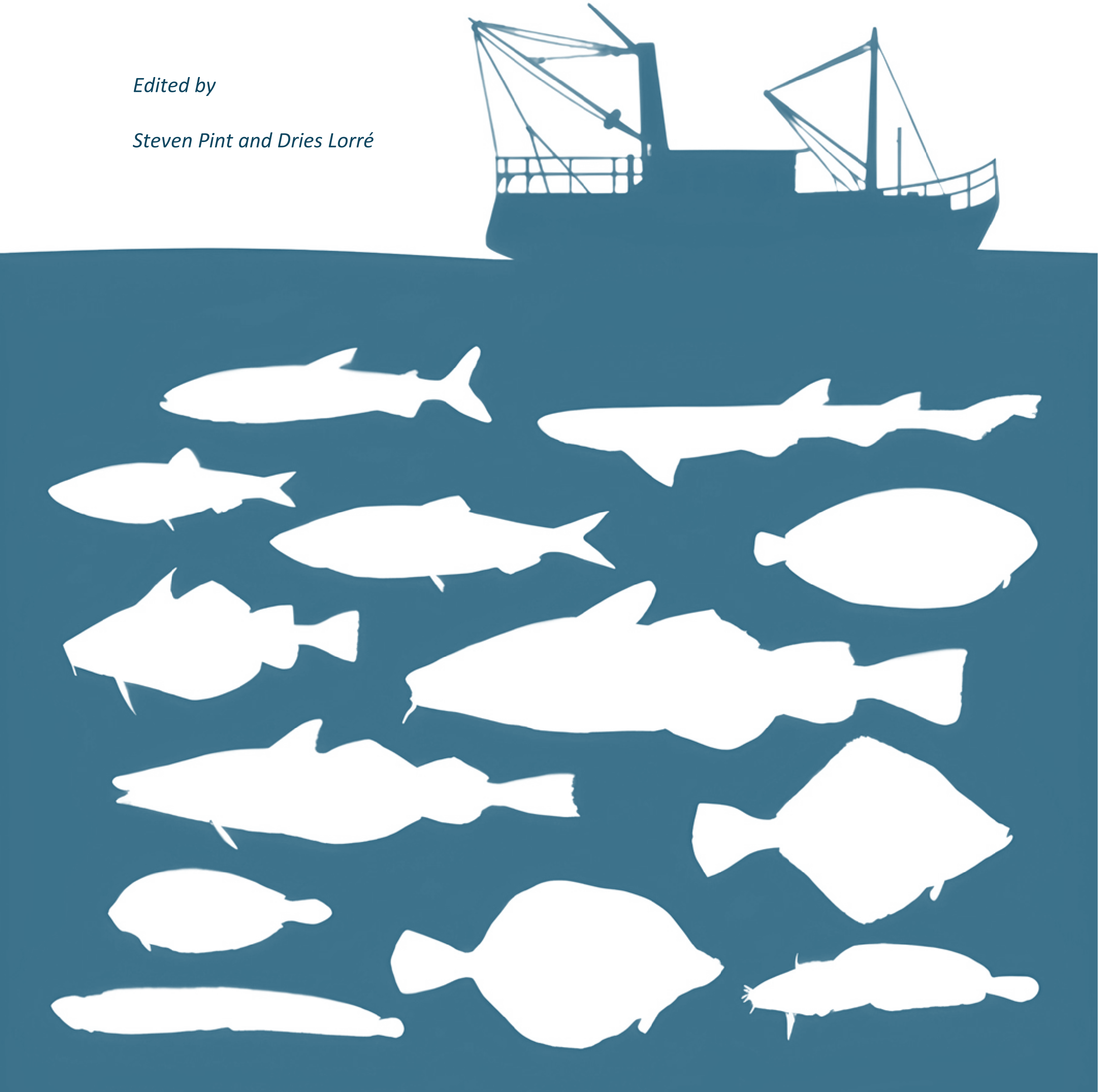
Ecopath with Ecosim model of the Southern Bight of the North Sea:

Technical report (version 4)

Edited by

Steven Pint and Dries Lorré



Copyright or Publication info /

Authors and affiliations:

Pint Steven[1,2]* (steven.pint@vliz.be), Lorré Dries[3,]* (Dries.Lorre@UGent.be), Stevens Martha[1,2], De Troch Marleen[2], Heymans Sheila[4], van Oevelen Dick[5], Everaert Gert[1]

1. Flanders Marine Institute, Ostend, Belgium
2. Ghent University, Marine Biology Research Group, Ghent, Belgium
3. Ghent University, Blue Growth Research Lab, Ghent, Belgium
4. European Marine Board, Ostend, Belgium
5. Royal Netherlands Institute for Sea Research, Yerseke, Netherlands

*Corresponding authors

Contents

1 Introduction

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 Ecopath with Ecosim (EwE). 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 in 2021 and gradually updated (Pint et al., 2024c).

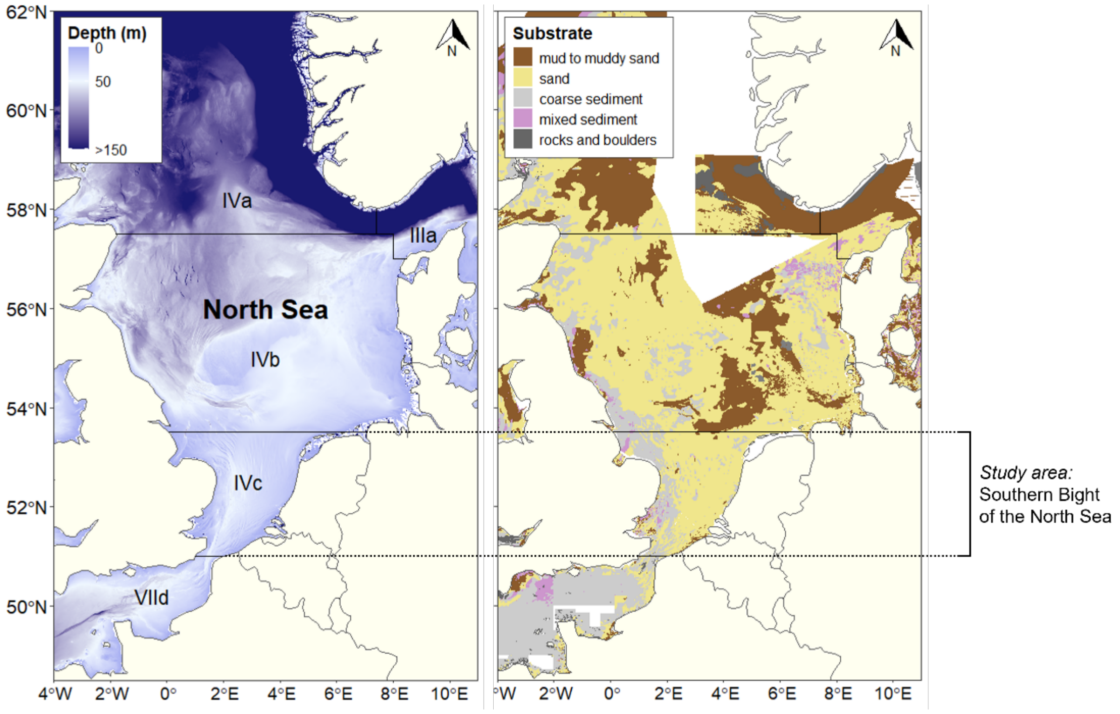
Ecopath with Ecosim (EwE) is an ecosystem modelling software (https://ecopath.org/) established in 1984 by Polovina (1984) and updated through the years by Christensen and Pauly (1992) and Walters et al. (1997). It has three main components: 1) Ecopath: a mass-balance snapshot of the ecosystem; 2) Ecosim: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

In this technical report, we describe an Ecopath with Ecosim model for the Southern Bight of the North Sea (SBNS; ICES area IVc) from 1991 until 2023. The initial 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 model parameters, such as vulnerability.

We provide an overview of our model parameterisation, and temporal dynamics with time series data and fitting. All steps undertaken to obtain a well-fit model are described in this manuscript. 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?".

1.1 Study area

The Southern Bight of the North Sea (SBNS; ICES area IVc; 63633.86 km^2)(Fig. 1) is a unique ecosystem within the Greater North Sea due to its distinct bathymetry and hydrology (ICES, 2024). Its southern limit is the English Channel (50.97° N), and its northern limit is at the latitude of the Dutch island Schiermonniksoog (53.49° N) (Fig. 1). The anticlockwise circulation in the North Sea transports water from the North Atlantic southwards along the coast of the UK into the SBNS, whereas an opposite current runs along the Belgian and Dutch coast transporting water from the English Channel northward (Turrell et al., 1992). These Atlantic influences determine the salinity of offshore regions, but in coastal areas, salinity is more strongly influenced by riverine input from the Scheldt, Reine, Meuse and Seine leading to salinity levels that vary between 29 and 35 PSU (Lacroix et al., 2004). High natural disturbance due to waves and tides in the relatively shallow SBNS (<50m) have resulted gravel beds in addition to more common sandy sediments (Fig. 1), and this disturbance also causes the water column to be well-mixed year-round (ICES, 2024). The combination of this strong mixing and high riverine nutrient input leads to high primary productivity in the region. These environmental conditions have resulted in an ecosystem with a distinct ecology and high levels of economic exploitation (Dauwe et al., 2022).



Study area: Southern Bight of the North Sea

Figure 1: Map of the Greater North Sea ICES Ecoregion divided into subregions (Iva, IVb and IVc) for bathymetry (left) and seabed substrate (right). Our study area, the Southern Bight of the North Sea, is indicated (see note to the right of the figure).

Human activities in the Southern Bight of the North Sea include shipping, wind farms, gas and oil exploration and production, dredging, aggregate extraction, aquaculture and fishing (Dauwe et al., 2022). Commercially important fish species in the Southern North Sea include the brown shrimp (*Crangon crangon*), caught by commercial shrimpers, and plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), and sole (*Solea solea*) caught by demersal trawlers and seiners (Stäbler et al., 2018). Beam trawlers, which are primarily used in the Southern North Sea, catch mainly flatfish (Pleuronectiformes), cod (*Gadus morhua*), herring (*Clupea harengus*), and whiting (*Merlangius merlangus*) (Stäbler et al., 2018). Recreational fishermen target similar species as commercial fishermen, and anglers favour sea bass (*Dicentrarchus labrax*), mackerel (*Scomber scombrus*), and horse mackerel (*Trachurus trachurus*) as well (Verleye et al., 2022).

2 Ecopath: an ecosystem model of the Southern Bight of the North Sea

As a first step towards understanding food web dynamics in the Southern Bight of the North Sea, an Ecopath model was developed, describing a snapshot of the ecosystem in 1991. The year 1991 was chosen because it was the “ICES Year of the Stomach” during which a large-scale, coordinated effort at fish stomach sampling has been conducted. This provides valuable insight into species' dietary intake, which is key to understanding its trophic interrelations in addition to population and community dynamics within an ecosystem. Moreover, an Ecopath model of 1991 accommodates a sufficient time span (1991-2022; 33 years) to serve as a basis for the subsequent development of an Ecosim model (see section 3).

This report describes the updated version of the Ecopath with Ecosim model of Pint et al. (2024c). Major changes to the Ecopath model are *Crangon crangon* is not a multi-stanza, a blue mussel (reefs) group was added, and diets were adjusted accordingly. These changes are highlighted in ***bold-italic***.

2.1 Model overview

This food web model for the SBNS in 1991 consists of 43 functional groups (Figure 2, Section 2.1.1), five recreational fisheries fleets, nine commercial fisheries fleets and commercial mussel aquaculture (Section 2.1.2). Functional groups to include in the model were selected based on their ecological or commercial importance, and groups of commercial interest with altered ecological niches in different life stages were divided into age classes, i.e. multi-stanza groups (Section 2.1.1.1). Recreational fisheries fleets were defined as per Verleye et al. (2019) in the Belgian part of the North Sea, whereas commercial fleets were selected based on gear types defined by the Scientific, Technical and Economic Committee for Fisheries (Table 1)(STECF, 2017).

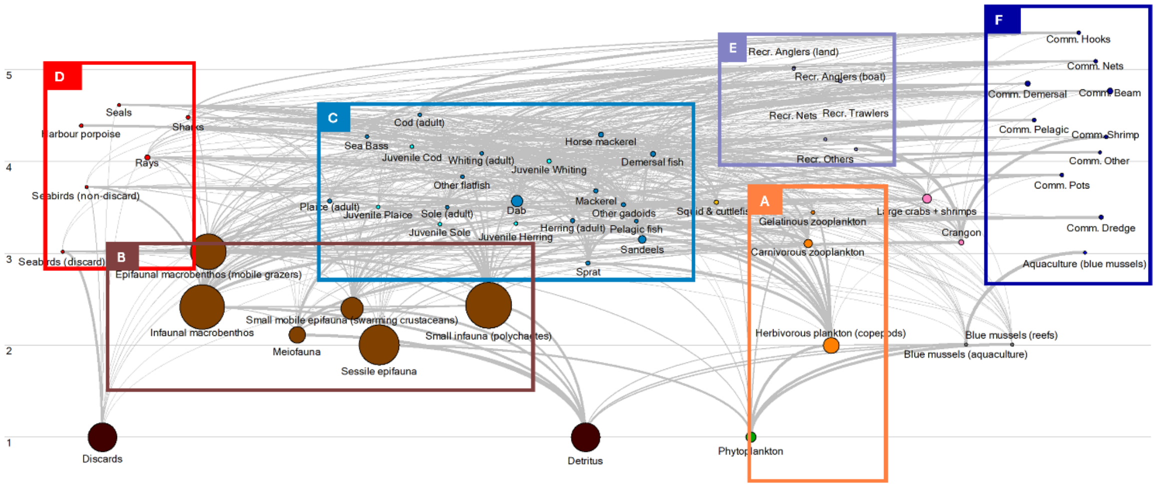


Figure 2: The dietary relationships between 43 functional groups and 14 fisheries fleets for a mass-balanced Ecopath food web model of the Southern Bight of the North Sea in 1991. Circle size represents functional group biomass with trophic level visualised on the Y-axis, whereas lines depict dietary relationships with their thickness indicating the amount of each flow. Boxes highlight related functional groups and fisheries fleets: (A) plankton, (B) benthos, (C) fish, (D) apex predators, (E) recreational fisheries and (F) commercial fisheries including mussel aquaculture.

2.1.1 Functional groups

2.1.1.1 Fish

Fish species of ecological or economic importance have been included as a unique group when sufficient data was available resulting in a functional group for *seabass* (*Dicentrarchus labrax*), *sprat* (*Sprattus sprattus*), *mackerel* (*Scomber scombrus*), *horse mackerel* (*Trachurus trachurus*), *sandeels* (*Ammodytidae*) and *dab* (*Limanda limanda*). Since fisheries focus on adult individuals, species of particular interest for either commercial or recreational fisheries have been included as multi-stanza groups to make a distinction between juvenile and adult individuals. This was the case for *cod* (*Gadus morhua*), *whiting* (*Merlangius merlangus*), *herring* (*Clupea harengus*), *plaice* (*Pleuronectes platessa*) and *sole* (*Solea solea*). Note that adults were defined as individuals with an age of two years or higher, with the exception of herring, which was considered to mature at the age of one. To reduce complexity in the model, other species have been grouped into broader functional groups as described below.

A functional group for *sharks* includes most common sharks in the SBNS, namely, the spurdog (*Squalus acanthias*), school shark (*Galeorhinus galeus*), small-spotted catshark (*Scyliorhinus canicula*) and smooth-hound (*Mustelus spp.*). In a functional group for *rays* the 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) were included.

Demersal fish have been grouped into a single functional group as well, encompassing common demersal fish species, gurnards, and dragonets in the SBNS. This functional group includes 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*).

Some flatfish in the SBNS, i.e. plaice, dab and sole, are included as unique functional groups whereas others are grouped into a functional group called *other flatfish*. These species are European flounder (*Platichthys flesus*), lemon sole (*Microstomus kitt*), turbot (*Scophthalmus maxima*) and brill (*Scophthalmus rhombus*).

Gadoid species that have not been included as unique functional groups were also grouped, resulting in the *other gadoids* functional group. This 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).

Finally, a miscellaneous filter feeding *pelagic fish* group was also include in the model which consist of shad (*Alosa* sp.), anchovy (*Engraulis encrasicolus*) and European pilchard (*Sardina pilchardus*).

2.1.1.2 Marine mammals

Three marine mammal species occur in the SBNS regularly: harbour porpoise (*Phocoena phocoena*), common seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*). Both seal species were integrated into a single functional group, resulting in two marine mammal groups: *harbour porpoise* and *seals*. Other species such as the bottlenose dolphin and minke whale are 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.

2.1.1.3 Seabirds

Seabirds were divided into two functional groups based on their diets, i.e. discard feeders and non-discards feeders. Large flocks of gulls 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) (Henry and Cumming, 2017).

The following species were included in the *discard feeders* functional 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 *non-discard feeders* functional group includes the following species: 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*). The great crested grebe is common in freshwater areas but also in estuaries and shallow coastal waters and thus included in the model (Stienen and Vanermen, 2018). The common tern 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 and Vanermen, 2018).

2.1.1.4 Invertebrates

Brown shrimp (*Crangon crangon*) was originally included as a multi-stanza functional group called *Crangon* because of their importance for commercial fisheries (Pint et al., 2024a). This, however, created instability in the model as the multi-stanza option was developed for fish species and not invertebrates. ***As a result, the* Crangon *is not a multi-stanza group anymore***. Other shrimp and crab species were grouped in a *large crabs & shrimp* functional group which included edible crab (*Cancer pagurus*), common spider crab (*Maja brachydactyla*) and velvet swimming crab (*Necora puber*). Shrimp species included are C*rangon allmanni*, *Eualus pusiolus*, *Pandalus montagui*, *Spirontocaris lilljeborgi*, *Processa nouveli*, and *Pandalina* spp. Note that European lobster (*Homarus gammarus*) is also included in this functional group. Note that *Pandalus borealis* and *Nephrops norvegicus* are not included in our model as they have a low occurrence in our study area.

Three species of squid and cuttlefish, i.e. veined squid (*Loligo forbesii*), European squid (*Loligo vulgaris*) and common cuttlefish (*Sepia officinalis*), were included in the model as a single functional group called *squid & cuttlefish*.

Benthic species were included in the model with six distinct functional groups as per Mackinson and Daskalov (2007): *epifaunal macrobenthos (mobile grazers)*, *infaunal macrobenthos*, *small mobile epifauna (swarming crustaceans)*, *small infauna (polychaetes)*, *sessile epifauna* and *meiofauna*. Two additional groups, ***blue mussels (reefs)*** and *blue mussels (aquaculture)* were included for blue mussels (*Mytilus edulis*) in a natural and an aquaculture context, respectively.

2.1.1.5 Plankton

A *carnivorous zooplankton* functional group in the model included krill species of the order Euphausiacea, e.g. *Thysanoessa inermis*, *Meganyctiphanes norvegica*. *Herbivorous & omnivorous plankton (copepods)* is an additional functional group that consist of several copepod species, e.g. *Pseudocalanus elongatus*, *Paracalnus parvus*, *Microcalanus pusillus*, *Acartia* spp. and *Temora longicornis*. The *gelatinous zooplankton* functional group represents common jellyfish in the SBNS, i.e. moon jellyfish (*Aurelia aurita*), blue jellyfish (*Cyanea lamarckii*) and lion's mane jellyfish (*Cyanea capillata*). A *phytoplankton* group was included as well.

2.1.1.6 Detritus & discards

A *detritus* functional group included in the model encompasses both dissolved and particulate organic matter (DOM & POM). A *discards* group was included in the model as well.

2.1.2 Fisheries fleets & aquaculture

2.1.2.1 Commercial fleets

Nine commercial fleets were distinguished using gear types distinguished by the Scientific, Technical and Economic Committee for Fisheries (STECF). In the SBNS, a total of 17 gear types were included in the STECF database (STECF, 2017). These gear types were assigned to nine corresponding EwE fleets (Table 3).

Table 1: Gear type allocation to commercial fleets in the Southern Bight of the North Sea model

Gear description	STECF Gear type	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*

2.1.2.2 Recreational fleets

Recreational fisheries were included based on monitoring efforts covering the Belgian coast by Verleye et al. (2019) as Belgium is of particular interest for the authors. In addition, this is to the best of our knowledge the most complete current monitoring program of recreational fisheries in the Southern Bight of the North Sea. Five recreational fleets were defined based on the fisheries methodologies observed by Verleye et al. (2019): *anglers (boat)*, *trawlers*, *anglers (land)*, *nets* and *others*. Note that this assumes similar recreational fisheries interests in the Netherlands and the United Kingdom (UK).

2.1.2.3 Mussel aquaculture

An *aquaculture (blue mussels)* fleet was included to answer potential research questions regarding this topic.

2.2 Model parametrisation

The baseline mass-balanced snapshot in Ecopath is obtained using the two Ecopath master equations (Christensen and Walters, 2004; Pauly et al., 2000; Polovina, 1984). The first equation (**Error! Reference source not found.**) represents the conservation of energy within a functional group, where total consumption is allocated to production, respiration, and unassimilated food:

$$\left(\frac{Q}{B}\right)_i \cdot B_i = \left(\frac{P}{B}\right)_i \cdot B_i + R_i + UN_i \qquad \text{Eq. 1}$$

With for each functional group (i)

- $\left(\frac{Q}{B}\right)_i \cdot B_i$: Consumption (t km^{-2} year^{-1})
- $\left(\frac{P}{B}\right)_i \cdot B_i$: Production (t km^{-2} year^{-1})
- R_i: Respiration (t km^{-2} year^{-1}).
- UN_i: Unassimilated food (t km^{-2} year^{-1})

The second equation (Eq. 1) describes the total production of a functional group, which is influenced by predation, fishing mortality, biomass accumulation, net migration, and other sources of mortality:

$$\left(\frac{P}{B}\right)_i \cdot B_i = \sum_{j=1}^{n} \left(\frac{Q}{B}\right)_j \cdot B_j \cdot DC_{ji} + Y_i + BA_i + E_i + \left(\frac{P}{B}\right)_i \cdot B_i \cdot (1 - EE_i) \qquad \text{Eq. 2}$$

With for each functional group (i)

- $\left(\frac{P}{B}\right)_i \cdot B_i$: Production (t km^{-2} year^{-1})
- $\left(\frac{Q}{B}\right)_j \cdot B_j \cdot DC_{ji}$: Predation mortality of i due to predation of functional group j (t km^{-2} year^{-1})
- Y_i: Fishing mortality (t km^{-2} year^{-1})
- BA_i: Biomass accumulation (t km^{-2} year^{-1})
- E_i: Net migration (t km^{-2} year^{-1})
- $\left(\frac{P}{B}\right)_i \cdot B_i \cdot (1 - EE_i)$: Other mortality (t km^{-2} year^{-1})

The construction of an Ecopath model requires data of three of the five following parameters for each functional group; **biomass** (B; t km^{-2}), **productivity-biomass ratio** (PB; y^{-1}), **consumption-biomass ratio** (QB; y^{-1}), **production-consumption ratio** (PQ; y^{-1}) and **ecotrophic efficiency** (EE). Additionally, a **diet composition** matrix that includes all functional groups, and **fisheries catch** data including both landings and discards (t km^{-2}) are needed.

2.2.1 Biomass, productivity & consumption

For functional groups where such data was available, **biomass** (B) in the SBNS was estimated based on ICES stock assessments (ICES Stock Assessment Database) which were downscaled to estimate a stocks' biomass in the SBNS using location-specific catch per unit effort (CPUE) data from the International Bottom Trawl Survey in the North Sea (NS-IBTS, ICES, 2024). For functional groups without an available stock assessment, biomass was either (1) extracted from scientific literature, (2) inferred from models with overlapping study areas Mackinson and Daskalov (2007) and Stäbler et al. (2016) or (3) estimated following the method of Sparholt (1990).

The **production-biomass ratio (PB)** and **consumption-biomass ratio (QB)** of fish were determined at 10°C (Mackinson and Daskalov, 2007) using empirical formulas from Pauly (1980), Pauly et al. (1990), and of birds from Nilsson and Nilsson (1976). For fish, the stoichiometries required in these calculations were obtained from FishBase (Froese and Pauly, 2023), whereas for birds they were inferred from scientific literature. The PB and QB for other species were distilled from other models and literature. The following section will elaborate on these estimation methods as well as indicate for which functional groups they were applied.

Table 2: An overview of the input parameters used to develop the model: biomass (B), total mortality (Z), production–biomass ratio (PB), consumption–biomass (QB), production–consumption ratio (PQ), and ecotrophic efficiency (EE). Multi-stanza groups are depicted in grey, and for each functional group all data sources used to obtain the input parameters are listed.

Functional group	**B (t km^{-2})**	**Z (y^{-1})**	**PB (y^{-1})**	**QB (y^{-1})**	**EE**	**PQ**
Harbour porpoise	0.03		0.02	24.64		
Seals	0.01		0.09	26.84		
Seabirds (discard)	0.0004		0.10	60.52		
Seabirds (non-discard)	0.002		1.12	48.20		
Sharks	0.03		0.54	3.37		
Rays	1.53		0.30	2.89		
Cod						
Juvenile Cod	0.17	2.10		8.29		
Cod (adult)	0.22	1.14		3.20		
Whiting (adult)						
Juvenile Whiting	0.94	2.80		13.41		
Whiting (adult)	0.35	1.31		5.41		
Other gadoids	0.65		0.95	5.23		
Demersal fish	1.60		1.56	4.94		
Herring						
Juvenile Herring	0.22	3.54		19.06		
Herring (adult)	0.76	1.20		6.78		
Sprat	0.63		2.70	9.01		
Mackerel	0.92		1.34	4.81		
Horse mackerel	1.53		0.90	4.96		
Sandeels	4.39		2.00	9.59		
Plaice						

Juvenile Plaice	0.51	2.30		10.44		
Plaice (adult)	0.85	0.89		3.63		
Dab	9.63		0.60	5.58		
Other flatfish	0.40		1.10	6.90		
Sole						
Juvenile Sole	0.19	1.10		10.46		
Sole (adult)	0.32	1.15		5.56		
Sea Bass	0.03		0.57	3.81		
Pelagic fish			4.00	10.19	0.98	
Squid & cuttlefish	0.70		4.50	20.00		
Carnivorous zooplankton			4.00		0.99	0.32
Herbivorous plankton (copepods)	16.00		9.20	30.00		
Gelatinous zooplankton	0.25		2.86			0.45
Large crabs + shrimps	5.60		1.20			0.20
Blue mussels (reefs)	1E-06		0.36	2.67		
Blue mussels (aquaculture)	1E-06		0.36	2.67		
Epifaunal macrobenthos (mobile grazers)	78.00		0.60			0.20
Infaunal macrobenthos	136.00		1.00			0.30
Crangon	1.30		6.00	18.00		
Small mobile epifauna (swarming crustaceans)	30.00		3.65			0.35
Small infauna (polychaetes)	150.00		1.80			0.30
Sessile epifauna	105.00		0.26			0.20
Meiofauna			35.00	125.00	0.99	
Phytoplankton	7.50		286.70			
Detritus	50.00					
Discards	50.00					

2.2.1.1 Fish

ICES stock assessments were available and hence used to estimate **biomass (B)** for *cod (adult)*, *whiting (adult)*, *herring (adult)*, *plaice (adult)*, *sole (adult)*, *sprat*, *dab*, *mackerel* and *sandeels* (Table 3). Because fish stocks often cover a larger geographical area than just the SBNS, stock assessments were corrected for their relative abundance in the SBNS compared to the entire stock area using location-specific catch per unit effort (CPUE) data from the International Bottom Trawl Survey in the North Sea (NS-IBTS) (ICES, 2024) (Eq. 3). An overview of the geographical range of each stock is provided in Table 3.

$$B = B_{ICES\ stock} \cdot \frac{CPUE_{ICES\ area\ IVc}}{CPUE_{ICES\ sock\ range}} \qquad \text{Eq. 3}$$

Whenever a stock assessment was not available, fish biomass was estimated according to the method of Sparholt (1990). Here, CPUE data from the NS-IBTS (ICES, 2024) is used to calculate the abundance ratio between the cumulative abundance of all species included in a functional group and a reference species of similar ecological niche for which a stock assessment is available. This abundance ratio was then multiplied with the biomass of the reference species in the SBNS which is estimated as described above based on ICES stock assessments (Eq. 4). This method was applied to estimate biomass for *sharks*, *rays*, *sea bass*, *demersal fish*, *horse mackerel*, *other flatfish* and *other gadoids*. Note that for *pelagic fish* biomass could not be estimated with the data available, instead ecotrophic efficiency (EE) was estimated which was assumed to be the same as in the North Sea model of Mackinson and Daskalov (2007).

$$B = B_{ref.species} \cdot \frac{CPUE_{functional\ group}}{CPUE_{ref.species}} \qquad \text{Eq. 4}$$

Table 3: Biomass estimation methods for fish

Functional group	Stock assessment				Sparholt Method
	Stock coverage area	Stock code	Year	Key	Reference species
Sharks					Cod and Whiting
Rays					Plaice
Cod (adult)	Subarea 4, in divisions 6.a and 7.d, and in Subdivision 20 (North Sea, West of Scotland, eastern English Channel, Skagerrak)	cod.27.46a7d20	2024	18716	
Whiting (adult)	Subarea 4 and in Division 7.d (North Sea, eastern English Channel)	whg.27.47d	2024	18694	
Other gadoids					Cod and Whiting
Demersal fish					Cod and Whiting
Herring (adult)	Subarea 4 and in divisions 3.a and 7.d; autumn spawners (North Sea, Skagerrak, Kattegat, eastern English Channel)	her.27.3a47d	2024	19293	
Sprat	Division 3.a and Subarea 4 (Skagerrak, Kattegat, North Sea)	spr.27.3a4	2024	18543	
Mackerel	Subareas 1–8 and 14 and in Division 9.a (Northeast Atlantic and adjacent waters)	mac.27.nea	2024	19137	
Horse mackerel					Herring
Sandeels	Divisions 4.b and 4.c, Sandeel Area 1r (central and southern North Sea, Dogger Bank)	san.sa.1r	2024	18515	
Plaice (adult)	Subarea 4 (North Sea) and in Subdivision 20 (Skagerrak)	ple.27.420	2024	18688	
Dab					Plaice
Other flatfish					Plaice
Sole (adult)	Subarea 4 (North Sea)	sol.27.4	2024	19295	
Sea bass	Divisions 4.b, 4.c, 7.a, and 7.d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, Celtic Sea)	bss.27.4bc7ad-h	2024	19277	Cod and Whiting

Productivity and consumption parameters for fish were determined using empirical formulas from Pauly (1980) and Pauly et al. (1990) as described below. For functional groups composed of multiple species, a weighted mean was calculated of the included species' parameters with their biomass as weight. Note that for all calculations the temperature was set to 10°C (Mackinson and Daskalov, 2007), the average annual temperature for the Southern Bight of the North Sea around 1991.

The **production to biomass ratio** (PB) of fish is equal to their total mortality (Z) which equals fishing mortality (F) plus natural mortality (M) (Eq. 5). The value for these mortality parameters was calculated using Eq. 6, Eq. 7 and Eq. 8 as explained below. Note that for multi-stanza groups, total mortality of juvenile groups was calculated with F and M estimates from ICES reports (for plaice, cod, whiting, and sole it was taken from ICES, 2019; and for herring, ICES, 2020)

$$\frac{P}{B} = Z = F + M \qquad \text{Eq. 5}$$

In which fishing mortality (F) is equal to the functional group's catch (C; see section 2.2.3) divided by its biomass (B, Eq. 1 and Eq. 2) (Eq. 4).

$$F = \frac{C}{B} \qquad \text{Eq. 6}$$

Whereas natural mortality (M) is calculated according to the empirical formula of Pauly (1980) using temperature (T; i.e. 10°C), the species' growth coefficient (K) and either asymptotic length (Linf; Eq. 5) or asymptotic weight (Winf; Eq. 6) depending on data availability.

$$log\ M = \ -0.0066 - 0.279\ \ log\ L_{inf} + 0.6543\ \ log\ K + 0.4634\ \ log\ T \qquad \text{Eq. 7}$$

$$log\ M = \ -0.2107 - 0.0824\ \ log\ W_{inf} + 0.6757\ \ log\ K + 0.4627\ \ log\ T \qquad \text{Eq. 8}$$

The **consumption to biomass ratio** (QB) was estimated using an empirical formula as per Pauly et al. (1990) (Eq. 9). The value for Pf (apex and/or pelagic predators and/or zooplankton feeders) is equal to 1 for top predators and zooplanktivores and equal to 0 for detritivores and herbivores. Hd (herbivores and detritivores) equals 1 for herbivores and 0 for carnivores.

$$log\,\frac{Q}{B} = \ 6.37 - 1.5045\ \left(\frac{1000}{(T+273.1)}\right) - 0.168\ \ log\ W_{inf} + 0.1399\ \ log\ Pf + 0.2765\ \ log\ Hd \qquad \text{Eq. 9}$$

Values for the parameters K, Linf and Winf required for Eq. 7, Eq. 8 and Eq. 9 for each species, as well as an estimate for weight at maturity over asymptotic weight (Wmat / Winf) which is in additional requirement for multi-stanza groups, were obtained from Fishbase (Froese and Pauly 2023) through the Life history tool.

Due to a lack of data availability for the *pelagic fish* functional group, these calculations were not possible. Instead, **PB** and **QB** were assumed to be the same as in the North Sea model of Mackinson and Daskalov (2007).

2.2.1.2 Marine mammals

For marine mammals, i.e. harbour porpoise and seals, no stock assessments or CPUE data is available in the North Sea. Instead, *harbour porpoise* **biomass** was estimated based on density data from OSPAR – SCANS III (0.607 individuals km^2) (Hammond et al., 2017)) which was multiplied with the average weight per individual (0.055 t; Bjørge and Tolley, 2009) resulting in a biomass of 0.03 t km^{-2} y^{-1}. The **production-biomass ratio** (PB) of 0.02 y^{-1} for harbour porpoise was assumed to be similar to the values of toothed whales from the Southern North Sea model of Stäbler et al. (2016). To estimate the **consumption-biomass ratio** (QB) of harbour porpoise, a daily rate of 6.75% of the body weight was assumed (Kastelein et al., 1997), resulting in a consumption-biomass ratio of 24.64 y^{-1}.

The **biomass, PB, and QB** for *seals* were assumed to be 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}.

2.2.1.3 Seabirds

Biomass for *discard feerders* (0.0004 t km^{-2} y^{-1}) and *non-discard feeders* (0.002 t km^{-2} y^{-1}) was estimated 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 assumed to be the same as in the North Sea model of Mackinson and Daskalov (2007), whereas **QB** was estimated using an empirical formula by Nilsson and Nilsson (1976)(Eq. 10).

$$\frac{Q}{B} = e^{\frac{-0.293 + 0.85 * \log(0.00162 * area\,IVc * 1000)}{0.00162 * area\,IVc * 1000}} * 365 \qquad \text{(Eq. 10)}$$

2.2.1.4 Invertebrates

The* Crangon functional *is not a multi-stanza group as previously was the case *(Pint et al., 2024c, a)*. ***The adult and juveniles were grouped together and biomass estimate changed to (1.30 t km^{-2} y^{-1}). The total mortality (Z or PB) (6.00 y^{-1}) and QB (18.00 y^{-1}) (Stäbler et al. (2016), after*** *Hufnagl et al. (2010)*, *Tulp et al. (2016)*)**.**

For the *large crabs & shrimp* functional group, **biomass** for crabs and shrimp (other than *Crangon Crangon*) in the SBNS was estimated separately. Shrimp species' biomass was estimated by calculating the abundance ratio between the SBNS and the greater 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 was multiplied with the best estimate biomass for the greater North Sea of Mackinson and Daskalov (2007, Table 11.8). The total biomass of all shrimp species was then added to the total large crab biomass, which was assumed to be equal to that of the entire North Sea (Mackinson and Daskalov, 2007). For production and consumption parameters, a weighted mean of the **PB** and **PQ** values for all relevant shrimp and crab functional groups from Stäbler et al. (2016) was calculated (with biomass as weight). Note that this assumes that the ratio between the functional groups in the SBNS is similar to the ratio in the central and southern North Sea.

Biomass for *squid and cuttlefish* was estimated by calculating the mean ratio from 1999 until 2019 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). **PB** (4.5 y-1) and **QB** (20.00 y-1) were based on the North Sea model from Mackinson and Daskalov (2007).

Biomass, **PB** and **PQ** for benthic functional groups, i.e. *epifaunal macrobenthos (mobile grazers)*, *infaunal macrobenthos*, *small mobile epifauna (swarming crustaceans)*, *small infauna (polychaetes)* and *sessile epifauna*, were assumed to be the same as in the greater North Sea as per Mackinson and Daskalov (2007). Note that for *meiofauna,* **ecotrophic efficiency** (EE) was estimated instead of biomass alongside **PB** and **QB** as per Mackinson and Daskalov (2007) as well.

The *blue mussels (aquaculture)* and ***blue mussels (reefs)*** groups have been introduced in the model for case studies in a later stage. Our interest lies in the cultivation of mussels in Belgium, which was not yet started in 1991. Hence the starting **biomass** in 1991 was estimated at a minimal value. **PB** and **QB** estimates were assumed to be the same as in an Ecopath model of the northern Wadden Sea (Horn et al., 2021).

2.2.1.5 Plankton

Input parameters for *phytoplankton* (**B** and **PB**) and *herbivorous & omnivorous plankton (copepods)* (**B**, **PB** and **QB**) were assumed to be similar in the SBNS as in the North Sea model of Mackinson and Daskalov (2007). For *carnivorous zooplankton*, **ecotrophic efficiency** (EE) was estimated instead of biomass. This value for EE, as well as **PB** and **PQ**, was assumed to be the same as in Mackinson and Daskalov (2007) as well.

For *gelatinous zooplankton* **biomass**, **PB** and **PQ** were assumed to be the same in the SBNS as in the Southern North Sea model from Stäbler et al. (2016).

2.2.1.6 Detritus & discards

For detritus and discards the only input parameter required is **biomass**. For *detritus*, the biomass of two relevant functional groups from the North Sea model of Mackinson and Daskalov (2007) (i.e. particulate organic matter and dissolved organic matter) was combined. *Discards* biomass was assumed to be equal in our study area compared to that of the Southern North Sea model (Stäbler et al., 2016).

2.2.2 Diets

The diet for each functional group was calculated based on the diets from a model with an overlapping study area (Southern North Sea model; Stäbler et al., 2016) and Mackinson and Daskalov (2007), which relied on the detailed dietary information for fish available for the year 1991, which was the ICES Year of the Stomach. The complete dietary matrix can be consulted in Table 4.

Since the model from Stäbler et al. (2016) included more functional groups, the diets for some groups were merged to reflect the functional groups in our model. Groups were merged by calculating 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 group. For example, gurnards, dragonets, and small demersal fish are distinct functional groups in Stäbler et al. (2016), but in our model they were merged into a single functional group, i.e. demersal fish, and thus had a single diet. Their corresponding biomass was used as the weight for calculating the weighted mean for each prey group.

In addition, several functional groups in the model of Stäbler et al. (2016) did not occur in our model. These groups were eliminated from the diets of our functional groups and the diet proportions were recalculated to a total of one while keeping the diet items ratio equal.

Note that there are three exceptions to our methodology to estimate diets: the *blue mussels (aquaculture)*, ***blue mussels (reefs)***, and *sea bass* functional group. The blue mussels, as filter feeders, mainly feed on phytoplankton, detritus, and herbivorous zooplankton as per Horn et al. (2020). Sea bass' diet was obtained from CEFAS fish stomach records (Pinnegar, 2014) and scientific literature (Henry and Cumming, 2017; Leeman et al., 2001).

Table 4: Dietary matrix of the Southern Bight of the North Sea.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Harbour porpoise	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Seals	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Seabirds (discard)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Seabirds (non-discard)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Sharks	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Rays	0	0	0	0	0	0	0	0.001107	0	0	0	2.72E-05	0	0	0	0	0	0	0	0
7	Juvenile Cod	0.036596	0.038233	0.005417	0.002305	0	0.008458	0.006218	0.009825	0	0.001111	0	0.005128	0	0	0	0.001984	0	0	0	0
8	Cod (adult)	0	0.07695	0	0	0	0	0	0.009522	0	0	0	0	0	0	0	0	0	0	0	0
9	Juvenile Whiting	0.030423	0.005203	0.013334	0.018036	0.002247	0.004954	0.017541	0.053943	0.000961	0.019293	0.000312	0.014929	0	0	0	5.73E-05	0.03331	0	0	0
10	Whiting (adult)	0.093621	0.083363	0	0	0.108001	0.004479	0	0.087064	0	0.000134	0	0	0	0	0	0	0	0	0	0
11	Other gadoids	0.069518	0.033636	0	0.000501	0.120878	0.033081	0.029187	0.026685	0.001094	0.00757	0.017611	0.015068	0	0	0	0.000396	0.004278	0	0	0
12	Demersal fish	0.000587	0.128943	0.002602	0.000901	0.012927	0.001054	0.053307	0.035938	0.060835	0.02142	0.019565	0.05268	0	0	0	0.001452	0.071494	0	0	0
13	Juvenile Herring	0.001617	1.04E-05	0	0	0.001777	0.003625	0.004671	0.016873	0.002444	0.029023	0	0.000354	0	0	0	0.012748	0.004592	0	0.000203	0
14	Herring (adult)	0.00485	0.00738	0.048337	0.059118	0.190339	0.013013	0.003223	0.102229	0	0	0	0	0	0	0	0	0	0	0	0
15	Sprat	0.153439	0.003388	0.044378	0.054509	0.038772	0.00444	0.018668	0.011011	0.014291	0.297891	0.004053	0.009371	0	0	0	0.029168	0.032556	0	0	0
16	Mackerel	0.028806	0	0.006042	0.02014	0.102805	0	0	4.98E-05	0	0	0	0.000302	0	0	0	8.04E-06	0	0	0	0
17	Horse mackerel	0.018078	0.015003	0	0	0.017376	0	0.00084	0.002988	0.001535	0.009883	0	3.95E-05	0	0	0	0.101912	0.084369	0	0	0
18	Sandeels	0.401382	0.364545	0.209182	0.333266	0.036159	0.334233	0.107437	0.047746	0.161665	0.326235	0.00104	0.28928	0	0	0	0.119565	0.020047	0	0.007627	0
19	Juvenile Plaice	0	0	0.002709	0.000301	0	0	1.73E-05	0.03763	0	0	0	0	0	0	0	0	0	0	0	0
20	Plaice (adult)	0	0.074409	0	0	0.05404	0.002057	0	0.004629	0	0	0	0	0	0	0	0	0	0	0	0
21	Dab	0	0.05977	0	0.0001	0.018199	0.01292	0.003577	0.117104	0.000699	0.000119	0.0052	0.023965	0	0	0	0	0.00607	0	0	0
22	Other flatfish	0	0.055656	0	0	0	0	0	0.003181	3.27E-06	0.001316	0	0	0	0	0	0	0	0	0	0
23	Juvenile Sole	0	0	0.000208	0	0	0.001186	0.001876	0.003485	0.001226	0.000533	0	0	0	0	0	0	0	0	0	0
24	Sole (adult)	0	0.044404	0	0	0.000139	0.003099	0	0	0	0	0	0.000292	0	0	0	0	0	0	0	0
25	Sea Bass	4.51E-07	0.000106	2.00E-06	6.92E-07	9.93E-06	8.10E-07	4.10E-05	2.76E-05	0	1.64E-05	1.50E-05	4.05E-05	0	0	0	1.12E-06	5.49E-05	0	0	0
26	Pelagic fish	0	0	0.002604	0	0.000472	0	0.000116	5.55E-05	0.000493	1.77E-05	0	0	0	0	0	0	0	0	0	0
27	Squid & cuttlefish	0.161082	0	0.003854	0.0001	0.060883	0.00293	0.074473	0.196968	0.023677	0.00961	0.000832	0.019642	0	0	0	0.008099	0.113729	0	0	0
28	Carnivorous zooplankton	0	0	0.014585	0.0001	0.006099	0.004897	0.022591	0.000791	0.223793	0.048656	0.104516	0.01644	0.2733	0.3093	0	0.065997	0.295734	0.066254	0	0
29	Herbivorous plankton (copepods)	0	0	0.005313	0.000601	0	7.21E-07	6.50E-06	0	0.006555	0.002799	0.312193	0.053614	0.6748	0.6701	0.888889	0.484844	0.058876	0.640907	0	0
30	Gelatinous zooplankton	0	0	0	0	0.03508	0	0.001791	0.001001	0.004575	0.003672	0	0	0	0	0	0.084915	8.48E-05	0	0.003458	0
31	Large crabs + shrimps	0	0	0.039794	0.010421	0.093515	0.153146	0.157159	0.077805	0.023325	0.043923	0.017774	0.186088	0	0	0	0.0228	0.070986	0	0.016928	0.108855
32	Blue mussels (reefs)	0	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	0	0	0	0	0	1.00E-11	1.00E-11	1.00E-11
33	Blue mussels (aquaculture)	0	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	1.00E-11	0	0	0	0	0	0	0	0
34	Epifaunal macrobenthos (mobile grazers)	0	0	0.000105	0	0.047784	0.139601	0.129258	0.100892	0.109784	0.08996	0.135152	0.088498	0	0	0	0.024951	0.172634	0.00084	0.104951	0.021278
35	Infaunal macrobenthos	0	0	0.016043	0.36012	0.023124	0.006508	0.082484	0.037439	0.026005	0.037204	0.176833	0.045785	0	0	0	0.000212	0.000874	0.00588	0.174715	0.436463
36	Crangon	0	0	0.002709	0	0.00846	0.026258	0.165263	0.012878	0.092238	0.018347	0.000355	0.006957	0	0	0	0.000395	0.003194	0	6.90E-05	0.010122
37	Small mobile epifauna (swarming crustaceans)	0	0	0	0	0.006376	0.145022	0.004439	2.49E-05	0.013533	0.001951	0.028656	0.098016	0.0519	0.0206	0	0.009074	0.019335	0.016275	0.196479	0.051271
38	Small infauna (polychaetes)	0	0	0.005209	0.000501	0.012773	0.082874	0.115667	0.000847	0.231217	0.029215	0.175895	0.055172	0	0	0	0.003355	0.007782	0.196871	0.476874	0.360665
39	Sessile epifauna	0	0	0.02396	0.106814	0.001041	0	0.000148	0.000261	4.79E-05	0.0001	0	4.62E-06	0	0	0	0.005979	0	0	0.014238	0
40	Meiofauna	0	0	0	0	0.000726	0.002161	0	0	3.27E-06	0	0	0.018305	0	0	0	1.00E-06	0	0.050189	0.003458	0.010346
41	Phytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.111111	0.022087	0	0.022785	0	0
42	Detritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	Discards	0	0.009001	0.485869	0.032165	0	0.010002	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.001
	Import	0	0	0.067744	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	(1 - Sum)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4: Dietary matrix of the Southern Bight of the North Sea (continued)

	Prey \ predator	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	Harbour porpoise	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Seals	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Seabirds (discard)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Seabirds (non-discard)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Sharks	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Rays	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Juvenile Cod	0	0.005002	0	0	0	0	0.011306	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Cod (adult)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	Juvenile Whiting	0	0.000981	0	0	0.001495	0	0.000951	0	0	0	0	0	0	0	0	0	0	0	0	0
10	Whiting (adult)	0	0	0	0	0.003486	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	Other gadoids	0	0.002953	0	0	0.019589	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	Demersal fish	0	0.012011	0.01279	0	0.020781	0	0.005701	0	0	0	0	0	0	0	0	0	0	0	0	0
13	Juvenile Herring	0	0.000122	0	0	0	0	0.000951	0	0	0	0	0	0	0	0	0	0	0	0	0
14	Herring (adult)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	Sprat	0	0.014859	0	0	0	0	0.011306	0	0	0	0	0	0	0	0	0	0	0	0	0
16	Mackerel	0	0	0	0	0.133138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Horse mackerel	0	0	0	0	0.066735	0	0.011306	0	0	0	0	0	0	0	0	0	0	0	0	0
18	Sandeels	0	0.015771	0	0	0.002988	0	0.045118	0	0	0	0	0	0	0	0	0	0	0	0	0
19	Juvenile Plaice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	Plaice (adult)	0	0	0	0	0	0	0.005706	0	0	0	0	0	0	0	0	0	0	0	0	0
21	Dab	0	0.051657	0	0	0	0	0.005706	0	0	0	0	0	0	0	0	0	0	0	0	0
22	Other flatfish	0	0.052364	0	0	0	0	0.011411	0	0	0	0	0	0	0	0	0	0	0	0	0
23	Juvenile Sole	0	0	0	0	0.010564	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	Sole (adult)	0	0	0	0	0.0011	0	0.005706	0	0	0	0	0	0	0	0	0	0	0	0	0
25	Sea Bass	0	9.23E-06	9.82E-06	0	1.60E-05	0	4.38E-06	0	0	0	0	0	0	0	0	0	0	0	0	0
26	Pelagic fish	0	0	0	0	0.068939	0.0531	0.0224	0	0	0	0	0	0	0	0	0	0	0	0	0
27	Squid & cuttlefish	0	0	0	0	0.008808	0.0056	0.025008	0	0	0.073614	0	0	0	0	0	0	0	0	0	0
28	Carnivorous zooplankton	0	0.038884	0	0	0	0.1489	0.23066	0.058258	0	0.294013	0.005615	0	0	0	0	0	0	0	0	0
29	Herbivorous plankton (copepods)	0.0125	0	0	0	0.209592	0.6949	0.336479	0.826714	0	0.294013	0.01123	0.01	0.01	0	0	0.000272	0	0	0	0
30	Gelatinous zooplankton	0	0.053729	0	0	0	0.0332	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	Large crabs + shrimps	0.010658	0.063365	0	0.054422	0.372514	0.00948	0.014399	0	0	0.048463	0.002245	0	0	0	0	0.001142	0	0	0	0
32	Blue mussels (reefs)	1.00E-11	1.00E-11	0	0	0	0	0	0	0	0	1.00E-11	1.00E-11	1.00E-11	1.00E-11	0	0	0	0	0	0
33	Blue mussels (aquaculture)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	Epifaunal macrobenthos (mobile grazers)	0.2582	0.18712	0.0128	0.011102	0.001053	0.0266	0	0	0	0	0.353173	0	0	0.059141	0	0.000349	0	0	0	0
35	Infaunal macrobenthos	0.2397	0.088637	0.1154	0.012708	0	0	0	0	0	0	0.375879	0	0	0.276562	0	4.11E-05	0	0	0	0
36	Crangon	0.000342	0.003186	0	0	0.070368	0.00492	0.007472	0	0	0.025152	0.000805	0	0	0	0	0	0	0	0	0
37	Small mobile epifauna (swarming crustaceans)	0.3278	0.114992	0	0	0	0.0122	0.169693	0.115028	0	0.117664	0.029829	0	0	0.059141	0.034482	0.008844	0.099985	0	0	0
38	Small infauna (polychaetes)	0.1379	0.197567	0.4221	0.920768	0	0.0111	0.0224	0	0	0	0.138779	0	0	0.295703	0.189655	0.036484	0	0.090909	0	0
39	Sessile epifauna	0.011	0.095791	0	0	0	0	0	0	0	0	0.066215	0	0	0	0	0.003074	0	0	0	0
40	Meiofauna	0.0009	0	0.4359	0	0	0	0	0	0	0	0.01123	0	0	0	0.086206	0.942701	0.230734	0.272727	0	0.1
41	Phytoplankton	0	0	0	0	0	0	0.056318	0	0.947368	0.147081	0	0.85	0.85	0.059141	0	0	0	0	0.333	0
42	Detritus	0	0	0	0	0	0	0	0	0.052632	0	0	0.14	0.14	0.241562	0.689656	0	0.669282	0.636364	0.667	0.9
43	Discards	0.001	0.001	0.001	0.001	0	0	0	0	0	0	0.005	0	0	0.008751	0	0.007093	0	0	0	0
	Import	0	0	0	0	0.008837	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	(1 - Sum)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

2.2.3 Landings and discards

2.2.3.1 Commercial fleets

Historical commercial catch data for **1991** is available through the International Council for the Exploration of the Sea (ICES Historical nominal catches 1950-2010). However, historical catch data as provided by ICES does not include information concerning what fisheries fleet contributed to a particular catch. Therefore, in the 1991 model, catches were assigned to each fleet based on the earliest available data collection for fleet contributions as per Stäbler et al. (2016) and Bentley et al. (2019). For this purpose, data on landings and discards at age for the SBNS (ICES are IVc) from 2003 – 2017 were obtained from the Scientific, Technical and Economic Committee for Fisheries (STECF) Fisheries Dependent Information (FDI) (STECF, 2017). First, all catches of 1991 (from ICES) and 2003 (from STECF FDI) were allocated to the functional groups of the EwE model (e.g. pouting catches were assigned to the *other gadoids* group). Next, the contribution of each fleet to the catches of the functional groups was calculated for 2003, which was then multiplied with the catches for EwE functional groups in 1991. This resulted in total landings biomass for each functional group and fleet (Table 5). As such, the relative contribution of commercial fleets to catches in 2003 based on STECF fisheries dependent information gear type (STECF, 2017) was extrapolated to 1991 catches.

Historical catch data does not include any information concerning discards either (ICES Historical nominal catches 1950-2010). Hence, for the 1991 model, the ratio of landings to discards in 2003 was calculated for each commercial fleet (based on STECF gear type) per functional group included in the model, and also extrapolated to 1991 (Table 7). Regarding the discards of commercial fleets, it was assumed that discards mortality rates are 100% (which is the standard setting).

Note that due to missing data on Dutch contributions to catches in the early years of the time series, adjustments were made to the 1991 landings and discards of some functional groups. In particular, the contributions for Dab, Other gadoids, and Other flatfish were estimated and added retrospectively, resulting in a rescaling of landings and discards for these groups. Further details on this adjustment are provided in Section 3.2.2.

2.2.3.2 Recreational fleets

Recreational fisheries landings and discards were included based a monitoring program at the Belgian coast from on Verleye et al. (2019). As this program started in 2017, the landings and discards data available for Belgian waters were extrapolated to the entire SBNS based on surface area for the 2018 model. However, for in the 1991 model, due to a lack of historical data, recreational landings and discards for target species, such as cod, sea bass, mackerel, plaice, sole and brown shrimp were included as conservative estimates (i.e. near zero) in this Ecopath model (Table 6 & 8). For recreational fisheries, the discards mortality rates were set lower than for commercial fleets, i.e. at 0.5, as studies show that the survival rate after release is higher with recreational fishing ((Ferter et al., 2013; Lewin et al., 2018; Skov et al., 2023; Weltersbach et al., 2018; Weltersbach and Strehlow, 2013)).

2.2.3.3 Mussel aquaculture

Even though there was no mussel aquaculture ongoing in the Belgian part of the North Sea in 1991, it was included to allow future assessment of management scenarios in this area of interest. As such, mussel aquacultures and landings were estimated at zero t km^{-2} y^{-1}.

Table 5. The landings of the commercial fishing fleets in the Southern Bight of the North Sea in t km^{-2} y^{-1}. Grey highlighted groups indicate that the group has a multi-stanza.

	Group name	Comm. Other	Comm. Demersal	Comm. Nets	Comm. Beam	Comm. Shrimp	Comm. Pelagic	Comm. Pots	Comm. Hooks	Comm. Dredge	Aquaculture (blue mussels)
1	Harbour porpoise	0	0	0	0	0	0	0	0	0	0
2	Seals	0	0	0	0	0	0	0	0	0	0
3	Seabirds (discard)	0	0	0	0	0	0	0	0	0	0
4	Seabirds (non-discard)	0	0	0	0	0	0	0	0	0	0
5	Sharks	0	0.00111	0.00316	0.000719	1.31E-06	0	3.48E-06	0.00434	0	0
6	Rays	0	0.00261	0.00141	0.0126	1.11E-05	5.43E-07	3.72E-05	0.00268	7.52E-07	0
	Cod										
7	Juvenile Cod	0	0	0	0	0	0	0	0	0	0
8	Cod (adult)	0	0.0345	0.0175	0.0712	0.00344	0.00179	3.67E-05	0.015	1.23E-05	0
	Whiting										
9	Juvenile Whiting	0	0	0	0	0	0	0	0	0	0
10	Whiting (adult)	0	0.0714	0.000914	0.0457	0.0117	0.00153	0	0.000228	8.42E-06	0
11	Other gadoids	0	0.004465402	0.003785884	0.01829844	0	0	0	2.42E-05	0	0
12	Demersal fish	0	0.01209146	0.0110412	0.01209146	0.000123608	0	0.000267143	0.002504467	0	0
	Herring										
13	Juvenile Herring	0	0	0	0	0	0	0	0	0	0
14	Herring (adult)	0	0.00088	0.000523	0.00133	0	0.184	0	0	0	0
15	Sprat	6.25E-05	0.0199	0.000185	4.57E-08	4.95E-06	0.0234	0	1.75E-06	7.30E-07	0
16	Mackerel	0	0.0452	0.000192	2.75E-05	6.84E-05	0.015	0	1.89E-06	0	0
17	Horse mackerel	0	0.00378	6.58E-07	4.97E-05	2.14E-06	0.0345	0	0	0	0
18	Sandeels	0	0.0453	0	0	0	0.000681	1.79E-07	0	0	0
	Plaice										
19	Juvenile Plaice	0	0	0	0	0	0	0	0	0	0
20	Plaice (adult)	1.11E-06	0.00518	0.000941	0.379	0.00153	7.79E-05	0	2.91E-07	4.73E-07	0
21	Dab	1.53E-07	0.01363854	0.000273	0.05003153	0.003243569	0.00015	0	6.52E-06	1.02E-05	0
22	Other flatfish	3.62E-07	0.002566632	0.001188756	0.0986127	0.000141	1.45E-05	0	6.82E-05	2.20E-06	0
	Sole										
23	Juvenile Sole	0	0	0	0	0	0	0	0	0	0
24	Sole (adult)	3.12E-05	0.0039	0.00712	0.165	0.000819	1.76E-05	0.000183	8.84E-06	2.66E-07	0
25	Sea Bass	0	0.000294	0.000336	0.000281	6.43E-06	0	3.40E-07	6.48E-05	0	0
26	Pelagic fish	0	0.000213	3.24E-06	5.86E-07	0	0.0408	0	0	0	0
27	Squid & cuttlefish	0	0.000914	0.000738	0.00129	0	8.84E-07	9.36E-05	1.84E-06	0	0
28	Carnivorous zooplankton	0	0	0	0	0	0	0	0	0	0
29	Herbivorous plankton (copepods)	0	0	0	0	0	0	0	0	0	0
30	Gelatinous zooplankton	0	0	0	0	0	0	0	0	0	0
31	Large crabs + shrimps	0	0.000455	9.70E-05	0.001	0.000371	5.56E-07	0.025	9.62E-06	8.34E-09	0
32	Blue mussels (reefs)	0	0	0	0	0	0	0	0	0	0
33	Blue mussels (aquaculture)	0	0	0	0	0	0	0	0	0	1.00E-11
34	Epifaunal macrobenthos (mobile grazers)	0	5.13E-07	0	6.66E-06	0	0	0	0	0.000158	0
35	Infaunal macrobenthos	0	2.64E-06	0	3.49E-05	2.28E-06	0	0.044	0	0.733	0
36	Crangon	0	0.00298	0	8.59E-06	0.121	0	0.000167	0	0	0
37	Small mobile epifauna (swarming crustaceans)	0	0	0	0	0	0	0	0	0	0
38	Small infauna (polychaetes)	0	0	0	0	0	0	0	0	0	0
39	Sessile epifauna	0	0	0	0	0	0	0	0	0.0494	0
40	Meiofauna	0	0	0	0	0	0	0	0	0	0
41	Phytoplankton	0	0	0	0	0	0	0	0	0	0
42	Detritus	0	0	0	0	0	0	0	0	0	0
43	Discards	0	0	0	0	0	0	0	0	0	0
49	Sum	9.53E-05	0.2713812	0.04940874	0.8572822	0.1424648	0.301963	0.06978864	0.02494042	0.7825934	1.00E-11

Table 6. The landings of the recreational fishing fleets in the Southern Bight of the North Sea in t km^{-2} y^{-1}. Grey highlighted groups indicate that the group has a multi-stanza.

	Group name	Recr. Anglers (boat)	Recr. Trawlers	Recr. Anglers (land)	Recr. Nets	Recr. Others
1	Harbour porpoise	0	0	0	0	0
2	Seals	0	0	0	0	0
3	Seabirds (discard)	0	0	0	0	0
4	Seabirds (non-discard)	0	0	0	0	0
5	Sharks	0.000105806	0	0	3.50E-06	0
6	Rays	0	0	0	0	0
	Cod					
7	Juvenile Cod	0	0	0	0	0
8	Cod (adult)	0.002506789	1.00E-20	3.76E-05	1.21E-05	0
	Whiting					
9	Juvenile Whiting	0	0	0	0	0
10	Whiting (adult)	0.009059928	1.20E-05	0.003422688	4.05E-05	0.000107294
11	Other gadoids	0.000322267	0	3.46E-05	0	0
12	Demersal fish	0.000422502	0	5.33E-05	2.41E-06	1.18E-05
	Herring					
13	Juvenile Herring	0	0	0	0	0
14	Herring (adult)	8.03E-07	2.51E-06	0	9.34E-07	0
15	Sprat	0	0	0	0	0
16	Mackerel	0.006215811	0	0	8.81E-06	0
17	Horse mackerel	0.00014945	0	5.07E-06	1.05E-05	0
18	Sandeels	2.24E-06	0	0	0	0
	Plaice					
19	Juvenile Plaice	0	0	0	0	0
20	Plaice (adult)	0.000710647	5.16E-06	8.33E-06	3.80E-06	1.84E-05
21	Dab	0.008306923	3.24E-05	0.000829753	3.47E-05	0.000422515
22	Other flatfish	0.00121625	1.50E-05	0.000283179	6.07E-05	0.000324832
	Sole					
23	Juvenile Sole	0	0	0	0	0
24	Sole (adult)	0.004860761	1.95E-05	0.000309717	0.000181589	0.000306895
25	Sea Bass	0.001526011	0	0.000810768	0.000236894	0
26	Pelagic fish	0	0	0	0	0
27	Squid & cuttlefish	0	0	0	1.99E-05	0
28	Carnivorous zooplankton	0	0	0	0	0
29	Herbivorous plankton (copepods)	0	0	0	0	0
30	Gelatinous zooplankton	0	0	0	0	0
31	Large crabs + shrimps	0	0	0	0	0
32	Blue mussels (reefs)	0	0	0	0	0
33	Blue mussels (aquaculture)	0	0	0	0	0
34	Epifaunal macrobenthos (mobile grazers)	0	0	0	0	0
35	Infaunal macrobenthos	0	0	0	0	0
36	Crangon	0	0.01546715	0.000126404	0	0.005354121
37	Small mobile epifauna (swarming crustaceans)	0	0	0	0	0
38	Small infauna (polychaetes)	0	0	0	0	0
39	Sessile epifauna	0	0	0	0	0
40	Meiofauna	0	0	0	0	0
41	Phytoplankton	0	0	0	0	0
42	Detritus	0	0	0	0	0
43	Discards	0	0	0	0	0
49	Sum	0.03540619	0.01555371	0.005921416	0.000616322	0.006545861

Table 7. The discards of the commercial fishing fleets in the Southern Bight of the North Sea in t km^{-2} y^{-1}. Grey highlighted groups indicate that the group has a multi-stanza.

	Group name	Comm. Other	Comm. Demersal	Comm. Nets	Comm. Beam	Comm. Shrimp	Comm. Pelagic	Comm. Pots	Comm. Hooks	Comm. Dredge	Aquaculture (blue mussels)
1	Harbour porpoise	0	0	0	0	0	0	0	0	0	0
2	Seals	0	0	0	0	0	0	0	0	0	0
3	Seabirds (discard)	0	0	6.00E-08	0	0	0	0	6.15E-06	0	0
4	Seabirds (non-discard)	0	0	3.15E-05	0	0	0	0	1.93E-06	0	0
5	Sharks	0	0.001658934	0.00035454	4.57E-05	0	0	0	0	0	0
6	Rays	0	0.003200906	1.54E-06	0.006435434	0	0	0	0	0	0
	Cod										
7	Juvenile Cod	0	0.005879791	8.00E-05	0.003888941	4.05E-06	0.00030421	0	1.32E-05	0	0
8	Cod (adult)	0	0.000283666	1.26E-05	0.00027716	5.82E-07	8.38E-05	0	6.58E-06	0	0
	Whiting										
9	Juvenile Whiting	0	0.09519688	0	0.8768977	0.000994955	0	0	0	0	0
10	Whiting (adult)	0	0.11556	0	0	0	0	0	0	0	0
11	Other gadoids	0	0.00245842	0.000175	0.004213856	0	0	0	0	0	0
12	Demersal fish	0	0.3304094	0.000844188	0.000693363	8.35E-07	0	0	0	0	0
	Herring										
13	Juvenile Herring	0	8.63E-06	0	0.008243455	0	5.23E-08	0	0	0	0
14	Herring (adult)	0	0	0	0	0	0	0	0	0	0
15	Sprat	4.16E-12	1.26E-07	9.87E-11	0	6.20E-06	0	0	0	0	0
16	Mackerel	0	0.4152901	0	0	0	9.05E-08	0	0	0	0
17	Horse mackerel	0	0.01210895	0	0	0	8.33E-07	0	0	0	0
18	Sandeels	0	0	0	0	0	0	0	0	0	0
	Plaice										
19	Juvenile Plaice	0	0.001733315	1.58E-05	0.2312031	0.000152748	7.93E-08	0	0	0	0
20	Plaice (adult)	0	0.000850132	1.43E-05	0.1337709	0	5.94E-08	0	0	0	0
21	Dab	0	0.1144011	1.87E-05	0.2762402	0.001902216	0.000101	0	0	0	0
22	Other flatfish	6.19E-09	0.000798024	1.38E-05	0.008589833	8.69E-06	1.21E-06	0	0	0	0
	Sole										
23	Juvenile Sole	0	1.88E-05	0	0	0.01578015	0	0	0	0	0
24	Sole (adult)	0	4.89E-05	0	0	0	0	0	0	0	0
25	Sea Bass	0	2.90E-06	0	0	0	0	0	0	0	0
26	Pelagic fish	0	0	0	0	0	0	0	0	0	0
27	Squid & cuttlefish	0	4.30E-06	0	0	0	0	0	0	0	0
28	Carnivorous zooplankton	0	0	0	0	0	0	0	0	0	0
29	Herbivorous plankton (copepods)	0	0	0	0	0	0	0	0	0	0
30	Gelatinous zooplankton	0	0	0	0	0	0	0	0	0	0
31	Large crabs + shrimps	0	0.000546368	3.28E-06	0.001907516	0	1.85E-09	0	0	0	0
32	Blue mussels (reefs)	0	0	0	0	0	0	0	0	0	0
33	Blue mussels (aquaculture)	0	0	0	0	0	0	0	0	0	0
34	Epifaunal macrobenthos (mobile grazers)	0	0	0	0	0	0	0	0	0	0
35	Infaunal macrobenthos	0	0	0	0	0	0	0	0	0	0
36	Crangon	0	0	0	0	0	0	0	0	0	0
37	Small mobile epifauna (swarming crustaceans)	0	0	0	0	0	0	0	0	0	0
38	Small infauna (polychaetes)	0	0	0	0	0	0	0	0	0	0
39	Sessile epifauna	0	0	0	0	0	0	0	0	0	0
40	Meiofauna	0	0	0	0	0	0	0	0	0	0
41	Phytoplankton	0	0	0	0	0	0	0	0	0	0
42	Detritus	0	0	0	0	0	0	0	0	0	0
43	Discards	0	0	0	0	0	0	0	0	0	0
49	Sum	6.19E-09	1.10046	0.001565309	1.552407	0.01885043	0.000491336	0	2.79E-05	0	0

Table 8. The discards of the recreational fishing fleets in the Southern Bight of the North Sea in t km^{-2} y^{-1}. Grey highlighted groups indicate that the group has a multi-stanza.

	Group name	Recr. Anglers (boat)	Recr. Trawlers	Recr. Anglers (land)	Recr. Nets	Recr. Others
1	Harbour porpoise	0	0	0	0	0
2	Seals	0	0	0	0	0
3	Seabirds (discard)	0	0	0	0	0
4	Seabirds (non-discard)	0	0	0	0	0
5	Sharks	9.86E-05	1.33E-05	0	4.66E-06	0
6	Rays	0	0	0	0	5.74E-06
	Cod					
7	Juvenile Cod	0	0	0	0	0
8	Cod (adult)	0.00020316	3.60E-06	3.31E-05	0	0
	Whiting					
9	Juvenile Whiting	0.00137712	1.63E-05	0.000188735	5.69E-06	5.98E-06
10	Whiting (adult)	0.001376958	8.40E-05	0.000247478	9.18E-07	0
11	Other gadoids	0.000353803	0	0.000181504	0	0
12	Demersal fish	0.000353338	1.39E-05	0.000325414	0.000134822	1.45E-05
	Herring					
13	Juvenile Herring	0	1.57E-07	0	4.44E-08	1.48E-06
14	Herring (adult)	5.99E-07	2.50E-05	0	0	0
15	Sprat	0	0	0	0	0
16	Mackerel	0.000441094	0	3.74E-06	6.34E-08	8.04E-07
17	Horse mackerel	0.000348203	0	2.38E-06	2.27E-05	0
18	Sandeels	9.74E-07	0	1.29E-07	0	0
	Plaice					
19	Juvenile Plaice	3.02E-05	2.86E-06	3.68E-06	5.85E-06	2.38E-05
20	Plaice (adult)	2.34E-05	2.28E-05	1.01E-05	5.23E-06	0
21	Dab	0.000758136	8.30E-05	8.20E-05	3.47E-06	2.46E-05
22	Other flatfish	0.002346647	3.42E-05	0.000820747	6.43E-05	0.000113479
	Sole					
23	Juvenile Sole	0.000174994	6.93E-06	1.70E-05	1.46E-06	4.01E-05
24	Sole (adult)	6.12E-05	2.97E-05	7.54E-06	7.54E-06	1.87E-05
25	Sea Bass	0.003683315	1.32E-06	0.002154128	0.000411044	4.70E-05
26	Pelagic fish	0	0	0	6.52E-05	0
27	Squid & cuttlefish	0	1.54E-06	0	1.58E-06	1.12E-05
28	Carnivorous zooplankton	0	0	0	0	0
29	Herbivorous plankton (copepods)	0	0	0	0	0
30	Gelatinous zooplankton	0	0	0	0	0
31	Large crabs + shrimps	0	0	0	0	0
32	Blue mussels (reefs)	0	0	0	0	0
33	Blue mussels (aquaculture)	0	0	0	0	0
34	Epifaunal macrobenthos (mobile grazers)	0	0	0	0	0
35	Infaunal macrobenthos	0	0	0	0	0
36	Crangon	0	0	0	0	0
37	Small mobile epifauna (swarming crustaceans)	0	0	0	0	0
38	Small infauna (polychaetes)	0	0	0	0	0
39	Sessile epifauna	0	0	0	0	0
40	Meiofauna	0	0	0	0	0
41	Phytoplankton	0	0	0	0	0
42	Detritus	0	0	0	0	0
43	Discards	0	0	0	0	0
49	Sum	0.01163174	0.000338607	0.004077675	0.000734572	0.000307383

2.2.4 Pedigree

A pedigree index was assigned to each parameter, representing the confidence of each estimate. These values highlight uncertainties in the parameter estimates for each functional group and can be used to calculate an uncertainty interval around the input values when running Monte-Carlo simulations. The pedigree aids decision making during the model balancing and fitting process. The pedigree is available with the EwE model (Pint et al., 2024b).

2.3 Mass-balancing

The ecopath model (Pint et al., 2024a) was mass-balanced following best practices described by Heymans et al. (2016). Pre-balance diagnostics were applied to identify ecological inconsistencies in the model as per Link (2010), and to subsequently balance it to obey the rules of thermodynamics (Christensen and Walters, 2024). After minor changes to the ecopath model, i.e. *Crangon* not a multi-stanza and including a new functional group, *blue mussels (reefs)*, the model was unbalanced again, and several steps were taken to balance the model again (Table 9).

Table 9: Overview of changes made to ecopath 1991 model.

	Functional groups	Change
1	Crangon	Multi-stanza Crangon was merged using the tool in EwE.
2	blue mussels (reefs)	Added new functional group, blue mussels (reefs), with low biomass and low proportion in predators' diets.
3	blue mussels (aquaculture)	Decreased biomass, proportion in predators' diets similarly to blue mussels (reefs). Landings were also decreased to ensure EE < 1.
4	Sea bass Horsemackerel	Recreational landings and discards added, resulting in EE > 1 for Sea bass and Horsemackerel. Biomass of both FGs was increased and discard mortality fate of recreational fisheries was set to 0.5.
5	Whiting (adults) Juvenile whiting	Diets were adjusted based on Mackinson & Dakalov (2007) as the trophic level of adults was lower than juveniles.
6	Rays Plaice (adults) Juvenile plaice Dab Other flatfish Sole (adults) Juvenile sole Large crabs + shrimps Crangon Epifaunal macrobenthos (mobile grazers) Seals	Discard proportions was included in FGs diets with low proportion. Additionally, fish species were excluded from Crangon's diet. Both changes were made as per Hill et al. (2021).
7	Cod (adults) Juvenile cod	Diet proportion of Squid & cuttlefish in cods' diet was increased, which resulted in an EE > 1 for Squid & cuttlefish. Squid & cuttlefish biomass was increased to 0.7 t km^{-2}.

3 Ecosim: a temporal dynamic model of the Southern Bight of the North Sea

To simulate ecosystem dynamics over time, the static Ecopath model was extended using Ecosim. Ecosim builds upon the mass-balanced snapshot provided by Ecopath and introduces temporal dynamics by integrating time series data using a series of coupled differential equations, which are based on the Ecopath master equations (Eq. 1 and 2). This enables the examination of how biomass and catch evolve in response to changing anthropogenic pressures (i.e. fisheries) and environmental conditions.

Ecosim models are grounded in foraging arena theory (Ahrens et al., 2012; Walters et al., 1997), in which predator-prey interactions are regulated by predator vulnerabilities, vij. These parameters define how prey move between vulnerable and invulnerable states for their predator, influencing the consumption rate of their predators (Eq. 11) and thus their consumption over time. When fitting a model to reference time series, these vulnerabilities are adjusted through vulnerability multipliers (kij), as vij equals kij multiplied by the baseline predation mortality (Qij/Bi). A vulnerability multiplier of two is the default, representing mixed control, whereas values closer to one suggest bottom-up control, and higher values than two reflect top-down control (Christensen and Walters, 2024). For each predator-prey interaction consumptions rates, Qij, of i predating on j are calculated as:

$$Q_{ij} = \frac{v_{ij} a_{ij} B_i B_j T_i T_j S_{ij} M_{ij} / D_j}{v_{ij} + v_{ij} T_i M_{ij} + a_{ij} M_{ij} B_j S_{ij} T_j / D_j / A} \cdot f(Env_t) \qquad \text{Eq. 11}$$

With for each interaction between prey (i) and predator (j):

- Q_{ij}: Consumption rate of j predating on i (t km−2 y−1).
- v_{ij}: Vulnerability, expressing the rate with wich prey i move between a vulnerable and non-vulnerable state. The default value is two.
- a_{ij}: Effective search rate for predator j feeding on a prey i.
- B_i and B_j: Prey and predator biomass respectively.
- T_i and T_j: Prey and predator feeding time respectively.
- S_{ij}: User defined seasonal or long-term forcing effects.
- M_{ij}: Mediation forcing effects.
- A: Foraging arena size proportional to total area.
- $f(Env_t)$: An environmental response function that affects the size of the foraging area to consider external environmental drivers changing over time (e.g., temperature and salinity).
- D_j: Effects of handling time as a limit to consumption rate, $1/D_j$ is proportion of time spent feeding.

Through this structure, Ecosim allows for dynamic simulations where each time step reflects changing system conditions. These changes are driven by temporal inputs, including anthropogenic time series (changing effects of fishing) and environmental forcing functions (changing environmental conditions).

3.1 Stability testing

Before running stability simulations, feeding time adjustment rates were assigned to functional groups in accordance with guidance fromChristensen and Walters (2024). In Ecosim, the feeding time adjustment rate controls how quickly a group can alter its relative foraging time to stabilise consumption (Q/B) at the Ecopath base rate. Values range from 0 to 1, where 0 indicates no behavioural adjustment—i.e., the group is assumed to forage at a constant rate—while higher values allow for dynamic compensation in response to changes in group biomass or prey availability. This parameter is particularly relevant for modelling compensatory growth and foraging plasticity, as it allows organisms to maintain Q/B by varying foraging time (when feeding time adjustment rate is set above zero). Christensen and Walters (2024) recommend that feeding time adjustments be enabled only for functional groups likely to exhibit such behavioural flexibility, such as marine mammals, seabirds, top predators, and early life stages. Following these recommendations, we applied a value of 0.5 to marine mammals and birds to reflect their foraging adaptability. Juvenile groups were assigned a value of 0.25. This resulted in increased stability for multi-stanza groups, as also observed in (Bentley et al., 2019a). Likewise, a value of 0.25 was applied to top predators in our model (i.e., sharks and cod) to represent their capacity to alter foraging behaviour (Christensen and Walters, 2024). All other groups were assigned a value of 0, meaning they were considered incapable of adjusting their foraging effort dynamically.

After assigning feeding time adjustment rates, the Ecopath model was subjected to stability tests under altered fishing regimes. Three scenarios were considered for stability evaluation: a permanent stop to all fishing activities, a temporary halt of fishing activities for 10 years followed by a return to baseline effort, and a temporary doubling of fishing effort for 10 years before resuming baseline levels. These tests enabled evaluation of how well the model responded to abrupt shifts in external pressure and whether trophic dynamics remained stable under such conditions.

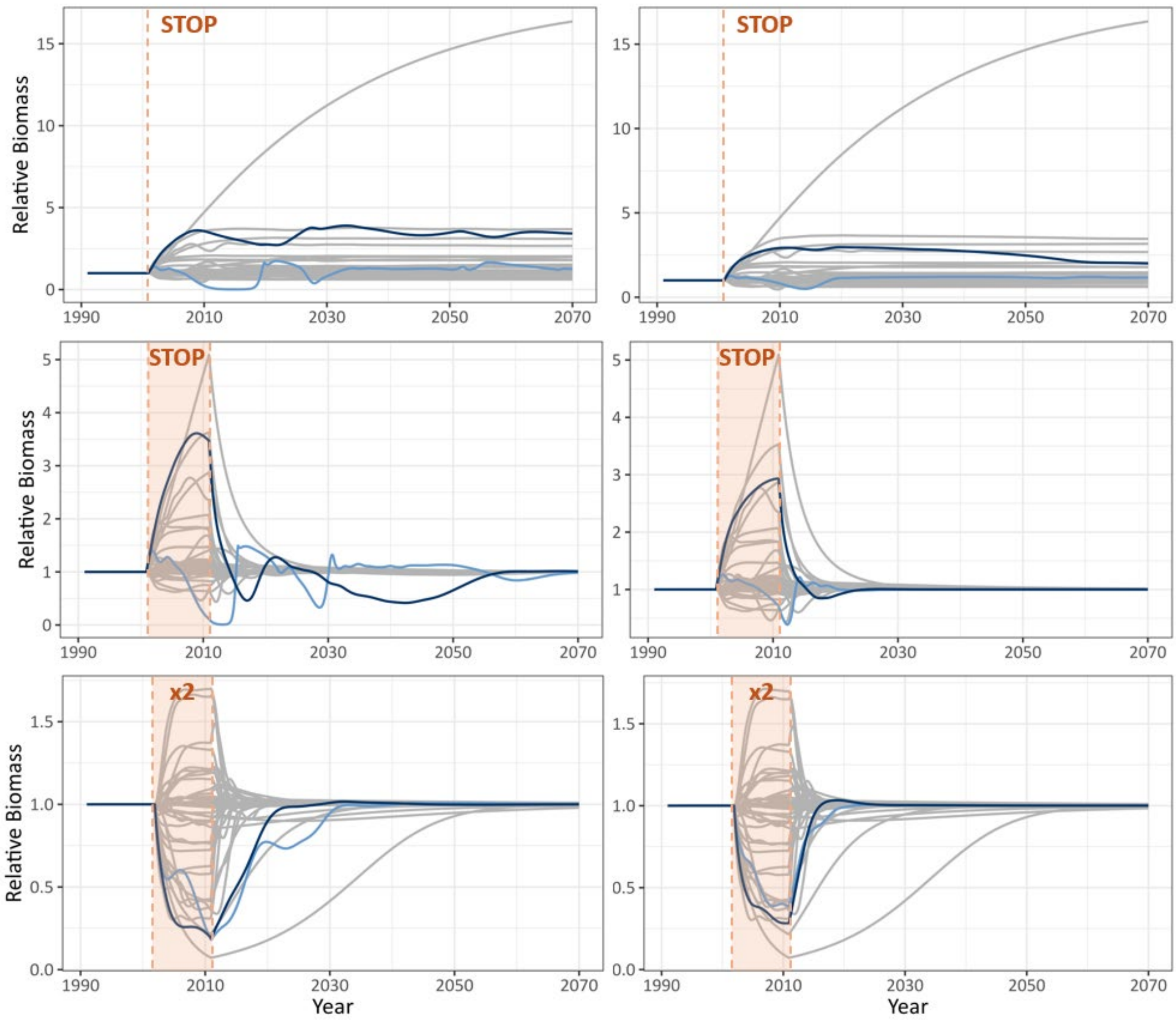


Figure 3: Model stability testing results under three fishing scenarios: (1) a complete cessation of fishing activities, (2) a temporary halt in fishing for 10 years followed by a return to baseline levels, and (3) a short-term doubling of fishing pressure for 10 years before resuming baseline levels. The temporal dynamics of Plaice (adult) are represented by the dark blue line, while Plaice (juvenile) is depicted by the light blue line. All other groups are shown in gray. The left panels illustrate model outcomes before adjustments to reproduction and growth parameters for the Plaice multi-stanza groups, highlighting instability across fishing scenarios. The right panels present results after modifications, demonstrating improved stability.

Plaice (adult) and *Plaice (juvenile)* exhibited unstable responses under each of the tested scenarios (Fig. 3, left). In the model, plaice is represented as a multi-stanza group, initially parameterised with a von Bertalanffy growth coefficient (K) of 0.18 year^{-1}, and a maturity ratio ($W_{maturity}/W_{inf}$) of 0.173. While these values were derived from empirical data available via FishBase (FishBase), Life-history tool), life-history parameters may vary depending on geographical region (Wang et al., 2020; Wilson et al., 2019). To better reflect local conditions in the SBNS study area, stanza parameters for plaice were revised based on available growth and mortality data from the North Sea Subarea IV. The growth coefficient (K) was increased to 0.18 year^{-1}, and the maturity ratio was adjusted to 0.173. These modifications resulted in an ecotrophic efficiency (EE) greater than 1 for *Small infauna (polychaetes),* and a reduced EE for both Plaice (juvenile) and Plaice (adult). To restore mass balance, *Plaice* *(adult)* biomass was slightly reduced from 0.899 to 0.85 t.km^{-2}. These adjustments successfully improved model stability across all tested fishing scenarios (Fig. 3, right).

3.2 Parametrization, data sources and treatment

Ecosim distinguishes between two types of time series: forcing data and reference data. Forcing data are used to introduce temporal dynamics into the model. Reference data correspond to the output variables generated by Ecosim and are used to calibrate the model such that its outputs align with observed trends. In the SBNS model, time series are implemented for the period 1991-2023. Three types of forcing data are included: fishing effort, fishing mortality and environmental (abiotic) forcing. Reference data include historical biomass and catch trends. A total of 37 reference time series were included for model calibrations. This section details the data sources and preprocessing of the time series used in the model.

3.2.1 Biomass

For *Cod*, *Herring*, *Mackerel*, *Plaice*, *Sandeels*, *Seabass*, *Sole*, *Sprat*, *Whiting,* and *Horse Mackerel*, ICES stock assessment biomass trends were available covering the period 1991 to the present (Table 10). For *Squid and cuttlefish*, the ratio from 1999 until 2019 between the abundance in the SBNS and the greater North Sea based on the ICES NS-IBTS data was calculated and multiplied the ratio with the total biomass of the North Sea model (Mackinson & Daskalov, 2007). To obtain biomass trends for other functional groups, *Sharks*, *Rays*, *Other gadoids*, *Demersal fish*, *Dab* and *Other flatfish*, and the Sparholt (1990) method, i.e. using a reference species to estimate the biomass, was applied as previously done for the ecopath model (Section 2.2.1.1, Table 3). For each year (1991–2023), the NS-IBTS CPUE ratio between the North Sea and SBNS (Eq. 3) was calculated for the reference species to estimate reference species' biomass in SBNS and was multiplied with the NS-IBTS CPUE ratio between target species and reference species (Eq. 4) to estimate the target species biomass. These biomass trends, expressed relative to the base year 1991, were used for the respective species as biomass reference time series.

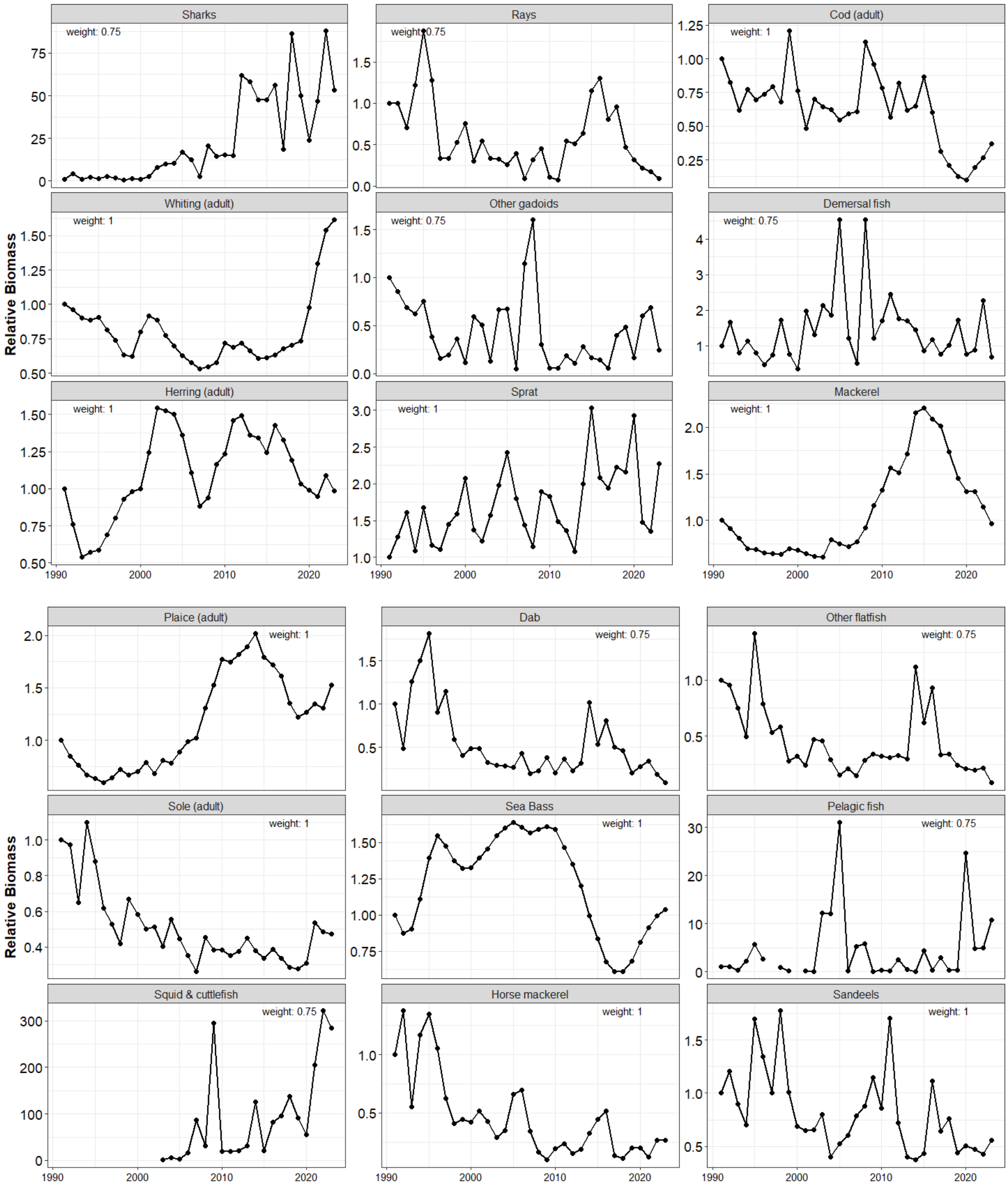


Figure 4: Relative biomass time series data for 1991–2023. (data accessible in attached .csv file tab 8 timeseries)

3.2.2 Catch

Catch time series were calculated for each functional group as total landed weight from ICES division IVc. Two overlapping datasets (Historical Nominal Catches 1950-2010, ICES and Official Nominal Catches 2006-2021, (ICES, n.d.)) were combined in order to include both historic data, reaching up to 2010, and more recent data up to 2021. For multi-stanza groups, reported catch was assigned to the adult group.

For *Rays*, historic catch data until 2008 are mostly not resolved up to species level, but reported as "Raja rays nei". Data reported as "Raja rays nei" were therefore included in the catch data for the model group *Rays* and resulted in a consistent overlap with the more recent dataset.

For *Dab*, and species included in the functional group *Other flatfish* no catch has been reported by the Netherlands between 1991 and 1997. Similarly, for the model group *Other gadoids* the Netherlands did not report any catch data between 2000 and 2010 (as illustrated by the blue line in Figure 5). To assess the Netherlands' contribution to the total catch of each model group, the percentage of catch attributed to the Netherlands was calculated for years with reported data. The average percentual contribution was utilized to estimate the Netherlands' catch in the years where these data were missing (illustrated by the red line in Figure 5). These estimated contributions were subsequently added to the time series for the respective years to provide more realistic catch estimates. This adjustment notably affected the 1991 values, which are included in the Ecopath model. Consequently, landings and discards for *Dab*, *Other flatfish*, and *Other gadoids* were rescaled to align with the updated 1991 catch estimates.

All catch time series used to calibrate the Ecosim model are provided in Figure 6.

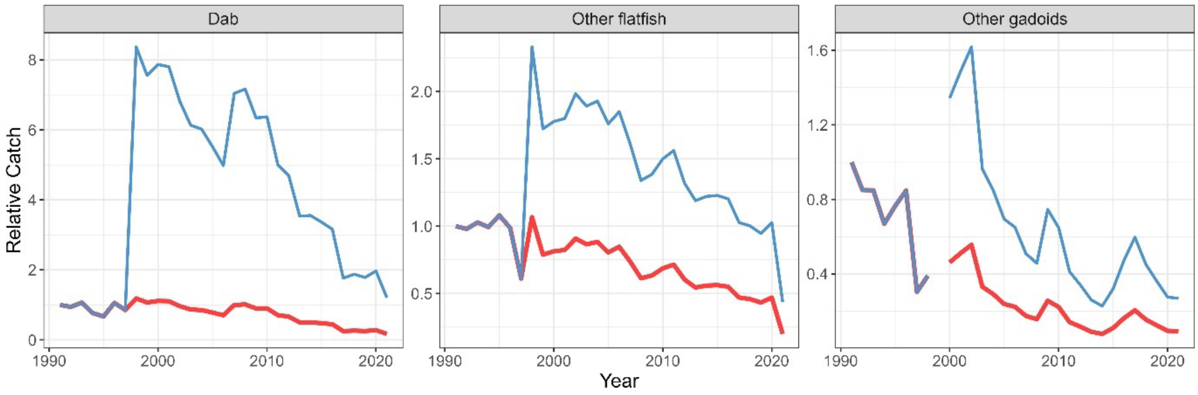
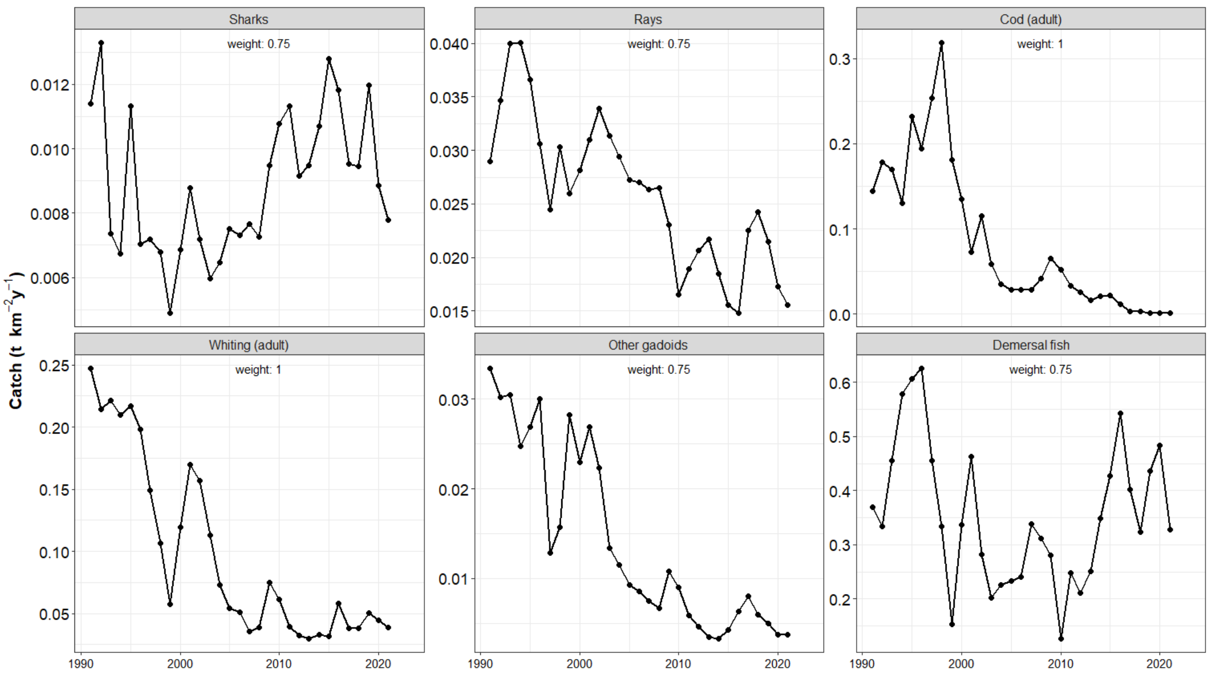
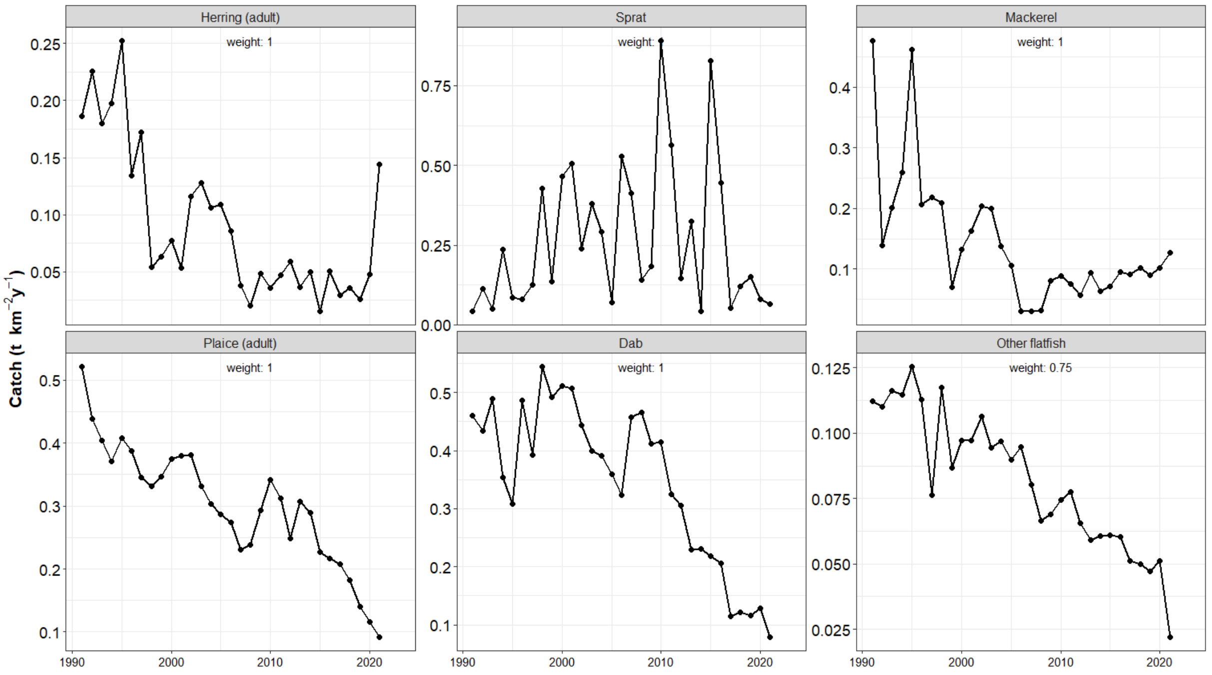


Figure 5: Relative time series of catch for Dab, Other flatfish, and Other gadoids relative to 1991. The blue line represents time series with partially missing Netherlands contribution in the first years. The red line indicates the adjusted trends, including estimated Netherlands contributions for these initial years. For comparison, these trends are plotted as relative time series, however, absolute catch time series were used for fitting the model.


Sharks
weight: 0.75
Rays
weight: 0.75
Cod (adult)
weight: 1
Whiting (adult)
weight: 1
Other gadoids
weight: 0.75
Demersal fish
weight: 0.75
Catch (t km⁻² y⁻¹)
0.012
0.010
0.008
0.006
0.040
0.035
0.030
0.025
0.020
0.015
0.3
0.2
0.1
0.0
0.25
0.20
0.15
0.10
0.05
0.03
0.02
0.01
0.6
0.5
0.4
0.3
0.2
1990
2000
2010
2020


Herring (adult)
weight: 1
Sprat
weight:
Mackerel
weight: 1
Plaice (adult)
weight: 1
Dab
weight: 1
Other flatfish
weight: 0.75
Catch (t km⁻² y⁻¹)
0.25
0.20
0.15
0.10
0.05
0.75
0.50
0.25
0.00
0.4
0.3
0.2
0.1
0.5
0.4
0.3
0.2
0.1
0.125
0.100
0.075
0.050
0.025
1990
2000
2010
2020

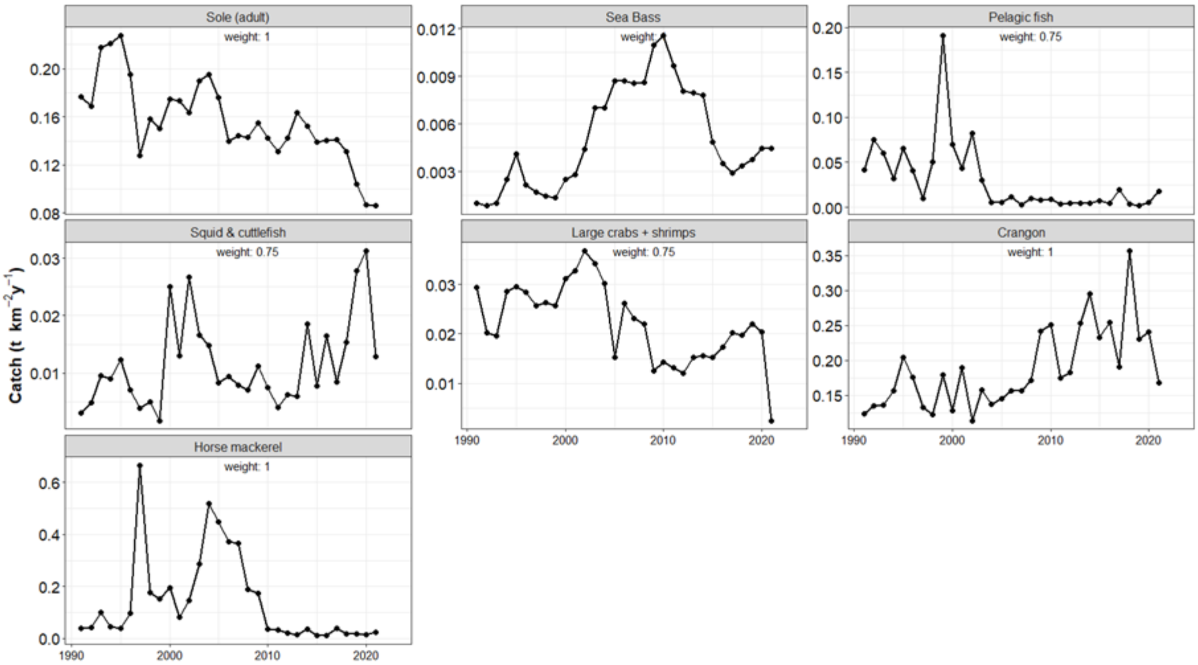


Figure 6: Catch time series data for 1991–2023. (data accessible in attached .csv file tab 8 timeseries)

3.2.3 Effort

In Ecosim, fishing effort is applied to fleets, which is then translated into species-specific partial F values based on the catch composition defined in Ecopath. Fishing effort time series were derived from three datasets. For EwE fleets “beam”, “demersal”, “pelagic” and “shrimp” fishing effort trends, relative to 1991, up to 2003 were based on the data reported by Mackinson and Daskalov (2007) and its updates. For all other fleets, relative effort was assumed constant (set to 1) during this period. From 2003 to 2016, total effort for all EwE fleets were obtained from spatially resolved data in ICES statistical rectangles falling within area IVc (STECF Expert Working Group 17-05, (Maksims et al., 2022; Zanzi and Holmes, 2017) and scaled relative to 2003 levels. For the period from 2016 onward, effort trends for all fleets in ICES subarea IVc were derived from STECF Expert Working Group 23-10 (Motova-Surmava et al., 2024)

Following implementation of the fishing effort time series, catch trends were visually assessed for inconsistencies. Due to missing data for most fleets prior to 2003, the modelled catch dynamics between 1991 and 2003 were evaluated with particular attention to their continuity with the period for which effort data were available (post-2003). Catches of *large crabs and shrimp* were consistently underestimated in the early years, whereas modelled catches after 2003 better reflected observed trends. Notably, the 2003 effort value for the “pots” fleet appeared unrealistically low compared to subsequent years, resulting in unreliable catch predictions for its primary target group (*large crabs and shrimp*). To address this, the mean effort across the first five years of available data (2003–2007) was used to represent the 1991–2003 period, rather than relying solely on the 2003 value. The effort time series was then rescaled relative to this mean, which improved the alignment between modelled and observed catch trends. The final fishing effort time series applied in the temporal analysis are presented in Figure 7.

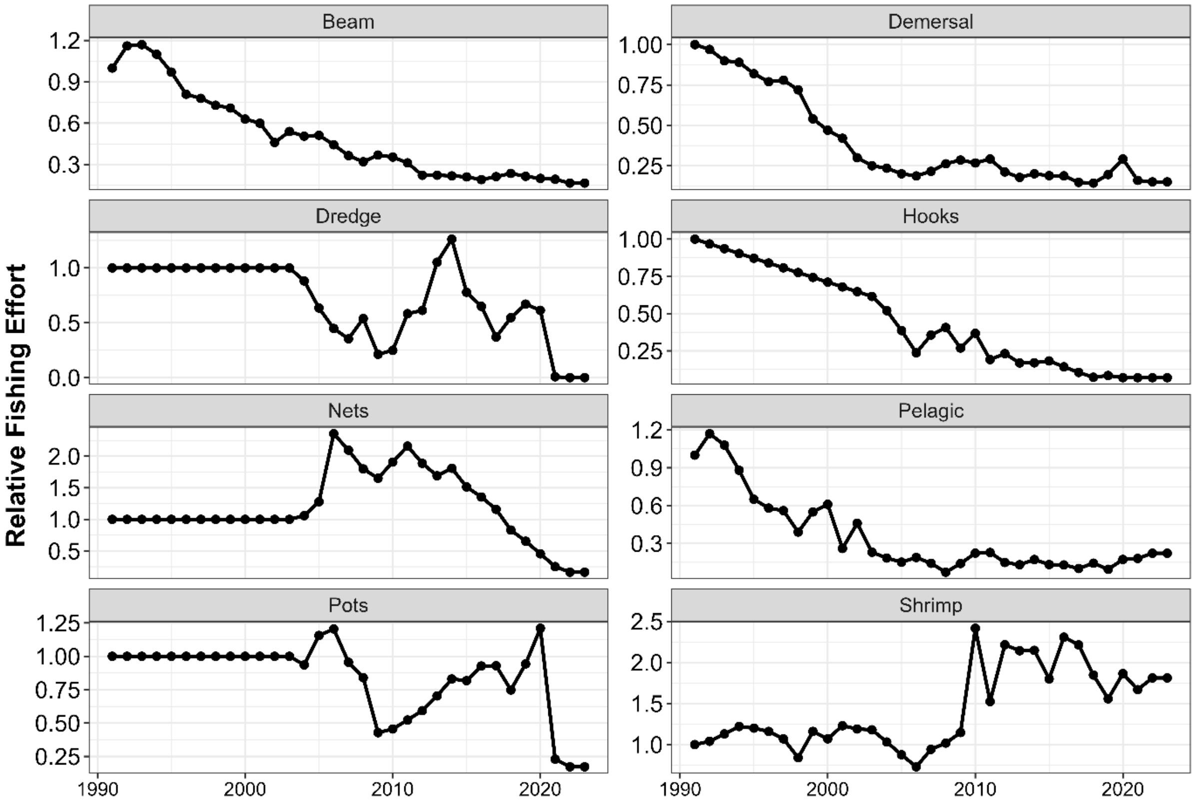


Figure 7: Fishing effort trends implemented for the EwE fleets. For each fleet, trends are scaled relative to the 1991 base year effort. (data accessible in attached .csv file tab 8 timeseries and tab 10 fishing effort)

3.2.4 Fishing mortality

Single-species stock assessments for the (Greater) North Sea are available for most commercially exploited species. In cases where effort-based estimates failed to reproduce observed biomass or catch trends, fishing mortality (F) from ICES stock assessments (Table 10) was introduced as a forcing function in the model. If applied, fishing mortality forcing overwrites mortality estimates derived from fleet-specific effort data.

ICES stock assessment data covering the full study period (1991–present) were available for *Cod*, *Herring*, *Mackerel*, *Plaice*, *Sandeels*, *Seabass*, *Sole*, *Sprat*, and *Whiting.* Fishing mortality time series were only included in the model when effort-based estimates failed to reproduce observed biomass and catch trends. As such, fishing mortality from ICES stock assessments was used as a forcing function for *Herring*, *Plaice*, *Seabass*, *Sole* and *Sprat,* as it improved the fit to biomass and/or catch trends for these species. A detailed overview of all available stock assessments is provided in Table 10.

Table 10: Overview of ICES stock assessments available for the study area and period (1991–present).

Species	Region	Stock code	Year	Key
Cod (*Gadus morhua*)	Subarea 4, in divisions 6.a and 7.d, and in Subdivision 20 (North Sea, West of Scotland, eastern English Channel, Skagerrak)	cod.27.46a7d20	2024	18716
Herring * (*Clupea harengus*)	Subarea 4 and in divisions 3.a and 7.d; autumn spawners (North Sea, Skagerrak, Kattegat, eastern English Channel)	her.27.3a47d	2024	19293
Mackerel (*Scomber scombrus*)	Subareas 1–8 and 14 and in Division 9.a (Northeast Atlantic and adjacent waters)	mac.27.nea	2024	19137
Plaice * (*Pleuronectes platessa*)	Subarea 4 (North Sea) and in Subdivision 20 (Skagerrak)	ple.27.420	2024	18688
Sandeels (*Ammodytes*)	Divisions 4.b and 4.c, Sandeel Area 1r (central and southern North Sea, Dogger Bank)	san.sa.1r	2024	18515
Seabass * (*Dicentrarchus labrax*)	Divisions 4.b, 4.c, 7.a, and 7.d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, Celtic Sea)	bss.27.4bc7ad-h	2024	19277
Sole * (*Solea solea*)	Subarea 4 (North Sea)	sol.27.4	2024	19295
Sprat * (*Sprattus sprattus)*	Division 3.a and Subarea 4 (Skagerrak, Kattegat, North Sea)	spr.27.3a4	2024	18543
Whiting * (*Merlangius merlangus*)	Subarea 4 and in Division 7.d (North Sea, eastern English Channel)	whg.27.47d	2024	18694

***** *species for which assessment-based fishing mortality (F) was used as a forcing function in the Ecosim model.*

Horse mackerel enter the North Sea only intermittently from southern regions (Abaunza et al., 2003; Nasri et al., 2024) posing a challenge for the model in accurately reproducing biomass and catch trends for this functional group. To address this issue, fishing mortality was estimated directly from available catch and biomass data specific to the Southern Bight of the North Sea (SBNS). This estimated fishing mortality (F = C/B) was then implemented as a forcing function in the Ecosim model. This improved model performance and produced biomass and catch trends that closely aligned with historical observations.

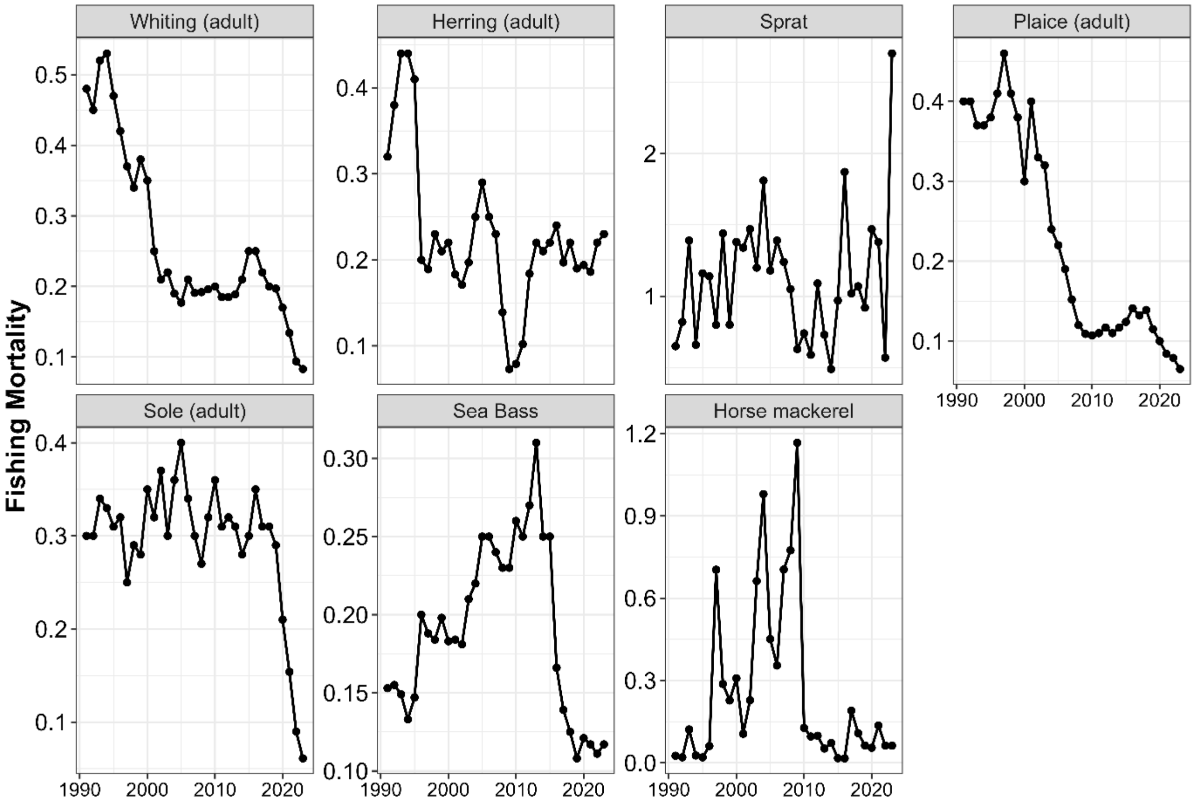


Figure 8: Time series of fishing mortality used as forcing functions in model fitting. Data were obtained from ICES stock assessments for all species, except horse mackerel, for which fishing mortality was estimated from catch and biomass data. (data accessible in attached .csv file tab 8 timeseries and tab 11 fishing mortality)

3.2.5 Environmental drivers and functional responses

In order to include temporal (abiotic) environmental variation, time series of salinity and sea surface temperature (SST) were implemented as forcing functions in Ecosim. Salinity describes the salt concentration in seawater [g.kg^{-1}]. SST is used as a proxy for sea temperature of the well-mixed waters of the SBNS (Christensen et al., 2024). Both historical time series were derived from the Copernicus Marine Service (Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis dataset; CMEMS). For each year from 1991 to 2023, annual average salinity and SST values were computed by spatially averaging all monthly gridded data points falling within the SBNS study area. The salinity and SST trend included in the model are shown in Figure 9.

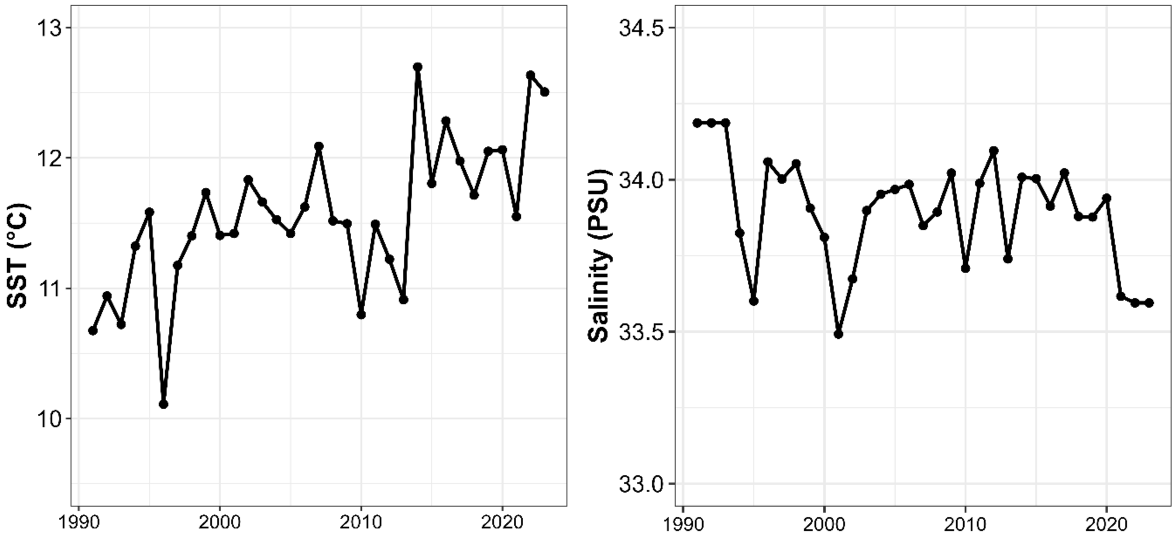


Figure 95: Time series for temperature and salinity for the SBNS between 1991 and 2023. Data were obtained from the Copernicus Marine Service (Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis, CMEMS). These environmental variables were used as forcing functions in the Ecosim model by linking species-specific response functions to the respective time series.

Response curves for temperature and salinity were derived from species-specific environmental envelope data obtained through AquaMaps (AquaMaps: Predicted range maps for aquatic species), which combines global species occurrence data with habitat preferences (Kesner-Reyes et al., 2020). AquaMaps provides computer-generated, standardized distribution maps for over 33,500 marine species, as well as expert-reviewed data products for certain species. Expert-reviewed data products were preferred over computer-generated ones whenever they were available, and only data for the Northeast Atlantic (FAO area 27) was used in this study to accurately represent regional habitat preferences. AquaMaps Expert mapping data was incorporated for *cod*, *whiting, sprat*, *horse mackerel*, *plaice*, *dab*, *sole*, *blue mussels* and *crangon*. For three species (*herring*, *horse mackerel* and *sea bass*), expert-reviewed environmental preferences from Musimwa et al. (2025) were used instead.

For each functional group, four thermal and salinity tolerance values were extracted from either the AquaMaps database (Skyttner, 2020) or Musimwa et al. (2025): the absolute minimum, preferred minimum (10th percentile), preferred maximum (90th percentile), and absolute maximum. For functional groups containing multiple species (e.g., other flatfish), a biomass-weighted average of these species-specific values was used to construct a trapezoidal environmental response curve. A double logistic function was applied to these trapezoidal responses as per NOAA SEFSC (2025) to create continuous environmental envelopes. The general equations for the double logistic function are described below:

$$f_1(x) = \frac{1}{(1+e^{B_1C_1}\cdot e^{-B_1x})^S}$$ (Increasing logistic equation where $x <$ midpoint)

$$f_2(x) = 1 - \frac{1}{(1+e^{B_1C_1}\cdot e^{-B_1x})^S}$$ (Decreasing logistic equation where $x \geq$ midpoint)

- For which 1 is the horizontal asymptote value when $x \rightarrow -\infty$, and 0 is the value of the horizontal asymptote when $x \rightarrow +\infty$
- B_1 and B_2, describe the rate of curve transitions between the two asymptotes.
- S describes the asymmetry of the curve. (The curve is symmetric when $S = 1$.)
- C is a location parameter

Linking the response curves to their corresponding forcing function (i.e. temperature or salinity), resulted in a scaling factor between 0 and 1, f(Envt), that modifies a group's consumption rate (Equation X) to simulate their respective response to (un)suitable habitat. Depending on the environmental conditions, this factor increases or decreases the consumption rate according to the shape of the environmental response curve.

Note that response curves for depth and distance to land are included in the Ecosim model using the same methodology described above. However, these are not currently linked to any forcing functions and are included solely for future interest in Ecospace modelling.

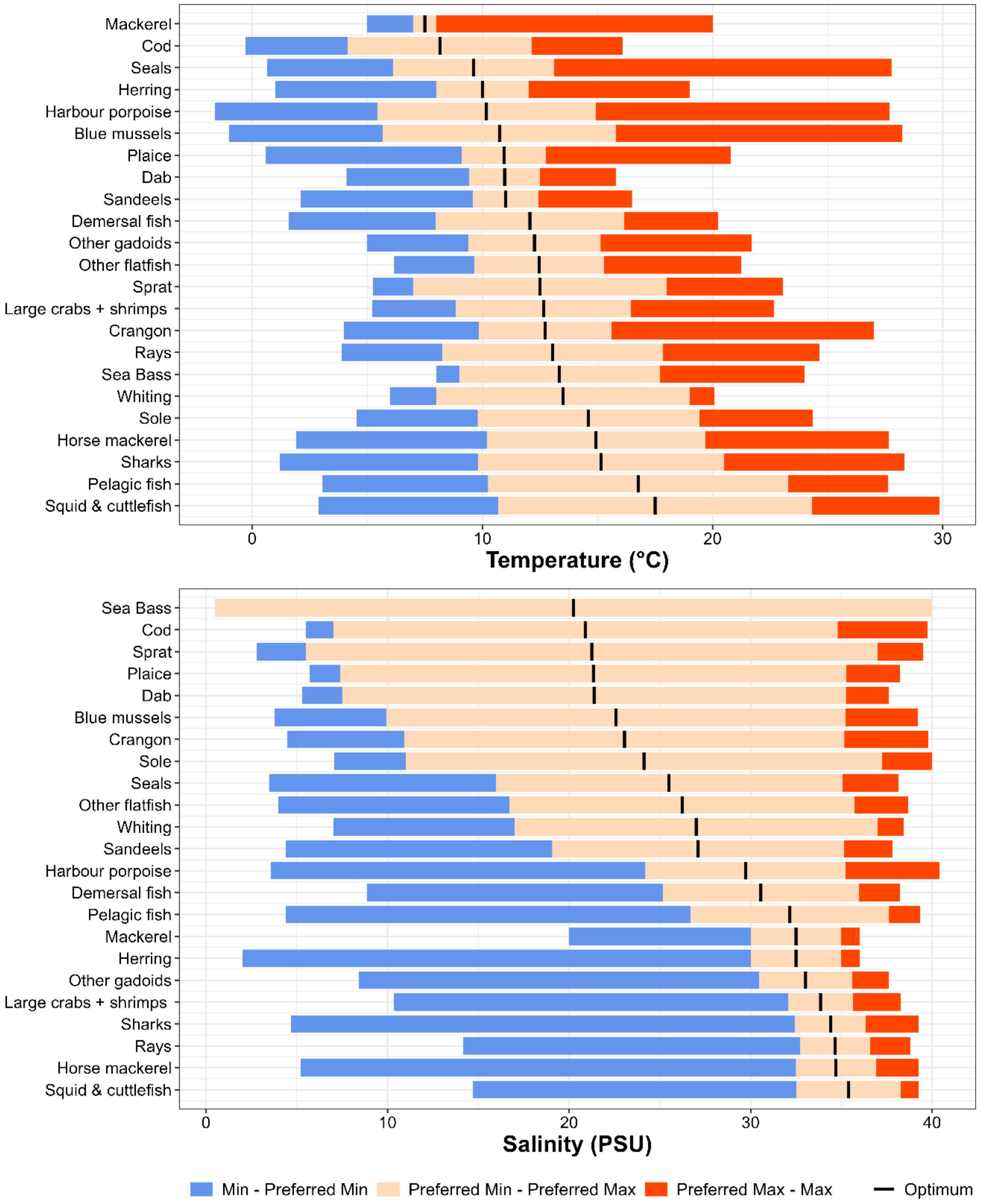


Figure 60: Thermal (top) and salinity (bottom) tolerance ranges for marine functional groups. Bars represent the full reported range for each group, subdivided into: minimum to preferred minimum (10th percentile, blue), preferred range (10th–90th percentile, light orange), and preferred maximum to maximum (90th percentile to maximum, red). The black vertical line indicates the thermal or salinity optimum, defined as the midpoint of the preferred range. Functional groups are ordered by increasing optimum value.

3.2.6 Recruitment

To assess the relationships between fish recruitment rates and climate variability, we performed a correlation analysis between species-specific recruitment indices and large-scale climate indicators (i.e. the Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO) and NAO winter index (December - March). AMO and NAO time series were obtained from the National Oceanic and Atmospheric Administration (NOAA.org). Recruitment data for the multi-stanza groups were obtained from ICES stock assessments (Table 10).

Recruitment data for *cod*, *whiting*, *herring*, *plaice*, and *sole* were log-transformed to improve distributional properties and stabilise variance prior to analysis. Normality was tested using the Shapiro–Wilk test, and since many variables showed significant deviations from normality, non-parametric Spearman correlation was used. Recruitment and environmental time series are often strongly autocorrelated, as values from one year are often closely related to those in preceding years (Pyper and Peterman, 1998). Classical correlation tests that do not account for autocorrelation may therefore yield inflated Type I error rates (Jenkins and Watts, 1968). To correct for this, as per Bentley et al. (2019a), we calculated Spearman's rank correlation coefficient (ρ) between each recruitment and climate variable pair and adjusted the statistical significance based on the effective number of independent observations.

We estimated the effective sample size (N*) using the method proposed by Chelton (1984) and modified by Pyper and Peterman (1998), which accounts for the autocorrelation structure in both time series:

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_{j=1}^{k} r_{xx}(j) \cdot r_{yy}(j)$$

Where N is the actual sample size, and (j) and (j) are the autocorrelation coefficients at lag j for the recruitment and climate series, respectively. We used up to $k=\lfloor N/5 \rfloor$ lags in line with Pyper and Peterman (1998). The autocorrelations were estimated using the Box–Jenkins approach (Box et al., 1976), as modified by Chatfield (1989), which corrects for bias at higher lags.

An adjusted t-statistic was then calculated based on the effective sample size, and a two-tailed p-value was derived using a t-distribution with −2 degrees of freedom. Correlations with $p < 0.05$ were considered statistically significant.

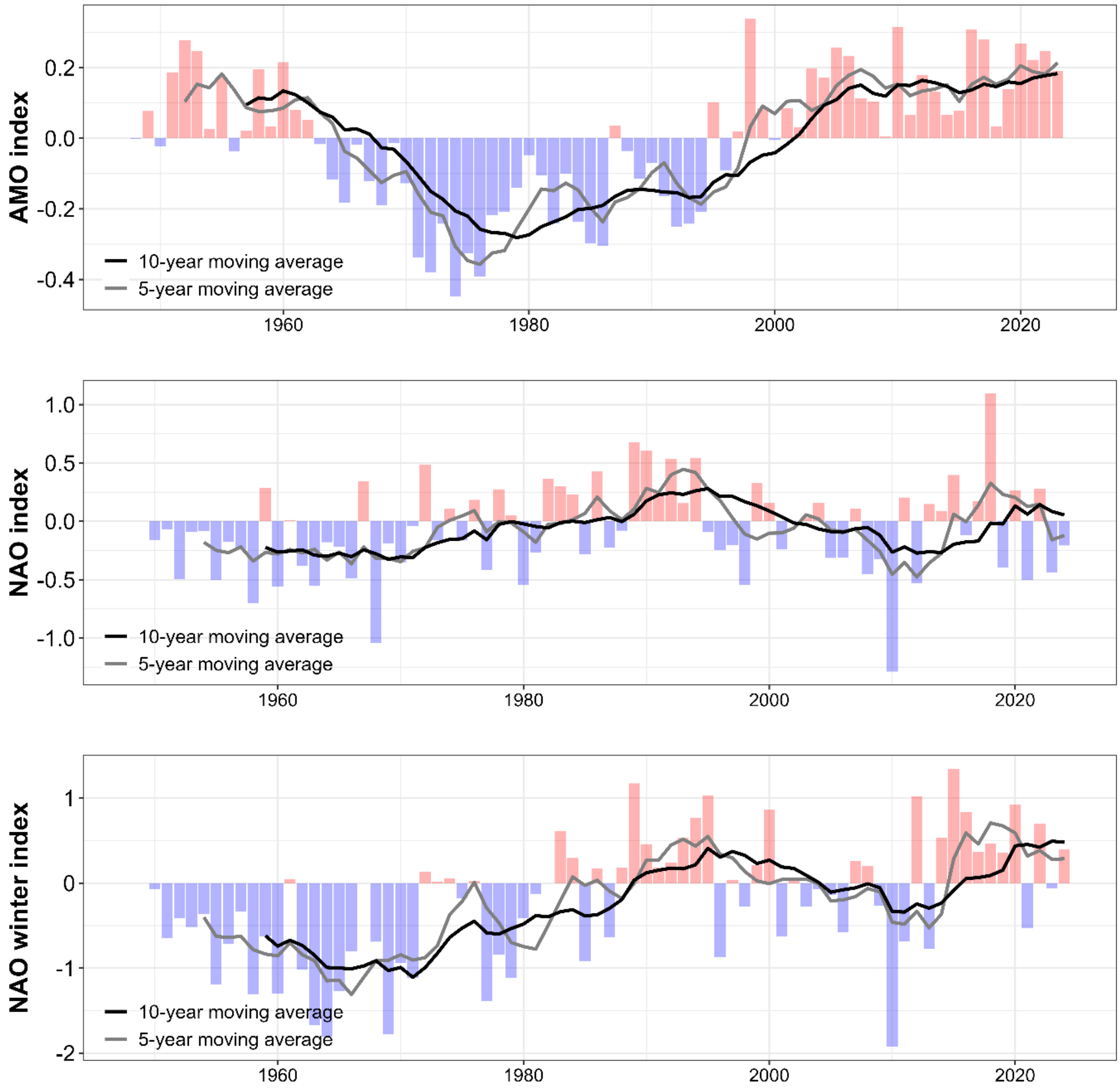
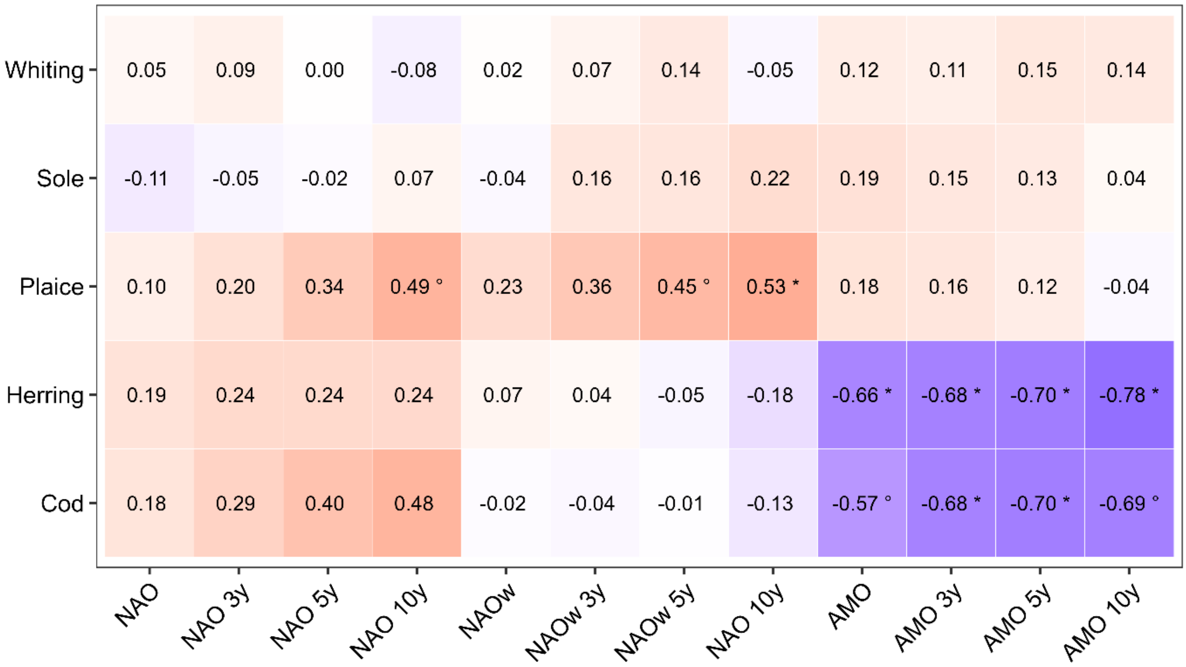


Figure 11: Time series of large-scale environmental indices used in the recruitment correlation analysis: Atlantic Multidecadal Oscillation (AMO; top), North Atlantic Oscillation (NAO; middle), and North Atlantic Oscillation winter index (NAOw; bottom). The annual index is shown by the blue and red bars, with 5-year and 10-year lagged moving averages overlaid in grey and black, respectively. These smoothed trends were evaluated to identify potential lagged effects of environmental variability on fish recruitment and were subsequently used as environmental forcing functions in the Ecosim model for groups showing significant correlations.

Recruitment of *plaice* was best explained by the 10-year moving average of the North Atlantic Oscillation (NAO) index (Figure 11), while recruitment rates of *herring* and *cod* were highly negatively correlated with the Atlantic Multidecadal Oscillation (AMO) index. These environmental trend effects were incorporated into the model as time series forcing functions applied to egg production. In Ecopath with Ecosim, egg production represents the spawning output of a population relative to its biomass and serves as the basis for recruitment, with environmental forcing functions modulating the rate of egg production over time to reflect observed environmental variability. Recruitment rates for *sole* and *whiting* did not show significant correlations with any of the evaluated NAO or AMO trends (Figure 12). Accordingly, in the Ecosim model, egg production was forced using the 10-year moving average of the NAO for *plaice*, the inverse 10-year moving average of the AMO for *herring*, and the inverse 5-year moving average of the AMO for *cod*.



	NAO	NAO 3y	NAO 5y	NAO 10y	NAOw	NAOw 3y	NAOw 5y	NAO 10y	AMO	AMO 3y	AMO 5y	AMO 10y
Whiting	0.05	0.09	0.00	-0.08	0.02	0.07	0.14	-0.05	0.12	0.11	0.15	0.14
Sole	-0.11	-0.05	-0.02	0.07	-0.04	0.16	0.16	0.22	0.19	0.15	0.13	0.04
Plaice	0.10	0.20	0.34	0.49 °	0.23	0.36	0.45 °	0.53 *	0.18	0.16	0.12	-0.04
Herring	0.19	0.24	0.24	0.24	0.07	0.04	-0.05	-0.18	-0.66 *	-0.68 *	-0.70 *	-0.78 *
Cod	0.18	0.29	0.40	0.48	-0.02	-0.04	-0.01	-0.13	-0.57 °	-0.68 *	-0.70 *	-0.69 °

Figure 72: Correlation between environmental indices and recruitment rates for multi-stanza groups included in the Ecosim model. Shown are Spearman correlation coefficients between the North Atlantic Oscillation (NAO), the NAO winter index (NAOw), and the Atlantic Multidecadal Oscillation (AMO) indices and recruitment rates of whiting, sole, plaice, herring, and cod. For each index, lagged moving averages over 3, 5, and 10 years (denoted as "3y", "5y", and "10y") were tested. Significant correlations ($p < 0.05$) are indicated with an asterisk (*), and marginally significant ones ($p < 0.1$) with a degree symbol (°).

3.3 Time series fitting

3.3.1 Time series

In Ecosim, inter-specific interactions are modeled as vulnerabilities based on the foraging arena theory (Ahrens et al., 2012), which captures how spatial and temporal constraints modulate predator-prey dynamics through both top-down and bottom-up processes. To improve the model's fit to observed temporal trends, we applied an automated stepwise fitting procedure developed (Scott et al., 2015). This approach systematically explores multiple model configurations to identify the combination of ecological mechanisms that yields the best statistical fit, evaluated using the residual sum of squares and Akaike's Information Criterion (AIC), defined as:

$$AIC = N \cdot \ln\left(\frac{SS}{N}\right) + 2 \cdot K$$

where N is the number of observations, SS is the residual sum of squares, and K is the number of estimated parameters.

The fitting process accounted for key ecological drivers, including fishing effort, predator-prey vulnerabilities, and anomalies in primary production (PP) represented with up to four spline points (Scott et al., 2015). In this model, vulnerabilities were estimated by predator. The stepwise procedure enabled estimation of up to 36 parameters, aligned with the availability of 37 catch and biomass time series. Limiting the number of parameters to one fewer than the number of time series helps maintain statistical robustness in the model.

The best obtained fit had a SS of 569, an AIC of -789, and AICc of -788, with 23 vulnerabilities and 3 spline points for the anomaly.

3.3.2 Uncertainty analysis (Monte Carlo)

Ecosim simulations are sensitive to changes in key input parameters, including biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), and ecotrophic efficiency (EE). As well as landings and discards. To assess this sensitivity, the Monte Carlo routine in Ecosim was applied to the best-fitting model identified through the stepwise fitting procedure. This routine evaluates the impact of uncertainty in basic input estimates by generating new values from a uniform distribution centered on the original Ecopath inputs, with a coefficient of variation (CV) of 0.01 applied uniformly across all functional groups (Christensen et al., 2008). A total of 2,000 Ecosim simulations and 10,000 Ecopath runs were performed to determine whether variability in basic estimates could improve the model's statistical fit (based on residual sum of squares, SS) or significantly influence temporal trends and dynamics.

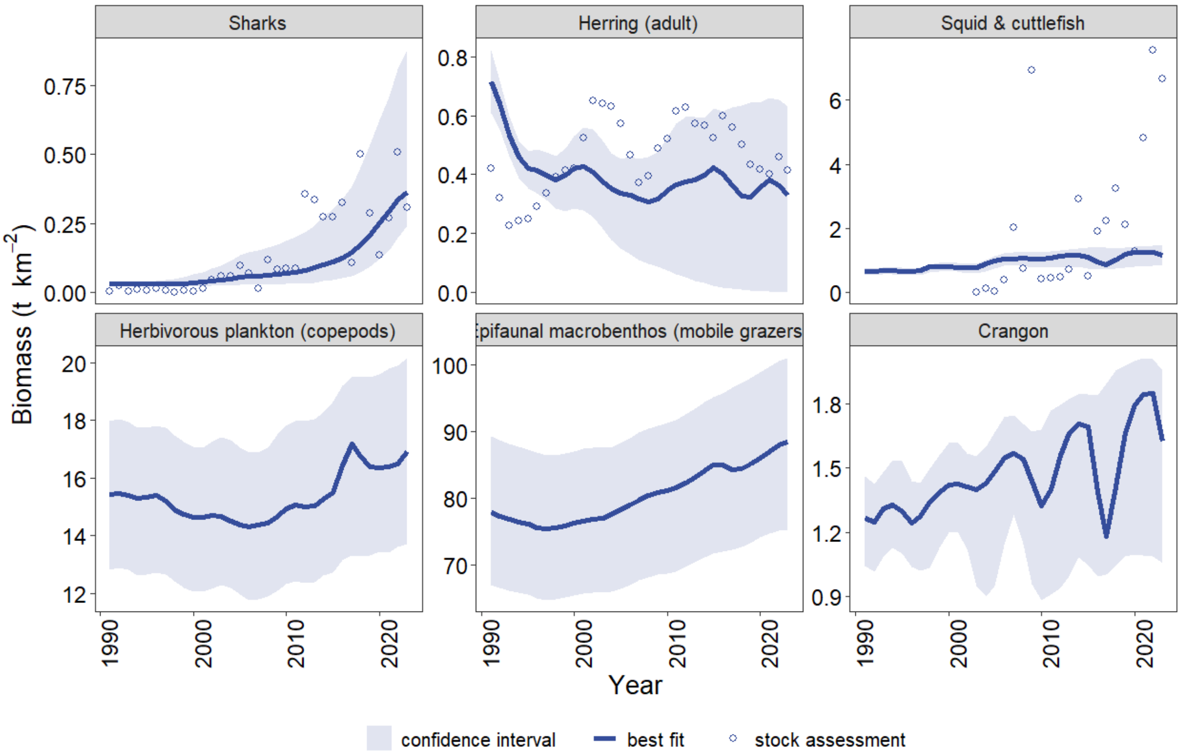


Figure 13: Biomass (t km^{-2} y^{-1}) from 1991 until 2023 for functional groups Sharks (Fig. 2: (D) apex predators), Herring (adult) (Fig. 2: (C) fish), Squid & cuttlefish, Herbivorous plankton (copepods) (Fig. 2: (A) plankton), Epifaunal macrobenthos (mobile grazers) (Fig. 2: , (B) benthos) and Crangon.

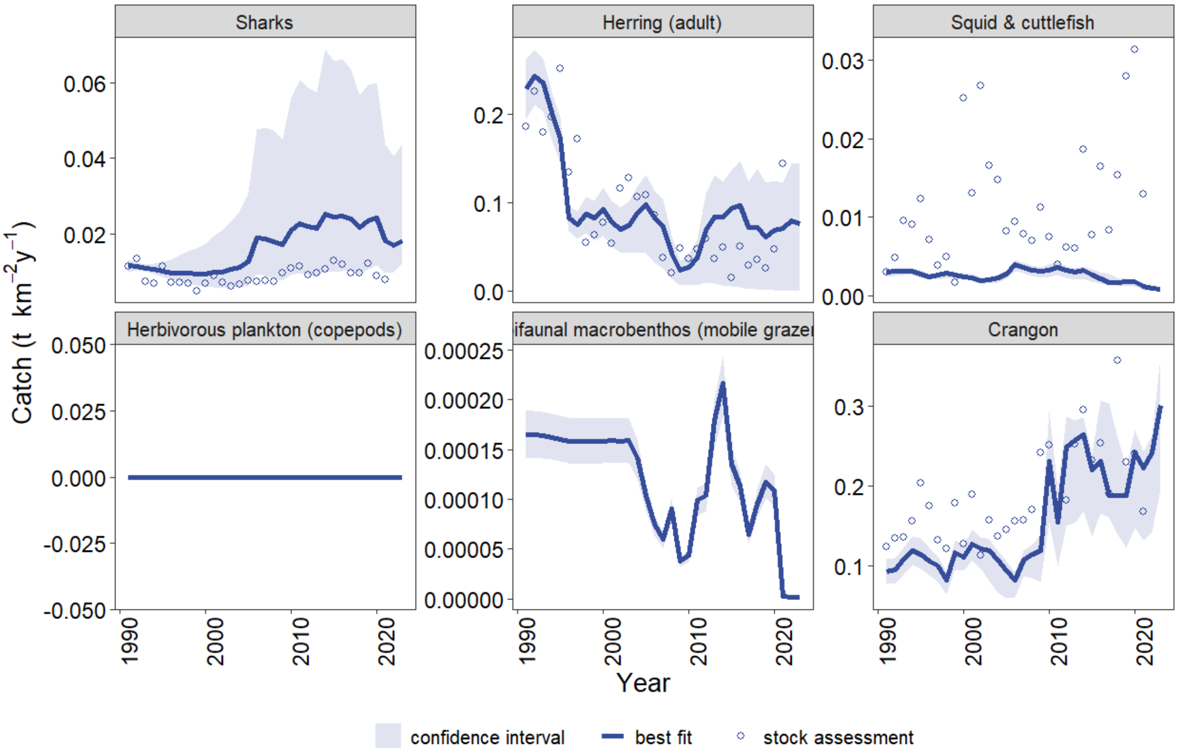


Figure 14: Catch (t km^{-2} y^{-1}) from 1991 until 2023 for functional groups Sharks (Fig. 2: (D) apex predators), Herring (adult) (Fig. 2: (C) fish), Squid & cuttlefish, Herbivorous plankton (copepods) (Fig. 2: (A) plankton), Epifaunal macrobenthos (mobile grazers) (Fig. 2: , (B) benthos) and Crangon.

4 Data availability

The input data, R scripts, and EwE model can be accessed by https://github.com/vlizBE/SBNS_foodweb_model and should be cited as follows:
Pint, S., & Lorré, D. (2026). Southern Bight of the North Sea Food Web Model: Data, code, model (v1.0.1). Zenodo. https://doi.org/10.5281/zenodo.18281264

5 Citation

Pint, S.; Lorré, D.; Stevens, M.; De Troch, M.; Heymans, S.; van Oevelen, D.; Everaert, G. (2026). Ecopath with Ecosim model of the Southern Bight of the North Sea. Version 4. Flanders Marine Institute (VLIZ): Ostend. 52 pp. https://dx.doi.org/10.48470/129

6 References

Abaunza, P., Gordo, L., Karlou-Riga, C., Murta, A., Eltink, A. T. G. W., García Santamaría, M. T., Zimmermann, C., Hammer, C., Lucio, P., Iversen, S. A., Molloy, J., and Gallo, E.: Growth and reproduction of horse mackerel, Trachurus trachurus (carangidae), Rev Fish Biol Fish, 13, 27–61, https://doi.org/10.1023/A:1026334532390, 2003.

Ahrens, R. N. M., Walters, C. J., and Christensen, V.: Foraging arena theory, Fish and Fisheries, 13, 41–59, https://doi.org/10.1111/j.1467-2979.2011.00432.x, 2012.

Anon: ICES Database on Trawl Surveys (DATRAS), 2024.

Bentley, J., Serpetti, N., Fox, C. J., Reid, D. G., and Heymans, J. J.: Modelling the food web in the Irish Sea in the context of a depleted commercial fish community. Part 2: ICES Ecopath with Ecosim Key Run, Oban. U.K, 2019a.

Bentley, J. W., Hines, D., Borrett, S., Serpetti, N., Fox, C., Reid, D. G., and Heymans, J. J.: Diet uncertainty analysis strengthens model-derived indicators of food web structure and function, Ecol Indic, 98, 239–250, https://doi.org/10.1016/j.ecolind.2018.11.008, 2019b.

Bicknell, A. W. J., Oro, D., Camphuysen, K. C. J., and Votier, S. C.: Potential consequences of discard reform for seabird communities, https://doi.org/10.1111/1365-2664.12072, June 2013.

Box, G. E., Jenkins, G. M., Reinsel, G. C., and Ljung, G. M.: Time series analysis: forecasting and control, John Wiley & Sons, 1118674928., 1976.

Brodie, B., Mowbray, F. and Power, D.: DFO Newfoundland and Labrador Region Ecosystem Trawl Surveys. Version 1 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/, 2013, Accessed on 29/06/2020.

Buhl-Mortensen, L.: MAREANO - Base-line mapping of hyperbenthic crustacea fauna obtained with RP-sledge. Institute of Marine Research, Norway https://doi.org/10.15468/gecvl4, 2014

Chatfield, C.: The analysis of time series: an introduction., Chapman and Hall/CRC, 1989.

Chelton, D. B.: Short-term climatic variability in the northeast Pacific Ocean. The Influence of Ocean Conditions on the Productivity of Salmonids in the North Pacific., 1984.

Christensen, V. and Pauly, D.: ECOPATH II-a software for balancing steady-state ecosystem models and calculating network characteristics *, Ecological Modelling, 169–185 pp., 1992.

Christensen, V. and Walters, C. J.: Ecopath with Ecosim: methods, capabilities and limitations, Ecol Modell, 172, 109–139, https://doi.org/10.1016/j.ecolmodel.2003.09.003, 2004.

Christensen, V. and Walters, C. J.: Ecosystem Modelling with EwE, edited by: Christensen, V. and Steenbeek, J., The University of British Columbia, Vancouver, BC, 2024.

Dauwe, S., Verleye, T., Pirlet, H., Martens, C., Sandra, M., De Raedemaecker, F., Devriese, L., Lescrauwaet, A.-K., Depoorter, M., and Moulaert, I.: Kennisgids Gebruik Kust en Zee 2022 - Compendium voor Kust en Zee. Compendium voor Kust en Zee = Compendium for Coast and Sea, edited by: Mees, J., Vlaams Instituut voor de Zee (VLIZ), Oostende, 275 pp., 2022.

DFO: Central and Arctic Multi-Species Stock Assessment Surveys Version 6 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/, 2016, Accessed on 29/06/2020.

E.U. Copernicus Marine Service Information (CMEMS): Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis.

Ferter, K., Weltersbach, M. S., Strehlow, H. V., Vølstad, J. H., Alós, J., Arlinghaus, R., Armstrong, M., Dorow, M., de Graaf, M., van der Hammen, T., Hyder, K., Levrel, H., Paulrud, A., Radtke, K., Rocklin, D., Sparrevohn, C. R., and Veiga, P.: Unexpectedly high catch-and-release rates in European marine recreational fisheries: implications for science and management, ICES Journal of Marine Science, 70, 1319–1329, https://doi.org/10.1093/icesjms/fst104, 2013.

Flanders Marine Institute (VLIZ). Taxonomic Information System for the Belgian coastal area. 10 Aug 2004, Oostende, Belgium, Accessed on 29/06/2020.

Froese, R. and D. Pauly. Editors. 2025. FishBase. World Wide Web electronic publication. www.fishbase.org, version (04/2025).

Hammond, P. S., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., Macleod, K., Ridoux, V., Santos, M. B., Scheidat, M., Teilmann, J., Vingada, J., Øien, N., Gillespie, D., Leaper, R., Sveegaard, S., and Antonio Vázquez, J.: Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys, 2017.

Hassel, A.: MAREANO - Base-line mapping of epifauna obtained with Beamtrawl. Institute of Marine Research, Norway https://doi.org/10.15468/iomgfj, 2014.

Henry, D. A. W. and Cumming, G. S.: Can waterbirds with different movement, dietary and foraging functional traits occupy similar ecological niches?, Landsc Ecol, 32, 265–278, https://doi.org/10.1007/s10980-016-0449-8, 2017.

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., and Christensen, V.: Best practice in Ecopath with Ecosim food-web models for ecosystem-based management, Ecol Modell, 331, 173–184, https://doi.org/10.1016/j.ecolmodel.2015.12.007, 2016.

Hill, Clare & Bentley, Jacob & Serpetti, Natalia & Fox, Clive & Heymans, Johanna & Angus (nee Laurenson), C.H.: Modelling the trophic interaction, structure, and function of the northern North Sea food web. Ecopath Technical Report. 10.13140/RG.2.2.11303.06561, 2021

Horn, S., Coll, M., Asmus, H., and Dolch, T.: Food web models reveal potential ecosystem effects of seagrass recovery in the northern Wadden Sea, Restor Ecol, 29, https://doi.org/10.1111/rec.13328, 2021.

Hufnagl, M., Temming, A., Siegel, V., Tulp, I., and Bolle, L.: Estimating total mortality and asymptotic length of Crangon crangon between 1955 and 2006, ICES Journal of Marine Science, 67, 875–884, https://doi.org/10.1093/icesjms/fsq003, 2010.

ICES Historical Plankton Dataset (1901-1912). The International Council for the Exploration of the Sea, Copenhagen. Online source: http://ecosystemdata.ices.dk., 2010.

ICES: Greater North Sea ecoregion – Ecosystem overview. In Report of the ICES Advisory Committee, 2024. ICES Advice 2024, Section 7.1, 2024.

ICES: Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), 2019.

ICES: Report of the Herring Assessment Working Group for the Area South of 62° N (HAWG), 2020.

ICES: Historical Nominal Catches 1950-2010, https://ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stockassessment.aspx.

ICES Stock Assessment Database. Copenhagen, Denmark. ICES. 2025. https://standardgraphs.ices.dk

Institut Français de Recherche pour l'Exploitation de la Mer – IFREMER: COMARGIS: Information System on Continental Margin Ecosystems https://doi.org/10.15468/0djslr, 2016.

Jenkins, G. M. and Watts, D. G.: Spectral Analysis and Its Applications, Holden-Day. San Francisco, 1968.

Kaschner, K., Kesner-Reyes, K., Garilao, C., Segschneider, J., Rius-Barile, J. Rees, T., & Froese, R. (2019, October). AquaMaps: Predicted range maps for aquatic species. Retrieved from https://www.aquamaps.org.

Kastelein, R. A., Hardeman, J., and Boer, H.: Food consumption and body weight of harbour porpoises (Phocoena phocoena), in: The biology of the harbour porpoise, edited by: Read, A. J., Wiepkema, P. R., and Nachtigall, P. E., De Spil Publishers, Woerden, The Netherlands, 217–233, 1997.

Kesner-Reyes, K., Garilao, C., Kaschner, K., Barile, J., and Froese, R.: AquaMaps: algorithm and data sources for marine organisms., version (10/2019)., edited by: Froese, R. and Pauly, D., FishBase, https://www.fishbase.org, 2020.

Lacroix, G., Ruddick, K., Ozer, J., and Lancelot, C.: Modelling the impact of the Scheldt and Rhine/Meuse plumes on the salinity distribution in Belgian waters (southern North Sea), J Sea Res, 52, 149–163, https://doi.org/10.1016/j.seares.2004.01.003, 2004.

Leeman, L. W., Colwell, M. A., Leeman, T. S., and MATHI, R. L.: Diets, Energy Intake, and Kleptoparasitism of Nonbreeding Long-Billed Curlews in a Northern California Estuary, Wilson Bull, 113, 194–201, https://doi.org/10.1676/0043-5643(2001)113[0194:DEIAKO]2.0.CO;2, 2001.

Lewin, W.-C., Strehlow, H. V., Ferter, K., Hyder, K., Niemax, J., Herrmann, J.-P., and Weltersbach, M. S.: Estimating post-release mortality of European sea bass based on experimental angling, ICES Journal of Marine Science, 75, 1483–1495, https://doi.org/10.1093/icesjms/fsx240, 2018.

Libby, D. A.: Maine Department of Marine Resources Inshore Trawl Survey, 2000 – 2009. Maine Department of Marine Resources, PO Box 8, West Boothbay Harbor, Maine 04575, 2010.

Link, J. S.: Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL, Ecol Modell, 221, 1580–1591, https://doi.org/10.1016/j.ecolmodel.2010.03.012, 2010.

Mackinson, S. and Daskalov, G.: An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation Science Series Technical Report no.142, 2007.

Maksims, K., Gibin, M., Maciej Adamowicz, Zanzi, A., and Hekim, Z.: Fisheries landings & effort: data by c-square., 2022.

Marine Biological Association of the UK (MBA): DASSH: The UK Archive for Marine Species and Habitats Data, 2016.

Meurisse, L., Semal, P.: Royal Belgian Institute of Natural Sciences Crustacea collection, 2020

Miller, R, Nozères, C, Kennedy, M.: DFO Quebec Region MLI museum collection. Version 2. OBIS Canada Digital Collections. Published by OBIS http://www.iobis.org/, 2014. Accessed on 29/06/2020.

Motova-Surmava, A., Zanzi, A., and Hekim, Z. (Eds.): Scientific Technical and Economic Committee for Fisheries (STECF) – Fisheries Dependent Information FDI (STECF 23-10), Publications Office of the European Union, doi:10.2760/676073, JRC136194., Luxembourg, 2024.

Musimwa, R., Standaert, W., Stevens, M., Fernández Bejarano, S. J., Muñiz, C., Debusschere, E., Pint, S., and Everaert, G.: Climate-induced habitat suitability modelling for pelagic fish in European seas, Front Mar Sci, 12, https://doi.org/10.3389/fmars.2025.1501751, 2025.

Nasri et al., H.: Ecology, Anatomy, Reproduction, and Diet of the Atlantic Horse Mackerel, Trachurus trachurus: A Comprehensive Review, Egypt J Aquat Biol Fish, 28, 517–539, https://doi.org/10.21608/ejabf.2024.358854, 2024.

National Museum of Natural History, Smithsonian Institution NMNH Invertebrate Zoology Collection Database. National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. N.W., Washington, DC 20560-0193, Version 3.2.04 (0802221), 2001.

Nilsson, S. G. and Nilsson, I. N.: Numbers, Food Consumption, and Fish Predation by Birds in Lake Möckeln, Southern Sweden, Scandinavian Journal of Ornithology), 61–70 pp., 1976.

NOAA Fisheries Southeast Fisheries Science Center GitHub Organization, https://github.com/SEFSC/CEFI-GoMCLIM-DataSynth, 2025.

NOAA's National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center.: Northeast Fisheries Science Center Bottom Trawl Survey Data. NOAA's National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center. Woods Hole, Massachusetts, United States of America, 2005.

Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, U.S. Department of Commerce. NEFSC Benthic Database. Northeast Fisheries Science Center, 166 Water Street, Woods Hole Laboratories, Woods Hole, MA 02543.Retrieved from http://www.usgs.gov/obis-usa/, 2010.

OBIS Canada: FRB Eastern Arctic Investigations: The Calanus Series. OBIS Canada Digital Collections. OBIS Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, Version 2, Digital, retrieved from http://iobis.org/, 2011.

Parr, J. Marine Life Information Network (MarLIN) marine survey data (Professional). Marlin, Collated Marine Life Survey Datasets, Marine Biological Associaton of the UK, Plymouth, UK

Pauly, D.: On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks, J. Cons. int. Explor. Mer, 175–192 pp., 1980.

Pauly, D., Christensen, V., and Sambilay, V.: Some features of fish food consumption estimatives used by ecosystem modellers, ICES Counc. Meet., 657, 1–8, 1990.

Pauly, D., Christensen, V., and Walters, C.: Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries, ICES Journal of Marine Science, 57, 697–706, https://doi.org/10.1006/jmsc.2000.0726, 2000.

Pinnegar, J. K.: DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. Version 4.7, Lowestoft, 39 pp., 2014.

Pint, S., Stevens, M., Musimwa, R., Standaert, W., De Troch, M., van Oevelen, D., Heymans, J. J., and Everaert, G.: A food web model of the Southern Bight of the North Sea, Ocean Coast Manag, 255, 107256, https://doi.org/10.1016/j.ocecoaman.2024.107256, 2024a.

Pint, S., Stevens, M., De Troch, M., van Oevelen, D., Heymans, J. J., and Everaert, G.: Data - Ecopath model of the Southern Bight of the North Sea, 2024b.

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

Polovina, J. J.: Coral Reefs Model of a Coral Reef Ecosystem I. The ECOPATH Model and Its Application to French Frigate Shoals, Coral Reefs, 1–11 pp., 1984.

Potiek, A., Vanermen, N., Middelveld, R. P., De Jong, J., Stienen, E. W. M., and Fijn, R. C.: Spatial and temporal distribution of different age classes of seabirds in the North Sea Analysis of ESAS database, 2019.

Pyper, B. J. and Peterman, R. M.: Comparison of methods to account for autocorrelation in correlation analyses of fish data, Canadian Journal of Fisheries and Aquatic Sciences, 55, 2127–2140, https://doi.org/10.1139/f98-104, 1998.

Rees, H.L. et al.: A comparison of benthic biodiversity in the North Sea, English Channel and Celtic Seas - Epifauna. Centre for Environment, Fisheries and Aquaculture Science; Burnham Laboratory, 12 Apr 2005, Essex, UK.

Reeves, S. and Furness, R. W.: Net Loss-Seabirds Gain? Implications of Fisheries Management for Seabirds Scavenging Discards in the Northern North Sea, 2002.

Santos, R.: Zariquiey Collection. Biological Reference Collections ICM CSIC. Institute of Marine Sciences (ICM-CSIC). https://dx.doi.org/10.15470/cqtmj1, 2016

Scientific, Technical and Economic Committee for Fisheries (STECF) – Fisheries Dependent - Information – Classic (STECF-17-09). Publications Office of the European Union, Luxembourg, ISBN 978-92-79-67481-5, doi:10.2760/561459, JRC107598, 2017.

Scott, E., Serpetti, N., Steenbeek, J., and Heymans, J. J.: A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models, SoftwareX, 5, 25–30, https://doi.org/10.1016/j.softx.2016.02.002, 2015.

Sherley, R. B., Ladd-Jones, H., Garthe, S., Stevenson, O., and Votier, S. C.: Scavenger communities and fisheries waste: North Sea discards support 3 million seabirds, 2 million fewer than in 1990, Fish and Fisheries, 21, 132–145, https://doi.org/10.1111/faf.12422, 2020.

Skov, C., Ferter, K., Jepsen, N., Pedersen, L.-F., Lewin, W.-C., Gundelund, C., and Weltersbach, M. S.: Post-release effects of catch and release angling for sea trout: Mortality, growth and wound healing, Fish Res, 261, 106637, https://doi.org/10.1016/j.fishres.2023.106637, 2023.

Skyttner, M.: aquamapsdata: Curated Data From AquaMaps.Org, 2020.

Sparholt, H.: An estimate of the total biomass of fish in the North Sea, J. Cons. int. Explor. Mer, 200–210 pp., 1990.

Stäbler, M., Kempf, A., Mackinson, S., Poos, J. J., Garcia, C., and Temming, A.: Combining efforts to make maximum sustainable yields and good environmental status match in a food-web model of the southern North Sea, Ecol Modell, 331, 17–30, https://doi.org/10.1016/j.ecolmodel.2016.01.020, 2016.

Stäbler, M., Kempf, A., and Temming, A.: Assessing the structure and functioning of the southern North Sea ecosystem with a food-web model, Ocean Coast Manag, 165, 280–297, https://doi.org/10.1016/j.ocecoaman.2018.08.017, 2018.

Stienen, E. and Vanermen, N.: Dichtheid van vogels op zee., edited by: In B. Staat (editor), Actualisatie van de initiële beoordeling voor de Belgische mariene wateren. Kaderrichtlijn Mariene Strategie – Art 8 lid 1a & 1b: België 2018-2024, Federale Overheidsdienst Volksgezondheid, Veiligheid van de Voedselketen en Leefmilieu., 198 pp., 2018.

Swedish county administration boards, Swedish municipalities, Swedish coalitions of water conservation, Swedish Meteorological and Hydrological Institute, et al.: SHARK - Regional monitoring and monitoring projects of Epibenthos in Sweden since 1994, 2017.

The Norwegian Oil Industry Association: Offshore reference stations, North/Norwegian sea. The Norwegian Oil Industry Association (OLF), Akvaplan-niva and Det Norske Veritas, Norway, 2001.

Tulp, I., Chen, C., Haslob, H., Schulte, K., Siegel, V., Steenbergen, J., Temming, A., and Hufnagl, M.: Annual brown shrimp (Crangon crangon) biomass production in Northwestern Europe contrasted to annual landings , ICES J Mar Sci, 73, 2539–2551, https://doi.org/10.1093/icesjms/fsw141, 2016.

Türkay, M.: Senckenbergisches Sammlungsverwaltungssystem, SeSam. Senckenbergische Naturforschende Gesellschaft, Frankfurt, Germany. http://sesam.senckenberg.de/

Turrell, W. R., Henderson, E. W., Slesser, G., Payne, R., and Adams, R. D.: Seasonal changes in the circulation of the northern North Sea, Cont Shelf Res, 12, 257–286, https://doi.org/10.1016/0278-4343(92)90032-F, 1992.

Van Guelpen, L.: Atlantic Reference Centre Museum of Canadian Atlantic Organisms - Invertebrates and Fishes Data. Version 4 In OBIS Canada Digital Collections. Bedford Institute of Oceanography, Dartmouth, NS, Canada. Published by OBIS, Digital http://www.iobis.org/, 2016. Accessed on 29/06/2020.

Van Guelpen L and Pohle, G.: Bay of Fundy Species List. v1.2. Canadian node of the Ocean Biogeographic Information System (OBIS Canada). Dataset/Occurrence.

Verleye, T. J., Dauwe, S., van Winsen F., and Torreele, E.: Beleidsinformerende Nota: Recreatieve zeevisserij in België anno 2018 - Feiten en cijfers, Oostende, 86 pp., 2019.

Verleye, T. J., Lanssens, T., Dauwe, S., and Torreele, E.: Recreatieve visserij in het Belgisch deel van de Noordzee: Een continue meerjaarlijkse datareeks van 2017 tot 2021, Oostende, 2022.

Waggitt, J. J., Evans, P. G. H., Andrade, J., Banks, A. N., Boisseau, O., Bolton, M., Bradbury, G., Brereton, T., Camphuysen, C. J., Durinck, J., Felce, T., Fijn, R. C., Garcia-Baron, I., Garthe, S., Geelhoed, S. C. V., Gilles, A., Goodall, M., Haelters, J., Hamilton, S., Hartny-Mills, L., Hodgins, N., James, K., Jessopp, M., Kavanagh, A. S., Leopold, M., Lohrengel, K., Louzao, M., Markones, N., Martínez-Cedeira, J., Ó Cadhla, O., Perry, S. L., Pierce, G. J., Ridoux, V., Robinson, K. P., Santos, M. B., Saavedra, C., Skov, H., Stienen, E. W. M., Sveegaard, S., Thompson, P., Vanermen, N., Wall, D., Webb, A., Wilson, J., Wanless, S., and Hiddink, J. G.: Distribution maps of cetacean and seabird populations in the North-East Atlantic, Journal of Applied Ecology, 57, 253–269, https://doi.org/10.1111/1365-2664.13525, 2020.

Walters, C., Christensen, V., and Pauly, D.: Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments, Reviews in Fish Biology and Fisheries, 139–172 pp., 1997.

Wang, H.-Y., Shen, S.-F., Chen, Y.-S., Kiang, Y.-K., and Heino, M.: Life histories determine divergent population trends for fishes under climate warming, Nat Commun, 11, 4088, https://doi.org/10.1038/s41467-020-17937-4, 2020.

Weltersbach, M. S. and Strehlow, H. V.: Dead or alive - Estimating post-release mortality of Atlantic cod in the recreational fishery, ICES Journal of Marine Science, 70, 864–872, https://doi.org/10.1093/icesjms/fst038, 2013.

Weltersbach, M. S., Strehlow, H. V., Ferter, K., Klefoth, T., de Graaf, M., and Dorow, M.: Estimating and mitigating post-release mortality of European eel by combining citizen science with a catch-and-release angling experiment, Fish Res, 201, 98–108, https://doi.org/10.1016/j.fishres.2018.01.010, 2018.

Wilson, K. L., De Gisi, J., Cahill, C. L., Barker, O. E., and Post, J. R.: Life-history variation along environmental and harvest clines of a northern freshwater fish: Plasticity and adaptation, Journal of Animal Ecology, 88, 717–733, https://doi.org/10.1111/1365-2656.12965, 2019.

Zanzi, A. and Holmes, S.: Fisheries data from DCF Fishing Effort Regimes data calls, European Commission, Joint Research Centre (JRC) [Dataset] PID: http://data.europa.eu/89h/9f8002cc-c6fc-4adb-86cd-466f935a7bda, 2017.