1} respectively.

b) Diet (pre-balanced model)

The diet of small zooplankton is assumed to include 90% phytoplankton, 5% detritus, and 5% small zooplankton (Mackinson and Daskalov, 2007).

c) Balancing changes

This group was balanced in the model with an EE of 0.683 and a $\mathrm{P/Q}$ of 0.306 yr^{-1}. Minke whale, hake, and small demersal fish were added as additional predators of small zooplankton. Also, the proportion of small zooplankton in the diet of seabirds, whiting, haddock, Norway pout, small and other pelagic fish, flatfish and squid & octopus groups were increased (for full description of changes to diet refer to predator group descriptions) whilst the proportion of small zooplankton in the diet of large zooplankton was decreased. With these changes the EE was 0.934 and the biomass was 16 $t.km^{-2}$ in the balanced model.

1.4.6 Primary Producers

1.4.6.1 FG40: Seaweed

a) Biomass, P/B, Q/B, catch (pre-balanced model)

The seaweed group in the model contains kelp (*Laminaria hyperborea*, *Saccharina latissima*, *Saccorhiza polyschides*, *Laminaria digitate*), bladder wrack (*Fucus vesiculosus*), toothed wrack (*Fucus serratus*), and knotted wrack (*Ascophyllum nodosum*). Burrows *et al.,* (2018) estimated a combined biomass of 18.9 million t of kelp and seaweed for North East Scotland, Orkney and Shetland Islands. This estimate was added to a biomass estimate for that part of the Norwegian coastline included within the model area of 18.9 million t (Gundersen *et al.*, 2011). Combined, these estimates give a group biomass estimate of 26.8 million t, or 101.5 t.km^{-2}. A $\mathrm{P/B}$ of 1 was used for this group as this is likely to represent the biological turnover rate of seaweed in the North East Atlantic (M. Burrows, pers. comm.).

Velvet crab consume the highest proportion of seaweed in the model, reflecting the importance of coastal seaweeds in their diet (Tallack, 2002). Sea urchins and kelp in the Northeast Atlantic (especially towards Norway and Russia) also have an important trophic relationship (Norderhaug and Christie, 2009). This relationship cycles from top-down sea urchin grazing pressure to bottom-up kelp re-vegetation, depending upon their relative abundances (Norderhaug and Christie, 2009). This relationship was represented in the model by the main predation upon kelp being from the urchins within the epifauna functional group (20% of their diet consists of kelp).

b) Balancing changes

Seaweed was balanced in the model with an EE of 0.217, although this is high in comparison to other North East Atlantic EwE models (Serpetti *et al.*, 2017; Bentley *et al.*, 2018). Therefore, the consumption of kelp by sea urchins in the epifauna group was reduced and the difference moved to detritus (Table 41) to reflect their probable ingestion of detrital kelp rather than the toxin heavy live fronds. Seaweed in the proportion of velvet crab diet was increased slightly (by 0.4%), and new predators of seaweed were added including edible crab (Table 37), and crabs & lobsters (Table 38). With these changes the EE of seaweed in the balanced model is 0.127. This estimate is closer to the EE for seaweed groups in the Irish Sea (EE 0.169) (Bentley *et al.*, 2018), and West Coast of Scotland (EE 0.037) (Serpetti *et al.*, 2017) EwE models.

1.4.6.2 FG41: Phytoplankton

For phytoplankton the biomass (7.5 t.km^{-2}) and P/B (268 yr^{-1}) estimates for the North Sea EwE models were used (Mackinson and Daskalov, 2007; ICES, 2016). During balancing, no changes were made to the phytoplankton functional group estimates.

1.4.7 Detritus

The detritus in the model includes two functional groups: fisheries discards and other detritus.

1.4.7.1 FG42: Discards

The discard group consists of the total fisheries discards for all the functional groups in the model. We estimated the biomass of this group using area-based estimates for each functional group from ICES stock assessments, STECF ratios for 1991 landings, and discard rates estimated using the whole North Sea for 1991 (Heath and Cook, 2015; Cook and Heath, 2018). The total discards biomass was estimated as 0.56 t.km^{-2}. The total discards for the fishing fleets in the model also total to this estimate of 0.56 t.km^{-2}. Sherley (2020) estimated discards across the whole North Sea were approx. 510,000 t in 1991 or approx. 0.89 t.km^{-2}. The discard estimate used in the model is 37% lower than the total North Sea discard estimate for 1991 (Sherley *et al.*, 2020). The consumers of discards in the model include seabirds (high and low discard diet), turbot, edible crab, crabs & lobsters, Norway lobster, shrimp, scallops, epifauna, and infauna groups (Table 43).

1.4.7.2 FG43: Detritus

The detritus group includes both dissolved- (DOM) and particulate organic matter (POM). Excreted and unassimilated food, dead organisms (other than fisheries discards) flow into this group in the model. The value of the biomass of this group is nominal and does not impact the overall balance of the model. Total combined POM and DOM were taken from Christensen (1995) at 50 t.km^{-2} (Christensen, 1995; Mackinson and Daskalov, 2007). The proportions of discards and detritus in the diets of their predator groups in the model are summarised in Table 43.

1.4.7.3 FG42 & FG43 Balancing changes to detrital groups

The discards group was unbalanced in the initial model with an EE of 26.641 but detritus was balanced with an EE of 0.046. Due to the high EE for discards, the methods for estimating biomass for this group were revisited. To balance the model we adopted the North Sea EwE model (Mackinson and Daskalov, 2007) biomass estimate for discards of 50 t.km^{-2}, with the discard fate directed to the discards functional group. Using this method the total discards of the fishing fleets in the model remained the same as their original estimate of 0.56 t.km^{-2}.

Table 43 *Proportions of discards and detritus in predator diets in the pre-balanced and balanced model.*

Prey	Discard diet proportion		Detritus diet proportion	
	Pre-balanced	Balanced	Pre-balanced	Balanced
Seals	-	0.009	-	-
Seabirds (HDD)	0.458	0.400	-	-
Seabirds (LDD)	0.002	0.002	-	-

Skates & Rays	0	0.010	-	-
Saithe	-	-	-	0.008
Turbot	0.079	0.079	0	0
Flatfish	-	0.001	0	0.075
Lrg. zooplankton	-	-	0.050	0.122
Sm. zooplankton	-	-	0.050	0.050
Edible crab	0.128	0.030	0.100	0.198
Velvet crab	-	-	0.094	0.094
Crabs & lobsters	0.128	0.0015	0.100	0.208
Nephrops	0.010	0.001	0.050	0.050
Shrimp	0.050	0.005	0.200	0.240
Scallops	0.050	0.010	0.350	0.390
Epifauna	0.050	0.001	0.150	0.199
Infauna	0.100	0.001	0.600	0.6981

Therefore, in the balanced model the same biomass estimates for detrital groups as used in the North Sea EwE model are reflected, (25 t.km^{-2} for POM and 25 t.km^{-2} for DOM, gives 50 t.km^{-2} for all detritus) and discards of 50 t.km^{-2} (FG42: Discards). With these changes the total biomass of the detrital groups in the model totals 100 t.km^{-2} similar to existing EwE models for the North Sea (Mackinson and Daskalov, 2007) and West coast of Scotland (Serpetti *et al.*, 2017). With these changes the discards group was balanced in the model with an EE of 0.913, with the detritus group having an EE of 0.132.

Section 2: Defining fleets and assigning landings & discards.

2.1 Allocation of fleets by gear: Landings

The Scientific, Technical and Economic Committee for Fisheries (STECF) provides fleet, species, and ICES rectangle specific landings and area specific discards from 2003-2017 (https://stecf.jrc.ec.europa.eu/dd/effort/graphs-annex) (STECF, 2018). Because there are no data for 1991, the ratio of landings by functional group for the northern North Sea in 2003 was applied to the landings by functional group and gear type in 1991 to derive landing proportions by fleet for input into the model (Figure 21). Using this method assumes that the landing patterns by gear type did not change during the period 1991-2003. Of course, this assumption might not be true but is necessitated by the lack of reliable landings data by fleet for the early 1990s. The structure of fleets in the northern North Sea Ecopath model and the allocation of gear types was simplified into seven fleets: beam trawl (BT1, BT2) otter trawl (TR3, TR1), *Nephrops* trawl (TR2), pelagic (PEL_TRAWL, PEL_SEINE), dredge (DREDGE), gill nets (and trammel nets, GN1, GT1), and pots (POTS) (STECF, 2018).

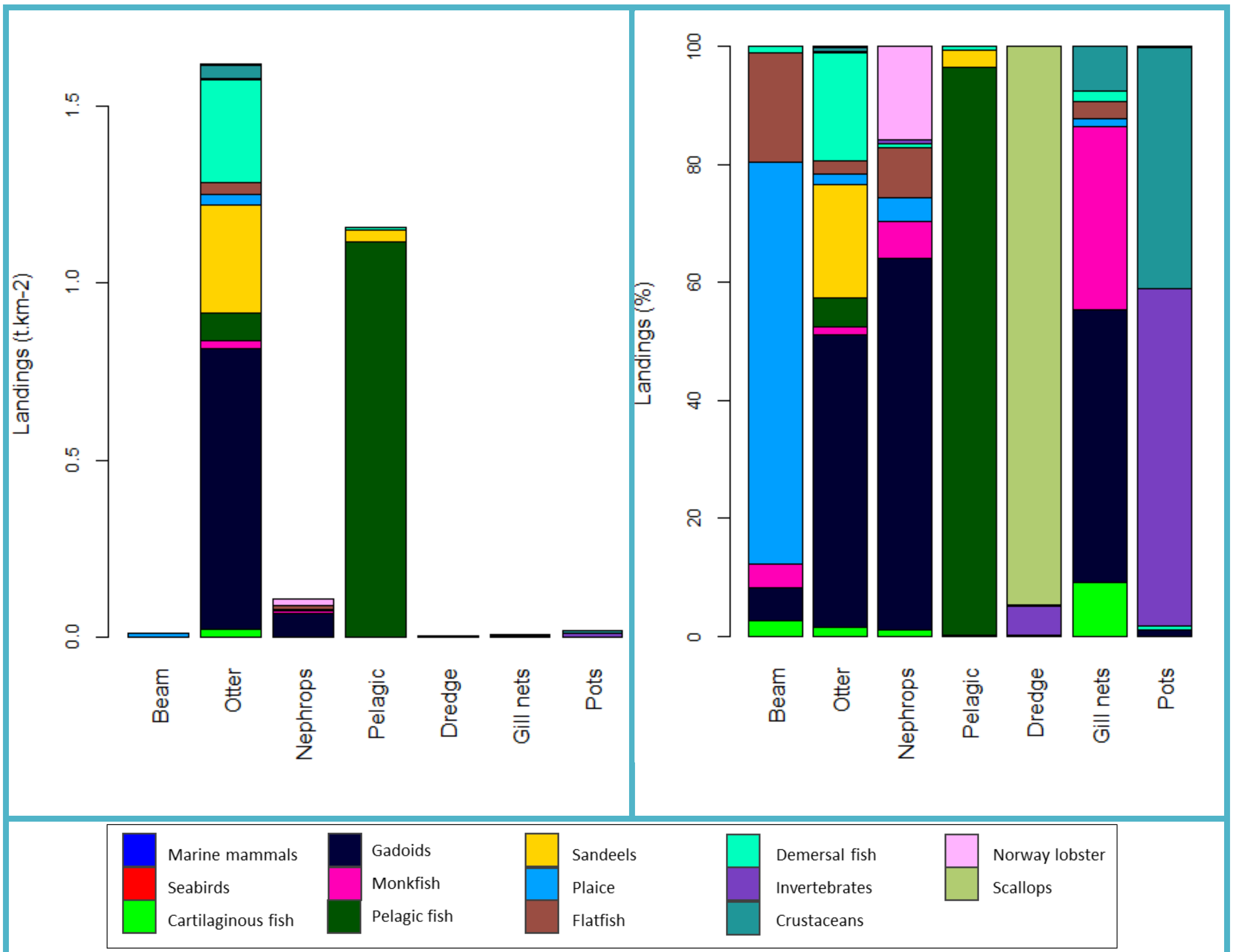


Figure 21 *Landings by Ecopath fleet 1991 in the model area. Functional groups combined into: Marine mammals (minke whales, toothed whales, seals), seabirds (seabirds with low & high discard diets), cartilaginous fish (sharks, skates & rays), gadoids (cod, haddock, whiting, saithe, hake, ling), monkfish, pelagic fish (herring, small & other pelagic fish), sandeels, plaice, flatfish(turbot, other flatfish), demersal fish (Norway pout, small & large demersal fish), invertebrates (squid & octopus, small, large & gelatinous zooplankton, epifauna, infauna), crustaceans (edible crab, velvet crab, shrimp), Norway lobster, scallops.*

2.2 Allocation of fleets by gear: Discards

STECF discards by gear type are only available for the whole North Sea area between 2003 and 2017. Species specific discards for 2003 by gear type were allocated to the corresponding functional group in order to estimate discards in 1991. With no data available by area, and no data available before 2003, it was assumed that the discarding patterns were spatially constant and similar in 1991 to 2003. The ratio of discards by functional group for northern North Sea in 1991 was applied to the discards by functional group and gear type in 2003 to derive discard proportions by fleet for input into the model (Figure 22).

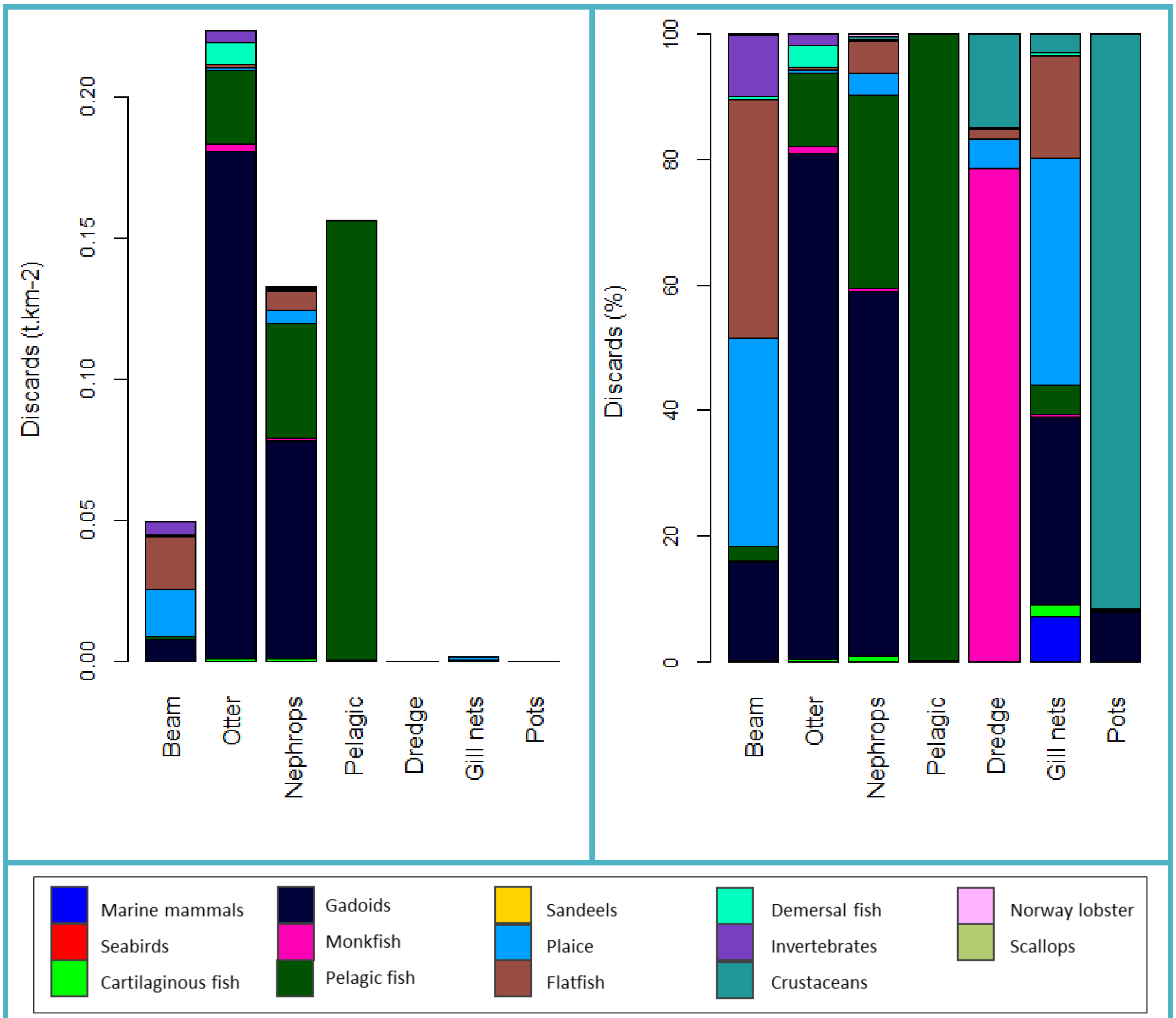


Figure 22 *Discards by Ecopath fleet 1991 in the model area. Functional groups combined the same as* Figure 21 *using the same colour palette.*

Table 44 *Basic estimates from the balanced model of the northern North Sea. Numbers in blue have been estimated by Ecopath.*

	Functional group	TL	Biomass ($t.km^{-2}$)	P/B (yr^{-1})	QB (yr^{-1})	EE	P/Q
1	Minke whale	3.882	0.089	0.02	6.580	0.022	0.003
2	Toothed whales	4.637	0.026	0.02	14.777	0.107	0.001
3	Seals	4.717	0.021	0.06	14.393	0.027	0.004
4	Seabirds (high discard diet)	3.115	0.002	0.4	65.038	0.033	0.006
5	Seabirds (low discard diet)	4.239	0.003	0.4	67.865	0.020	0.006
6	Sharks	4.042	0.277	0.377	3.770	0.363	0.100
7	Skates & Rays	3.971	0.230	0.486	3.241	0.384	0.150
8	Atlantic cod (juv.)	3.914	0.246	1.732	7.641	0.766	0.227
9	Atlantic cod (adult)	4.155	0.160	0.776	2.927	0.934	0.265
10	Whiting (juv.)	3.999	0.097	1.606	11.29	0.915	0.142
11	Whiting (adult)	4.285	0.154	0.961	5.297	0.898	0.181
12	Haddock (juv.)	3.690	0.342	1.743	10.383	0.882	0.168
13	Haddock (adult)	3.859	0.197	0.77	4.107	0.851	0.187
14	Saithe	4.130	1.213	0.685	3.290	0.811	0.208
15	Hake	4.591	0.052	1.143	3.850	0.907	0.297
16	Common ling	4.324	0.064	0.967	3.248	0.952	0.298
17	Norway pout	3.296	1.566	1.481	7.407	0.927	0.200
18	Monkfish	4.599	0.084	0.539	2.476	0.912	0.218
19	Atlantic herring	3.372	2.600	1.311	6.553	0.983	0.200
20	Small pelagic fish	3.321	1.700	1.897	9.486	0.984	0.200
21	Other pelagic fish	3.669	2.554	0.539	4.832	0.900	0.112
22	Sandeels	3.047	2.800	2.127	8.506	0.983	0.250
23	European plaice	3.287	0.140	0.601	3.653	0.988	0.165
24	Turbot	3.531	0.024	0.801	3.947	0.984	0.203
25	Flatfish	3.484	1.519	0.717	4.333	0.900	0.165
26	Small demersal fish	3.358	0.809	1.012	6.747	0.900	0.150
27	Large demersal fish	4.074	0.316	0.452	3.622	0.893	0.125
28	Squid & Octopus	3.268	1.264	2.000	15.000	0.950	0.133
29	Large zooplankton	2.385	15.620	4.000	12.500	0.900	0.320
30	Small zooplankton	2.053	16.000	9.167	30.000	0.935	0.306
31	Gelatinous zooplankton	3.207	0.780	0.537	1.790	0.957	0.300
32	Edible crab	2.937	0.125	1.245	8.302	0.899	0.150
33	Velvet crab	2.313	0.001	1.580	10.533	0.836	0.150
34	Crabs & lobsters	2.947	1.097	2.140	10.700	0.909	0.200
35	Norway lobster	2.981	0.450	1.130	7.533	0.835	0.150
36	Shrimp	2.896	0.735	3.300	22.000	0.900	0.150
37	Scallops	2.263	0.161	1.140	7.600	0.690	0.150
38	Epifauna	2.458	1.429	20.000	80.000	0.900	0.250
39	Infauna	2.001	3.001	20.000	80.000	0.900	0.250
40	Seaweed	1.000	101.485	1.000		0.127	
41	Phytoplankton	1.000	7.500	286.00		0.297	
42	Discards	1.000	50.000	0.685		0.913	
43	Detritus	1.000	50.000	1.143		0.132	

Table 45 *Landings by fleet (t.km^{-2}) in the northern North Sea model.*

	FG	Beam	Otter	Nephrops	Pelagic	Dredge	Gill	Pots	Total
1	Minke whale	-	-	-	-	-	-	-	0
2	Toothed whales	-	-	-	-	-	-	-	0
3	Seals	-	-	-	-	-	-	-	0
4	Seabirds (HDD)	-	-	-	-	-	-	-	0
5	Seabirds (LDD)	-	-	-	-	-	-	-	0
6	Sharks	8.3x10-6	0.019	0.001	7.1x10-5	-	0.001	-	0.021
7	Skates & Rays	0.0003	0.005	0.0003	1.6x10-8	3.2x10-7	0.0001	-	0.005
8	Juv. cod	7.9x10-5	0.038	0.004	6.6x10-6	-	0.001	1.1x10-5	0.044
9	Adult cod	0.0002	0.076	0.008	1.3x10-5	-	0.002	2.1x10-5	0.087
10	Juv. Whiting	4.0x10-5	0.015	0.004	1.6x10-7	1.8x10-9	1.1x10-7	3.5x10-7	0.019
11	Adult Whiting	0.0001	0.039	0.011	4.2x10-7	4.7x10-9	2.7x10-7	9.0x10-7	0.050
12	Juv. Haddock	6.3x10-5	0.073	0.011	0.0001	-	7.3x10-6	4.4x10-6	0.084
13	Adult Haddock	6.7x10-5	0.078	0.011	0.0001	-	7.8x10-6	4.7x10-6	0.090
14	Saithe	5.1x10-5	0.393	0.014	0.0011	6.8x10-09	0.0005	0.0001	0.409
15	Hake	6.4x10-5	0.043	0.002	3.0x10-5	-	0.0005		0.046
16	Ling	6.2x10-5	0.034	0.002	1.6x10-6	-	0.0005	3.9x10-5	0.037
17	Norway pout	-	0.250	-	0.009	-	-	-	0.258
18	Monkfish	0.001	0.024	0.007	2.0x10-6	2.4x10-6	0.003	9.8x10-7	0.034
19	Herring	-	0.030	-	0.880	-	-	-	0.911
20	Sm. pelagic fish	-	0.017	-	0.001	-	-	-	0.018
21	Other pelagic fish	-	0.028	1.5x10-6	0.232	2.6x10-6	7.0x10-8	2.1x10-6	0.260
22	Sandeels	-	0.305	-	0.033	-	-	-	0.339
23	Plaice	0.009	0.031	0.004	5.1x10-8	1.1x10-06	0.0001	-	0.044
24	Turbot	0.002	0.006	0.001	2.0x10-7	-	0.0003	-	0.009
25	Other flatfish	0.001	0.029	0.008	2.3x10-6	4.1x10-7	1.4x10-5	7.8x10-7	0.037
26	Sm. demersal fish	7.9x10-5	-	-	-	-	-	-	0.000
27	Lrg.demersal fish	5.0x10-5	0.043	0.001	5.2x10-5	-	0.0002	0.0001	0.044
28	Squid & Octopus	-	0.002	0.001	-	-	-	-	0.002
29	Large zoo.	-	-	-	-	-	-	-	0
30	Small zoo.	-	-	-	-	-	-	-	0
31	Gel. zoo.	-	-	-	-	-	-	-	0
32	Edible crab	-	4.7x10-8	5.1x10-6	-	7.7x10-6	1.6x10-5	0.006	0.006
33	Velvet crab	-	1.0x10-9	1.6x10-7	-	2.4x10-7	5.0x10-7	0.000	0.000

34	Crabs & lobsters	-	4.6x10-6	5.2x10-6	-	-	0.001	0.001	0.002
35	Nephrops	6.9x10-6	0.003	0.017	1.5x10-7	-	-	2.7x10-5	0.020
36	Shrimp	-	0.013	0.0001	-	-	-	4.7x10-5	0.013
37	Scallops	4.4x10-6	9.6x10-7	4.3x10-7	-	0.004	-	-	0.004
38	Epifauna	-	-	8.3x10-5	-	-	-	0.011	0.011
39	Infauna	-	-	-	-	0.0002	-	4.0x10-6	0.000

Table 46 *Discards by fleet (t.km^{-2}) in the northern North Sea model.*

	FG	Beam	Otter	Nephrops	Pelagic	Dredge	Gill	Pots	Total
1	Minke whale	-	-	-	-	-	4.0x10-5	-	4.0x10-5
2	Toothed whales	-	-	-	5x10-7	-	5.6x10-5	-	5.7x10-5
3	Seals	-	-	-	-	-	3.4x10-5	-	3.4x10-5
4	Seabirds (HDD)	-	-	-	-	-	-	-	0
5	Seabirds (LDD)	-	-	-	-	-	-	-	0
6	Sharks	1.9x10-5	1.7x10-4	6.3x10-5	8.0x10-8	-	7.8x10-7	2.8x10-10	0.0003
7	Skates & Rays	0.0001	0.001	0.001	2.6x10-6	-	3.3x10-5		0.002
8	Juv. cod	0.002	0.015	0.006	6.9x10-6	-	0.0002	8.9x10-8	0.023
9	Adult cod	1.5x10-5	0.0002	6.0x10-5	6.8x10-8	-	1.7x10-06	8.7x10-10	0.0002
10	Juv. Whiting	0.001	0.001	0.003	1.6x10-5	-	6.1x10-5	1.3x10-9	0.006
11	Adult Whiting	0.005	0.003	0.013	6.0x10-5	-	0.0002	4.9x10-9	0.021
12	Juv. Haddock	0.0002	0.065	0.048	0.0001	-	2.8x10-5	7.9x10-8	0.114
13	Adult Haddock	2.0x10-6	0.001	0.001	1.29x10-6	-	3.5x10-7	9.9x10-10	0.001
14	Saithe	4.6x10-6	0.083	0.003	0.0002	-	4.6x10-5	1.0x10-11	0.087
15	Hake	4.9x10-7	0.001	0.0001	1.3x10-8	-	5.4x10-6	4.6x10-12	0.001
16	Ling	1.7x10-5	0.011	0.002	5.9x10-8	-	6.0x10-6	1.0x10-12	0.013
17	Norway pout	-	-	-	-	-	-	-	0
18	Monkfish	7.1x10-5	0.002	0.001	1.25x10-6	1.7x10-5	9.6x10-6	1.6x10-10	0.003
19	Herring	0.001	0.003	0.027	0.141	-	2.7x10-6	7.3x10-10	0.171
20	Sm. pelagic fish	0.0003	0.0003	2.2x10-5	2.2x10-5	-	9.0x10-6	0	0.001
21	Other pelagic fish	7.0x10-5	0.023	0.014	0.015	-	7.1x10-5	6.0x10-9	0.052
22	Sandeels	-	-	-	-	-	-	-	0
23	Plaice	0.016	0.001	0.005	5.73x10-6	9.9x10-7	0.001	1.1x10-10	0.022
24	Turbot	6.0x10-5	9.0x10-7	3.1x10-6	1.0x10-8	0	1.2x10-06	0	6.5x10-5
25	Other flatfish	0.019	0.001	0.007	6.9x10-06	3.4x10-7	0.0003	3.0x10-09	0.027
26	Sm. demersal fish	0.0002	3.5x10-5	6.2x10-05	7.6x10-11	4.1x10-8	3.1x10-07	4.8x10-12	0.000
27	Lrg.demersal fish	0.0001	0.008	0.0003	6.3x10-8	-	8.6x10-06	8.7x10-10	0.008
28	Squid & Octopus	4.7x10-5	0.0003	0.0002	-	-	-	-	0.001
29	Large zoo.	-	-	-	-	-	-	-	0
30	Small zoo.	-	-	-	-	-	-	-	0
31	Gel. zoo.	-	-	-	-	-	-	-	0
32	Edible crab	0.0001	0.0002	0.0004	2.3x10-9	3.2x10-6	5.4x10-5	2.0x10-6	0.001
33	Velvet crab	-	-	-	-	-	-	-	0
34	Crabs & lobsters	-	-	-	-	-	-	-	0
35	Nephrops	6.0x10-6	4.0x10-5	0.001	3.0x10-9	-	5.1x10-8	4.0x10-11	0.001

36	Shrimp	-	-	-	-	-	-	-	0
37	Scallops	-	-	-	-	-	-	-	0
38	Epifauna	0.005	0.003	-	-	-	-	-	0.008
39	Infauna	-	-	-	-	-	-	-	0

Table 47 *Diet matrix of the balanced northern North Sea EwE. Diets are weighted proportions (sum to 1).*

	Prey \ predator	Minke whale	Toothed whales	Seals	Seabirds (HDD)	Seabirds (LDD)	Sharks	Skates & Rays	J.cod	A. cod	J. whiting	A. whiting	J. haddock	A. haddock	Saithe	Hake	Ling	Norway pout	Monkfish	Herring
1	Minke whale																			
2	Toothed whales																			
3	Seals																			
4	Seabirds (HDD)				0.0002															
5	Seabirds (LDD)				0.0002															
6	Sharks		0.040																0.007	
7	Skates & Rays			0.020			0.027			0.002										
8	J. cod	0.016	0.005	0.184		0.028	0.021			0.001					0.032		0.096		0.090	
9	A. cod		0.003	0.020			0.008			0.0003							0.020		0.046	
10	J. Whiting	0.014	0.120	0.014		0.028		0.002	0.004	0.012	0.009		0.001	0.002	0.001	0.013		0.001	0.007	
11	A. Whiting		0.130	0.020				0.001	0.000	0.001				0.001		0.007			0.004	
12	J. Haddock	0.010	0.050	0.002		0.050			0.080	0.030			0.001	0.0003	0.003				0.017	
13	A. Haddock		0.023	0.001						0.020		0.010		0.001	0.001				0.034	
14	Saithe		0.133	0.305		0.028					0.007						0.100		0.009	
15	Hake		0.003	0.001		0.000	0.004			0.003										
16	Ling		0.002	0.008		0.000	0.006													
17	Norway pout	0.005	0.058	0.018	0.006	0.028	0.017	0.002	0.104	0.213	0.100	0.100	0.017	0.107	0.029	0.016			0.077	
18	Monkfish			0.010			0.0007													
19	Herring	0.016	0.070	0.021	0.072		0.045	0.010	0.000	0.084	0.100	0.159			0.150	0.015	0.145		0.227	
20	Sm. pelagic fish	0.029	0.004	0.020	0.000	0.220	0.050	0.009	0.002	0.025	0.153	0.117	0.007	0.001	0.073	0.068			0.017	
21	Lrg. pelagic fish	0.060	0.014	0.000	0.072	0.000	0.065	0.024	0.000	0.006	0.000	0.176		0.0004	0.014	0.760	0.099		0.332	
22	Sandeels	0.500	0.300	0.237	0.221	0.588		0.527	0.221	0.196	0.143	0.292	0.070	0.329	0.200	0.001	0.020		0.005	0.050
23	Plaice			0.008			0.010	0.003	0.000	0.002		0.001							0.00003	
24	Turbot			0.001						0.005	0.001									
25	Other flatfish			0.021			0.046	0.001	0.093	0.000	0.023	0.0001	0.050	0.037	0.011	0.002	0.007		0.087	
26	Sm. demersal fish		0.0003	0.015			0.107	0.050	0.006	0.065	0.000	0.057	0.0002	0.006	0.050	0.092	0.085		0.015	
27	Lrg. demersal fish		0.010	0.055		0.020	0.010	0.002	0.007	0.003	0.000	0.0004	0.000	0.0004		0.002	0.050		0.005	
28	Squid & Octopus	0.020	0.036	0.006			0.081	0.104	0.021	0.008	0.091	0.048	0.179	0.110	0.120	0.001	0.084		0.020	
29	Lrg. zooplankton	0.220			0.133	0.008	0.003	0.001	0.207	0.0002	0.005	0.002	0.116	0.004	0.007	0.017	0.001	0.359		0.755
30	Sm. zooplankton	0.110			0.095				0.067	0.0001	0.169	0.002	0.090	0.002	0.00002	0.0002	0.0001	0.304		0.148
31	G. zooplankton						0.012		0.001	0.0005	0.019	0.00001	0.009	0.005	0.030	0.004	0.000	0.001		
32	Edible crab			0.001			0.015		0.003	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.010			
33	Velvet crab				0.0010		0.0003	0.0001		0.0010		0.0003		0.0003		0.0003	0.00001			
34	Crabs & lobsters			0.001			0.193	0.018	0.001	0.016	0.141	0.001		0.010	0.200	0.000	0.050	0.025		
35	Nephrops						0.001		0.059	0.216	0.000	0.00002		0.006						
36	Shrimp			0.001			0.006	0.048	0.030	0.012	0.031	0.016	0.020	0.009	0.00001	0.00004	0.0002	0.010	0.00001	
38	Scallops													0.002						
39	Epifauna			0.000	0.000		0.169	0.182	0.087	0.074	0.002	0.015	0.380	0.284	0.069	0.001	0.230	0.231	0.001	0.047
40	Infauna			0.000	0.000		0.102	0.006	0.005	0.004	0.006	0.003	0.029	0.083	0.002	0.000	0.003	0.069	0.000	0.000
41	Seaweed			0.000	0.000															
42	Phytoplankton			0.000	0.000															
43	Discards			0.009	0.400	0.002		0.010												
44	Detritus			0.000											0.008					

Table 42 *continued: Diet matrix balanced northern North Sea EwE. Diets are weighted proportions (sum to 1).*

	Prey \ predator	Lrg. pelagic fish	Sandeels	Plaice	Turbot	Flatfish	Sm. demersal fish	Lrg. demersal fish	Squid & Octopus	Lrg. zooplankton	Sm. zooplankton	G. zooplankton	Edible crab	Velvet crab	Crabs & lobsters	Norway lobster	Shrimp	Scallops	Epifauna	Infauna
1	Minke whale																			
2	Toothed whales																			
3	Seals																			
4	Seabirds (HDD)																			
5	Seabirds (LDD)																			
6	Sharks																			
7	Skates & Rays																			
8	J. cod																			
9	A. cod																			
10	J. Whiting																			
11	A. Whiting																			
12	J. Haddock																			
13	A. Haddock																			
14	Saithe																			
15	Hake																			
16	Ling																			
17	Norway pout	0.036			0.094	0.074		0.112												
18	Monkfish																			
19	Herring	0.030					0.040	0.224	0.015											
20	Sm. pelagic fish	0.165			0.028				0.020											
21	Lrg. pelagic fish					0.027	0.010	0.099												
22	Sandeels	0.040	0.010	0.073	0.055	0.020	0.050	0.060	0.010											
23	Plaice																			
24	Turbot								0.0001											
25	Flatfish				0.010			0.007	0.020											
26	Sm. demersal fish				0.009	0.009		0.165												
27	Lrg. demersal fish							0.010												
28	Squid & Octopus	0.050		0.003	0.008	0.008			0.005							0.010				
29	Lrg. zooplankton	0.488	0.163		0.006	0.006	0.003	0.001	0.227	0.050		0.450					0.090			
30	Sm. zooplankton	0.084	0.667		0.005	0.009	0.021	0.0001	0.397	0.300	0.050	0.450					0.500	0.250	0.095	
31	G. zooplankton					0.020						0.050								
32	Edible crab																			
33	Velvet crab																			
34	Crabs & lobsters				0.082	0.053	0.050						0.001	0.067	0.001					
35	Norway lobster												0.010		0.015					
36	Shrimp	0.001			0.172	0.150	0.007	0.0002	0.030				0.001		0.001	0.010	0.010			
38	Scallops								0.006						0.001					
39	Epifauna	0.091	0.015	0.451	0.270	0.355	0.389	0.290	0.196				0.356	0.104	0.355	0.350	0.155		0.005	
40	Infauna		0.077	0.473	0.182	0.192	0.430	0.029	0.022				0.394	0.031	0.395	0.429			0.350	0.001
41	Seaweed												0.010	0.704	0.023				0.100	0.005
42	Phytoplankton		0.068						0.052	0.528	0.900	0.050				0.150		0.350	0.250	0.295
43	Discards				0.079	0.001							0.030		0.002	0.001	0.005	0.010	0.001	0.001
44	Detritus					0.075				0.122	0.050		0.198	0.094	0.208	0.050	0.240	0.390	0.199	0.698

The pre-balance (PREBAL) diagnostics described by Link (2010) were used to judge the ecological quality of our balanced Ecopath model. Criteria used are listed below and describe how our model performed against each ecological rule in the section below (Table 48, Figure 23 through to 28 and Table 49).

Table 48 *PREBAL diagnostic criteria* (Link, 2010) *used to test the quality of our model, model results and comments on model performance.*

PREBAL criteria	Northern North Sea EwE model results	Comments
The range of biomass should span 5-7 orders of magnitude.	Biomass range spans 3-4 orders of magnitude; see Figure 23.	Order of magnitude lower than criteria. Biomass pans from 0.001 $t.km^{-2}$ for velvet crab to 101 $t.km^{-2}$ for seaweed.
The slope of biomass (on a log scale) should be in the order of approx. 5-10% decline with increasing trophic level.	6.5% decline see Figure 23.	Groups that are noticeably below the slope line are seabirds which have a low biomass due to their relatively light body mass; and velvet crab which have a very low biomass in the model year but important to present day shellfish catch.
P/Q should fall between 0.1 and 0.3 for all finfish and <1 for all functional groups.	Criteria met; see Figure 24.	-
P/B ratio should decline with increasing trophic level (this rule excludes homeotherms).	Criteria mostly met; see Figure 25.	When excluding homeotherms, seaweed and scallops fall notably blow the line whilst epifauna, infauna, and phytoplankton are above the line.
Q/B should decline with increasing trophic level (this rule excludes homeotherms).	Criteria met; see Figure 26.	When excluding homeotherms gelatinous zooplankton and scallops fall noticeably below the line whilst epifauna, infauna, shrimp and juvenile whiting are above.
Phytoplankton functional group should have a greater P/B than every other group.	Criteria met; see Figure 25.	-
P/R should be <1 for all functional groups.	Criteria met; see Figure 27.	-
EE should be <1 for all functional groups	Criteria met; see Figure 28.	-
The ratio between predator and prey biomass should be < 1 by approx. 1-2 decimal places, depending upon trophic level.	70% = <1 and >0.009 10% = <0.009 14% = >1 3% >10 4 % = cannibalism See table 3.4	Ratios below two decimal places are prominent for seals, seabirds, turbot, and their prey, and also for predators of sandeels and zooplankton. Ratios greater than 1 are most common when comparing predator biomass with high TL to low TL prey groups with low amounts of biomass in the model. This is seen for all predators of velvet crab (biomass 0.001 $t.km^{-2}$); flatfish (1.5 $t.km^{-2}$), squid & octopus (1.3 $t.km^{-2}$), and turbot (biomass 0.02 $t.km^{-2}$). Ratios greater than 1 are seen for high TL groups that predate upon each other, for example saithe (TL 4.1) predating upon juvenile whiting (TL 4).

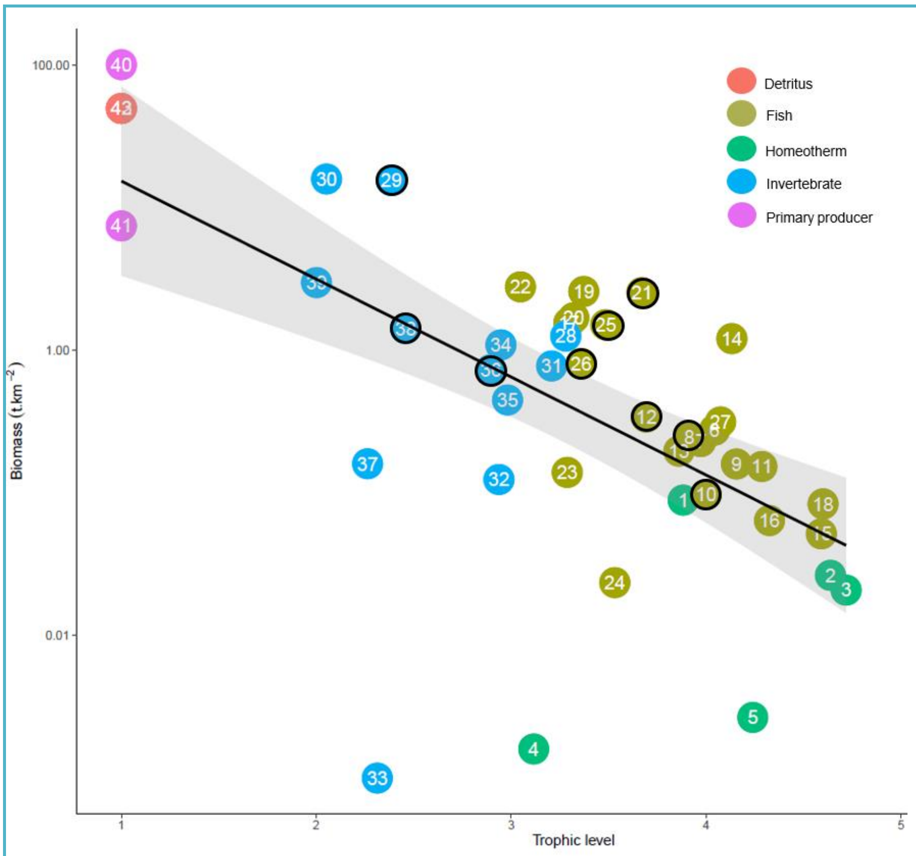


Figure 23 *Declining biomass with increasing trophic level. Line is linear regression of biomass and trophic level, grey bands represent S.E. Circles with black outline represent group biomass estimated by the model. Colours represent groupings for PREBAL analysis.*

	Functional group
1	Minke whale
2	Toothed whales
3	Seals
4	Seabirds (high discard diet)
5	Seabirds (low discard diet)
6	Sharks
7	Skates & Rays
8	Juvenile Cod
9	Adult Cod
10	Juvenile Whiting
11	Adult Whiting
12	Juvenile Haddock
13	Adult Haddock
14	Saithe
15	Hake
16	Ling
17	Norway pout
18	Monkfish
19	Herring
20	Small pelagic fish
21	Large pelagic fish
22	Sandeels
23	Plaice
24	Turbot
25	Flatfish
26	Small demersal fish
27	Large demersal fish
28	Squid & Octopus
29	Large zooplankton
30	Small zooplankton
31	Gelatinous zooplankton
32	Edible crab
33	Velvet crab
34	Crabs & lobsters
35	Norway lobster
36	Shrimp
37	Scallops
38	Epifauna
39	Infauna
40	Seaweed
41	Phytoplankton
42	Discards
43	Detritus

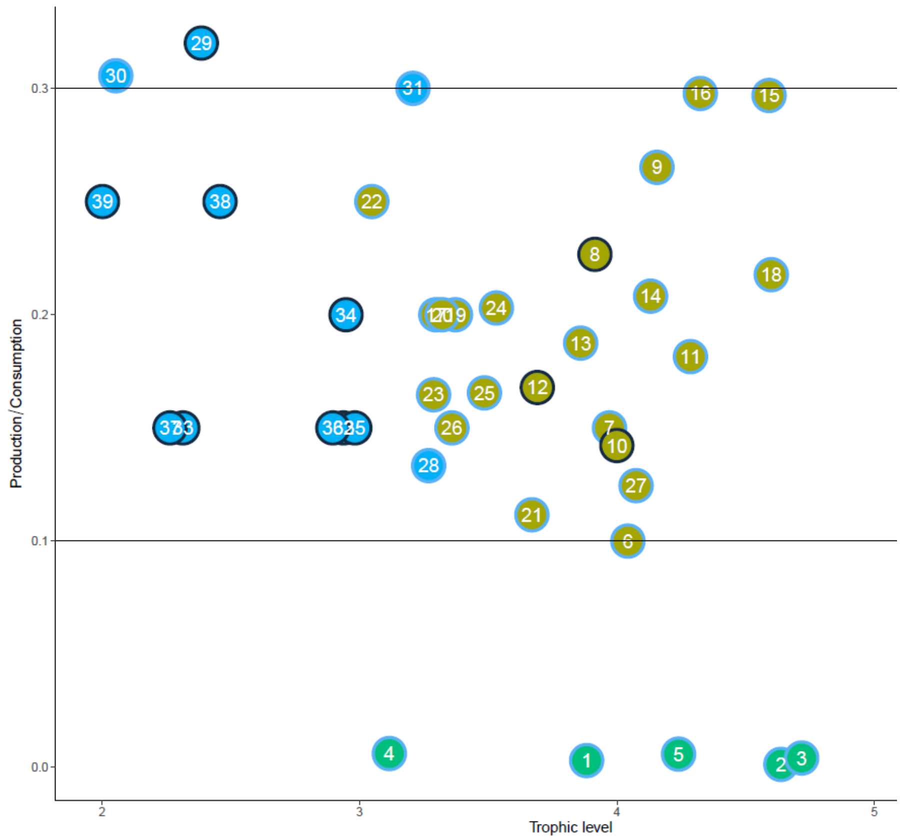
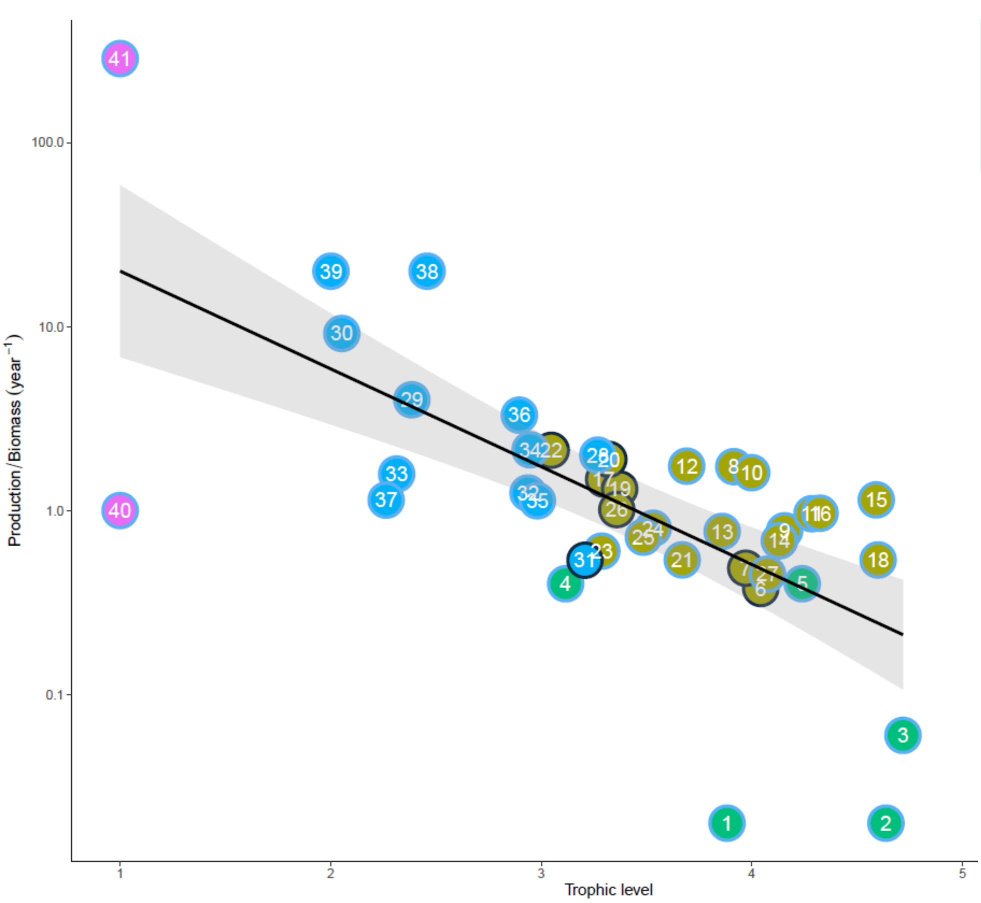
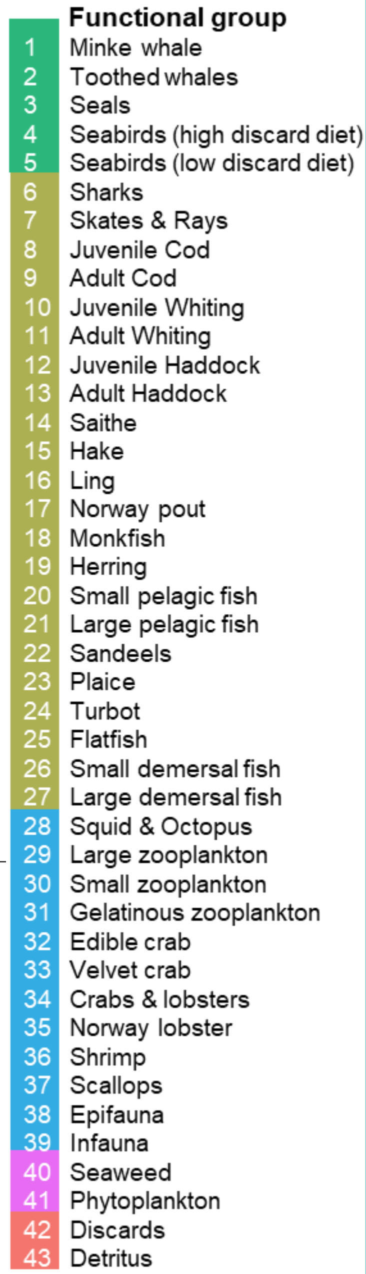


Figure 24 *Declining P/Q with increasing trophic level. Horizontal lines represent the ecological limits of finfish. Groups with P/Q estimated by the model outlined in black.*





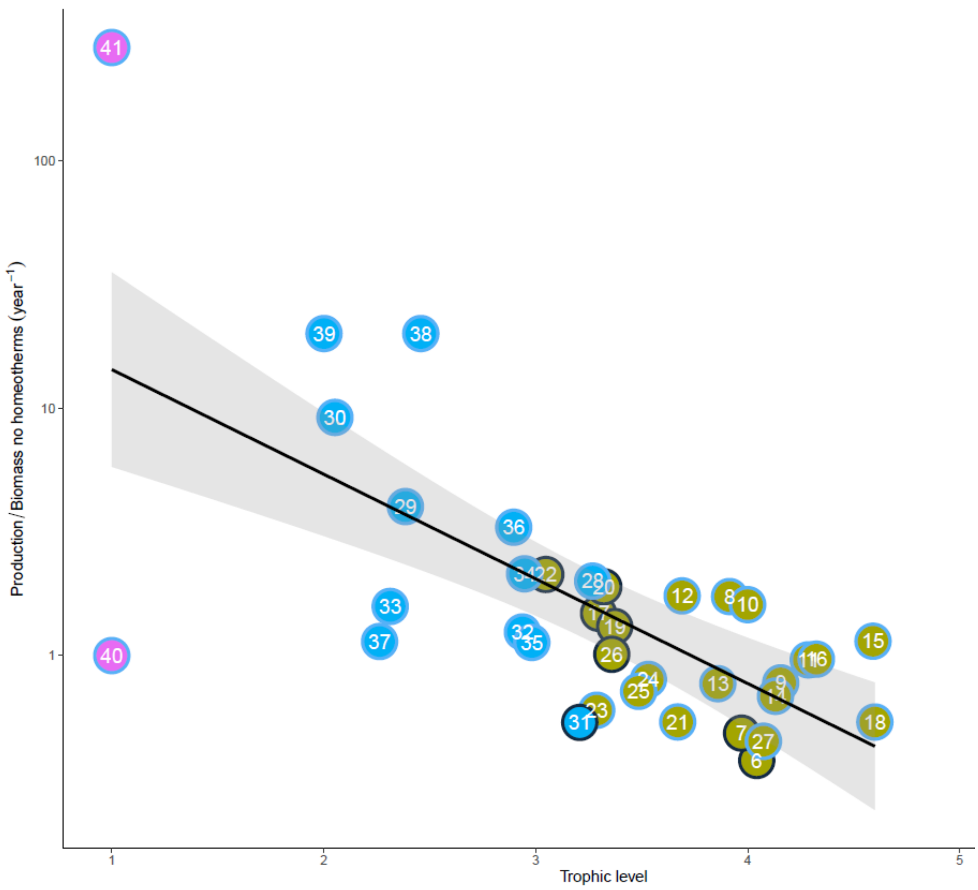


Figure 25 *Declining P/B with increasing trophic level (above: all groups included, below: homeotherms excluded). Line is linear regression of PB and trophic level. Grey bands represent the standard error of the regression line. Circles with black outline representing PB estimated by the model. Colours represent groupings for PREBAL analysis.*

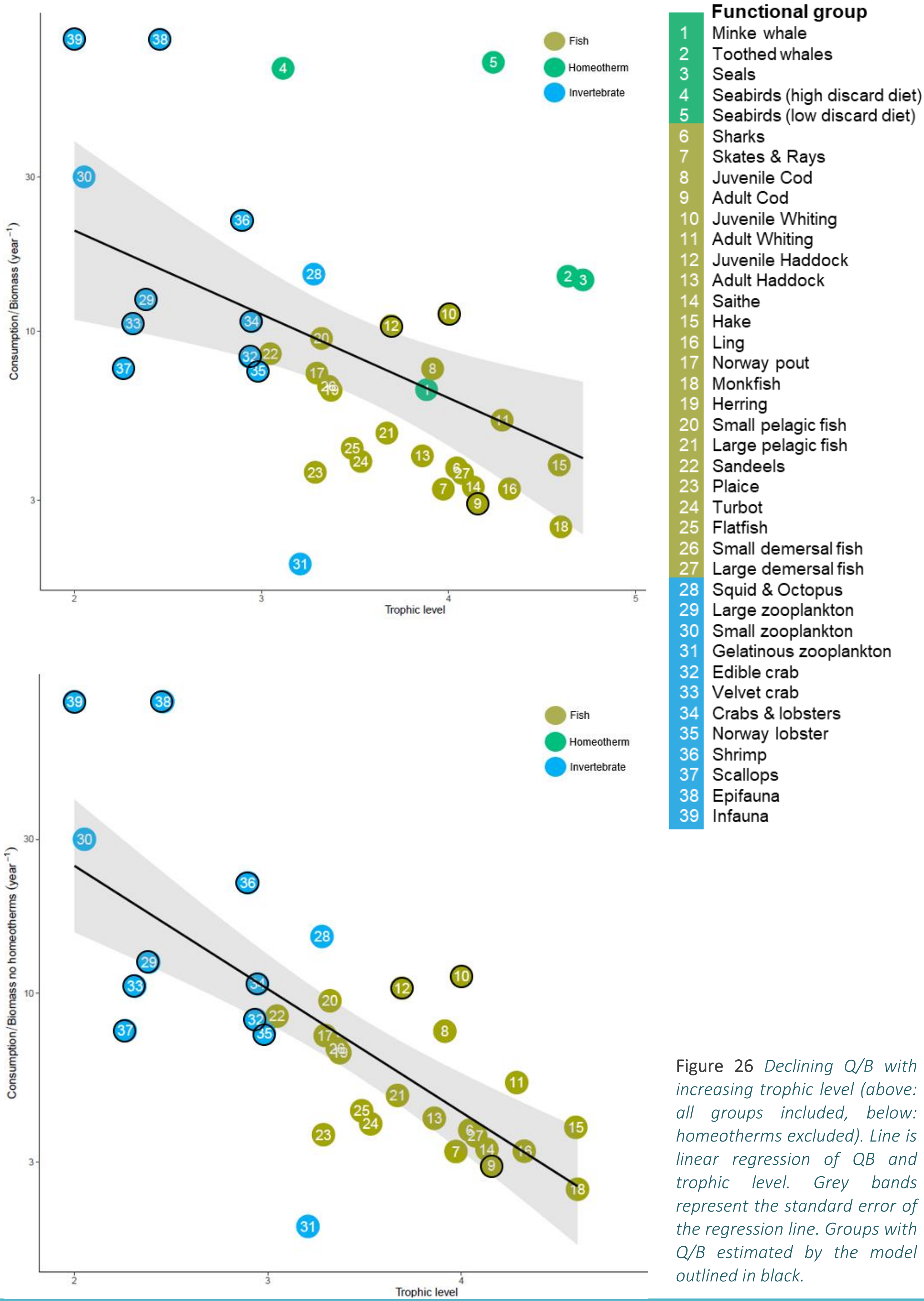


Figure 26 *Declining Q/B with increasing trophic level (above: all groups included, below: homeotherms excluded). Line is linear regression of QB and trophic level. Grey bands represent the standard error of the regression line. Groups with Q/B estimated by the model outlined in black.*

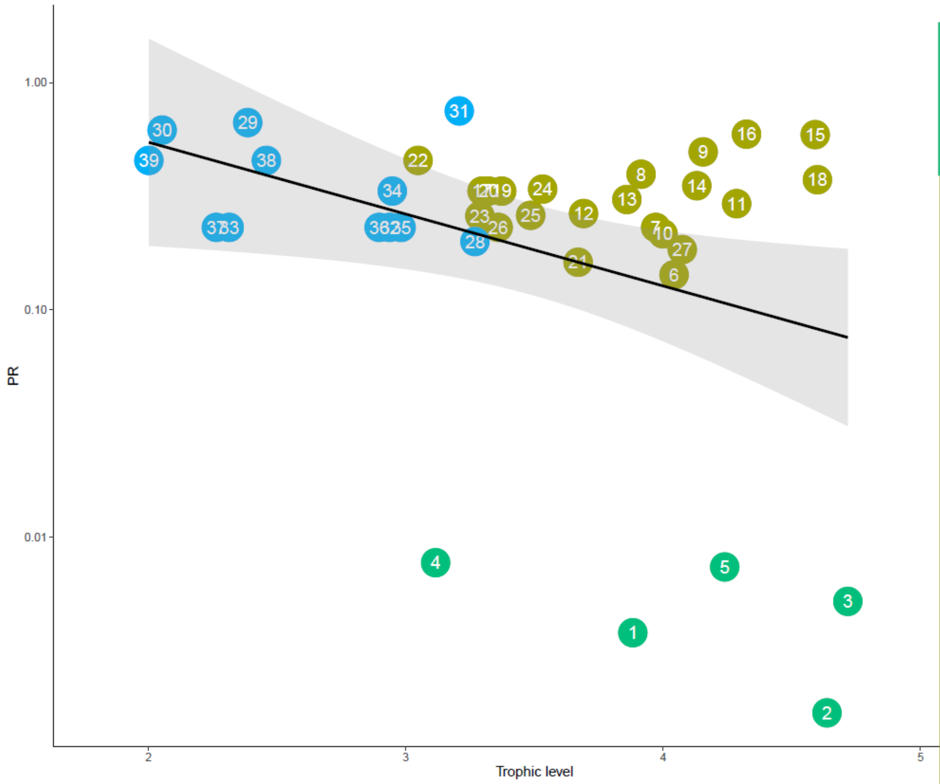


Figure 27 *Declining Production/Respiration (PR) ratio with increasing trophic level. Line is linear regression of PR and TL with grey bands representing the standard error of the regression line. Colours represent groupings used in PREBAL analysis.*

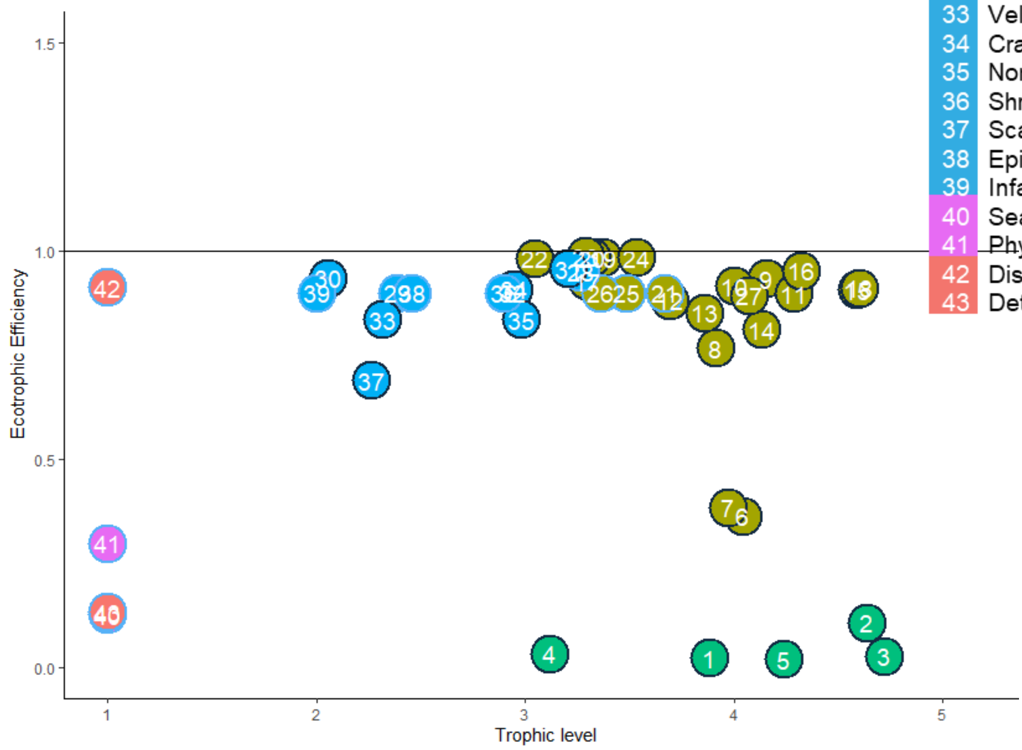


Figure 28 *Ecotrophic efficiency (EE) for all groups falls below one (the horizontal line) in the mass balanced model. Colours represent groupings used in PREBAL analysis.*

Table 49 *Predator – prey biomass ratios in the balanced model. Green = <1 and >0.009; blue = cannibalism; orange = <0.009, bright red = >1 and dark red >10. All ratios are rounded up to the nearest integer.*

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
1	Minke whale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Toothed whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Seals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Seabirds (high discard diet)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Seabirds (low discard diet)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Sharks	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Skates & Rays	-	-	0	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Juvenile cod	0	0	0	-	0	1	-	-	1	-	-	-	-	5	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Adult cod	-	0	0	-	-	2	-	-	1	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Juvenile Whiting	1	0	0	-	0	-	2	3	2	1	2	4	2	>10	1	-	>10	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Adult Whiting	-	0	0	-	-	-	1	-	1	-	1	-	1	8	0	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Juvenile Haddock	0	0	0	-	0	-	-	1	0	-	-	1	1	4	-	-	-	0	-	-	7	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
13	Adult Haddock	-	0	0	-	-	-	-	-	1	-	1	-	1	6	-	-	-	0	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
14	Saithe	-	0	0	-	0	-	-	-	-	0	-	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Hake	-	1	0	-	-	5	-	-	3	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Ling	-	0	0	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Norway pout	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	-	-	0	-	-	2	-	-	0	1	-	0	-	-	-	-	-	-	-	-	-	-	-	-
18	Monkfish	-	-	0	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	Herring	0	0	0	0	-	0	0	0	0	0	0	-	-	0	0	0	-	0	-	-	1	-	-	-	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-
20	Small pelagic fish	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	-	-	0	-	-	2	-	-	0	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
21	Large pelagic fish	0	0	-	0	-	0	0	-	0	-	0	-	0	0	0	0	-	0	-	-	-	-	-	-	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-
22	Sandeels	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	-	0	1	-	1	1	0	0	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-
23	Plaice	-	-	0	-	-	2	2	-	1	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	Turbot	-	-	1	-	-	-	-	-	7	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	>10	-	-	>10	-	-	-	-	-	-	-	-	-	-	-
25	Other flatfish	-	-	0	-	-	0	0	0	-	0	0	0	0	1	0	0	-	0	-	-	-	-	-	0	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-
26	Small demersal fish	-	0	0	-	-	0	0	0	0	-	0	0	0	2	0	0	-	0	-	-	-	-	-	0	2	-	0	-	-	-	-	-	-	-	-	-	-	-	-
27	Large demersal fish	-	0	0	-	0	1	1	1	1	-	0	-	1	4	0	0	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
28	Squid & Octopus	0	0	0	-	-	0	0	0	0	0	0	0	0	1	0	0	-	0	-	-	2	-	0	0	1	-	-	1	-	-	-	-	-	-	0	-	-	-	-
29	Large zooplankton	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	-	0	-	-	-	-	0	-	-	-
30	Small zooplankton	0	-	-	0	-	-	-	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	-	0	0	0	0	0	1	1	0	-	-	-	-	0	0	0	-
31	Gelatinous zooplankton	-	-	-	-	-	0	-	0	0	0	0	0	0	2	0	-	2	-	3	2	-	-	-	-	2	-	-	2	-	-	1	-	-	-	-	-	-	-	-
32	Edible crab	-	-	0	-	-	2	-	2	-	-	-	3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33	Velvet crab	-	-	-	2	-	>10	>10	-	>10	-	>10	-	>10	>10	-	-	-	-	-	-	-	-	-	-	>10	-	>10	>10	-	-	-	-	-	-	-	-	-	-	-
34	Crabs & lobsters	-	-	0	-	-	0	0	0	0	0	0	-	0	1	0	0	1	-	-	-	-	-	-	0	1	1	0	-	-	-	-	0	0	1	-	-	-	-	-
35	Nephrops	-	-	-	-	-	1	-	1	0	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	2	-	-	-	-	-
36	Shrimp	-	-	0	-	-	0	0	0	0	0	0	0	0	2	0	0	2	0	-	-	3	-	-	0	2	1	0	2	-	-	-	0	-	1	1	1	-	-	-
37	Scallops	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	7	-	-	-	-	-
38	Epifauna	-	-	-	-	-	0	0	0	0	0	0	0	0	1	0	0	1	0	2	1	2	2	0	0	1	1	0	1	-	-	-	0	0	1	0	1	-	1	-
39	Infauna	-	-	-	-	-	0	0	0	0	0	0	0	0	0	-	0	1	0	-	-	-	1	0	0	1	0	0	0	-	-	-	0	0	0	0	-	-	0	1
40	Seaweed	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	-	-	0	0
41	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	0	2	2	0	-	-	-	0	-	0	0	0
42	Discards	-	-	0	0	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	0	-	0	0	0	0	0	0
43	Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0	0	-	-	-	0	0	-	0	0	0	0	0	0	0	0

The flow of energy between functional groups and fishing fleets in the model are depicted in Figure 29.

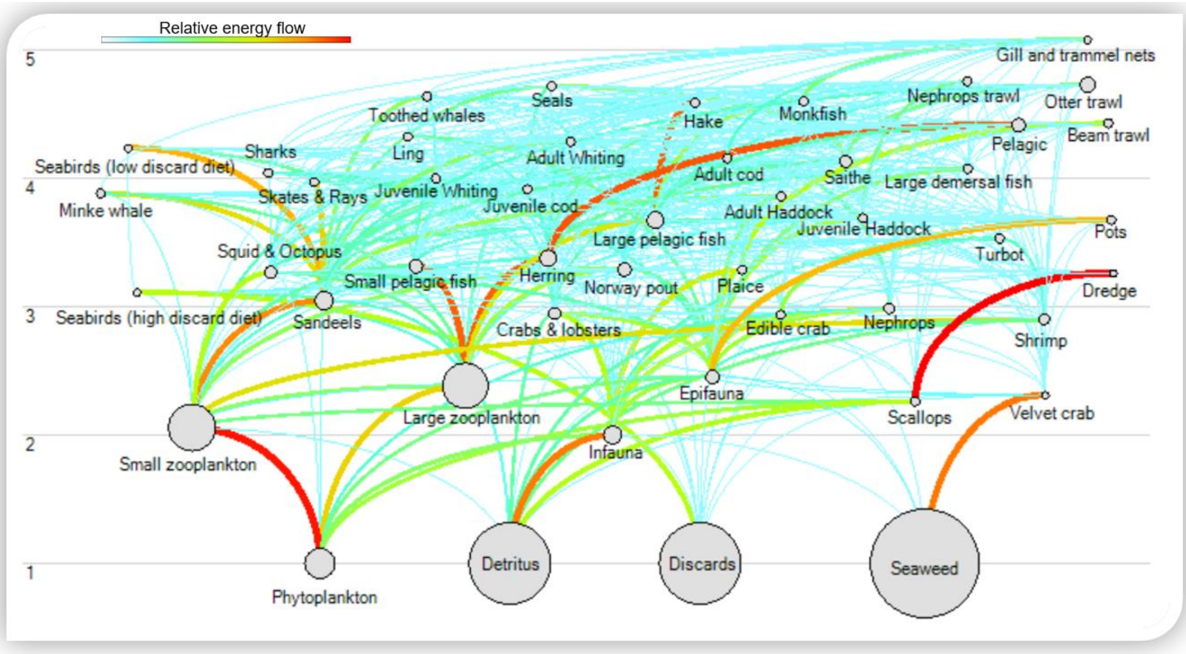


Figure 29 *Energy flow and biomass diagram of the northern North Sea Ecopath food web model. Nodes represent functional groups. Relative size of nodes represents functional group biomass in the system and catch volume of fleets. Lines indicate the flow of energy and y-axis the trophic levels. Width and colour of the lines represent the relative size of energy flow between the groups.*

Section 4: Conclusion

This report describes the construction of an Ecopath model for the northern North Sea, representing the food-web and fishing interactions (Figure 29). Commonly used methods for the calculation of production and consumption parameters were adopted in the parameterisation of this model. For data limited fish, the model incorporates area-based biomass estimates for the northern North Sea based on IBTS DATRAS data, guided by Greenstreet *et al.* (2007). The model included evaluation of diets for northern North Sea predators using DAPSTOM diet records combined with new diet data from NAFC stomach samples collected from Shetland demersal mixed fisheries in 2017. This model is intended to form the baseline for Ecosim simulations which will be used to explore the ecosystem consequences of changes to fisheries management in the northern North Sea.

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