Ecopath model of the Southern Bight of the North Sea (version 3)

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Contents

Preface

In this technical report, we describe the required data, the pre-processing steps taken and the methodologies used to develop a fully calibrated ecosystem model for the southern part of the North Sea. The ecosystem model was developed in both Ecopath with Ecosim (EwE) and Rpath, which is a R implementation of the commonly used EwE software. The model will serve as a tool to explore the ecosystem's natural history and its evolution throughout the years. A first version of the model was developed between July 2020 and February 2021.

Ecopath with Ecosim (EwE) is an ecosystem modelling software (https://ecopath.org/) established in 1984 by Polovina (1984) and updated through the years by Christensen and Pauly (1992) and Walters et al. (1997). It has three main components: 1) Ecopath: a mass-balance snapshot of the ecosystem; 2) Ecosim: a time dynamic simulation of the system; and 3) Ecospace: a spatial and time dynamic module.

In this technical report, we describe an Ecopath model for the Southern Bight of the North Sea (SBNS; ICES area IVc) in 1991. The year of the model, 1991, was chosen for three main reasons: 1) it is the year with the most complete diet data, i.e. North Sea Year of the Stomach; 2) it is the base year in the "mother model", the North Sea model of Mackinson and Daskalov (2007); and 3) the period between 1991 and 2023 is a long time span for time series fitting in Ecosim to understand the influence of parameters, such as vulnerability.

We provide an overview of our basic input parameters, the fisheries included in this model, our data sources, and methods to estimate basic input parameters. Steps undertaken to assess and balance the model are described in this manuscript as well. We are using an ecosystem modelling approach, i.e. an Ecopath with Ecosim model of the SBNS, to address our research question: "What does the food web in the SBNS look like, and how did it evolve over time?".

1. Basic input parameters

1.1. Introduction to Southern Bight of the North Sea

We developed an ecosystem model for the Southern Bight of the North Sea (SBNS). The SBNS (ICES area IV division c) has a surface area of 63,633.86 km^{-2} (ICES Spatial Facility, Fig. 1a). It is a relatively shallow (<50 m) part of the North Sea (Fig. 1b). The southern limit of the SBNS is determined by the English Channel and its northern limit is at the latitude of the island Schiermonniksoog, Netherlands. Apart from extreme observations, surface water temperatures vary seasonally between 5°C and 20°C. The salinity varies between 29 to 35 PSU and is strongly influenced by the inflow of Atlantic water (offshore) and the river plumes of the Scheldt, Rhine, Seine, and Meuse in the coastal zones (Lacroix et al., 2004). An anticlockwise circulation in the North Sea brings water from the North Atlantic along the coast of the UK in the west of the SBNS and water from the English Channel in the east, along the Belgian and Dutch coast (Turrell, 1992). The sediment in SBNS consists mainly of sands (Fig. 1c, ICES, 2008).

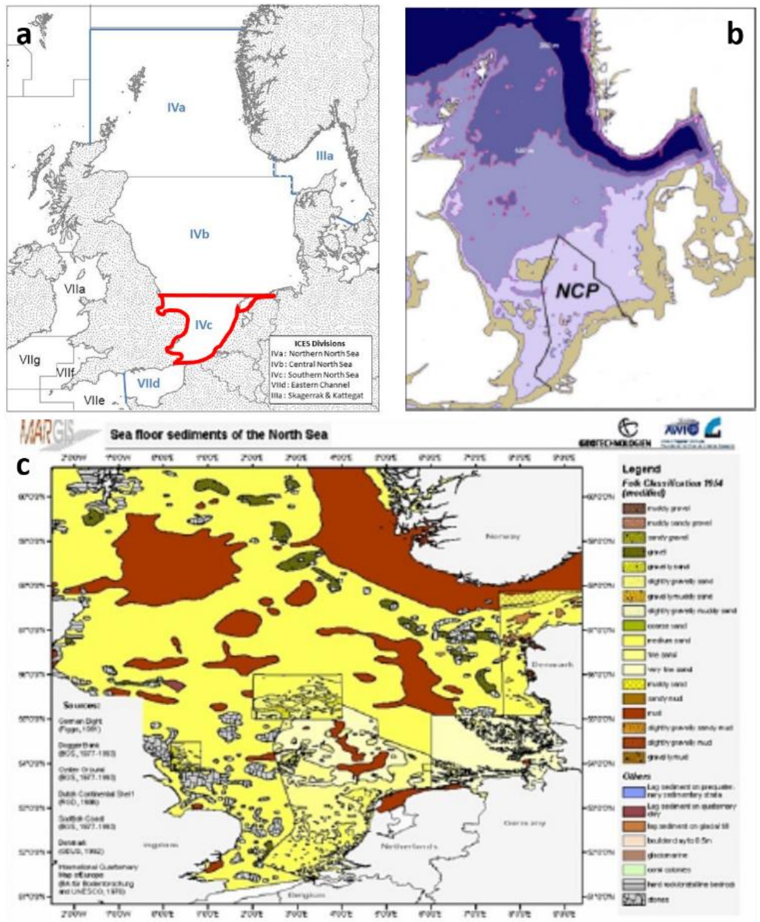

Figure 1: The geographical location of our study area (a), the Southern Bight of the North Sea (ICES area IVc, in red) adjusted from SWD/2016/0272 final - 2016/0238 (COD) and the environmental setting, (b) bathymetry of the North Sea (source RIVO – alternative from ICES, 2008) and (c) seabed sediment types of the North Sea. http://www.awi-bremerhaven.de/GEO /Marine_GIS/Margis%20homepage/index.html.

1.2. Data sources for the Southern Bight of the North Sea model

Ecopath models are mass-balance snapshots of the ecosystem, and the input data are expressed in mass-based units. To feed a SBNS specific model, we collected a range of data from multiple sources. Here, we give an overview of how we estimated input parameters, e.g. biomass (wet mass in t km^{-2} y^{-1}) and QB (Fig. 2). To estimate the biomass for our study area, we relied on biomass estimates from stock assessments and catch per unit effort (CPUE) data. For most commercial fish species, biomass data is available from ICES expert group reports such as HAWG, WGWIDE and WGNSSK. For species that were not included in ICES expert group reports, e.g. sea bass, seabirds and brown shrimp, estimates from research papers were used instead. In the specific case of harbour porpoise, we used an abundance estimate from OSPAR and the average weight per individual (Bjørge and Tolley, 2009). For some groups, such as plankton, we did not find a good estimate of the biomass in the SBNS. Hence, we assumed similar biomass compared to the study area of the other EwE models, the North Sea model (Mackinson and Daskalov, 2007) and the Southern North Sea (SNS; Stäbler et al., 2016). CPUE data was collected from the International Bottom Trawl survey in the North Sea (NS-IBTS, ICES Database of Trawl Surveys (DATRAS), 2020; https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx).

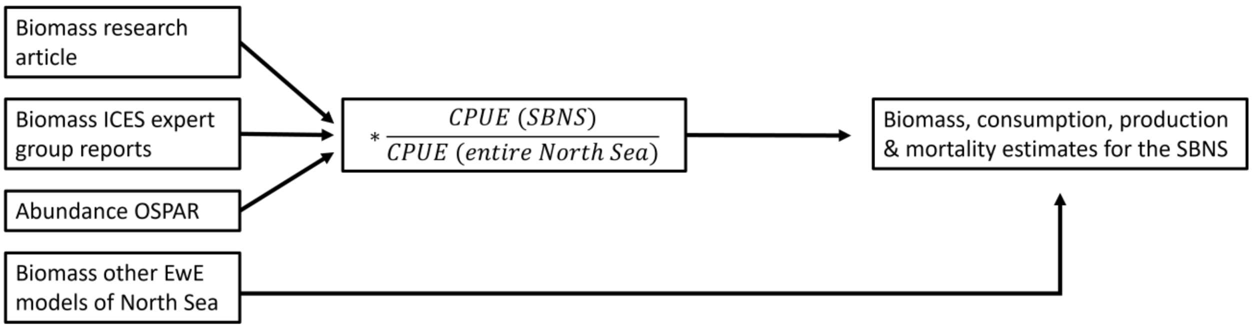

Figure 2: An overview of estimating the biomass and other parameters for the Southern Bight of the North Sea (SBNS) EwE model.

Catch related data was obtained from STECF (mainly for information about fishing gear types, landings, and discards) and ICES (mainly for historical catch data). The diets in the SNS model of Stäbler et al. (2016) were adjusted to our study area. Diets of the species that were not included in the SNS model of Stäbler et al. (2016) were taken from CEFAS fish stomach records (https://www.cefas.co.uk/data-and-publications/fish-stomach-records/) and scientific literature. Detailed information concerning data sources for the input data in our model is described in the following sections.

1.3. Functional group input parameters

We determined the functional groups (FGs), i.e. a biomass groups representing one or multiple species, based on the SNS model of Stäbler et al. (2016). The ecosystem model of Stäbler et al. (2016) was focused on ICES areas IVb and IVc. Functional groups that had a low occurrence in our study area (ICES area IVc), based on the ICES ecosystem map (https://ecosystemdata.ices.dk/Map/index.aspx?Action=AddLayer&DataSet=657&LatN=&LatS=&LonE=&LonW=&Sdate=&Edate), were left out of our model. Other functional groups, i.e. functional groups that are not within our focus or have less economic value, were clustered together to decrease the complexity in the model. We obtained a total of 43 functional groups, for which an overview of the input data and their sources can be consulted in Table 1.

Table 1: An overview of the input parameters (biomass (B), total mortality (Z), production over biomass (PB), consumption over biomass (QB), production over consumption (PQ), and ecotrophic efficiency (EE), and references per functional group. The grey shaded area indicates a functional group with a multi-stanza.

Functional group	Input parameters						Data sources
	B (t km^{-2})	Z (y^{-1})	PB (y^{-1})	QB (y^{-1})	PQ	EE	
Harbour porpoise	0.03		0.02	24.64			Bjørge and Tolley (2009), Hammond et al. (2017; OSPAR-SCAN III), Stäbler et al. (2016)
Seals	0.008		0.09	26.84			Mackinson and Daskalov (2007)
Seabirds (discard feeders)	0.0004		0.1	60.52			Bicknell et al. (2013), Mackinson and Daskalov (2007), Nilsson and Nilsson (1976), Potiek et al. (2019), Reeves and Furness (2002), Sherley et al. (2020), Waggitt et al. (2020)
Seabirds (non-discard feeders)	0.002		1.12	48.2			Bicknell et al. (2013), Mackinson and Daskalov (2007), Nilsson and Nilsson (1976), Potiek et al. (2019), Reeves and Furness (2002), Sherley et al. (2020), Waggitt et al. (2020)
Sharks	0.0003		0.54	3.37			ICES Database of Trawl Surveys (DATRAS), Sparholt (1990)
Rays	1.51		0.30	2.89			ICES Database of Trawl Surveys (DATRAS), Sparholt (1990)
Cod							
Juvenile Cod		1.13		7.05			ICES (2019a)
Cod (adult)	0.22	1.13		3.20			Fishbase – Life history tool*, ICES Stock Assessment Database, ICES – Historical Nominal Catches 1950-2010
Whiting							
Juvenile Whiting		2.80					ICES (2019a)
Whiting (adult)	0.09	1.31		5.41			Fishbase – Life history tool*, ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Other gadoids	0.06		0.85	5.23			ICES Database of Trawl Surveys (DATRAS), Sparholt (1990)
Demersal fish	0.05		2.49	4.94			ICES Database of Trawl Surveys (DATRAS), Sparholt (1990)
Herring							
Juvenile Herring		0.87					ICES (2020)
Herring (adult)	0.76	0.87		6.78			Fishbase – Life history tool*, ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Sprat	0.21		0.80	9.01			ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Mackerel	0.92		1.34	4.81			ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Horse mackerel	1.51		0.34	4.96			ICES Stock Assessment Database, Sparholt (1990)
Sandeels	4.38		1.00	9.59			ICES Stock Assessment Database
Plaice							
Juvenile Plaice		0.49					ICES (2019a)
Plaice (adult)	0.90	0.89		3.63			Fishbase – Life history tool*, ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Dab	9.64		0.46	5.58			ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Other flatfish	0.15		0.84	6.90			ICES Database of Trawl Surveys (DATRAS), Sparholt (1990)
Sole							
Juvenile Sole		0.54					ICES (2019a)
Sole (adult)	0.32	1.15		5.56			Fishbase – Life history tool*, ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Sea Bass	0.00004		0.56	3.81			ICES Stock Assessment Database, ICES Database of Trawl Surveys (DATRAS)
Pelagic fish			4.00	10.19		0.98	Mackinson and Daskalov (2007)
Squid & cuttlefish	0.13		11.02	20.00			ICES Database of Trawl Surveys (DATRAS), Mackinson and Daskalov (2007)
Carnivorous zooplankton			4.00		0.32	0.99	Mackinson and Daskalov (2007)
Herbivorous zooplankton	16.00		9.20	30.00			Mackinson and Daskalov (2007)
Gelatinous zooplankton	0.09		2.86		0.45		Stäbler et al. (2016)
Large crabs & shrimp	2.30		1.05		0.20		Mackinson and Daskalov (2007), OBIS**, Stäbler (2016)
Blue mussels (aquaculture)	0.06		0.36	2.67			Horn et al. (2020)
Epifaunal macrobenthos (mobile grazers)	78.00		0.39		0.20		Mackinson and Daskalov (2007)
Infaunal macrobenthos	136.00		1.00		0.30		Mackinson and Daskalov (2007)
C. crangon							
Crangon (below 5cm)		12.50					Hufnagl et al. (2010a), Stäbler et al. (2016)
Crangon (commercial size)	0.36	6.50		10.00			Hufnagl et al. (2010a), Tulp et al. (2016), Stäbler et al. (2016)
Small mobile epifauna (swarming crustaceans)	30.00		1.90		0.35		Mackinson and Daskalov (2007)
Small infauna (polychaetes)	150.00		0.90		0.30		Mackinson and Daskalov (2007)
Sessile epifauna	105.00		0.26		0.20		Mackinson and Daskalov (2007)
Meiofauna			35.00	125.00		0.99	Mackinson and Daskalov (2007)
Phytoplankton	7.50		286.70				Mackinson and Daskalov (2007)
Detritus	50.00						Mackinson and Daskalov (2007)
Discards	0.00						Stäbler et al. (2016)

* Asila and Ogari (1988); Beddington and Cooke (1983); Beverton and Holt (1957); Beverton and Holt (1964); Beverton (1992); Blueweiss et al. (1978); Froese and Binohlan (2000); Froese et al. (in prep.); Gulland (1971); Musick (1999); Palomares (1991); Palomares and Pauly (1999); Pauly (1979); Pauly (1980); Pauly (1984); Pauly (1986); Pauly (1989); Pauly and Christensen (1998); Pauly et al. (1998); Ricker (1975); Taylor (1958)

** Brodie et al. (2013); Buhl-Mortensen (2014); DFO (2016); Hassel (2014); ICES (2010); IFREMER (2016); Libby (2014); MBA (2016); Meurisse and Semal (2020); Miller et al. (2014); National Museum of Natural History (2001); NOAA's National Marine Fisheries Service (2005); Northeast Fisheries Science Center (2010); OBIS Canada (2011); Parr (n.d.); Rees et al. (n.d.); Santos (2016); Swedish county administration boards et al. (2017); The Norwegian Oil Industry Association (2001); Türkay (n.d.); Van Guelpen (2016); Van Guelpen and Pohle (2014); VLIZ (2004)

1.3.1. Marine mammals

Three marine mammals regularly occur in the SBNS: harbour porpoise (*Phocoena phocoena*), common seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*). Other species such as the bottlenose dolphin and minke whale are uncommon in this area and sighted rarely. As they are irregular inhabitants of the SBNS and more likely to just travel through or arrive by accident, they are not included in the model.

Harbour porpoise

A density of 0.607 individuals km^{-2} was obtained from OSPAR – SCANS III (Hammond et al., 2017) and multiplied with the average weight per individual of about 0.055 t (Bjørge and Tolley, 2009). We calculated a biomass of 0.03 t km^{-2} y^{-1} for our model. Production-biomass ratio (PB) of 0.02 y^{-1} and consumption-biomass ratio (QB) of 17.63 y^{-1} for harbour porpoise were assumed to be similar to the values of toothed whales from the SNS model of Stäbler et al. (2016).

Seals

We assumed that the parameters, such as biomass, PB, and QB for seals, i.e. grey and common seal were the same as in the North Sea model of Mackinson and Daskalov (2007). Thus, the biomass for seals was 0.008 t km^{-2} y^{-1}, PB 0.09 y^{-1} and QB 26.84 y^{-1}.

1.3.2. Seabirds

We divided the seabirds into two functional groups, i.e. discard feeders and non- discards feeders. We did this because discards can be a large portion of some species' diets. Large flock of seabirds are often observed feeding on discards thrown overboard by fishermen. Other seabirds, such as divers and northern gannets do not feed on discards (or do so to a limited extent).

Discard feeders

Discard feeders consist of seabirds whose diet relies for a large part on discards. The following species were included in this group: European herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), lesser black-backed gull (*Larus fuscus*), common gull (*Larus canus*), black-legged kittiwake (*Rissa tridactyla*), and great skua (*Stercorarius skua*). The biomass of discard feeders was estimated to be 0.0004 t km^{-2} y^{-1} based on scientific literature from Bicknell et al. (2013), Potiek et al. (2019), Reeves and Furness (2002), Sherley et al. (2020) and Waggitt et al. (2020). PB was taken from the North Sea model of Mackinson and Daskalov (2007) and estimated to be 0.10 y^{-1}, whereas QB was estimated using the empirical formula of Nilsson and Nilsson (1976) resulting in 60.52 y^{-1}.

Non-discard feeders

Non-discard feeders consist of seabirds where discards do not (or to a limited extend) contribute to their diet. The following species were included in this group: Great crested grebe (*Podiceps cristatus*), Northern gannet (*Morus bassanus*), little gull (*Hydrocoloeus minutus*), common tern (*Sterna hirundo*), common murre (*Uria aalge*), razorbill (*Alca torda*), scoter sp. (*Melanitta sp*.), loon (Gaviidae) and tern (Sternidae). Podiceps cristatus is common in freshwater areas but also in estuaries and shallow coastal waters (Stienen & Vanermen, 2018). Sterna hirundo is also a common bird at freshwater bodies, such as rivers and lakes, but is also common around saltwater bodies, such as lagoons, and coastal waters (Bicknell et al., 2013; Potiek et al, 2019; Stienen & Vanermen, 2018). The biomass of non-discard feeders was estimated at 0.002 t km^{-2} y^{-1} based on several research papers: Bicknell et al. (2013), Potiek et al. (2019), Reeves and Furness (2002), Sherley et al. (2020) and Waggitt et al. (2020). PB (1.12 y^{-1}) was taken from the North Sea model (Mackinson and Daskalov, 2007), and QB was estimated with the empirical formula of Nilsson and Nilsson (1976) resulting in 48.20 y^{-1}.

1.3.3. Fish

The functional groups containing fish were chosen based on their importance for fisheries, both commercial and recreational. The PB of fish was calculated using equation 1. The total mortality (Z) equals fishing mortality (F) plus the natural mortality (M, Eq. 1). Fishing mortality is equal to the catch (C) over biomass (B, Eq. 2). The natural mortality is calculated according to the empirical formula of Pauly (1980) using asymptotic length (L_{inf}; Eq. 3) or asymptotic weight (W_{inf}; Eq. 4) depending on which parameter was known.

$$\frac{P}{B} = Z = F + M \quad (1)$$

$$F = \frac{C}{B} \quad (2)$$

$$log\ M = -0.0066 - 0.279\ \ log\ L_{inf} + 0.6543\ \ log\ K + 0.4634\ \ log\ T \quad (3)$$

$$log\ M = -0.2107 - 0.0824\ \ log\ W_{inf} + 0.6757\ \ log\ K + 0.4627\ \ log\ T \quad (4)$$

In equation 3 and 4, K is the growth coefficient and T is the temperature (°C), i.e. 10°C. Consumption-biomass ratio (QB; Eq. 5) was estimated using the empirical formula of Pauly et al. (1990). Pf (apex and/or pelagic predators and/or zooplankton feeders) is 1 for top predators and zooplanktivores and 0 for detritivores and herbivores. Hd (herbivores and detritivores) is 1 for herbivores and 0 for carnivores. The values for the parameters; K, L_{inf} and W_{inf} were obtained from Fishbase (Froese and Pauly 2023) through the Life history tool (Asila and Ogari, 1988); Beddington and Cooke, 1983; Beverton and Holt, 1957; Beverton and Holt, 1964; Beverton, 1992; Blueweiss et al., 1978; Froese and Binohlan, 2000; Froese et al., in prep.; Gulland, 1971; Musick, 1999; Palomares, 1991; Palomares and Pauly, 1999; Pauly, 1979; Pauly, 1980; Pauly, 1984; Pauly, 1986; Pauly, 1989; Pauly and Christensen, 1998; Pauly et al., 1998; Ricker, 1975; Taylor, 1958) for each species. For FGs composed of multiple species, we took a weighted mean of the species' parameters with their biomass as weight.

$$log\ \frac{Q}{B} = \ 6.37 - 1.5045\ (\frac{1000}{(T+273.1)}) - 0.168\ \ log\ W_{inf} + 0.1399\ \ log\ Pf + 0.2765\ \ log\ Hd \quad (5)$$

Table 1 provides an overview of all model parameter estimates.

Cod

We divided cod (*Gadus morhua*) into two stanza groups as they are a target species for fisheries, which focus on adult individuals. For adult cod (2+) we estimated the biomass to be 0.02 t km^{-2} y^{-1}. We obtained this biomass estimate by multiplying the spawning stock biomass of cod in the greater North Sea (North Sea, English Channel and Skagerrak; ICES Stock Assessment Database) with the ratio of cod in the SBNS compared to those in the greater North Sea based on CPUE data (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)). PB and QB were calculated as 1.14 y^{-1} and 3.20 y^{-1} for adult cod. Total mortality of juvenile cod was calculated using F and M from ICES (2019a) and was estimated at 1.13 y^{-1}. For multi-stanza functional groups such as Cod, weight at maturity over asymptotic weight ($W_{maturity}$ / $W_{infinity}$) which were retrieved from Fishbase – Life history tool (Asila and Ogari, 1988; Beddington and Cooke, 1983; Beverton and Holt, 1957; Beverton and Holt, 1964; Beverton, 1992; Blueweiss et al., 1978; Froese and Binohlan, 2000; Froese et al., in prep.; Gulland, 1971; Musick, 1999; Palomares, 1991; Palomares and Pauly, 1999; Pauly, 1979; Pauly, 1980; Pauly, 1984; Pauly, 1986; Pauly, 1989; Pauly and Christensen, 1998; Pauly et al., 1998; Ricker, 1975; Taylor, 1958), is required as basic input in Ecopath. For this, a value of 0.137 was obtained.

Whiting

We divided whiting (*Merlangius merlangus*) in two stanza groups as they are a target species for fisheries. For adult whiting (2+), we estimated the biomass to be 0.09 t km^{-2} y^{-1}. This estimate was obtained based on the ratio of whiting in the SBNS compared to the greater North Sea based on CPUE data (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total spawning whiting stock biomass in the greater North Sea (North Sea and English Channel; ICES Stock Assessment Database). PB and QB were calculated as 1.31 y^{-1} and 5.41 y^{-1} for adult whiting. Total mortality of juvenile whiting was calculated using F and M from ICES (2019a) and was estimated at 2.80 y^{-1}. Maturity over asymptotic weight ($W_{maturity}$ / $W_{infinity}$) for whiting was estimated at 0.182 (Fishbase – Life history tool; Asila and Ogari, 1988); Beddington and Cooke, 1983; Beverton and Holt, 1957; Beverton and Holt, 1964; Beverton, 1992; Blueweiss et al., 1978; Froese and Binohlan, 2000; Froese et al., in prep.; Gulland, 1971; Musick, 1999; Palomares, 1991; Palomares and Pauly, 1999; Pauly, 1979; Pauly, 1980; Pauly, 1984; Pauly, 1986; Pauly, 1989; Pauly and Christensen, 1998; Pauly et al., 1998; Ricker, 1975; Taylor, 1958).

Herring

We divided herring (*Clupea harengus*) into two stanza groups as they are a target species for fishery. For adult herring (1+), we estimated the biomass to be 0.76 t km^{-2} y^{-1}. This estimate was obtained based on the ratio of herring in the SBNS compared to the greater North Sea using CPUE data (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total spawning stock biomass of herring in the greater North Sea (North Sea, English Channel and Skagerrak; ICES Stock Assessment Database). PB and QB were calculated as 0.87 y^{-1} and 6.78 y^{-1} for adult herring. Total mortality of juvenile herring was calculated using F and M from ICES (2020) and was 0.87 y^{-1}. Maturity over asymptotic weight ($W_{maturity}$ / $W_{infinity}$) for herring was 0.207 obtained from FishBase – Life history tool (Asila and Ogari, 1988); Beddington and Cooke, 1983; Beverton and Holt, 1957; Beverton and Holt, 1964; Beverton, 1992; Blueweiss et al., 1978; Froese and Binohlan, 2000; Froese et al., in prep.; Gulland, 1971; Musick, 1999; Palomares, 1991; Palomares and Pauly, 1999; Pauly, 1979; Pauly, 1980; Pauly, 1984; Pauly, 1986; Pauly, 1989; Pauly and Christensen, 1998; Pauly et al., 1998; Ricker, 1975; Taylor, 1958).

Plaice

We divided plaice (*Pleuronectes platessa*) into two stanza groups, as they are a target species for fisheries. For adult plaice (2+), we estimated the biomass to be 0.90 t km^{-2} y^{-1}. This estimate was based on the ratio of plaice landings in the SBNS compared to the North Sea (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total stock biomass of plaice in the North Sea (North Sea and Skagerrak; ICES Stock Assessment Database). PB and QB were calculated as 0.89 y^{-1} and 3.64 y^{-1} for adult plaice. Total mortality of juvenile plaice was calculated using F and M from ICES (2019a) and was 0.49 y^{-1}. A $W_{maturity}$ / $W_{infinity}$ value of 0.147 was estimated for plaice using FishBase – Life history tool (Asila and Ogari, 1988); Beddington and Cooke, 1983; Beverton and Holt, 1957; Beverton and Holt, 1964; Beverton, 1992; Blueweiss et al., 1978; Froese and Binohlan, 2000; Froese et al., in prep.; Gulland, 1971; Musick, 1999; Palomares, 1991; Palomares and Pauly, 1999; Pauly, 1979; Pauly, 1980; Pauly, 1984; Pauly, 1986; Pauly, 1989; Pauly and Christensen, 1998; Pauly et al., 1998; Ricker, 1975; Taylor, 1958).

Sharks

The most common sharks in the SBNS are the spurdog (*Squalus acanthias*), school shark (*Galeorhinus galeus*), small-spotted catshark (*Scyliorhinus canicula*) and smooth-hound (*Mustelus spp*.). We estimated their biomass following the approach of Sparholt (1990). We calculated the ratio of sharks to the sum of cod and whiting for the SBNS using CPUE data from the International Bottom Trawl survey in the North Sea (NS-IBTS, ICES Database of Trawl Surveys (DATRAS)). We then multiplied this ratio with the sum of cod and whiting biomass in the SBNS. We obtained a biomass of 0.0003 t km^{-2} y^{-1}. The PB was estimated to be 0.54 y^{-1} and QB 3.37 y^{-1}.

Rays

Ray species included in this functional group are thornback ray (*Raja clavata*), spotted ray (*Raja montagui*), starry ray (*Amblyraja radiata*, low abundance), rajids unid., blue skate (*Dipturus batis*, low abundance) and cuckoo ray (*Leucoraja naevus*, low abundance). We estimated their biomass according to the approach of Sparholt (1990). We calculated the ray-plaice ratio of the SBNS using CPUE data of the NS-IBTS (ICES Database of Trawl Surveys (DATRAS)). Then we multiplied the ray-plaice ratio with the calculated total stock biomass of plaice. We obtained a biomass of 1.51 t km^{-2} y^{-1}. The PB was estimated to be 0.30 y^{-1} and QB 2.90 y^{-1}.

Sea Bass

We estimated sea bass' (*Dicentrarchus labrax*) biomass following the approach of Sparholt (1990). We calculated the ratio of ratio sea bass compared to the sum of cod and whiting in the SBNS using CPUE data of the NS-IBTS (ICES Database of Trawl Surveys (DATRAS)). We then multiplied this ratio with the sum of cod and whiting biomass in the SBNS. We obtained a biomass of 0.0004 t km^{-2} y^{-1}. The PB was estimated to be 0.56 y^{-1} and QB 3.81 y^{-1}.

Demersal fish

The demersal fish FG includes demersal fish, gurnards, and dragonets. The most common species in this FG are john dory (*Zeus faber*), eelpout (*Zoarces viviparus*), shorthorn sculpin (*Myoxocephalus Scorpius*), longspined bullhead (*Taurulus bubalis*), hooknose (*Agonus cataphractus*), striped sea snail (*Liparis liparis*), greater weever (*Trachinus draco*), lesser weever (*Echiichthys vipera*) and surmullet (*Mullus surmuletus*). We estimated their biomass following the approach of Sparholt (1990). We calculated the ratio of demersal fish compared to the sum of cod and whiting in the SBNS using CPUE data from the NS-IBTS (ICES Database of Trawl Surveys (DATRAS)). Then, we multiplied this ratio with the sum of cod and whiting biomass in the SBNS. We obtained a biomass of 0.05 t km^{-2} y^{-1}. The PB was estimated to be 2.49 y^{-1} and QB 4.94 y^{-1}.

Sprat

Biomass was estimated based on the ratio of sprat (*Sprattus sprattus*) in the SBNS compared to the greater North Sea based on CPUE data (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total spawning stock biomass of sprat in the greater North Sea (North Sea, Skagerrak and Kattegat; ICES Stock Assessment DatabaseWe calculated a biomass of 0.21 t km^{-2}. PB and QB were calculated as 0.80 y^{-1} and 9.01 y^{-1}.

Mackerel

Mackerel (*Scrombus scrombus*) biomass was estimated based on the ratio of mackerel landings in the SBNS compared to the greater North Sea (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total spawning stock biomass of mackerel in the greater North Sea (North Sea, English Channel and Skagerrak). The greater North Sea spawning stock biomass required for this calculation was estimated for the North Sea by taking the North Sea portion (stock) of the spawning stock biomass in the Atlantic (ICES Stock Assessment Database). This resulted in a biomass estimate of 0.92 t km^{-2} y^{-1}. PB and QB were calculated as 1.34 y^{-1} and 4.81 y^{-1}.

Horse mackerel

We estimated the biomass of horse mackerel (*Trachurus trachurus*) following the approach of Sparholt (1990). We calculated the horse mackerel-herring ratio of the SBNS using data from the NS-IBTS (ICES Database of Trawl Surveys (DATRAS)). Then we multiplied the horse mackerel-herring ratio with the calculated biomass of whiting. We obtained a biomass of 1.51 t km^{-2} y^{-1}. The PB was estimated to be 0.34 y^{-1} and QB 4.96 y^{-1}.

Sandeels

Sandeel (*Ammodytidae*) biomass was estimated based on the ratio of sandeel landings in the SBNS compared to the North Sea (sandeel area 1r; ICES Stock Assessment Database), which was then multiplied with the total stock biomass of sandeels in the North Sea (sandeel area 1r; ICES Stock Assessment Database). This resulted in a biomass estimate of 4.39 t km^{-2} y^{-1}. PB and QB were calculated as 1.00 y^{-1} and 9.59 y^{-1}.

Dab

We estimated dab's (*Limanda limanda*) biomass based on the ratio of dab in the SBNS compared to the North Sea based on CPUE data (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total stock biomass of dab in the North Sea (ICES Stock Assessment Database). We obtained a biomass of 9.64 t km^{-2} y^{-1}. The PB was estimated to be 0.46 y^{-1} and QB 5.58 y^{-1}.

Sole

We divided sole (*Solea solea*) in two stanza groups as they are a target species for fisheries. For adult sole (2+), we estimated the biomass to be 0.32 t km^{-2} y^{-1}. This estimate was based on the ratio of sole landings in the SBNS compared to the North Sea (NS-IBTS; ICES Database of Trawl Surveys (DATRAS)), which was then multiplied with the total stock biomass of sole in the North Sea (North Sea; ICES Stock Assessment Database). PB and QB were calculated at 1.15 y^{-1} and 5.56 y^{-1} for adult sole. Total mortality of juvenile sole was calculated using F and M from ICES (2019a) and was 0.54 y^{-1}. A $W_{maturity}$ / $W_{infinity}$ value of 0.185 was estimated for sole using FishBase – Life history tool (Asila and Ogari, 1988); Beddington and Cooke, 1983; Beverton and Holt, 1957; Beverton and Holt, 1964; Beverton, 1992; Blueweiss et al., 1978; Froese and Binohlan, 2000; Froese et al., in prep.; Gulland, 1971; Musick, 1999; Palomares, 1991; Palomares and Pauly, 1999; Pauly, 1979; Pauly, 1980; Pauly, 1984; Pauly, 1986; Pauly, 1989; Pauly and Christensen, 1998; Pauly et al., 1998; Ricker, 1975; Taylor, 1958).

Other flatfish

The other common flatfish in the SBNS (besides plaice, dab and sole) are European flounder (*Platichthys flesus*), lemon sole (*Microstomus kitt*), turbot (*Scophthalmus maxima*) and brill (*Scophthalmus rhombus*). We estimated their biomass according to the approach of Sparholt (1990). We calculated the 'other flatfish-plaice' ratio of the SBNS using data from the NS-IBTS (ICES Database of Trawl Surveys (DATRAS)). Then, we multiplied the 'other flatfish-plaice' ratio with the calculated total stock biomass of plaice. We obtained a biomass of 0.15 t km^{-2} y^{-1}. The PB was estimated to be 0.83 y^{-1} and QB 6.90 y^{-1}.

Other gadoids

The FG of the other gadoids consists of fivebeard rockling (*Ciliata mustela*), poor cod (*Trisopterus minutus*), pouting (*Trisopterus luscus*), three-bearded rockling (*Gaidropsarus vulgaris*, low abundance), fourbeard rockling (*Enchelyopus cimbrius*, low abundance) and silvery pout (*Gadiculus argenteus*, low abundance). We estimated their biomass following the approach of Sparholt (1990). We calculated the ratio of other gadoids to the sum of cod and whiting in the SBNS using data from the NS-IBTS (ICES Database of Trawl Surveys (DATRAS)). We then multiplied this ratio with the sum of the biomass of cod and whiting in the SBNS. We obtained a biomass of 0.06 t km^{-2} y^{-1}. The PB was estimated to be 0.85 y^{-1} and QB 5.23 y^{-1}.

Miscellaneous filter feeding pelagic fish

The miscellaneous filter feeding group consist of shad (*Alosa* sp.), anchovy (*Engraulis encrasicolus*) and European pilchard (*Sardina pilchardus*). We could not estimate the biomass of miscellaneous filter feeding pelagic fish with the data available to us. Instead, we took the values of the North Sea model of Mackinson and Daskalov (2007) for which PB is 4.00 y^{-1} and the QB is 10.19 y^{-1}. Trophic efficiency was set to 0.98.

1.3.4. Invertebrates

Squid & cuttlefish

We included three species of squid and cuttlefish in this FG, i.e. veined squid (*Loligo forbesii*), European squid (*Loligo vulgaris*) and common cuttlefish (*Sepia officinalis*). We estimated the biomass for squid and cuttlefish by calculating the mean ratio from 1999 until 2018 between the abundance in the SBNS and the greater North Sea based on the ICES NS-IBTS data and multiplying this ratio with the total biomass of the North Sea model (Mackinson and Daskalov, 2007). The resulting biomass was 0.13 t km^{-2} y^{-1}. We based PB (11.02 y^{-1}) and QB (20.00 y^{-1}) on the North Sea model (Mackinson and Daskalov, 2007).

Large crabs + shrimps

Common large crabs with commercial value in the SBNS are edible crab (*Cancer pagurus*), common spider crab (*Maja brachydactyla*) and velvet swimming crab (*Necora puber*). Note that European lobster

(*Homarus gammarus*) is also included in this FG. Shrimp species included are *Crangon allmanni*, *Eualus pusiolus*, *Pandalus montagui*, *Spirontocaris lilljeborgi*, *Processa nouveli*, and *Pandalina* spp. We estimated the biomass of shrimp species by calculating the abundance ratio of the SBNS and North Sea (Brodie et al., 2013; National Museum of Natural History, 2001; Northeast Fisheries Science Center, 2010; Türkay, n.d.; NOAA's National Marine Fisheries Service, 2005; DFO, 2016; Hassel, 2014; Swedish county administration boards et al., 2017; Buhl-Mortensen, 2014; Parr, n.d.; Rees et al., n.d.; Miller et al., 2014; ICES, 2010); Van Guelpen, 2016; OBIS Canada, 2011; Santos, 2016; Meurisse and Semal, 2020; MBA, 2016; IFREMER, 2016; VLIZ, 2004; Libby, 2014; Van Guelpen and Pohle, 2014; The Norwegian Oil Industry Association, 2001), which we then multiplied with the best estimate biomass of Mackinson and Daskalov (2007, Table 11.8). *Pandalus borealis* and nephrops (*Nephrops norvegicus*) are not included in our model as they have a low occurrence in our study area. The total biomass of all shrimp species was added to the total large crab biomass, which we assumed to be equal to the entire North Sea (Mackinson and Daskalov, 2007). This resulted in an estimated biomass of 2.30 t km^{-2} y^{-1}. For PB, a weighted mean was taken from all relevant functional groups from Stäbler et al. (2016) (with biomass as weight) which resulted in an estimate of 1.05 y^{-1} and production-consumption (P/Q) ratio, 0.20. For these estimates, we assumed that the ratio between the functional groups in the SBNS is similar to the ratio in the North Sea.

Epifaunal macrobenthos (mobile grazers)

The biomass, PB and production over consumption (PQ) for the epifaunal macrobenthos were taken from Mackinson and Daskalov (2007). The biomass was 78 t km^{-2}; the PB 0.39 y^{-1}, and the PQ was 0.20.

Infaunal macrobenthos

The biomass, PB and production over consumption (PQ) for the infaunal macrobenthos were taken from Mackinson and Daskalov (2007). The biomass was 136 t km^{-2}; the PB 1.00 y^{-1}, and the PQ was 0.30.

Small mobile epifauna (swarming crustaceans)

The biomass, PB and production over consumption (PQ) for the small mobile epifauna were taken from Mackinson and Daskalov (2007). The biomass was 30 t km^{-2}; the PB 1.90 y^{-1}, and the PQ was 0.35.

Small infauna (polychaetes)

The biomass, PB and production over consumption (PQ) for the small infauna were taken from Mackinson and Daskalov (2007). The biomass was 150 t km^{-2}; the PB 0.90 y^{-1}, and the PQ was 0.30.

Sessile epifauna

The biomass, PB and production over consumption (PQ) for the sessile epifauna were taken from Mackinson and Daskalov (2007). The biomass was 105 t km^{-2}; the PB 0.26 y^{-1}, and the PQ was 0.20.

Meiofauna

The PB, QB and EE for the meiofauna were taken from Mackinson and Daskalov (2007). The PQ was 35 y^{-1}; the QB 125 y^{-1}, and the EE was 0.99.

Crangon crangon

We divided brown shrimp (*Crangon crangon*) into two stanza groups as they are a target species for fisheries. *Crangon crangon* larger than 50 mm were considered adults, because this is the length at recruitment for fishery. For adult *Crangon crangon* (> 50 mm), we based the biomass on a research study of Tulp et al. (2016) to be 0.36 t km^{-2} y^{-1}. The total mortality (Z) of the adults, 6.50 y^{-1}, was based on Stäbler et al. (2016), after Hufnagl et al. (2010a). Z for juveniles, 12.50 y^{-1}, was estimated in the same manner (Hufnagl et al., 2010a. Stäbler et al., 2016). The QB was set to 10.00 y^{-1} (Stäbler et al., 2016). The von Bertalanffy growth function K for *Crangon crangon* was found to be 1.17 (Hufnagl et al., 2010a). The asymptotic length of *Crangon crangon* is 79.32 mm, length at 'maturity' is 50 mm length, i.e. length at recruitment to fisheries. From both, we calculated the corresponding weight according to Hufnagl et al. (2010b; section 3.1.4). The resulting weight at maturity over asymptotic weight ($W_{maturity}$ / $W_{infinity}$) required as basic input to Ecopath is 0.24.

Blue mussels (aquaculture)

This functional group was introduced in the model for a case study in a later stage. We directed our attention to the cultivation of mussels in Belgium, commencing with a minimal initial biomass, i.e. 0.055 t km^{-2}. This was because there was no existing mussel aquaculture in Belgium in 1991. The PB and QB were taken from an Ecopath model of the northern Wadden Sea (Horn et al., 2020), and are 0.36 y^{-1} and 2.67 y^{-1} respectively.

1.3.5. Plankton

Carnivorous zooplankton

In this FG we included krill species of the order Euphausiacea, e.g. *Thysanoessa inermis*, *Meganyctiphanes norvegica*. We assumed that the carnivorous zooplankton PB, production-consumption ratio and ecotrophic efficiency in the SBNS were the same as in the North Sea (Mackinson and Daskalov, 2007). The PB is 4.00 y^{-1}, the production-consumption ratio is 0.32, and the ecotrophic efficiency is 0.99.

Herbivorous & omnivorous plankton (copepods)

The herbivorous & omnivorous plankton consist of several copepod species, e.g. *Pseudocalanus elongatus, Paracalnus parvus, Microcalanus pusillus, Acartia spp. and Temora longicornis.* We assumed that the herbivorous & omnivorous zooplankton biomass, PB and QB in the SBNS were similar to those of the North Sea model (Mackinson and Daskalov, 2007). The biomass is 16.00 t km^{-2} y^{-1}, the PB is 9.20 y^{-1} and the QB is 30.00 y^{-1}.

Gelatinous zooplankton

The gelatinous zooplankton are jellyfish, i.e. moon jellyfish (*Aurelia aurita*), blue jellyfish (*Cyanea lamarckii*) and lion's mane jellyfish (*Cyanea capillata*). We assumed that the gelatinous zooplankton biomass, PB and P/Q ratio in the SBNS were the same as in the SNS model (Stäbler et al., 2016). The biomass is 0.09 t km^{-2} y^{-1}, the PB is 2.86 y^{-1} and the production-consumption ratio is 0.45.

Phytoplankton

We assumed that the phytoplankton biomass and PB in the SBNS were the same as for the entire North Sea (Mackinson and Daskalov, 2007). The biomass is 7.50 t km^{-2} y^{-1} and the PB is 286.70 y^{-1}.

1.3.6. Detritus

We combined the two detritus groups (POM and DOM) from the North Sea model of Mackinson and Daskalov (2007). The sum of the biomass of these two groups resulted in the detritus biomass in our model: 50.00 t km^{-2} y^{-1}.

Discards

The biomass of the discards in the SBNS were estimated at 0.0001 t km^{-2} y^{-1}. We assumed that the discards biomass in our study area was equal to that of the SNS (Stäbler et al., 2016).

1.4. Diets

We based the diets of our functional groups on Stäbler et al. (2016), which were adjusted to fit our functional groups. To achieve this, the diets for some functional groups from Stäbler et al. (2016) were merged by taking the weighted mean of the functional groups' diets assuming that the biomass ratio between functional groups remained equal. The weight used for calculating the weighted mean was the biomass of the corresponding functional groups. For example, we grouped gurnards, dragonets, and small demersal fish into a single functional group, i.e. demersal fish, and thus a single diet. We used their corresponding biomass' as the weight for taking the weighted mean for each prey item. Several functional groups of the SNS model of Stäbler et al. (2016) did not occur in our model. We eliminated these functional groups from the diets of our functional groups and recalculated the diet proportions back to a total of one while keeping the diet items ratio equal. Note that there is one exception to our methodology to estimate diets: the diet of blue mussels. Their diet was based on Horn et al. (2020) and as filter feeders, they mainly feed on phytoplankton, detritus, and herbivorous zooplankton. An overview of all diets is provided in Table 2.

Table 2: An overview of the diets in the Southern Bight of the North Sea.

	Prey \ predator	1	2	3	4	5	6	7	8
1	Harbour porpoise								
2	Seals								
3	Seabirds (discard)								
4	Seabirds (non-discard)								
5	Sharks								
6	Rays								1.11E-03
7	Juvenile Cod	3.66E-02	3.82E-02	5.42E-03	2.30E-03		8.46E-03	6.22E-03	9.83E-03
8	Cod (adult)		7.69E-02						9.52E-03
9	Juvenile Whiting	3.04E-02	5.20E-03	1.33E-02	1.80E-02	2.25E-03	4.95E-03	1.75E-02	5.40E-02
10	Whiting (adult)	9.36E-02	8.34E-02			1.08E-01	4.48E-03		8.71E-02
11	Other gadoids	6.95E-02	3.36E-02		5.01E-04	1.21E-01	3.31E-02	2.92E-02	2.67E-02
12	Demersal fish	5.87E-04	1.38E-01	2.60E-03	9.01E-04	1.29E-02	1.05E-03	5.33E-02	3.59E-02
13	Juvenile Herring	1.62E-03	1.04E-05			1.78E-03	3.62E-03	4.67E-03	1.69E-02
14	Herring (adult)	4.85E-03	7.38E-03	4.83E-02	5.91E-02	1.90E-01	1.30E-02	3.22E-03	1.58E-01
15	Sprat	1.53E-01	3.39E-03	4.44E-02	5.45E-02	3.88E-02	4.44E-03	1.87E-02	1.10E-02
16	Mackerel	2.88E-02		6.04E-03	2.01E-02	1.03E-01			4.98E-05
17	Horse mackerel	1.81E-02	1.50E-02			1.74E-02		8.40E-04	2.99E-03
18	Sandeels	4.01E-01	3.65E-01	2.09E-01	3.33E-01	3.62E-02	3.34E-01	1.07E-01	4.78E-02
19	Juvenile Plaice			2.71E-03	3.01E-04			1.73E-05	3.76E-02
20	Plaice (adult)		7.44E-02			5.40E-02	2.06E-03		4.63E-03
21	Dab		5.98E-02		1.00E-04	1.82E-02	1.29E-02	3.58E-03	2.17E-01
22	Other flatfish		5.57E-02						3.18E-03
23	Juvenile Sole			2.08E-04			1.19E-03	1.88E-03	3.49E-03
24	Sole (adult)		4.44E-02			1.39E-04	3.10E-03		
25	Sea Bass	4.51E-07	1.06E-04	2.00E-06	6.92E-07	9.93E-06	8.10E-07	4.10E-05	2.76E-05
26	Pelagic fish			2.60E-03		4.72E-04		1.16E-04	5.55E-05
27	Squid & cuttlefish	1.61E-01		3.85E-03	1.00E-04	6.09E-02	2.93E-03	6.14E-03	1.07E-02
28	Carnivorous zooplankton			1.46E-02	1.00E-04	6.10E-03	4.90E-03	2.26E-02	7.91E-04
29	Herbivorous plankton (copepods)			5.31E-03	6.01E-04		7.21E-07	6.50E-06	
30	Gelatinous zooplankton					3.51E-02		1.79E-03	1.00E-03
31	Large crabs + shrimps			3.98E-02	1.04E-02	9.35E-02	1.53E-01	1.57E-01	1.08E-01
32	Blue mussels (aquaculture)		1.15E-04	1.04E-04	1.00E-04				1.13E-04
33	Epifaunal macrobenthos (mobile grazers)			1.05E-04		4.78E-02	1.40E-01	1.97E-01	1.01E-01
34	Infaunal macrobenthos			1.60E-02	3.60E-01	2.31E-02	6.51E-03	8.25E-02	3.74E-02
35	Crangon (below 5cm)			2.71E-03		6.12E-03	1.90E-02	1.26E-01	9.44E-03
36	Crangon (commercial size)					2.34E-03	7.26E-03	3.96E-02	3.44E-03
37	Small mobile epifauna (swarming crustaceans)					6.38E-03	1.55E-01	4.44E-03	2.49E-05
38	Small infauna (polychaetes)			5.21E-03	5.01E-04	1.28E-02	8.29E-02	1.16E-01	8.47E-04
39	Sessile epifauna			2.40E-02	1.07E-01	1.04E-03		1.49E-04	2.61E-04
40	Meiofauna					7.26E-04	2.16E-03		
41	Phytoplankton								
42	Detritus								
43	Discards			4.86E-01	3.22E-02				
	Import			6.77E-02					

Table 2: An overview of the diets in the Southern Bight of the North Sea (continued).

	Prey \ predator	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
1	Harbour porpoise								
2	Seals								
3	Seabirds (discard)								
4	Seabirds (non-discard)								
5	Sharks								
6	Rays				2.72E-05				
7	Juvenile Cod	2.26E-03	1.11E-03		5.13E-03				1.98E-03
8	Cod (adult)								
9	Juvenile Whiting	9.61E-04	1.93E-02	3.12E-04	1.49E-02				5.73E-05
10	Whiting (adult)		1.34E-04						
11	Other gadoids	1.09E-03	7.57E-03	1.76E-02	1.51E-02				3.96E-04
12	Demersal fish	6.08E-02	2.14E-02	1.96E-02	5.27E-02				1.45E-03
13	Juvenile Herring	2.44E-03	2.90E-02		3.54E-04				1.27E-02
14	Herring (adult)								
15	Sprat	1.43E-02	2.92E-01	4.05E-03	9.37E-03				2.92E-02
16	Mackerel				3.02E-04				8.04E-06
17	Horse mackerel	1.53E-03	9.88E-03		3.95E-05				1.02E-01
18	Sandeels	1.62E-01	3.26E-01	1.04E-03	2.89E-01				1.20E-01
19	Juvenile Plaice								
20	Plaice (adult)								
21	Dab	6.99E-04	1.19E-04	5.20E-03	2.40E-02				
22	Other flatfish	3.27E-06							
23	Juvenile Sole	1.23E-03	5.33E-04						
24	Sole (adult)				2.92E-04				
25	Sea Bass	4.67E-05	1.64E-05	1.50E-05	4.05E-05				1.12E-06
26	Pelagic fish	4.93E-04	1.77E-05						
27	Squid & cuttlefish	8.37E-02	9.60E-03	8.32E-04	1.96E-02				8.10E-03
28	Carnivorous zooplankton	1.32E-01	4.86E-02	1.05E-01	1.64E-02	2.73E-01	3.09E-01		6.60E-02
29	Herbivorous plankton (copepods)	6.55E-03	3.09E-03	3.12E-01	5.36E-02	6.75E-01	6.70E-01	8.89E-01	4.85E-01
30	Gelatinous zooplankton	4.57E-03	4.05E-03						8.49E-02
31	Large crabs + shrimps	1.33E-01	4.39E-02	1.78E-02	1.86E-01				2.28E-02
32	Blue mussels (aquaculture)		1.10E-04		9.07E-05				
33	Epifaunal macrobenthos (mobile grazers)	7.98E-02	8.99E-02	1.35E-01	8.85E-02				2.50E-02
34	Infaunal macrobenthos	2.60E-02	4.10E-02	1.77E-01	4.58E-02				2.12E-04
35	Crangon (below 5cm)	7.48E-02	1.51E-02	2.57E-04	5.32E-03				3.95E-04
36	Crangon (commercial size)	1.74E-02	3.21E-03	9.79E-05	1.64E-03				
37	Small mobile epifauna (swarming crustaceans)	1.35E-02	2.15E-03	2.87E-02	9.80E-02	5.19E-02	2.06E-02		9.07E-03
38	Small infauna (polychaetes)	1.81E-01	3.22E-02	1.76E-01	5.52E-02				3.35E-03
39	Sessile epifauna	4.79E-05	1.00E-04		4.62E-06				5.98E-03
40	Meiofauna	3.27E-06			1.83E-02				1.00E-06
41	Phytoplankton		2.54E-05					1.11E-01	2.21E-02
42	Detritus								
43	Discards								
	Import								

Table 2: An overview of the diets in the Southern Bight of the North Sea (continued).

	Prey \ predator	17	18	19	20	21	22	23	24
1	Harbour porpoise								
2	Seals								
3	Seabirds (discard)								
4	Seabirds (non-discard)								
5	Sharks								
6	Rays								
7	Juvenile Cod						5.00E-03		
8	Cod (adult)								
9	Juvenile Whiting	3.33E-02					9.81E-04		
10	Whiting (adult)								
11	Other gadoids	4.28E-03					2.95E-03		
12	Demersal fish	7.15E-02					1.20E-02	1.28E-02	
13	Juvenile Herring	1.31E-01		2.03E-04			1.22E-04		
14	Herring (adult)								
15	Sprat	3.26E-02					1.49E-02		
16	Mackerel								
17	Horse mackerel	8.44E-02							
18	Sandeels	2.00E-02		7.63E-03			1.58E-02		
19	Juvenile Plaice								
20	Plaice (adult)								
21	Dab	6.07E-03					5.17E-02		
22	Other flatfish						5.24E-02		
23	Juvenile Sole								
24	Sole (adult)								
25	Sea Bass	5.49E-05					9.23E-06	9.82E-06	
26	Pelagic fish								
27	Squid & cuttlefish	1.14E-01							
28	Carnivorous zooplankton	1.70E-01	6.63E-02				3.89E-02		
29	Herbivorous plankton (copepods)	5.89E-02	6.41E-01			1.25E-02			
30	Gelatinous zooplankton	8.48E-05		3.46E-03			5.37E-02		
31	Large crabs + shrimps	7.10E-02		1.69E-02	1.09E-01	1.07E-02	6.34E-02		5.44E-02
32	Blue mussels (aquaculture)								
33	Epifaunal macrobenthos (mobile grazers)	1.73E-01	8.40E-04	1.05E-01	2.13E-02	2.58E-01	1.87E-01	1.28E-02	1.11E-02
34	Infaunal macrobenthos	8.74E-04	5.88E-03	1.75E-01	4.36E-01	2.40E-01	8.86E-02	1.15E-01	1.27E-02
35	Crangon (below 5cm)	2.24E-03		5.90E-05	8.60E-03	2.47E-04	2.30E-03		
36	Crangon (commercial size)	9.58E-04		1.00E-05	1.52E-03	9.50E-05	8.82E-04		
37	Small mobile epifauna (swarming crustaceans)	1.93E-02	1.63E-02	1.96E-01	5.13E-02	3.29E-01	1.15E-01		
38	Small infauna (polychaetes)	7.78E-03	1.97E-01	4.78E-01	3.62E-01	1.38E-01	1.99E-01	4.23E-01	9.22E-01
39	Sessile epifauna			1.42E-02		1.10E-02	9.58E-02		
40	Meiofauna		5.02E-02	3.46E-03	1.03E-02	9.00E-04		4.36E-01	
41	Phytoplankton		2.28E-02						
42	Detritus								
43	Discards								
	Import								

Table 2: An overview of the diets in the Southern Bight of the North Sea (continued).

	Prey \ predator	25	26	27	28	29	30	31	32
1	Harbour porpoise								
2	Seals								
3	Seabirds (discard)								
4	Seabirds (non-discard)								
5	Sharks								
6	Rays								
7	Juvenile Cod			1.13E-02					
8	Cod (adult)								
9	Juvenile Whiting	1.49E-03		9.51E-04					
10	Whiting (adult)	3.49E-03							
11	Other gadoids	1.96E-02							
12	Demersal fish	2.08E-02		5.70E-03					
13	Juvenile Herring			9.51E-04					
14	Herring (adult)								
15	Sprat			1.13E-02					
16	Mackerel	1.33E-01							
17	Horse mackerel	6.67E-02		1.13E-02					
18	Sandeels	2.99E-03		4.51E-02					
19	Juvenile Plaice								
20	Plaice (adult)			5.70E-03					
21	Dab			5.70E-03					
22	Other flatfish			1.14E-02					
23	Juvenile Sole	1.06E-02							
24	Sole (adult)	1.10E-03		5.70E-03					
25	Sea Bass	1.60E-05		4.38E-06					
26	Pelagic fish	6.89E-02	5.31E-02	2.24E-02					
27	Squid & cuttlefish	8.81E-03	5.60E-03	5.63E-02			7.36E-02		
28	Carnivorous zooplankton		1.49E-01	2.31E-01	5.83E-02		2.94E-01	5.62E-03	
29	Herbivorous plankton (copepods)	2.10E-01	6.95E-01	3.36E-01	8.27E-01		2.94E-01	1.12E-02	1.00E-02
30	Gelatinous zooplankton		3.32E-02						
31	Large crabs + shrimps	3.73E-01	9.48E-03	1.44E-02			4.85E-02	2.25E-03	
32	Blue mussels (aquaculture)								
33	Epifaunal macrobenthos (mobile grazers)	1.05E-03	2.66E-02					3.53E-01	
34	Infaunal macrobenthos							3.61E-01	
35	Crangon (below 5cm)	3.55E-02	3.56E-03	5.40E-03			1.82E-02	5.83E-04	
36	Crangon (commercial size)	3.49E-02	1.36E-03	2.07E-03			6.96E-03	2.23E-04	
37	Small mobile epifauna (swarming crustaceans)		1.22E-02	1.70E-01	1.15E-01		1.18E-01	2.98E-02	
38	Small infauna (polychaetes)		1.11E-02	2.24E-02				1.39E-01	
39	Sessile epifauna							8.62E-02	
40	Meiofauna							1.12E-02	
41	Phytoplankton			5.63E-02		9.47E-01	1.47E-01		8.50E-01
42	Detritus					5.26E-02			1.40E-01
43	Discards								
	Import	8.84E-03							

Table 2: An overview of the diets in the Southern Bight of the North Sea (continued).

	Prey \ predator	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
1	Harbour porpoise								
2	Seals								
3	Seabirds (discard)								
4	Seabirds (non-discard)								
5	Sharks								
6	Rays								
7	Juvenile Cod								
8	Cod (adult)								
9	Juvenile Whiting								
10	Whiting (adult)								
11	Other gadoids								
12	Demersal fish				5.07E-03				
13	Juvenile Herring								
14	Herring (adult)								
15	Sprat								
16	Mackerel								
17	Horse mackerel								
18	Sandeels								
19	Juvenile Plaice				4.52E-04				
20	Plaice (adult)								
21	Dab								
22	Other flatfish				1.62E-03				
23	Juvenile Sole								
24	Sole (adult)								
25	Sea Bass				3.89E-06				
26	Pelagic fish								
27	Squid & cuttlefish								
28	Carnivorous zooplankton								
29	Herbivorous plankton (copepods)				2.88E-03				
30	Gelatinous zooplankton								
31	Large crabs + shrimps				1.21E-02				
32	Blue mussels (aquaculture)								
33	Epifaunal macrobenthos (mobile grazers)	5.91E-02			3.69E-03				
34	Infaunal macrobenthos	2.37E-01			4.34E-04				
35	Crangon (below 5cm)			4.31E-03	4.14E-02				
36	Crangon (commercial size)								
37	Small mobile epifauna (swarming crustaceans)	5.91E-02	3.45E-02		8.29E-02	1.54E-01			
38	Small infauna (polychaetes)	2.96E-01	1.90E-01		3.86E-01		9.09E-02		
39	Sessile epifauna				2.19E-02				
40	Meiofauna		8.62E-02	9.96E-01	4.42E-01	2.31E-01	2.73E-01		2.00E-01
41	Phytoplankton	5.91E-02						3.33E-01	
42	Detritus	2.37E-01	6.90E-01			6.15E-01	6.36E-01	6.67E-01	8.00E-01
43	Discards	5.38E-03							
	Import								

2. Defining fleets and assigning landings and discards

2.1. Fleets (commercial) distinguished by STECF gear types

Nine commercial EwE fleets were distinguished using STECF gear types. In total, 17 gear types were included in the STECF data for the SBNS (STECF, 2017; https://stecf.jrc.ec.europa.eu/dd/effort/graphs-annex). These gear types were allocated to their corresponding EwE fleet (Table 3).

Table 3: Structure of the EwE fleets in the Southern Bight of the North Sea model and the allocation of gear types

Gear description	Gear types	EwE fleet
Beam trawls ≥ 120 mm	BT1	beam
Beam trawls ≥ 80 mm and < 120 mm	BT2	
Beam trawls > 31 mm and < 80 mm or missing mesh size	BEAM	
Bottom trawls and seines ≥ 100 mm	TR1	demersal
Bottom trawls and seines ≥ 16 mm and < 32 mm	TR3	
Bottom trawls and seines ≥ 70 mm and < 100 mm	TR2	
Danish seine ≥ 90 mm	DEM_SEINE	
OTTER ≥ 32 mm and < 70 mm or missing mesh size	OTTER	
Dredges	DREDGE	dredge
Longlines	LL1	hooks
Gill nets, entangling nets	GN1	nets
Trammel nets	GT1	
Unspecified gear type	NONE	other
Pelagic seine (all mesh size)	PEL_SEINE	pelagic
Pelagic trawls (all mesh size)	PEL_TRAWL	
Pots	POTS	pots
Beam trawls < 31 mm and < 90 mm	BEAM	shrimp

2.2. Assigning 1991 landings to fleets

Catch data, i.e. landings and discards at age, from 2003 – 2017 for the SBNS (ICES are IVc) was obtained from STECF FDI (STECF, 2017; https://stecf.jrc.ec.europa.eu/dd/effort/graphs-annex). Historical catch data from ICES (https://www.ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx) was obtained for the catches of 1991 in the SBNS. We applied methods used by Bentley et al. (2018) and Stäbler et al. (2016) to estimate the landings and discards for the SBNS in 1991. Catches of both 1991 and 2003 were first allocated to the EwE FGs of the model. Next, the contribution of each fleet to the catches of 2003 was calculated. Because this fleet data was not available for 1991, the landings of the 1991 EwE FGs were multiplied with the contribution of fleets in 2003. This resulted in total landings biomass for each functional group and fleet. Note that for multi-stanza FGs, we assumed that all landings belonged to the adult group of that multi-stanza.

2.3. Calculating discards for 1991

We estimated the discards for 1991 by calculating the ratio of landings and discards in 2003 per fleet and per FG. We multiplied the landing-discard ratio of 2003 with the landings of 1991 per FG and per fleet to estimate the discards in 1991 assuming the ratio remained the same from 1991 to 2003. We also assumed that all discards in multi-stanza FGs belonged to the juvenile group of that FG.

2.4. Recreational fishery

We included Belgian recreational fisheries based on Verleye et al. (2019). We incorporated the recreational fleets (i.e. anglers (boat), trawlers, anglers (land), nets and others) grouped according to Verleye et al. (2019). As only data from 2018 onwards is available for Belgian recreational fisheries, the recreational catch for target species, such as cod, sea bass, mackerel, plaice, sole and brown shrimp was limited in the model.

3. Balancing of the Ecopath model

The previous chapter describes an unbalanced EwE model of the SBNS. Initially thirteen FGs were unbalanced when using the basic input parameters from chapter 1. Energy ‘imbalance’ is determined by examining each group’s ecotrophic efficiency (EE). A group’s EE exceeding 1 indicates that the energy demand placed upon that group exceeds its PB and therefore needs to be reduced.

3.1. Pre-balance diagnostics

We used pre-balance (PREBAL) diagnostics as described in Link (2010) to identify ecological issues in the model and to balance it obeying the rules of thermodynamics and ecology. Group biomass should span 5 to 7 orders of magnitude and the slope should decline by 5 to 10% with each increasing trophic level. PB and QB ratios should also show a general decline with increasing trophic level, whilst P/Q ratios should fall between 0.1 and 0.3 (Darwall et al., 2010, Heymans et al., 2016). Respiration/assimilation should be below 1 as the proportion of biomass lost through respiration cannot exceed the biomass of food assimilated (Heymans et al., 2016).

Table 4: Basic estimates from the initial unbalanced model of the Southern Bight of the North Sea. Numbers highlighted in red indicate unbalances, i.e. the ecothrophic efficiency is too high (>1), blue values are estimated by Ecopath.

Functional group	Ecopath parameters								
	TL	B (t km^{-2})	Z (y^{-1})	PB (y^{-1})	QB (y^{-1})	EE	PQ (y^{-1})	BA (t km^{-2})	BA rate (y^{-1})
Harbour porpoise	4.42	0.03		0.02	24.64	0.00	0.00		
Seals	4.67	0.01		0.09	26.84	0.00	0.00		
Seabirds (discard)	3.03	0.0004		0.10	60.52	0.17	0.00		
Seabirds (non-discard)	3.74	0.0016		1.12	48.20	0.02	0.02		
Sharks	4.50	0.0003		0.54	3.37	66.26	0.16		
Rays	4.09	1.51		0.30	2.89	0.06	0.10		
Cod									
Juvenile Cod	4.16	0.01	1.13		7.05	27.65	0.16		
Cod (adult)	4.53	0.02	1.13		3.20	38.81	0.35		
Whiting									
Juvenile Whiting	4.16	0.24	2.80		13.41	0.49	0.21		
Whiting (adult)	4.10	0.09	1.31		5.41	1.09	0.24		
Other gadoids	3.54	0.06		0.85	5.23	9.05	0.16		
Demersal fish	4.11	0.05		2.49	4.94	7.53	0.50		

Table 4: Basic estimates from the initial unbalanced model of the Southern Bight of the North Sea. Numbers highlighted in red indicate unbalances, i.e. the ecothrophic efficiency is too high (>1), blue values are estimated by Ecopath (continued).

Functional group	**Ecopath parameters**								
	TL	**B (t km^{-2})**	**Z (y^{-1})**	**PB (y^{-1})**	**QB (y^{-1})**	**EE**	**PQ (y^{-1})**	**BA (t km^{-2})**	**BA rate (y^{-1})**
Herring									
Juvenile Herring	3.33	0.04	0.87		18.00	35.34	0.05		
Herring (adult)	3.36	0.76	0.87		6.78	0.19	0.13		
Sprat	2.89	0.21		0.80	9.01	4.57	0.09		
Mackerel	3.69	0.92		1.34	4.81	0.21	0.28		
Horse mackerel	4.34	1.51		0.34	4.96	3.23	0.07		
Sandeels	3.17	4.39		1.00	9.59	0.80	0.10		
Plaice									
Juvenile Plaice	3.55	0.11	0.49		9.39	1.31	0.05		
Plaice (adult)	3.60	0.90	0.89		3.63	0.11	0.25		
Dab	3.61	9.63		0.46	5.58	0.08	0.08		
Other flatfish	3.86	0.15		0.84	6.90	1.13	0.12		
Sole									
Juvenile Sole	3.40	0.14	0.54		9.74	0.13	0.06		
Sole (adult)	3.54	0.32	1.15		5.56	0.10	0.21		
Sea Bass	4.30	0.00		0.56	3.81	31.18	0.15		
Pelagic fish	3.36	0.03		4.00	10.19	0.98	0.39		
Squid & cuttlefish	3.64	0.13		11.03	20.00	1.03	0.55		
Carnivorous zooplankton	3.13	2.34		4.00	12.50	0.99	0.32		
Herbivorous plankton (copepods)	2.00	16.00		9.20	30.00	0.42	0.31		
Gelatinous zooplankton	3.48	0.09		2.86	6.35	1.78	0.45		
Large crabs + shrimps	3.60	2.30		1.05	5.27	1.32	0.20		
Blue mussels (aquaculture)	2.01	0.06		0.36	2.67	0.01	0.13		
Epifaunal macrobenthos (mobile grazers)	2.98	78.00		0.39	1.94	0.99	0.20		
Infaunal macrobenthos	2.44	136.00		1.00	3.33	0.41	0.30		
C. crangon									
Crangon (below 5cm)	3.25	0.58	12.50		25.14	0.09	0.50		
Crangon (commercial size)	3.43	0.36	6.51		10.00	0.05	0.65		
Small mobile epifauna (swarming crustaceans)	2.52	30.00		1.90	5.43	1.30	0.35		
Small infauna (polychaetes)	2.48	150.00		0.90	3.00	1.45	0.30		
Sessile epifauna	2.00	105.00		0.26	1.30	0.07	0.20		
Meiofauna	2.25	22.63		35.00	125.00	0.99	0.28		
Phytoplankton	1.00	7.50		286.70		0.24			
Detritus	1.00	50.00				1.14		-370.91	-7.42
Discards	1.00	0.00				5.16			

3.1.1. Biomass

The biomass (log scale) in the unbalanced SBNS model spans seven orders of magnitude, falling within the ecological range (5-7 orders) and the slope declines by 130 %, falling below the ecological range (5-10%) suggested by Link (2010; Fig. 3). Several groups show variance from the trend line. The PREBAL ecological rules of thumb from Link et al. (2010) are applicable to poikilotherms and not so much to homeotherms. Marine mammals and seabirds consequently show large divergence. Sandeels and dab seem to have a high biomass and may be overestimated.

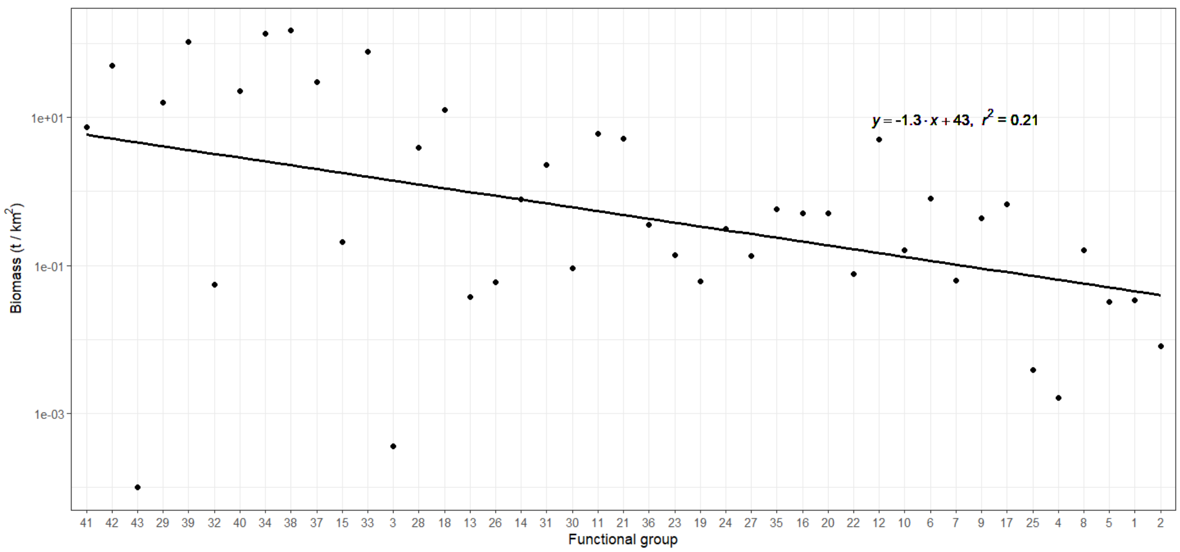

Figure 3: PREBAL diagnostic biomass. Functional groups are ordered by increasing trophic level.

3.1.2. Production/biomass

PB (log scale) in the unbalanced SBNS model spans five orders of magnitude, falling within the ecological range (5-7 orders) and the slope declines by 120%, falling below the ecological range (5-10%) suggested by Link (2010; Fig. 4). Overall, there is little variance from the trend line apart from seabirds, marine mammals, phytoplankton, juvenile brown shrimp (*Crangon crangon*), and squid and cuttlefish. The homeotherms, i.e. seabirds and marine mammals have higher consumptive demands per unit of body mass than poikilotherms.

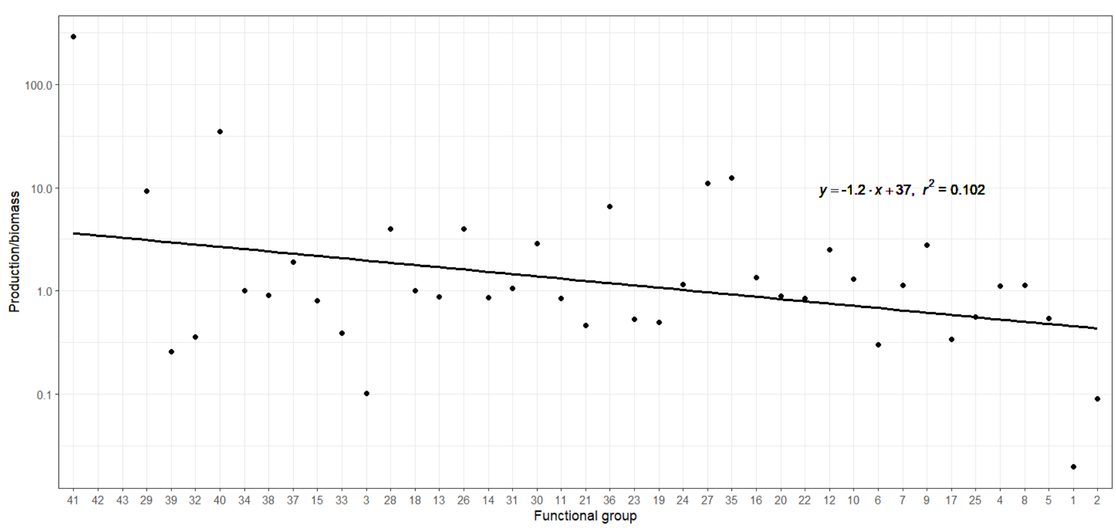

Figure 4: PREBAL diagnostic production/biomass. Functional groups are ordered by increasing trophic level.

3.1.3. Consumption/biomass

QB is expected to decline with increasing trophic level following basic energetic assumptions. QB (log scale) in the unbalanced SBNS model spans two orders of magnitude and the slope declines by 28 % (Fig. 5). Blue mussels (aquaculture) and benthos have low QB ratios. The opposite is true for seabirds and marine mammals being homeotherms, which demands a high amount of energy. These deviances may affect the trend line.

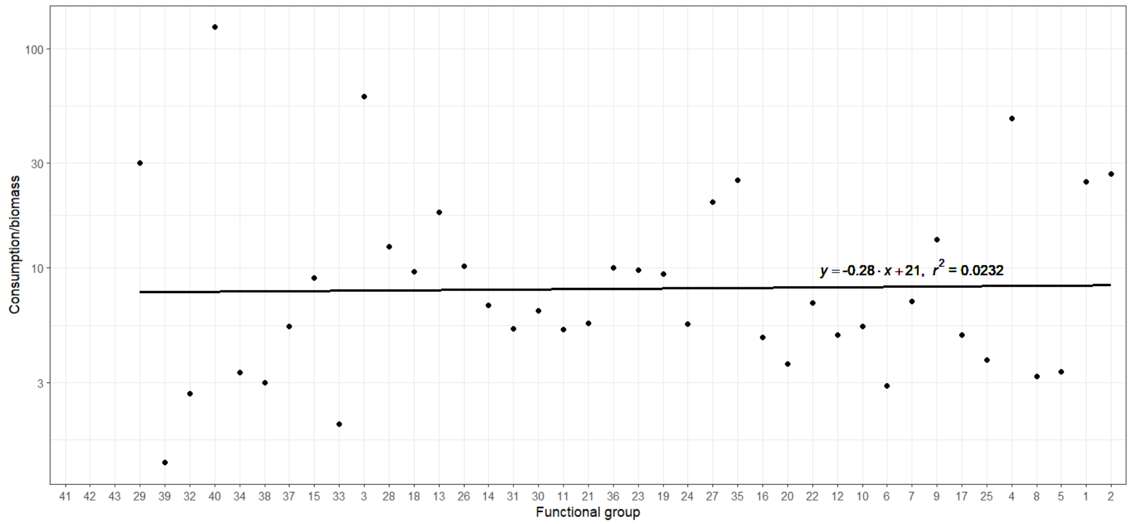

Figure 5: PREBAL diagnostic consumption/biomass. Functional groups are ordered by increasing trophic level.

3.1.4. Production/consumption

There are several FGs falling outside the suggested P/Q range of 0.1 - 0.3 (Fig. 6). However, most fish groups fall within or close to the range, with few exceptions such as pelagic fish and demersal fish. There are invertebrate species such brown shrimp (*Crangon crangon*), squid and cuttlefish that have high P/Q. These ratios are similar to values found by Stäbler et al. (2016). Nevertheless, it is advised to revise the ratios of the FGs that fall outside the advised range. Marine mammals and seabirds are slow producing and the energy from consumption is prioritised for other physiological processes such as thermoregulation.

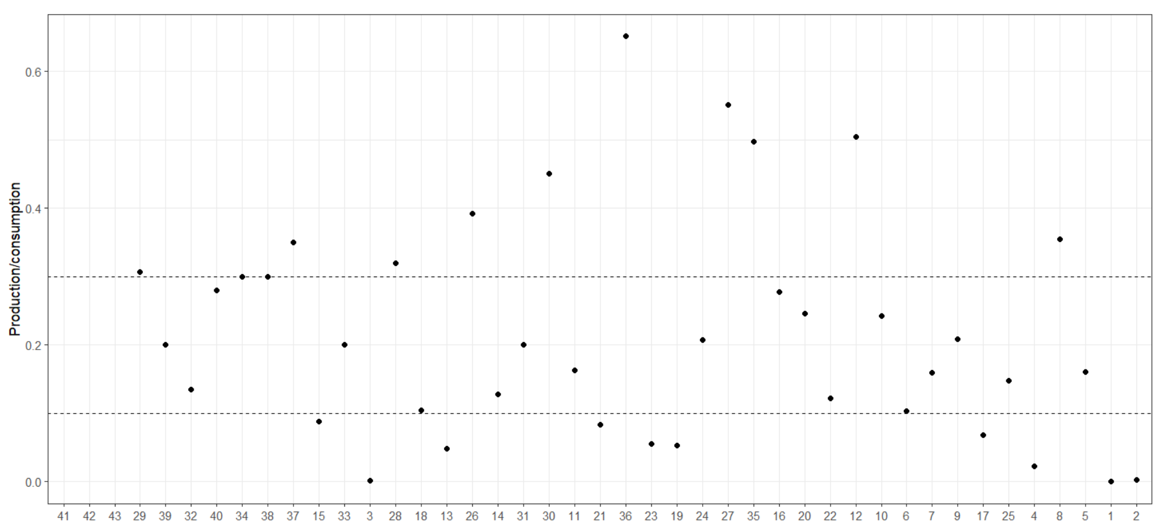

Figure 6: PREBAL diagnostic production/consumption. Functional groups are ordered by increasing trophic level.

3.1.5. Respiration/assimilation

All respiration/assimilation values fall below 1.

3.2. Revision of the input data

By altering the basic input parameters and group diet composition based on the PREBAL diagnostics, we balanced the basic estimates. Groups with the highest EE estimates were adjusted first as suggested by (Heymans et al., 2016). By doing so, other imbalances may improve as well. The diets of functional groups were adjusted in case high cannibalism was present in the FG. The vast majority of imbalances in the model were corrected by adjusting functional group input parameters, either to fix ecological issues or to reduce EE estimates. The adjustments to our input parameters were performed keeping the mother models, i.e. North Sea (Mackinson and Daskalov, 2007), and SNS (Stäbler et al., 2016), in mind. The changes made to the input parameters are listed below. The balanced food web is illustrated in Figure 8. Below in Table 5, we provide the input parameters of the balanced model of the SBNS. In Table 6, the revised diet composition is provided. In addition, the basic estimates are shown in Table 6.

Table 5: Balancing steps towards a balanced Ecopath model of the Southern Bight of the North Sea. Ecotrophic efficiency (EE), biomass (B), total mortality (Z), production over consumption (PQ), production over biomass (PB) and functional group (FG).

Balancing step	Functional group	Issue	Parameter	Initial value	Adjusted value	Unit
1	Sharks	EE: 66	B	0.00	0.03	t km^{-2}
2	Juvenile herring	EE: 34 & PQ: 0.048	Z	0.87	5.70	y^{-1}
3	Sea Bass	EE= 77	B	0.00004	0.00380	t km^{-2}
4	Juvenile cod	EE: 14.135	Z	1.13	1.70	y^{-1}
5	Adult cod	PQ: 0.333	B	0.02	0.22	t km^{-2}
6	Demersal fish	EE: 8.914 & PQ: 0.5	Z	2.49	1.48	y^{-1}
			B	0.05	0.95	t km^{-2}
7	Other gadoids	EE: 8.083	B	0.01	0.06	t km^{-2}
8	Sprat	EE: 5.306 & PQ: 0.089	PB	0.80	2.60	y^{-1}
			B	0.21	0.35	t km^{-2}
9	Juvenile plaice	EE: 4.928 & PQ: 0.053	Z	0.50	2.30	y^{-1}
10	Discards	EE: 3.849	B	0.00	50.00	t km^{-2}
11	Adult whiting	EE: 3.666 & PQ: 2.242	B	0.09	0.35	t km^{-2}
12	Horse mackerel	EE: 2.383	PB	0.34	0.90	y^{-1}
13	Large crabs & shrimp	EE: 2.296	B	2.30	5.35	t km^{-2}
14	Gelatinous zooplankton	EE: 2.046	B	0.09	0.19	t km^{-2}
15	Squid & cuttlefish	EE: 1.681	Diet portion of FG 27 in diet of FG 27	0.06	0.03	y^{-1}
			Diet portion of FG 29 in diet of FG 27	0.31	0.34	y^{-1}
			PB	11.05	4.50	y^{-1}
			B	0.13	0.60	t km^{-2}
16	Other flatfish	EE: 2.044	B	0.15	0.40	t km^{-2}
			PB	0.84	0.95	y^{-1}
17	Sprat	EE: 1.719	B	0.35	0.58	t km^{-2}
			PB	2.60	2.70	y^{-1}
18	Sandeels	EE: 1.689	PB	1.00	2.00	y^{-1}
19	Small infauna (polychaetes)	EE: 1.501	PB	0.90	1.60	y^{-1}
20	Small mobile epifauna	EE: 1.412	PB	1.00	3.30	y^{-1}
21	Demersal fish	EE: 1.454	B	0.95	1.50	t km^{-2}
22	Juvenile cod	EE 1.500	PB	1.70	2.10	y^{-1}

Table 5: Balancing steps towards a balanced Ecopath model of the Southern Bight of the North Sea. Ecotrophic efficiency (EE), biomass (B), total mortality (Z), production over consumption (PQ), production over biomass (PB) and functional group (FG) (continued).

Balancing step	Functional group	Issue	Parameter	Initial value	Adjusted value	Unit
23	Epifaunal macrobenthos	EE: 1.273	PB	0.39	0.55	y^{-1}
24	Large crabs & shrimp	EE: 1.145	B	5.35	5.50	t km^{-2}
			PB	1.05	1.20	y^{-1}
25	Gelatinous zooplankton	EE: 1.192	B	0.19	0.25	t km^{-2}
26	Sea bass	EE: 1.199	B	0.00	0.01	t km^{-2}
27	Other gadoids	EE: 1.065	B	0.59	0.65	t km^{-2}
28	Sprat	EE: 1.021	B	0.58	0.63	t km^{-2}
29	Epifuanal macrobenthos	EE: 1.026	PB	0.55	0.60	y^{-1}
30	Small infauna (polychaetes)	EE: 1.082	PB	1.60	1.80	y^{-1}
31	Small mobile epifauna	EE: 1.055	PB	2.30	3.65	y^{-1}
32	Squid & cuttlefish	EE: 1.00	B	0.60	0.62	t km^{-2}
33	Detritus	EE: 1.546	Unassim. Consumption (FG: 29, 39, 40)	0.20	0.40	y^{-1}
			Diet portion of FG 40 in diet of FG 40	0.20	0.10	y^{-1}
			Diet portion of FG 42 in diet of FG 40	0.80	0.90	y^{-1}
34	Discards	EE: 5.942	Diet portion of FG 34 in diet of FG 33	0.24	0.28	y^{-1}
			Diet portion of FG 42 in diet of FG 33	0.24	0.24	y^{-1}
			Diet portion of FG 43 in diet of FG 33	0.05	0.01	y^{-1}
35	Juvenile Sole	PQ: 0.055	Z	0.54	1.10	y^{-1}
36	Demersal fish	EE: 1.03	PB	1.41	1.55	y^{-1}
37	Dab	PQ: 0.083	PB	0.48	0.60	y^{-1}

3.3. Balanced model

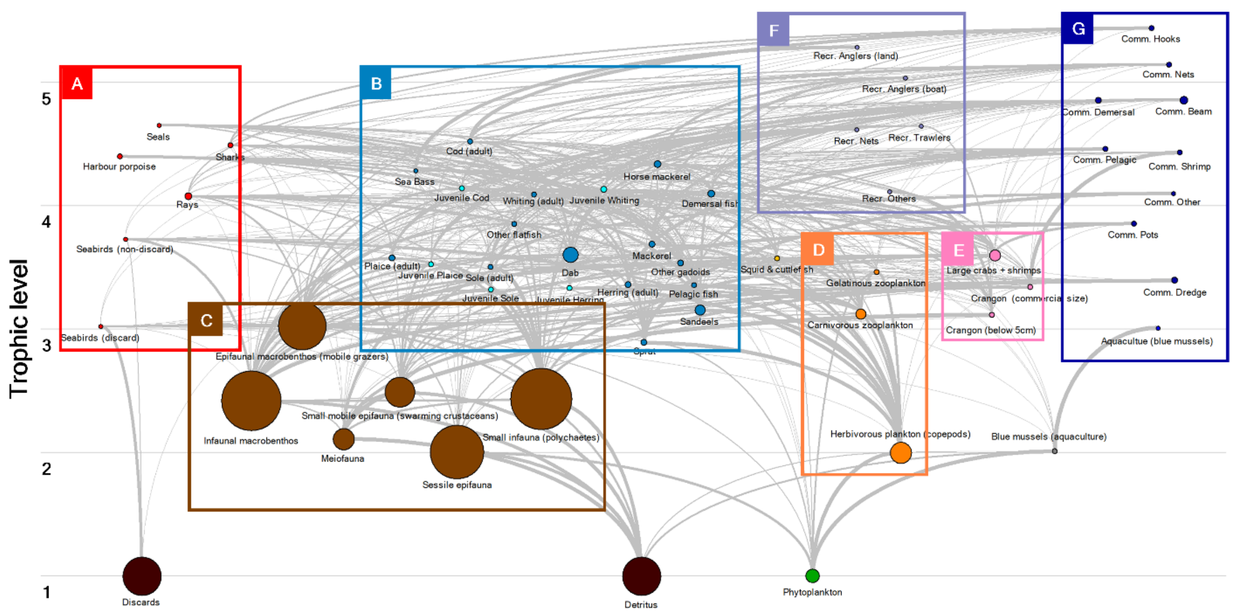

Figure 7: Visual representation of the balanced food web model for the Southern Bight of the North Sea. Each functional group and fisheries fleet is represented with a circle indicating its estimated biomass, with trophic level represented on the y-axis. Boxes highlight related functional groups and fisheries fleets: (A) apex predators, (B) fish species, (C) zooplankton, (D) crabs and shrimp, (E) recreational fisheries and (F) commercial fisheries including mussel aquaculture.

Table 6: Basic estimates from the balanced Ecopath model of the Southern Bight of the North Sea. Values in are estimated by Ecopath.

Functional group	Ecopath parameters								
	TL	B (t km^{-2})	Z (y^{-1})	PB (y^{-1})	QB (y^{-1})	EE	PQ (y^{-1})	BA (t km^{-2})	BA rate (y^{-1})
Harbour porpoise	4.40	0.03		0.02	24.64	0.00	0.001		
Seals	4.65	0.01		0.09	26.84	0.00	0.003		
Seabirds (discard)	3.02	0.0004		0.10	60.52	0.17	0.002		
Seabirds (non-discard)	3.73	0.0016		1.12	48.20	0.02	0.02		
Sharks	4.49	0.03		0.54	3.37	0.66	0.16		
Rays	4.08	1.51		0.30	2.89	0.07	0.10		
Cod									
Juvenile Cod	4.14	0.17	2.10		8.29	0.92	0.25		
Cod (adult)	4.52	0.22	1.14		3.20	0.66	0.35		
Whiting									
Juvenile Whiting	4.13	0.94	2.80		13.41	0.57	0.21		
Whiting (adult)	4.09	0.35	1.31		5.41	0.95	0.24		
Other gadoids	3.53	0.65		0.85	5.23	0.97	0.16		
Demersal fish	4.10	1.50		1.55	4.94	0.96	0.31		
Herring									
Juvenile Herring	3.33	0.21	5.70		26.33	0.98	0.22		
Herring (adult)	3.36	0.76	0.87		6.78	0.60	0.13		
Sprat	2.89	0.63		2.70	9.01	0.94	0.30		
Mackerel	3.68	0.92		1.34	4.81	0.42	0.28		
Horse mackerel	4.34	1.51		0.90	4.96	0.99	0.18		
Sandeels	3.15	4.39		2.00	9.59	0.94	0.21		
Plaice									
Juvenile Plaice	3.52	0.34	2.30		12.54	0.34	0.18		
Plaice (adult)	3.57	0.90	0.89		3.63	0.78	0.25		
Dab	3.60	9.63		0.60	5.58	0.13	0.11		
Other flatfish	3.85	0.40		0.95	6.90	0.94	0.14		
Sole									
Juvenile Sole	3.32	0.19	1.10		10.46	0.20	0.11		
Sole (adult)	3.50	0.32	1.15		5.56	0.75	0.21		
Sea Bass	4.29	0.01		0.56	3.81	0.92	0.15		
Pelagic fish	3.36	0.10		4.00	10.19	0.98	0.39		
Squid & cuttlefish	3.57	0.62		4.50	20.00	0.97	0.23		
Carnivorous zooplankton	3.12	4.18		4.00	12.50	0.99	0.32		
Herbivorous plankton (copepods)	2.00	16.00		9.20	30.00	0.63	0.31		
Gelatinous zooplankton	3.46	0.25		2.86	6.35	0.91	0.45		
Large crabs + shrimps	3.60	5.50		1.20	6.00	0.99	0.20		
Blue mussels (aquaculture)	2.01	0.06		0.36	2.67	0.05	0.13		
Epifaunal macrobenthos (mobile grazers)	3.02	78.00		0.60	3.00	0.97	0.20		
Infaunal macrobenthos	2.42	136.00		1.00	3.33	0.70	0.30		
C. crangon									
Crangon (below 5cm)	3.12	0.58	12.50		25.14	0.23	0.50		
Crangon (commercial size)	3.34	0.36	6.51		10.00	0.22	0.65		
Small mobile epifauna (swarming crustaceans)	2.49	30.00		3.65	10.43	1.00	0.35		
Small infauna (polychaetes)	2.43	150.00		1.80	6.00	1.00	0.30		
Sessile epifauna	2.00	105.00		0.26	1.30	0.14	0.20		
Meiofauna	2.11	17.00		35.00	125.00	0.99	0.28		
Phytoplankton	1.00	7.50		286.70		0.24			
Detritus	1.00	50.00				0.95		150.11	3.00
Discards	1.00	50.00				0.97			

3.4. Post-balance diagnostics

3.4.1. Biomass

The biomass (log scale) in the balanced SBNS model spans seven orders of magnitude and the slope declines by 5.7%, falling within the ecological range suggested by Link (2010; Fig. 8). Still, some groups show variance from the trend line, i.e. blue mussels (aquaculture) and benthos. A possibility to improve the benthos group is to split this FG in multiple FGs.

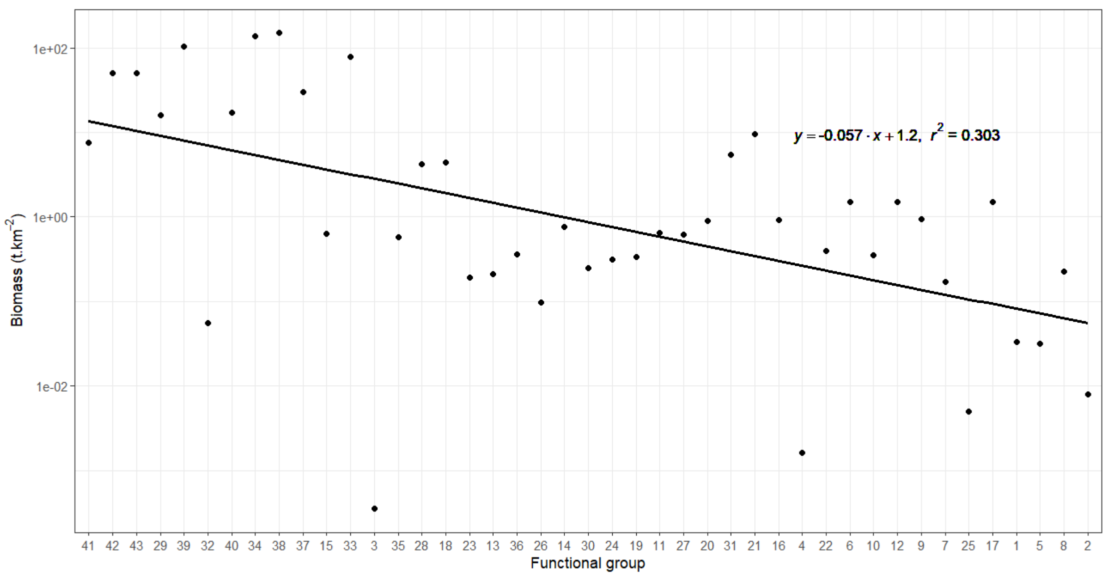

Figure 9: POSTBAL diagnostic biomass. Functional groups are ordered by increasing trophic level.

3.4.2. Production/biomass

PB (log scale) in the balanced SBNS model spans five orders of magnitude and the slope declines by 2.7 % (Fig. 9). This decrease falls still below the suggested decline (Link, 2010). Overall, there is little variance from the trend line except for phytoplankton, juvenile brown shrimp (*Crangon crangon*), and squid and cuttlefish. However, these PB values are similar to the PB values of Stäbler et al. (2016) for the central and SNS and Mackinson and Daskalov (2007) for the entire North Sea.

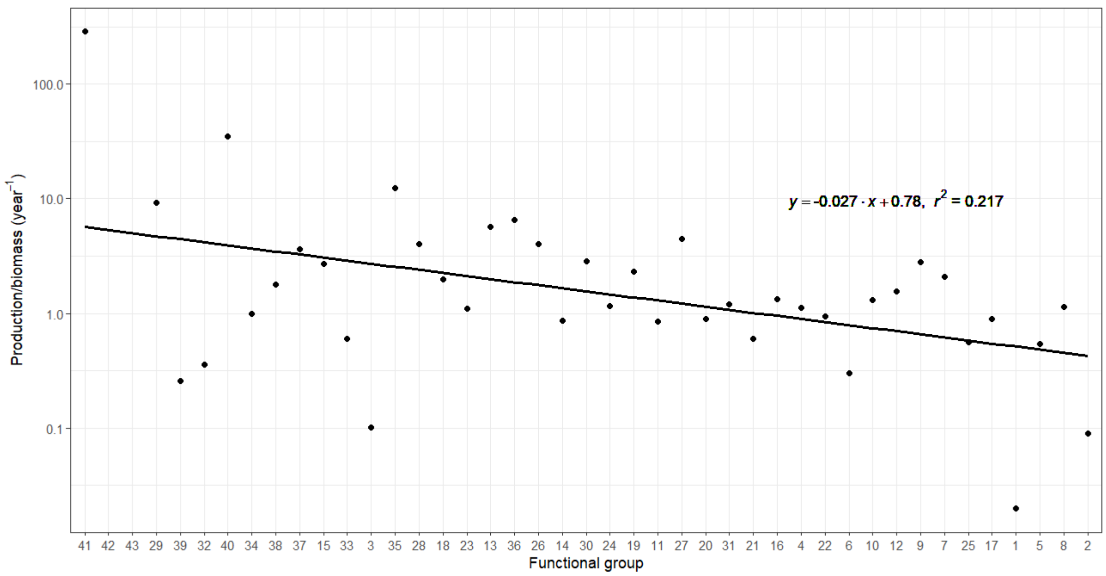

Figure 10: POSTBAL diagnostic production/biomass. Functional groups are ordered by increasing trophic level.

3.4.3. Consumption/biomass

QB is expected to decline with increasing trophic level following basic energetic assumptions. QB (log scale) in the balanced SBNS model spans two orders of magnitude and the slope declines by 0.5 % (Fig. 10). It did not improve, but it follows the decline with increasing trophic levels.

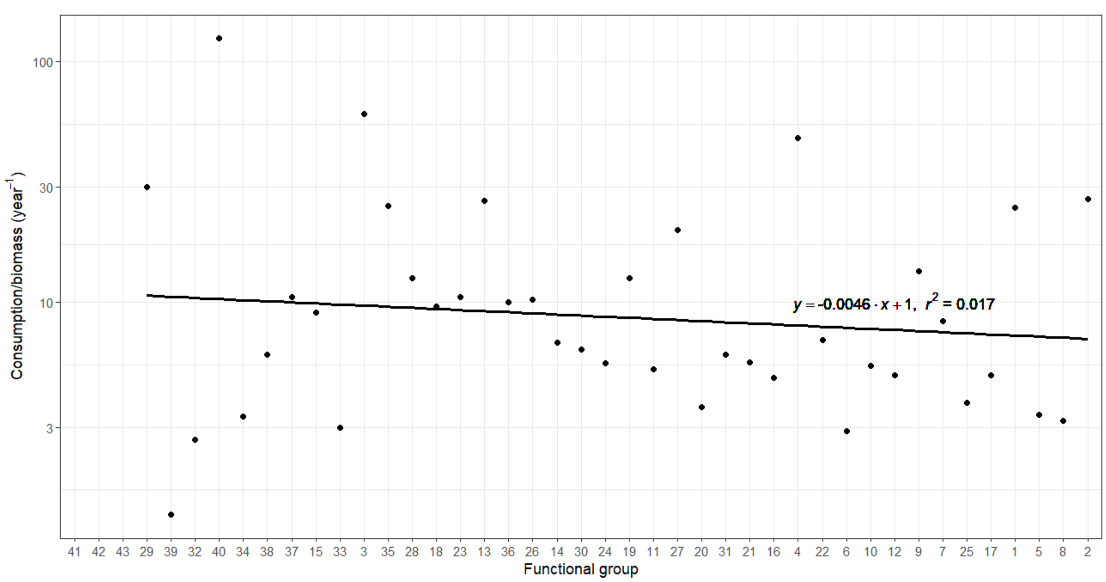

Figure 11: POSTBAL diagnostic consumption/biomass. Functional groups are ordered by increasing trophic level.

3.4.4. Production/consumption

Most FGs fall inside the suggested P/Q range of 0.1 - 0.3 (Fig. 11). The groups that fall outside the ideal range, were compared to the mother models' values and are in line with the P/Q values of the mother models (Mackinson and Daskalov, 2007; Stäbler et al., 2016). Some invertebrate species such brown shrimp (*Crangon crangon*), squid and cuttlefish that have high P/Q.

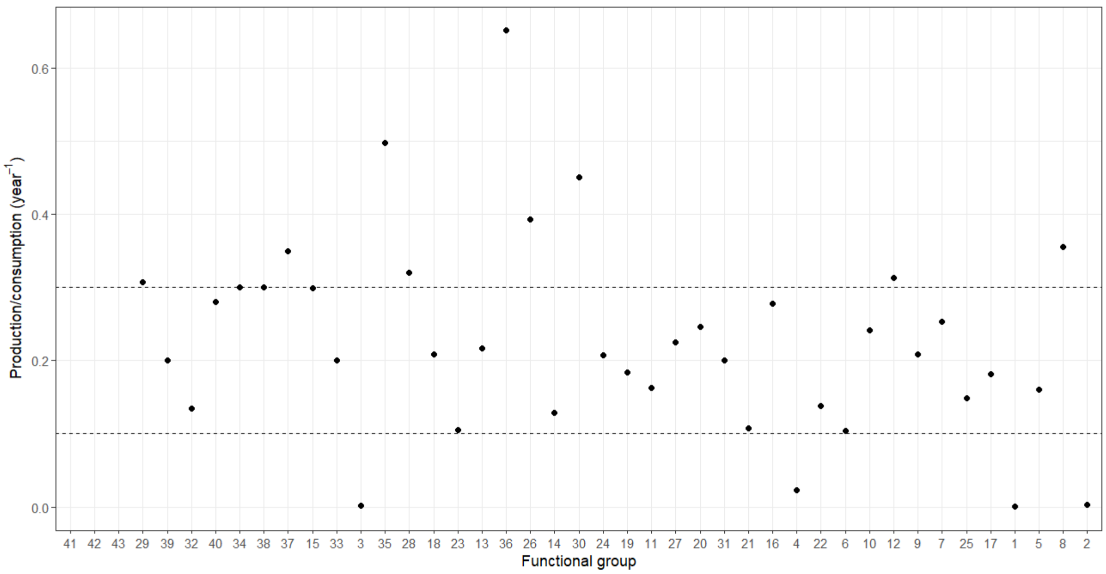

Figure 12: POSTBAL diagnostic production/ consumption. Functional groups are ordered by increasing trophic level.

Abbreviations

B:	Biomass
C:	Catch
CEFAS:	Centre for Environment, Fisheries, and Aquaculture Science
CPUE:	Catch Per Unit Effort
EwE:	Ecopath with Ecosim
F:	Fishing mortality
FG:	Functional group; plural FGs: functional groups
HAWG:	Herring Assessment Working Group for the area south of 62° N
Hd:	Herbivores and detritivores
ICES:	International Council for the Exploitation of the Sea
K:	von Bertalanffy growth function
L_{inf}:	asymptotic length, i.e. the length fish of a population would reach if they were to grow indefinitely
M:	Natural mortality
NS-IBTS:	International Bottom Trawl Survey North Sea
OBIS:	Ocean Biodiversity Information System
OSPAR:	the mechanism by which 15 Governments & the EU cooperate to protect the marine environment of the North-East Atlantic. (OSlo and PAris convention)
OSPAR - SCANS III:	Small Cetacean Abundance in the European Atlantic and North Sea
PB:	Production over biomass
P/Q:	Production-consumption ratio
Pf:	Apex and/or pelagic predators and/or zooplankton feeders
QB:	Consumption
SBNS:	Southern Bight of the North Sea
SNS:	Southern North Sea
SSB:	Spawning Stock Biomass
STECF:	Scientific, Technical and Economic Committee for Fisheries
STECF FDI:	Fisheries-Dependent Information
T:	Temperature
TSB:	Total Stock Biomass
WGNSSK:	Working Group on the assessment of Demersal Stocks in the North Sea and Skagarrak
WGWIDE:	Working Group on Widely Distributed Stocks
W_{inf}:	Asymptotic weight, i.e. the weight fish of a population would reach if they were to grow indefinitely
$W_{maturity}$:	The mean weight at which fish of a given population mature for the first time
Z:	Total mortality

Data availability

The input data, Rscripts and Ecopath model can be accessed by https://doi.org/10.14284/668 and should be cited as follows:

Pint, S.; Stevens, M.; De Troch, M.; van Oevelen, D.; Heymans, J.J.; Everaert, G.; Flanders Marine Institute; Ghent University; Royal Netherlands Institute for Sea Research; University of the Highlands and Islands; (2024): Data - Ecopath model of the Southern Bight of the North Sea. Marine Data Archive. https://doi.org/10.14284/668

Citation

Pint S., Stevens M., De Troch M., van Oevelen D., Heymans J. J., Everaert G.: Ecopath model of the Southern Bight of the North Sea (version 3), https://dx.doi.org/10.48470/74, 2024.

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