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Modelling the food web in Icelandic waters

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Titill:
Modelling the food web in Icelandic waters

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Ágrip:
Lýst er þróun Ecopath líkans fyrir íslenska hafsvæðið, þar sem gerð er ítarleg greining á þeirri aðferðarfræði sem var beitt, auk þess sem nauðsynlegum inntaksgögnum líkansins er lýst. Tilgangur skýrslunnar er að tryggja gagnsæi í ferli líkanasmíðarinnar, og að auki að varpa ljósi á þær takmarkanir sem kunna að koma til, og þar með á þá fyrirvara sem fylgja útkomunni. Ecopath líkan er svokallað jafnstöðulíkan sem rekur flæði orku, næringarefna og lífmassa innan vistkerfis í jafnvægi og er undirstaðan fyrir hermanir í Ecosim hluta líkansins. Í Ecosim er hægt er að herma eftir umhverfisbreytingum, breytingum á veiðiálagi og breytingum á lífmassa og þannig spá fyrir um áhrif þessara breytinga á lífverur innan vistkerfisins.

Skýrslan er hluti af doktorsverkefni sem snýr að þróun vistkerfislíkans og er hluti af stærra verkefni “Fiskveiðar til framtíðar: Samspil vistkerfis og félagshagrænna þátta við nýtingu sjávarauðlinda” en Landbúnaðarháskóli Íslands hlaut öndvegisstyrk frá Rannsóknarsjóði Íslands – Rannís, fyrir verkefnið. Verkefnastjórar eru Erla Sturludóttir lektor við Landbúnaðarháskólann og Gunnar Stefánsson prófessor við Raunvísindastofnun Háskóla Íslands en verkefnið er unnið í samstarfi við Hafrannsóknarstofnun og erlenda vísindamenn.

Abstract:
This report describes the development of an Ecopath model of Icelandic waters, detailing the methodology and data used to construct the model. It is intended to provide transparency to the model construction process and highlight the limitations of the data and thus the caveats attached to model output. Ecopath is a mass-balance model that represents the flow of energy and nutrients through the ecosystem. Ecosim builds upon the Ecopath model, and allows for simulations of changes over time, such as environmental variations, fishing pressure, and alterations in species biomass.

This work was undertaken as a part of the PhD titled "Development of marine ecosystem modelling: increasing its potential as a supporting tool for the ecosystem approach to fisheries management" funded via the Icelandic Research Fund - Rannís and as a part of a larger project "Fishing into the future: Operationalizing linkages in the ecosystem approach to fisheries". Project managers are Erla Sturludóttir, assistant professor at the Agricultural University of Iceland, and Gunnar Stefánsson, professor at the University of Iceland. The project is carried out in collaboration with the Marine and Freshwater Research institute.

Lykilorð: Ecopath, food web, ecosystem model, ecosystem

Undirskrift verkefnisstjóra:

Undirskrift forstöðumanns sviðs:

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An introduction to Icelandic waters

Iceland has an exclusive economic zone (EEZ) of 200 nautical miles (758,000 km2). The continental shelf extends from 20 to 100 km offshore, and at the shelf break the depth drops from a few hundred meters to 1,000-1,500 m (Malmberg 2004; Malmberg and Magnússon 1982). Many authors have provided descriptions of the hydrography of the waters surrounding Iceland (Stefánsson 1962, Valdimarsson and Malmberg 2003, Valdimarsson et. al. 2012), which form one of the most hydrographically complicated regions in the North-Atlantic (Hansen and Østerhus 2000). In general, the ecoregion is made up of four subareas which vary in both physical oceanographic characteristics and faunal composition between areas. The first two areas are on the continental slope south and north of Iceland at depths less than 500 m. The southern area is characterized by a mix of coastal and warm Atlantic water, but the northern area carries a mixture of coastal, warm Atlantic and cold Arctic water. The third and fourth areas are below the slope at depths greater than 500 m. The deeper southern area is characterized by Atlantic water and the area in the north by cold Arctic water (Hansen and Østerhus 2000). Sediment on the Icelandic shelf is mostly sand and sandy mud, with patches of rocks and boulders, whereas off the shelf the sediment types are more mixed, with large areas of mud and sandy mud (Figure 1).

The Marine and Freshwater Research Institute (former Marine Research Institute, but hereafter referred to as MFRI) carries out various environmental research in Icelandic waters with the objective to monitor long term changes in Icelandic waters. Quarterly hydrographic cruises for monitoring of environmental conditions, such as temperature, salinity, and nutrients, have been conducted annually on fixed stations since 1970. Results from those surveys can be found in numerous reports (e.g., Olafsdottir et al. 2020) and on the website of MFRI oceanographic research (https://sjora.hafro.is/). Results are also contextualized in relation to comparable observations from other areas in the North Atlantic in annual reports of the International Council for the Exploration of the Sea (ICES) on the state of the sea in the North Atlantic (see e.g., González-Pola et al. 2023).

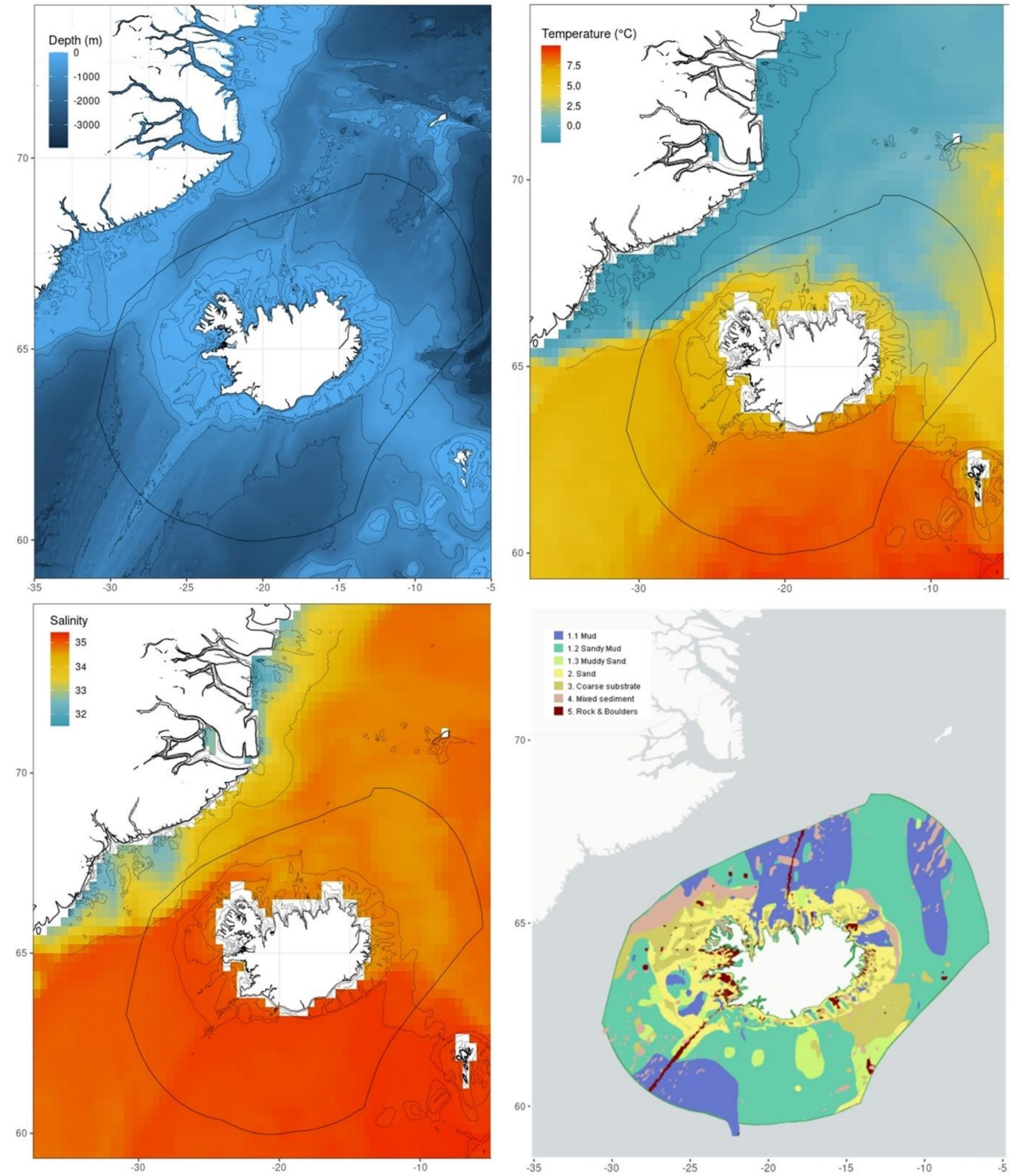

Figure 1. Physical characteristics of Icelandic waters and adjacent areas. The black line shows the boundaries of the Icelandic exclusive economic zone (EEZ) (black line). The map shows bathymetry from 0-3000 meters (upper left), sea surface temperature and salinity (time period 1993-1999, extracted from the Global Ocean Reanalysis and Simulations (Jean-Michel et al. 2021)), and substrate types (compiled by EMODnet Seabed Habitats; www.emodnet-seahabitats.eu).

Main changes in the ecosystem in past decades

For the past three decades, the oceans north and south of Iceland have been warmer than the previous three decades (Figure 2). Since 1996, mean temperatures at selected stations (see Figure 2) at depths ranging grom 50-150 m, mean annual temperatures have increased by 0.83°C in the north and by 0.58 °C in the south. Changes in temperature can have major impacts on ecosystems, for instance through distributional shifts of marine species, recruitment processes and through the food chain by affecting the onset of phytoplankton bloom.

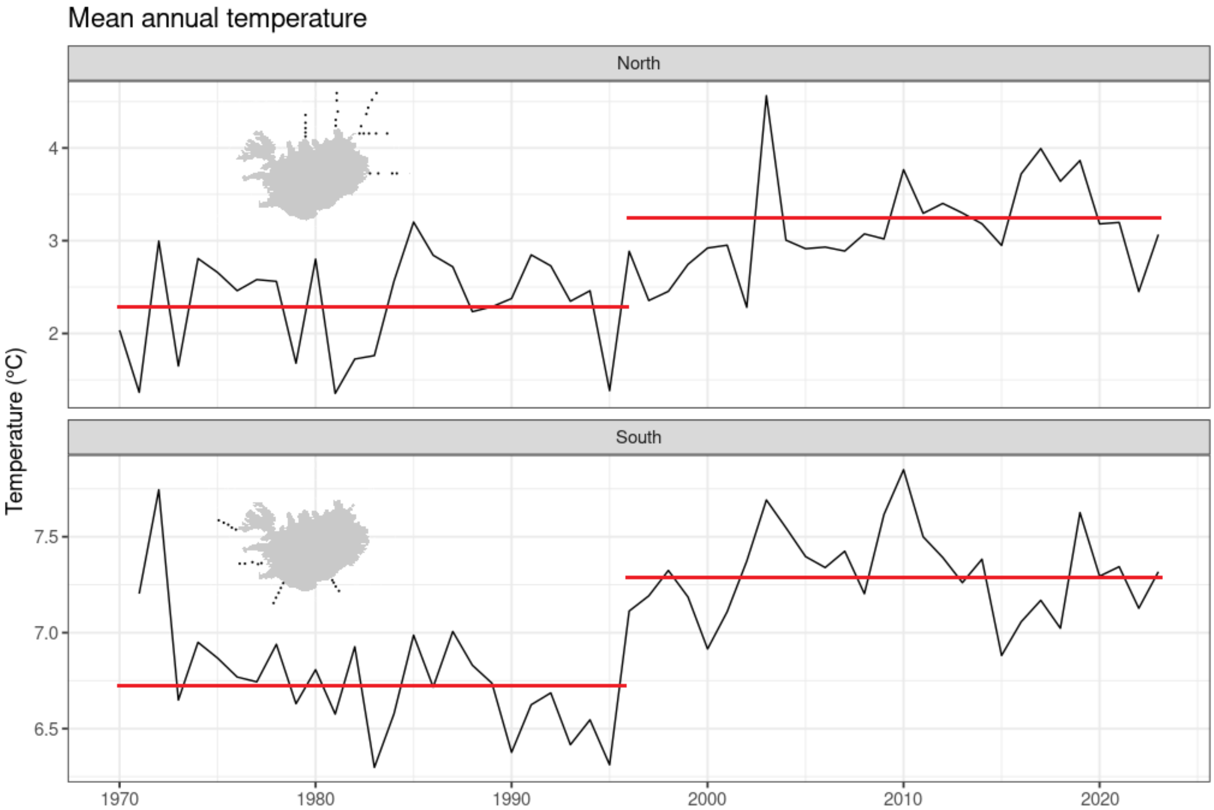

Figure 2. Mean annual temperatures at fixed stations north and south of Iceland from 1970-2023 at depths ranging from 50-150 m. The data is from the Marine and Freshwater Research Institute's quarterly hydrographic cruises for the monitoring of environmental conditions in Icelandic waters. Red lines are the mean from 1970-1995 and 1996-2023. Black dots are the selected stations north and south of Iceland.

Changes in temperature may affect growth rates and reproduction (Pankhurst 2011), as well as having an impact on feeding success and survival of species (Gobler 2018). In the seas around Iceland, changes in assemblage structure and arrangement of species have been noticed, where species are either retreating, declining in abundance, or moving to more suitable areas (Stefánsdóttir et al. 2010, Campana et al. 2020). Also, rare species and vagrants have been recorded more frequently, for instance flounder (*Platichthys flesus*), brown shrimp (*Crangon crangon*), rock crab (*Cancer irroratus*), and more recently, European sprat (*Sprattus sprattus*), which have gained a foothold in Icelandic waters (Koberstein 2013, Henke 2018, Gíslason et al. 2013, Palsson et al. 2022). New species can have significant impacts on the existing ecosystem, by outcompeting native species and by disrupting established food webs (Astthorsson et al. 2007, Pálsson and Björnsson 2011, Valdimarsson et al. 2012).

Changes in temperature have also impacted the migration patterns of foraging species in Icelandic waters. For example, at the time of warming in early 2000s, Atlantic mackerel (*Scomber scombrus*) extended its feeding grounds from the Norwegian Sea to Icelandic waters ecoregion (Astthorsson 2012), summer feeding grounds of capelin (*Mallotus villosus*) moved westwards from Icelandic waters into Greenlandic waters (Jansen 2021) and the Norwegian spring spawning herring (*Clupea harengus*) reappeared at its traditional feeding grounds east and north of Iceland (Óskarsson 2018). These changes have impacted commercial fisheries, for instance where targeted species have located elsewhere or declined in abundance at preferred fishing grounds.

Phytoplankton and zooplankton

Phytoplankton biomass in Icelandic waters varies both in space and time and the variation is explained by temperature, surface salinity, light availability, currents, and nutrients (Gudmundsson 1998). Phytoplankton growth rate is highest during warmer months when light is abundant. During favorable conditions, spring bloom starts to develop in late March/early April and peaks in May (Sakshaug and Slagstad 1991) (Figure 3). Secondary producers, such as copepods and other zooplankton, largely depend on phytoplankton for growth and spawning success, and thus, the timing and duration of the phytoplankton bloom may be of key importance for the survival of fish larvae that feed on zooplankton. As phytoplankton provides the base of the food web, it is an important indicator of the overall health and productivity of marine ecosystem and thus, monitoring timing and duration is important. The MFRI has conducted annual monitoring of primary productivity since 1958 and variation in phytoplankton biomass has been explained by differences in physical factors (Gudmundsson 1998).

Since 1970, zooplankton biomass and species composition has been monitored by the MFRI annually in late May and early June. The most dominant species of zooplankton in Icelandic waters is *Calanus finmarchicus* (Astthorsson 1995, Gislason and Astthorsson 1998, Gislason and Astthorsson 2004). A significant relationship between zooplankton abundance and cod larvae abundance has been demonstrated, where zooplankton biomass explained 42% of the variation in 0-group cod abundance (Astthorsson 1995) and thus, secondary production in marine food webs is highly important in relation to recruitment and larval success.

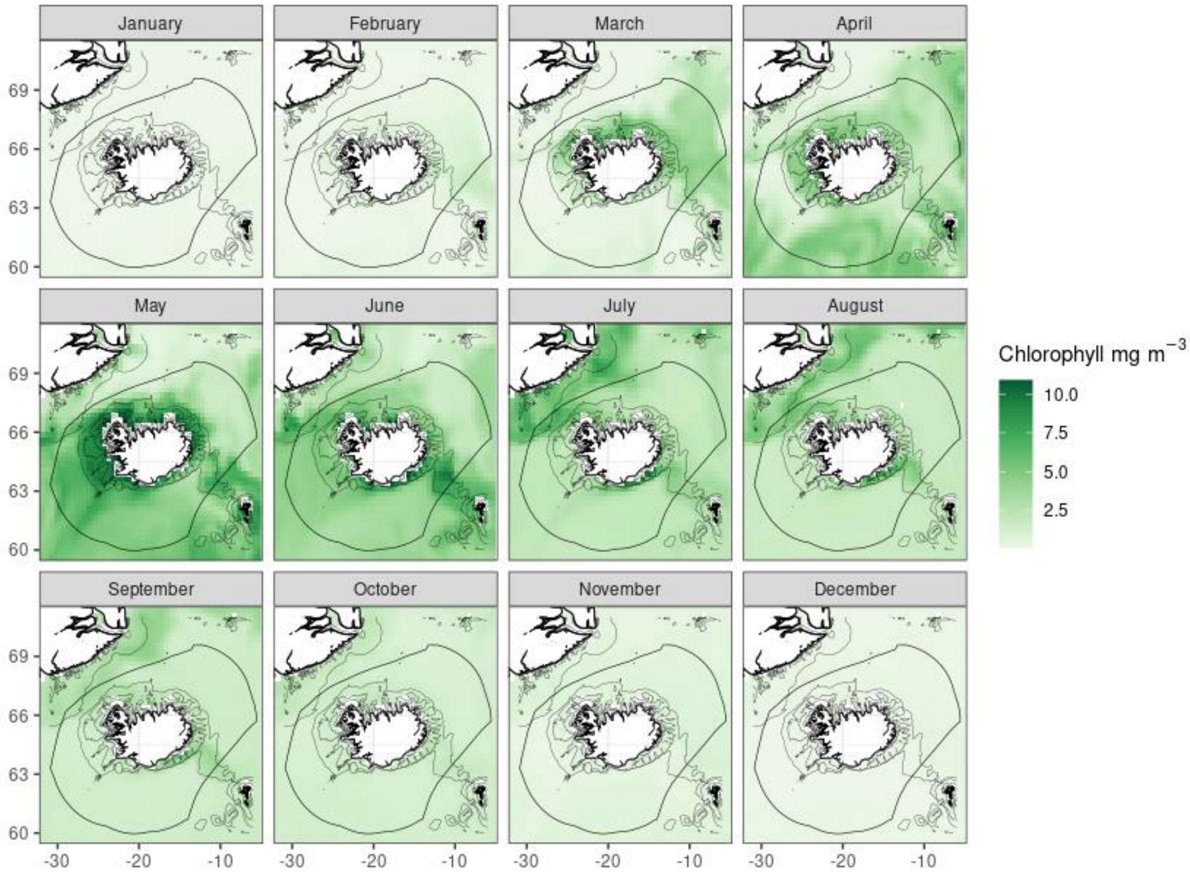

Figure 3. Phytoplankton abundance and distribution in 1996 (Extracted from the Global Ocean Reanalysis and Simulations (Jean-Michel et al. 2021)).

Commercial fisheries over the past century - fish and shellfish

Over 40 stocks of fish and invertebrates are harvested in Icelandic waters. Demersal fisheries are mixed, i.e. more than one species is targeted at the time, while pelagic fisheries target single species. Total annual landings have fluctuated throughout the years and were highest in 1997, when total annual landings were just under two million tonnes (Figure 4). After 2002, total annual landings have been lower, compared to the previous years. Cod and capelin are the most commercially important species in Icelandic waters. Cod is mainly targeted by bottom trawls and longlines and capelin by pelagic gear (purse seine).

Norway lobster (*Nephrops norvegicus*), northern shrimp (*Pandalus borealis*) and, since 2008, sea cucumber (*Cucumaria frondosa*) are the most commercially important invertebrate species fished in Icelandic waters. Lobster and shrimp are mainly fished in bottom trawls, while sea cucumber, scallop and sea urchins are fished by dredge. Since 2000, total annual landings of invertebrates have decreased substantially (Figure 6). The offshore shrimp stock has decreased since 1997, and inshore shrimp stocks have also declined and in some places collapsed. The scallop fisheries halted in 2003, due to stock collapse and lobster fishing was discontinued in 2022.

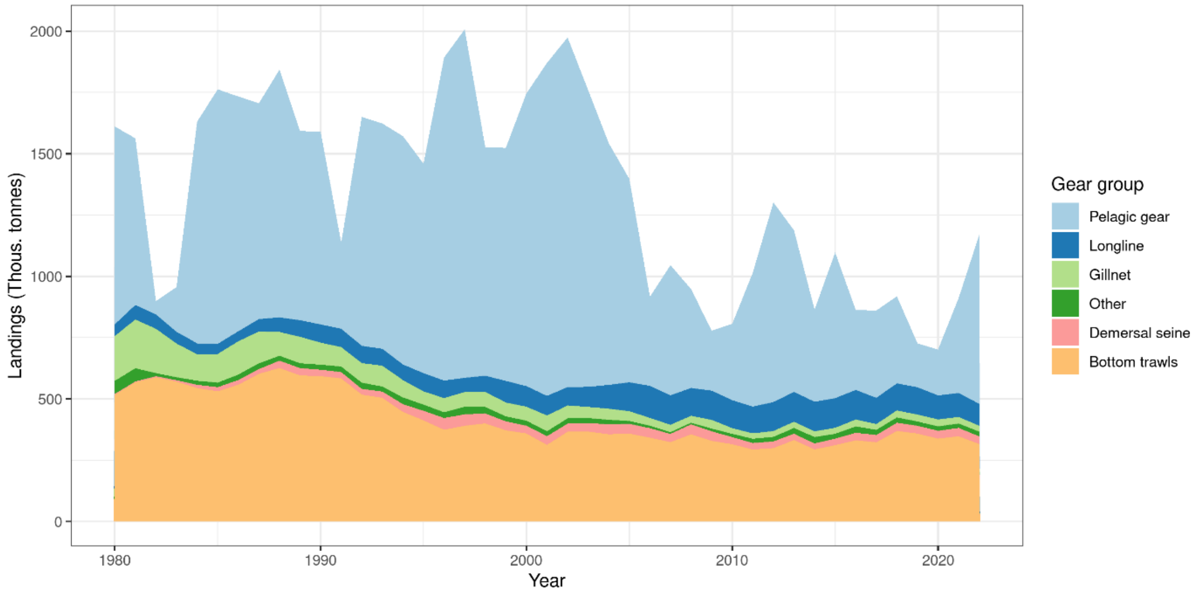

Figure 4. Total annual landings (thousand tonnes) from Icelandic fishing grounds in 1980-2022 by gear groups defined in the Icelandic Ecopath model.

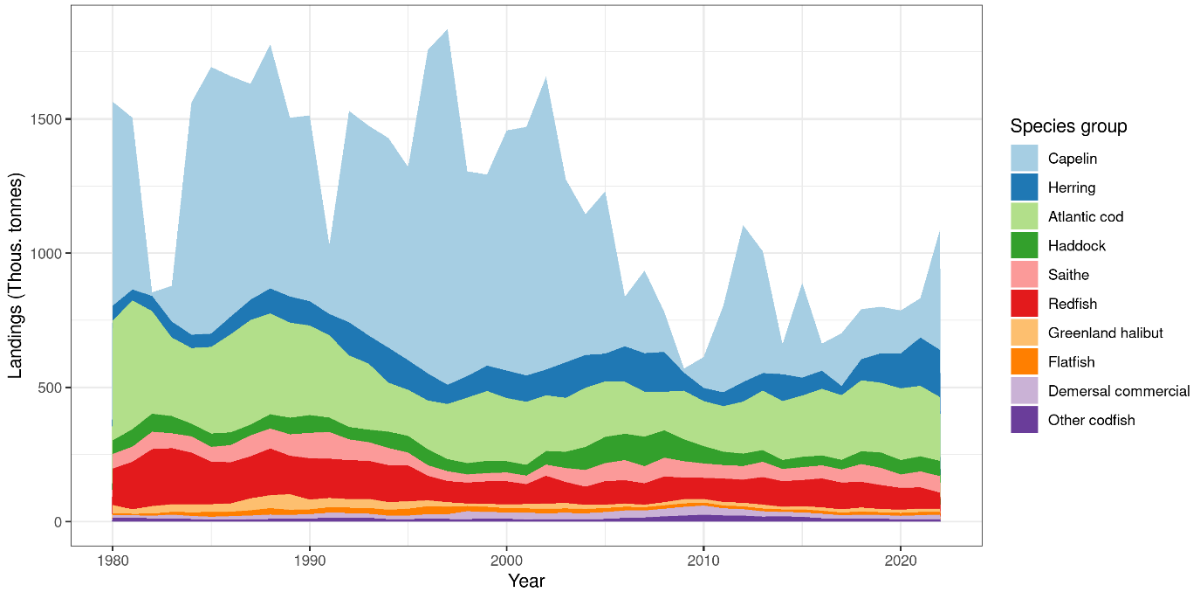

Figure 5. Total annual landings (thousand tonnes) from Icelandic fishing grounds in 1980-2022 of the main fish functional groups in the Icelandic Ecopath model.

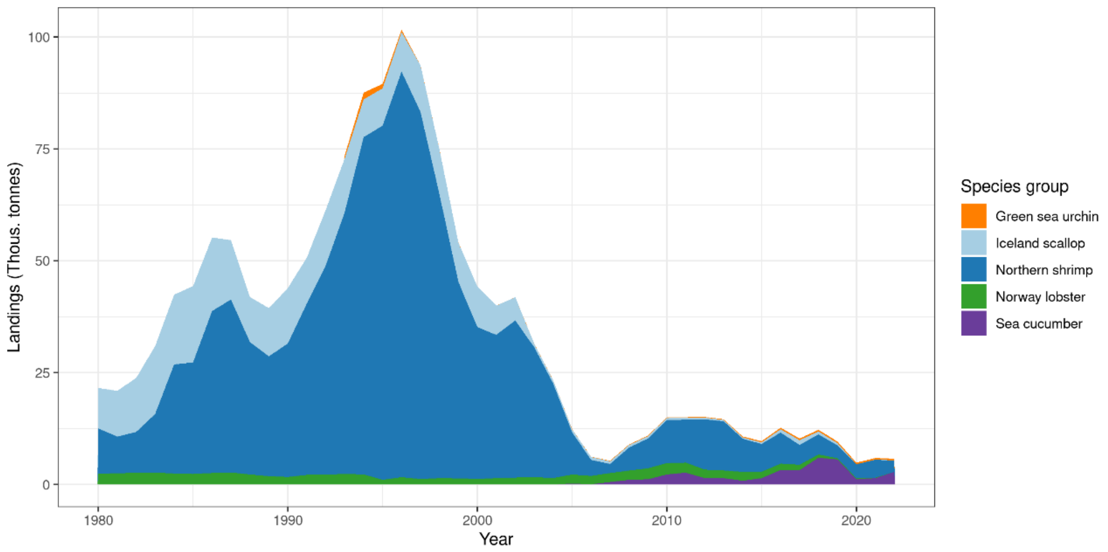

Figure 6. Total annual landings (thousand tonnes) from 1980-2022 of invertebrate species on Icelandic fishing grounds.

Fishing on Icelandic grounds are mostly managed by the Icelandic authorities, but some stocks are managed under the Northeast Atlantic Fisheries Commission (NEAFC) and in accordance with agreements between coastal states (Iceland, Greenland, Faroe Islands, and Norway). The MFRI provides advice on fisheries in Icelandic waters, in collaboration with international organizations such as the International Council for the Exploration of the Sea (ICES). The International Whaling Commission (IWC) issues specific measures (such as catch limits) for conservation of whales, while advice on the hunting and protection of marine mammals is provided by the North Atlantic Marine Mammal Commission (NAMMCO).

An introduction to Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a modelling framework that was first established by Jeff Polovina in 1984 and is used to create mass balanced models of marine and aquatic ecosystems i.e., describe the structure and flow of energy through the system. Initially it was presented for estimating biomass and food consumption of the elements (species or groups of species) of an aquatic ecosystem. The software and its techniques have subsequently been updated and improved to include methods of comparing ecosystems (Christensen and Pauly 1992), to model dynamic changes using Ecosim (Walters et al. 1997) and to model spatial changes using Ecospace (Walters et al. 1999). EwE can be used to evaluate the ecosystem effects of fishing, explore management policy options, investigate the impact and placement of marine protected areas and evaluate the effect of environmental change on marine food webs. EwE software is open source and freely available at www.ecopath.org. An R implementation of Ecopath and Ecosim, called Rpath was recently developed by Lucey et al. (2020) and is meant to be a complement to the existing software. Rpath allows for cross-platform use of EwE algorithms and increases reproducibility of studies (Lucey et al. 2020). The Icelandic EwE model was built using Rpath (version 0.0.1.3).

Ecopath

Ecopath models are parameterized using two master equations, one to describe the production term and one for the energy balance of each group. Equation 1 models the total production rate (Pi) for each group (i) assuming mass balance over a specified period, usually one year (Christensen et al. 2005):

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i) \qquad (1)$$

where P_i represents the total production rate of (i), Y_i is the total fishery catch rate of (i), B_i is the biomass of (i), $M2_i$ is the total predation rate for group (i), E_i the net migration rate (emigration minus immigration), BA_i is the biomass accumulation rate for (i) and $Pi \cdot (1\text{-}EE_i)$ is the ‘other mortality’ rate for (i), or the fraction of the production unaccounted for by the model. EE_i is the ecotrophic efficiency of a group (i) and is a measure of the proportion of its production or total mortality (where production to biomass ratio, P/B, is equals the total mortality rate, Z) that is accounted for in the model.

Normally, biomass, P/B and Q/B, along with diets and catches, are input parameters, while EE is an output of the model. However, in situations where biomass data are unavailable, EE values may be adjusted to enable the model to estimate missing parameters.

The energy input and output of all living groups must be balanced and to ensure mass balance between groups, Ecopath also employs a series of parameterization algorithms to estimate missing parameters. Once the missing parameters have been estimated, energy balance is ensured within each group using equation 2 (Christensen et al. 2005):

$$\text{Consumption} = \text{Production} + \text{respiration} + \text{unassimilated food} \qquad (2)$$

Ecosim

Ecosim simulates the interaction between different species/groups in an ecosystem over time, using the output of the Ecopath model as a starting point. It then incorporates information on growth, mortality, and recruitment rates of different species/groups. The changes in biomass dynamics over time are determined by a series of coupled differential equations (equation 3) which are derived from the initial parameters of equation 1

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right) \sum Q_{ji} - \sum Qij + I_i - B_i \cdot (M_i + F_i + e_i) \qquad (3)$$

where dB is the biomass growth rate of group (i) during the time interval dt, (P/Q) is the group's net growth efficiency (production/consumption), Q_{ji} is the total consumption of predator group (i), Q_{ij} is the predation by all predators on the same prey group (i). I_j is the group immigration rate, B_i is the biomass of group (i), M_i is the non-predatory ('other') natural mortality of group I (estimated from the ecotrophic efficiency), F_i is the fishing mortality rate of group (i) and e_i is the emigration rate of group (i).

Data sources for the Icelandic Ecopath model

The Icelandic Ecopath model represents the ecosystem as it was in 1996. This year was chosen due to the availability of biomass estimate information for the majority of commercially exploited fish species in Icelandic waters and most other groups used in the model. Biomass of commercially exploited fish stocks and invertebrates in the model are from stock assessments. Biomass estimates for whale species were based on whale counting, where the Marine and Freshwater Research Institute undertook extensive whale sighting surveys in Icelandic and adjacent waters as a part of joint international effort (North Atlantic Sightings Surveys) of several North Atlantic nations (see Sigurjónsson 1989, Sigurjónsson et al. 1991, Sigurjónsson et al. 1996). Seabird abundance was based on estimates from the ICES Working Group on Seabird Ecology (WGSE). Biomass estimates for seals are based on counting from aerial surveys.

Landings data for exploited fish stocks, invertebrates and whales were obtained from the Directorate of Fisheries in Iceland and of seabirds from the Environmental Agency of Iceland.

The stomach data in the model is mainly from the MFRI and from literature when missing. Stomach content has been analyzed for the past decades and during various surveys (see below). In the model, stomach content analysis from 1979–2022 was used.

Diet

Stomach content from fish has been collected during various surveys conducted by the MFRI throughout the years but mainly during the groundfish surveys in March and October (IGFS and AGS). The sampling approach differs between surveys and sampling effort varies between years. In 1992 (March, July, and November), an increased effort was put in stomach sampling, as a part of the Multi-species Research Program (Fjölstofnarannsóknir 1997). More recently, stomach sampling has been included in the offshore shrimp survey (SMR) in July and inshore shrimp surveys (SMG) in fall and winter. In some years, special stomach sampling trips on commercial vessels have been undertaken, mostly in July. In total, 402,824 stomachs have been analyzed in the period between 1979-2022. Mackerel stomach data is excluded from the model since they appeared in the ecosystem much later, or in 2006. The diet ratio in the model does not take into account spatial or temporal variation.

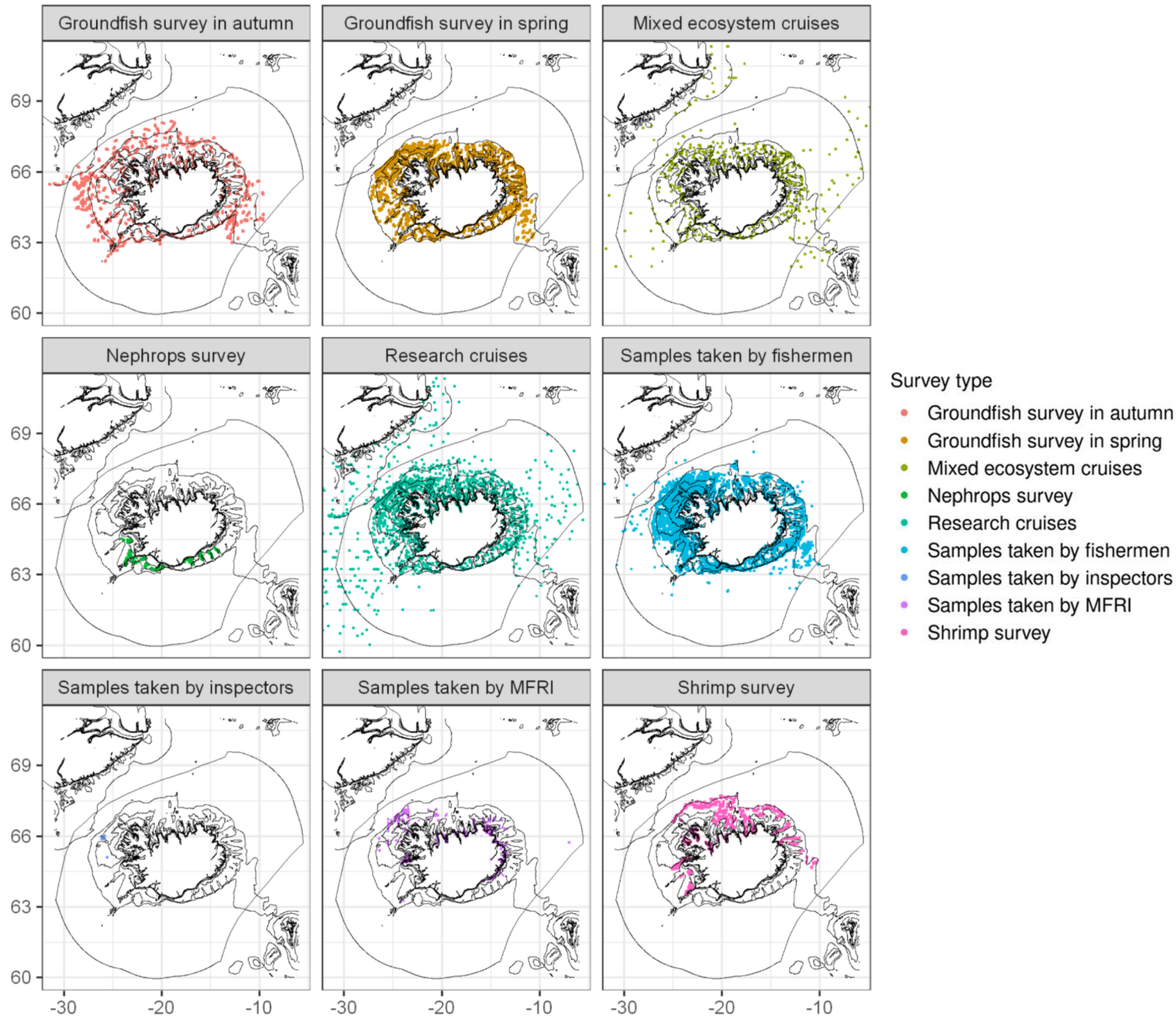

Figure 7. Various surveys from where fish stomach content has been analyzed. Colored points indicate sampling location.

Table 1. Number of stomachs with prey analyzed per functional groups according to the model.

Code	Functional groups	Number of stomachs analyzed
SB	Seabirds	2,359
PIN	Pinniped	1,230
WMW	Minke whale	20,423
WHB	Baleen whale	4,024
WHT	Tooth whale	2,523
SSR	Skates	4,989
SSD	Small sharks	5,541
SSH	Large sharks	5
FCD	Cod	229,705
FHA	Haddock	69,916
FSA	Saithe	18,499
FRF	Redfish	9,013
FFF	Flatfish	5,795
GHL	Greenland halibut	14,206
FHE	Herring	1,136
FCA	Capelin	124
FMI	Blue whiting	928
FOC	Other codfish	6,926
FDC	Demersal commercial fish	3,691
FDF	Other demersal fish	1,770
FSD	Sand eel	4
FBP	Small pelagic fish	17

The Icelandic groundfish survey in the spring

The Icelandic Groundfish Survey (IGFS), or the spring survey, was initiated in spring 1985 by the Marine Research Institute (MRI, later MFRI), and the survey has been carried out annually in March since then. The survey gear and methods have been more or less unchanged over the study period. The IGFS covers the continental shelf of Iceland to depths of 500 m and has a relatively dense station net (approximately 550 stations). All fish species are identified, and length measured to the nearest cm. In addition, commercially important species are weighted, sexed and otolith sampled for age determination. Further description of the survey can be found in Jónsdóttir et al. (2023).

The Icelandic autumn groundfish survey

The Icelandic autumn groundfish survey (AGS) has been conducted in October since 1996 and covers larger area than the IGFS. It is conducted on the continental shelf and slopes and extends to depths down to 1,500 m. The number of stations has varied around 380, and thus the distance between stations is often greater than in IGFS. The objective is to gather fisheryindependent information on biology, distribution and biomass of demersal species at greater depths than the IGFS covers. As in IGFS, biological information is collected, such as length, weight, sex, stomach content and age. Further description on the autumn survey is found in Jakobsdóttir et al. 2023.

Shrimp surveys

In 1988, MFRI initiated the annual offshore shrimp survey (SMR) and the annual inshore shrimp survey (SMG). SMR was conducted annually in June-August from 1988 to 2018, but since 2018, the survey has been conducted biannually. The SMR covers the north and the northeast areas of the Icelandic continental shelf and slope, at depths ranging from 200-700 m and the purpose is to provide an index for the northern shrimp stock biomass and to inform fishery management. SMG covered nine inshore areas (Arnarfjörður, Ísafjarðardjúp, Húnaflói, Skagafjörður, Skjálfandi, Öxarfjörður, Snæfellsnes and areas around Eldey) from 1988-2018, but since then, only Ísafjörður and Arnarfjörður have been surveyed. All species are identified, and length measured, and additionally cod, haddock, withing and Greenland halibut are aged, sexed and the stomach content analyzed. Further description of the two surveys is found in Jónsdóttir (2022).

Nephrops survey

The Nephrops survey was initiated in 1973 to measure the stock size and to provide fisheries advice for Norway lobster in Icelandic waters. The survey was conducted annually in May/June but due to poor state of the stock in 2016, the survey changed from trawling to burrow counting from images. From 2008-2016, stomach samples from cod and haddock were collected during surveys to estimate predation on Norway lobster (Jónsdóttir and Jónasson 2018).

Acoustic surveys

Acoustical measurements by the MFRI on the Icelandic summer-spawning herring have been conducted annually in March and October since 1973 on the feeding grounds of adult herring. Additionally, measurements on the juvenile part of the stock began in 1980 on rearing grounds in fjords in the west and north. The area surveyed each year varies spatially but is considered to cover the whole stock each year as the area surveyed is determined with information regarding the distribution of the fisheries. Results from the surveys are used to calculate biomass indices and to give advice.

In 1978, the MFRI initiated acoustic surveys to monitor and measure the stock size of capelin. The surveys are conducted annually in fall and winter, and the results are used for capelin fisheries advice. Biological sampling is conducted during the surveys but in the period, stomach content from 124 capelin has been analyzed.

Seabirds, pinniped and whale monitoring

A long-term project spanning from 1984 to 2009 conducted by Arnþór Garðarsson, a professor at the University of Iceland, involved a thorough assessment of seabird breeding populations. These assessments involved counts at specific locations with five-year intervals (Garðarsson et al. 2019). In 2006, the Northeast Iceland Nature Conservation Center took over the execution of the fixed site counts and expanded the number of sites and increased the frequency to annual counts in collaboration with other nature conservation centers (www.nna.is) The Icelandic Institute of Natural history carried out the third comprehensive assessment of seabird breeding populations from 2021-2022 (www.ni.is). Seabird diet was a part of the forementioned Multi-species Research Program (Fjölstofnarannsóknir 1997). During the increased sampling effort, diet of six seabird species was examined in the summer of 1994 and 1995 in five areas around Iceland (south, west, east, northwest and northeast). A total of 1481 stomachs were collected, and the stomach content analyzed (Lillendahl and Sólmundsson 1997). Additionally, stomachs from European shag and great cormorant were collected in 1996-2000 (Lillendahl et al. 2004). No regular monitoring is of seabird diet.

Harbour seal population monitoring in Iceland began in 1980 and has been conducted approximately every three years since 1985 in late July-September (Granquist 2022). Population monitoring of grey seals began two years later where population size estimates were based on pup population (Hauksson 2007, Granquist and Hauksson 2019), but in both cases, the monitoring involved counting seals from air around Iceland. Diet of pinnipeds was analyzed in 1992-1994 (Hauksson and Bogason 1997) where approximately 2000 stomachs of seals were collected. No regular monitoring is of seal diet in Iceland.

The distribution and abundance of cetaceans in the Central North Atlantic (CNA) have been monitored regularly with the North Atlantic Sightings Surveys (NASS and TNASS) since 1987 and include six large scale surveys (1987, 1989, 1995,2001, 2007, 2005) (Pike et al. 2019a). The CNA is covered by Icelandic, Faroese, and Norwegian research effort and since 1986, seven aerial surveys covering the coastal waters of Iceland have been conducted (Pike et al. 2019b). No regular monitoring is of whale diet, but smaller projects have been undertaken by the MFRI where stomachs have been collected systematically, e.g. in 1976-1988 when 247 stomachs from caught sei whales were analyzed (Sigurjónsson and Vikingsson 1997) and in 2003-2007 when 200 stomachs of minke whale were analyzed (Vikingsson et al. 2011)). Stomach content of landed fin whales has also been analyzed by the MFRI but infrequently (Vikingsson 1997, Garcia-Vernet et al. 2021).

Other sampling

In addition to collecting fish stomach content during the above surveys, samples have been collected by inspectors, by fishermen and by the MFRI throughout the years. Projects have also been undertaken where stomachs, mainly from cod and saithe, have been collected throughout the year by fishermen (between the year 2001-2017). This was done to get a year around estimate of diet consumption of these species. All available data on stomach content was used in this analysis.

Determination of functional groups

The Icelandic Ecopath model incorporates a total of 332 species that have been observed in Icelandic waters during various surveys (including those found in stomachs). Additionally, the model includes 108 different class/family/phylum (serving as prey), which have not been identified at the species level.

Species were allocated to 37 functional groups according to their taxonomic rank and/or their ecological and behavioral similarities (Table 3). Other functional groups are detritus, discards and seven gear groups (bottom trawls, demersal seine, longline, gillnet, harpoon, pelagic gear, and other gear).

Cod, haddock and saithe were split into multi-stanza groups (juveniles and adults) to capture ontogenetic diet shifts and/or different exploitation patterns. Cod and saithe were split at age 3 (juveniles age 0-3, adults age 4+) and haddock at age 2 (juveniles age 0-2, adults age 3+). The model requires estimates of diet, predation, catches and discards for each stanza, as well as the total mortality, the von Bertalanffy K parameter, and the estimate of weight at maturity as a fraction of weight at infinity (W_{mat}/W_{∞}). W_{mat}/W_{∞} determines how productive the juvenile stanza are at low spawning stock biomass and has a direct influence on the recovery and depletion rates in Ecosim.

Table 2. Structure of the functional groups in the Icelandic Ecopath model

	Code	Functional groups	Main species
1	SB	Seabirds	**Razorbill** (*Alca torda*), **great cormorant** (*Phalacrocorax carbo*) **northern fulmar** (*Fulmarus glacialis*), **common murre** (*Uria aalge*), **Atlantic puffin** (*Fratercula arctica),* **black-legged kittiwake** (*Rissa tridactyla*), **thick-billed murre** (*Uria lomvia*), **European shag** (*Phalacrocorax aristotelis*)
2	PIN	Pinniped	**Harbour seal** (*Phoca vitulina*), **grey seal** (*Halichoerus grypus*)
3	WMW	Minke whale	**Common minke whale** (*Balaenopterus acutorostrata*)
4	WHB	Baleen whale	**Sei whale** (*Balaenoptera borealis*), **blue whale** (*Balaenoptera musculus*), **fin whale** (*Balaenoptera physalus*), **humpback whale** (*Megaptera novaeangliae*)
5	WHT	Tooth whale	**Harbour porpoise** (*Phocoena phocoena*), **northern bottlenose whale** (*Hyperoodon ampullatus*)
6	WTO	Other tooth whale	**White-beaked dolphin** (*Lagenorhynchus albirostris*), **long-finned pilot whale** (*Globicephala melas*), **killer whale** (*Orcinus orca*), **Atlantic white-sided dolphin** (*Lagenorhynchus acutus*)
7	SSR	Skates	**Thorny skate** (*Amblyraja radiata*), **spinetail ray** (*Bathyraja spinicauda*), **round ray** (*Rajella fyllae*), **Arctic skate** (*Amblyraja hyperborea*), **common skate** (*dipturus batis*), **sailray** (*Rajella lintea*), ***deepwater ray*** (*Rajella bathyphila*)
8	SSD	Small sharks	**Iceland catshark** (*Apristurus laurussonii*), **black dogfish** (*Centroscyllium fabricii*), **Portuguese dogfish** (*Centroscymnus coelolepis*), **longnose velvet dogfish** (*Centroscymnus crepidater*), **dogfish** (*Squalus acanthias*), **greater lantern shark** (*Etmopterus princeps*), **velvet belly** (*Etmopterus spinax*), **mouse catshark** (*Galeus murinus*), **leafscale gulper shark** (*Centrophorus squamosus*), **pale catshark** (*Apristurus aphyodes*).
9	SSH	Large sharks	**Basking shark** (Cetorhinus maximus), **porbeagle** (*Lamna nasus*), **Greenland shark** (*Somniosus microcephalus*)
10	FCD	Cod 0-3	**Atlantic cod** (*Gadus morhua*) age 0-3
11		Cod 4+	**Atlantic cod** (*Gadus morhua*) age 4+
12	FHA	Haddock 0-2	**Haddock** (*Melanogrammus aeglefinus*) age 0-2
13		Haddock 2+	**Haddock** (*Melanogrammus aeglefinus*) age 3+
14	FSA	Saithe 0-3	**Saithe** (*Pollachius virens*) age 0-3
15		Saithe 4+	**Saithe** (*Pollachius virens*) age 4+
16	FRF	Redfish	**Golden redfish** (*Sebastes norvegicus*), **demersal beaked redfish** (*Sebastes mentella*), **Norway haddock** (*Sebastes viviparus*)
17	FFF	Flatfish	**Atlantic halibut** (*Hippoglossus hippoglossus*), **witch** (*Glyptocephalus cynoglossus),* **megrim** (*Lepidorhombus whiffiagonis*), **plaice** (*Pleuronectes platessa*), **dab** (*Limanda limanda*), **long rough dab** (*Hippoglossoides platessoides*), **lemon sole (***Microstomus kitt*).
18	GHL	Greenland halibut	**Greenland halibut** (*Reinhardtius hippoglossoides*)
19	FHE	Herring	**Herring** (*Clupea harangus*)
20	FCA	Capelin	**Capelin** (*Mallotus villosus*)
21	FMI	Blue whiting	**Blue whiting** (*Micromesistius poutassou*)
22	FOC	Other codfish	**Whiting** (*Merlangius merlangus*), **ling** (*Molva molva*), **blue ling** (*Molva dypterygia*), **tusk** (*Brosme brosme*)
23	FDC	Demersal commercial	**Atlantic wolffish** (*Anarhichas lupus*), **spotted wolffish** (*Anarhichas minor*), **greater argentine** (*Argentina silus*), **lumpfish** (*Cyclopterus lumpus*), **monkfish** (*Lophius piscatorius*)

	Code	Functional groups	Main species
24	FDF	Other demersal fish	Eels, Eelpouts, rocklings, sculpins, bullheads (Table 34)
25	FSD	Sand eel	**Sand eel** (*Ammodytes tobianus*), **Raitt´s sand eel** (*Ammodytes marinus*), **greater sand eel** (*Hyperoplus lanceolatus*)
26	FBP	Small pelagic fish	**Pearlside** (*Maurolicus muelleri*), **polar cod** (*Boreogadus saida*), **glacier lanternfish** (*Benthosema glaciale*), **whitespotted lanternfish** (*Diaphus rafinesquii*), **spotted lanternfish** (*Myctophum punctatum*), **pilchard** (*Sardina pilchardus*), **mirror lanternfish** (*Lampadena speculigera*), **jewel lanternfish** (*Lampanyctus inticarius*), **rakery beaconlamp** (*Lampanyctus macdonaldi*), **Arctic telescope** (*Protomyctophum arcticum*), **diamondcheek lanternfish** (*Lampanyctus intricarius*)
27	LOB	Norway lobster	**Norway lobster** (*Nephrops norvegicus*)
28	PWN	Shrimp	**Northern shrimp** (*Pandalus borealis*) and other shrimp in Icelandic waters (see appendix Table 38)
29	FEP	Epifauna	**Mollusca** (Gastropoda), **Arthropoda** (Malacostraca, Hexanauplia), **Bryozoa**, **Cnidaria** (Anthozoa), **Echinodermata** (Echinoidea, Ophiuroidea, Holothuroidea, Asteroidea), **Chordata** (Ascidiacea) (see appendix Table 35
30	FIN	Infauna	**Mollusca** (Bivalvia), **Annelida** (Polychaeta), **Cephalorycha** (Priapulida), **Nematoda**, **Platyhelminthes**, **Nemertea** (see appendix Table 36)
31	FLC	Lobsters and crabs	**Arthropoda** (Malacostraca) (see appendix Table 37)
32	CEP	Cephalopod	**Bobtail squid** (*Rossia glaucopis*), **Boreoatlantic armhook squid** (*Gonatus fabricii*), **Atlantic bobtail** (*Sepiola atlantica*), **European flying squid** (*Todarodes sagittatus*)
33	FKR	Krill	**Northern krill** (*Meganyctiphanes norvegica*), **krill** (*Thysanoessa inermis*, *Thysanoessa longicaudata*, *Thysanoessa raschii*, **Mysidae** (*Boreomysis nobilis, Boreomysis arctica, Erythrops abyssorum, Erythrops erythropthalma, Erythrops serrata, Mysideis insignis, Mysis mixta, Mysis oculate, Pseudomma truncatum)*
34	ZG	Gelatinous zooplankton	**Jellyfish** *(Aurelia aurita)*. Phylum: Sagitta, Cnidaria, Ctenophora, Chaetognatha
35	ZL	Large zooplankton	Zooplankton species > 2mm in length (see appendix Table 39)
36	ZS	Small zooplankton	Zooplankton species < 2mm in length (see appendix Table *39*)
37	Phytoplankton		
38	Detritus		

Functional group parameters

Cetaceans are important top predators in Icelandic waters. A total of 23 species have been recorded on Icelandic grounds (Hersteinsson 2004) but 12–14 species inhabit the area regularly. In the Icelandic Ecopath model, the cetacean group is split into four groups, i.e. baleen whales, minke whale, tooth whales and other tooth whale (Delphinidae) (see species in Table 2).

Baleen whales

Five species of baleen whales inhabit the Icelandic ecoregion i.e., the common minke whale (Balaenoptera acutorostrata), the sei whale (*Balaenoptera borealis*), blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*) and humpback whale (*Megaptera novaeangliae*). Population estimates are based on observations from the NASS surveys in 1995 to represent biomass in 1996.

The common minke whale is a widespread species and seasonally abundant in the North Atlantic Ocean. In Icelandic waters, the common minke whale is the most abundant mammalian top predator, mainly on the continental shelf and is present from March-November (Sigurjónsson and Vikingsson 1997). The population inhabiting Icelandic waters was estimated to be around 20,000 animals in 1996 (abundance in 1996 with 95% CI (14,077-28,930)) (Pike et al. 2009b). As they are only present in the ecosystem for approximately eight months, biomass in the model is set to 13,500 animals. To estimate biomass in tonnes, the mean weight of minke whale (5,251 kg, Lockyer 1976) is multiplied with number of animals or 70,889 tonnes. In the beginning of last century and up until 1950, common minke whale was hunted and consumed domestically, averaging about 50 animals annually (Sigurjónsson 1989). The export market gradually increased and from 1974–1986, around 200 minke whales were hunted annually. In 1986, whaling of minke whales was discontinued in conformity with the International Whaling Commission moratorium on commercial whaling but resumed in 2003 under Scientific Permit and in 2006, commercial whaling continued. Landing in the model (1996) are zero. Minke whale diet has been well studied in Icelandic waters (Sigurjónsson et al. 2000, Vikingsson et al. 2011, Vikingsson et al. 2014) and data used in the model is from Sigurjónsson et al. (2000).

Table 3. Diet proportion of minke whales in the Icelandic Ecopath model. Data is from Skern-Mauritzen (2022).

Code	Functional group	Diet proportion
FCD.adult	Adult cod	< 0.01
FCA	Capelin	0.25
FHE	Herring	< 0.01
FSD	Sand eel	0.36
FKR	Krill	0.38

Sei whale is found in all oceans, both on shelves and in offshore waters (Sigurjónsson 1995) and in summer, sei whales migrate to higher/colder latitudes to their feeding grounds (Horwood 2009). In Icelandic waters, sei whales are spotted in late summer but migration patterns are irregular. Sei whale distribution has been found to be driven by depth, sea surface temperatures in spring and sea surface height anomaly (Houghton et al. 2019). The population in 1996 was estimated to be around 10,000 animals. As they only appear in late summer and leave in October, the biomass in the model is set to 2,500 animals times mean weight of sei whale (19,919 kg, Vikingsson et al. 1988), or 49,798 tonnes. Substantial whaling in the mid-last century led to a depletion of the species and since 1970, sei whales are listed as endangered under the Endangered Species Act. (Perry 1999). In 1982, the International Whaling Commission voted to ban commercial whaling in Iceland which took effect in 1986. However, whaling for scientific purposes continued until 1989. Diet data is taken from Sigurjónsson and Vikingsson (1997) where 247 stomachs from sei whale caught in 1976–1988 were analyzed. 98% had eaten planktonic crustaceans, 1% sand eels, 0.5% capelin and 0.5% lumpfish (Sigurjónsson and Vikingsson 1997)

Blue whales are distributed from the Northern Hemisphere south into the Mediterranean. They are very rare or absent in the Northeast Atlantic (Pike et al. 2009a). In Icelandic waters, blue whales are most commonly sighted off western Iceland, and to a lesser extent northeast of Iceland. Blue whales are only seen in summer, usually from May–October, but in winter they migrate southward. The population inhabiting Icelandic waters was estimated to be around 1,200 animals in 1996. As they are only present in the ecosystem for five months, biomass in the model is set to 500 animals. To estimate biomass in tonnes, mean weight of blue whale (69,235 kg, Lockyer 1976) is multiplied with number of animals or 34,618 tonnes. Blue whales are listed as endangered under the Endangered Species Act and protected under the Marine Mammal Protection Act and have not been targeted in Iceland since 1959 when six blue whales were landed. Blue whales feed exclusively on euphausiids (Hjort 1929).

Fin whales are found in all oceans but are most common in the cold temperate and temperate belt. Fin whales are migratory and exhibit seasonal north-south movements as they feed in higher latitudes in summer and breed in lower latitudes in winter. In Icelandic waters, they usually appear in May and leave in August (Sigurjónsson 1995) and are most abundant on the shelf edge west and southwest of Iceland. The population in 1996 was estimated to be around 15,000 individuals and as they inhabit Icelandic waters for approximately four months, biomass in the model is estimated to be 5,000 individual's times mean weight of fin whales (42,279 kg, Vikingsson 1988) or 211,395 tonnes. Fin whales are considered endangered under the Endangered Species Act since and depleted under the Marine Mammal Protection Act since 1973. However, commercial whaling did not end until 1989. From 1948–85 the average annual catch was 234 animals. From 1986 and 1989, 292 fin whales were sampled for scientific research. From 1990–2006, no fin whales were caught but fishing resumed in 2006 when the government issued licenses for sustainable commercial whaling. Data on fin whale diet was collected by MFRI in the period from 1967-2015. Fin whales feed exclusively on euphausiids (*Meganictiphanes norvegica*).

Humpback whales are found in oceans around the world. They feed in colder latitudes and migrate long distances to tropical or subtropical waters to breed. They can be found all around Iceland, both inshore and offshore from May until September (Sigurjónsson 1995) but a small number of animals may remain in high latitude areas throughout the year (In Icelandic waters and on Norwegian summer feeding grounds) (Pike et al. 2005). Abundance estimates in 1995 were approximately 10,500 animals (Pike et al. 2009a). As they inhabit Icelandic waters for five months of the year, biomass is estimated as 4,375 individual's times mean weight of humpback whales (31,782 kg, Lockyer 1976), or 139,046 tonnes. The International Whaling Commission established a moratorium in 1955. The MFRI collected stomach samples from humpback whales in April 2002 and they were found to feed exclusively on capelin (*Mallotus villosus*) (MFRI database). Other research suggests that humpback whales also feed on euphausiids and Sigurjónsson (1997) concluded that the fish crustacean ratio was 52:48, respectively. This ratio is used in the model (Table 4). The diet was weighted with biomass of each species in the group.

Table 4. The diet proportion of baleen whales (WHB) in the Ecopath model. Data is from the MFRI and from Skern-Mauritzen (2022) and Sigurjónsson and Vikingsson (1997).

Code	Functional group	Diet proportion				
		Sei whale	Blue whale	Fin whale	Humpback whale	Weighted proportion
FCA	Capelin	0.005	-	-	0.52	0.17
FDC	Demersal commercial fish	0.005	-	-	-	<0.01
FSD	Sand eel	0.01	-	-	-	<0.01
FKR	Krill	-	1	1	0.48	0.71
ZL	Zooplankton large	0.98	-	-	-	0.11

P/B values for baleen whales are based on expert opinion of total mortality estimates obtained from scientists at the Institute of Marine Research, Bergen. These values were used in the Ecopath model for the Norwegian Sea and the Barents Sea (Dommasnes 2001), or 0.03 $year^{-1}$.

The consumption rate (DR or daily rate of fish consumed in g) was estimated from Innes et al. (1987) as:

$$\mathrm{DR} = 0.1 * W^{0.8} \tag{4}$$

where *W* is biomass weighted mean body weight of the species in kg. Q/B is an annual measure and was therefore derived as DR/W*365. The Q/B ratios were estimated 6.58 $year^{-1}$ for minke whale and 4.41 $year^{-1}$ for other baleen whales.

Toothed whales

Harbour porpoise (*Phocoena phocoena*) is distributed throughout most of the Icelandic continental shelf area (Pike et al. 2019) and the distribution largely overlaps with the operational area of the Icelandic coastal fisheries. Abundance estimates in 1995 were 5,156 animals (Pike et al. 2009a) and biomass is is calculated as number of animals times mean weight (39 kg, MFRI, unpubl. data) or 201 tonnes. The harbour porpoise is not targeted by the Icelandic fleet but due to its distributional patters, harbour porpoise is common as bycatch in the cod and lumpsucker gillnet fisheries. The MFRI estimated mean annual bycatch to be 528 animals in 2014-2018 (MFRI 2019). The main prey of harbour porpoise is capelin (57%), sand eels (21%), cephalopods (10%), redfish (3.5%), whiting (2%), haddock (1%) and Norway pout (1%) (Vikingsson 2003).

Northern bottlenose whale (*Hyperoodon ampullatus*) is found all over the North Atlantic Ocean and around Iceland, they are occasionally sighted in deeper waters off southeast and eastern Iceland in warmer months. Abundance in 1995 was estimated to be 27,879 animals (Pike et al. 2003), and since the northern bottlenose whale inhabits Icelandic waters for approximately six months per year, the biomass is estimated to be mean weight of the animal (5,418 kg, Benjaminsen and Christensen 1979) times number animals or, 75,524 tonnes.

No diet data has been collected from northern bottlenose whales in Iceland but according to Skern-Mauritzen (2022), they feed solely on cephalopods.

Six dolphin species of the Delphinidae family are found on Icelandic fishing grounds and the most common is the **white-beaked dolphin** (*Lagenorhynchus albirostris*). The largest dolphin species is the **killer whale** *(Orchinus orca*) which is common in shallower waters. On deeper grounds, the **long-finned pilot whale** (*Globicephala melas*) and the **Atlantic white-sided dolphin** (*Lagenorhynchus acutus*) are more common and move in larger groups. Some less common dolphin species on Icelandic fishing grounds are **short-beaked common dolphin** (*Delphinus delphis*) and the **striped dolphin** (*Stenella coeruleoalba*). No biomass estimates are available for the last two.

Killer whales are found in all oceans but are most abundant in colder waters. In Iceland they are most frequently sighted on seasonal herring grounds in the East fjords as well as on the south and west coast. They can be observed all year around, but they are not targeted by fishermen. Population estimates for killer whales is based on counting in 1987-1989 where it was estimated to be 4,736 animals (Øien 1993). Biomass is estimated as mean weight (2,350 kg, Christensen 1982) times 4,736 or 11,129 tonnes. Diet proportions in the model is based on Skern-Mauritzen (2022) where they feed exclusively on herring.

Long-finned pilot whale is widely distributed in the North Atlantic and occurs offshore as well as in coastal areas (Buckland et al. 1993). In Iceland, they are observed in the south and west during warmer months. Abundance estimates are from 1989 (80,867 animals) (Butterworth 1996). As they inhabit Icelandic waters only in summer months, biomass is estimated to be 26,955 times mean weight (789 kg, Bloch and Lockyer 1989), or 21,268 tonnes. Long-finned pilot whales feed mainly on cephalopods (91%). Other diet is mainly blue withing and crustaceans (Skern-Mauritzen 2022). Pilot whales are not targeted by the Icelandic fleet.

Atlantic white sided dolphin and the **white beaked dolphin** are distributed through the North Atlantic Ocean and are observed in Icelandic waters all year round. Biomass estimates in the model for white sided dolphin in 1996 is 37,622 individual's times mean weight (190 kg, Watson 1981) or 7,148 tonnes. For the white beaked dolphin, biomass is estimated as 12,341 individuals (in 1996) times mean weight (225 kg, MFRI, unpubl. data) or a total of 2,777 tonnes. Consumption in the model is based on Skern-Mauritzen (2022).

Few other species of toothed whales and dolphins have been sighted around Iceland. Narwhale (*Monodon monoceros*), white whale (*Delphinapterus leucas*), bowhead whale (*Balaena mysticetus*) and sperm whales (*Physeter macrocephalus*) sightings in Iceland are rare, and they are only occasionally sighted in the far north. Sowersby´s beaked whale (*Mesoplodon bidens*) and Cuvier´s beaked whale (*Ziphius cavirostris*) has been sighted in waters deep south of Iceland, but sightings are also rare.

Table 5. Diet proportion of toothed whale group (WHT) in the Icelandic model taken from the MFRI data base and from Skern-Mauritzen (2022) and Vikingsson et al. (1998).

Code	Functional group	Diet proportion of toothed whales (WHT)		
		Harbour porpoise	Northern bottlenose	Weighted
FRF	Redfish	0.034	-	<0.001
FSD	Sand eel	0.208	-	<0.001
FCA	Capelin	0.572	-	0.0016
FCD	Commercial demersal	0.038	-	<0.001
FHA.adult	Adult haddock	0.011	-	<0.001
CEP	Cephalopods	0.101	1	0.9976
FBP	Small pelagic fish	0.011	-	<0.001

Table 6. Diet of the other toothed whale (WTO) in the Icelandic model taken from the MFRI data base and from Skern-Maurizen (2022).

Code	Functional group	Diet proportion of other toothed whale (WTO)			Weighted proportion
		Dolphins	Killer whale	Pilot whale	
FCA	Capelin	0.2	-	-	0.015
FHE	Herring	0.1	1	-	0.357
FMI	Migratory fish	-	-	0.06	0.034
FOC	Other codfish	0.005	-	-	0.004
FCD	Adult cod	0.03	-	-	0.022
FHA	Adult haddock	0.061	-	-	0.004
FSA	Adult saith	0.203	-	-	0.015
CEP	Cephalopods	0.11	-	0.91	0.532
FBP	Small pelagic fish	0.23	-	-	0.017
PWN	Shrimp	-	-	0.03	0.017

Pinnipeds

Six species of seals have been observed in Icelandic waters and the most common is the **harbour seal** (*Phoca vitulina*) and **grey seal** (*Halichoerus grypus*), which also breed in Iceland. The four other less common visitors are harp seal (*Phoca groenlandica*), bearded seal (*Erignathus barbatus*), hooded seal (*Cystophora cristata*) and ringed seal (*Phoca hispida*). Only harbour seals and grey seals are included in the model.

The harbour seal (*Phoca vitulina*) is the most common seal around Iceland, mainly on the north-west coast but they are distributed through the Northern Hemisphere. The harbour seal is not known to migrate long distances and older animals come back year after year to their own birth colonies. The grey seal is distributed in the temperate areas of the North-Atlantic and occur throughout the year around Iceland. The highest abundance is observed on the west- and northwest shores and on the southeast coast, where they breed.

Population estimates of the Icelandic harbour seal and the grey seal have been conducted regularly by separate aerial surveys during the pupping period since 1980 and 1982, respectively (Hauksson 2007, Hauksson 2010). In the beginning of the time series, the harbour seal population was estimated to be 33,327 animals (Hauksson 2010) and grey seal 9,200 animals. The harbour seal population has decreased since and in 2006, the population was estimated to be around 12,000 animals. The grey seal population increased from 1982 until 1990 but decreased substantially thereafter. The last aerial survey was in 2012 where the lowest abundance was observed in the period, or 4,200 animals. Population estimates for the date of the model is estimated to be the same as in 1995, or 13,578 animals of harbour seal and 7,758 of grey seal. The mean weight of adult harbour seals is estimated to be 110 kg (males) and 85 kg (females) (Burns 2009). For grey seals, the mean weight of adults is 233 kg (male) and 155 kg (females). Here, the population is considered to have an equal sex ratio and since the surveys have been conducted during the pupping period for both species, the population size estimates are based on pup production. The average weight of harbour seal pups of 23.6 kg (Cottrell et al. 2002), and grey seal pups 38.85 kg (Bonner 1981). Biomass is estimated as the mean weight multiplied with the number of individuals (*Harbour seal*: 4,524*110 kg + 4,524*85 kg + 4,524*23.6 kg = 989 tonnes; *Grey seal*: 2,586*233 kg +2,586*155 kg + 2586*38.85 kg = 1,104 tonnes. Total biomass: 989+1104 = 2,093 tonnes).

In 2006, when the harbour seal population was estimated to be the lowest since the beginning of monitoring and the Icelandic government introduced a management objective, stating that the harbour seal population should not decrease below 12,000 animals. The same was done for the grey seal in 2005, with 4,100 animals as a minimum count.

In 2019, the MFRI estimated the bycatch of harbour and grey seal in the cod and lumpsucker gillnet fisheries to be 9-20% and 8-25%, respectively (MFRI 2019). The percentage is considered to be at the lower end, as population estimates have great variance (Sigurðsson, MFRI. pers. comm). The landings (bycatch) used in the model is thus, 8.5% of biomass.

In 1991, the Marine Research Institute commenced a Multi-species Research program, with the aim to obtain knowledge and understanding of the ecosystem of Icelandic waters. A part of this program was to investigate food and feeding habits of seals and their role as top-predators in Icelandic waters. During 1992-1993, seal stomachs were sampled around Iceland and the diet analyzed. A total of 1,059 samples were collected from grey seal (737 contained food) and 799 samples from harbour seal (493 with food). The total biomass of prey in a stomach was estimated by summing the estimated wet weight of all prey items (aged otoliths were assigned to the species and wet weight assumed).

Table 7. Pinniped diet in the Icelandic Ecopath model, taken from Hauksson and Bogason 1997.

Code	Functional group	Diet proportion		Weighted proportion
		Harbour seal	Grey seal	
FCD.adult	Adult cod	0.48	0.24	0.35
FDC	Demersal commercial	0.07	0.22	0.15
FCA	Capelin	0.04	0.004	0.02
FFF	Flatfish	0.06	0.09	0.08
FHE	Herring	0.07	0.01	0.04
FSA.adult	Adult saithe	0.08	0.11	0.10
FHA.adult	Adult haddock	-	0.02	0.01
FDF	Other demersal fish	0.02	0.03	0.03
FOC	Other codfish	0.02	-	0.01
FRF	Redfish	0.08	0.003	0.04
FSD	Sand eel	0.08	0.23	0.16

A biomass weighted average of P/B is 0.042, or 4%. The Q/B was estimated using equation 4. Q/B is an annual measure and was therefore derived as **DR/W*365**. The Q/B ratios were estimated 15.48 year^{-1} for harbour seals and 13.54 year^{-1} for grey seals using mean daily rations. A biomass weighted average of Q/B was used, or 14.45 year^{-1}.

Seabirds

In Iceland, the most common seabird species are razorbill (*Alca torda*), great cormorant (*Phalacrocorax carbo*) northern fulmar (*Fulmarus glacialis*), common murre (*Uria aalge*), Atlantic puffin (*Fratercula arctica),* black-legged kittiwake (*Rissa tridactyla*), thick-billed murre (*Uria lomvia*) and European shag (*Phalacrocorax aristotelis*). All species, except for the great cormorant and the European shag migrate after the breeding season and are most abundant in spring until fall. They breed all around Iceland, mainly in cliffs and on islets in fjords.

Biomass is estimated for each species by multiplying the total population number estimated by the Working Group on Seabird Ecology (2002) with mean weight of the species (from www.fuglavefur.is). For migrating species, biomass was estimated for the time they inhabit Icelandic grounds. The total biomass of seabirds in the model is 4,612 tonnes. Catch is based on numbers from the Environmental agency of Iceland in 1998. Seabirds are also caught as bycatch in the gillnet fishery (Sigurðsson 2023).

Table 8. Estimated number of seabirds in Icelandic waters, their mean weight in kg, biomass in kg, biomass ratio and months inhabiting Icelandic grounds.

Species	**Total number**	**Mean weight (kg)**	**Biomass (kg)**	**Biomass ratio**	**Months in Iceland**
Northern fulmar	3,000,000	0.8	1,600,000	0.3468	8
Great cormorant	6,300	3	18,900	0.0040	12
European shag	13,200	2	26,400	0.0057	12
Black-legged kittiwake	1,262,000	0.4	231,367	0.0501	5.5
Common murre	1,980,000	1	990,000	0.2146	6
Thick billed murre	1,160,000	1	386,667	0.0838	4
Razorbill	760,000	0.6	209,000	0.0453	5.5
Atlantic puffin	5,520,000	0.5	1,150,000	0.2493	5
Total	13,701,500		4,612,334		

Q/B was estimated by using equation 4 and as Q/B is an annual measure and was derived as D**R/W*365,** where *W* is the mean body weight of species (g). Here, the weighted biomass average mean weight was used (0.771 kg), resulting in Q/B of or 38.44 year^{-1}. The DR is estimated to be 0.1 as in the North-Sea Ecopath model (Dommasnes 2001).

All available diet data from the eight included seabird species collected by the MFRI was used in the model. To estimate weight ratio of diet, species count in stomachs was multiplied with individual mean weight. The weight ratio was weighted with the biomass of seabird species.

Table 9. Diet ratio of seabirds in the Icelandic EwE model. Ratio is biomass weighted.

Code	**Functional group**	**Diet proportion of seabirds**
FSD	Sand eel	0.44
FCA	Capelin	0.20
FKR	Krill	0.08
CEP	Cephalopods	0.06
FDF	Other demersal fish	0.05
ZL	Large zooplankton	0.04
FMI	Migratory fish	0.03
FSA.juv	Juvenile saithe	0.01
FBP	Small pelagic fish	0.01
FCD.juv	Juvenile cod	0.01
Other *		0.07

*FRF, FDC, FRF, FDC, FFF, FHE, FIN, PWN, FHA.juv, FEP, ZG, FLC, LOB, FOC, ZS

Fish

A total of 20 out of 37 functional groups presented in the Icelandic EwE model belong to fish and includes roughly 120 species. Empirical equations and data sources which apply to the majority of fish functional groups are presented below.

Length weight relationships

For parameter calculations, (such as consumption/biomass ratios (Q/B), natural mortality estimations etc., see below), length (cm) and weight parameters (kg) for all fish groups were needed. Mean weights at length were estimated using equation 5 (Ricker 1973, Ricker 1975)

$$W = \alpha \cdot L^{b} \quad (5)$$

where *W* is weight in kg, L is length in cm and a (intercept) and *b* (slope) are conversion factors estimated using linear regression through natural logarithmic transformation (ln*W*=ln *a* + *b* · ln *L*). For multi-species groups, a biomass-weighted average was used in P/B and Q/B estimations.

Production/Biomass

The production/biomass (P/B) ratio is equivalent to the instantaneous rate of total mortality (Z) (Allen 1971).

$$PB = Z \quad and \quad Z = M + F \quad (6)$$

where *Z* is instantaneous total mortality, *M* is natural mortality and *F* is fishing mortality. P/B ratios for all groups are found in Table 11.

Fishing mortality

Fishing mortality is from stock assessment for assessed groups. For unassessed groups fishing mortality is estimated as

$$Fishing\ mortality = catch + discard/biomass \quad (7)$$

Where biomass is missing, fishing mortality is based on “guestimate”.

Natural mortality

Natural mortality (M) for fish was estimated using Pauly´s (1980) empirical equations:

$logM = -0.2107 - 0.0824 * logW_{\infty} + 0.675logK + 0.4687logT$, or (8)

$$logM = -0.0066 - 0.279 * logL_{\infty} + 0.643logK + 0.4634logT \quad (9)$$

Where W_∞ and L_∞ are the wet weight (g) and total length (cm) at infinity for the population (the species asymptote or maximum weight), K is the curvature parameter of the von Bertalanffy growth function and *T* is the mean annual temperature (°C).

Consumption/Biomass

Q/B values were calculated using the empirical model of Pauly et al. (1990) and Christensen and Pauly (1992):

$$logQB = 6.37 - 1.5045\,T' - 0.168 logW_\infty + 1.399Pf + 0.2765Hd \qquad (10)$$

Where T´ is the mean annual temperature (Kelvin), Pf characterizes feeding behavior (apex predators, pelagic predators, and zooplankton feeders = 1; other feeding types = 0) and Hd characterizes food type (herbivores = 1; predators = 0).

Landings and discard

Fish landings on Icelandic fishing grounds are given by the Icelandic Directorate of Fisheries. Catch of seabirds are from The Environment Agency of Iceland and landings/bycatch and discard data are obtained from the Directorate of Fisheries.

Twelve gear types (plus one various) are included in the model. They are assigned to seven fleets for implementation into Ecopath (Table 10). Total annual landings by pelagic gear and bottom trawls account for the majority of landings over the period. Total annual landings from pelagic gear fluctuated throughout the period, peaking in 1997 and 2002, when over 1.4 million tonnes were landed. Total annual landings by bottom trawls were highest in 1988 but have been relatively stable since 2000. Total annual landings by longlines and demersal seiners have more than doubled in the time period while total annual landings by gillnets have decreased substantially (Figure 4).

According to Icelandic law, discarding catch at sea of species with commercial value is illegal in Icelandic waters. Since 2001, the MFRI has monitored length-based discards of cod and haddock where length distributions at sea are compared to length distributions of landed fish. Combined discards of all gears since 2001, has fluctuated between 0.08% - 4.75%. In 2001, discard was estimated to be 1.03% (Sigurðsson 2020) and this percentage was used in the model for all gears, except harpoon.

Table 10. Structure of fleets in the Icelandic Ecopath model, recorded landings in 1996 and allocation of gear types.

Ecopath fleet	Landings (tonnes)	Gears included
Bottom trawls	374,410	Bottom trawl, nephrops trawl, shrimp trawl, dredge
Longline	71,392	Longline
Pelagic gear	1,317,702	Pelagic trawl, purse seine
Gillnets	57,897	Gillnet
Demersal seine	47,776	Demersal seine
Other	23,278	Hand line, trap, various
Harpoon	-	Harpoon

Biomass accumulation

When the biomass in the model is known at the beginning of the year and at the beginning of the next year, the biomass accumulation (BA) can be calculated as the difference between these biomasses (in this case, the biomass in 1996 and 1997) and that value divided with biomass in 1996 (BA/B). The default value is 0 (indicating no change in biomass during the modelled period), a negative value indicates a reduction in biomass over the period and a positive value indicates an increase. BA/B is a flow term, with a rate unit of tonnes year^{-1} and is calculated for all species with known biomass (from assessment).

Unassimilated consumption

Unassimilated consumption is an estimate of the percentage of consumed food that is not utilized for growth. In the model, the values are based on Winberg (1956) where the default value for carnivorous fish is 0.2 (20% of consumption is directed to the detritus) and 0.35 for herbivores.

Table 11. Parameter estimates for fish functional groups in 1996, including biomass of functional group, the proportion of species biomass in aggregated groups, total landings, the source of data, fishing mortality (F), natural mortality (M) and calculated production over biomass value (P/B). Blue values are “guestimates”.

Functional group	Biomass			Landings		F	M	P/B
	tonnes	FG prop	Source	tonnes	Source			
Atlantic cod	-	-						
· Juvenile	-			1820	-	-	0.3065	0.3175
· Adult	517623.8		MFRI stock assessment	180162	Directorate of Fisheries	0.3471	0.1444	0.4915
Haddock	-	-						
· Juvenile	-			588	-	0.0158	0.4179	0.4363
· Adult	108526.51		MFRI stock assessment	58246	Directorate of Fisheries	0.5377	0.2898	0.8188
Saithe	156403.1	-	MFRI stock assessment					
· Juvenile			-	396	-	0.0139	0.3956	0.4096
· Adult	127959.8		-	39195	Directorate of Fisheries	0.4411	0.1592	0.6003
Redfish	496681.4	-	MFRI stock assessment	91756		0.1847	0.2220	0.4075
· Golden Redfish	324123.7	0.6525	-	56993	Directorate of Fisheries	-	-	-
· Demersal beaked redfish	165271	0.3327	-	34741	Directorate of fisheries	-	-	-
· Norway haddock	7286.7	0.0146	-	21.8	Directorate of Fisheries	-	-	-
Flatfish	77425	-		29523		0.4105	0.2512	0.6617
· Atlantic halibut	670	0.0009	MFRI stock assessment	955	Directorate of Fisheries	-	-	-
· Witch	1143	0.0158	MFRI stock assessment	1529	Directorate of Fisheries	-	-	-
· Megrim	278	0.0038	MFRI stock assessment	395	Directorate of Fisheries	-	-	-
· Plaice	11689	0.1625	MFRI stock assessment	11281	Directorate of Fisheries	-	-	-
· Dab	11336	0.1576	MFRI stock assessment	8012	Directorate of Fisheries	-	-	-
· Long rough dab	49457	0.6876	MFRI stock assessment	6379	Directorate of Fisheries	-	-	-
· Lemon sole	2852	0.0396	MFRI stock assessment	973	Directorate of Fisheries	-	-	-
Greenland halibut	147582.3	-	MFRI stock assessment	21925	Directorate of Fisheries	0.1485	0.1585	0.3071
Herring	322215		MFRI stock assessment	100558	Directorate of Fisheries	0.3120	0.5317	0.8438
Capelin	1632994	-	MFRI stock assessment	1232994	Directorate of Fisheries	0.7619	0.5300	1.2936
Migratory fish	600000	-	Guestimate	501	Directorate of Fisheries	0.2 [1)]	0.4643	0.6643
Other commercial fish	46153.38	-	MFRI stock assessment	10432		0.4206	0.1842	0.6049
· Ling	20484.9	0.4438	-	4125	Directorate of Fisheries	-	-	-
· Blue ling	572.9	0.0124	-	1195	Directorate of Fisheries	-	-	-
· Tusk	18558.59	0.4027	-	6471	Directorate of Fisheries	-	-	-
· Whiting	7109.9	0.1540	-	429	Directorate of Fisheries	-	-	-
Demersal commercial	138212.7	-	MFRI stock assessment	17484		0.1255	0.1710	0.2966
Atlantic wolffish	59288.9	0.4289	-	14781	Directorate of Fisheries	-	-	-

Functional group	Biomass			Landings		F	M	P/B
	tonnes	FG prop	Source	tonnes	Source			
Spotted wolffish	10993.3	0.0795	-	902	Directorate of Fisheries	-	-	-
Monkfish	305.2	0.0022	-	796	Directorate of Fisheries	-	-	-
Lumpfish	9677	0.0700	-	120	Directorate of Fisheries	-	-	-
Greater silversmelt	57948	0.4192	-	881	Directorate of Fisheries	-	-	-
Demersal fish	-	-		119		-	-	1.1800
Sand eel	-	-		0	Directorate of Fisheries	0.005	0.3998	0.4048
Small pelagic fish	-	-		0		-	0.6027	0.6027
Skates and rays	50000	-	Guestimate	1681	Directorate of Fisheries	0.1	0.1762	0.2762
Large sharks	1000	-	Guestimate	36	Directorate of Fisheries	0.05	0.0145	0..0645
Small sharks	5000	-	Guestimate	188	Directorate of Fisheries	0.05	0.1087	0.1587

1) Assumed value

Table 12. Parameter estimates for fish functional groups, including length infinity (cm), weight infinity (W_∞), von Bertalanffy growth coefficient (K) and calculated consumption/biomass (Q/B).

Functional group	a	b	Linf (cm)	Winf (kg)	K	Q/B
Atlantic cod (0-3)	-	-	-	1.275	0.2	3.15
Atlantic cod (4+)	0.01	3.00000	150	33.750	0.0979	1.81
Haddock (0-2)	-	-	-	0.752	0.3[4)]	3.44
Haddock (3+)	0.008850	3.02587	81.9	5.449	0.21	2.47
Saithe (0-3)	-	-	-	1.599	0.3[4)]	3.03
Saithe (4+)	0.024980	2.75674	140	20.602	0.102	1.97
Greenland	0.017580	2.843870	115.5[1)]	12.904	0.100[1)]	2.13
Redfish	0.00520	3.256000	46.4	1.387	0.126	3.10
Flatfish	0.01605	3.38752	45.18	6.487[2)]	0.181[2)]	2.39
Herring	0.004306	3.173190	36.24	0.382	0.389	4.43
Capelin	0.00363[1)]	3.21[1)]	17.8	0.062	0.610	5.23
Migratory fish	0.006002	3.004555	33.2	0.2231	0.299	4.22
Other commercial fish	0.005232	3.127967	108.49	12.171[2)]	0.123[2)]	2.53
Demersal commercial fish	0.010000	2.95	92.30	6.271[2)]	0.102[2)]	2.41
Demersal fish	-	-	-	-	-	3.10[3)]
Sand eel	-	-	37	0.238	0.4[1)]	4.90
Small pelagic	-	-	8.5[1)]	0.044	0.4[1)]	6.52
Skates and rays	0.010442	2.985197	71.4	3.568	0.1[1)]	3.12
Large sharks	-	-	550[1)]	1.000	0.008[1)]	1.19
Small sharks	-	-	152	23.7	0.1[1)]	2.24

1) From fishbase.org

2) Biomass weighted average

3) Hutchings, J. A. (2002)

4) Guestimate

Sharks

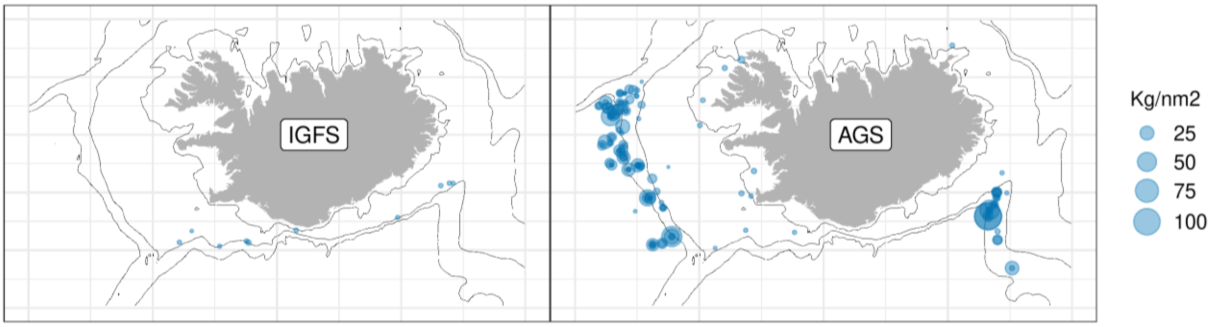

Figure 8. Geographical distribution and abundance of small sharks on Icelandic fishing grounds from the Icelandic groundfish survey (IGFS) in spring and the groundfish survey in autumn (AGS) in 1996.

In the model, sharks are categorized into two distinct functional groups: namely, large sharks (SSH) and small sharks (SSD). Although sharks can be found in the Icelandic ecosystem, they are not as abundant as in other regions of the world. The most common species of large sharks observed around Iceland is the Greenland shark (*Somniosus microcephalus*), but Greenland shark is the only shark that inhabits the coldest oceans in the Arctic and has been observed all around Iceland. They are known to feed on mostly fish, squid, and even marine mammals (Jónsson 2013). The basking shark (*Cetorhinus maximus*) is mainly pelagic and has been observed all around Iceland but is more common in warmer oceans south and southwest of Iceland. They are filter feeders, and their diet primarily consists of plankton (Jónsson 2013). Porbeagle (*Lamna nasus*) has been observed all around Iceland but is typically seen far away from the coastline.

Growth parameters of Greenland shark were used for the large shark group. Natural mortality was estimated with equation 8 (Table 11) with L_∞ of 550 cm and K of 0.008 (fishbase.org). Fishing mortality was assumed to be 0.05, resulting in a P/B of 0.0645 year^{-1}. Q/B was estimated with equation 10 with max weight of 1000 kg (1.19 year^{-1}). Biomass in the model was set to 1000 tonnes ("guestimated" value). Diet from Icelandic surveys was used in the model. Table 2 lists the ten smaller shark species, which are typically bottom-dwellers (Jónsson 2013) but mostly feed in upper layers of the water column. No targeted fishing is on this group and they rarely appear as bycatch. The assumed fishing mortality in the model is 0.01 and their natural mortality is estimated using equation 8 with L_∞ of 152 cm (based on Icelandic surveys), which yields a P/B value of 0.11 year^{-1}. Q/B was estimated with equation 10 with a maximum weight of 23,7 kg used as $W_{\infty,}$ resulting in Q/B value of 2.24 year^{-1}. Biomass was set to 5000 tonnes in the model ("guestimated" value).

Diet data from Icelandic surveys are used in the model and smaller sharks predominantly feed on pelagic fish (31%), demersal fish (17.5%), cephalopods (14%), crustaceans (17%) and zooplankton (20%), but temporal and ontogenetic variation in smaller shark diet in Icelandic waters has recently been analyzed (Sólmundsson et al. 2024). Large sharks predominantly feed on demersal fish (69%) and small pelagic fish (30%) (Table 13).

Table 13. Diet proportion of large sharks (SSH) and small sharks (SSD) in the Icelandic Ecopath model. Data from MFRI.

Code	Functional group	Diet proportion	
		Large sharks	Small sharks
FBP	Small pelagic fish	0.30	0.21
PWN	Shrimp	-	0.16
ZG	Gelatinous zooplankton	-	0.16
CEP	Cephalopods	-	0.14
FDF	Other demersal fish	< 0.01	0.09
FMI	Migratory fish	-	0.07
FRF	Redfish	0.51	0.04
FKR	Krill	-	0.04
FDC	Demersal commercial fish	0.18	0.02
Other*		-	0.03

*FSD, FHA.juv, FHE, FEP, ZL, FLC, FCD.juv, FCA, FIN

Skates and rays

Figure 9. Geographical distribution and abundance of thorny skate on Icelandic fishing grounds from the Icelandic groundfish survey (IGFS) in spring and the groundfish survey in autumn (AGS) in 1996.

Rays in Icelandic waters all belong to the Rajidae family, and the most common species is the thorny skate, also known as starry ray (Amblyraja radiata). Other species included in this groups are species that have analyzed diet data, i.e. the spinetail ray (Bathyraja spinicauda), round ray (Rajella fyllae), Arctic skate (Amblyraja hyperborea), common skate (Dipturus batis), sailray (Rajella lintea) and deepwater ray (Rajella bathyphila). Thorny skate is the most abundant species in this group and the only species that is targeted by the fisheries, but thorny skate is distributed all around Iceland and depths ranging from 20-1,000 m (Figure 9). As such, input parameters for this group are based on thorny skate life history parameters. Thorny skate is primarily caught as a bycatch species in the longline fishery, with the majority of its landings occurring in autumn due to demand. Fishing mortality is assumed to be 0.1 in the model, and natural mortality is estimated using equation 8 (Table 11). W_∞ estimated with length to weight conversion factor (equation 5, Table 12) and Q/B was estimated to be 3.12 $year^{-1}$ using equation 10. Diet information is from the Icelandic groundfish surveys.

Skates and rays in the Icelandic ecosystem primarily feed on demersal fish (36%), pelagic fish (28%), zooplankton (17%) and crustaceans (15%) (Table 14). Temporal and ontogenetic variation by species of skates and rays in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 14. Stomach content weight rations for skates and rays in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FDF	Other demersal fish	0.14
PWN	Shrimp	0.12
FCA	Capelin	0.12
FKR	Krill	0.10
FIN	Infauna	0.09
FMI	Migratory fish	0.08
ZL	Large zooplankton	0.08
FRF	Redfish	0.06
FHE	Herring	0.03
FSD	Sand eel	0.03
Other*		0.13

* FCD.juv, FSA.juv, FLC, FFF, CEP, FEP, SSR, FBP, ZG, FHA.juv, FDC, LOB

Cod

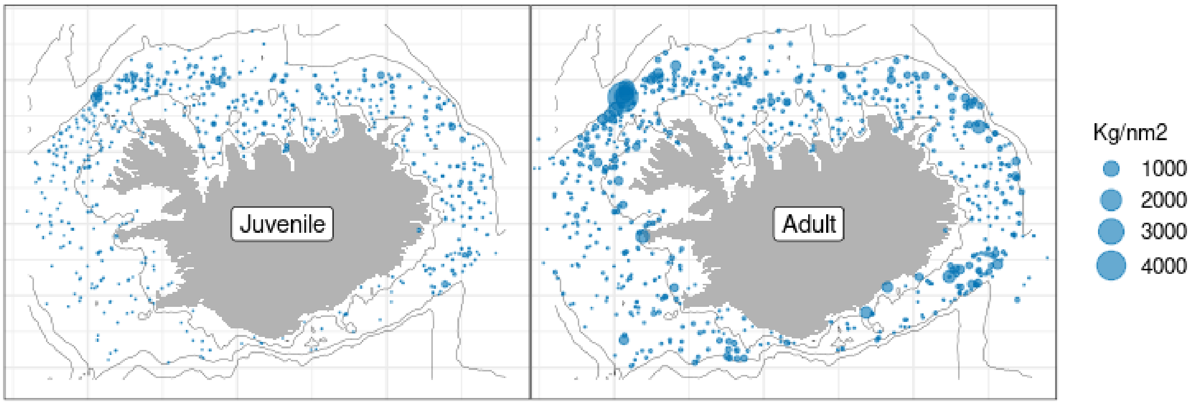

Figure 10. Geographical distribution and abundance of juvenile and adult cod from the Icelandic groundfish survey in spring (IGFS) and the autumn groundfish survey (AGS) in 1996.

Atlantic cod (*Gadus morhua*) is the most important commercially exploited demersal species on Icelandic fishing grounds. It is also the most thoroughly studied fish species in Icelandic waters and its biology is well known (Jónsdóttir et al. 2006, Pétursdóttir et al. 2006, Jónasson et al. 2009). Cod is found all around Iceland (Figure 10) and is most common at depths ranging from 100-400 m (MFRI, 2023a). Cod were split into two functional groups (stanza groups) i.e., juveniles (age 0-3, length 0-45 cm) and adults (age 4+ and length>45 cm). Ecopath requires the von Bertalanffy K for both stanzas, and length infinity (L_∞) to estimate production and consumption parameters, as well as to estimate weight at maturity and weight at infinity to link mature cod to immature cod. These parameters were estimated with age and length data from IGFS. L_∞ of adult cod is 150 cm and K is 0.0979. W_{mat} for cod was calculated to be 3.080 kg using a generalized linear model with weight data from IGFS. W_∞ was estimated with length to weight conversion factor (equation 5, Table 12), resulting in W_{mat}/W_∞ of 0.09124642.

Biomass estimates from assessment were used in the model. Biomass of juveniles was estimated to be 180,294 tonnes and for adult cod 517,633 tonnes in 1996. Biomass accumulation rate (BA/B) for juveniles was -0.0600 year^{-1} and 0.0809 year^{-1} for adults.

P/B and Q/B parameters are estimated for each stanza separately, and thus, growth parameters for separate stanza are required. W_∞ for juvenile cod was set to maximum weight of 0-3 year old cod in IGFS and K set to 0.2. Natural mortality was estimated using equation 8 (Table 11), resulting in P/B of 0.32 year^{-1} for juveniles and 0.49 year^{-1} for adults. Equation 10 was used to calculate Q/B, resulting in Q/B of 5.17 year^{-1} for juveniles and 1.82 year^{-1} for adults.

Cod diet in Icelandic waters has been well studied (Astthorsson, 1987, Pálsson and Björnsson 2011, Jónsdóttir et al. 2012). All stomach content data collected by MFRI is incorporated in the model. Juvenile cod mainly feed on capelin (53%), shrimp (15%) and krill (10%). Adult cod predominantly feed on capelin (57%) (Table 15). Spatial, temporal, and ontogenetic variation in cod diet can be seen in Sólmundsson et al. (2024).

Table 15. Stomach content weight rations for juvenile and adult cod in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion	
		Juvenile cod	Adult cod
FCA	Capelin	0.53	0.57
PWN	Shrimp	0.15	0.08
FKR	Krill	0.10	0.03
ZL	Large zooplankton	0.04	0.01
FSD	Sand eel	0.03	0.03
FCD.juv	Juvenile cod	0.03	0.02
FIN	Infauna	0.02	0.003
FDF	Other demersal fish	0.02	0.03
FLC	Lobsters and crabs	0.01	0.007
FHE	Herring	0.01	0.04
Other		0.04*	0.15**

*FHA.juv, FFF, FEP, ZG, FBP, FRF, FMI, FDC, CEP, FOC, LOB, FSA.juv, ZS
** FHA.juv, FFF, FEP, ZG, FBP, FRF, FMI, , FDC, CEP, FOC, LOB, FSA.juv, ZS, FHA.adult, SSR, FGH.

Haddock

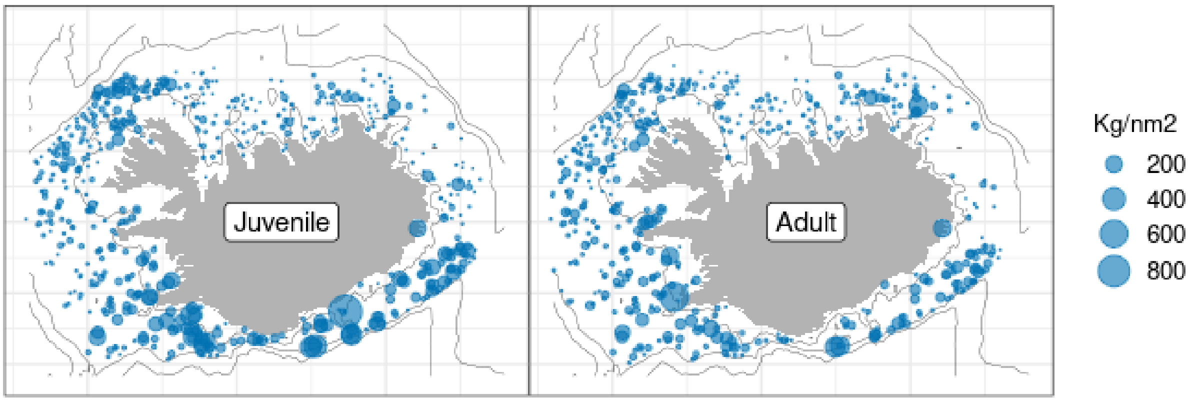

Figure 11 Geographical distribution and abundance of juvenile and adult haddock from the Icelandic Groundfish Survey in spring (IGFS) and the Autumn Groundfish Survey (AGS) in 1996.

Haddock were split into two functional groups: juvenile (age 0-2, length 0-30 cm) and adults (age 2+, length>30 cm). The distribution of haddock spans across all the Icelandic fishing grounds but juveniles were more abundant on the south coast (Figure 11). Haddock is found in relatively warm waters at depths ranging from 10-200 m (MFRI 2023b). Haddock is targeted after age 2 and according to logbooks from the Directorate of Fisheries, mostly by bottom trawls and longlines, south, southwest, and west of the country at depths less than 200 meters.

Juveniles and adults were linked via multi-stanza connection using the same methods as described for cod above. L_∞ and K parameters are estimated with von Bertalanffy (L_∞ = 81.9 cm and K = 0.21). W_∞ is 5,449 kg (estimated with length to weight conversion factor (equation 5, Table 12) and W_{mat} was calculated to be 0.958 kg using a generalized linear model with weight data from IGFS, resulting in W_{mat}/W_∞ of 0.1758.

Biomass estimates from assessment were used in the model. The biomass of adults in the model is 180,323 tonnes but biomass of juveniles is highly uncertain and was estimated by the model. Biomass accumulation rate (BA/B) for juveniles was 0.0431 year^{-1} and -0.4608 year^{-1} for adults.

Natural mortality was estimated using equation 8 (Table 11) and fishing mortality with equation 7, resulting in P/B of 0.44 year^{-1} for juveniles and 0.82 year^{-1} for adults. Equation 10 was used to calculate Q/B, resulting in Q/B of 5.94 year^{-1} for juveniles and 2.47 year^{-1} for adults. Juvenile haddock primarily feed on the infauna group (38%) but as adults, they mostly feed on capelin (48%) (Table 16). Spatial, temporal, and ontogenetic variation in haddock diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 16. Stomach content weight rations for juvenile and adult haddock in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	**Functional group**	**Diet proportion**	
		Juvenile haddock	**Adult haddock**
FIN	Infauna	0.38	0.15
FEP	Epifauna	0.17	0.17
FKR	Krill	0.11	0.09
PWN	Shrimp	0.09	0.02
FSD	Sand eel	0.08	0.03
FCA	Capelin	0.07	0.48
ZL	Large zooplankton	0.04	-
FLC	Lobsters and crabs	0.02	0.01
FDF	Other demersal fish	0.005	0.007
ZG	Gelatinous zooplankton	0.004	0.01
Other		0.009*	0.01**

*CEP, FBP, FHE, FRF, FCD.juv, FHA.juv, FMI, LOB, FDC, ZS
** CEP, FBP, FHE, FRF, FCD.juv, FHA.juv, FMI, LOB, FDC, ZS, FFF, FOC, FSA.juv, SSR

Saithe

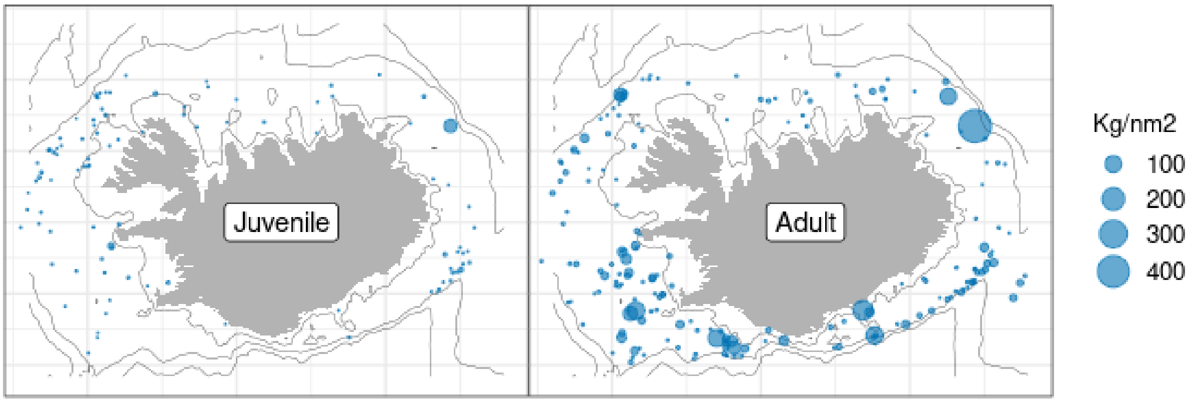

Figure 12 Geographical distribution and abundance of juvenile and adult Saithe from the Icelandic groundfish Survey in spring (IGFS) and the Autumn Groundfish Survey (AGS) in 1996.M

Saithe (*Pollachius virens*) were split into two functional groups: juveniles (age 0-3, length 0-45 cm) and adults (age 4+, length>45 cm). 0-2 year old saithe tend to be closer to shore and often in fjords around Iceland. In Figure 12, the juvenile distribution reflects the 0-3 year old saithe, which have similar distribution as the adults i.e., further offshore, and preferably in warmer waters, south, southeast, and west of the coast (Figure 12). They are mainly targeted by bottom trawls at depths ranging from 150-200 m (MFRI, 2023c).

Juveniles and adults were linked via multi-stanza connection using the same methods as seen for cod and haddock above. L_∞ and K parameters are estimated with von Bertalanffy (L_∞ = 140 cm and K = 0.102). W_∞ is 20,6 kg (estimated with length to weight conversion factor (equation 5, Table 12) and W_{mat} was calculated to be 3,162 kg using a generalized linear model with weight data from IGFS, resulting in W_{mat}/W_∞ of 0.1534645.

The estimated biomass of saithe in the model is based on stock assessments. In 1996, the biomass of adult saithe was estimated to be 127,945 tonnes. The biomass of juveniles was estimated by the EwE model. Biomass accumulation rate (BA/B) for juveniles was -0.0002 $year^{-1}$ and -0.0672 $year^{-1}$ for adults.

Natural mortality was estimated using equation 8 (Table 11) and fishing mortality from assessment used (MFRI 2023c) resulting in P/B of 0.40 $year^{-1}$ for juveniles and 0.59 $year^{-1}$ for adults. Equation 10 was used to calculate Q/B, resulting in Q/B of 5.43 $year^{-1}$ for juveniles and 1.97 $year^{-1}$ for adults.

Juvenile saithe primarily feed on pelagic fish (33%), demersal fish (36%) and invertebrates (31%). Adult saithe feed mostly on capelin (49%), other pelagic fish (11%), demersal fish (23%)

and invertebrates (17%) (Table 17). Spatial, temporal, and temporal variation in saithe diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 17. Stomach content weight rations for juvenile and adult saithe in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Prey group	Functional group	Diet proportion	
		Juvenile saithe	Adult saithe
FCA	Capelin	0.30	0.5
FKR	Krill	0.30	0.12
FSD	Sand eel	0.26	0.06
FDF	Other demersal fish	0.06	0.06
FHE	Herring	0.03	0.06
FMI	Migratory fish	0.02	0.09
ZL	Large zooplankton	0.01	0.02
FBP	Small pelagic fish	0.009	0.04
PWN	Shrimp	0.009	0.009
FHA.juv	Juvenile haddock	0.006	0.02
Other		0.01*	0.02**

*FOC, FCD.juv, FIN, ZG, CEP, FEP, FLC, FFF, FRF, FDC
** FOC, FCD.juv, FIN, ZG, CEP, FEP, FLC, FFF, FRF, FDC, FSA.juv

Commercial demersal fish

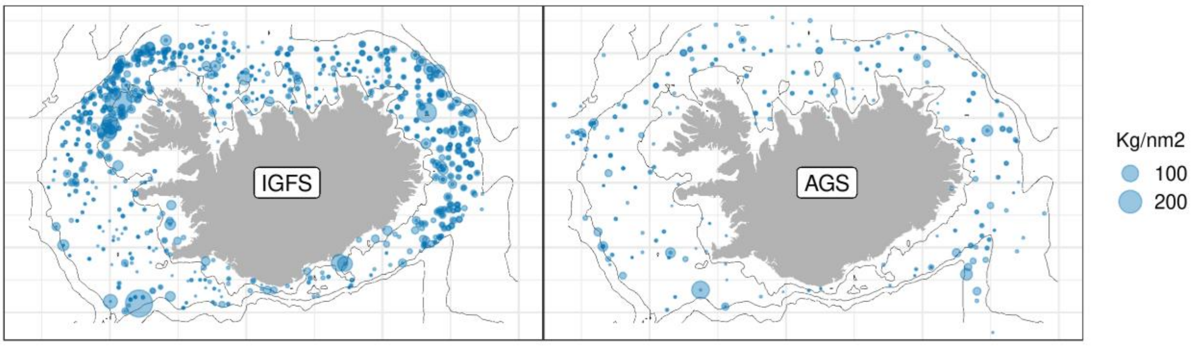

Figure 13 Geographical distribution and abundance of commercial demersal fish (FDC) in spring (IGFS) and autumn (AGS) in 1996.

Fish species in the commercial demersal group (FCD) are Atlantic wolffish (*Anarhichas lupus*), spotted wolffish (*Anarhichas minor*), greater argentine (*Argentina silus*), lumpfish (*Cyclopterus lumpus*) and monkfish (*Lophius piscatorius*). Northern wolffish (*Anarhichas denticulatus*) is also included in the group as prey. They are distributed all around Iceland and are observed in higher abundance in the spring (IGFS) (Figure 13).

The estimated biomass of this group in the model is based on survey biomass estimates (stock assessments). In 1996, the total biomass of the group was 73,595 tonnes (Atlantic wolffish: 38,918 tonnes, spotted wolffish: 11,017 tonnes, monkfish: 320 tonnes, lumpfish 4,839 tonnes and greater silversmelt: 18,502 tonnes. Biomass accumulation rate (BA/B) for the group was -

0.0141 year^{-1}. W_∞ was estimated with length to weight conversion factor (equation 5, Table 12) with biomass weighted average of L_∞ for Atlantic wolffish, spotted wolffish and greater silversmelt. Growth parameters from von Bertalanffy were weighted with biomass. Natural mortality was estimated using equation 8 (Table 11) and fishing mortality estimated with equation 7, resulting in P/B of 0.29 year^{-1} and Q/B was estimated with equation 10 (2.41 year^{-1}). Diet proportions of commercial demersal fish are in Table 18. Temporal and ontogenetic variation in Atlantic wolffish, monkfish and lumpfish diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 18. Stomach content weight rations for commercial demersal fish (FDC) in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FEP	Epifaula	0.21
FCD.juv	Juvenile cod	0.14
FRF	Redfish	0.14
FFF	Flatfish	0.08
FHE	Herring	0.07
FDC	Demersal commercial fish	0.07
FCA	Capelin	0.07
FHA.adult	Juvenile haddock	0.04
FOC	Other codfish	0.03
Other*		0.15

*ZG, SSR, FIN, FHA.juv, FDF, FSA.juv, FLC, PWN, FKR, ZL, FMI, CEP, FBP, LOB, FGH, ZS

Other codfish

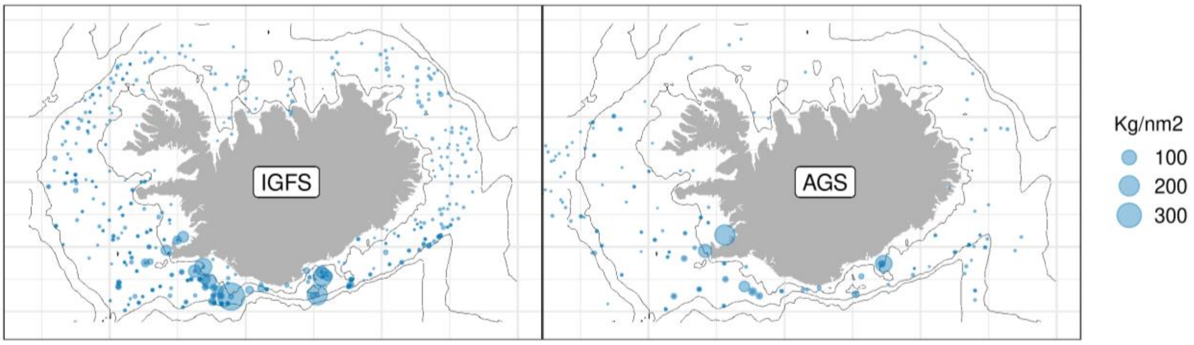

Figure 14. Geographical distribution and abundance of other codfish (FOC) in spring (IGFS) and autumn (AGS) in 1996.

Species in the other codfish group (FOC) are whiting (*Merlangius merlangus*), ling (*Molva molva*), blue ling (*Molva dypterygia*) and tusk (*Brosme brosme*).

The estimated biomass of this group in the model is based on survey biomass estimates (here the spawning stock biomass from stock assessments). In 1996, the total spawning stock biomass of the group was 46,153 tonnes (whiting: 7,110 tonnes, ling: 20,485 tonnes, tusk:

18,559 tonnes, blue ling 572.9 tonnes in the year 2000. Biomass accumulation rate (BA/B) for the group was -0.1858 year^{-1}. W_∞ was estimated with length to weight conversion factor (equation 5, Table 12) with biomass weighted average of L_∞ for whiting, ling, tusk and blue ling. Growth parameters (L_∞ and K) from von Bertalanffy were weighted with biomass. Natural mortality was estimated using equation 8 (Table 11) and fishing mortality estimated with equation 7, resulting in P/B of 0.60 year^{-1}. Q/B was estimated with equation 10, resulting in Q/B of 2.53 year^{-1}. Fish from this group predominantly feed on other fish species i.e. blue whiting (29%), herring (21%) and demersal fish (17%) (Table 19). Temporal and ontogenetic variation in ling, blue ling and tusk diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 19. Stomach content weight rations other codfish (FOC) in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FMI	Migratory fish	0.29
FHE	Herring	0.20
FDF	Other demersal fish	0.18
FBP	Small pelagic fish	0.05
PWN	Shrimp	0.04
FOC	Other codfish	0.03
FCD.juv	Juvenile cod	0.03
FCA	Capelin	0.03
FSD	Sand eel	0.02
FDC	Demersal commercial fish	0.02
Other*		0.09

*FSA.juv, FHA.juv, FRF, CEP, FKR, FLC, LOB, FFF, ZL, FEP, FIN, ZB, SSR

Other demersal fish

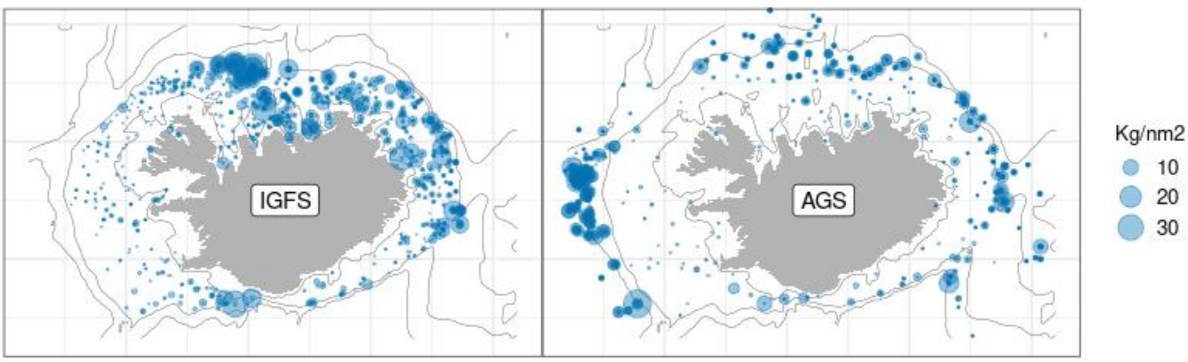

Figure 15. Geographical distribution and abundance of other demersal fish (FDF) in spring (IGFS) and autumn (AGS) in 1996.

Species in the other demersal fish group (FDF) are unexploited demersal fish such as sculpins, rocklings, eels, eelpouts and more (see appendix Table 34 for species list).

The biomass of this group is unknown, and thus, estimated by the model with EE of 0.95. The P/B was set as 0.265 year^{-1} and Q/B as 3.100 year^{-1} (Ribeiro et al. 2018). No species in this group is landed.

Table 20. Stomach content weight rations of demersal fish (FDF) in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FKR	Krill	0.25
PWN	Shrimp	0.24
FDF	Other demersal fish	0.12
ZG	Gelatinous zooplankton	0.10
FCA	Capelin	0.08
ZL	Large zooplankton	0.06
CEP	Cephalopods	0.04
FIN	Infauna	0.03
Other*		0.06

*FEP, FBP. FLC, FSD, FMI, FFF, FHE, FRF, ZS, FGH

Greenland halibut

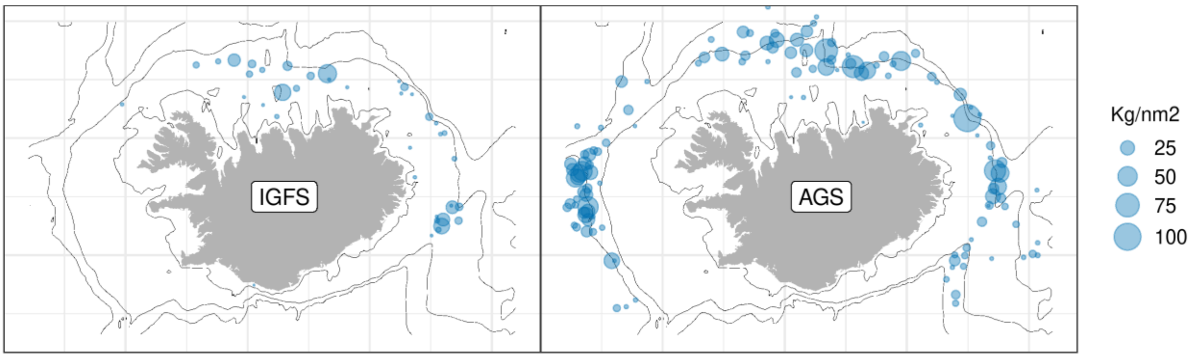

Figure 16. Geographical distribution and abundance of Greenland halibut in spring (IGFS) and autumn (AGS) in 1996.

Greenland halibut (*Reinhardtius hippoglossoides*) is mainly distributed on the shelf edge west, north and northeast of the country (Figure 16). Biomass in 1996 was 147,582.3 tonnes (from stock assessment). Biomass accumulation rate (BA/B) was -0.0130 year^{-1}.

Growth parameters were obtained from fishbase.org (L_∞ = 115.5 cm, K = 0.1), and W_∞ was estimated with length to weight conversion factor (equation 5, Table 12). Natural mortality was estimated using equation 8 (Table 11) and fishing mortality was calculated with equation 7, resulting in P/B of 0.30 year^{-1}. Q/B was estimated with equation 10, resulting in Q/B of 2.13 year^{-1}.

Greenland halibut feeds primarily on pelagic fish such as capelin, herring, and other small pelagic fish (46%), demersal fish (33%) and invertebrates (21%) (Table 21). Spatial, temporal, and ontogenetic variation in Greenland halibut diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 21. Stomach content weight rations of Greenland halibut (FGH) in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FCA	Capelin	0.36
FMI	Migratory fish	0.16
FDF	Other demersal fish	0.14
FHE	Herring	0.10
CEP	Cephalopods	0.08
FKR	Krill	0.07
PWN	Shrimp	0.06
FRF	Redfish	0.01
FBP	Samm pelagic fish	0.09
FSD	Sand eel	0.07
Other*		0.03

*ZL, ZG, FCD.juv, FSA.juv, FGH, FDC, SSR, FHA.juv, FEP, FIN, FFF, FOC, FLC

Flatfishes

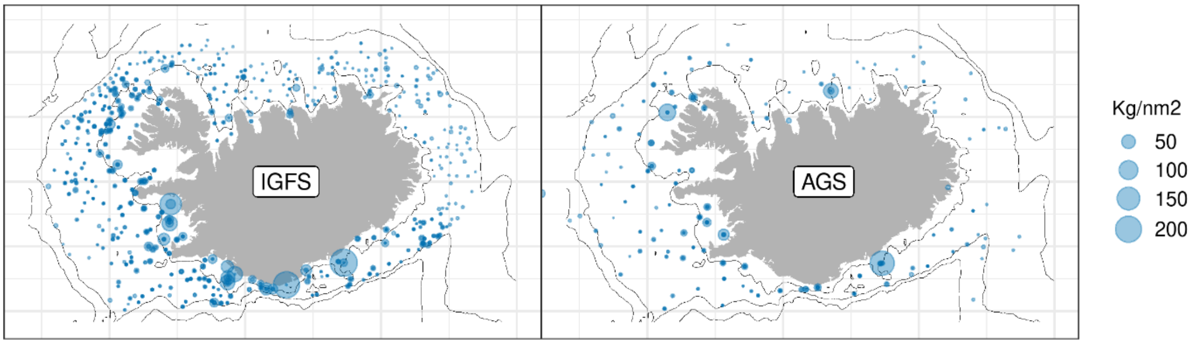

Figure 17. Geographical distribution and abundance of flatfish in spring (IGFS) and autumn (AGS) in 1996.

A flatfish group in the model include Atlantic halibut (*Hippoglossus hippoglossus*), witch (*Glyptocephalus cynoglossus*), megrim (*Lepidorhombus whiffiagonis*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), long rough dab (*Hippoglossoides platessoides*) and lemon sole (*Microstomus kitt*). They are distributed all around Iceland, mainly at depths ranging from 20-500 m.

The biomass in 1996 is the sum of the spawning stock biomasses or 76,918 tonnes (Atlantic halibut: 670 tonnes, witch: 1,143 tonnes, megrim: 278 tonnes, plaice: 11,689 tonnes, dab: 11,336 tonnes, long rough dab: 49,457 tonnes, lemon sole: 2,852 tonnes). Growth parameters

K and L_∞ parameters were estimated with von Bertalanffy, resulting in a K of 0.18 and L_∞ 45.18. W_∞ was estimated with length to weight conversion factor (equation 5, Table 12). Natural mortality was estimated using equation 8 (Table 11) and fishing mortality calculated with equation 7, resulting in P/B of 0.66 $year^{-1}$. Q/B was estimated with equation 10, resulting in Q/B of 2.39 $year^{-1}$. Species in the flatfish group feed primarily on invertebrates (54%), pelagic fish (28%) and demersal fish (12%) (Table 22). Temporal and ontogenetic variation in halibut, plaice, dab and long rough dab diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 22. Stomach content weight rations of the flatfish group (FFF) in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FEP	Epifauna	0.31
FIN	Infauna	0.18
FCA	Capelin	0.16
FSD	Sand eel	0.12
FRF	Redfish	0.10
PWN	Shrimp	0.03
FKR	Krill	0.03
Other*		0.07

*FDF, FHE, FFF, LOB, FDC, FMI, CEP, ZG, FBP, ZS, FCD.juv, FHA.juv, FLC, ZL

Redfish

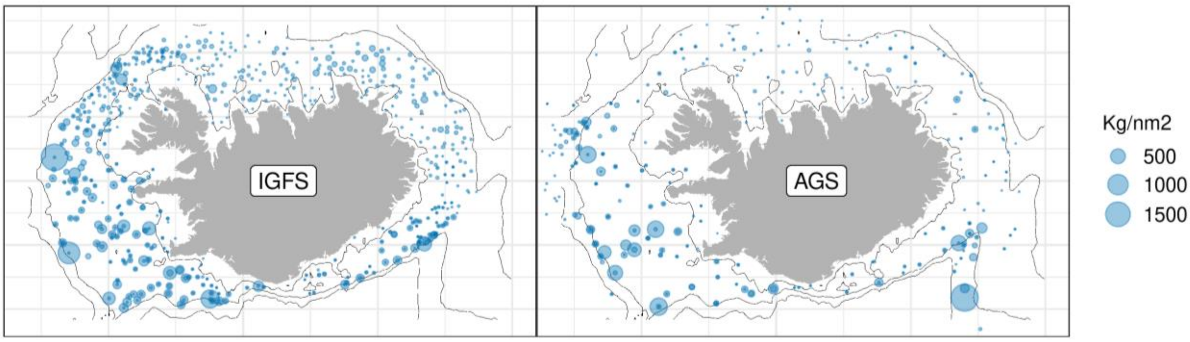

Figure 18. Geographical distribution and abundance of redfish in spring (IGFS) and autumn (AGS) in 1996.

Redfish group in the model include the three redfish species inhabiting Icelandic waters, that is golden redfish (*Sebastes norvegicus*), Norway haddock (*Sebastes viviparus*) and demersal beaked redfish (*Sebastes mentella*). They are most common in the warmer seas in the west, southwest, south, and southeast (Figure 18) at depths ranging from 30-600 m.

The biomass in 1996 is the sum of the spawning stock biomass (of demersal beaked redfish and Norway haddock) and the number at age times stock weights (golden redfish) (demersal beaked redfish: 165,271 tonnes, Norway haddock: 7,287 tonnes, golden redfish: 324,124 tonnes). Biomass accumulation rate (BA/B) was -0.0408 year^{-1}.

Growth parameters K and L_∞ parameters were estimated with von Bertalanffy (K = 0.126, L_∞ = 46.4 cm). W_∞ was estimated with length to weight conversion factor (equation 5, Table 12). Natural mortality was estimated using equation 8 (Table 11) and fishing mortality with equation 7, resulting in P/B of 0.40 year^{-1}. Q/B was estimated with equation 10, resulting in Q/B of 3.10 year^{-1}.

The redfish group feeds mostly on krill (39.7%), capelin (13.4%), and Shrimp (12.5%) (Table 23). Spatial, temporal and ontogenetic variation in golden redfish and demersal beaked redfish diet in Icelandic waters can be seen in Sólmundsson et al. (2024).

Table 23. Stomach content weight rations of the redfish group (FRF) in the Icelandic Ecopath model. Stomach content collected by the MFRI from 1979-2022.

Code	Functional group	Diet proportion
FKR	Krill	0.40
FCA	Capelin	0.13
PWN	Shrimp	0.13
ZL	Large zooplankton	0.09
FBP	Small pelagic fish	0.06
FDF	Other demersal fish	0.04
FSD	Sand eel	0.04
ZG	Gelatinous zooplankton	0.03
CEP	Cephalopods	0.03
FMI	Migratory fish	0.02
Other*		0.04

*FIN, FHA.juv, FHE, FRF, FCD.juv, FOC, FFF, FLC, FEP, ZS, FDC, FSA.juv

Herring

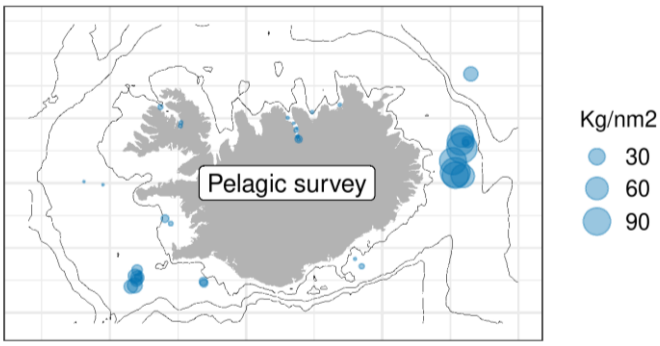

Figure 19. Geographical distribution and abundance of herring in herring survey in 1996.

The Icelandic summer-spawning herring (*Clupea harengus*) is a pelagic fish found all around Iceland at depths ranging from surface down to 400 m (MFRI 2023d). Since 2008, the parasite *Icthyophonus hoferi* has been persistent in the Icelandic summer-spawning herring, causing an increase in mortality rates. The infection was particularly high in 2009-2011 and 2016-2018 (Óskarsson et al. 2018) and after 2007, the stock steadily declined (MFRI 2023d). Since 2020, spawning stock biomass and recruitment has increased substantially. The estimated biomass in 1996 is based on the herring survey biomass estimates and in 1996, the total biomass of the group was 322,215 tonnes. Biomass accumulation rate (BA/B) was -0.1726 $year^{-1}$.

Growth parameters, K and L_∞, were estimated with von Bertalanffy (K = 0.39, L_∞ = 36.2 cm). W_∞ was estimated with length to weight conversion factor (equation 5, Table 12). Natural mortality was estimated using equation 8 (Table 11) and fishing mortality with equation 7, resulting in P/B of 0.84 $year^{-1}$. Q/B was estimated with equation 10, resulting in Q/B of 4.54 $year^{-1}$.

Stomach content from herring was extensively collected from 2008-2016. Herring mainly feeds on large zooplankton (*Calanus finmarchicus*) and krill species (Euphausiacea). Landings are from the Directorate of Fisheries, and from 1996-2013 herring was mainly targeted by purse seine and pelagic trawls. In 2014, fishing pattern changed, and fisheries moved from small inshore areas west of the coast to offshore areas west and east off the country. Since then, herring has primarily been targeted by pelagic trawls.

Table 24. Diet proportion of herring (FHE) in the Icelandic Ecopath model.

Code	Functional group	Diet proportion
ZL	Large zooplankton	0.54
FKR	Krill	0.38
FCA	Capelin	0.02
FIN	Infauna	0.02
ZS	Small zooplankton	0.009
FSD	Sand eel	0.009
FLC	Lobsters and crabs	0.003
FDF	Other demersal fish	0.002
FEP	Epifauna	0.002
ZG	Gelatinous zooplankton	0.001

Capelin

Capelin (*Mallotus villosus*) is one of the most important commercially exploited species in Icelandic waters and has a key role in the food chain as a link between zooplankton and larger fish. During its migration from hatching grounds north of Iceland to spawning grounds in the south, capelin becomes the main food of many species, and are especially important to cod (Pálsson and Björnsson 2011). The biomass of capelin in Icelandic waters has been assessed since 1978 during annual autumn acoustic surveys. In 1996, the biomass was estimated to be

1.632,994 tonnes (Landings from the Directorate of Fisheries) + 400,000 tonnes (advice rule in 1996). Biomass accumulation rate (BA/B) was 0.0260 year^{-1}.

Growth parameters, K and L_∞, were estimated with von Bertalanffy and W_∞ was estimated with length to weight conversion factor (equation 5, Table 12). Natural mortality was estimated using equation 8 (Table 11) and fishing mortality with equation 7, resulting in P/B of 1.29 year^{-1}. Q/B was estimated with equation 10, resulting in Q/B of 5.23 year^{-1}.

Capelin feed on large zooplankton (*Calanus* spp. 92%) and krill (8%) (Astthorsson, O. S. & Gislason, A. 1997).

Capelin landings are highly seasonal and most of them take place from January-March. In 1996, 1.280,052 tonnes were landed but have steadily declined since then. In 2019 and 2020, no fishing took place as only small amounts of mature capelin were observed in acoustic surveys in autumn and winter. Landings in 1996 were the highest in the time series and have since gradually declined (Figure 5).

Migratory fish

Blue whiting (*Micromesistius poutassou*) is a migratory fish and is widely distributed throughout the North- and Northeast-Atlantic (Trenkel et al. 2014, Huse et al. 2015). Blue whiting spawns west off the British Isles, and during summer and autumn, juveniles often migrate into Icelandic waters where they stay until reaching maturity. Biomass indices of one-year-old blue whiting in Icelandic waters have been monitored since 1996 during the Icelandic Groundfish Survey in spring. Biomass of one-year olds in Icelandic waters is highly related to recruitment success and strong year classes. Total biomass in Icelandic waters is unknown and "guesstimated" to be 600,000 tonnes in the model. Growth parameters, K and L_∞, were estimated with von Bertalanffy and W_∞ was estimated with length to weight conversion factor (equation 5, Table 12). Natural mortality was estimated using equation 8 (Table 11) and fishing mortality assumed to be 0.2, resulting in P/B of 0.54 year^{-1}. Q/B was estimated with equation 10, resulting in Q/B of 5.18 year^{-1}.

Sand eel

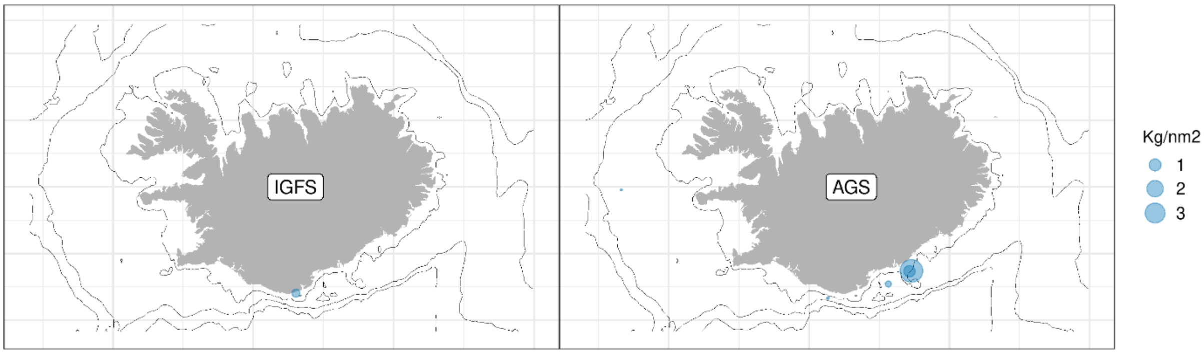

Figure 20. Geographical distribution and abundance of sand eel in spring survey (IGFS) and autumn survey (AGS) in 1996.

There are three species of sand eels found in Icelandic waters i.e., lesser sand eel (*Ammodytes tobianus*), Raitt´s sand eel (*Ammodytes marinus*) and greater sand eel (*Hyperoplus lanceolatus*). Lesser and greater sand eel are distributed at the south coast of Iceland but Raitt´s sand eel is also distributed further north and in deeper waters. They are not commercially exploited but serve as important prey for many numerous fish stocks, seabirds and marine mammals (Jónsson 2013).

The biomass of sand eels in Icelandic waters is unknown and thus, estimated by the model with EE of 0.9, resulting in an estimated biomass of 2.171,560 tonnes. No targeted fishing is on sand eels in Iceland and the fishing mortality is assumed to be 0.005% in the model. Sand eels were measured during pelagic surveys (length and weight) in 1998 and 1999 and those measurements are used for further calculations of L_∞ and W_∞. Natural mortality is estimated using equation 9 with maximum length from measurements (17 cm), and growth factor K from fishbase.org (0.4), resulting in M of 0.39, yielding a P/B of 0.4 year^{-1}. Q/B was estimated to be 4.90 year^{-1} using equation 10 with maximum weight from measurements as W_∞.

Diet of sand eel in Icelandic waters has not been studied, but the MFRI has collected and analyzed a total of 23 stomachs from Raitt´s sand eel in 1981 and 2008. The stomach content weight ratio for the sand eel group is based on those data and they are assumed to prey on krill (80%) and large zooplankton (20%).

Small pelagic fish

Species in the small pelagic fish group (FBP) are usually found at 75-150 m (depths during the day (also found in deeper waters), but migrate to near-surface waters at night (Prihartato 2015). Species in this group are pearlside (*Maurolicus muelleri*), polar cod (*Boreogadus saida*), glacier lanternfish (*Benthosema glaciale*), whitespotted lanternfish (*Diaphus rafinesquii*), spotted lanternfish (*Myctophum punctatum*), mirror lanternfish (*Lampadena speculigera*), jewel lanternfish (*Lampanyctus inticarius*), rakery beaconlamp (*Lampanyctus macdonaldi*), Arctic telescope (*Protomyctophum arcticum*) and diamondcheek lanternfish (*Lampanyctus intricarius*), This group is not targeted by fisheries (apart from pearlside fisheries in 2008-2014, Directorate of Fisheries) and no landings were reported in 1996. The biomass of small pelagic fish in Icelandic waters is unknown and thus, estimated by the model with EE of 0.9.

Lantern fish species (of family Myctophidae) served as 72% of occurrence as prey, and thus, growth parameters for glacier lanternfish were used to calculate production and consumption (from fishbase.org). Equation 9 was used to calculate P/B with L_∞ and growth factor K from fishbase.org (8.5 cm and 0.4, respectively). P/B is equal to natural mortality (0.6027), as the fishing mortality is 0. Q/B was calculated with equation 10 with W_∞ as maximum weight of myctophidae from surveys (0.044 kg), resulting in Q/B of 6.52 year^{-1}.

Diet is based on Knutsen et al. (2023), where glacier lanternfish diet was studied in Icelandic waters and across the North Atlantic.

Invertebrates

Nephrops norvegicus

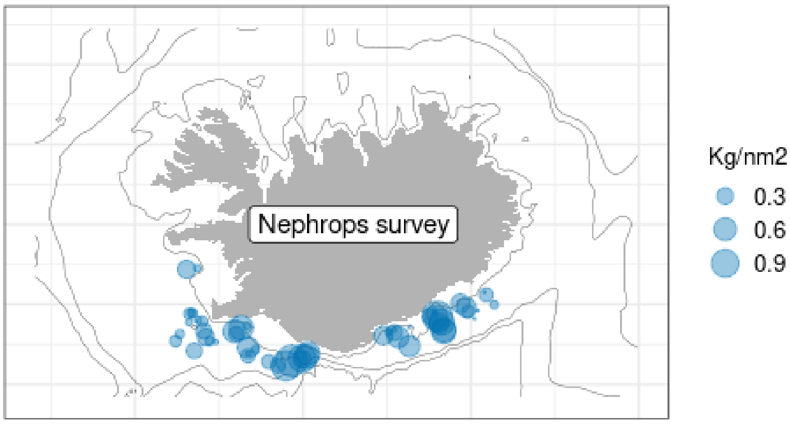

Figure 21. Geographical distribution and abundance of Norway lobster during nephrops survey in 1996.

Up until recently, Norway lobster (*Nephrops norvegicus*) was found on the southern shelf of Iceland in 10 distinct areas (Figure 21), at depths ranging from 100-300 m. In 2010, the stock began to collapse and in late 2021, all fishing of Norway lobster was banned on Icelandic fishing grounds. Biomass in 1996 was estimated at 12,625 tonnes (biomass of age 6+: 11,109 tonnes + 75.8 million recruits estimated to be 20 g). L_∞ is 80 mm (Eiríksson and Jónasson 2018), W_∞ is maximum weight from surveys and K is 0.06 (Bjarnason, 2016). P/B was assumed to be

1.5 $year^{-1}$ as in the Ecopath model of the North Atlantic (Gunétte et al. 2001). Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.15 (Christensen 1995).

Diet of Norway lobster in Icelandic waters is unknown and assumed to be the same as in the North Sea (Mackinson and Daskalov, 2007), where they primarily feed on infauna (45%), epifauna, (25%), demersal fish (10%), phytoplankton (15%) and detritus (5%).

Shrimp

Numerous species of shrimp are found in Icelandic waters (see species in appendix Table 38). The most abundant species is northern shrimp (*Pandalus borealis*), which has been commercially exploited in Icelandic waters since the early 1970´s. Northern shrimp are found all around Iceland, both offshore and in fjords. Other species of shrimp are found in less abundance and some only occasionally (Eydal and Jónsdóttir 2018). In the model, landings of northern shrimp is used as it is by far the most abundant. The biomass of shrimp in Icelandic waters is unknown and thus, estimated by the model with EE of 0.95. P/B was assumed to be the same as in the Norwegian Sea Ecopath model (Christensen, 2001) or 1.25 $year^{-1}$. Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.15 (Christensen 1995).

Diet of shrimps in Icelandic waters has not been investigated and assumed to be the same as in the North Sea (Mackinson and Daskalov, 2007). Shrimp mainly feed on detritus (32%), phytoplankton (27%), zooplankton (15%), epifauna (15%) and infauna (10%).

Epifauna

The key species included in the epifauna functional groups (FEP) are the common whelk (*Buccinum undatum*) and green sea urchins (*Strongylocentrotus droebachiensis*). Other species are sea cucumbers, starfish species (Ophiuroidea, Asteroidea) bryozoans, and other species of mollusks and urchins (see appendix Table 35). Available landings are taken from the Directorate of Fisheries (urchins 491.3 t and whelk 524.3 t). No available biomass estimates are available for epifauna in Icelandic waters and thus, estimated by the model with EE of 0.95. P/B was estimated using an empirical model for marine benthos (Tumbiolo and Downing 1994):

$$LogP = 0.24 + 0.96LogB - 0.21LogWm + 0.03T - 0.16Log(D + 1) \quad (11)$$

where B is the biomass of the functional group, Wm is the maximum body weight, T is surface temperature and D is depth. As biomass is unknown, a biomass "guestimate" of one million tonnes was used for the equation and the most common weight of the group in stomachs of predators (10 g) as maximum body weight, resulting in P/B of 0.78 year^{-1}. Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.15 (Christensen 1995).

Diet of epifauna in Icelandic waters is unknown and assumed to be the same as in the North Sea (Mackinson and Daskalov 2007). Epifauna mainly feeds on infauna (45%), phytoplankton (25%), detritus (20%) and other epifauna (10%).

Infauna

The infauna group (FIN) includes bivalves, annelids, and other burrowing sea worms (see species in appendix Table 36. As biomass is unknown, a biomass "guestimate" of one million tonnes was used for the equation and the most common weight of the group in stomachs of predators (17.6 g) as maximum body weight, resulting in P/B of 0.76 year^{-1}. Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.30 (Christensen 1995).

Diet of infauna in Icelandic waters is unknown and assumed to be 100% detritus in the model.

Lobsters and crabs

Several species of lobsters and crabs (FLC) are found in Icelandic waters, and the most common species are spider crab (*Hyas araneus*), European green crab (*Carcinus maenas*), Arctic lyre crab (*Hyas coarctatus*) and hermit crabs (*Pagarus pubescens*). Other species of crabs and lobsters are listed in appendix Table 37. Crabs are mostly found near the shore but are also common down to a few hundred meters.

The stock size of crabs (Decapoda: Brachyura) in Icelandic waters is poorly studies. Apart from stock size measurements of spider crabs in the 1980´s (Einarsson 1988), and more recently, stock size measures of a newly established population of rock crabs in Icelandic waters (Gíslason 2021a), little is known about the stock structure of other species. Crabs are mainly targeted by traps but crab harvesting is mostly experimental due to low marketing demands. The total biomass of lobsters and crabs in Icelandic waters is unknown and thus, estimated by the model with EE of 0.95. P/B and diet of lobsters and crabs in Icelandic waters has not been investigated and assumed to be the same as for Norway lobster. Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.15 (Christensen 1995).

Cephalopoda

The cephalopoda group (CEP) includes squids and octopuses. Only one squid species has been commercially exploited in Iceland i.e., the European flying squid (*Todarodes sagittatus*). Other squid species included in the model are bobtail squid (*Rossia glaucopis*), Boreoatlantic armhook squid (*Gonatus fabricii*) and Atlantic bobtail *(Sepiola atlantica*). Other species included in the model have not been identified to genus level from stomach content analysis (Genus: Todarodes, Cirroteuthis, Octopus, Histioteuthis, Gonatus, Rossia, Sepiola). The biomass of cephalopods in Icelandic waters is unknown and thus, estimated by the model with EE of 0.95. P/B, Q/B and diet was assumed to be the same as in the Norwegian Seas and Barents Sea Ecopath model (P/B = 2.44 $year^{-1}$, Q/B = 12 $year^{-1}$, Dommasnes et al. 2001). Cephalopods primarily feed on large zooplankton (62%), krill (15.3%) and small zooplankton (15.3%).

Krill

The krill group contains four species of euphausiids that are commonly found in Icelandic water i.e. *Meganyctiphanes norvegica*, *Thysanoessa inermis*, *Thysanoessa longicaudata* and *Thysanoessa raschii* (Einarsson 1945). Species of the Mysidae family occurring as prey are also included in this group. They are *Boreomysis nobilis*, *Boreomysis arctica, Erythrops abyssorum*, *Erythrops erythropthalma*, *Erythrops serrata*, *Mysideis insignis*, *Mysis mixta*, *Mysis oculate* and *Pseudomma truncatum*.

Krill plays an important ecological role and serves as an important link between phytoplankton and higher trophic levels (Astthorsson et al. 2007). Krill is known to be an important prey for both demersal (Pálsson and Björnsson 2011) and pelagic fish (Óskarsson et al. 2016), seabirds (Lilliendahl and Solmundsson 1997) and marine mammals (Sigurjónsson and Vikingsson 1997).

Krill is not harvested in Icelandic waters, but experimental fishing has been attempted in Ísafjarðardjúp in 2013 (Gíslason 2021b) and 2018 (Sigurðardóttir and Gíslason 2021). The biomass of krill in Icelandic waters is unknown and thus, estimated by the model with EE of 0.95. P/B and diet ratios are based on the Norwegian Seas and Barents Sea Ecopath model (Dommasnes et al. 2001). Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.15 (Christensen, 1995).

Krill primarily feeds on phytoplankton (50%), detritus (25%) and large zooplankton (25%) (Dommasnes et al. 2001).

Zooplankton

Zooplankton is split into three functional groups i.e., small zooplankton (<2 mm), large zooplankton (>2 mm) and gelatinous zooplankton. Small zooplankton include *Temora longicornis, Vargula norvegica* and *Discoconchoecia elegans*. Species in the large zooplankton group are listed in appendix Table 39. Gelatinous zooplankton are species belonging to family/class/phylum Hydrozoa, Scyphozoa, Sagittoidea and Ctenophora.

Zooplankton biomass abundance and species composition in Icelandic waters has been monitored annually in late May and early June since 1970. The copepod *Calanus finmarchicus* is the most abundant species of zooplankton in Icelandic waters (Gíslason and Astthorsson 2004). Zooplankton biomass is generally highest northeast off Iceland and lowest on the coastal shelves (Gíslason and Astthorsson 2004). P/B and diet rations are based on the Norwegian Seas and Barents Sea Ecopath model (Dommasnes et al. 2001). Q/B was estimated by the model by providing a production/consumption (P/Q) ratio of 0.15 (Christensen 1995).

Primary production

Primary production (uptake of ^{14}C) has been monitored annually in Icelandic waters since 1958 and the overall means range from 4.3-9.2 mg $Cm^{-2}h^{-2}$ (Gudmundsson 1998). The phytoplankton flora ranges in size from 1-300 µm and consists mainly of diatoms in spring, with flagellates and dinoflagellates later in the year (Pálsson et al. 2012). Zhai et al. (2012), evaluated the annual primary production in Icelandic waters with data from years 1958 to 1982. Primary production south of Iceland was estimated to be 309 g Cm^{-2} y^{-1} and 251 g Cm^{-2} y^{-1} in the north. The average primary production is 280 g C m^{-2} y^{-1}. Total primary production (average from April-August) in Icelandic waters amounts to 2,800 g wet wt m^{-2} y^{-1} (based on 0.1 g C=0.2 g dry weight = 1 g wet weight) (Matthews and Heimdal 1980). The maximum reported phytoplanktonic biomass was approximately 1,800 mg Cm^{-2}, with average phytoplankton standing stock biomass in April-August being approx. 1,150 mg Cm^{-2} (11.5 g wet wt m^{-2} using the above conversion). Using a biomass of 11.5 g wet wt m^{-2} and productivity of 2,800 g wet wt m^{-2}, a P/B ratio of 243.47 $year^{-1}$ was calculated.

Unbalanced Ecopath model

Eight functional groups were unbalanced when using the basic input parameters, i.e. the energy demand placed upon these groups exceeded its production (Table 25). The diet for the unbalanced model is shown in Table 26.

Table 25. Basic estimates from the initial unbalanced model. Numbers highlighted in red signify unbalanced or ecological issues. Numbers highlighted in blue have been estimated by Ecopath.

Code	Functional group	TL	Biomass	P/B	Q/B	EE
FCD.juv	Juvenile cod	4.270	165513.08	0.317500	5.1749	2.3138616
FCD.adult	Adult cod	4.514	517632.80	0.491519	1.8178	0.7706288
FHA.juv	Juvenile haddock	3.540	39982.04	0.436300	5.9442	3.2317567
FHA.adult	Adult haddock	4.061	108323.00	0.818770	2.4700	0.8251171
FSA.juv	Juvenile saithe	4.216	52744.46	0.403000	5.4280	2.9666086
FSA.adult	Adult saithe	4.440	127945.60	0.595700	1.9749	0.6150822
FGH	Greenland halibut	4.523	147582.30	0.307135	2.1300	0.5212503
FRF	Redfish	3.909	496681.40	0.407500	3.1000	2.2191458
FHE	Herring	3.567	322215.00	0.843800	4.5389	1.6656283
FCA	Capelin	3.613	1680052.0	1.293693	5.2300	1.8769453
FMI	Migratory fish	3.669	600000.00	0.540600	5.1800	0.7483758
FFF	Flatfish	4.172	1155613.8	0.661718	2.3981	0.7000000
SSR	Skates and rays	4.247	50000.00	0.276293	3.1200	0.8650722
SSD	Small sharks	4.380	5000.00	0.158793	2.2400	0.7606710
SSH	Large sharks	4.927	1000.00	0.060000	1.1900	0.6011856
PIN	Seals	5.118	2093.00	0.142000	14.457	0.5985915
LOB	Norway lobster	3.093	12625.00	1.500000	16.666	0.5332504
FSD	Sand eel	3.451	2171560.5	0.400000	4.9000	0.9000000
FDF	Other demersal fish	3.953	986287.32	1.315000	3.1000	0.9000000
FBP	Small pelagic fish	3.496	967628.72	0.602700	6.5200	0.9000000
PWN	Shrimps	2.602	1256920.3	1.250000	8.3333	0.9500000
FOC	Other codfish	4.709	46153.38	0.604900	2.5300	1.1635854
FDC	Demersal commercial	4.668	138212.70	0.296601	2.4100	9.2427540
CEP	Cephalopods	3.560	413756.20	2.440000	12.000	0.9500000
WHT	Toothed whale	4.560	75725.00	0.040000	5.7304	0.0000003
WMW	Minke whale	4.105	70889.00	0.030000	6.5802	0.0000004
WTO	Other toothed whale	4.587	44118.00	0.030000	10.277	0.0003701
WHB	Baleen whale	3.636	434857.00	0.030000	4.4100	0.0000000
SB	Seabirds	4.601	2500.84	0.110000	39.340	0.6213853
FEP	Epifauna	2.611	13441759.	0.780000	5.2000	0.9500000
FIN	Infauna	2.000	46910179.7	0.756500	2.5216	0.9500000
FLC	Lobsters and crabs	3.794	71233.37	2.500000	16.666	0.9500000
FKR	Krill	2.407	8249711.3	2.500000	8.3333	0.9500000
ZG	Gelatinous	3.296	42955.68	10.000000	22.222	0.9500000
ZL	Large zooplankton	2.631	9407303.5	5.000000	16.666	0.9500000
ZS	Small zooplankton	2.000	7086179.3	13.000000	43.333	0.9500000
Phytoplankto		1.000	12151000.0	243.000000	0.0000	0.1304158
Detritus		1.000	5680279270	0.500000	0.0000	0.0674937

Table 26. Diet matrix from the unbalanced Ecopath model. Diets are weighted proportions (sum to 1).

Prey	1	2	3	4	5	6	7	8	9	10	11	12
1. Cod juvenile	0.0305819	0.0214689	0.0006532	0.0007010	0.0024792	0.0031821	0.0042421	0.0013666	-	-	-	-
2.Cod adult	-	-	-	-	-	-	-	-	-	-	-	-
3. Haddock juvenile	0.0083725	0.0209606	0.0006532	0.0007284	0.0056854	0.0167034	0.0019828	0.0097159	-	-	-	0.0000013
4. Haddock adult		-	-	-	-	-	-	-	-	-	-	-
5. Saithe juvenile	0.0001189	0.0019476	-	0.0000434	-	0.0004885	0.0032200	0.0000177	-	-	-	0.0153998
6. Saithe adult	-	-	-	-	-	-	-	-		-		-
7.Greenland halibut	-	0.0002739	-	-	-	-	0.0029348	-	-	-	-	-
8. Redfish	0.0038762	0.0168866	0.0007465	0.0014151	0.0001025	0.0025133	0.0109080	0.0168071	-	-	-	0.0848114
9. Herring	0.0105417	0.0463131	0.0008399	0.0062361	0.0257866	0.0672353	0.1024152	0.0080464	-	-	-	0.0091791
10. Capelin	0.5274779	0.5675059	0.0700946	0.4780249	0.2959348	0.4969310	0.3351124	0.1325170	0.0245512	-	0.0068457	0.1379933
11. Migratory fish	0.0025601	0.0378255	0.0004666	0.0003458	0.0172739	0.0863967	0.1637690	0.0229711	-	-	0.0042953	0.0003740
12.Flatfish	0.0067942	0.0291684	0.0044795	0.0038736	0.0002485	0.0005577	0.0003333	0.0008692	-	-	0.1284580	0.0096971
13. Skates and rays	-	0.0003489	-	0.0000130	-	-	0.0025739	-	-	-	-	-
14. Small sharks	-	-	-	-	-	-	-	-	-	-	-	-
15. Large sharks	-	-	-	-	-	-	-	-	-	-	-	-
16. Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-
17. Nephrops	0.0003245	0.0095667	0.0004666	0.0017733	-	-	-	-	-	-	-	0.0015776
18. Sand eel	0.0325602	0.0267234	0.0799130	0.0303747	0.2573725	0.0605393	0.0073576	0.0369209	0.0089698	-	-	0.1057660
19. Demersal fish	0.0183707	0.0355792	0.0047407	0.0067808	0.0612945	0.0572264	0.1371283	0.0420001	0.0028883	-	-	0.0162760
20. Small pelagic fish	0.0047735	0.0079489	0.0023330	0.0015671	0.0090532	0.0369361	0.0091684	0.0572884	-	-	0.0041074	0.0001349
21. Shrimp	0.1517538	0.0843213	0.0924978	0.0239664	0.0087612	0.0087537	0.0583017	0.1233566	-	-	0.0015436	0.0290933
22. Other codfish	0.0004022	0.0020880	-	0.0000905	0.0034485	0.0018804	0.0001673	0.0009075	-	-	-	-
23. Demersal commercial fish	0.0009063	0.0101254	0.0000933	0.0005825	0.0000932	0.0000230	0.0026499	0.0000238	-	-	-	0.1144903
24. Cephalopods	0.0008424	0.0023789	0.0027063	0.0004399	0.0005281	0.0067031	0.0762223	0.0264055	-	-	-	0.0003234
25. Tooth whale	-	-	-	-	-	-	-	-	-	-	-	-
26. Minke whale	-	-	-	-	-	-	-	-	-	-	-	-
27. Other toothe whale	-	-	-	-	-	-	-	-	-	-	-	-
28. Baleen whale	-	-	-	-	-	-	-	-	-	-	-	-
29. Seabirds	-	-	-	-	-	-	-	-	-	-	-	-
30. Epifauna	0.0088885	0.0054780	0.1746745	0.1718928	0.0004349	0.0024939	0.0012388	0.0000603	0.0027651	-	0.0002684	0.2705232
31. Infauna	0.0227600	0.0033904	0.3835308	0.1547763	0.0012209	0.0007518	0.0003360	0.0106341	0.0224577	-	0.0014765	0.1545158
32. Lobsters and crabs	0.0138655	0.0073674	0.0216975	0.0142610	0.0003200	0.0002945	0.0000319	0.0004370	0.0036926	-	0.0000134	0.0133418
33. Krill	0.1087035	0.0284808	0.1174926	0.0685213	0.2936497	0.1218427	0.0673898	0.3919944	0.3800005	0.0800000	0.7770171	0.0263941
34. Gelatinous zooplankton	0.0057051	0.0203824	0.0037002	0.0106040	0.0011557	0.0049794	0.0060112	0.0275373	0.0015766	-	0.0000134	0.0003110
35. Large zooplankton	0.0398185	0.0134695	0.0382082	0.0229718	0.0151557	0.0235666	0.0065041	0.0900757	0.5437304	0.9200000	0.0759607	0.0097527
36. Small zooplankton	0.0000007	0.0000000	0.0000110	0.0000154	-	-	-	0.0000464	0.0093673	-	-	0.0000417
37. Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-
Detritus	-	-	-	-	-	-	-	-	-	-	-	-

Table 27 continued. Diet matrix from the unbalanced Ecopath model. Diets are weighted proportions (sum to 1).

Predator/Prey	13	14	15	16	17	18	19	20	21	22	23	24
1. Cod juvenile	0.0275000	0.0003000	-	0.3614000	-	-	-	-	-	0.0304000	0.139	-
2.Cod adult							-	-	-	-	-	
3. Haddock juvenile	0.0008578	0.0080528	-	0.0097096	-	-	-	-	-	0.0166455	0.0138074	-
4. Haddock adult		-	-	-	-	-	-	-	-	-	0.0365696	-
5. Saithe juvenile	0.0209706	-	-	0.0979951	-	-	-	-	-	0.0175207	0.0109632	-
6. Saithe adult				-	-	-	-	-	-	-	-	-
7.Greenland halibut	-	-	-	-	-	-	-	-	-	-	0.0002149	-
8. Redfish	0.0618156	0.0446615	0.5109056	0.0402769	-	-	-	-	-	0.0162446	0.1352918	-
9. Herring	0.0352981	0.0058812	-	0.0381416	-	-	0.0019617	-	-	0.2089033	0.0740270	-
10. Capelin	0.1234258	0.0003981	-	0.0214870	-	-	0.0850553	-	-	0.0252261	0.0676111	-
11. Migratory fish	0.0800128	0.0780255	-	-	-	-	0.0035891	-	-	0.2892236	0.0017402	-
12.Flatfish	0.0181309	-	-	0.0791602	-	-	0.0021692	-	-	0.0029588	0.0820768	-
13. Skates and rays	0.0090797	-	-	-	-	-	-	-	-	0.0000593	0.0230818	-
14. Small sharks	-	-	-	-	-	-	-	-	-	0.0035439	-	-
15. Large sharks	-	-	-	-	-	-		-	-	-	-	-
16. Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-
17. Nephrops	0.0000629	-	-	-	-	-		-	-	0.0073283	0.0002315	-
18. Sand eel	0.0321283	0.0181505	-	0.1627259	-	-	0.0042019	-	-	0.0216080	0.0262503	-
19. Demersal fish	0.1450743	0.0983874	0.0055926	0.0258473	0.095238	-	0.1428779	-	-	0.1762952	0.0135039	-
20. Small pelagic fish	0.0052167	0.2083348	0.2984228	-	-	-	0.0084038	-	-	0.0534696	0.0003354	0.0705645
21. Shrimp	0.1250770	0.1649909	-	-	-	-	0.235156	-	0.0100000	0.0434305	0.0031317	-
22. Other codfish	-	-	-	0.0096646	-	-		-	-	0.0345492	0.0294799	-
23. Demersal commercial fish	0.0003279	0.0239775	0.1850788	0.1535781	-	-		-	-	0.0212397	0.0694357	-
24. Cephalopods	0.0162297	0.1393230	-	-	-	-	0.0375606	-	-	0.012908	0.0009816	-
25. Tooth whale	-	-	-	-	-	-	-	-	-	-	-	-
26. Minke whale	-	-	-	-	-	-	-	-	-	-	-	-
27. Other tooth whale	-	-	-	-	-	-	-	-	-	-	-	-
28. Baleen whale	-	-	-	-	-	-	-	-	-	-	-	-
29. Seabirds	-	-	-	-	-	-	-	-	-	-	-	-
30. Epifauna	0.0100376	0.0046525	-	-	0.2380952	-	0.0272073	-	0.1500000	0.0008791	0.2149981	-
31. Infauna	0.0941869	0.0002967	-	-	0.4285714	-	0.0307868	0.0000000	0.1000000	0.0004910	0.0196324	-
32. Lobsters and crabs	0.0199725	0.0004107	-	-	-	-	0.0068123	-	-	0.0078066	0.0093290	-
33. Krill	0.0950917	0.0412949	-	-	-	0.8039216	0.2494565	0.5200000	-	0.0079112	0.0027938	0.1542338
34. Gelatinous zooplankton	0.0014573	0.1619252	-	-	-	-	0.1051264	-	-	0.0002534	0.0231402	-
35. Large zooplankton	0.0779873	0.0008378	-	-	-	0.1960784	0.0596285	0.4500000	0.1500000	0.0010290	0.0019499	0.6209677
36. Small zooplankton	-	-	-	-	-	-	0.0000052	0.0300000	-	-	0.0000052	0.1542338
37. Phytoplankton	-	-	-	-	0.1904761	-	-	-	0.2700000	-	-	-
Detritus	-	-	-	-	0.0476190	-	-	-	0.3200000	-	-	-

Table 28 continued. Diet matrix from the unbalanced Ecopath model. Diets are weighted proportions (sum to 1).

Predator/Prey	25	26	27	28	29	30	31	32	33	34	35	36
1. Cod juvenile	-	-	-	-	0.0287000	-	-	-	-	-	-	-
2.Cod adult	0.0001000	0.0069721	0.0238388	-	-	-	-	-	-	-	-	-
3. Haddock juvenile	-	-	-	-	0.0004140	-	-	-	-	-	-	-
4. Haddock adult	0.0000291	-	0.0047614	-	-	-	-	-	-	-	-	-
5. Saithe juvenile	-	-	-	-	0.0502622	-	-	-	-	-	-	-
6. Saithe adult	-	-	0.0160830	-	-	-	-	-	-	-	-	-
7.Greenland halibut	-	-	-	-	-	-	-	-	-	-	-	-
8. Redfish	0.0000902	-	-	-	0.0022357	-	-	-	-	-	-	-
9. Herring	-	0.0069721	0.3022931	-	0.0033618	-	-	-	-	-	-	-
10. Capelin	0.0015181	0.2490039	0.0158714	0.1668436	0.2333923	-	-	-	-	-	-	-
11. Migratory fish	-	-	0.0365042	-	0.0101849	-	-	-	-	-	-	-
12.Flatfish	-	-	-	-	0.0263317	-	-	-	-	-	-	-
13. Skates and rays	-	-	-	-	-	-	-	-	-	-	-	-
14. Small sharks	-	-	-	-	-	-	-	-	-	-	-	-
15. Large sharks	-	-	-	-	-	-	-	-	-	-	-	-
16. Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-
17. Nephrops	-	-	-	-	-	-	-	-	-	-	-	-
18. Sand eel	0.0005500	0.3585657	-	0.0011451	0.4399727	-	-	-	-	-	-	-
19. Demersal fish	-	-	-	-	0.0866961	-	-	0.3460674	-	-	-	-
20. Small pelagic fish	0.0000291	-	0.0188340	-	0.0173889	-	-	-	-	-	-	-
21. Shrimp	-	-	0.0188340	-	0.0002914	-	-	0.0007490	-	0.0279474	-	-
22. Other codfish	-	-	0.0003914	-	0.0241788	-	-	-	-	-	-	-
23. Demersal commercial fish	-	-	-	0.0005700	0.0068727	-	-	-	-	-	-	-
24. Cephalopods	0.9976834	-	0.5625883	-	0.0119668	-	-	-	-	0.0817541	-	-
25. Tooth whale	-	-	-	-	-	-	-	-	-	-	-	-
26. Minke whale	-	-	-	-	-	-	-	-	-	-	-	-
27. Other toothe whale	-	-	-	-	-	-	-	-	-	-	-	-
28. Baleen whale	-	-	-	-	-	-	-	-	-	-	-	-
29. Seabirds	-	-	-	-	-	-	-	-	-	-	-	-
30. Epifauna	-	-	-	-	0.0006040	0.1000000	-	0.2666666	-	0.0199942	-	-
31. Infauna	-	-	-	-	0.0005532	0.4500000	-	0.2973782	-	-	-	-
32. Lobsters and crabs	-	-	-	-	0.0006422	-	-	0.0157303	-	0.0538733	-	-
33. Krill	-	0.3784860	-	0.7192158	0.0421970	-	-	-	-	-	-	-
34. Gelatinous zooplankton	-	-	-	-	0.0000763	-	-	-	-	-	-	-
35. Large zooplankton	-	-	-	0.1122253	0.0136332	-	-	-	0.2500000	0.3265723	0.0500000	-
36. Small zooplankton	-	-	-	-	-	-	-	-	-	0.3265723	0.5500000	-
37. Phytoplankton	-	-	-	-	-	0.2500000	-	0.0734082	0.5000000	0.1632861	0.2500000	0.9500000
Detritus	-	-	-	-	-	0.2000000	1	-	0.2500000	-	0.1500000	0.0500000

Pre-balancing

To improve the model, a set of pre-balancing diagnostics were performed on the data to identify issues of model structure and data quality. These pre-balancing diagnostics were performed on biomasses, biomass ratios between trophic levels, vital rates, vital rate ratios, total production, and total removals (and slopes thereof) across the taxa and trophic levels in any given energy budget (Link 2010). In addition, the diet matrix was thoroughly examined prior to pre-balancing diagnostics.

Visualization of fish diet data

The diet matrix is one of the first components in the model that is revisited and adjusted to achieve model balance (Heymans et al. 2016). Diet information for this model was generated using stomach sample data from the MFRI fish stomach database, collected between 1979-2022. To examine whether the average ratio of the whole period used in the model reflects true dynamics, an exploration of stability between years is crucial.

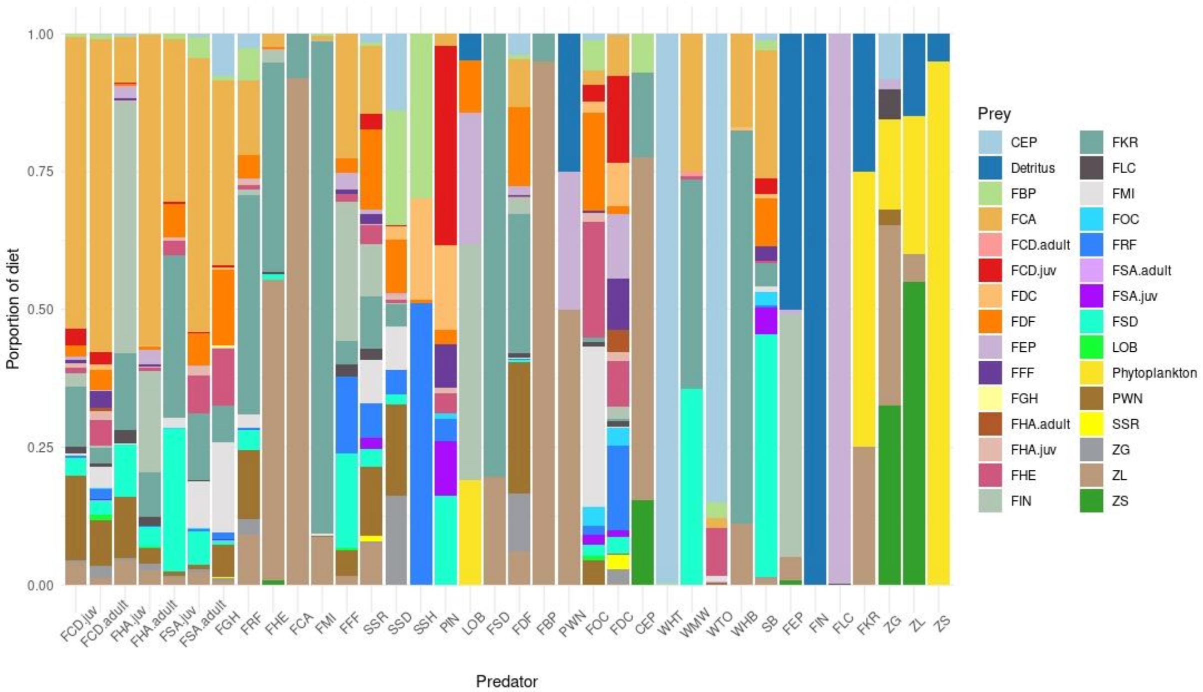

Figure 22. Proportion of diet for each functional group in the Icelandic Ecopath model. The data includes analyzed stomachs from the Marine and Freshwater Research Institute and for missing groups, ratio from literature.

Using long-term primary data creates the opportunity to generate a range of plausible diet ratios which can be used to address the uncertainty in the model outcome. The MFRI has collected and analyzed a total of 402,824 stomachs with prey in the period between 1979-2022. The amount of analyzed stomach content differs between groups in the model (Table 1), and for some groups, the number of stomachs is low. Small pelagic fish, sand eel and capelin, for instance only have few stomachs analyzed, while cod stomachs account for more than half of all analyzed stomachs. Prey in stomachs can also vary between years, and the range in proportion, and thus, visualizing the data in time can be useful during the balancing process.

Cod diet

Figure 23 and Figure 24 show the total biomass weighted proportion of prey group found in juvenile and adult cod stomachs in all available years. Cod diet has been stable throughout the years, where they mostly feed on capelin, prawn, and krill.

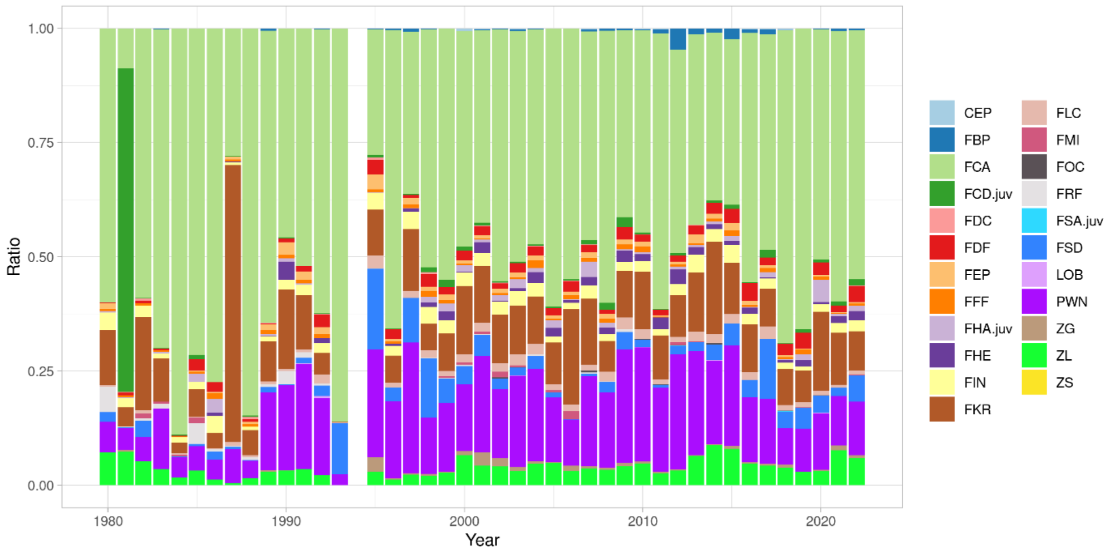

Figure 23. Prey weight ratio of juvenile cod (FCD.juv) from 1980-2022.

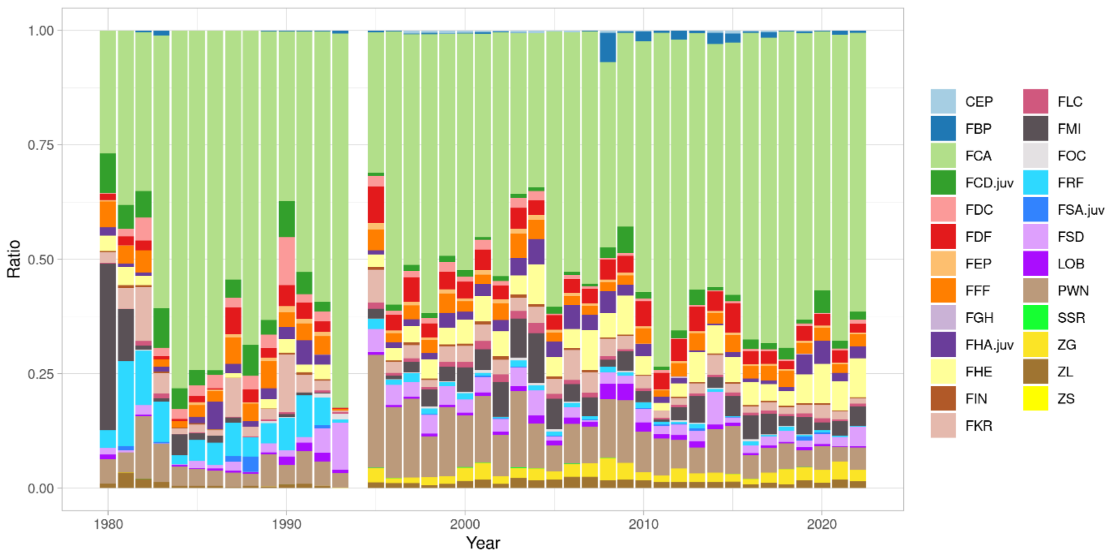

Figure 24. Prey weight ratio of adult cod (FCD.adult) from 1980-2022.

Haddock diet

Most of the juvenile haddock data is from 1997-2022. The ratio is relatively stable throughout the period but in the beginning of the period from 1997-2003, they mostly consumed sand eel, shrimp, infauna and epifauna. Later, sand eel became less abundant in stomachs of juveniles and adults. This shift can be explained by the difference in sampling but in 2006, stomach sampling of haddock during IGFS began. Prior to 2006, haddock stomach content had mostly been collected during summer months (Sólmundsson et al. 2024). The year 1979 is highly distinct from other years, where they prey solely on large zooplankton (Figure 25).

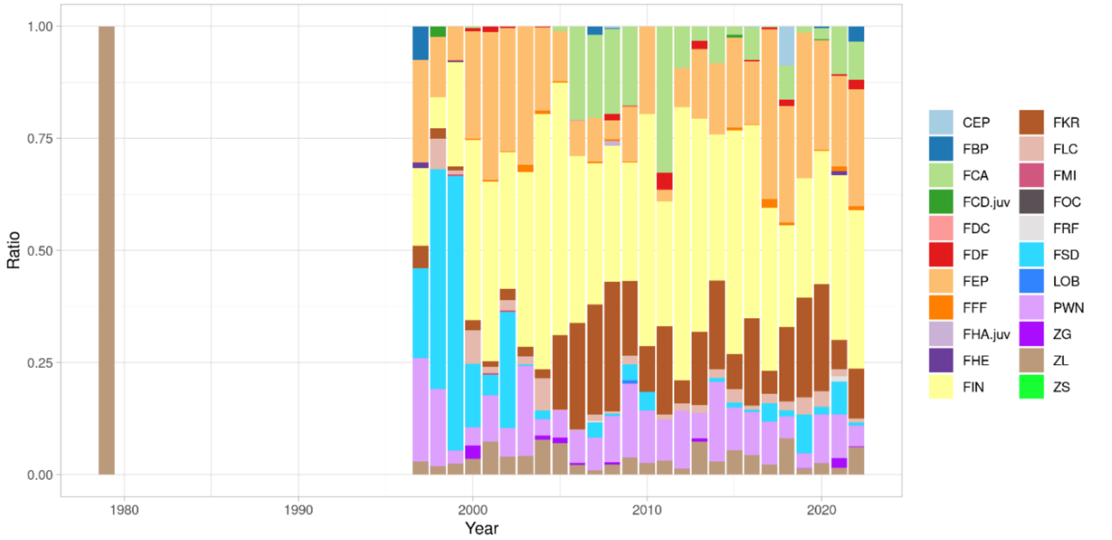

Figure 25. Prey weight ratio of juvenile haddock (FHA.juv) from 1979-2022.

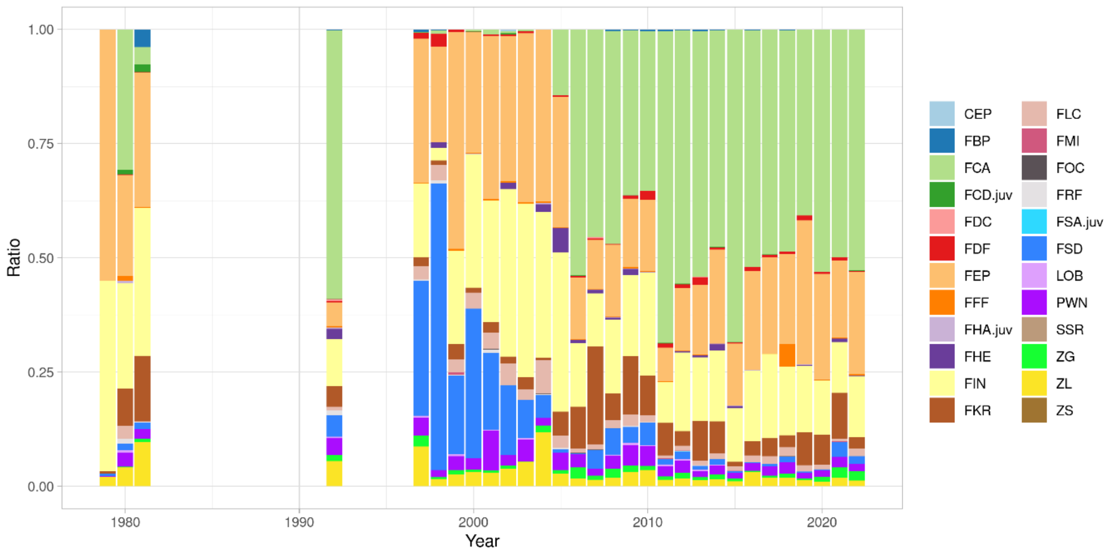

Figure 26. Prey weight ratio of adult haddock (FHA.adult) from 1980-2022.

Saithe diet

The juvenile saithe diet mainly consists of sand eel, capelin, and krill. From 1998, sand eel as prey has gradually declined, but the same is seen in adults and other species, such as haddock. Adult saithe diet is more variable, but capelin has become more important throughout the years. In 2016, the IGFS (which takes place in spring) included sampling of saithe stomachs, and capelin is abundant during that time of the year (Figure 28).

Figure 27. Prey weight ratio of juvenile saithe (FSA.juv) from 1980-2021.

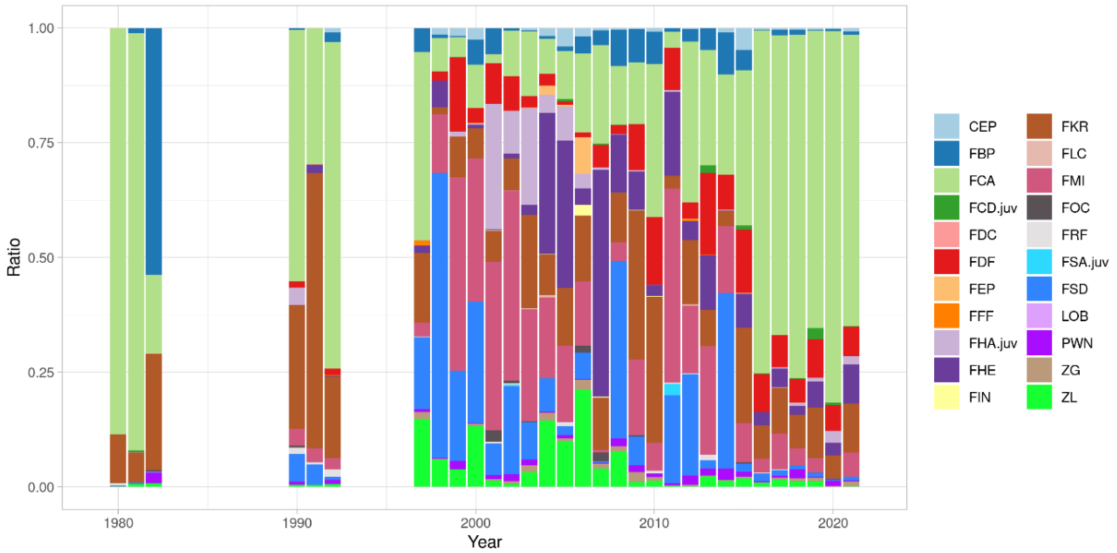

Figure 28. Prey weight ratio of adult saithe (FSA.adult) from 1980-2021.

Greenland halibut diet

Greenland halibut diet ratios have shifted from high proportion of capelin in stomachs to higher proportions of herring. Other ratios have been relatively consistent throughout the period (Figure 29). The year 1981 has an unusually high ratios of large zooplankton but few samples are behind (only five fish analyzed).

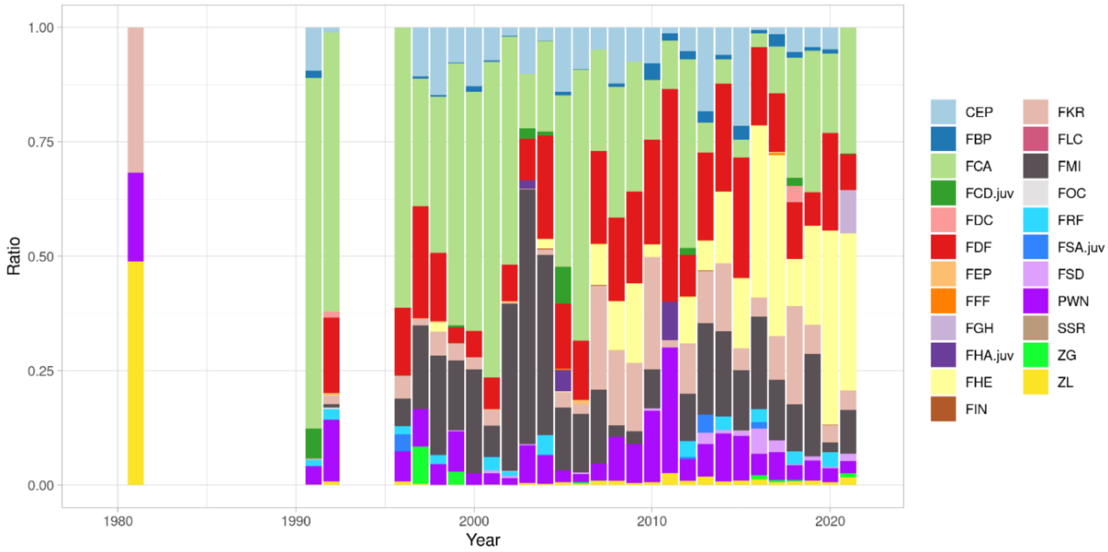

Figure 29. Prey weight ratio of Greenland halibut (FGH) from 1981-2021.

Redfish diet

Redfish diet ratios have been more or less stable since 1980, where they mainly feed on krill (FKR) and shrimp (PWN) (Figure 30).

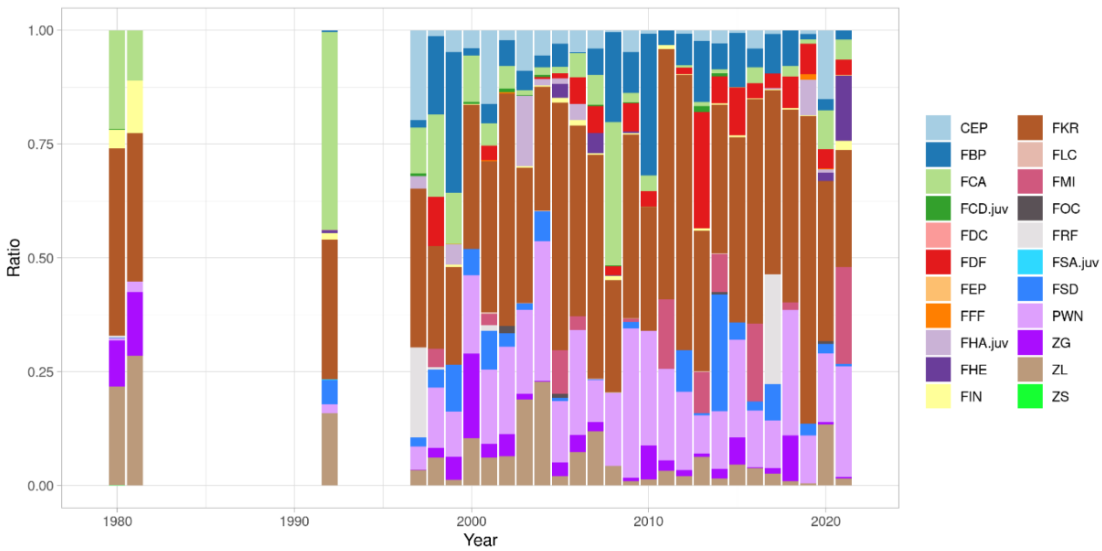

Figure 30. Prey weight ratios of redfish (FRF) from 1980-2021

Flatfish diet

Flatfish diet ratios are highly variable. The reason for this is that from 1980-2005, long rough dab was predominantly analyzed. From 2008-2013, long rough dab was not present in samples but more effort was put on plaice sampling. In the most recent years, only halibut has been examined and only a few samples collected. Due to halibut size, the preference of prey is different, as they feed on larger prey (Figure 30).

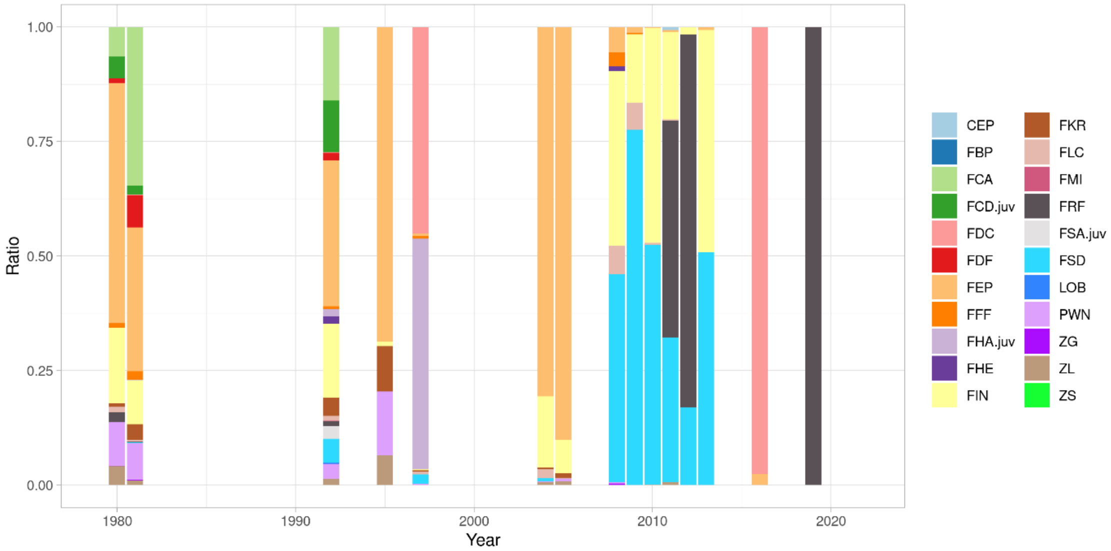

Figure 31. Prey weight rations of the flatfish (FFF) group from 1980-2019.

Herring diet

Herring diet has been sporadically analyzed. Apart from 2017, herring primarily feeds on krill and large zooplankton (ZL). In 2017, one Norway pout was in one herring sample and therefore does not reflect the herring diet.

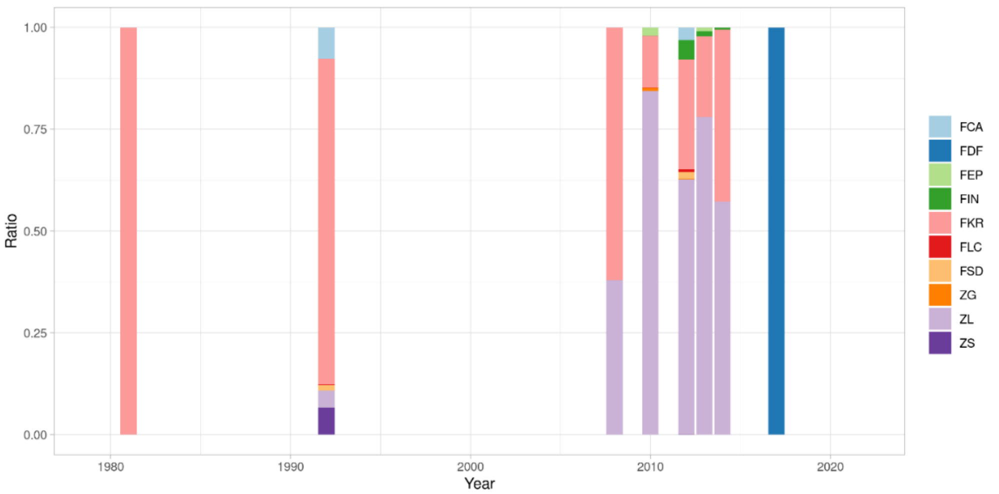

Figure 32. Prey weight rations of herring (FHE) from 1981-2017.

Skates and rays diet

The food composition of skates and rays is variable between years and no obvious pattern can be observed. In some years, large zooplankton is predominant as prey, but in other years, demersal or pelagic fish are in greater quantity. In 2002, one redfish was consumed by a spinetail ray.

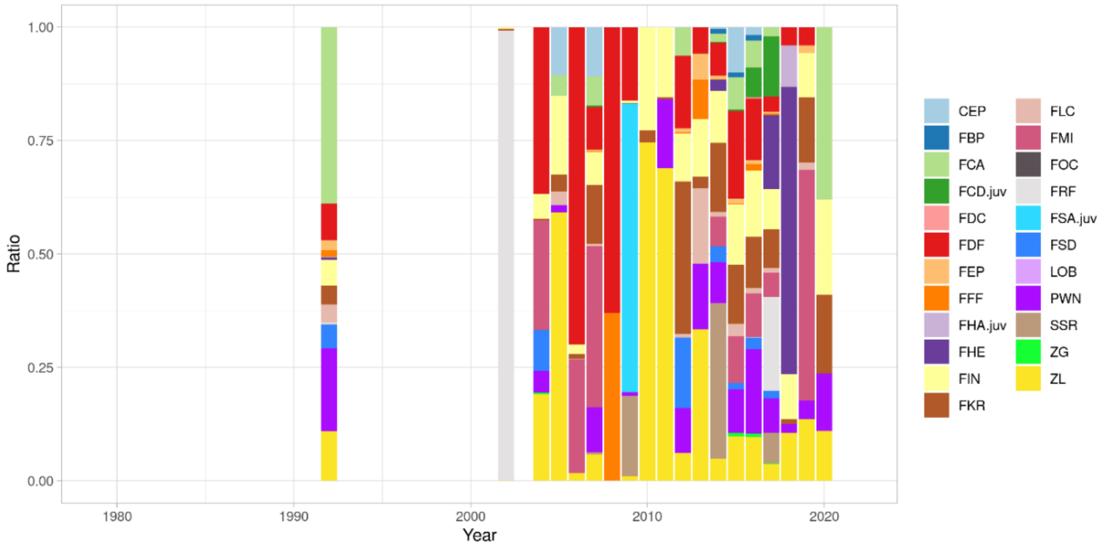

Figure 33. Prey weight ratio of skates and rays (SSR) from 1992-2020.

Small shark diet

Small shark diet ratios are relatively stable throughout the period, where they feed on both demersal and pelagic fish, as well as on invertebrates and zooplankton.

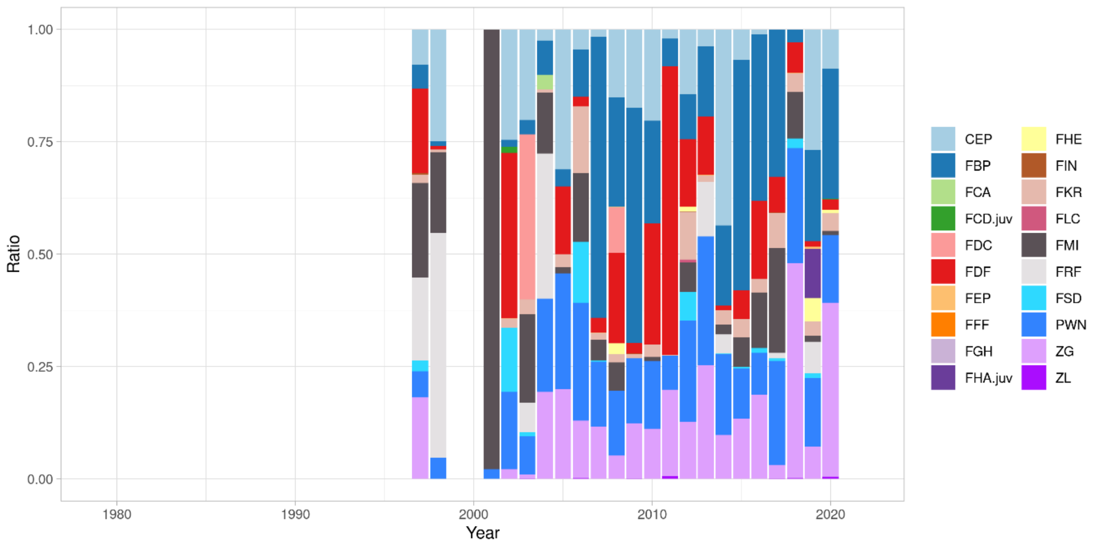

Figure 34. Prey weight ratio of small sharks (SSD) from 1997-2020.

Large shark diet

All stomach samples from the large sharks group (SSH) are from Greenland shark, which feeds on both demersal and pelagic fish.

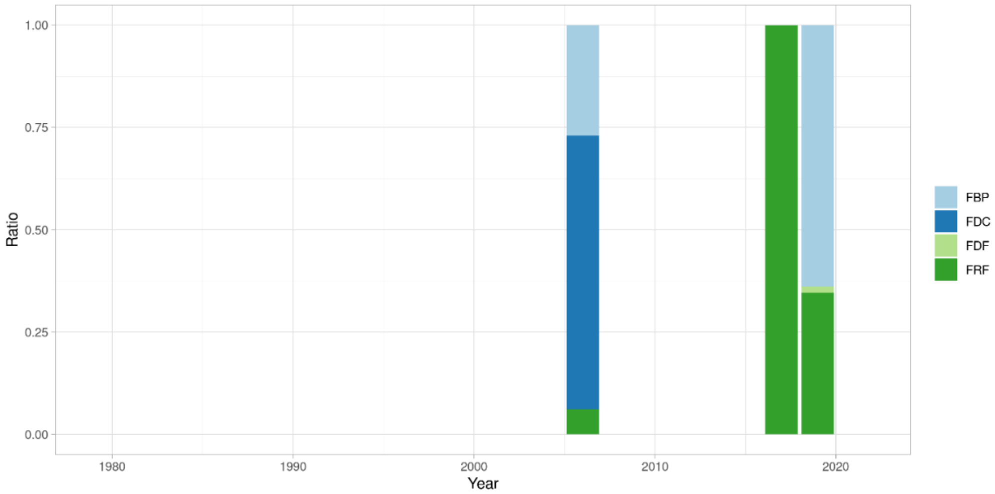

Figure 35. Prey weight ratio of large sharks (SSH) in 2009, 2018 and 2019.

Demersal fish diet

Species in the demersal fish group mainly feed on Shrimp and krill. Two years, 1980, 1998, 2003 and 2009 are different, probably due to fewer samples those years.

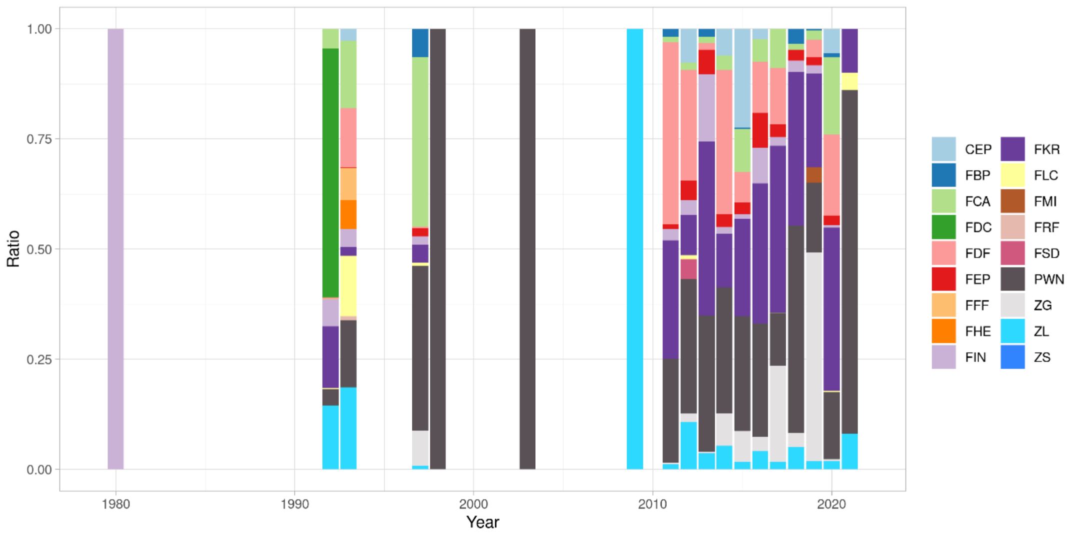

Figure 36. Prey weight ratio of demersal fish group (FDF) from 1980-2021.

Commercial demersal fish diet

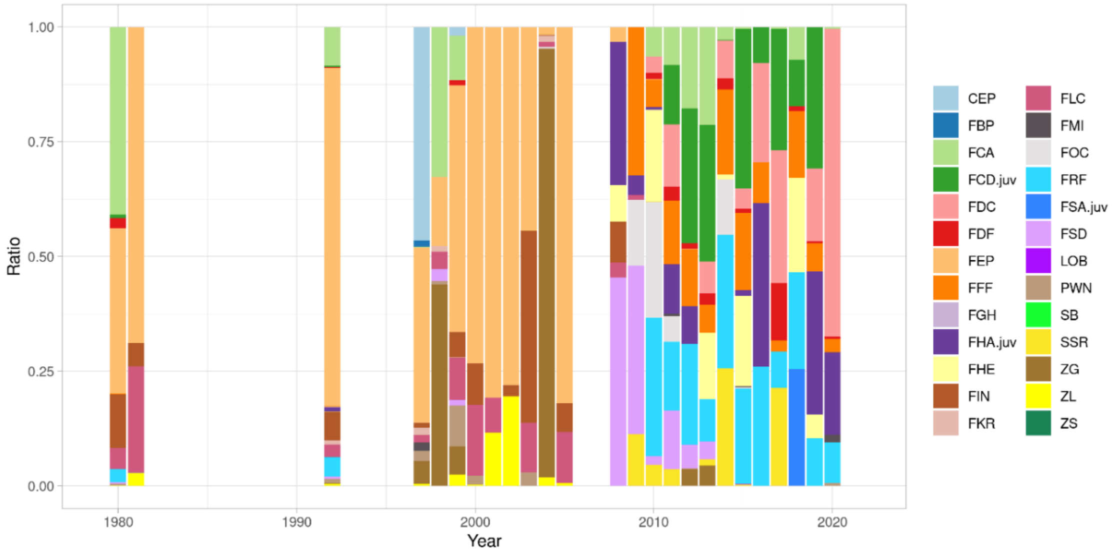

Figure 37. Prey weight ratio of commercial demersal fish group (FDC) from 1980-2020.

The prey weight ratio of species in the commercial demersal group (FDC) from 1980-2005 is different from the ratio in 2009-2020. In the former period, they primarily preyed on epifauna (FEP) and zooplankton. In the later period, the ratio is more diverse, where they prey on more fish groups. The reason could be that more of Atlantic wolffish diet was analyzed in the previous period and more of monkfish diet in the later period.

Other codfish diet

The prey weight ratio of other codfish group (FOC) is relatively stable throughout the period, where they mainly feed on pelagic fish and demersal fish.

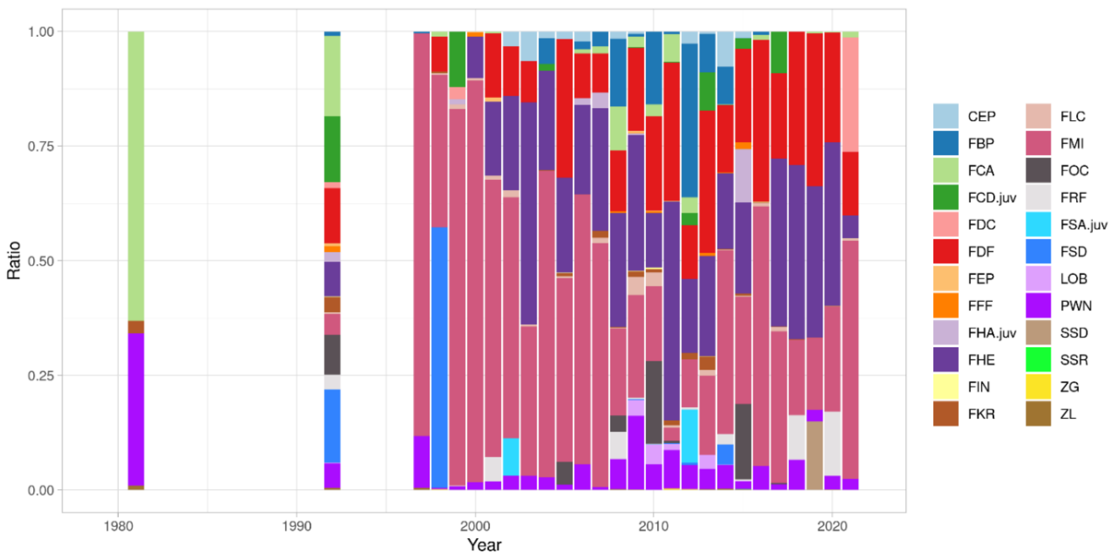

Figure 38. Prey weight ratio of other codfish group (FOC) from 1981 to 2021.

Diet modification

- In 1979, juvenile haddock diet consisted exclusively of large zooplankton (ZL), but from 1997-2022, the proportion of that group is low (Figure 25). The juvenile haddock diet was modified and mean values from 1997-2022 were used (year 1979 excluded).
- Halibut diet may not be representative of overall flatfish group (FFF) consumption (due to its size). In some cases, halibut stomach content was removed from the flatfish group. For example, in 2019, only one flatfish (halibut) was examined which had eaten one redfish (Figure 31). The consumption ratio of flatfish (FFF) on redfish (FRF) was lowered substantially. Also, in 2016, one halibut ate one spotted wolffish. Predation of the flatfish group (FFF) on the demersal commercial fish group (FDC) was lowered from 11% to 0.03 %.
- Juvenile saithe (FSA.juv) consumed one halibut in 2010 (Figure 27) and was removed, as juvenile saithe did not consume flatfish in any other year.
- Self-predation of redfish (FRF) only occurred in high ratios in 1997 and 2017 (Figure 59). Self-predation of redfish was lowered from 1.6% to 0.2%.
- Self-predation of the flatfish group (FFF) in the period is rare (Figure 31) and was lowered by 50%.
- Small sharks (SSD) were present in other codfish group (FOC) diet in 2019 (Figure 38). In this case, a large tusk ate a small velvet belly. As this is uncommon, SSD was removed from FOC diet.
- The flatfish group (FFF) as prey was removed from migratory fish (FMI) diet to balance.
- The juvenile-adult ratio of haddock in stomachs of demersal commercial fish group (FDC) was adjusted. Juvenile ratio was increased, and adult ratio lowered.
- The demersal fish group (FDF) was removed from herring diet (FHE), as in 2017, one herring sample had one Norway pout in the stomach, accounting for 100 percent of the diet that year.
- The year 1981 was removed from Greenland halibut diet.

Trophic level

In marine ecosystems, organisms can be classified according to their feeding relationships to trophic levels. Energy is transferred from prey to predator up the food chain and each organism or a group at a certain trophic level produces energy at a certain rate which must be less than the rate of energy ingestion by that trophic level. Detritus and primary producers are assigned to trophic level 1, the organisms feeding on trophic level 1, such as herbivores and detritivores are assigned to trophic level 2, and ultimately the higher order carnivores are assigned to trophic levels ranging from 3-5 (Trites 2001).

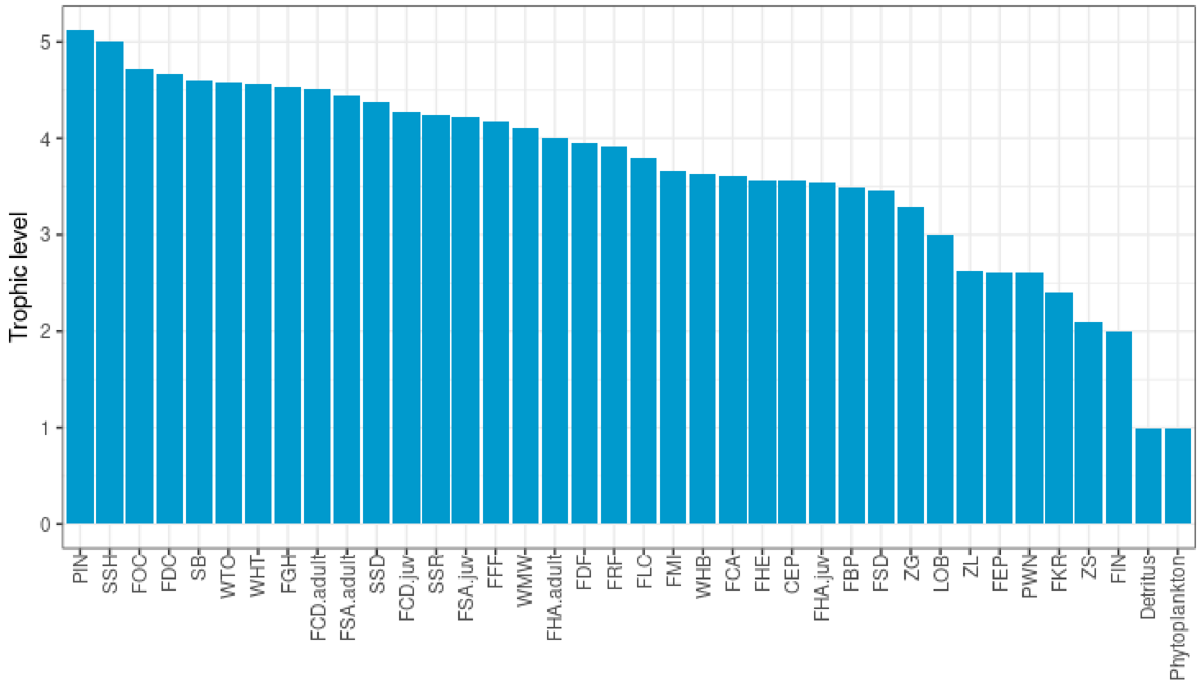

Figure 39. The trophic level of functional groups in the unbalanced Ecopath model.

Biomass

The range of biomass spans 6.754 orders of magnitude across trophic levels, falling close to the ecological range suggested by Link (2010) (5-7 orders). According to Link (2010), biomass across trophic levels is expected to decline from smaller organisms at lower trophic levels to lower abundance of larger organisms at upper trophic levels. Log Biomass (base of 10) was plotted against trophic level to visualize the slope (excluding phytoplankton and detritus) (Figure 40). In aquatic systems, the slope of the log 10 biomass is expected to decline about 5-10% with increasing trophic level across all taxa and in this system the slope has a 11.26% decline, indicating that biomass at lower trophic levels is too high or that biomass at higher trophic levels is too low.

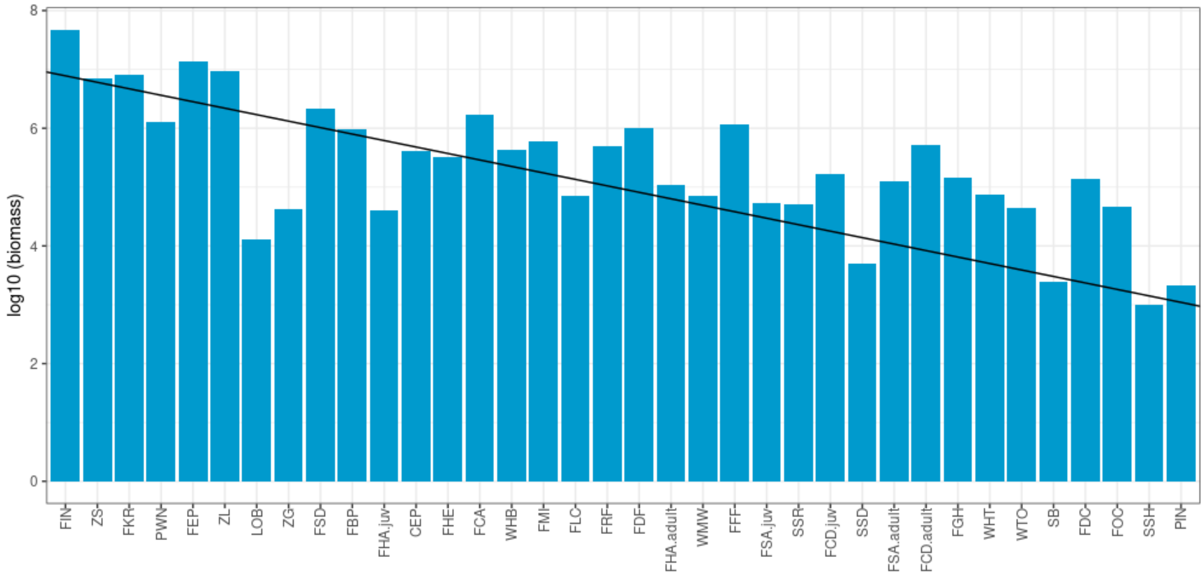

Figure 40. log (base 10) biomass with increasing trophic level (increased from left to right on x-axis).

Biomass ratios

The total biomass of prey in an ecosystem should be more than the biomass of the predator. Biomass summed at a given trophic level should be higher than that at the next higher trophic level.

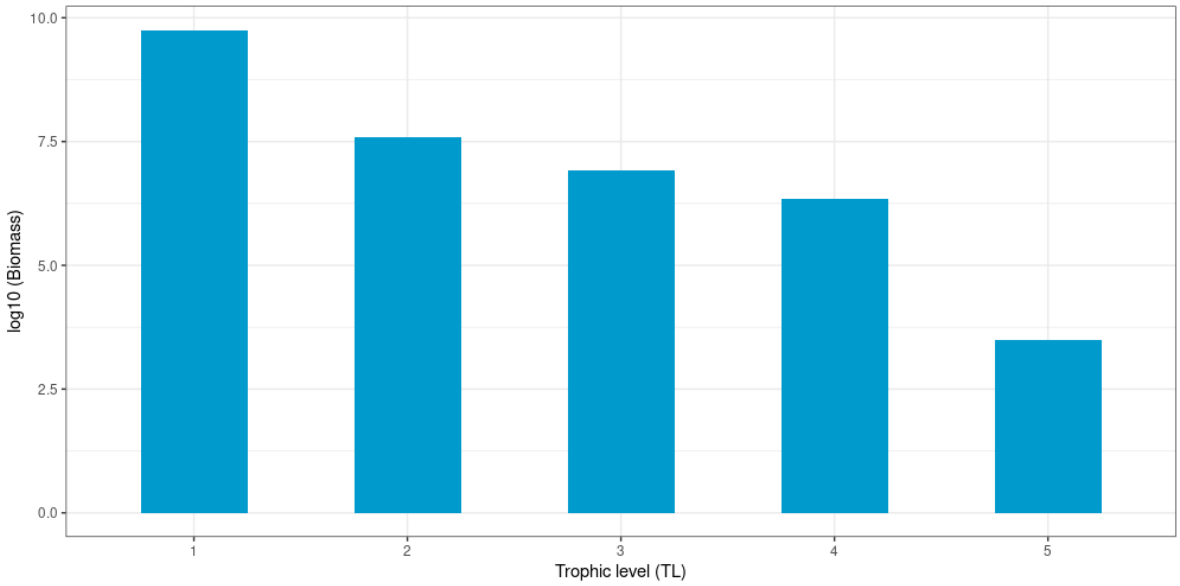

Figure 41. Total log (base 10) biomass at a given trophic level (TL).

To analyze whether estimated predation pressure is too high on a given prey group (imbalance in the system structure), the ratio between predator and prey biomass was analyzed. In general, the biomass of a predator should be less than of its prey. When the ratio approaches 1, it indicates that there may possibly be too much predation pressure on the prey groups. If there are too many zeros after the decimal point, it indicates that the predator is preying on a prey at a trophic level far from its own.

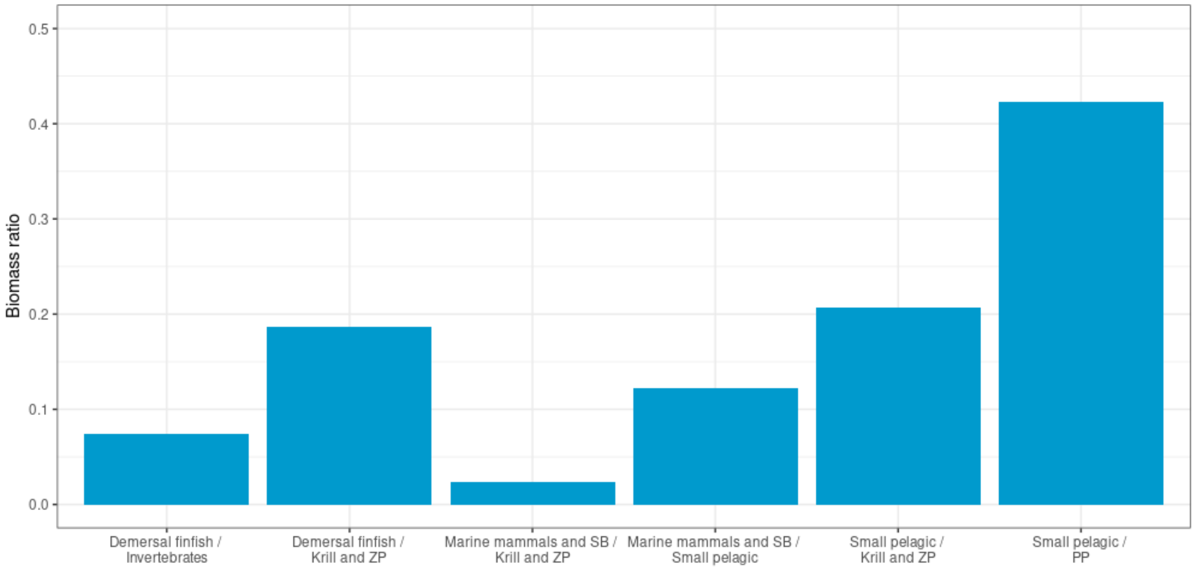

Figure 42. Biomass ratios of predator groups to prey groups. Names on x-axis below bars refer to combined groups of predators and prey.

Vital rates across taxa and trophic levels

The vital rates of organisms are reflective of an entire suite of physiological processes. These vital rates are the processes of consumption (Q), production (P) and respiration (R) and represent the balance of energy consumed and used by an organism which are strongly related to body size and biomass (Link, 2010).

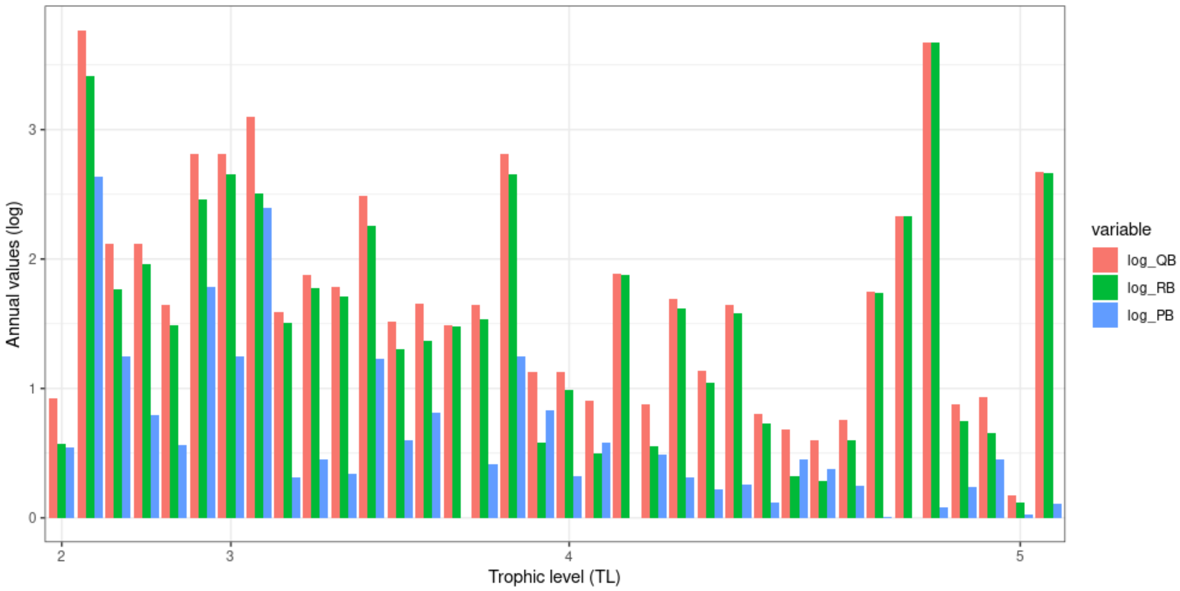

Figure 43. Vital rates across trophic levels in the unbalanced Ecopath model.

According to Link (2010), there needs to be a general decline with increasing trophic level, except for log consumption/biomass (log Q/B) and log respiration/biomass (log R/B) at upper trophic levels (marine mammals and seabirds) due to a highly energy demanding lifestyle (Peters, 1986). log P/B values are expected to decrease with increasing trophic level.

Vital rates ratios

Ratios of vital rates provide insight into additional processes among groups, bioenergetic constraints within groups, and the relative relationship across vital rates. In balanced ecosystems, vital rates of predator (consumption, production, and respiration (C, P and R) should be less than that of their prey. If the ratio exceeds 1, predation pressure on a particular prey is too high.

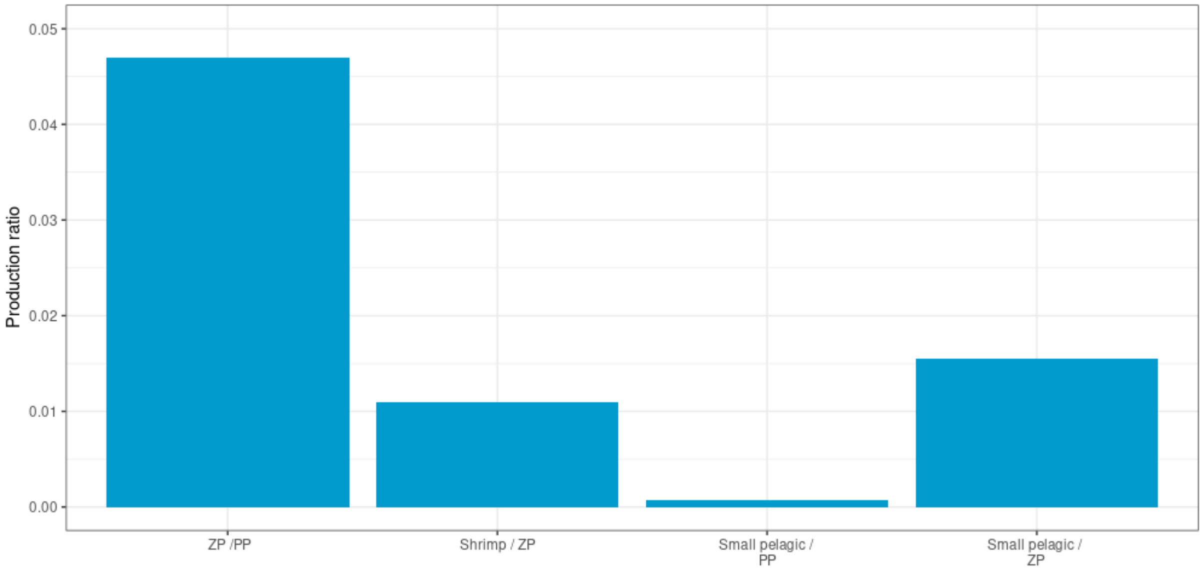

Figure 44. Vital rates ratios of specific groups on the unbalanced Ecopath model

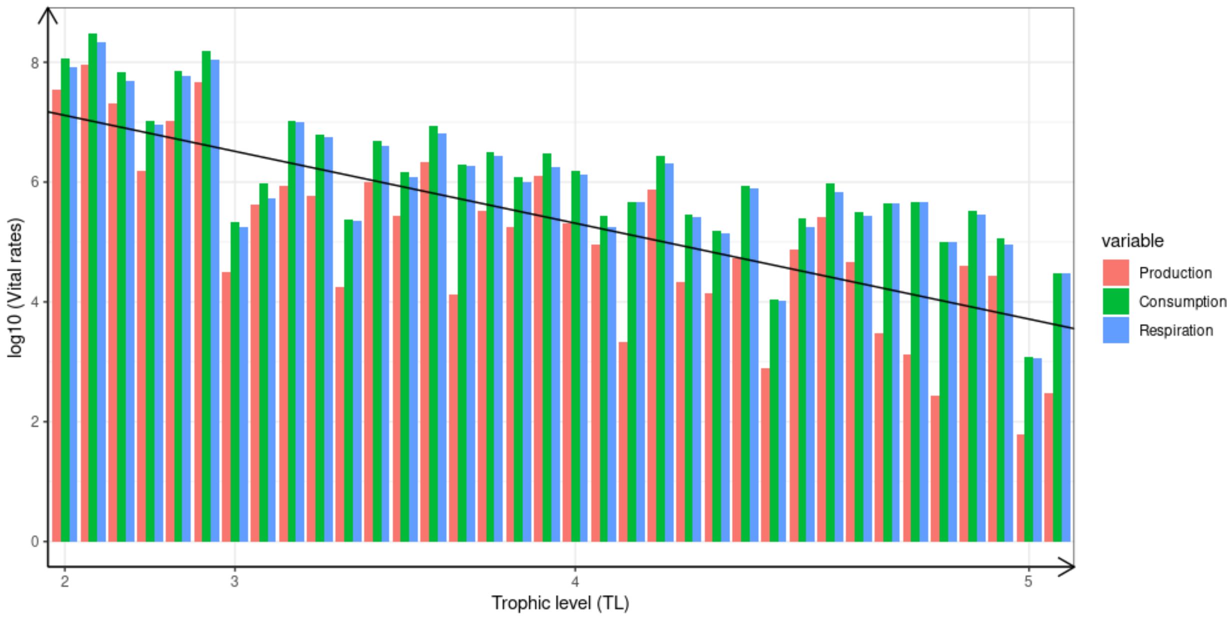

Figure 45. log (base 10) vital rates (Production, consumption, and respiration) across trophic levels.

No group should have a biomass (B) and production (P) rate relative to primary producers (PP) greater, or even close to 1. In the unbalanced model, the infauna (FIN) and epifauna (FEP) group exceed one, which warrants a closer examination of those groups (Figure 46).

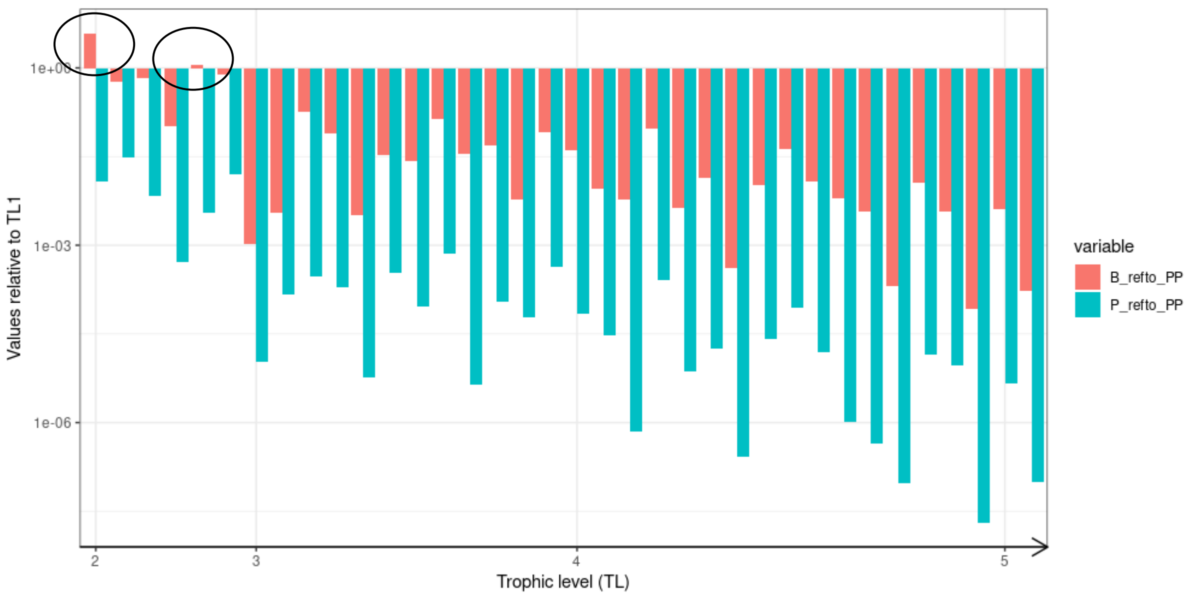

Figure 46. Biomass and production in reference to biomass and production of primary producers.

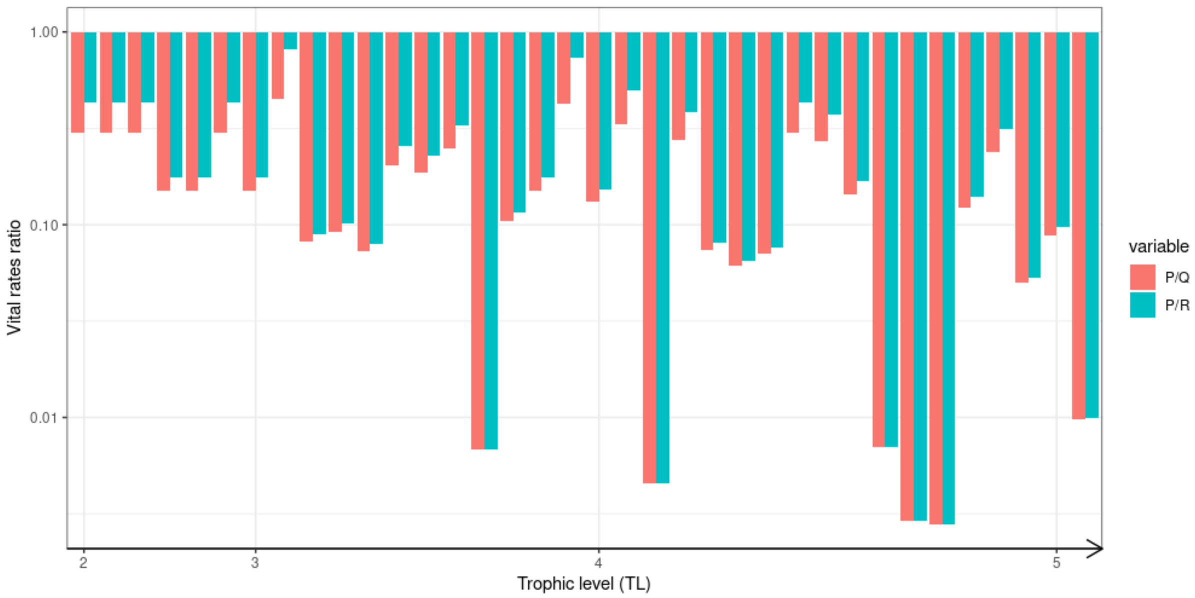

Figure 47. Production over consumption ratio (P/Q) and production over respiration ratio (P/R) across trophic levels.

According to Link (2010), production (P) should not exceed consumption (Q), i.e. a group cannot produce more than what is eaten. Similarly, production (P) should not exceed respiration (R).

Eight groups were adjusted to achieve model balance (listed below).

- P/B value of juvenile haddock (FHA.juv) was increased from 0.31 to 1.27 year^{-1}.
- P/B value of juvenile cod (FCD.juv) was increased from 0.43 to 1.5 year^{-1}.
- P/B value of juvenile saithe (FSA.juv) was increased from 0.402 to 0.87 year^{-1}.
- P/B value of redfish (FRF) was increased from 0.41 to 0.49 year^{-1}.
- P/B value of demersal commercial fish (FDC) was increased from 0.30 to 0.46 year^{-1} as well as the Q/B value was lowered from 2.41 to 2.17 year^{-1}.
- P/B value of other commercial fish (FOC) was increased from 0.60 to 0.70 year^{-1}.
- P/B value of capelin (FCA) increased from 1.29-2.13 year^{-1}.
- P/B value of herring (FHE) was increased from 0.84-1.35 year^{-1}.
- Production over consumption (P/C) of epifauna was increased from 0.15 to 0.25 (addressing the problem with biomass and production in reference to biomass and production of primary producers (Figure 46).
- Biomass of capelin was increased by 5% to balance. Biomass in the model was assumed to be total annual landings in 1996 plus 400.000 tonnes (The harvest control rule aimed to leave at least 400.000 tonnes of mature capelin at the time of spawning in March (MFRI 1996). A 5% increase results in a total biomass of 1,764.055 tonnes.

Post-balance

Table 29. Basic estimates from the balanced model. Numbers highlighted in blue have been estimated by Ecopath.

Code	Functional group	TL	Biomass	P/B	Q/B	EE
FCD.juv	Juvenile cod	4.26912	165513.08	1.271548	5.17496	0.55905387
FCD.adult	Adult cod	4.50161	517632.80	0.491519	1.81780	0.77173588
FHA.juv	Juvenile haddock	3.70044	39982.04	1.500000	5.94426	0.88480993
FHA.adult	Adult haddock	4.05975	108323.00	0.818770	2.47000	0.87367637
FSA.juv	Juvenile saithe	4.21276	54185.86	0.870000	4.47060	0.37426424
FSA.adult	Adult saithe	4.42318	127945.60	0.595700	1.97499	0.27082874
FGH	Greenland halibut	4.50351	147582.30	0.307135	2.13000	0.52133327
FRF	Refdish	3.89096	496681.40	0.489000	3.10000	0.92433033
FHE	Herring	3.56303	322215.00	1.350080	4.53890	0.99175030
FCA	Capelin	3.61368	1764054.60	2.134593	5.23000	0.99573155
FMI	Migratory fish	3.44686	600000.00	0.540600	5.18000	0.76262637
FFF	Flatfish	3.84468	230410.40	0.661718	2.39813	0.70000000
SSR	Skates and rays	4.22214	50000.00	0.276293	3.12000	0.82395524
SSD	Small sharks	4.36279	5000.00	0.158793	2.24000	0.34568629
SSH	Large sharks	4.91138	1000.00	0.060000	1.19000	0.60118569
PIN	Seals	5.08692	2093.00	0.142000	14.45760	0.59859147
LOB	Nephrops	3.09330	12625.00	2.500000	16.66668	0.48405568
FSD	Sand eel	3.45175	1626254.00	0.400000	4.90000	0.90000000
FDF	Other demersal fish	3.95188	787809.30	1.315000	3.10000	0.90000000
FBP	Small pelagic fish	3.49632	959936.70	0.602700	6.52000	0.90000000
PWN	Shrimp	2.60243	1070211.00	1.250000	8.33333	0.95000000
FOC	Other codfish	4.63978	46153.38	0.695635	2.53000	0.94518778
FDC	Demersal	4.63577	138212.70	0.459731	2.16900	0.97889357
CEP	Cephalopods	3.56069	405518.1	2.440000	12.00000	0.95000000
WHT	Toothed whale	4.56084	75725.00	0.040000	5.73042	0.00000033
WMW	Minke whale	4.10545	70889.00	0.030000	6.58028	0.00000047
WTO	Other toothed whale	4.57792	44118.00	0.030000	10.27753	0.00037010
WHB	Baleen whale	3.63664	434857.00	0.030000	4.41000	0.00000008
SB	Seabirds	4.42573	2500.84	0.110000	39.34026	0.33694405
FEP	Epifauna	2.61111	4734918.00	0.780000	3.12000	0.95000000
FIN	Infauna	2.00000	11573420.00	0.756500	2.52167	0.95000000
FLC	Lobsters and crabs	3.79370	52331.66	2.500000	16.6666	0.95000000
FKR	Krill	2.40789	7407259.00	2.500000	8.33333	0.95000000
ZG	Gelatinous	3.29625	35986.59	10.000000	22.22222	0.95000000
ZL	Large zooplankton	2.63158	8831366.00	5.000000	16.66667	0.95000000
ZS	Small zooplankton	2.00000	6653240.00	13.000000	43.33333	0.95000000
Phytoplankton		1.00000	12151000.00	243.000000	0.00000	0.11782076
Detritus		1.00000	5628683900.38	0.500000	0.00000	0.03088763

Table 30. Diet matrix from the balanced Ecopath model. Diets are weighted proportions (sum to 1).

Prey	1	2	3	4	5	6	7	8	9	10	11	12
1. Cod juvenile	0.0305819	0.0214324	0.0087170	0.0007010	0.0024792	0.0031821	0.0042943	0.0013864	-	-	-	0.0000017
2.Cod adult	-	-	-	-	-	-	-		-	-	-	-
3. Haddock juvenile	0.0083725	0.0167128	0.0054054	0.0007284	0.0056855	0.0167034	0.0020073	0.0098570	-	-	-	0.0000017
4. Haddock adult	-	0.0058720	-	-	-	-	-		-	-	-	-
5. Saithe juvenile	0.0001189	0.0019444	-	0.0000434	-	0.0004885	0.0032597	0.0000180	-	-	-	-
6. Saithe adult	-	-	-	-	-	-	-	-	-	-	-	-
7.Greenland halibut	-	0.0002734	-	-	-	-	0.0029707	-	-	-	-	-
8. Redfish	0.0038762	0.0168586	0.0084112	0.0014151	0.0001025	0.0025133	0.0104234	0.0025236	-	-	-	-
9. Herring	0.0105417	0.0462363	0.0078473	0.0062361	0.0257867	0.0672353	0.1036764	0.0081633	-	-	-	0.0117538
10. Capelin	0.5274779	0.5665643	0.0945814	0.4780249	0.2959348	0.4969310	0.3392393	0.1344421	0.024622	-	0.0078547	0.1766996
11. Migratory fish	0.0025601	0.0377627	0.0033533	0.0003458	0.0172740	0.0863967	0.1657858	0.0233049		-	0.0049285	0.0004789
12.Flatfish	0.0067942	0.0291200	0.0058437	0.0038736	0.0002485	0.0005577	0.0003375	0.0008819	-	-	-	0.0062568
13. Skates and rays	-	0.0003483		0.0000130	-	-	0.0042144	-	-	-	-	-
14. Small sharks	-	-	-	-	-	-	-	-	-	-	-	-
15. Large sharks	-	-	-	-	-	-	-	-	-	-	-	-
16. Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-
17. Nephrops	0.0003245	0.0095509	0.0076575	0.0017733	-	-	-	-	-	-	-	0.0020201
18. Sand eel	0.0325602	0.0266791	0.1087702	0.0303747	0.2573726	0.0605393	-	0.0374573	0.008996	-	-	0.1354327
19. Demersal fish	0.0183707	0.0355202	0.0103283	0.0067808	0.0612946	0.0572264	0.1381415	0.0426103	-	-	-	0.0208414
20. Small pelagic fish	0.0047735	0.0079357	0.0242001	0.0015671	0.0090533	0.0369361	0.0092813	0.0581207	-	-	0.0047128	0.0001728
21. Shrimp	0.1517538	0.0841814	0.0997696	0.0239664	0.0087612	0.0087537	0.0532937	0.1251487	-	-	0.0017712	0.0372538
22. Other codfish	0.0004022	0.0020845	-	0.0000905	0.0034486	0.0018804	0.0001694	0.0009207	-	-	-	-
23. Demersal commercial fish	0.0009063	0.0101086	0.0026705	0.0005825	0.0000932	0.0000230	0.0011059	0.0000241	-	-	-	0.0005902
24. Cephalopods	0.0008424	0.0023749	0.0287435	0.0004399	0.0005282	0.0067032	0.0771610	0.0267891	-	-	-	0.0004141
25. Tooth whale	-	-	-	-	-	-	-	-	-	-	-	-
26. Minke whale	-	-	-	-	-	-	-	-	-	-	-	-
27. Other toothe whale	-	-	-	-	-	-	-	-	-	-	-	-
28. Baleen whale	-	-	-	-	-	-	-	-	-	-	-	-
29. Seabirds	-	-	-	-	-	-	-	-	-	-	-	-
30. Epifauna	0.0088885	0.0054689	0.0200861	0.1718928	0.0004350	0.0024939	0.0010280	0.0000612	0.002773	-	0.0003080	0.3464034
31. Infauna	0.0227600	0.0033848	0.3696685	0.1547763	0.0012210	0.0007518	0.0003402	0.0107886	0.022523	-	0.0016942	0.1978566
32. Lobsters and crabs	0.0138655	0.0073552	0.0236753	0.0142610	0.0003200	0.0002945	0.0000323	0.0004433	0.003703	-	0.0000154	0.0170841
33. Krill	0.1087035	0.0284335	0.1230590	0.0685213	0.2936498	0.1218427	0.0682197	0.3976892	0.381101	0.0800000	0.8915431	0.0337974
34. Gelatinous zooplankton	0.0057051	0.0203486	0.0085233	0.0106040	0.0011557	0.0049794	0.0001607	0.0279373	0.001581	0.0000000	0.0000154	0.0003982
35. Large zooplankton	0.0398185	0.0134471	0.0386309	0.0229718	0.0151557	0.0235666	0.0052801	0.0913843	0.545305	0.9200000	0.0871567	0.0124883
36. Small zooplankton	0.0000007	-	0.0000571	0.0000154	-	-	-	0.0000471	0.009394	-	-	0.0000534
37. Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-
Detritus	-	-	-	-	-	-	-	-	-	-	-	-

Table 31 continued. Diet matrix from the balanced Ecopath model. Diets are weighted proportions (sum to 1).

Predator/Prey	13	14	15	16	17	18	19	20	21	22	23	24
1. Cod juvenile	0.0275575	0.0003981	-	0.3614132	-	-	-	-	-	0.0305821	0.1394164	-
2.Cod adult	-	-	-	-	-	-	-	-	-	-	-	-
3. Haddock juvenile	0.0008578	0.0080528	-	0.0097096	-	-	-	-	-	0.0167047	0.0138074	-
4. Haddock adult	-	-	-	-	-	-	-	-	-	-	0.0365696	-
5. Saithe juvenile	0.0209706	-	-	0.0979951	-	-	-	-	-	0.0175830	0.0109632	-
6. Saithe adult	-	-	-	-	-	-	-	-	-	-	-	-
7.Greenland halibut	-	-	-	-	-	-	-	-	-	-	0.0002149	-
8. Redfish	0.0618156	0.0446615	0.5109056	0.0402769	-	-	-	-	-	0.0163023	0.1352918	-
9. Herring	0.0352981	0.0058812	-	0.0381416	-	-	0.0019617	-	-	0.2096462	0.0740270	-
10. Capelin	0.1234258	0.0003981	-	0.0214870	-	-	0.0850553	-	-	0.0253159	0.0676111	-
11. Migratory fish	0.0800128	0.0780255	-	-	-	-	0.0035891	-	-	0.2902522	0.0017402	-
12.Flatfish	0.0181309	-	-	0.0791602	-	-	0.0021692	-	-	0.0029694	0.0820768	-
13. Skates and rays	0.0090797	-	-	-	-	-	-	-	-	0.0000596	0.0230818	-
14. Small sharks	-	-	-	-	-	-	-		-	-	--	-
15. Large sharks	-	-	-	-	-	-	-	-	-	-	-	-
16. Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-
17. Nephrops	0.0000629	-	-	-	-	-	-	-	-	0.0073544	0.0002315	-
18. Sand eel	0.0321283	0.0181505	-	0.1627259	-	-	0.0042019	-	-	0.0216848	0.0262503	-
19. Demersal fish	0.1450743	0.0983874	0.0055926	0.0258473	0.0952381	-	0.1428779	-	-	0.1769222	0.0135039	-
20. Small pelagic fish	0.0052167	0.2083348	0.2984228	-	-	-	0.0084038	-	-	0.0536598	0.0003354	0.0705645
21. Shrimp	0.1250770	0.1649909	-	-	-	-	0.2351569	-	0.0100000	0.0435850	0.0031317	-
22. Other codfish	-	-	-	0.0096646	-	-	-	-	-	0.0346721	0.0294799	-
23. Demersal commercial fish	0.0003279	0.0239775	0.1850788	0.1535781	-	-	-	-	-	0.0213153	0.0694357	-
24. Cephalopods	0.0162297	0.1393230	-	-	-	-	0.0375606	-	-	0.0129544	0.0009816	-
25. Tooth whale	-	-	-	-	-	-	-	-	-	-	-	-
26. Minke whale	-	-	-	-	-	-	-	-	-	-	-	-
27. Other toothe whale	-	-	-	-	-	-	-	-	-	-	-	-
28. Baleen whale	-	-	-	-	-	-	-	-	-	-	-	-
29. Seabirds	-	-	-	-	-	-	-	-	-	-	-	-
30. Epifauna	0.0100376	0.0046525	-	-	0.2380952	-	0.0272073	-	0.1500000	0.0008822	0.2149981	-
31. Infauna	0.0941869	0.0002967	-	-	0.4285714	-	0.0307868	-	0.1000000	0.0004927	0.0196324	-
32. Lobsters and crabs	0.0199725	0.0004107	-	-	-	-	0.0068123	-	-	0.0078343	0.0093290	-
33. Krill	0.0950917	0.0412949	-	-	-	0.803922	0.2494565	0.5200000	-	0.0079393	0.0027938	0.1542339
34. Gelatinous zooplankton	0.0014573	0.1619252	-	-	-	-	0.1051264	-	-	0.0002543	0.0231402	-
35. Large zooplankton	0.0779873	0.0008378	-	-	-	0.196078	0.0596285	0.4500000	0.1500000	0.0010326	0.0019499	0.6209677
36. Small zooplankton	-	-	-	-	-	-	0.0000052	0.0300000	-	-	0.0000052	0.1542339
37. Phytoplankton	-	-	-	-	0.1904762	-	-	-	0.2700000	-	-	-
Detritus	-	-	-	-	0.0476190	-	-	-	0.3200000	-	-	-

Table 32 continued. Diet matrix from the balanced Ecopath model. Diets are weighted proportions (sum to 1).

Predator/Prey	25	26	27	28	29	30	31	32	33	34	35	36
1. Cod juvenile	-	-	-	-	0.0287331	-	-	-	-	-	-	-
2.Cod adult	0.0001000	0.0069721	0.0238388	-	-	-	-	-	-	-	-	-
3. Haddock juvenile	-	-	-	-	0.0004140	-	-	-	-	-	-	-
4. Haddock adult	0.0000291	-	0.0047614	-	-	-	-	-	-	-	-	-
5. Saithe juvenile	-	-	-	-	0.0502622	-	-	-	-	-	-	-
6. Saithe adult	-	-	0.0160830	-	-	-	-	-	-	-	-	-
7.Greenland halibut	-	-	-	-	-	-	-	-	-	-	-	-
8. Redfish	0.0000902	-	-	-	0.0022357	-	-	-	-	-	-	-
9. Herring		0.0069721	0.3022931	-	0.0033618	-	-	-	-	-	-	-
10. Capelin	0.0015181	0.2490039	0.0158714	0.1668436	0.2333923	-	-	-	-	-	-	-
11. Migratory fish	-	-	0.0365042	-	0.0101849	-	-	-	-	-	-	-
12.Flatfish	-	-	-	-	0.0263317	-	-	-	-	-	-	-
13. Skates and rays	-	-	-	-	-	-	-	-	-	-	-	-
14. Small sharks	-	-	-	-	-	-	-	-	-	-	-	-
15. Large sharks	-	-	-	-	-	-	-	-	-	-	-	-
16. Pinnipeds	-	-	-	-	-	-	-	-	-	-	-	-
17. Nephrops	-	-	-	-	0.0000099	-	-	-	-	-	-	-
18. Sand eel	0.0005500	0.3585657	-	0.0011451	0.4399727	-	-	-	-	-	-	-
19. Demersal fish	-	-	-	-	0.0866961	-	-	0.3460674	-	-	-	-
20. Small pelagic fish	0.0000291	-	0.0188340	-	0.0173889	-	-	-	-	-	-	-
21. Shrimp	-	-	0.0188340	-	0.0002914	-	-	0.0007490	-	0.0279475	-	-
22. Other codfish	-	-	0.0003914	-	0.0241788	-	-		-	-	-	-
23. Demersal commercial fish	-	-	-	0.0005700	0.0068727	-	-		-	-	-	-
24. Cephalopods	0.9976834	-	0.5625883	-	0.0119668	-	-		-	0.0817542	-	-
25. Tooth whale	-	-	-	-	-	-	-		-	-	-	-
26. Minke whale	-	-	-	-	-	-	-		-	-	-	-
27. Other toothe whale	-	-	-	-	-	-	-		-	-	-	-
28. Baleen whale	-	-	-	-	-	-	-		-	-	-	-
29. Seabirds	-	-	-	-	-	-	-		-	-	-	-
30. Epifauna	-	-	-	-	0.0006040	0.1000000	-	0.2666666	-	0.0199942	-	-
31. Infauna	-	-	-	-	0.0005532	0.4500000	-	0.2973782	-	-	-	-
32. Lobsters and crabs	-	-	-	-	0.0006422	-	-	0.0157303	-	0.0538733	-	-
33. Krill	-	0.3784860	-	0.7192158	0.0421970	-	-	-	-	-	-	-
34. Gelatinous zooplankton	-	-	-		0.0000763	-	-	-	-	-	-	-
35. Large zooplankton		-	-	0.1122253	0.0136332	-	-	-	0.2500000	0.3265723	0.0500000	-
36. Small zooplankton	-	-	-	-	-	-	-	-		0.3265723	0.5500000	-
37. Phytoplankton	-	-	-	-	-	0.2500000	-	0.0734082	0.5000000	0.1632862	0.2500000	0.9500000
Detritus	-	-	-	-	-	0.2000000	1		0.2500000	-	0.1500000	0.0500000

To examine the ecological quality of the Icelandic Ecopath model, the pre-balance criteria described by Link (2010) were applied post balance (Table 33, Figure 48, Figure 49).

Table 33. Post-balance diagnostics on the Icelandic Ecopath model (based on Link (2010)).

Criteria	Iceland model results	Comment
Biomass should span 5-7 orders of magnitude	Spans 6.750 orders of magnitude	Criteria met.
Biomass slope (on log scale) around 5-10% decline with increasing TL	The decline is 11% with increasing trophic level.	The decline is higher than preferred. Likely indicative of too high biomass estimates at lower trophic levels. When detritus group is excluded from the analysis, the percentage in decline is 10% and meets the criteria.
Functional groups biomasses above/below the line	Figure 49(f)	Most groups are close to the regression line. Exceptions are detritus (above) and phytoplankton and lobster (below)
Compared across taxa, the ratio between predator and prey biomass should be less than 1 with 1-2 decimal places, depending on the TL	Figure 48	Biomass ratios of predator and prey groups meet the criteria.
P/B should decline with increasing TL (excluding marine mammals and seabirds)	Figure 49(b)	Criteria met
Q/B should decline with increasing TL (excluding marine mammals and seabirds)	Figure 49(d)	Criteria met
No taxa should have a P/B greater than phytoplankton	Figure 49(a)	Criteria met
PQ should fall below 1 for all functional groups	Figure 49(g)	Criteria met
PR should fall below 1 for all functional groups	Figure 49(e)	Criteria met
EE should fall below 1 for all functional groups	Table 29	Criteria met
Total production and consumption should decrease with increasing TL	Figure 49(I) and Figure 49(j)	Criteria met

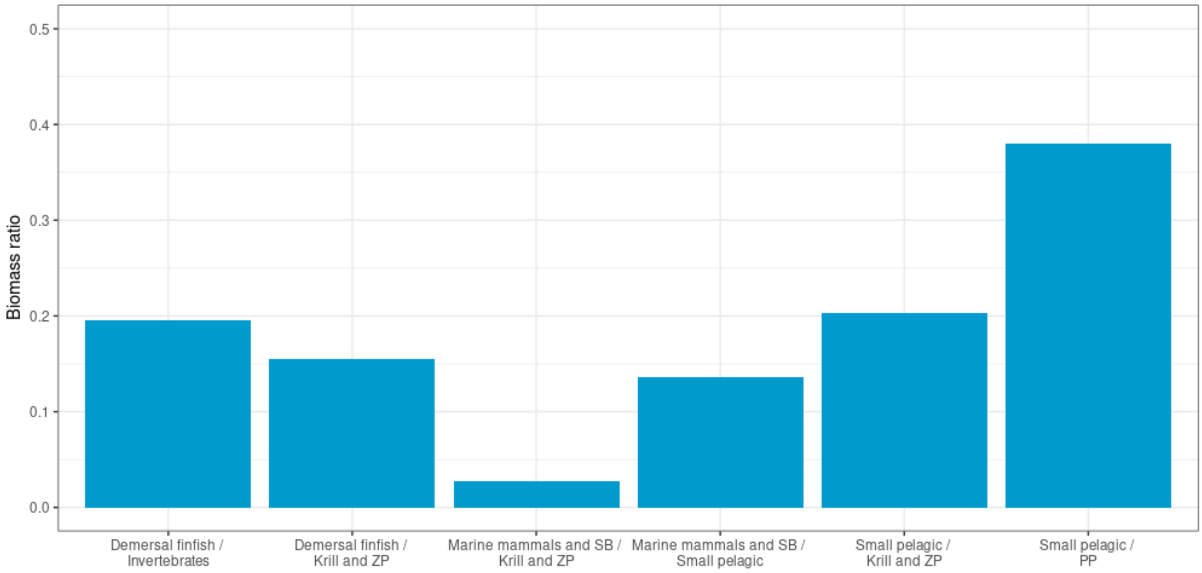

Figure 48. Biomass ratios of predator groups to prey groups post balancing. Names on x-axis below bars refer to combined groups of predators and prey.

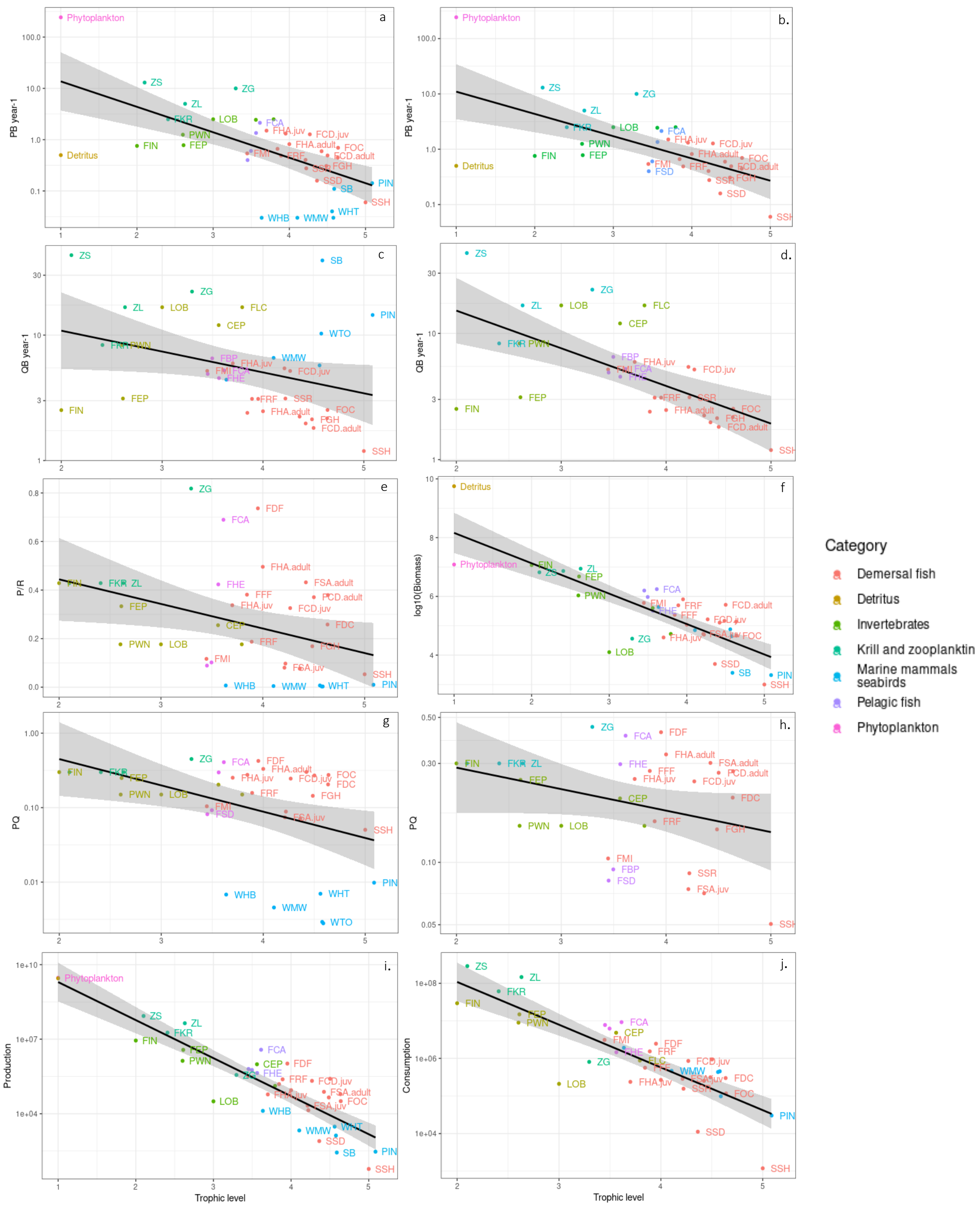

Figure 49. Production over biomass (P/B year⁻¹) across trophic levels (fig a. and b.), consumption over biomass (Q/B year⁻¹) across trophic levels (fig. c. and d.), production over respiration (P/R) across trophic levels (fig. e.), log(base=10)(biomass) across trophic levels (fig f.), production over consumption (PQ) across trophic levels (fig. g. and h.), production across trophic levels (fig i.) and consumption across trophic levels (fig j.). Figures b., d. and h. are without marine mammals and seabirds. The black lines in each graph are the regression line (X ~ TL) and the grey shaded areas are 95% confidence intervals of the regression lines.

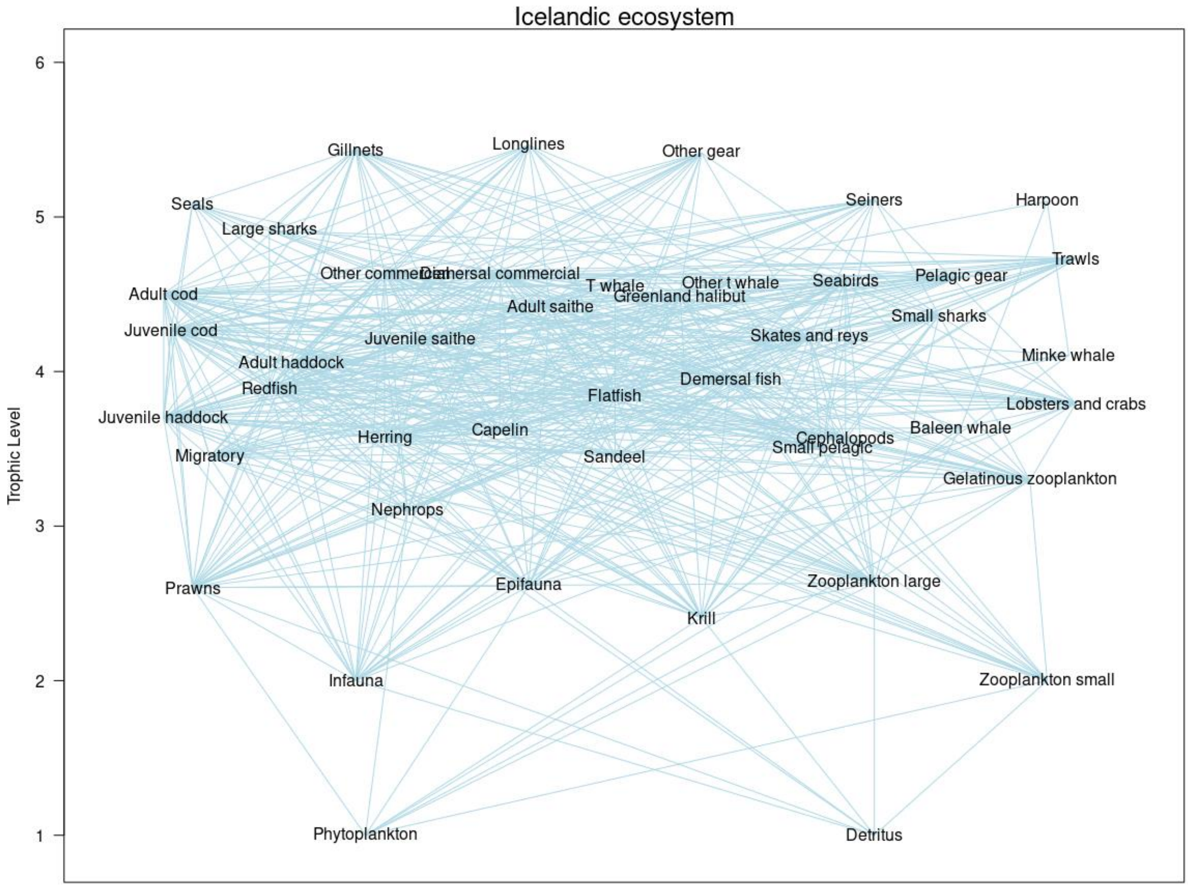

Figure 50. Energy flow diagram for the Icelandic Ecopath food web model. Lines represent the flow of energy and the y-axis denotes group trophic level.

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Appendix

Table 34. Species in the demersal fish functional group (FDF)

English name	Scientific name
Norway pout	*Trisopterus esmarkii*
Viperfish	*Chauliodus sloani*
Slender snipe eel	*Nemichthys scolopaceus*
Beans´s sawtoothed eel	*Serrivomer beanii*
Blackfin waryfish	*Scopelosaurus lepidus*
Arctic rockling	*Gaidropsarus argentatus*
Moustache sculpin	*Triglops murrayi*
Fourbearded rockling	*Enchelyopus cimbrius*
Atlantic poacher	*Leptagonus decagonus*
Atlantic hookear sculpin	*Artediellus atlanticus*
Polar sculpin	*Cottunculus microps*
Twohorn sculpin	*Icelus bicornis*
Esmark´s eelpout	*Lycodes esmarkii*
Goitre blacksmelt	*Bathylagus euryops*
Roundnose grenadier	*Coryphaenoides rupestris*
Black seasnail	*Paraliparis bathybius*
Shorthorn sculpin	*Myoxocephalus scorpius*
Hooknose	*Agonus cataphractus*
Rock gunnel	*Pholis gunnellus*
Blackbelly rosefish	*Helicolenus dactylopterus*
Arctic eelpout	*Lycodes reticulatus*
Boa dragonfish	*Stomias boa ferox*
Black scabbard fish	*Aphanopus carbo*
Greater forkbeard	*Phycis blennoides*
Grey gurnard	*Eutrigla gurnardus*
White hake	*Urophycis tenuis*
Baird´s smoothhead	*Alepocephalus bairdii*
Silver hatchetfish	*Argyropelecus olfersii*
Greenland argentine	*Nansenia groenlandica*
Lightless loosejaw	*Malacosteus niger*
Bluntsnout smoothhead	*Xenodermichthys copei*
Antarctic snaggletooth	*Borostomias antarcticus*
Black swallower	*Chiasmodon niger*
Snake pipefish	*Entelurus aequoreus*
Roughhead grenadier	*Macrourus berglax*
Cutthroat eel	*Synaphobranchus kaupii*
Gulper eel	*Saccopharynx ampullaceus*
Spark angelmouth	*Sigmops bathyphilus*
Gelatinous snailfish	*Liparis fabricii*
Benttooth bristlemouth	*Cyclothone acclinidens*
Veiled anglemouth	*Cyclothone microdon*

Norwegian topknot	*Zeugopterus norvegicus*
Short silver hatchetfish	*Argyropelecus hemigymnus*
Multipore searsid	*Normichthys operosus*
Pelican eel	*Eurypharynx pelecanoides*
Ribbed sculpin	*Triglops pingelii*
Fivebearded rockling	*Ciliata mustela*
Longfin snailfish	*Careproctus reinhardti*
Longear eelpout	*Lycodes seminudus*
Doubleline eelpout	*Lycodes eudipleurostictus*
Fish doctor	*Gymnelus viridis*
Aurora pout	*Gymnelus retrodorsalis*
Blackspot grenadier	*Coelorinchus caelorhincus*
Moray wolf eel	*Lycenchelys muraena*
Checkered wolf eel	*Lycenchelys kolthoffi*
Pale eelpout	*Lycodes pallidus*
Pallid sculpin	*Cottunculus thomsonii*
Largeeyed rhinofish	*Poromitra megalops*
Vahl´s eelpout	*Lycodes gracilis*

Other Family/Class/Phylum	
Macrouridae	Melamphaidae
Sternoptychidae	Sternoptychidae
Liparidae	Zoarchias
Lumpenus	Artediellus
Serrivomeridae	

Table 35. Species in the epifauna functional group (FEP)

Scientific name	
Aega psora	*Lepeta caeca*
Alvania jeffreysi	*Margarites groenlandicus*
Amauropsis islandica	*Margarites olivaceus*
Amphiura borealis	*Margarites vahlii*
Boreoscala greenlandica	*Moelleria costulata*
Boreotrophon clathratus	*Neptunea despecta*
Boreotrophon clavatus	*Odostomia unidentata*
Buccinum hydrophanum	*Oenopota tenuicostata*
Buccinum undatum	*Ondina divisa*
Bulbus smithii	*Onoba semicostata*
Calliostoma militare	*Ophiacantha bidentata*
Calliostoma occidentale	*Ophiacantha bidentata*
Cerithiella metula	*Ophiactis abyssicola*
Cryptonatica affinis	*Ophiura robusta*
Curtitoma decussata	*Ophiura signata*
Cylichna alba	*Piliscus commodus*
Diaphana hiemalis	*Pseudopolinices nanus*
Echinus esculentus	*Puncturella noachina*
Emarginula fissura	*Raphitoma linearis*
Euspira montagui	*Scissurella costata*
Euspira nitida	*Skenea trochoides*
Euspira pallida	*Strongylocentrotus droebachiensis*
Gorgonocephalus caputmedusae	*Trophonopsis barvicensis*
Iothia fulva	*Velutina plicatilis*
Laeocochlis sinistratus	*Volutomitra groenlandica*

Other Class/Family/Phylum	
Actiniaria	Heterobranchia
Anemonactis	Laomedea
Anthozoa	Ophiacantha
Ascidiacea	Ophiactis
Asteroidea	Ophiocten
Bryozoa	Ophioscolex
Cirripedia	Ophiura
Echinodermata	Prosobranchia
Eupagurus	Psolus
Gastropoda	Solaster

Table 36 . Species in the infauna functional group (FIN)

Scientific name	
Abra nitida	*Lyonsia arenosa*
Anomia squamula	*Lyonsia norwegica*
Aphrodita aculeata	*Macoma calcarea*
Arctica islandica	*Mendicula ferruginosa*
Astarte borealis	*Modiolus modiolus*
Astarte crenata	*Montacuta ferruginosa*
Astarte elliptica	*Musculus niger*
Astarte montagui	*Mya arenaria*
Astarte sulcata	*Mya truncata*
Bathyarca glacialis	*Mytilus edulis*
Bathyarca pectunculoides	*Nucula delphinodonta*
Cardium echinatum	*Nucula tenuis*
Cardium edule	*Nuculana minuta*
Chlamys islandica	*Nuculana pernula*
Ciliatocardium ciliatum	*Palliolum tigerinum*
Cochlodesma praetenue	*Panomya ampla*
Crenella decussata	*Parvicardium minimum*
Cyclopecten hoskynsi	*Parvicardium pinnulatum*
Cyprina islandica	*Priapulus caudatus*
Dacrydium vitreum	*Pseudamussium peslutrae*
Dosinia lupinus	*Spisula solida*
Gari fervensis	*Thyasira flexuosa*
Goethemia elegantula	*Venus ovata*
Hiatella arctica	*Yoldia hyperborea*
Limatula similaris	

Other Class/Family/Phylum	
Abra	Nephtyidae
Ampharetidae	Nereidae
Annelida	Nuculana
Anomiidae	Nuculanidae
Aphroditidae	Onuphidae
Aricidea	Opheliidae
Astarte	Orbiniidae
Astartidae	Parachaeta
Bivalvia	Pectinidae
Capitellidae	Phyllodocida
Cardiidae	Phyllodocidae
Cardium	Platyhelminthes
Cuspidariidae	Polynoidae
Eunicida	Priapulida
Eunicidae	Saxicavella
Flabelligeridae	Serpulidae
Glyceridae	Spionidae

Goniadidae	Spisula
Lumbrineridae	Sternaspidae
Lumbrineris	Syllidae
Maldanidae	Terebellidae
Mytilidae	Trichobranchidae
Nematoda	Ungulinidae
Nemertea	

Table 37. Species in the lobsters and crabs functional group (FLC)

English name	Scientific name
Atlantic rock crab	*Cancer irroratus*
European green crab	*Carcinus maenas*
Squat lobster	*Munida rugosa*
Three-spined geryon	*Geryon trispinosus*
Great spider crab	*Hyas araneus*
Arctic lyre crab	*Hyas coarctatus*
Flying crab	*Liocarcinus holsatus*
Northern stone crab	*Lithodes maja*
Rugose squat lobster	*Munida rugosa*
Porcupine crab	*Neolithodes grimaldii*
Toothed rock crab	*Cancer bellianus*
Deep-sea red crab	*Chaceon affinis*
Hermit crab	*Pagurus pubescens*
Narrow-legged squat lobster	*Munida tenuimana*
Deep-sea swimming crab	*Bathynectes maravigna*

Other Family/Class/Phylum	
Anapagurus	Macropipus
Brachyura	Macrura
Decapoda	Munida
Eupagurus	Pagurus
Hyas	Reptantia

Table 38. Species in the shrimp functional group (PWN)

Scientific name	
Crangon crangon	*Eualus gaimardii*
Pandalus borealis	*Eualus pusiolus*
Pandalus montagui	*Eudorellopsis deformis*
Pasiphaea multidentata	*Sabinea sarsii*
Pasiphaea tarda	*Sabinea septemcarinata*
Spirontocaris spinus	*Sclerocrangon boreas*
Brythocaris simplicirostris	*Sclerocrangon ferox*
Pandalina brevirostris	*Lebbeus polaris*
Systellaspis debilis	

Table 39. Species in the zooplankton functional groups (ZS, ZL)

Scientific name	
*Vargul norvegica**	*Halirages fulvocinctus*
*Discoconchoecia elegans**	*Haploops setosa*
*Temora longicornis**	*Hippomedon denticulatus*
Acanthonotozoma cristatum	*Ilyarachna hirticeps*
Aetideopsis multiserrata	*Leucothoe spinicarpa*
Anonyx compactus	*Liljeborgia fissicornis*
Anonyx lilljeborgi	*Maera loveni*
Anonyx nugax	*Neohela monstrosa*
Arrhis phyllonyx	*Paraeuchaeta glacialis*
Calanus glacialis	*Paraeuchaeta norvegica*
Calanus finmarchicus	*Paramphithoe hystrix*
Calanus hyperboreus	*Protomedeia fasciata*
Caprella ciliata	*Rhachotropis aculeata*
Centraloecetes pallidus	*Rostroculodes borealis*
Ceradocus torelli	*Stegocephalus inflatus*
Dulichia spinosissima	*Syrrhoe crenulata*
Dyopedos monacanthus	*Themisto abyssorum*
Gaetanus pileatus	*Themisto libellula*
Gaetanus tenuispinus	*Themisto gaudichaudii*
Gammarellus angulosus	*Tiron spiniferum*
Gammarus locusta	*Tmetonyx cicada*
Gammarus wilkitzkii	*Unciola leucopis*

Amphipoda	Metopa
Anonyx	Metridia
Calanoida	Oedicerotidae
Calanus	Paraeuchaeta
Cladocera	Phyllocarida
Eusirus	Pteropoda
Haploops	Pycnogonidae
Hyperiidea	Rhachotropis
Isaeidae	Ostracoda*

*Small zooplankton