Study on stomach content of fish to update databases and analyse possible changes in diet or food web interactions

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LIST OF ABBREVIATIONS

Term	Description
AMO	Atlantic Multidecadal Oscillation
BIAS	Baltic International Acoustic Survey
BITS	Baltic International Trawl Survey
BIOR	Institute of Food Safety, Animal Health, and Environment BIOR
CC	Creative commons
CEFAS	Centre for Environment, Fisheries and Aquaculture Science
CINEA	European Climate, Infrastructure and Environment Executive Agency
CS	Case study
DAPSTOM	Integrated database and portal for fish stomach records
DATRAS	The Database of Trawl Surveys
DTU	Technical University of Denmark
EAF	Ecosystem Approach to Fisheries
EASME	Executive Agency for Small and Medium-sized Enterprises
EC	European Commission
FI	File information
FMSY	Fishing mortality at Maximum Sustainable Yield
HH	Haul information
ICES	International Council for Exploration of the Sae
ILVO	Flanders Research Institute for Agriculture, Fisheries and Food
ISSG	Intersessional subgroup
ITIS	Integrated Taxonomic Information System
MAFF	Ministry of Agriculture, Fisheries and Food
MSY	Maximum Sustainable Yield
NAO	North Atlantic Oscillation
NMFRI	National Marine Fisheries Research Institute
PI	Predator information
PP	Prey information
RCG	Regional coordination groups
SDM	Species Distribution Model
SLU	Swedish University of Agricultural Sciences
SMS	Stochastic Multispecies Model
TI	Thünen Institute
TMB	Template model builder
TPL	Theoretic prey length
TSN	Taxonomic Serial Number
WGSAM	Working Group on Multispecies Assessment Methods
WMR	Wageningen Marine Research
YOTS	ICES Year of the Stomach dataset

Study on stomach content of fish to update databases and analyse possible changes in diet or food web interactions

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ABSTRACT

Fish stomach content is a compelling data source, as stomachs can provide information about diet of predators, distribution of prey fish, predator-prey preference or changes in diet over time. For instance, stomach samples have historically been used to inform the natural mortality of stock assessments in the Baltic and North Seas. Since stomach samples tend to vary substantially over time, due to differences in biomass of predator and prey, time series must be constructed to provide critical information on food web interactions in time and space. In this project, we aimed (1) to analyse new stomach samples, from the North and Baltic Seas; (2) to continue historical time series; (3) to update and create an online ICES database for the broader community to explore new and old data in conjunction; and (4) to perform preliminary analysis on the newly added data. In total, 10 087 new stomachs will be provided from the two case study areas. We analysed and uploaded 5 512 new stomach samples so far. Additionally, 27 744 historical Baltic cod stomach data have been uploaded. The analysis provided here show that the predation on *saduria* and sprat by cod in the Baltic Sea has changed over the last 30 years. In the North Sea, the new samples consisted primarily of unidentified matter, benthic food and crustaceans, whereas the historical samples contain a larger number of commercial fish.

RÉSUMÉ

Le contenu stomacal des poissons est une source de données intéressante, car les estomacs peuvent fournir des informations sur le régime alimentaire des prédateurs, la distribution des poissons proies, la préférence prédateur-proie ou l'évolution du régime alimentaire au fil du temps. Par exemple, les échantillons stomacaux ont été historiquement utilisés pour évaluer la mortalité naturelle dans les études d'évaluation de stocks dans la mer Baltique et la mer du Nord. Comme les échantillons stomacaux ont tendance à varier considérablement dans le temps, en raison des différences de biomasse du prédateur et de la proie, des séries chronologiques doivent être construites pour fournir des informations critiques sur les interactions du réseau trophique dans le temps et l'espace. Dans ce projet, nous avions pour objectif (1) d'analyser de nouveaux échantillons stomacaux provenant de la mer du Nord et de la mer Baltique ; (2) de poursuivre les séries chronologiques historiques ; (3) de mettre à jour et de créer une base de données CIEM en ligne pour permettre à la communauté élargie d'explorer conjointement les nouvelles et les anciennes données ; et (4) d'effectuer une analyse préliminaire sur les données nouvelles ajoutées. Au total, 10 087 nouveaux échantillons d'estomac provenant des deux zones d'étude seront ajoutés à la base de données CIEM. Jusqu'à présent, nous avons analysé et téléchargé 5 512 nouveaux échantillons d'estomac. En outre, 27 744 données historiques sur les estomacs de cabillaud de la Baltique ont été téléchargées. L'analyse fournie ici montre que la prédation du *saduria* et du sprat par le cabillaud en mer Baltique a changé au cours des 30 dernières années. En mer du Nord, les nouveaux échantillons se composaient principalement de matières non identifiées, de nourriture benthique et de crustacés, alors que les échantillons historiques contenaient un plus grand nombre de poissons commerciaux.

EXECUTIVE SUMMARY

Stomach content data are an important data source to obtain knowledge about ecological interactions, food web structure and abundance of predator and prey species. In this specific contract, we analysed a range of stomachs from predatory fish in the North and the Baltic Seas re-established a database to make the data available and conducted analysis on the data to determine the impact of predator-prey interactions in the two ecosystems. In total, we analysed 9 229 new stomach samples of cod (*Gadus morhua*), whiting (*Merlangius merlangus*), mackerel (*Scomber scombrus*) and a few other species which had a small number of saved samples from the 2022 and 2023 international marine surveys.

We re-established the ICES stomach content database, which had not been functional or available for several years. In the process of re-establishing this database, we developed a new exchange format which is able to handle the most relevant metadata for fish stocks, including stomach fullness, latitude, longitude, haul identification number and specific fish identification numbers that can be traced back to scientific surveys or even DNA registers when possible. The database is continuously being updated with historical data, and efforts are being made to have other projects (e.g., the fishery regional coordination groups (RCG)) upload their stomach content data upon availability. The database is currently functional and publicly available for researchers across the globe to be able to use the full breadth of stomach content data in ICES areas. In addition to the newly analysed data, a large number of historical samples were also digitalised and uploaded to the database. Additionally, work was done to make the database fully compatible with the CEFAS database DAPSTOM, which covers over a century of stomach samples. The two databases can be easily linked through a ShinyR tool that has been developed in this project as well.

We used the new (and historical data) to perform three case studies in the Baltic and North Seas. In case study 1, we showed how cod predation in the Baltic Sea has changed over time and space (Figure ES1) and how cod's prey has changed, with a shift from herring to a larger portion of sprat and the invertebrate saduria. The spatial mapping of cod predation is a novel result and may have important implications for the future management of the stock.
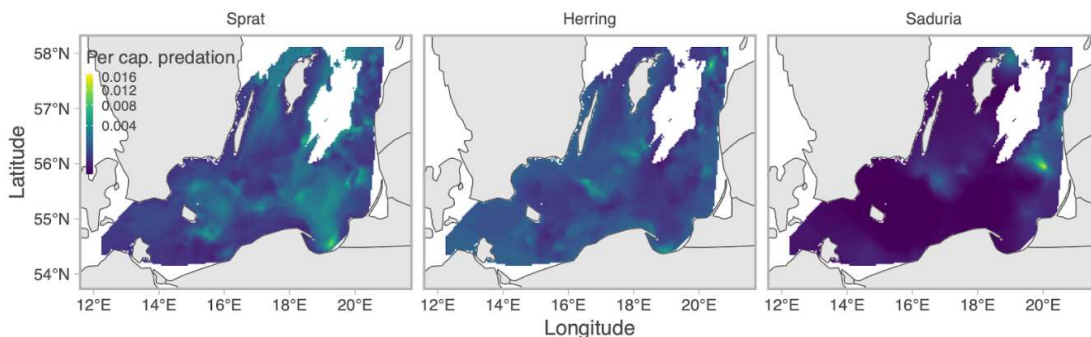
Figure ES1. Spatial variation in per capita predation for sprat, herring and saduria in the year 2000 and for cod of an average body length of 31 cm.

In case study 2.1, we presented how the predation of the three key species in the North Sea changed over time. We also show how the decline of the total cod population has caused its predation on other prey species to be at an all-time low. Whiting, on the other hand, is consuming more prey biomass. Mackerel has historically been a significant predator in the North Sea, primarily due to its large stock size. However, mackerel's

favourite prey is often planktonic, and recruited prey species only constitute a fraction of their diet. Finally, in case study 2.2, fish stomachs were used as samplers in a machine learning context and showed how temperature, fishing mortality and other environmental covariates influence the amount of piscivore, benthic and zooplanktivore fish stomachs.

Stomach samples have a wide variety of uses, and while complex to handle, stomach sample data contain a wide variety of valuable information about predators, prey, their interactions and their spatial availability. We support ongoing sampling and analysis of stomach content to have a continuous time series of diet information in the North Sea and Baltic Sea.

RÉSUMÉ EXÉCUTIF

Les informations sur le contenu stomacal constituent une source de données importante pour acquérir des connaissances sur les interactions écologiques, la structure du réseau trophique et l'abondance des espèces prédatrices et des espèces proies. Dans le cadre de ce contrat spécifique, nous avons analysé une série d'estomacs de poissons prédateurs de la mer du Nord et de la mer Baltique, rétabli une base de données pour rendre les données disponibles et effectué des analyses à partir de ces données afin de déterminer l'impact des interactions prédateur-proie dans les deux écosystèmes. Au total, nous avons analysé 9229 nouveaux échantillons stomacaux de cabillaud (*Gadus morhua*), de merlan (*Merlangius merlangus*), de maquereau (*Scomber scombrus*) et de quelques autres espèces pour lesquelles un petit nombre d'échantillons avaient été conservés lors des études internationales en mer de 2022 et 2023.

Nous avons rétabli la base de données du CIEM sur le contenu stomacal, qui n'était plus fonctionnelle ni disponible depuis plusieurs années. Dans le cadre du rétablissement de cette base de données, nous avons développé un nouveau format d'échange capable de traiter les métadonnées les plus pertinentes pour les stocks de poissons, y compris la plénitude de l'estomac, la latitude, la longitude, le numéro d'identification de la remontée et les numéros d'identification spécifiques des poissons qui peuvent être rattachés aux enquêtes scientifiques ou même aux registres d'ADN lorsque cela est possible. La base de données est régulièrement mise à jour avec des données historiques, et des efforts sont déployés pour que d'autres projets (par ex. les groupes de coordination régionale de la pêche (RCG)) téléchargent leurs données sur le contenu stomacal dès qu'elles sont disponibles. La base de données est actuellement fonctionnelle et accessible au public pour que les chercheurs du monde entier puissent utiliser l'ensemble des données sur le contenu stomacal dans les zones du CIEM. En plus des nouvelles données analysées, un grand nombre d'échantillons historiques ont également été numérisés et téléchargés dans la base de données. En outre, des travaux ont été réalisés pour rendre la base de données entièrement compatible avec la base de données DAPSTOM du CEFAS, qui couvre plus d'un siècle d'échantillons stomacaux. Les deux bases de données peuvent être facilement reliées grâce à un outil ShinyR qui a également été développé dans le cadre de ce projet.

Nous avons utilisé les nouvelles données (et les données historiques) pour réaliser trois études de cas dans la mer Baltique et la mer du Nord. Dans l'étude de cas n° 1, nous avons démontré comment la prédation du cabillaud dans la mer Baltique a évolué dans le temps et dans l'espace (Figure ES2) et comment les proies du cabillaud ont changé, passant du hareng à une plus grande portion de sprat et à l'invertébré *saduria*. La cartographie spatiale de la prédation du cabillaud est un résultat novateur qui pourrait avoir des implications importantes pour la gestion future du stock.
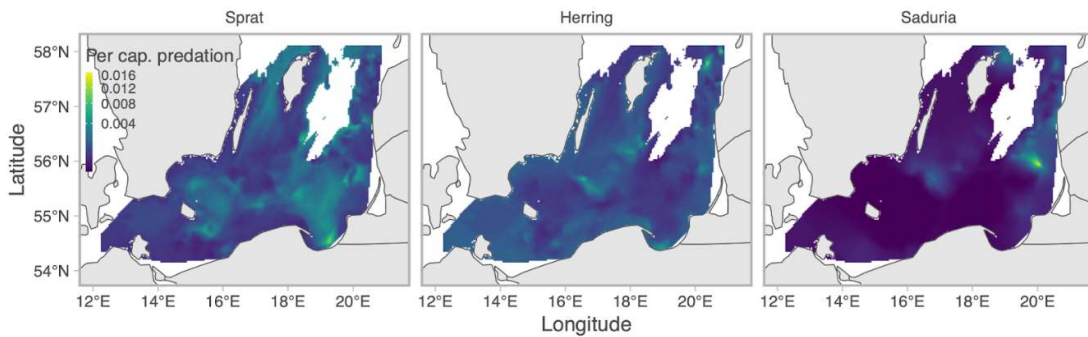
Figure ES2. Variation spatiale de la prédation par individu pour le sprat, le hareng et le *saduria* en l'an 2000 et pour le cabillaud d'une longueur corporelle moyenne de 31 cm.

Dans l'étude de cas 2.1, nous avons présenté l'évolution dans le temps de la prédation des trois espèces clés de la mer du Nord. Nous avons également expliqué comment le déclin de la population totale du cabillaud a provoqué une baisse historique de sa prédation sur d'autres espèces proies. Le merlan, en revanche, consomme davantage de biomasse de proies. Le maquereau a toujours été un prédateur important en mer du Nord, principalement en raison de la taille importante de son stock. Cependant, les proies préférées du maquereau sont souvent planctoniques et les espèces de proies recensées ne constituent qu'une fraction de son régime alimentaire. Enfin, dans l'étude de cas 2.2, les estomacs de poissons ont été utilisés comme échantillonneurs dans un contexte d'apprentissage automatique et ont montré comment la température, la mortalité par pêche et d'autres facteurs environnementaux influencent le contenu des estomacs de poissons piscivores, benthiques et zooplanctoniques.

Les échantillons stomacaux sont utilisés à des fins très diverses et, bien que complexes à manipuler, les données sur les échantillons stomacaux contiennent une grande variété d'informations précieuses sur les prédateurs, les proies, leurs interactions et leur disponibilité spatiale. Nous sommes favorables à l'échantillonnage et à l'analyse continus du contenu stomacal afin de disposer de séries chronologiques continues d'informations sur le régime alimentaire dans la mer du Nord et la mer Baltique.

1 INTRODUCTION

Stomach sample collection and analysis is vital to understand marine food webs and interactions by providing direct evidence of predator-prey overlap, evidence and inference on size-based interactions and as input to species distribution and multispecies models (1,2).

Stomach content observations are a critical component in analysis of biology of species, ecosystem functioning and understanding of predator-prey relationships. For instance, the diet content of species has historically been used to estimate the trophic level and position of species. This information can be used to extract indicators such as trophic level of the catch, mean trophic level in an ecosystem, or if trophic level has changed over time within a species due to changes in diet composition (3). Additionally, stomach observations are critical to fisheries management, as these observations are used to fuel and determine the interactions between species in multispecies models in the North Sea and Baltic Sea, which ultimately provides the size and age dependent natural mortality of species used in stock assessments (4). Stomach data analysis thus serves as an important tool to implement the ecosystem approach to fisheries (EAF) by providing information on the strength and importance of links between exploited species as part of dynamic ecosystems (5).

One challenge when analysing fish diet data within or across ecosystems is the scarcity and availability of repeat measurements, which often leads to incomplete time series, high noise to signal ratio and, thus, challenges in model integration (2,6). Additionally, fish undergo significant changes in their diet preference throughout their lives (by growing from millimetre-sized eggs to metre-long individuals); to obtain a complete picture of a species trophic role in an ecosystem, it is therefore essential to include size specific measurements of both predator and prey to get the highest quality output from a diet study. There are several other challenges with stomach content data, such as diverging evacuation of different types of food (e.g., hard part of crabs vs soft tissue in fish larvae) and changing rates of evacuation due to stomach fullness (7).

A distinctive advantage of building a time series of stomach content analysis is that it provides an outlet to estimate the diet preference and preferred predator-prey mass ratio of species. An important distinction between observed diet content and diet preference is that a predator's gut is likely to be filled with whichever prey item was most abundant in the sample year, despite that item not necessarily being the most preferred for food. By combining information from several years of predator and prey abundance, preference can be inferred and subsequently used to model and simulate potential future management objectives and directions. Ultimately, this information is crucial to implement EAF and determine appropriate management strategies to be implemented in the North Sea and the Baltic Sea.

The overarching goal of this project is to supplement the historical stomach data from the North and Baltic Sea with new data entries, to understand whether any temporal change has occurred in the interactions between predators and preys in these two case study areas. Additionally, historical stomach content data from the North and Baltic Sea are as of January 2023 stored in a non-functional database at ICES, making this data difficult to utilise for researchers and the general ICES community across the region.

This project seeks to expand the current database of stomach observations and will thus help understand the intricate relationships between predators and prey in the Baltic and North Sea, as well as provide an essential framework for researchers to use for a wide array of applications that are useful for EAF. The project will also provide a preliminary analysis of spatial diversity of Baltic cod food preference and may assist in providing an understanding of that stock's ecology.

The study presented here is a follow-up to the EU project MARE/2012/02 (8), which focused on conducting stomach content analysis across the Baltic and North Sea. The study aimed to analyse stomach content data of cod (and to a minor extent whiting) in the Baltic Sea and grey gurnard, mackerel and hake in the North Sea. The main focus of that tender was

the Baltic Sea. Additional stomach samples are also being processed in Regional Coordination Groups (RCGs).

The project was divided into three focus areas, all of which were necessary to restart the building of a database with concurrent and historical data available to researchers around the region:

- Analysis of newly collected stomach samples in the Baltic and North Sea
- Development and update of a common stomach content database hosted by ICES
- Preliminary analysis of new and historical stomach content data

Analysis of new stomach samples has been in large part a wet lab contribution to the project, where many stomach samples from 2022 and 2023 have been analysed in partner labs to obtain new datapoints for stomach samples. The second part of the project has focused on creating a database available to everyone and making sure that all uploaded data has all the correct metadata.

As per the 22nd of November 2023 all the work described in the report has been conducted, which is what was requested and more in the Terms of References. Additional work is ongoing.

2   STOMACH CONTENT ANALYSIS

The first main goal in this project was to analyse new stomach content data from the Baltic Sea and the North Sea. To achieve this goal, fish stomach samples were collected on board of research cruises during standard ichthyological analysis to get basic information about predators (total body length, total weight, sex etc.). Then samples were selected for further analysis based on the best possible spatiotemporal coverage. Subsequently, stomach samples were analysed in labs, and prey items were determined to the lowest possible taxonomic level, depending on the stage of decomposition. Finally, results of the stomach content analyses were uploaded to the ICES stomach database.

The activities in this part of the study were as follows:

- Make an inventory and selection of stomach samples;
- Conduct analysis of stomach content after information and samples exchange between institutes;
- Prepare the data to be uploaded in the ICES database.

Baltic Sea

In the Baltic Sea, the focus was on cod (*Gadus morhua*) and whiting (*Merlangius merlangus*). Samples of cod were provided by Latvia, Sweden, Poland and Denmark, while samples of whiting were provided by Germany. Although the aim was to analyse up to 2 500 new samples for this region, results were different (see Table 1).

Table 1. Number of stomach samples from the Baltic Sea. (selected – samples selected for stomach content analysis; analysed – samples analysed for diet composition; ICES database – number of stomachs analysed with results uploaded in ICES stomach content data https://stomachdata.ices.dk/inventory). Status on the 22nd of November 2023.

Species	Sampling period	Selected	Analysed	ICES database
Cod	2017-2022	5 895	5 293	3 146
Whiting	2020-2021	400	400	0
Total		*6 295*	*5 693*	*3 146*
Cod	1963-2014	27 663	27 663	27 663
Total		**33 958**	**33 356**	**30 809**

North Sea

In the North Sea, the focus was on mackerel, whiting and cod. Additionally, a small number of monkfish (*Lophius piscatorius)*, grey gurnard (*Eutrigla gurnardus)*, horse mackerel (*Trachurus trachurus)* and turbot (*Scophthalmus maximus)* samples have been included in the analysis for the North Sea. Several individuals of other fish species were also included. Although the aim was to analyse 2 800 new samples from this region, results were different (see table 2).

Table 2. Number of stomach samples from the North Sea. (selected – samples selected for stomach content analysis; analysed – samples analysed for diet composition; ICES database – number of stomachs analysed with results uploaded in ICES stomach content data https://stomachdata.ices.dk/inventory). Status on the 22nd of November 2023.

Species	Sampling period	Selected	Analysed	ICES database
Mackerel	2013-2014 & 2022	1 829	1 711	1 054
Whiting	2022-2023	1 506	972	972
Cod	2023	264	239	239
Grey gurnard	2012-2014 & 2022-2023	103	99	21
Monkfish	2022	23	23	23
Horse mackerel	2023	22	17	17
Turbot	2023	13	13	13
Spiny dogfish	2023	10	5	5
Brill	2023	4	4	4
Common ling	2023	4	4	4
Pollack	2023	4	4	4
Thornback ray	2023	4	4	4
Tub gurnard	2023	3	3	3
Atlantic halibut	2023	2	2	2
Cuckoo ray	2023	1	1	1
Total		**3 792**	**3 101**	**2 366**

2.1 Inventory and selection of stomach samples

A detailed inventory of samples is shown in Annex 1 (Table 6 and 7). The tables contain information about the number of samples that have been collected, location of sampling, sampled species, year and quarter of sampling. The unified template format from the EU project MARE/2012/02 was used for inventory purposes with all metadata required for further analysis.

We selected a larger subset of the samples for stomach content analysis. The most important criteria used for selection of the samples were the following: predator fish species (to align samples with previously collected data), area of sampling (to get the highest spatial coverage), time of sampling (to verify potential temporal changes) and samples preservation method (to avoid changes related with the used fixative – deformation of prey). In the Baltic Sea, case study species preferences were cod and whiting, while from the North Sea whiting, mackerel and grey gurnard. However, only few grey gurnard samples were available from the North Sea, while several cod stocks had been collected. These species have historical data or were covered by the EU project MARE/2012/02. The number of finally selected samples was limited by availability of the collected samples and project budget dedicated for stomach content analysis. Our initial estimation was that 5 300 samples in total from the two areas could be analysed, but this amount was largely exceeded (Annex 1, Table 8 and 9).

Baltic Sea

In the Baltic Sea, the focus was on whiting and cod. The samples were collected during scientific cruises (for example Baltic International Trawl Survey, BITS) but have not been analysed earlier, either due to the lack of funding or the lack of qualified experts. Samples were collected in different seasons and areas of the Baltic Sea.

While as many as up to 2 500 new samples from the Baltic Sea were expected for analysis, 6 295 samples have been provided and 5 293 of the cod stomachs (from Sweden, Denmark and Poland) and 400 of whiting stomachs have been analysed. Analysis of recently

collected samples from Latvia (around 600 cod stomachs) are not finished yet, but this analysis will be conducted (and results will be uploaded in the ICES stomach database) as soon as possible. Samples of whiting stomachs have been analysed, but the uploaders have yet to add them to the database. However, we expect this process to be completed before the project ends. Historical data (sampling 1963-2013) of cod stomachs (in total, 27 663 fish) were digitalised and are available in the database.

After the inventory of collected samples, stomachs were selected to provide the best possible spatiotemporal coverage Table 1. Samples representing prioritised predator fish species from different subregions in the Baltic Sea and different seasons have been chosen to achieve this goal, in accordance with the availability declared during the inventory process.

North Sea

Samples for North Sea case study were collected during scientific cruises but have not been analysed earlier due to the lack of funding. Samples contain fish stomachs, collected in different seasons and areas of the North Sea. Additional sampling was continued in first quarter of 2023. After a detailed inventory of collected samples, samples were selected to provide the best spatiotemporal coverage. In total, 3 792 samples were selected.

One of the partners has 289 samples available, collected between 2009-2013 (stomachs or whole fish) and preserved in formaldehyde. These samples were not included in the analysis due to inconsistency in preservation with the other samples used in this study.

Due to a freezer failure, 241 stomachs of whiting were lost, as the stomach content degraded when thawed. The final list of fish stomach samples collected and analysed in the North Sea case study is presented in **Error! Reference source not found.**.

2.2 Analysis of stomach content

Analysis protocol

Stomach content analyses were conducted according to the methodology agreed in the EU project MARE/2012/02 by the same experts involved in the analysis in that project (8).

The Baltic Sea partners BIOR and NMFRI did a cross-validation of sampling through sharing of pictures in a previous study; these prior agreements were implemented here. Also, the methodology of stomach content analyses described by the intersessional subgroup on stomach sampling (ISSG stomach) of the regional coordination groups in the North Atlantic, North Sea & Eastern Arctic (RCG NANSEA) and the Baltic (RCG BALTIC) was taken into account in the standardised protocol.

Transport and analyses of stomachs

Stomach content analyses were conducted in the institute that was responsible for sampling or after transfer of stomach samples between partners. Each stomach that needed to be transported was packed separately in a string bag and labelled with an individual unique code (FishID). Samples were then frozen for transport and further analysis in laboratory at the institutes.

Before analysis, each stomach was thawed on a Petri dish. Stomach samples were analysed individually in contrast to some of the previously conducted stomach content analysis where several stomachs were pooled in one analysis (e.g., a large range of data from the 80s and YOTS). Cross-sectioning of stomachs was conducted with due care to avoid damaging the content. Prey items were collected on separate Petri dishes after visual inspection using naked eye and stereomicroscope (Figure 1). The stomach wall was also inspected for the presence of prey or remains (e.g., otoliths, limbs etc). Each prey item was identified to the lowest possible taxonomic level (preferably species), depending on the degree of decomposition. Each prey item was counted, and information about its

presence and number of individuals was recorded on the analysis form. Length of fish and crustacean prey was measured or estimated to nearest cm below (fish – total length/standard length; crab – carapace width; shrimp – distance between bases of rostrum and uropods; isopod – total length or pleotelson for partially digested individuals; eggs were recorded as having length zero). Digestive stage was also recorded, matching the descriptions in the ICES database. Most of the invertebrates were identified at higher taxonomic levels than species, according to level of decomposition. Total prey weight and weight of individual prey items (fish and crustaceans) or prey groups were recorded. All obtained information and measurements were recorded on the analysis form and digitalised.

Baltic Sea

The Baltic Sea stomach samples have been analysed by partners: NMFRI (samples from Sweden, Germany and Poland); BIOR (samples from Latvia) and DTU (cod sampled in Denmark). Transportation of stomachs took place from Sweden and Germany to Poland. In total, 5 693 samples were analysed (Table 3).

Figure 1. Examples of *Saduria entomon* from a cod stomach in the Baltic Sea (photo by Joanna Pawlak, NMFRI).

Table 3. Baltic Sea. The conducted fish stomach content analysis. The whiting samples and some of the cod samples have been analysed but have not been uploaded to the database yet. Status on the 22nd of November 2023.

Species	Sampling year	Country	Stomachs sampled	Stomachs analysed	ICES database
Cod	1963-2013	Latvia	27 663	27 663	27 663
	2017	Latvia	836	836	
	2018	Denmark	901	901	901
	2018	Latvia	561	560	
	2019	Latvia	426	426	
	2020	Latvia	325	325	
	2021	Denmark	919	919	919
	2021	Latvia	446		
	2021	Poland	702	702	702
	2022	Latvia	155		
Whiting	2020-2021	Germany	400	400	
Total			**33 958**	**33 356**	**30 809**

North Sea

The fish stomach samples were provided by partners ILVO, DTU and WMR. Samples were not transported between partner institutes for the North Sea case study, as each institute analysed their own samples. In total, 3 101 stomachs have been analysed (Table 4).

The analysed fish included mackerel, whiting and cod. Additionally available samples of grey gurnard (*Eutrigla gurnardus),* monkfish (*Lophius piscatorius*), horse mackerel (*Trachurus trachurus*) and turbot (*Scophthalmus maximus)* were also included. However, the number of stomachs available were limited. Moreover, a few samples of spiny dogfish (*Squalus acanthias*), brill (*Scophthalmus rhombus*), common ling (*Molva molva*), pollack (*Pollachius pollachius*), thornback ray (*Raja lucerne*), tub gurnard (*Chelidonichthys lucerne*), Atlantic halibut (*Hippoglossus hippoglossus*) and a single specimen of cuckoo ray (*Leucoraja naevus*) were analysed. Samples contain fish stomachs, collected in different seasons and areas of the North Sea.

Table 4. North Sea. Fish stomach content analysis. Some older samples from WMR (e.g., the horse mackerel) have been analysed but not yet uploaded. Status on the 22nd of November 2023.

Country	Institute	Fish species of collected stomachs (predator)	Year of sampling	Number of collected stomachs	Analysed	ICES database
Netherlands	WMR	Mackerel	2013/2014	140	140	
Netherlands	WMR	Mackerel	2013/2014	164	164	
Netherlands	WMR	Mackerel	2013/2014	353	353	
Netherlands	WMR	Grey gurnard	2013/2014	54	54	
Netherlands	WMR	Grey gurnard	2012	24	24	
Netherlands	WMR	Whiting	2022	412	158	158
Netherlands	WMR	Cod	2023	175	150	150
Netherlands	WMR	Whiting	2023	300	195	195
Netherlands	WMR	Monkfish	2022	5	5	5
Netherlands	WMR	Horse mackerel	2023	22	17	17
Netherlands	WMR	Spiny dogfish	2023	10	5	5
Netherlands	WMR	Turbot	2023	10	10	10
Netherlands	WMR	Cuckoo ray	2023	1	1	1
Netherlands	WMR	Thornback ray	2023	4	4	4
Netherlands	WMR	Common ling	2023	1	1	1
Netherlands	WMR	Brill	2023	2	2	2
Denmark	DTU	Whiting	2022	185	185	185
Denmark	DTU	Monkfish	2022	18	18	18
Denmark	DTU	Whiting	2022	213	213	213
Denmark	DTU	Mackerel	2022	1 172	1 054	1 054
Denmark	DTU	Cod	2023	89	89	89
Denmark	DTU	Atlantic halibut	2023	2	2	2
Denmark	DTU	Brill	2023	2	2	2
Denmark	DTU	Common ling	2023	3	3	3
Denmark	DTU	Pollack	2023	4	4	4
Denmark	DTU	Tub gurnard	2023	3	3	3
Denmark	DTU	Turbot	2023	3	3	3
Belgium	ILVO	Whiting	2022	58	58	58
Belgium	ILVO	Grey gurnard	2022	17	17	17
Belgium	ILVO	Whiting	2023	25		
Belgium	ILVO	Grey gurnard	2023	4		
Belgium	ILVO	Whiting	2023	150		
Belgium	ILVO	Grey gurnard	2023	4	4	4
Belgium	ILVO	Whiting	2023	163	163	163
Total				**3 792**	**3 101**	**2 366**

2.3 Data preparation for uploading to ICES database

The data collected for the purpose of this study were digitalised using the protocol that has been implemented in the EU project MARE/2012/02. Uploading these data to the ICES database is conducted by the partner that collected the stomach samples. The individual number of samples uploaded are presented in Table 1 for the Baltic Sea and Table 2 for the North Sea. For both regions, more samples have been analysed than uploaded; however, we expect a continuous stream of uploads from historical data to continue.

Baltic Sea

The historical data were added to the ICES database but lack some of the metadata that are available for newly collected samples (e.g., sampling location).

In total so far, 30 809 analysed stomachs data were uploaded in ICES database for the Baltic Sea. In the case of the Baltic Sea, 2 147 cod stomachs data and 400 whiting stomach content analysis results should be delivered (Table 3

).

Database related with the prey items found in Baltic Sea predators consists of 46 353 records and 77 types of items have been described. In the Baltic Sea, the most frequently recorded preys were invertebrates *Mysis mixta* (17 961 records), *Saduria entomon* (4 903) and *Bylgides sarsi* (4 569) and a vertebrate often recorded was sprat (*Sprattus sprattus)* (6 071).

North Sea

Regarding the North Sea database, the total results of 2 366 stomachs analysed are uploaded, and the diet composition of 657 mackerels and 78 grey gurnards were analysed and will soon be added to the database (Table 4).

In the case of the North Sea, 4 292 unique records of prey items have been reported, and 73 types of items have been identified. Among the most frequently recorded items in the North Sea fish predator stomachs were representatives of invertebrates: Nematoda (978 records), Crustacea, Caridea, Arthropoda, Mysida, Brachyura and Decapoda. Meanwhile, most abundant fish prey were representatives of the Gadidae family - *Merlangius merlangus* (60 records) and representatives of the Clupeidae family (herring and sprat). The large (numerical) abundance of nematodes is most likely related to a parasitic infection in the fish in which they were found, rather than being an important prey item.

3 CONSTRUCTION OF ICES STOMACH DATABASE

The second aim in the project was to re-establish the ICES stomach database https://stomachdata.ices.dk/. In this study, ICES and participating institutes redesigned the stomach content database. The redesign included newly collected and historical stomach samples. ICES' role was primarily practical support for their online data portal, i.e. hosting, data support and helpdesk, bug fixes, developments to upload/view/download functions and updating the portal interface. The role of the institutes was to provide expert knowledge on the structure of collected stomach samples to redesign the database in a new format. Unfortunately, the new exchange format made it impossible to transfer previously published stomach data directly to the new format. The protocol for uploading new stomach content data to the ICES stomach database is published in the ICES data portal. The ICES stomach database is now publicly available.

As part of the EU project MARE/2012/02 in 2014, the DAPSTOM database was redesigned and substantially altered. Further reconstruction and refinement have been carried out under this study. The basic relational structure has been retained for DAPSTOM Version 6.3. Data from 127 additional sampling campaigns were added to the database as part of this most recent update. Some datasets were derived from scientists log-books or reports contained within the CEFAS archive, while others were donated by 'partners' or were digitised from published peer-reviewed papers, with specific relevance to the British Isles. An app used to combine DAPSTOM with the newly generated ICES database has been partly developed in the project and will be made available from the DAPSTOM webpage. Besides a clickable link that can be used to download the content from DAPSTOM and bind it with the ICES database, an API will also be made available for researchers to bulk download data, and combine it with stomach content data from the ICES database.

3.1 ICES stomach database

Update and maintenance of the ICES stomach database

ICES stomach content database interface consists of four sections – data submission, data downloading, description of file format and contact address information (Figure 2). In the proceeding paragraphs, detailed information about the structure and functionalities of each section is provided, including progress made at the time of this study.
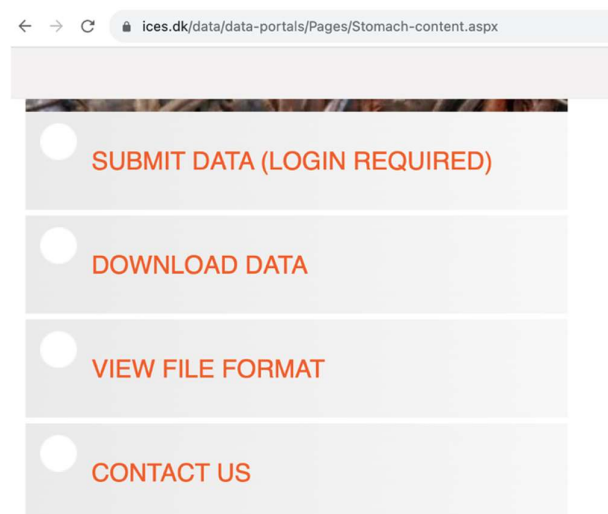
Figure 2. ICES Stomach content data base overview. Source: https://stomachdata.ices.dk/**.**

Data submission and screening

Submission of stomach content data is password protected and requires ICES login credentials to ensure data security and integrity. Data validation (data screening) is performed by the data screening utility (DATSU) upon data submissions to the ICES stomach content database (https://stomachdata.ices.dk/Account/Login) (Figure 3). The validation is an automated process which produces data quality reports with quality flagged data for the submitter to verify if the data needs any correction. If no corrections are needed, the data are uploaded to the database and can be downloaded right away.
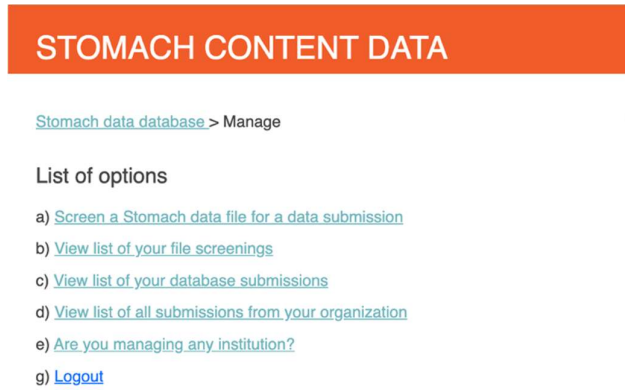
Figure 3. List of options in the data screening utility (DATSU) upon data submissions to the ICES stomach content database.

Exchange file format

The existing exchange format (used in EU project MARE/2012/02) was used as a starting point to build a new format for the database that will be published in the ICES data portal.

Updating process
ICES provided an older exchange format (Version 1) and asked the project partners for feedback. All comments and suggestions were included in a new version of the exchange format (version 2), which formed the basis for discussions in a Technical meeting at ICES Headquarters (February, 2023). Changes were suggested and incorporated in the exchange format, resulting in Version 3. After the Technical meeting, the fourth version of the exchange format was built, which was used to start uploading real stomach content data and testing the new database. The final tuning of exchange format, taking into account feedback from national institutes, was made in September 2023. The new exchange format consists of four parts:

1. FI – File information
2. HH – Haul information
3. PI – predator information
4. PP – prey information

Final Exchange format and Protocol for uploading to stomach content analysis
The latest version of exchange format is available under the link 'View file format' in http://datsu.ices.dk/web/selRep.aspx?Dataset=157 and in Annex 2 (Table 10 to

Table 13). All information needed for uploading stomach content data can be found on the ICES website.

1. File Information

The basic information about reporting country, institution and survey where stomach data were collected is included in File information (FI) file.

2. Haul Information

In the latest format sampling 'time of haul information' is required as a mandatory field. The aim of reporting 'time of haul information' is to exclude the overlap of different hauls on the same day and to ensure that duplicated events are not in the database. Haul positions are mandatory for recent data but are optional for historical data. For instance, the DATRAS survey database also has a corresponding unique haul information and has additional information, such as temperature, wind speed, or catch per unit effort of fish species caught in that haul.

3. Predator Information

To include improved information about predator biological information and methods of analyses, some additional predator specific fields were added to the new format, while some were changed from optional to mandatory. 'Preservation method' was changed to mandatory, and 'age data' in the new format is still mandatory, while it could be problematic for some historical data and for some fish species where age reading is stopped.

Additional fields describing 'Number of empty stomachs', 'Measurement Increment', 'Genetic sampling information' and 'Age source' were added to the exchange format of 'Predator Information'. If the predator has an empty stomach, then the value in the field StomachEmpty is '1', meaning that in the predator information file there should not be any information about stomach content.

4. Prey Information

To improve the available information on prey items, biological information and analysis method, some additional fields were added to the exchange format, and some were changed from optional to mandatory.

'PreySequency' was added as mandatory field to allow for adding a unique prey sequence ID number. An additional field 'AnalysingOrg' was included to register the organisation that conducted the stomach analyses, as register the organisation, as it is not always the same as the organisation that collected the stomach samples.

Data downloading

ICES stomach data are open access and freely available for scientific community. It is possible to download stomach data applying several criteria: Reporting organisation, Year, Country or Ecoregion (Figure 4).

Downloaded stomach data are provided in a ZIP file, containing a data disclaimer text file, as well as four csv files from exchange format (File information.csv, Haul information.csv, Predator information.csv and Prey information.csv).

To download stomach data from the database, a disclaimer with following conditions should be accepted:
- *All data products are by default publicly available, including those derived from restricted data.*
- *Only summary information for restricted records are publicly available for download.*
- *All public data are under the Creative Commons (CC BY 4.0) licence.*
- *You have sole responsibility for correct and appropriate data interpretation.*
- *Results, conclusions and/or recommendations derived from the data do not imply endorsement from ICES.*
- *You are requested to inform ICES of any suspected problems in the data.*

Figure 4. Data download interface of stomach content data.

Integration and standardisation of historical data

As an extension to the new stomach content exchange format for uploading, a large set of previously analysed data which had not been digitised before was prepared for the database.

Baltic Sea
Historical stomach content data were available on paper. A first step was to convert these paper files to Excel files. A second step was a quality check of these Excel files, using a comparison of biological analyses with trawling information, checking of outliers, etc.). A third step was to modify the format to fit the new ICES exchange format. Finally, the data were uploaded to the ICES stomach database.

The above described procedure was originally planned for approximately 12 000 juvenile cod stomach data from the Baltic Sea, covering a time period from 1963 to 2017.

However, due to the new format of the exchange file that requires additional metadata, it was not possible to transfer all the historical data directly into the new database. ICES could not solve this problem, since the YOTS data are at the national institutes. Additional contribution from each of the institutes is necessary to complete this task. It was not possible to finish the transfer of all the historical data by the end of this tender. Part of existing historical data is already transformed to the new format and uploaded in ICES stomach database. As a result, the total number of historical cod stomach data are several times higher than originally planned in the project (27 000 although firstly we estimated to do it for around 12 000). Historical data uploaded in the database consist of juvenile and adult cod. There will be continuous uploading of historical data from the North Sea and the Baltic Sea after this project concludes with funding from other projects.

Table 5. Overview of uploaded stomach (all species combined) data by country in ICES stomach database from 1963 – 2023. Status on the 22nd of November 2023.

Years	BE	DE	DK	LV	NL	PL	SE	Total
1963-1967				7 605				7 605
1968-1972				1 912				1 912
1973-1977				5 129				5 129
1978-1982				1 146				1 146
1983-1987				1 031				1 031
1988-1992				1				1
1993-1997				1 367				1 367
1998-2002				2 503				2 503
2003-2007				4 335				4 335
2008-2012				2 071				2 071
2013-2017				644				644
2018-2023	75	5	2 878		548	702	624	4 832
Total	**75**	**5**	**2 878**	**27 744**	**548**	**702**	**624**	**32 576**

3.2 DAPSTOM stomach database

DAPSTOM Version 6.3; development and coherence with ICES stomach database

DAPSTOM is an ongoing CEFAS initiative digitising fish stomach records (9). The database contains information collected between 1836-2023 on 210 predator species, most occurring in Northern European groundfish surveys. These data differ from ICES Year of The Stomach Dataset (YOTS) in that they are a collation of 741 surveys, many of which were not coordinated, from across the North Atlantic and Arctic Oceans, particularly the North Sea, Celtic Sea, Irish Sea and area around Spitzbergen. DAPSTOM therefore covers a much greater spatial and temporal scaled, with many more predator species compared with ICES stomach contents data but has some gaps in, e.g. prey biomass observations, because information has not been reported consistently across different surveys. In these cases, we have estimated prey biomass information thus aiding interoperability between the different stomach content data. This section describes the latest efforts to update and expand the DAPSTOM database for fish stomach content records. In this latest iteration (Version 6.3), an additional 26 767 records for 122 137 individual predator stomachs have been added to the dataset (including 31 488 cod stomachs), bringing the total up to 283 121 records from 481 476 stomachs. In this latest version, particular emphasis has been placed on digitising historical datasets from Scottish waters, the Faroe Islands, the coasts of Norway and the Irish Sea. The DAPSTOM database encompasses individuals ranging in size from 0.1 cm (a herring larva) to 768 cm for a basking shark caught in 1947.

This section describes efforts to substantially re-engineer the online portal and move away from Microsoft Access toward PostgreSQL. Postgres is a free and open-source relational database management system that can be linked to CEFAS' externally accessible server, as part of the 'CEFAS Open Science' initiative. Data from the DAPSTOM Version 6.3 database can be seamlessly combined with ICES stomach content data, with the intention to make it searchable and freely available to users via a dedicated R-shiny interface.

For a detailed description of newly added data to DAPSTOM, see Annex 3.

The database is available at: DAPSTOM (integrated database and portal for fish stomach records) - Cefas (Centre for Environment, Fisheries and Aquaculture Science)[1].

DAPSTOM structure and design

As part of the EU project MARE/2012/02 in 2014, the DAPSTOM database was redesigned and substantially altered. Further reconstruction and refinement have been carried out under this project. The basic relational structure has been retained for version 6.3 (Figure 5) although 'predators' and 'prey' in their stomachs have now been split into two separate tables, noting that there can be multiple prey records in the 'prey' table for each individual (or pooled) predator in the 'predator' table. In addition, a new 'prey qualifier' look-up table has been added, linked to the 'prey' table to differentiate between prey life stages, e.g. eggs, larvae, adults etc. (Table 14). Prey names as written in the original source material are retained in the 'prey table', but a TSN identifier (Taxonomic Serial Number) is assigned to provide an internationally recognised taxonomic scheme. TSN numbers are used as the linking variable to the 'prey taxonomy' table. Taxonomic Serial Numbers (TSN codes) are issued by the Integrated Taxonomic Information System (ITIS), a partnership formed in 1996 as an interagency group within the US federal government. TSN numbers were chosen to provide the primary taxonomic architecture for DAPSTOM in preference to other schemes (such as the WoRMS - World Register of Marine Species) because ITIS-TSN includes terrestrial, freshwater and marine organisms, whereas other schemes have gaps. It was necessary (in a few cases) to devise our own DAPSTOM/TSN codes for empty stomachs and inanimate objects etc. (see Table 15). WoRMS aphiaID numbers are provided, where available, to aid interoperability with ICES stomach content data.
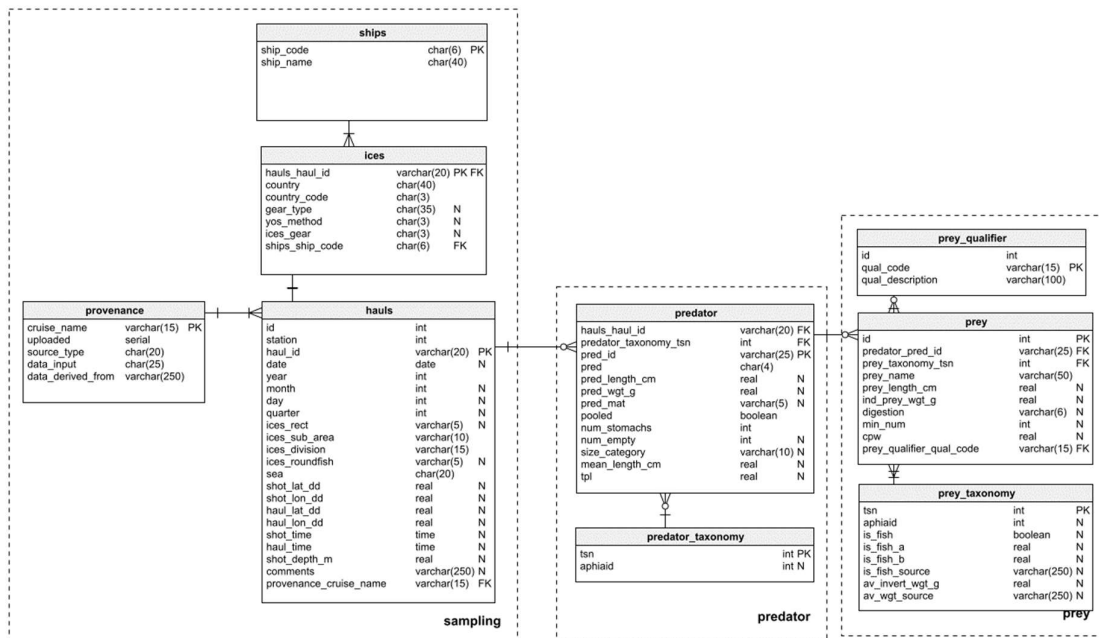
Figure 5. Structure of the revised DAPSTOM 6.3 relational database, including a list of the fields included (for a full description, see Appendix 1).

[1]https://www.cefas.co.uk/data-and-publications/dois/dapstom-integrated-database-and-portal-for-fish-stomach-records/

More complete data on average prey weights (invertebrates)

In preparing a previous version of the DAPSTOM database (Version 4.9), under the auspices of the EU project MARE/2012/02, a major task involved the construction of a new 'look-up table' of average prey wet weight that was further refined and expanded in version 5.5. A particularly important source of 'fresh weight' estimates was the CEFAS database of benthic surveys. Average wet weight of individuals by species were calculated, which provided coverage for most benthic invertebrates encountered in fish stomachs. Regarding planktonic invertebrates, information on various macroplankton types (jellyfish, chaetognaths, euphausiids, mysids, ctenophores, larvaceans etc.) was derived from Moriarty et al. (10), whereas information on mesozooplankton types (copepods, cladocerans, etc.) was based on the volume of different species, converted to wet biomass (see Pitois and Fox (11)). Estimates of 'fresh weight' for insects were primarily obtained from Studier & Sevick (12) and from Chown et al. (13).

Where prey weights could not be obtained from literature sources, we made use of weights of individuals actually observed in stomachs from the DAPSTOM database itself, where these existed. This was especially true for plant material (seaweeds and terrestrial plants) as well as colonial animals such as bryozoans, sponges and soft corals etc. For phytoplankton and micro-organisms (such as foraminifera) a nominal small value of 0.00001 g per individual was assumed.

More complete data on average prey weights (fish and cephalopods)

For all fish species observed as prey, average prey weight estimates were not used. Rather, weight-length exponents (a, b) were included (in the 'prey taxonomy' table), mostly derived from the CEFAS report by Silva et al. (14), and these exponents were in turn used to derive prey weight, based on the length of the predator. Within the 'predator' table, a field called 'TPL' (Theoretical Prey Length) had previously been included based on the observed relationship between predator length and prey length. Individual species' relationships (n=22) from Pinnegar et al. (15) and Scharf et al. (16) were averaged in order to create an overall relationship:

Prey length = (0.2057 x predator length) + 1.618

Weight-length exponents (in the 'prey taxonomy' table) were used with estimates of TPL (in the 'predator' table) to yield the wet weight of fish prey items.

In addition to fish, weight-length relationships were also available for cephalopods (squid, octopus and cuttlefish), most notably from Merella et al. (17) and Emam et al. (2014). For the frog *Rana temporaia*, exponents were obtained from (1984), for harbour porpoise *Phocoena phocoena* from Kastelein and Batum (18) and, for birds (*Anthus pratensis* and *Uria aalge*), from Victoria et al. (19). As part of DAPSTOM 6.3, notable new prey items included harbour seal (eaten by a 75.7 cm spurdog in 1966) and water vole (eaten by two chubs in 1964). Weight-length exponents for these species were taken from Markussen et al. (20) and Pisanu et al. (21), respectively.

Species, spatial and temporal coverage

Species coverage
The most recent version of the DAPSTOM dataset (Version 6.3, collated in August 2023) includes 283 121 records derived from 741 distinct research cruises, spanning the period 1836-2023. The database contains information from 481 476 individual predator stomachs and 210 predator species. As such, this database represents one of the largest and most diverse compilations of marine food web data anywhere in the world.

In this most recent upload, an additional 26 767 records were added to the database from 122 137 individual stomachs. The fact that the number of stomachs is substantially higher than the number of records reflects the fact that large quantities of 'pooled' data were digitised. For example, 4 210 records were obtained where cod was identified as the

predator, but these were derived from 31 488 stomachs (Figure 6). Similarly, 570 records were digitised for salmon, from 7 543 individual stomachs. By contrast, the situation was reversed for dab, plaice and horse mackerel, where the number of stomachs exceeded the number of records (dab: 4 291 records, 4 071 stomachs; plaice: 3 948 records, 3 158 stomachs; horse mackerel: 530 records, 280 stomachs), and this reflects the fact that, for these species, large quantities of recent data were uploaded, having been collected at the individual stomach level (e.g. from the CEFAS CSEMP cruises, from Hunt et al. (22), Rijnsdorp & Vingerhoed (23), Patel et al. (24) and Macer (25)).
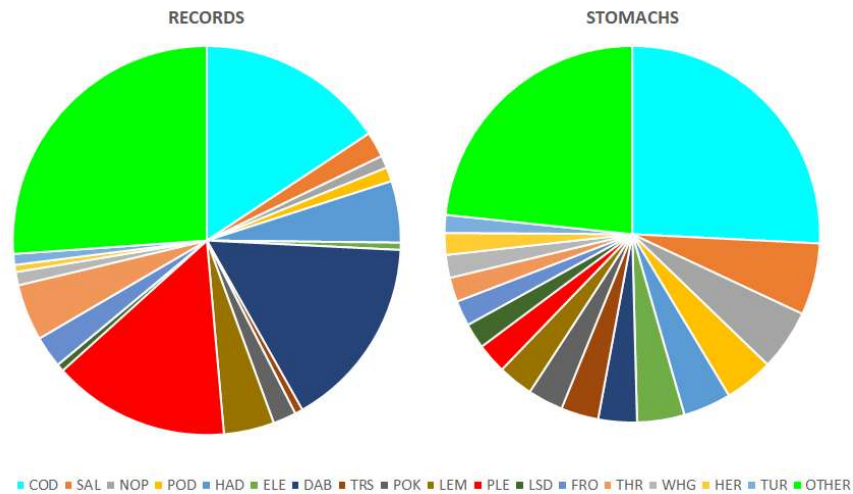
Figure 6. Composition of the newly added datasets by predator species, according to (a) the number of records and (b) the number of stomachs examined [for three-letter predator codes, see Annex 3].

Figure 7 shows that for the DAPSTOM Version 6.3 database as a whole, 26.8% of all records (75 923) relate to cod and 16.9% (47 929) relate to whiting. However, the importance of these species in terms of number of stomachs is much reduced (16.4% and 7.5% respectively), whereas plaice and herring represent a greater proportion of the stomachs examined (9.3% and 16.1% respectively) than of the number of records (6.8% and 2.8% respectively). For eighteen species (out of 212) in the database, only one individual stomach was examined.
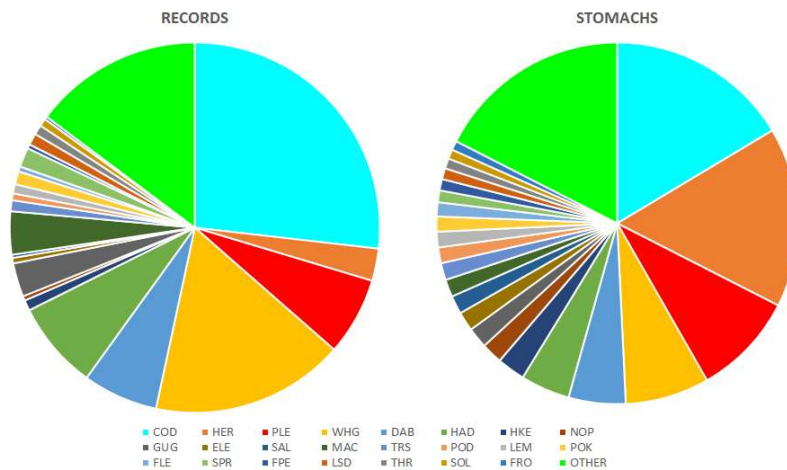
Figure 7. Composition of the DAPSTOM 6.3 database by predator species, according to (a) the number of records and (b) the number of stomachs examined [for three-letter predator codes, see Annex 3].

Spatial coverage
In this latest iteration of the DAPSTOM database (version 6.3), the largest proportion of newly added data (49%, 13 217 records) were derived from the North Sea, and this is also the case when expressed in terms of number of stomachs (53%, 64 680 stomachs). 13% of all records (3 576) were derived from the Irish Sea, but only 6% of all stomachs (7 365). Similarly, large quantities of data (11%, 1 257 records) were digitised from the Celtic Sea (including the Bristol Channel), although these records were derived from a smaller number of stomachs (5%, 5 831 stomachs). By contrast, a relatively small proportion of records were obtained for freshwater predatory fish (8%, 2 220 records), but these records were derived from a relatively large number of stomachs (12%, 14 675 stomachs).

As is apparent from Table 11, the updated DAPSTOM database (Version 6.3) includes information from sites all over the Northeast Atlantic. However, half (52.8%) of the records (52.6% of stomachs) relate to the North Sea, given that this has continued to be the main focus of survey work at CEFAS/MAFF in Lowestoft for the past 120 years. Relatively large numbers of records have also been digitised for the Irish Sea (10.7% records, 9.5% stomachs), Celtic Sea (8.8% records, 4.4% stomachs), as well as the area around Spitzbergen (9.0% records, 4.0% stomachs), where a MAFF survey vessel operated from 1949 to 1977 (26). Freshwater fish species represent only a small proportion of all records (2.6%) and stomachs (6.5%) in the database.

Temporal coverage
The earliest records in the DAPSTOM database are for 1836 and were digitised from Thompson (27) in *Annals of Natural History*. The most recent record is from the *RV CEFAS Endeavour* 'END01-23' cruise in January 2023. Figure 8 shows that data have been digitised from every decade after 1830. From the 1920s (6 737 records, 54 497 stomachs) onwards, the number of fish stomachs examined increased rapidly. Fewer stomachs were sampled in the 1940s, because activity ceased during the Second World War; however, sampling resumed quickly in the 1950s (Figure 8: 31 636 records, 55 641 stomachs). Many thousands of stomachs have been digitised for the 1970s (23 676 records; 73 124 stomachs), and progressively fewer stomachs have been sampled in decades since. However, it should be noted that, while additional stomach sampling effort was expended in 1981 and 1991 as part of the ICES 'Year of the Stomach' campaigns, these data are not included in the DAPSTOM database in order to avoid duplication with the open-access sources available through ICES (see www.ices.dk/marine-data/data-portals/Pages/Fish-stomach.aspx). The most recent iteration of the DAPSTOM database added large quantities of data from the 1960s and 1970s in particular (24 780 and 30 995 stomachs, respectively). In the current decade (2020-2023) 773 records (541 stomachs) were derived from the annual CSEMP (Clean Seas Environmental Monitoring Programme) monitoring cruises [END18-20, END06-21, END01-23].
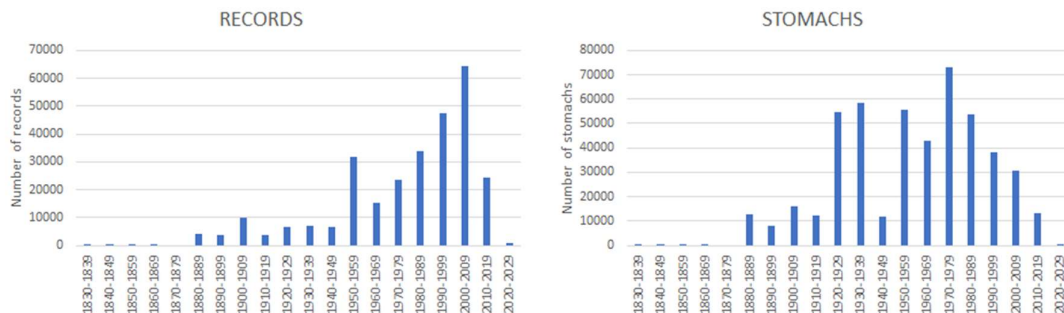
Figure 8. Temporal coverage of database records and stomachs sampled within the DAPSTOM 6.3 database.

Discussion – how the database can be used

Caveats and capabilities
As a result of efforts to estimate 'calculated prey weight', it is now possible to compare the nominal diet composition based on both number of prey items consumed, as well as the weight (mass) of prey consumed. For example, Figure 9 shows the results for dab and plaice >10cm total length in the North Sea. From this figure, it is clear that diet composition of dab includes large numbers of bivalve molluscs (23%) and ophiuroids (16%), whereas these prey types are less important in terms of weight (13 and 12%, respectively). By contrast, Anomurans (hermit crabs and squat lobsters), teleosts and brachyuran crabs represented only a small proportion of prey in terms of numbers consumed (7, 7 and 6%), but they are very important in terms of biomass (22, 13 and 14% respectively). In plaice, bivalve molluscs are important prey items both in terms of number and weight of prey items consumed (72 and 70%, respectively), but polychaetes were more important in terms of numbers in comparison with biomass (16% compared to 7%), whereas fish (teleosts) were less important in terms of numbers in comparison with biomass (2% compared to 10%). These results are largely indicative and are very sensitive to the assumed average size of an individual prey organism; however, the estimates should prove useful for future multi-species-modelling projects (e.g. Bentley et al. (28)).
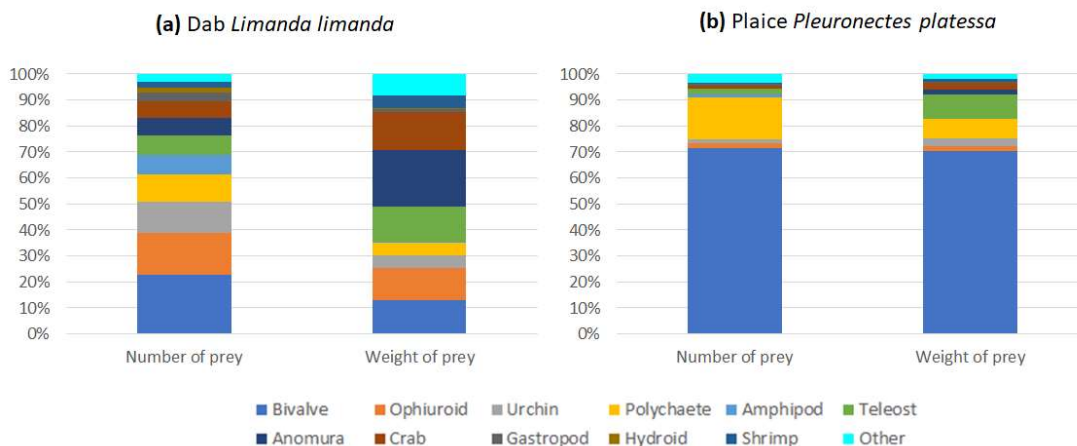
Figure 9. Diet composition of (a) dab (*Limanda limanda*) and (b) plaice (*Pleuronectes platessa*) based on the number and estimated biomass (wet weight) of prey items consumed.

A major limitation of the DAPSTOM Version 6.3 dataset is that it comprises a mixture of 'pooled' information together with data collected from individual fish. Sometimes only information on the number of stomachs containing a particular prey item was available (i.e. 'frequency of occurrence'), rather than the actual number of a particular prey item. Hence, in any data extraction, outputs should be viewed as providing information on the 'minimum number' of prey items consumed. This would have little impact in predator species that consume large prey items (e.g. fish feeders), and in most of the newer datasets submitted, but it could mean that in certain older datasets, the total number of prey items (and by extension the aggregate weight of prey items consumed) in plankton-eating species such as herring could be underestimated. An example of such data added in this most recent iteration includes that from Ogilvie (29) on herring and diets of larval haddock from Ogilvie (30) around Scotland.

Unlike the ICES 'Year of the Stomach' dataset, the DAPSTOM database includes considerable information on the prey consumed by fish larvae as well as adults. In effect, this means that any data extraction that does not take account of predator size (and for example exclude individuals smaller than 10cm) could yield a diet composition with unexpectedly high prominence of planktonic prey items such as copepods. The DAPSTOM database encompasses individuals ranging in size from 0.1cm (a herring larva) to 768 cm for a basking shark caught in 1947.

A ShinyR application has been prepared to seamlessly connect the DAPSTOM database with the ICES stomach database. The app has been constructed such that the column names in DAPSTOM correspond to the column names in the ICES database, and the two are thus easily joined in external software (such as R or Python). Specific CruiseID ensures that the entries in the two databases does not overlap. The application is still in alpha stage, but will be available from the DAPSTOM website[2] as soon as it is launched.

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[2] https://www.cefas.co.uk/data-and-publications/fish-stomach-records/

4   ANALYSIS OF STOMACH CONTENT DATA

As the last part of the project, we wanted to use the new (and existing) stomach data to perform a preliminary analysis feeding rates and predator-prey interactions of fish in the North Sea and the Baltic Sea. These analyses also investigated changes in food web interactions, energy pathways and food web structure, with potential implications for the maximum sustainable yield (MSY) of prey species in a multispecies context. This work will predominantly occur via three case studies (CS) covering the Baltic Sea (CS1) and North Sea (CS2.1 and CS2.2), the results of which are described in detail below.

We also provide a general overview of how the stomach database has been updated (i.e., what new data has been added) with respect to samples, species (both predators and prey) and the spatial extent of the data. This overview is specifically aimed at cod, whiting and mackerel in the North Sea and cod in the Baltic Sea. These species were prioritised because they have seen the greatest increase in data.

4.1 General overview of the ICES database

The summarised data of stomach samples calculated below are presented as number of individuals in the stomach, thus favouring species that are smaller and therefore often more abundant. In CS1–2 below, the prey is calculated per weight in both the North Sea and the Baltic Sea to get an overview of the total diet contribution per prey.

Baltic Sea

As shown in Figure 10, the main prey species of cod in the Baltic Sea was brown shrimp (*Crangon crangon*) which constituted 26.4% of the diet. Although brown shrimp is a benthic crustacean species, the new stomach data indicates that cod also feed on fish such as Gobiidae (22.9%), sprat (12.9%) and herring (4.9%).

New cod stomach content data were collected from five of the twelve ICES areas in the Baltic Sea. The highest-sampled area was IIId25 (958 stomachs) in the southern Baltic, followed by area IIId26 (424 stomachs). Stomachs were also added in area IIId24 (143), IIId28.2 (95) and IIId27 (63). The proportional contribution of prey species to the diet of cod in those five areas are presented in Figure 10 and Figure 11. Amongst these, the most varied diet was from cod in area IIId25, which is also the most sampled area, albeit many of the prey species only contributed a small amount (<1%).
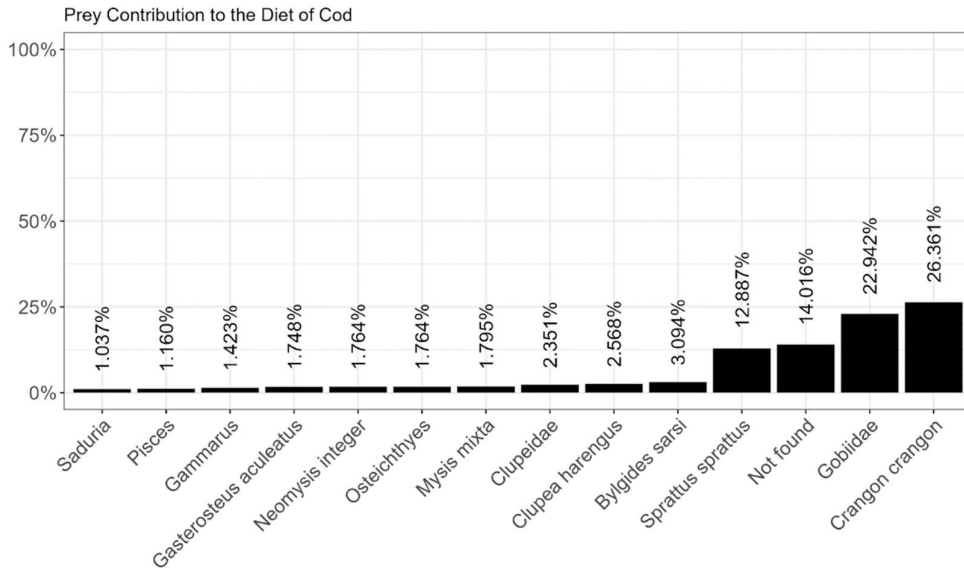
Figure 10. Proportional contribution of the different prey species to the diet of cod in the Baltic Sea. 'Not found' indicates the presence of an unidentifiable particle in the stomach. These unidentified particles were weighed and measured, but identification was not possible. Proportional values smaller than 1% have been removed to aid visualisation.

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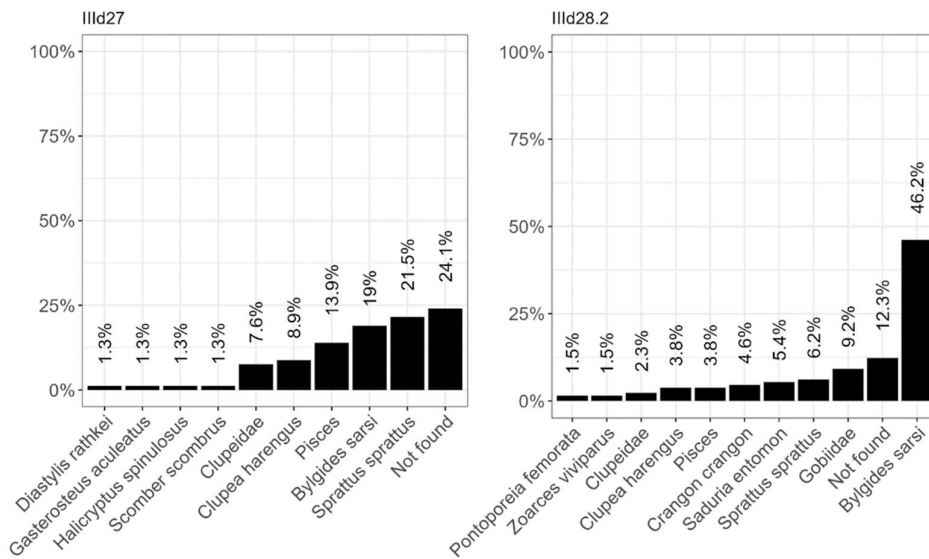
Figure 11. Proportional contribution of the different prey species to the diet of cod in ICES areas IIId27 and IIId28.2. Proportional values smaller than 1% have been removed to aid visualisation.
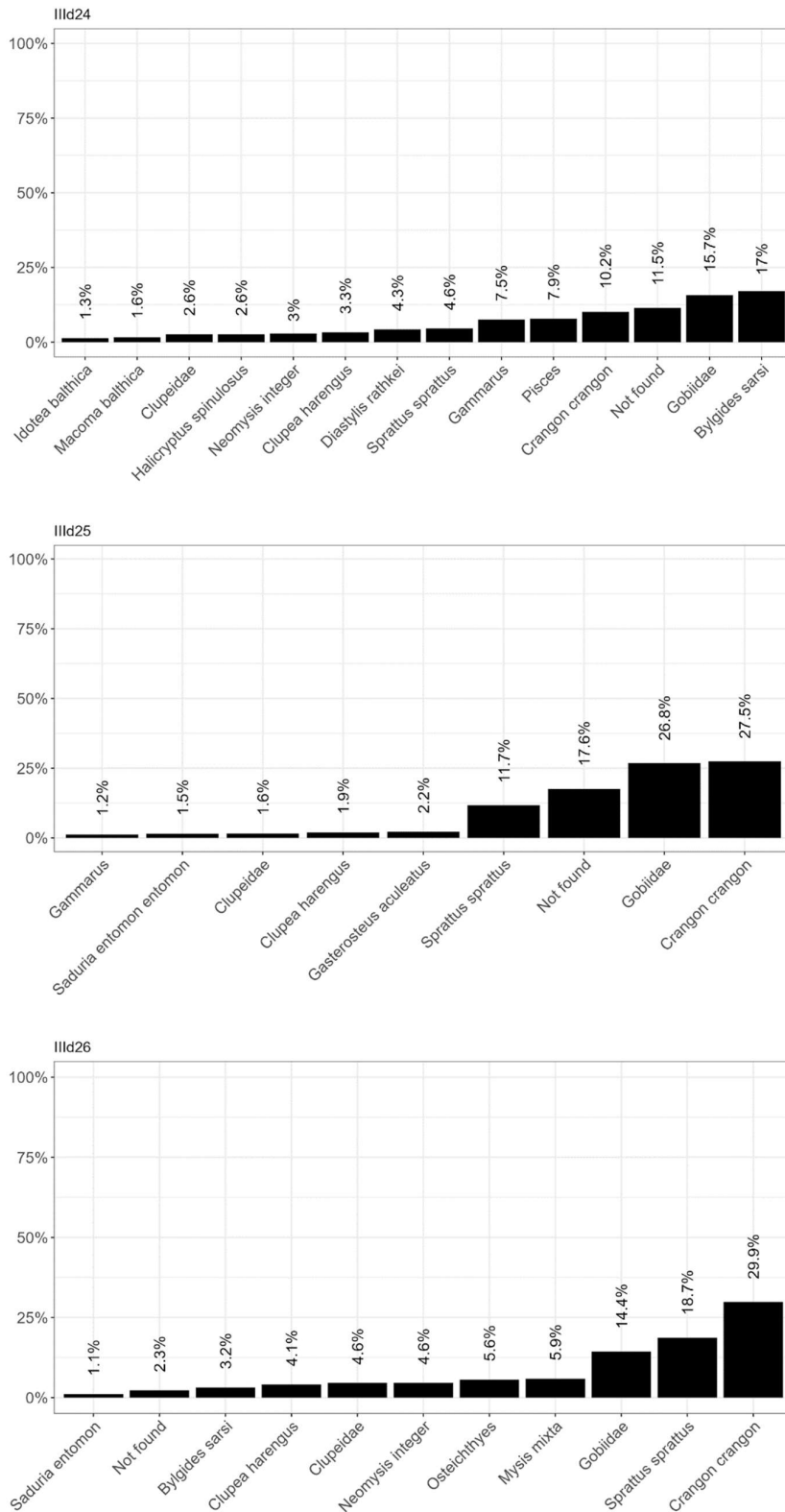
Figure 12. Proportional contribution of the different prey species to the diet of cod in ICES areas IIId24, IIId25 and IIId26. Proportional values smaller than 1% have been removed to aid visualisation.

In areas IIId28.2 and IIId24, *Bylgides sarsi* (polychaeta) is found to be the main prey species with a relative contribution of 46.2% and 17%, respectively. In areas IIId25 and IIId26, the main prey species was brown shrimp contributing 27.5% and 29.9%,

respectively. In comparison, Area IIId27 is the only area where a fish species (sprat) was found to be the main prey contributing to the diet of cod (21.5%) followed by *Bylgides sarsi* (19%). Unidentified fish species (Pisces; 13.9%), herring (8.9%) and Clupeidae (7.6%) were also found in the stomachs in cod in area IIId27. Area IIId27 is also the only area where Gobiidae are not found in the diet of cod. In all other areas, the Gobiidae family is well represented (9.2% in IIId28.2, 15.7% in IIId24, 26.8% in IIId25 and 14.4% in IIId26).

In summary, the results of the updated stomach content database indicate that Baltic Sea cod mainly prey upon a range of benthic species (including brown shrimp and fish in the Gobiidae family) as well as pelagic fish (herring and sprat).

North Sea

When analysing the relative contribution of different prey species to the diet of whiting, cod and mackerel in the North Sea, we found that whiting has the highest number of different prey species in their stomachs. In fact, 61 different prey species are found in the stomachs of whiting, including a prey group that is unidentifiable (Figure 13). In comparison, cod was found to have 44 different prey species and mackerel ten different prey species.

Cod stomachs in the North Sea were found to contain species from the phylum Nematoda (9.09%) and Arthropoda (6.58%) and the order Decapoda (5.80%) and Brachyura (true crabs; 4.45%). It should be noted that the observed Nematoda species in the stomach samples could be a parasite as opposed to a prey item. In general, the updated stomach content data indicates that cod mainly feed on benthic prey (e.g. Decapoda, Arthropoda etc.) as well as some other fish species including sprat (2.90%), herring (1.93%), whiting (1.74%) and haddock (1.16%).

Whiting has a more diverse prey list. The updated stomach content data indicates that whiting mainly feeds on benthic prey including Caridae (true shrimp; 10.93%), Gnathostomata (10.46%), Nematoda (8.06%), Arthropoda (5.99%) and Crustacea (5.27%). Whiting is also found to eat other small fish species including Clupeidae and Gobiidae. The data also indicates that whiting display cannibalism, with small traces of *M. merlangus* (2.47%) in the analysed stomach content.

Finally, mackerel is found to have a fairly limited diet in the North Sea. The updated stomach content data indicates that mackerel mainly feed on Nematoda (34.13%) and Crustacea (10.03%), albeit over 54% of the prey in the stomachs of mackerel were unidentifiable. As in cod, the observed Nematoda species could be a parasite (in either the predator or the prey it has eaten) as opposed to a prey item, and this possibility merits consideration.

A)

Prey Contribution to the Diet of Cod
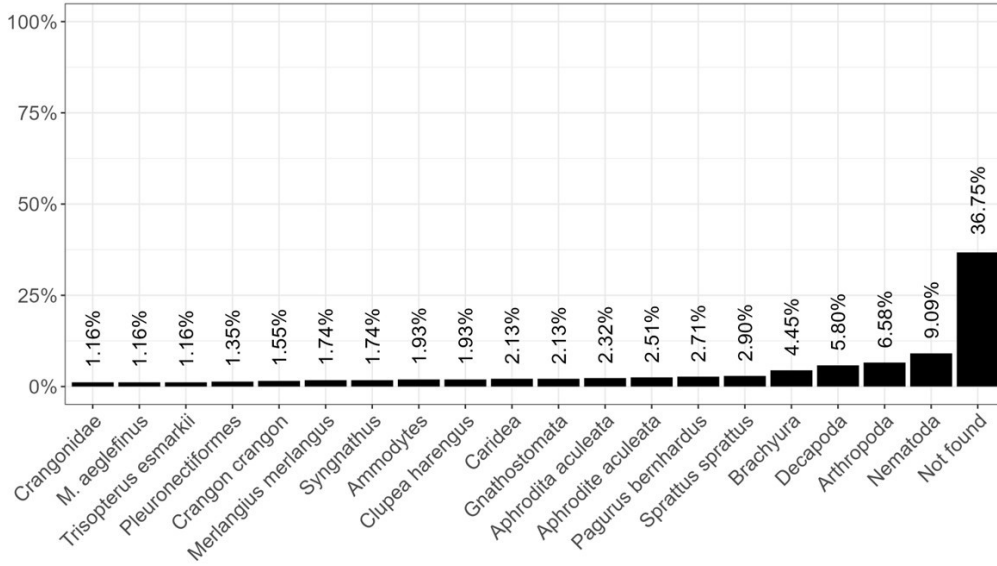
B)

Prey Contribution to the Diet of Whiting
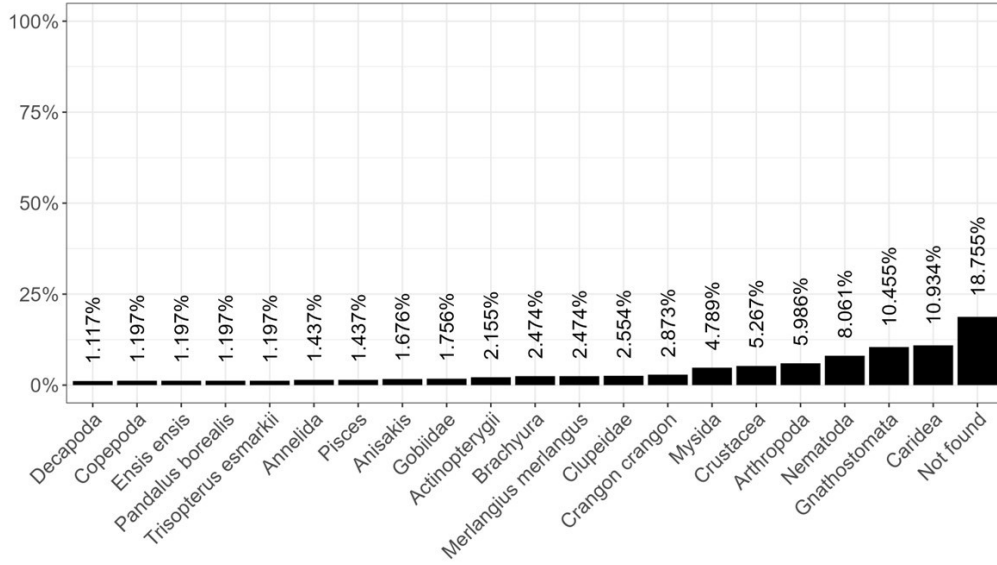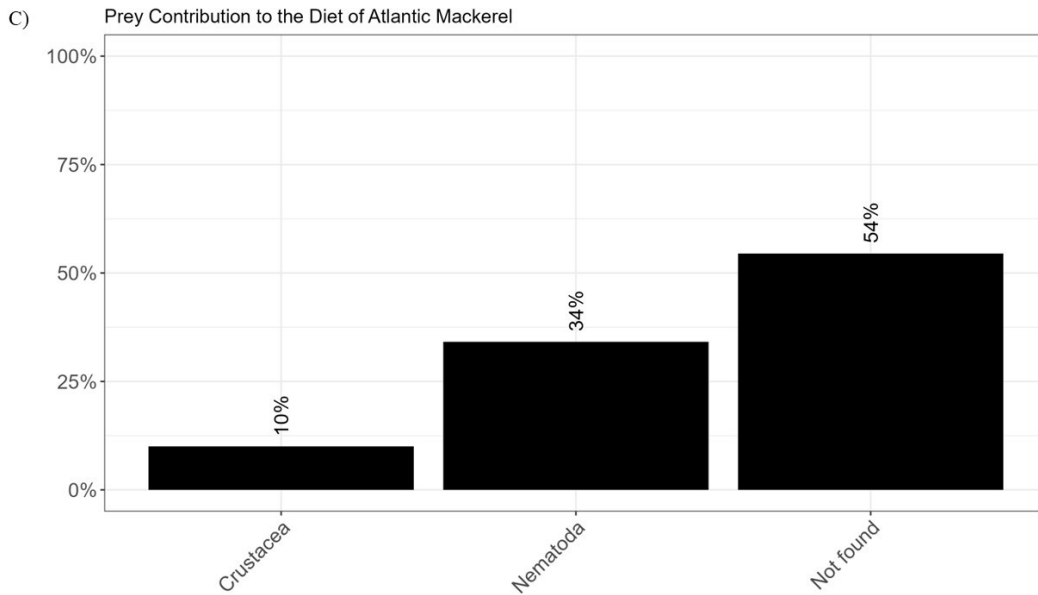
Figure 13. Proportional contribution of the different prey species to the diet of cod (A), whiting (B) and mackerel (C) in the North Sea. 'Not found' indicates the presence of an unidentifiable particle in the stomach. These unidentified particles were weighed and measured but identification was not possible. Proportional values smaller than 1% have been removed to aid visualisation.

In order to investigate the spatial extent of the updated stomach content database in the North Sea, we have first allocated ICES statistical rectangles to their respective ICES areas. New stomachs have been added in all five areas of the Greater North Sea: IVa, IVb, IVc, VIId and IIIa.

For cod, new stomachs have been added in IIIa (12), IVa (37), IVb (144) and IVc (5). Amongst these, the highest proportion of unidentified prey come from area IVa; within this area, the most common prey species are all benthic organisms (Figure 14). In comparison, in areas IVb and IIIa cod are found to eat benthic prey as well as fish species such as sprat and herring. The highest percentage of cannibalism in cod was found in area IIIa (4.3%).

IVa

IVb
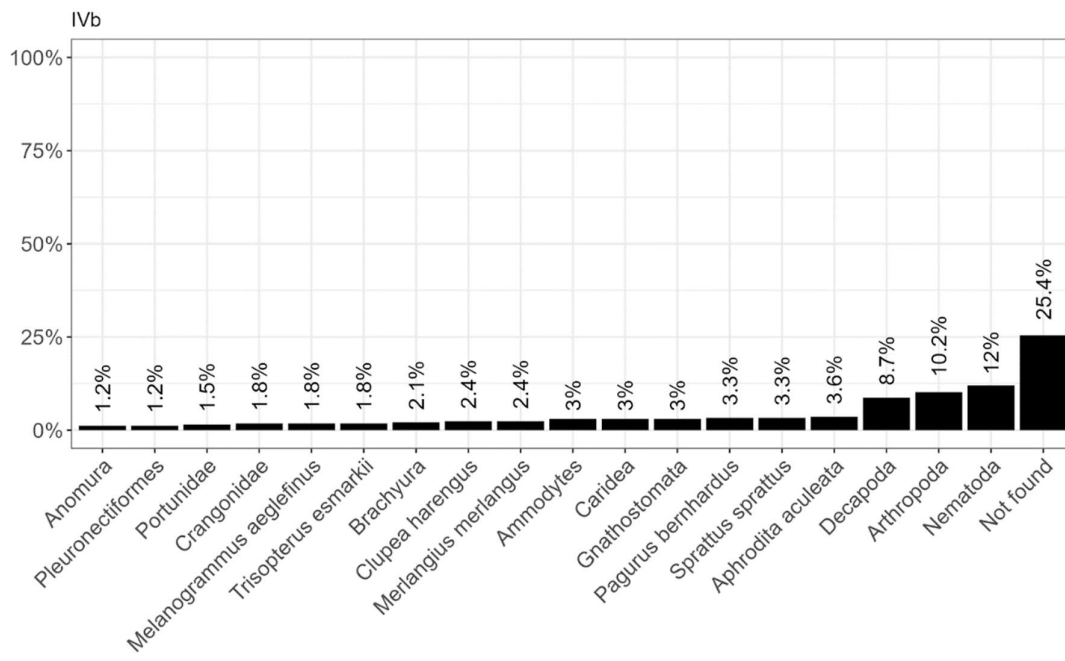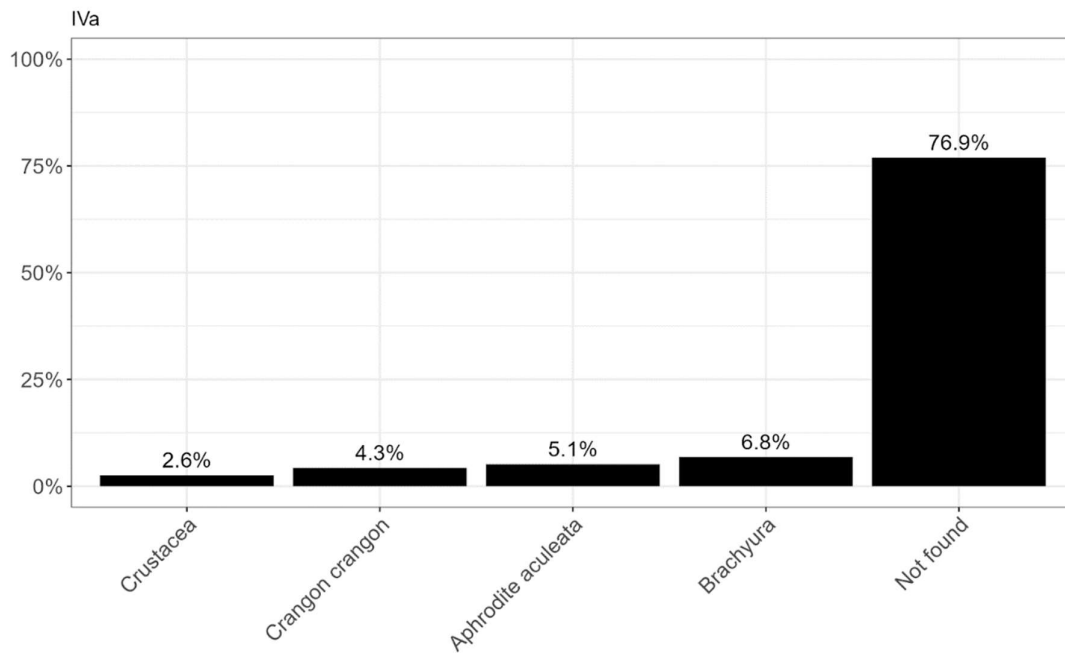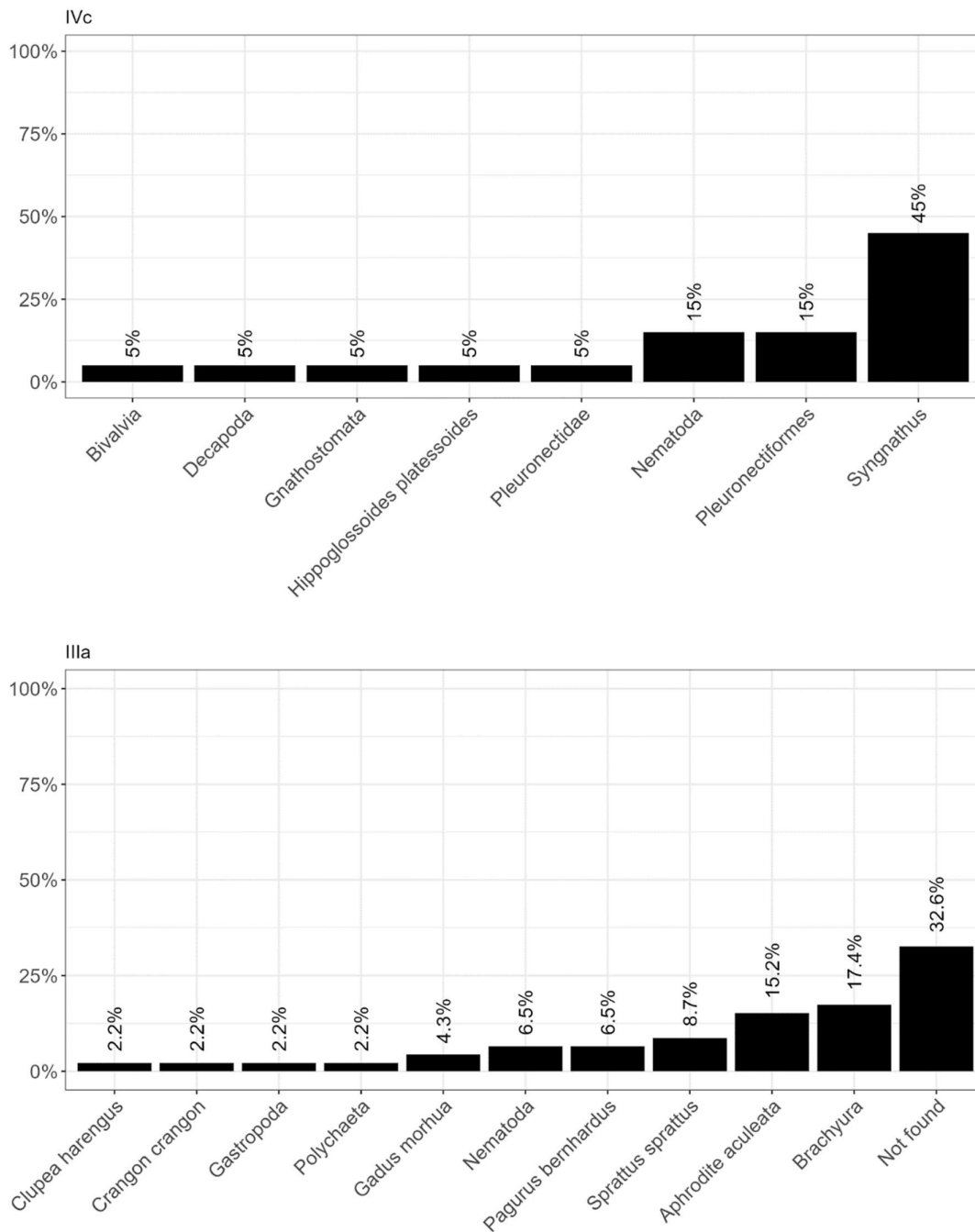
Figure 14. Proportional contribution of the different prey species to the diet of cod in different areas of the North Sea (IVa, IVb, IVc and IIIa). 'Not found' indicates the presence of an unidentifiable particle in the stomach. These unidentified particles were weighed and measured but identification was not possible. Proportional values smaller than 1% have been removed to aid visualisation.

Whiting stomachs were added in IVa (5), VIId (59), IIIa (20), IVb (417) and IVc (181). The highest variation in diet was observed in area IVc (Figure 15). Across all areas, whiting are found to feed predominantly on benthic species, albeit in areas VIId, IIIa and IVc, other fish species (Pisces) as well as Gnathostomata are also found to contribute a relatively high percentage to the diet of whiting (45.2%, 12.9% and 16.1%, respectively). Whiting are also found to eat other whiting in areas IVb (3.8%) and IIIa (3.2%). It is also likely that a higher percentage of the unidentified fish might be whiting as well.

Mackerel stomachs were added in areas IVa (148) and IVb (903). The data suggest a more varied diet in area IVb compared to area IVa, however this could be linked to large differences in sample size (Figure 16). The main prey in both areas was the same - Nematoda. In IVb, mackerel are found to feed on other fish species including whiting and Clupeidae, albeit the percentages are low (0.8% and 0.1%, respectively). In comparison, only benthic preys were found in the stomachs of mackerel in IVa.

IVb

IVc
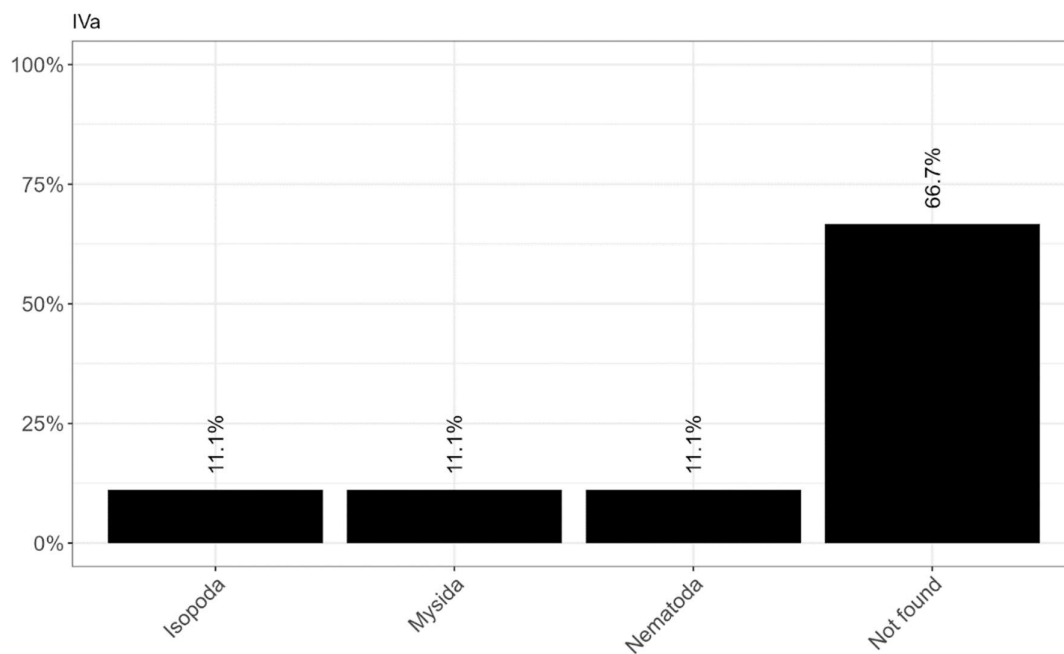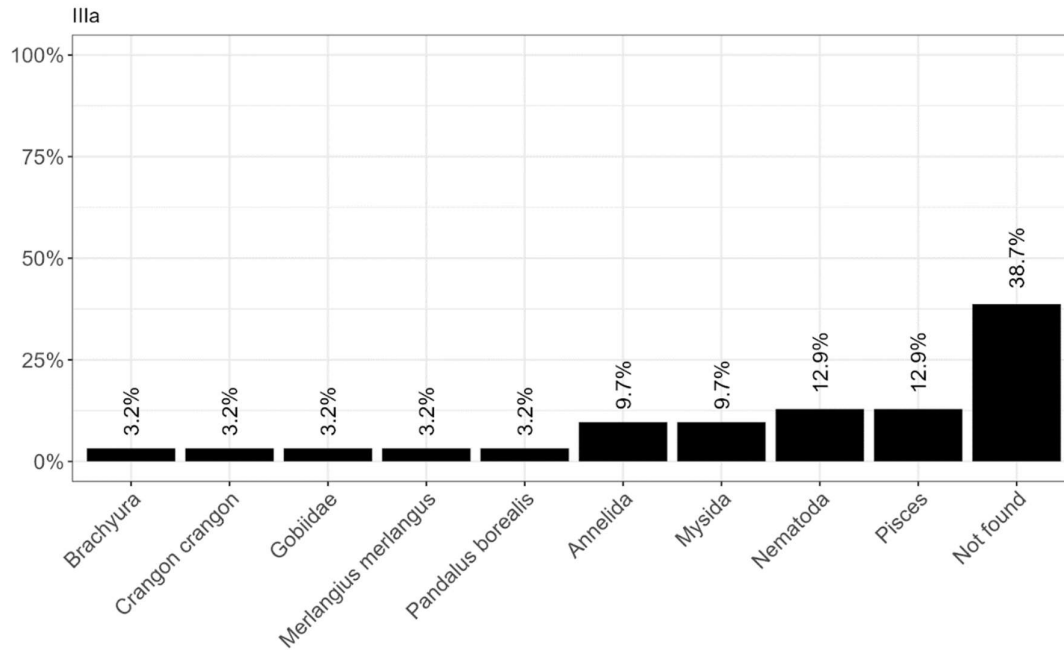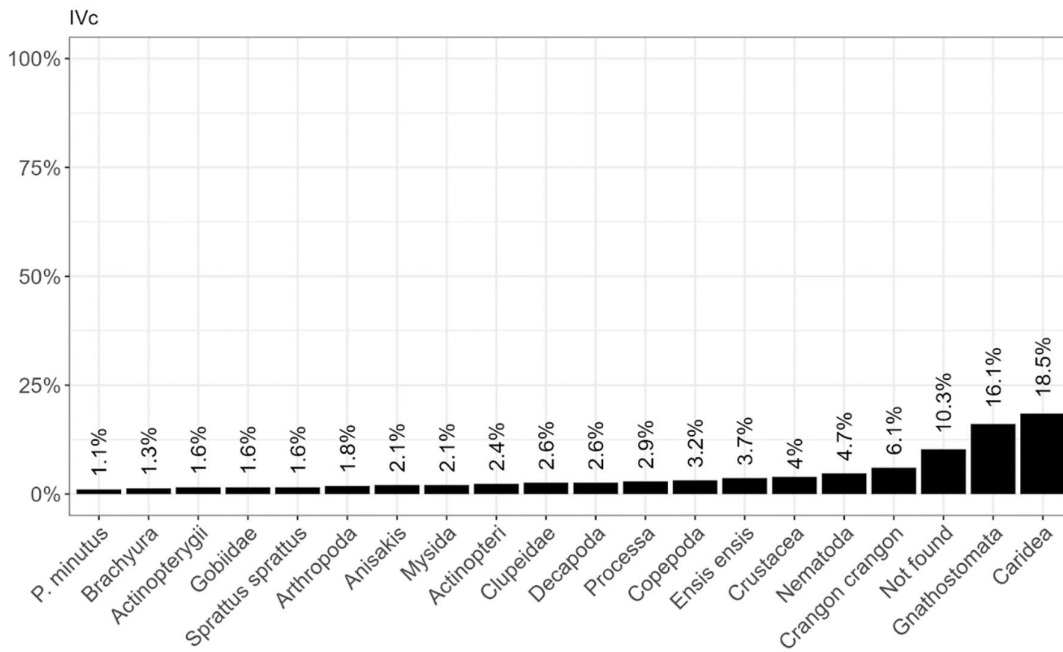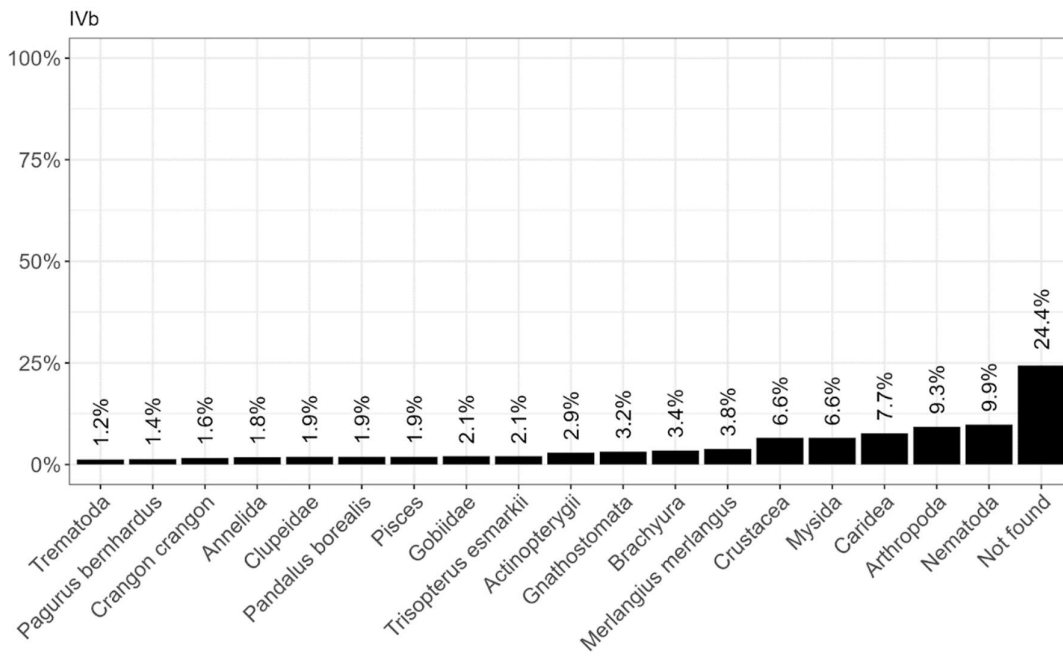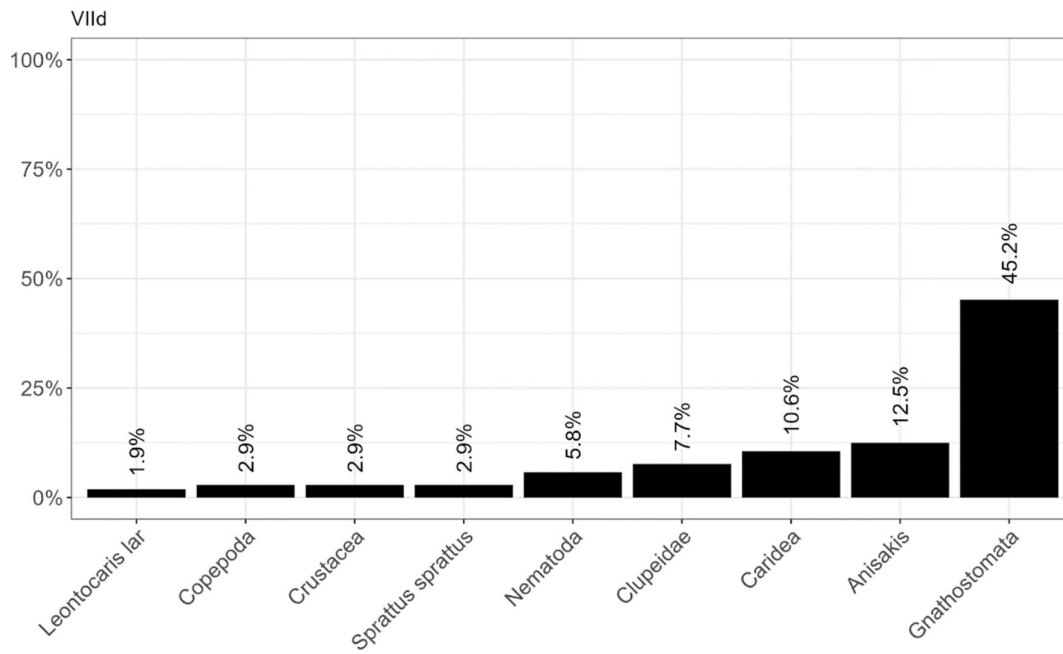
Figure 15. Proportional contribution of the different prey species to the diet of whiting in different areas of the North Sea (IIIa, IVa, IVb, IVc and VIId). 'Not found' indicates the presence of an unidentifiable particle in the stomach. These unidentified particles were weighed and measured but identification was not possible. Proportional values smaller than 1% have been removed to aid visualisation.
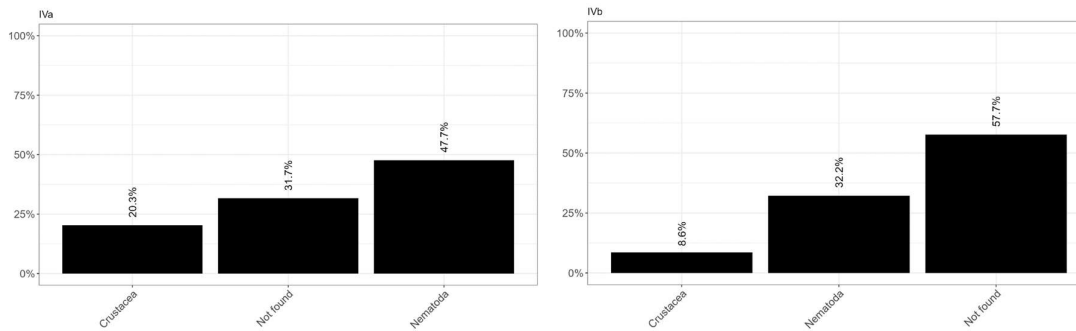
Figure 16. Proportional contribution of the different prey species to the diet of mackerel in different areas of the North Sea (IVa and IVb). 'Not found' indicates the presence of an unidentifiable particle in the stomach. These unidentified particles were weighed and measured but identification was not possible. Proportional values smaller than 1% have been removed to aid visualisation.

4.2 CS1: Spatiotemporal changes in the diet of Baltic Sea cod

Key messages

This case study used novel spatiotemporal models to study how the feeding patterns of Baltic Sea cod have changed in both space and time. Our main results show that feeding on both sprat and *saduria* by cod has increased: it was approximately three times higher in 2020 than it was in 1993. Although the spatial overlap between cod and sprat and cod and *saduria* is higher now than in the early 1990s, the relationship between spatial overlap and the amount of prey in stomachs of cod is not statistically strong, suggesting other factors might be impacting feeding patterns. By allowing us to statistically account for differences in both the spatial and temporal collection of stomach content data, these novel models provide a more complete picture of how predators like cod interact with their prey.

Background

The abundance of Atlantic cod in the Eastern Baltic Sea has been declining for much of the last 30 years after a period of record-high abundances in the 1980s. Cod abundance is now estimated to be below ICES biological reference points (29). These declines in stock size have been correlated with declines in individual body condition and growth (31–34). There are several potential reasons for this, involving fisheries, trophic interactions, biotic and abiotic drivers and climate, all of which act as multiple stressors and impact fish stock dynamics. As a consequence of the deteriorated state of the stock, fishing has also been declining, and the catch advice has been zero since 2019.

Previous studies have hypothesised that changes in the abiotic conditions of the Baltic Sea as well as changes in the quantity and quality of food might be driving the observed trends in condition, growth and stock size. In particular, changes in the abundance and spatial overlap between cod and its prey and increasing extension of hypoxic areas may have diminished both the availability of benthic prey and as well as cod appetite (32,35). However, our knowledge on the matter remains inconclusive, as the ability of these variables to explain the decline in condition varies between studies (33).

To explicitly link trends in condition and growth to changes in cod diets, stomach content data are needed. Cod stomach content data have been analysed before (36,37) and linked to the decline in individual growth and stock size (38). For instance, using a bioenergetic growth model and stomach content information, Neuenfeldt et al. (38) showed that reductions in growth of Eastern Baltic cod are correlated with reduced feeding levels on sprat and the isopod S*aduria entomon*. This decline was in turn hypothesised to be due to changes in prey availability. For *saduria*, the decline was attributed to lower abundances due to increasing hypoxia and for sprat due to a decline in sprat within the core distribution area of cod. However, some key knowledge gaps remain, not only in the spatiotemporal trends in the diet of cod, but also in the effect of prey availability. These gaps are predominantly because no study has estimated predator-prey overlap in a spatially explicit manner or directly related spatial predator-prey overlap to changes in the diet of cod.

Here, we expand on past work in four fundamental ways. First, we make use of the new and updated stomach content database that has been created by this project (including the addition of over 2000 new cod stomachs). Second, we use novel analytical methods which allow us to quantify changes in the diet of cod through space and time, as well as the predation intensity by cod of different prey species. These novel methods provide a significant advancement on past work where changes in space as well as variability across samples are often ignored. Third, we provide the first study in the Baltic that relates changes in diet to spatially explicit estimates of predator-prey overlap. Fourth, we explore key questions in relation to changes in population-level predation intensity and discuss how these changes may be related to the observed declines in stock size and individual growth/condition in the Baltic Sea.

Aims

Using historic and new stomach content data for cod in the Baltic Sea, CS1 addresses the following three research questions:

Q1. How has the diet of individual cod changed through space over time?

Q2. How has the predation intensity by cod on different prey species changed through space over time?

Q3. Are changes in population-level predation intensity due to changes in spatial overlap with prey or due to changes in per capita predation intensities?

Approach

Prey species and data
The following prey species, representing on average >80% of the cod diet in terms of biomass (cod with body lengths of 30-60 cm; (36,39)), are included in our statistical models of stomach content: *Saduria entomon*, Atlantic herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). We will also fit species distribution models to cod biomass from the Baltic International Trawl Survey (BITS) from the DATRAS database (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx) and use acoustic survey data from BIAS (Baltic International Acoustic Survey) and the primary literature to inform on the abundance and availability of these main prey species.

Spatiotemporal diet model
To quantify how individual cod diet has changed over time (Q1), we fitted spatiotemporal statistical models to individual level 'feeding ratios' (unit kg/kg). The feeding ratio is the weight of a specific prey species (sprat, herring and *Saduria entomon*, hereafter simply *saduria*) in the stomach relative to the weight of cod. Hereafter we refer to this metric as per capita predation. The model fits spatial random fields with the SPDE approach (Stochastic Partial Differential Equation, for a thorough explanation, see references (41) and (40), which informs about spatial deviations from the average feeding ratio that are constant through time. The main purpose of the spatial random field is to model processes that might cause spatial autocorrelation (the feature of spatial data where data closer in space are more similar to each other), which would otherwise limit our ability to make inference and quantify uncertainty because it means statistical assumptions about independence are not met, and they us to interpolate in space.

To model diet in space and time, we use data from 1993 in the Baltic Sea, as for those years we were able to combine the cod biomass data from DATRAS with environmental covariates (e.g., salinity and temperature) and prey biomass and biomass density estimates. Trends over time in the average feeding ratios (the intercept) are modelled as temporally varying coefficients following a random walk. This time-varying model on the year-effect allows us to constrain the annual means and interpolate averages in missing years. We also include the effect of cod body length (in centimetres) as a smoother with the basis function dimensions set to 3 to reduce the curvature and force the function to be unimodal (for instance, this allows sprat to increase in the diet of cod up to a certain size, then decline as cod start feeding on larger fish, such as flounder or smaller cod). We modelled sampling month as a random effect to borrow information across months when estimating each months' effect on the feeding ratio, and depth is modelled as a linear fixed effect. See Annex 4 for the conditional effects of these covariates. We assume the observation error follows a Tweedie distribution, since the ratios are non-negative and are zero-inflated. The Tweedie distribution is not bounded at 1, but the response variable is since it is the ratio of prey weight to predator weight. A theoretically sounder model would be e.g., a delta-beta model, but we chose the Tweedie because of better model diagnostics (shown by QQ-plots) and because the model predicts feeding ratios to be much smaller than 1. See Annex 3 equation 1 for the mathematical description of the full model.

Spatiotemporal biomass model

The spatiotemporal biomass model ('species distribution model') largely follows the diet model, but because of the greater data availability from the BITS survey, the model additional terms (see Lindmark et al. (33) for a description of the data and a similar model structure). The response variable is biomass density (kg/km^2) of cod larger than 15 cm, i.e., the minimum size when cod can feed on all above-mentioned prey species. In addition to a constant spatial random field, we also use a spatiotemporal random field, i.e., a spatial field that changes every year. This is to capture spatial processes that vary from each year, e.g., primary production or oceanographic variables. We model year as a factor (independent mean densities for each year) and include the following additional covariates: quarter (modelled as a spatially varying coefficient, i.e. a random field, to allow the spatial variation in cod density vary between quarters), salinity, temperature and depth (both variables also have a squared effect to model a unimodal 'preference' curve), as well as oxygen, modelled as a break-point function (or a 'hockey-stick' curve) representing the expectation that oxygen is positively related to cod biomass density only to a certain point. Oxygen data stem from the Baltic Sea Biogeochemistry Reanalysis and salinity and temperature come from the Baltic Sea Physics Reanalysis. Both were downloaded from the Copernicus Marine data portal,[3]. We use a delta-gamma model (logit and log link functions, respectively), which models presence/absence and positive biomass separately, as this added complexity (over e.g., a Tweedie distribution) leads to better model diagnostics (again shown by QQ-plots). See Annex Equation 2 for the mathematical description of the full model.

Model fitting

We fit all spatiotemporal models using the R-package 'sdmTMB' (41), which utilises the R-packages 'TMB' (42) for model fitting and 'R-INLA' (43) to set up the stochastic partial differential equation matrices.

Spatiotemporal model predictions and predator-prey overlap

These models were then used to predict per capita predation onto a prediction grid. This grid is a 3x3 km grid following the main boundary of the BITS survey (but limited to depths below 120m), with spatial covariates. Predicting from the models onto this grid allows us to spatially visualise how the diet, distribution (see Annex 4 Figure 41) and overlap between cod and its prey has changed through space over time (Q2). The grid-level estimates of per capita feeding (kg/kg) are then multiplied by the grid-level cod biomass density (kg/km^2), which yields a snapshot predation intensity metric in unit kg/km^2 (44). Hereafter, we refer to this predation intensity as a population-level predation metric.

We also use these gridded predictions to calculate annual averages of per capita and population-level predation. Finally, we use the gridded predictions of cod biomass density to calculate overlap in space between cod and the prey, both in space and as total overlap in space by year (Q3). We use the 'local index of collocation' metric (44,45), defined as follows:

$$\text{overlap} = \frac{\sum_i^n \left(p_{\text{pred}_i} \times p_{\text{prey}_i} \right)}{\sqrt{\left(p_{\text{pred}_i}^2 \times p_{\text{prey}_i}^2 \right)}}$$

which estimates co-occurrence using correlations between predator and prey densities at the grid-scale. For pelagic prey (sprat, herring), we are limited to quarter 4, when the acoustic survey (BIAS) takes place. For consistency and simplicity, we also limit our analysis of *saduria* feeding to quarter 4. We evaluate overlap at both the ICES rectangle level and the subdivision level, because these are the two scales pelagic densities are available at. For overlap with *saduria*, we used predicted *saduria* densities from Gogina et al. (46). Due to poor temporal resolution of *saduria* data, data were pooled to create a spatial prediction for years 1993–2019 and therefore are representative of the long-term

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[3] https://data.marine.copernicus.eu/products

core habitat and does not capture interannual variation in *saduria* density. Hence, changes in overlap with *saduria* are only driven by changes in cod distribution, while in reality, *saduria* also likely have changed their spatial distribution. To assess whether the overlap between cod and its prey on an annual basis is related to per capita feeding and the population-level predation intensity, we evaluate the relationship between these metrics and the overlap metric.

Results and discussion

Q1: Spatiotemporal changes in cod diets
Model predictions reveal clear spatial patterns in cod diets (per capita predation; Figure 17). Sprat feeding increases as a function of depth and is generally highest in the basins, while herring feeding declines with depth. Feeding on pelagic prey occurs throughout the spatial domain, while *saduria* feeding is more patchy and limited to areas where *saduria* are present in high densities, i.e., northeast of the Bornholm basin and along the Lithuanian and Latvian coast (see also Gogina et al. (46)).
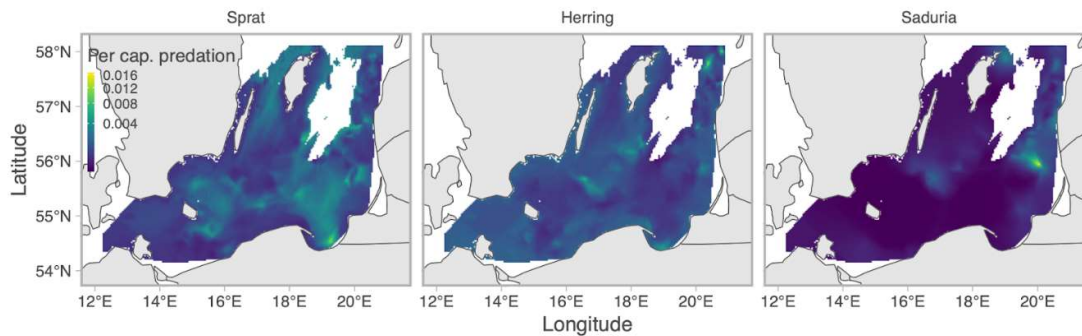
Figure 17. Spatial variation in per capita predation for sprat, herring and *saduria* in the year 2000 and for cod of an average body length of 31 cm. Per capita predation is the weight of a specific prey species in the stomach relative to the weight of the predator.

Over time, the average feeding patterns of cod in terms of per capita predation, calculated as the average of grid-level predictions of feeding ratio, are also found to have changed substantially. Feeding on sprat has increased twofold between 1993-2020 in an almost linear manner (Figure 18). Herring feeding increased until around 2007 and then declined steadily. In comparison, feeding on *saduria* did not change over time until the early 2000s, after which feeding increased rapidly and is now almost four times larger than in the early 1990s.
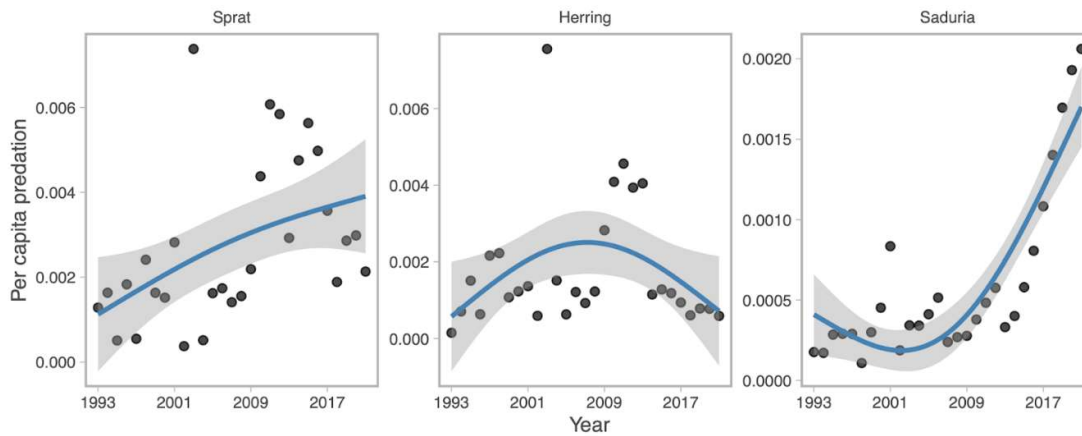
Figure 18. Spatially-averaged per capita predation by cod on sprat, herring and *saduria* by year. Lines depict generalised additive model fits (basis dimension k = 4) and the grey band its confidence interval. The lines and confidence intervals have been added to aid interpretation of the general trend over time by prey species. See Annex Fig. A3 for the confidence interval around annual averages.

Q2: Population-level changes in cod predation

The population-level predation trends are found to differ from the per capita trends both in space and time (Figure 19 and Figure 20). In other words, when accounting for cod biomass, the predation intensities are more pronounced in the southwest areas and not in the basins for both sprat and herring. In comparison, for *saduria* the per capita and population-level metrics are largely similar—likely a reflection of the more constrained spatial distribution of *saduria* biomass density and our data limitations for this prey species.
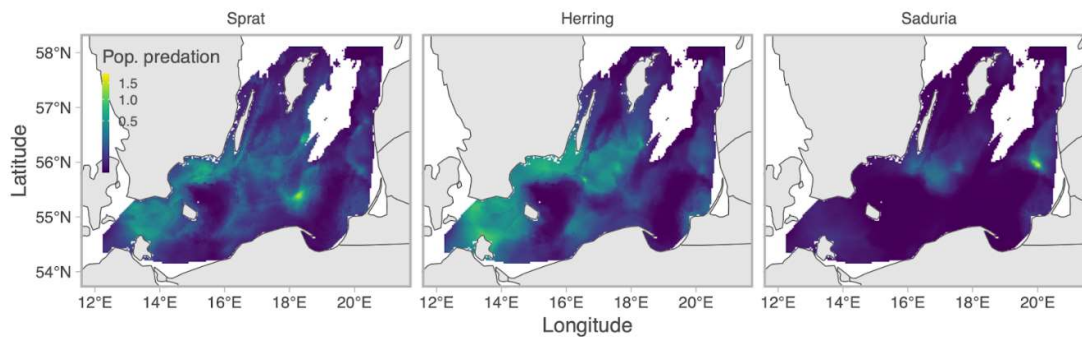
Figure 19. Spatial variation in predation intensity (per capita predation multiplied by cod biomass density) for sprat, herring and *saduria* in the year 2000 and for cod of an average body length of 31 cm.

The general temporal trends are found to be similar for herring, both showing an increase and a decrease at the start and end of the time series, respectively (comparison between Figure 18 and Figure 19). However, for sprat, the predation intensity declines after around 2010 (which the per capita predation does not), and for *saduria* there is also a decline towards the end of the time series, due to a decline in the biomass density of cod.
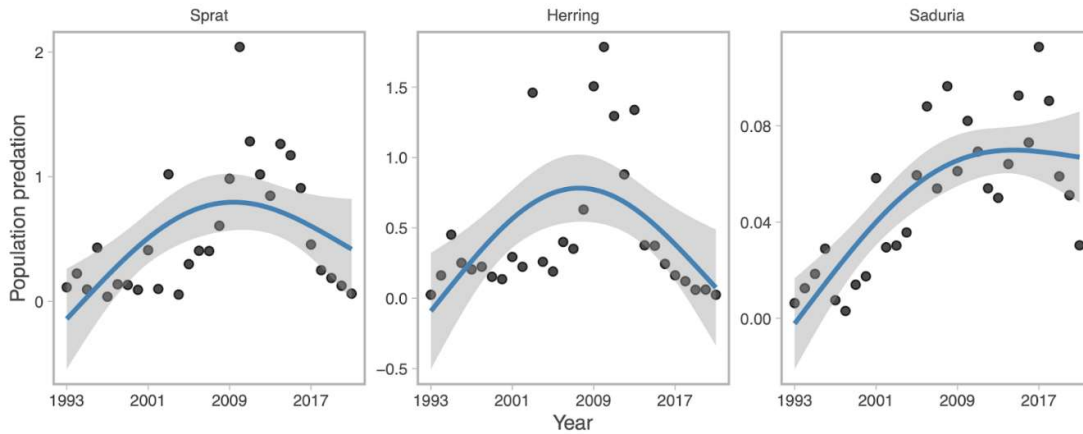
Figure 20. 1Spatially-averaged predation intensity by cod on sprat, herring and *saduria* by year. Lines depict generalised additive model fits (basis dimension k = 4) and the grey band its confidence interval. The lines and confidence intervals have been added to aid interpretation of the general trend over time by prey species.

Q3: Relationship between predator-prey overlap metric and total predation
The predator-prey overlap metrics also show considerable variation in space (Figure 21). Taking the year 2000 as an example, overlap between cod and sprat is mainly located along the Swedish and Latvian coasts, whereas the overlap with herring is highest in the southern part of the domain. Overlap between cod and *saduria* is found to be highest in the centre of the domain, northeast of the Bornholm basin. We also evaluated the centre of gravity of overlap in space (i.e., the average UTM coordinates weighed by the overlap metric), and how that has changed over time (Figure 22). This reveals that the average location of predator-prey overlap hotspots have changed over time. For sprat, the centre of gravity is similar now compared to in the early 1990s, for herring it has moved northeast and for saduria it has remained relatively stable over time.
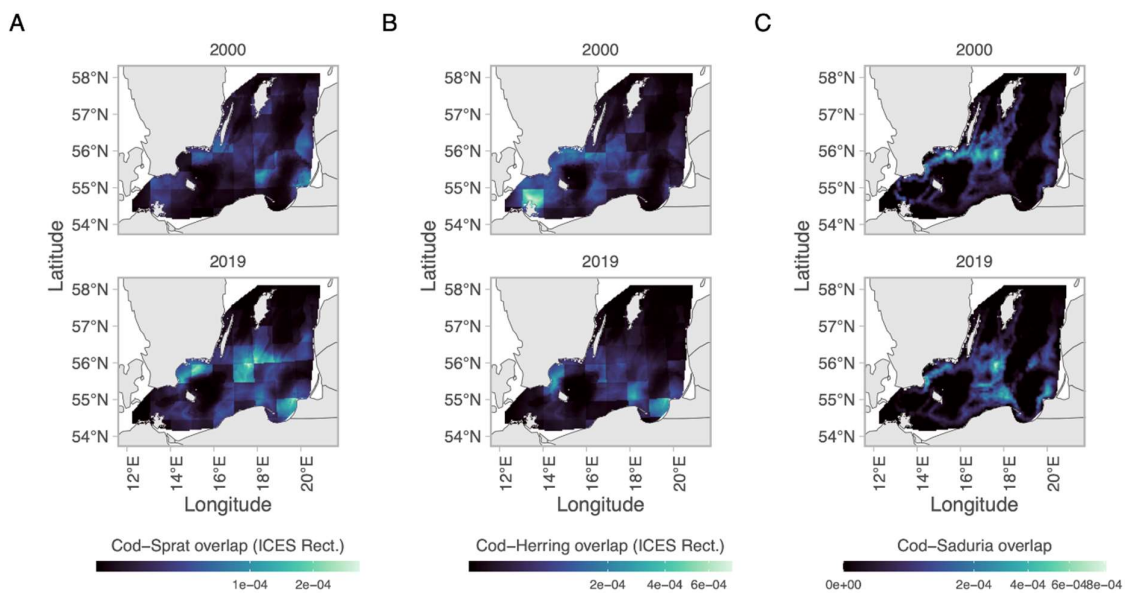
Figure 21. Predator-prey overlap (calculated as the 'local index of collocation') plotted in space for sprat (A), herring (B) and saduria (C) in quarter 4, using the years 2000 and 2019 as a examples. For sprat and herring, the colour scale is trimmed by setting values above the 99.9th quantile to equal the 99.9th quantile of the overlap metric.

When the spatially-explicitly overlap values are summed across space per year, a hump-shaped pattern emerges for herring, while for sprat there is an increase over time (Figure 23A). There is also a high level of agreement between the two scales of pelagic biomass estimates (ICES rectangle or ICES subdivision). For *saduria*, the overlap trends over time are similar to those for herring, i.e., increasing until around 2005, followed by a decline (Figure 23B). For *saduria*, there is high agreement between the overlap metrics calculated by quarter—only the magnitude differs (such that the overlap generally is lower in quarter one), not the temporal trend.
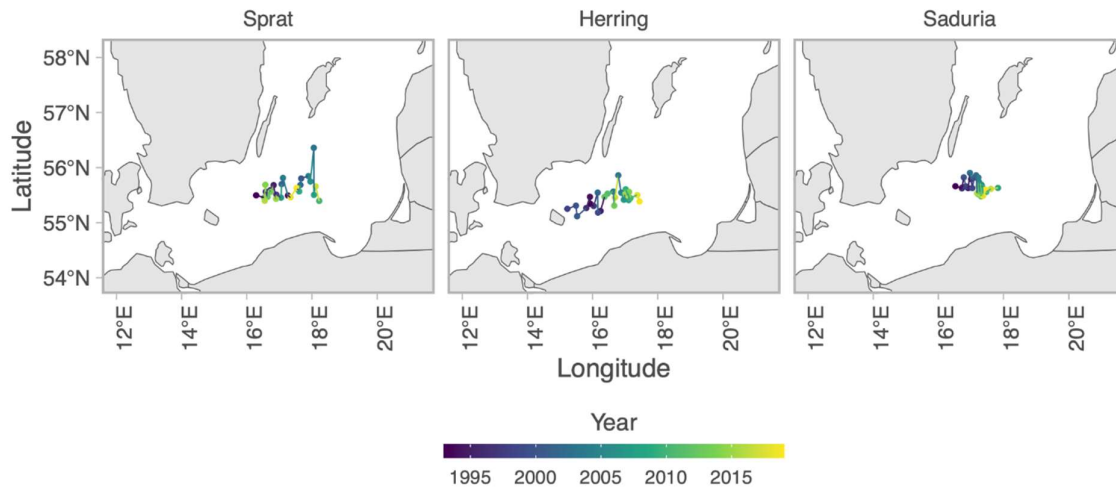
Figure 22. Average UTM coordinates weighted by the spatial overlap, which deptict the "center of gravity", for sprat, herring and saduria. Colors indicate years.

We also find that predation intensities (per capita or population-level) are in general not significantly associated with spatial overlap trends (Figure 24). The only exception to this lack of association occurs in the population-level predation on *saduria* (p = 0.024).
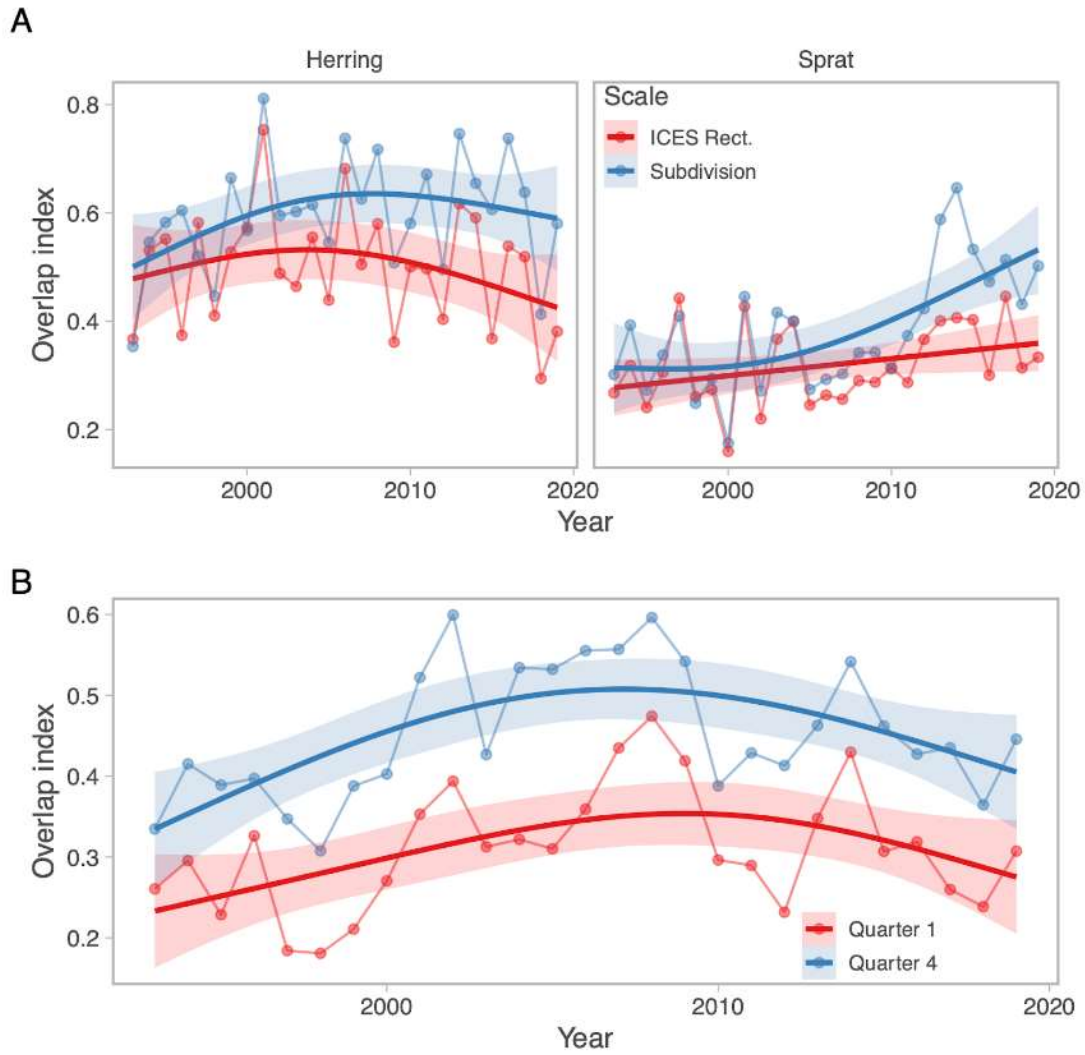
Figure 23. Predator-prey overlap (calculated as the 'local index of collocation') averaged in space by year to visualise temporal trends. In panel A, the overlap between cod-sprat and cod-herring is plotted, calculated for different scales of pelagic biomass (ICES rectangle in red and ICES subdivision in blue) and in the bottom panel (B), the overlap between cod and *saduria* is plotted, where colour indicates quarter (red is the first quarter, and blue depicts quarter 4, which is the main quarter used in this analysis).
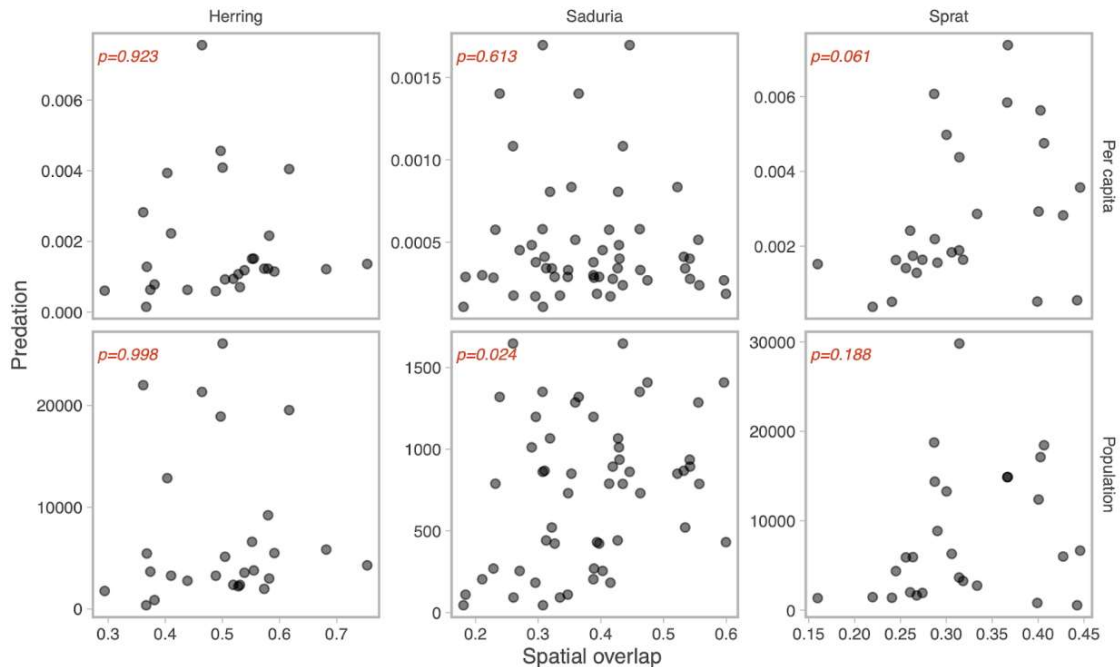
Figure 24. Relationship between annual average spatial overlap and predation metrics by cod on the three main prey species (top row: per capita predation, bottom row: population-level predation). Estimated p values are detailed in red and on the top right of each panel.

Conclusions

This case study sheds new light on the feeding patterns of Baltic Sea cod between the years 1993–2020 and how that relates to the availability of prey. Previous studies have identified that feeding on sprat and herring was lower between 1994–2014 than 1963–1988 (38). The time period 1994–2014 was characterised by a steep decline in body condition of cod lasting until around 2010, where cod body condition hit a low plateau (33,35). Therefore, to understand the link between feeding dynamics and the growth and condition of Baltic cod, it is important to understand the temporal dynamics within this recent time period and the years after.

Our analysis revealed that, over time, the length-corrected feeding on both sprat and *saduria* by individual cod increased and were approximately three times higher in 2020 than in 1993. On a population level, i.e., by combining per capita diet predictions with predicted local biomass densities of cod, we also found increases in predation on *saduria* and sprat, albeit the increases in population-level sprat predation were less than at the individual level and seem to have declined in recent years. In addition, we found that the spatial overlap between cod and sprat and cod and *saduria* is higher now than in the early 1990s, though for the former, overlap did decline again after 2020. Finally, the spatial predator-prey overlap and the per capita and population-level feeding intensity do not in general correlate well, and only for population-level predation on *saduria* does the spatial overlap have a significant effect (i.e., a significant p value). Consequently, these results suggest that there is no clear relationship between either temporal trends of sprat and *saduria* in cod stomachs and the decline in cod condition, nor does the spatial overlap seem to explain the temporal trends in cod feeding patterns. Future studies are needed to characterise temporal trends in diets over a longer time frame, including the period of exceptionally high growth and condition of cod in the 1980s (35). Also important is to continue collecting data and exploring the performance of data-demanding spatiotemporal models using tools such as spatiotemporal cross-validation.

Our results highlight the importance of predator-prey interactions, as well as the information that can be gained from stomach content data when correcting for space over time. Predator-prey interactions also play an important role in defining ecosystem functioning and the trophic structure of marine food webs (47–49). Therefore, understanding the relation between predator diets and species interactions in the Baltic Sea may increase our knowledge on what regulates food web structure and how it may have changed. Understanding both the temporal and spatial changes in food web interactions, including the prey targeted by pelagic fisheries, is important for developing food web considerations in the ecosystem-based approach to fisheries management.

4.3 CS2.1: Multispecies models in the North Sea (SMS)

Key messages

This case study explored trends over time in the biomass consumed by predators (cod, mackerel and whiting) in the North Sea. A stochastic multispecies model ('SMS') was used, which predicts the abundance, catch and interactions between predators and their prey based on survey, catch and stomach content data. Stomach content data is key to the application of SMS because it informs the model about who eats who in the North Sea food web. The main result of the case study was a clear trend in the biomass consumed by predators in the North Sea, which was linked to the population dynamics of each predator. For instance, a decline in cod abundance led to a decline in the amount of prey consumed by cod, making them less important predators in the food web. As the abundance decline is often a consequence of fishing, there is also a link between fishing and rates of predation. SMS is one of the few multispecies models that is used in stock assessment and advice and provides a reliable estimate of natural mortality for many stocks.

Background

The North Sea SMS ('Stochastic multispecies model') is a multispecies assessment model that uses surveys, catches and stomach content to predict the abundance, catch and interactions between predators and prey in the North Sea (4). The model is used to provide time-varied natural mortality rates for a range of exploited stocks, including cod (*Gadus morhua*) and herring (*Clupea harengus*), and thus serves as one of the few models which is actively used to implement ecosystem interactions in the practical management of exploited fish stocks (4).

The interactions between species are calculated based on a likelihood function that fits modelled stomachs to stomach content observations. The predator-prey interactions are assumed to be a function of both size and species identity. Currently, the stomach samples used to run the North Sea SMS model are comprised mainly of pre-1992 observations (ICES Year of the Stomach Dataset; YOTS).

The SMS model has seen a preliminary update in the ICES WGSAM (Working Group on Multispecies Assessment Methods) (2023) meeting. Unfortunately, due to the restricted geographical scope (see Annex 4: Figure 42, Figure 43, and Figure 44), high amount of unknown organic matter in the stomachs and limited time to properly analyse the stomach content in the right format, WGSAM decided to not include the newly analysed stomachs (from this tender) in the 2023 key run of the North Sea. A key run is a three-year recurring update of the multispecies models in the North and Baltic Sea, where the natural mortality output is being calculated and delivered to the stock assessment working groups. However, also discussed was that the samples could be used in future iterations of either SMS or other multispecies models, where input data should be used as stochastic observations rather than the 'average diet' input SMS takes now, which requires a broad geographical scale and a high number of stomachs to properly assess what is the average diet. The new data from the Baltic Sea are still in contention to be used for the next Baltic Sea SMS key run, which is scheduled to take place in 2025. The next North Sea Key run should occur in 2026.

To provide a formal comparison of the old and the new data here, we present the estimated average diet per species, calculated from each year of stomach samples. This information is calculated based on the 'FishStomachs' R-package, specifically designed to prepare stomach content data for SMS. Then, we provide the most recent estimates of natural mortality, who eats whom and general changes in the SMS model based on the preliminary run in order to show the potential utility of stomach content data.

Aims

The aims of this case study was to analyse how the stomach content has changed from the historical sampling (1980:1991) and in comparison with the new samples on a population scale. This population scale can be used to infer the predator-prey interactions in the North Sea through predation mortality; a crucial parameter used in stock-assessments.

Methods

We compiled all the uploaded data from the newly assigned ICES stomach database and continuously updated it whenever additional data was uploaded. The data was then run through the FishStomachs R-package[4], to assign all prey items to correct sizes and prey categories. All prey contributions have been weighted in the average based on the roundfish area (ICES rectangle) to properly use regurgitated stomachs. The observed preis that have non-specific species identification (i.e., often the terms 'gadoids' and 'clupeids' are used) were distributed on the respective families included in the model. For instance, clupeids were distributed between sprat and herring, based on their respective prey abundance in other stomachs in that roundfish area.

We here focus on three species (whiting, mackerel and cod), since these three species have had a significant addition of samples in the new database and are all used as dynamic predators in the 2023 SMS North Sea model.

To average the diet, stomach content per ICES roundfish area is calculated. If more than one sample is taken from a rectangle, the average stomach content for a predator length class is calculated as a weighted mean, using the number of stomachs sampled as weights. The average stomach content of a given predator and length class in a roundfish area are calculated as a weighted mean of the average stomach content per ICES square, weighted by the square root of the arithmetic mean of the observed number of stomachs within a rectangle. This calculation is a little different to the final SMS version, where the average weighting is done by the CPUE of the predator; however, as this was not readily available for the new data, we weighted it by number of stomach samples instead. The resulting output is the average relative diet per predator size of modelled prey, and the rest is attributed to the group 'other prey'. The total abundance of 'other prey' is quite important in the SMS model, as it effectively scales the total natural mortality up and down, by being an available resource to predators.

In the presentation of the results, the sandeel populations in SMS are divided into a 'north' and a 'south' population. This structure does not fit the actual structure of sandeel populations, which are currently considered to be four different populations (50).

Results

<u>Old and new data</u>
The newly collected samples from cod were mostly collected from the central North Sea, with very little coverage in the northern part of the ecosystem (Figure 42). The previous sampling efforts were tightly organised in a grid to cover the entire ecosystem. The same is true for whiting, where the new sampling was not as consistent as the YOTS dataset, where many of the samples are collected in the southern part of the North Sea.

Ideally, one would see a higher fraction of fish in the stomach samples, as the predator fish get older, as one would assume that older fish eat more fish. This rule is generally true for the old data of cod and to some degree true for the newer data (Figure 25), however, a large fraction of the new data are unidentified items. In comparison with the old data, one length class has a larger fraction of haddock (*Melanogrammus aeglefinus*) in their stomach, with generally lesser whiting observed than previously. There is a significant

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[4] https://github.com/MortenVinther/FishStomachs

number of herring (*Clupea harengus*) in both the new and the old data; however, the 2023 data has the herring confined to one size class (800-900 mm) as well.
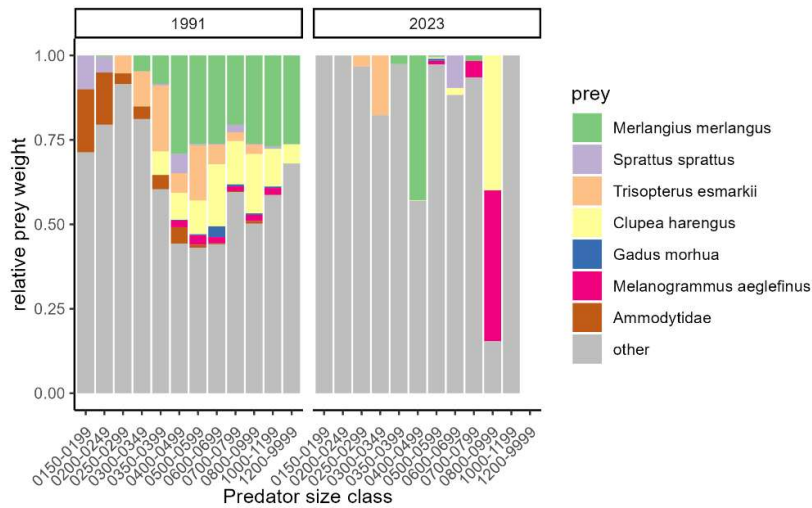
Figure 25. Cod stomach content data from 1991 and 2023. Predator size classes are in mm.

The mackerel stomachs contain a high number of 'other food', which is not very surprising, as this omnivore fish is often considered primarily a plankton eater (51), and fish larvae under 5 cm are allocated to the 'other food' category (Figure 26). Some sprat and herring were observed in one size class in the new data, which was also the most abundant prey in the 1991 YOTS data.
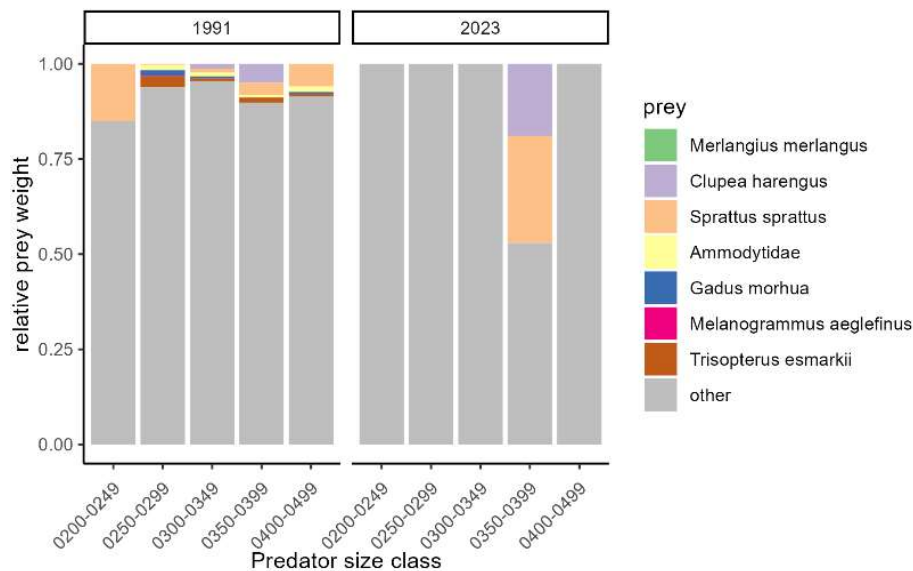
Figure 26. Mackerel stomachs from 1991 and 2022 prepared for SMS.

The whiting stomachs from 1991 contained a large fraction of Norway pout (*Trisopterus esmarkii*); however, this species was only identified in a small fraction of the new stomachs from 2023 (not in 2022). Many of the new stomachs had either clupeids (sprat or herring) or cannibalistic content, with some size classes having stomachs full of whiting (Figure 27).
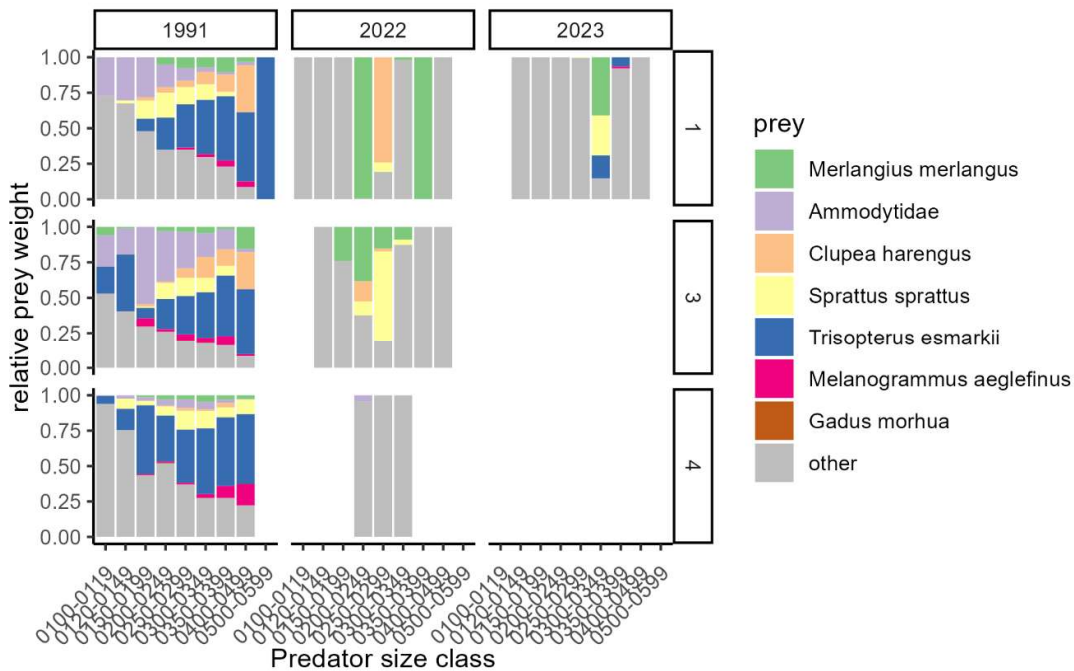
Figure 27. Whiting stomachs per quarter (1, 3, 4) in 1991 and the new samples from 2022 and 2023. The new samples contain a larger amount of unidentified prey in the stomachs.

Estimates of who eats whom in SMS

The new SMS 2023 key run has several updates to its structure, including updated data for seals, birds and evaluation of the North Sea cod stock, which has been divided into three substocks in the most recent benchmark. What we are presenting here is a preliminary run, as the final runs are scheduled to be published in the end of 2023. For details on the model structure, options used and changes from the last key run in 2022 see (52).

From the latest key run, one can see that the lower biomass of cod causes them to eat less biomass of prey than the two other predators considered here (Figure 28). The total biomass that mackerel consumes has also been declining in the last decade, primarily due to a lower population biomass in the last decade. Whiting, on the other hand, are an increasingly important predator in the North Sea. Cod has a varied prey diet with both haddock, sprat, sandeel and herring. The declining biomass of cod also means that the cannibalism is negligible in recent years (Figure 29). Mackerel consume a fair amount of small pelagic fish, including sandeel and sprat, which is not surprising as the pelagic realm is mackerel's main habitat. Whiting, like cod, has a varied diet which also includes quite a bit of Norway pout.
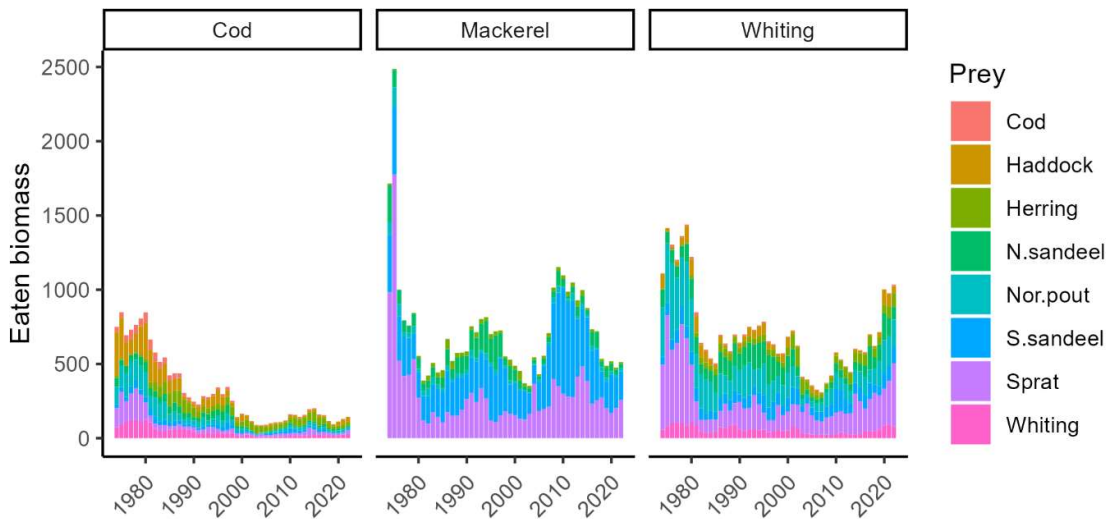
Figure 28. Biomass of prey eaten by predators cod (left), mackerel (middle) and whiting (right) in SMS.
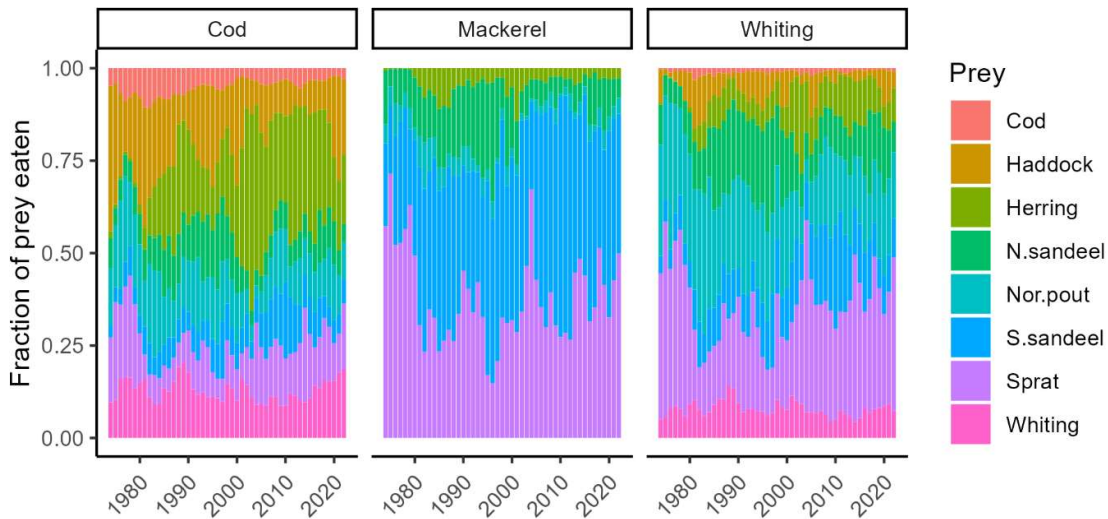
Figure 29. Fraction of prey eaten per predators cod (left), mackerel (middle) and whiting (right).

Conclusions

New data are still needed in the future to get the North Sea SMS model updated with most current information on who eats whom. This information is essential to properly calculate reference points (53) and in extension perform proper ecosystem-based fisheries management (54). The Baltic Sea and North Sea are two of only few ecosystems, where ecological effects (such as natural mortality) are included in the stock assessments of species included in SMS.

The results shown here (Figure 28 and Figure 29), show that there is a clear temporal trend in the biomass consumed by predators in the North Sea. The biomass consumed here is highly dependent on the population dynamics of the predators and therefore highly influenced by fisheries management. This indirect effect can cause changes to marine food webs (55–57) and are important to consider when creating management plans in marine ecosystems.

4.4 CS2.2: Estimating prey richness and biomass in the North Sea

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Key messages

This case study used machine learning approaches to investigate how ecosystem structure and function has changed in the North Sea over a 120-year period. The analysis revealed that the contribution of benthic prey in the stomachs of fish has declined through time. It also showed that body size and predator species were important variables, explaining both the amount of fish and the number of fish species that contributed to the diet of fish predators. This study highlights the potential to use stomach content data to establish long-term trends in species interactions and how they may have changed in response to climate change and fishing. It also shows how fish stomachs can be seen as samplers of their food web and may, when analysed appropriately, provide data and insight on areas, life stages and species that might otherwise be poorly sampled.

Background

Fishing and global environmental change are altering the structure and functioning of marine ecosystems with major implications for the sustainability of commercial fisheries (58–60) and associated economic systems (61). Because of these changes in structure and function, robust information on the distribution of biodiversity and areas important for ecosystem functioning are vital. This importance is especially true if we want to help mitigate deleterious impacts from human activities on ecosystems.

Many ecosystems have already experienced defaunation, trophic downgrading and extinctions (62). Such change can propagate through the food web, e.g., as trophic cascades (63), via species interactions which extend the impact of human pressure far beyond the time and location of the initial activity. Quantifying the relationships between change in species interactions with climate change and fishing mortality is therefore critical to help better assess and predict the effect of human pressures on marine ecosystem structure and functioning. Despite this necessity, international efforts to demonstrate change in species interactions empirically have been hampered by insufficient observations of food web interactions across many species, life stages and geographic ranges. Specifically, conventional marine biodiversity surveys (our key data source) are often unable to provide simultaneous observations across assemblages because of the need to change gear to sample microscopic organisms to top predators or to sample both the water column and the seabed. Such surveys also do not provide information on species interactions, which ultimately determine the structure and function of ecosystems.

Monitoring marine ecosystems is essential for effective management (64). This need to monitor has been formally enshrined in law as part of the Marine Strategy Framework Directive and the Convention on Law of the Sea (65). Indeed, stock assessments for fisheries have been commonplace for decades. However, a focus on commercially exploited species means that some aspects of the ecosystem remain poorly resolved and data can be patchy. A more holistic view of the ecosystem could be achieved with more sampling; however, sampling is time consuming and expensive, (66) and it often involves additional lethal collection methods (67).

A possible workaround, without the need for extra sampling, is to identify prey species within the stomachs of fish collected from fisheries monitoring. A single fish stomach sample can contain prey from across assemblages and habitats, and predators with differing foraging strategies, e.g., planktivores, benthivores and piscivores are often caught together. Fish stomachs can therefore provide samples (where the fish itself acts as a sampler) that integrate habitats and assemblages as well as behaviours and can be used to observe different components of an ecosystem simultaneously. Stomach samples also provide direct observations of species interactions because one gains information on both predator and prey. Although not without drawbacks, namely the need for taxonomic expertise for prey identification (65), using fish as samplers of the marine ecosystem has several advantages. Fish can 'sample' biodiversity from dangerous or logistically unfeasible

areas (such as near busy shipping lanes, wind farms or oil installations). Furthermore, biased samplers can reveal meaningful ecosystem changes (e.g. trophic shifts) before community composition changes are observed (68). Similar approaches using scavengers (shrimp) and molecular techniques have been used to monitor marine biodiversity previously (66). However, dietary records from routine fisheries monitoring exercises have yet to be used in this manner. Collectively, these dietary records constitute a vast resource. However, due to methodological differences in gathering the fish and the patchy spatial and temporal distribution of the data, dietary records often constitute a noisy and challenging dataset to analyse. Fortunately, advances in the application of machine learning in ecological research have yielded techniques with superior predictive abilities (compared to classical approaches (69)) well suited for rich and noisy datasets (70).

Here, we have combined fish stomach content data from the North Sea and utilised machine learning approaches to investigate spatial and temporal changes in prey over a 120-year period.

Aims

The aim of this case study is to harness machine learning approaches and use them to glean details about biodiversity and ecosystem change from the stomachs of fish. We use a stomach dataset concatenated from multiple sources (e.g., the ICES Year of the Stomach and the DAPSTOM database), spanning 120 years, to provide a long-term assessment of how marine ecosystem structure and functioning is changing in the North Sea in response to fishing and climate change alongside other environmental change gradients.

We explore the following three aspects and how they have changed in both space and time: (1) the relative quantity of plankton, benthos and fish prey biomass in the stomachs of fish; (2) the taxonomic richness of prey; and (3) how the contents of fish stomach relate to the pressures of fishing and temperature.

Approach

Database construction
Stomach data was sourced from ICES Year of the Stomach (71,72), DAPSTOM (73), Swedish-, Icelandic-, Norwegian-, French- and German-led surveys (e.g., FishNet[5]). The dataset was then processed with records missing ICES rectangles, year, predator or prey taxonomy, or number of stomach samples being omitted. Only records for which there were at least 30 predators per ICES rectangle per year sample were retained to prevent model overfitting. In total, 230 425 stomach samples spanning 120 years and including thirteen predator species fit all these criteria (Table 16). Where predator mass was missing, estimates were provided based on published length-mass relationships (14). Linear mixed-effect models of predator-prey body size scaling were used to estimate prey biomass where prey size information was unavailable (74). Predator and prey taxonomy were processed using the 'taxize' package (75) and assigned to 'zooplankton', 'benthos', 'fish' and 'other' functional groups as per Webb & Vanhoorne (76) using the 'worrms' package (75). The relative quantity of plankton, benthic and fish prey was calculated for each unique predator species, year and ICES rectangle combination by summing the weight of prey items belonging to each prey group and dividing by the sum of weight of all consumed functional groups. The richness of prey taxa belonging to each functional group was also calculated as a measure of prey diversity.

Climate, fishing and environmental change covariates
Monthly values of sea surface temperature and salinity were obtained from climate projections made by the CNRM-CM6-1-HR general circulation model, run by CNRM-CERFACS (CNRM: Centre National de Recherches Météorologiques; CERFACS: Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique). The dataset was generated as part of the internationally-coordinated Coupled Model Intercomparison

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[5] https://www.nationalpark-wattenmeer.de/wissensbeitrag/fishnet/

Project Phase 6 (CMIP6) as a resource for authors of the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC-AR6). We used data from the historical run, covering the period 1950 to 2014, version 'r1i1p1f2' (Centre National de Recherches Météorologiques; Centre Européen de Recherche et Formation Avancée en Calcul Scientifique, 2020).

The CNRM-CM6-1-HR climate model, released in 2017, includes the following components: aerosol: prescribed monthly fields computed by TACTIC_v2 scheme, atmos: Arpege 6.3, atmosChem: OZL_v2, land: Surfex 8.0c, ocean: Nemo 3.6, seaIce: Gelato 6.1. The model was run in native nominal resolutions: aerosol: 100 km, atmos: 100 km, atmosChem: 100 km, land: 100 km, ocean: 25 km, seaIce: 25 km. Data was downloaded at the original resolution and then interpolated to a 0.25° x 0.25° grid. Annual averages were obtained by averaging all twelve monthly means and were linked to the survey data collected from the same grid cell during each year.

We also included the mean annual index values for the Atlantic Multidecadal Oscillation (AMO) and the winter North Atlantic Oscillation (NAO). These two indices track large-scale environmental change associated with contrasting precipitation and warm and cool climate phases, the AMO being of lower frequency (60-80 years) relative to the NAO (<30 years; ((77–79)). Both indexes have been linked with changes in marine plankton, benthic invertebrates and fish assemblages, through to marine ecosystem-level change (80–82).

Time series of fishing mortality (F) were obtained from the most recent ICES stock assessments to describe the effect of fishing pressure on fish community structure. For herring, sole and plaice, these assessments covered ages 2-6; for cod and haddock ages 2-4; and for whiting ages 2-5. The dataset for herring already extended back to 1947, but for all other species it was necessary to extend these datasets backwards in time to 1950 using outputs for the North Sea provided by (83) (1996) [plaice], Millner and Whiting (84) [sole], or Pope & Macer (85) [cod, haddock and whiting]. A composite index of F for 'flatfish' (sole & plaice) and for 'gadoids' (cod, haddock and whiting) was constructed, using a similar technique to the 'living planet' index (see Loh et al. (86)). Data on the proportion of seafloor substrate (i.e., gravel, mud and sand), depth, distance to coast and seabed shear stress provide information on spatial environmental gradients and were sourced from Thompson et al. (51). We also include 'Year' as a predictor in our models to reveal any outstanding temporal variation in prey contributions not captured by our other temporally varying covariates (i.e., temperature, salinity, winter NAO, AMO and fishing mortality).

Machine Learning
Covariance of predictor variables was assessed using pairwise Pearson's correlation tests. Variables were removed if they correlated with another by >0.7 (Figure 30). A 'dummy' variable, randomly generated numbers between one and five, was assigned to each record of predation. Machine learning can overfit models; therefore, having a variable which is known to be noise can be used to diagnose and combat overfitting. Data were split into a test set (20% observation) and a training set (80%). Random Forest Analysis (87) using ten cross-validation folds was used to model each response with predator species, log10 transformed predator mass and the final set of spatial and temporal predictors (Figure 30, right panel) using the 'Caret' package (88). Models then underwent hyperparameter tuning using the 'tuneGrid' functionality in 'Caret' to further refine the model. The influence of predictor variables was visually assessed using a partial dependence and relative importance plots, and the fit of the final model was quantified on the withheld test data using the 'predict' function. All data processing and subsequent analyses were conducted in R version 4.02 (89).
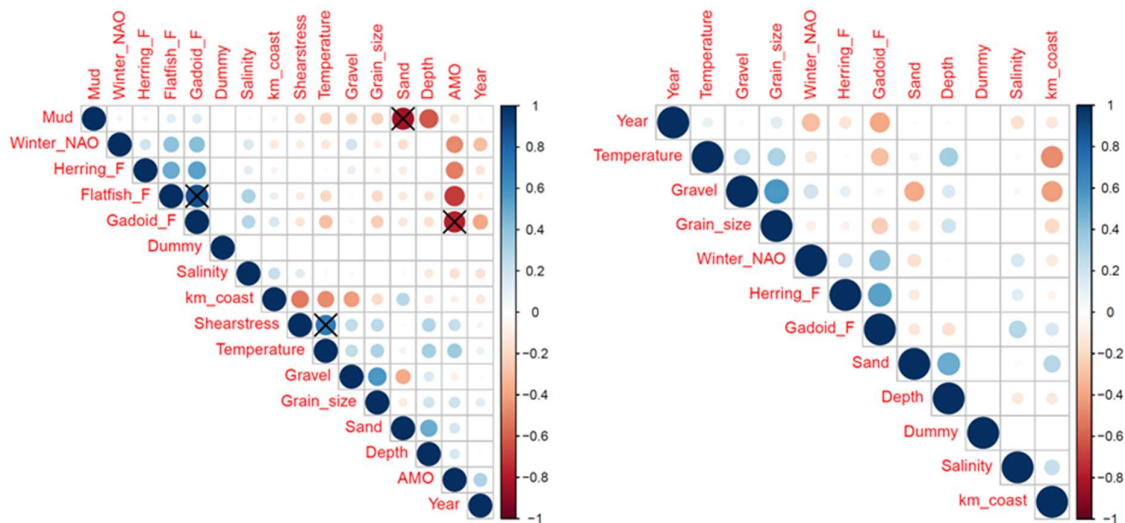
Figure 30. Pairwise Pearson correlation coefficients for all covariates considered in our analysis. Black crosses highlight correlations >0.7 using the full set of environmental variables considered (left panel) where we chose to exclude one of the covarying variables (right panel).

Results and discussion

Temperature and gadoid fishing mortality were both found to be important predictors of the relative contribution of prey biomass and prey richness across our models, particularly in relation to change in fish and benthic prey (Figure 31). The taxonomic richness of benthic prey and that prey's percentage biomass contribution to fish stomach contents declined over the study period (Figure 32 and Figure 33), although the latter increased again in the last 40 years, with limited unexplained temporal variation (i.e., change in relation to year) in our models of fish and zooplankton prey (Figure 34 and Figure 35). These results show that long-term and extensive changes in fish feeding behaviour, and thus ecosystem structure and functioning can be related to fishing as well as increasing temperature.

Our models for piscivory, benthivory and zooplanktivory (i.e. the percentage contribution of fish, benthos and zooplankton prey biomass) captured 39.3%, 41.7% and 52.7% of the variance, respectively. As gadoid fishing mortality increased, piscivory increased and benthivory decreased, while there was little change in zooplanktivory (Figure 34). As temperature increased, benthivory increased, with limited change in piscivory and zooplanktivory (Figure 35). Predator species, distance to coast and seabed shear stress were also important predictors of the relative contribution of prey across our models (Fig. 2). Turbot (*Scophthalmus maximus*), brill (*Scophthalmus rhombus*) and whiting (*Merlangius merlangus*) were the most piscivorous species; dab (*Limanda limanda*), plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) were the most benthivorous; and mackerel (*Scomber scombrus*), Atlantic horse mackerel (*Trachurus trachurus*) and saithe (*Pollachius virens*) were the most zooplanktivorous. Predator size was the most important predictor of piscivory (Figure 36) with larger predators being more piscivorous (Figure 37), zooplanktivory increased in smaller predators (Figure 38), while benthivory was highest in fish predators of approximately 10 g, decreasing in smaller and larger individuals (Figure 38).

Our models for the taxonomic richness of fish, benthic and zooplankton prey captured 34.9%, 45.3% and 48.2% of the variance, respectively. As gadoid fishing mortality increased, the average richness of fish prey per stomach sampled increased (Figure 35), while there was no clear direction of change in benthic or zooplankton prey richness (Figure 36 and Figure 37. There was also no clear direction of change in the taxonomic richness of fish, benthic and zooplankton prey in response to temperature, despite temperature being a relatively important predictor across those models (Figures 35-37). Predator species was

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the most important predictor across all models of prey richness (Figure 32). Typically, the most piscivorous, benthivorous and zooplanktivorous species had the most taxonomically rich diets for their respective prey groups. Exceptions were thornback ray (*Raja clavata*), which had higher benthic and fish prey richness in their diet compared to the more benthivorous and piscivorous plaice, dab and whiting, and saithe, which had higher fish prey richness in their diet compared to more piscivorous whiting. Increasing predator size was positively correlated with fish prey richness, but negatively related to zooplankton prey richness (Figure 34), with no clear relationship to benthic prey richness (Figure 36).

The dummy variable had negligible importance across our models (Figure 31) which suggests random noise could be discerned from the signal, and the risk of overfitting was limited. Smooth response variables were also observed across our partial dependence plots, confirming overfitting was not present in our final models.
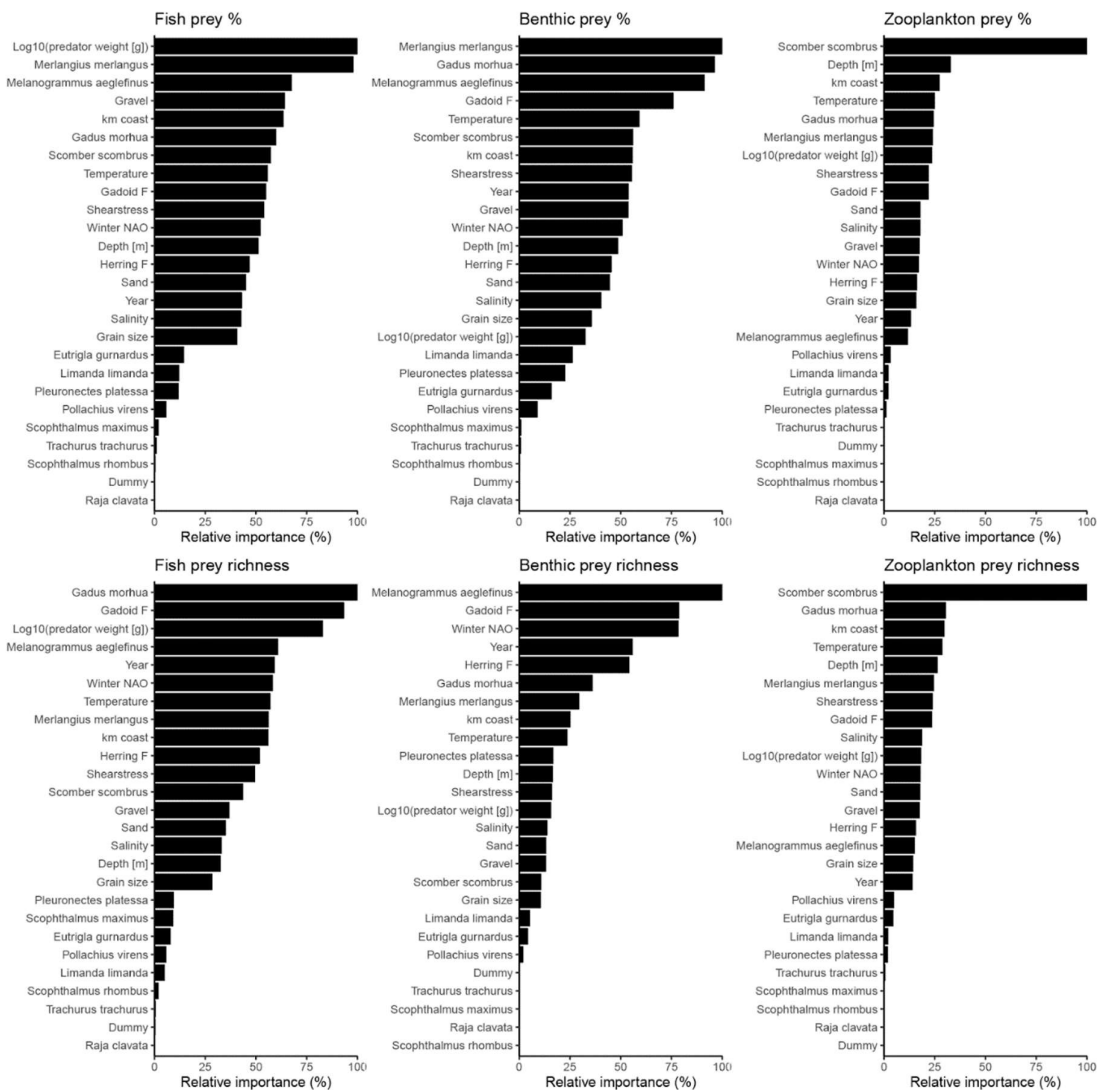
Figure 31. The relative importance of predictor variables in the final random forest models.
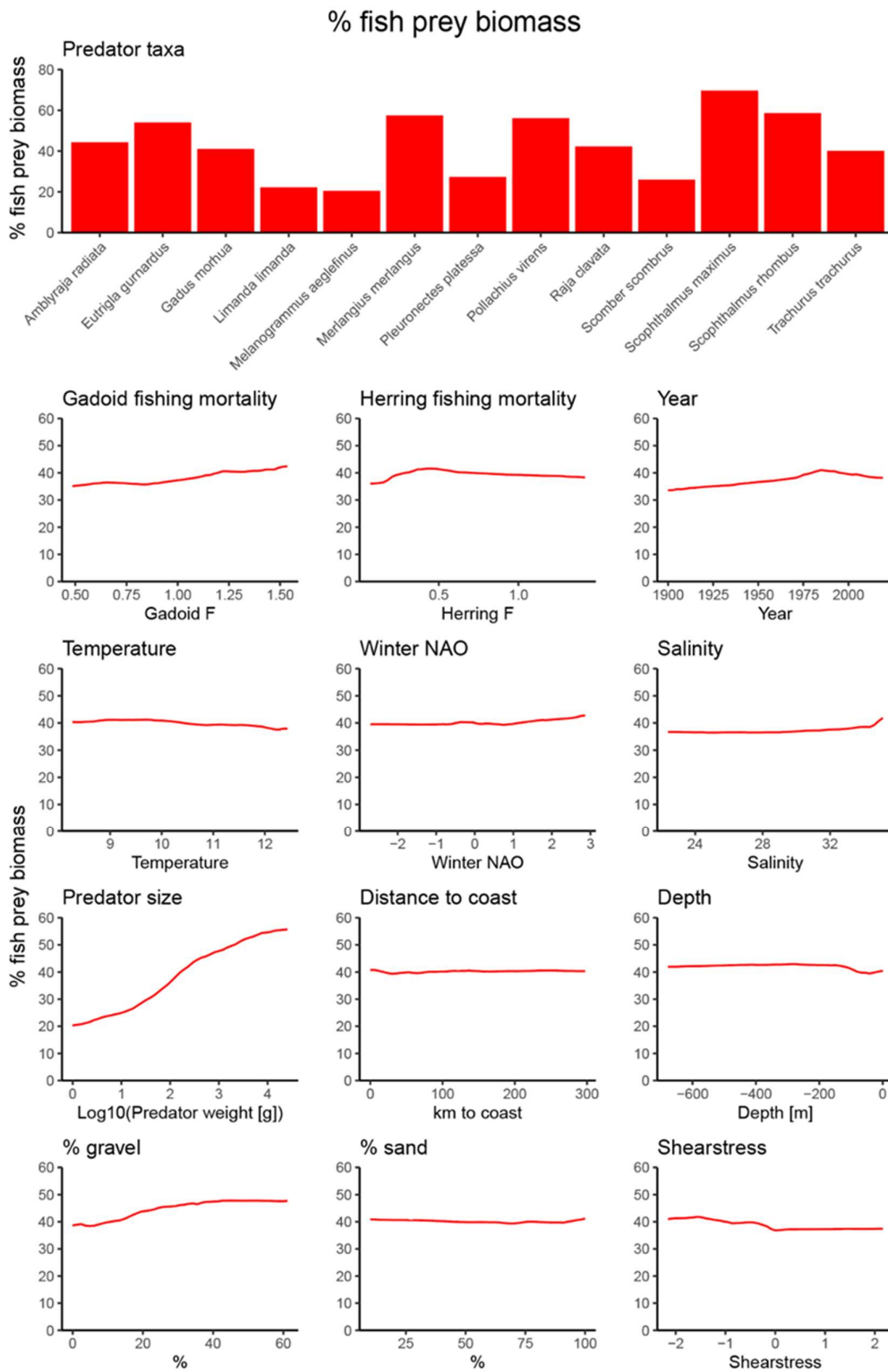
Figure 32. Partial dependence plots showing model predictions in red for the influence of predictor variables on the % fish prey biomass contribution to fish stomach contents while keeping other variables fixed at their average values.
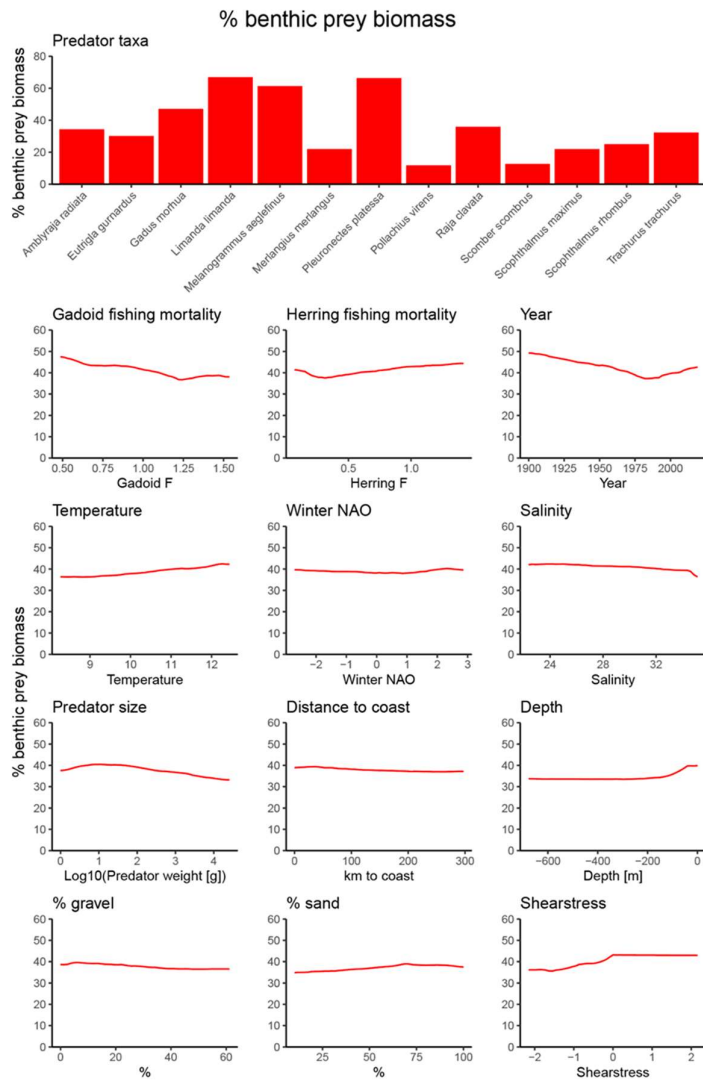
Figure 33. Partial dependence plots showing model predictions in red for the influence of predictor variables on the % benthic prey biomass contribution to fish stomach contents while keeping other variables fixed at their average values.
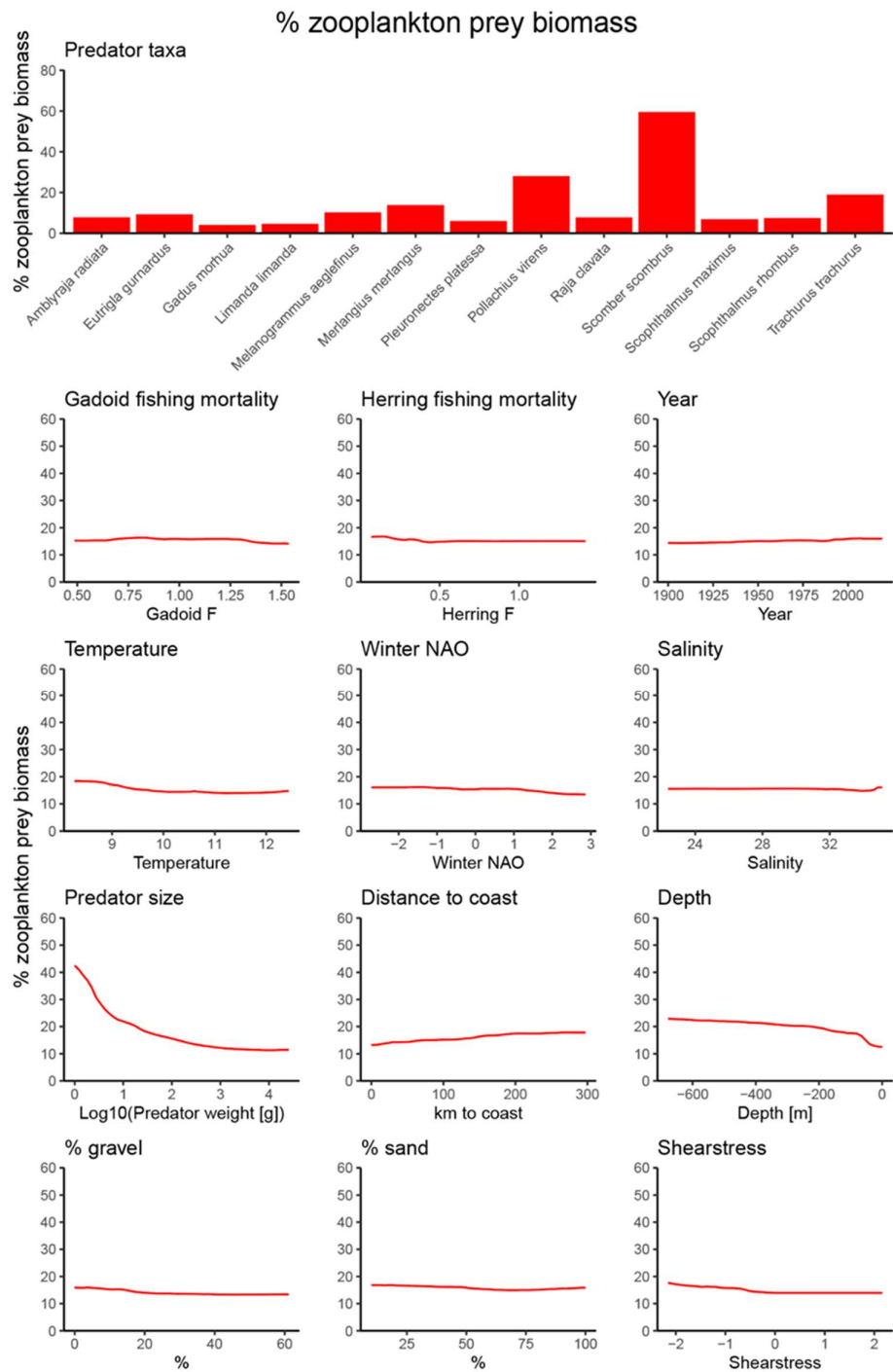
Figure 34. Partial dependence plots showing model predictions in red for the influence of predictor variables on % zooplankton prey biomass to fish stomach contents while keeping other variables fixed at their average values.
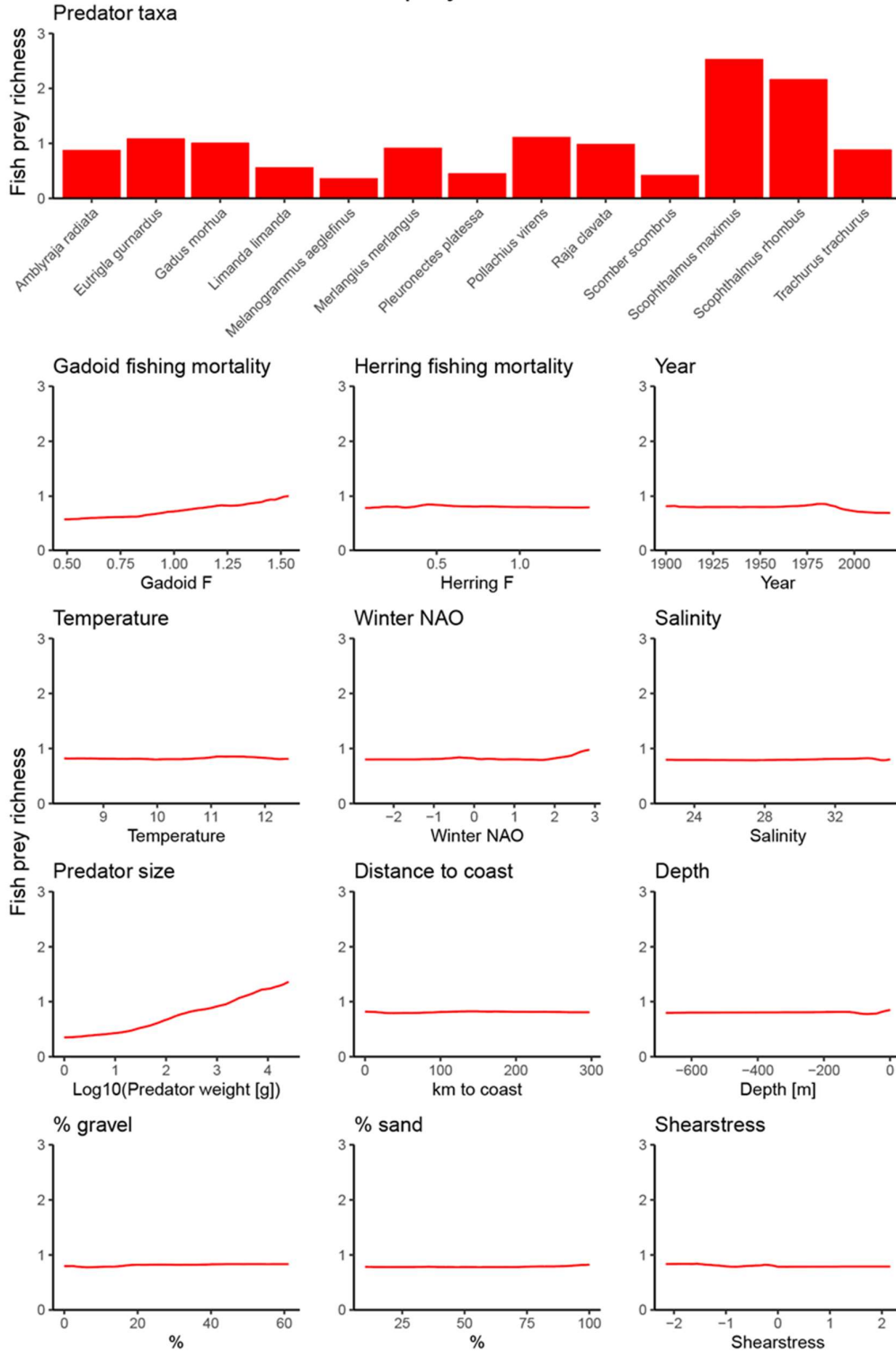
Figure 35. Partial dependence plots showing model predictions in red for the influence of predictor variables on the richness of fish prey to fish stomach contents while keeping other variables fixed at their average values.
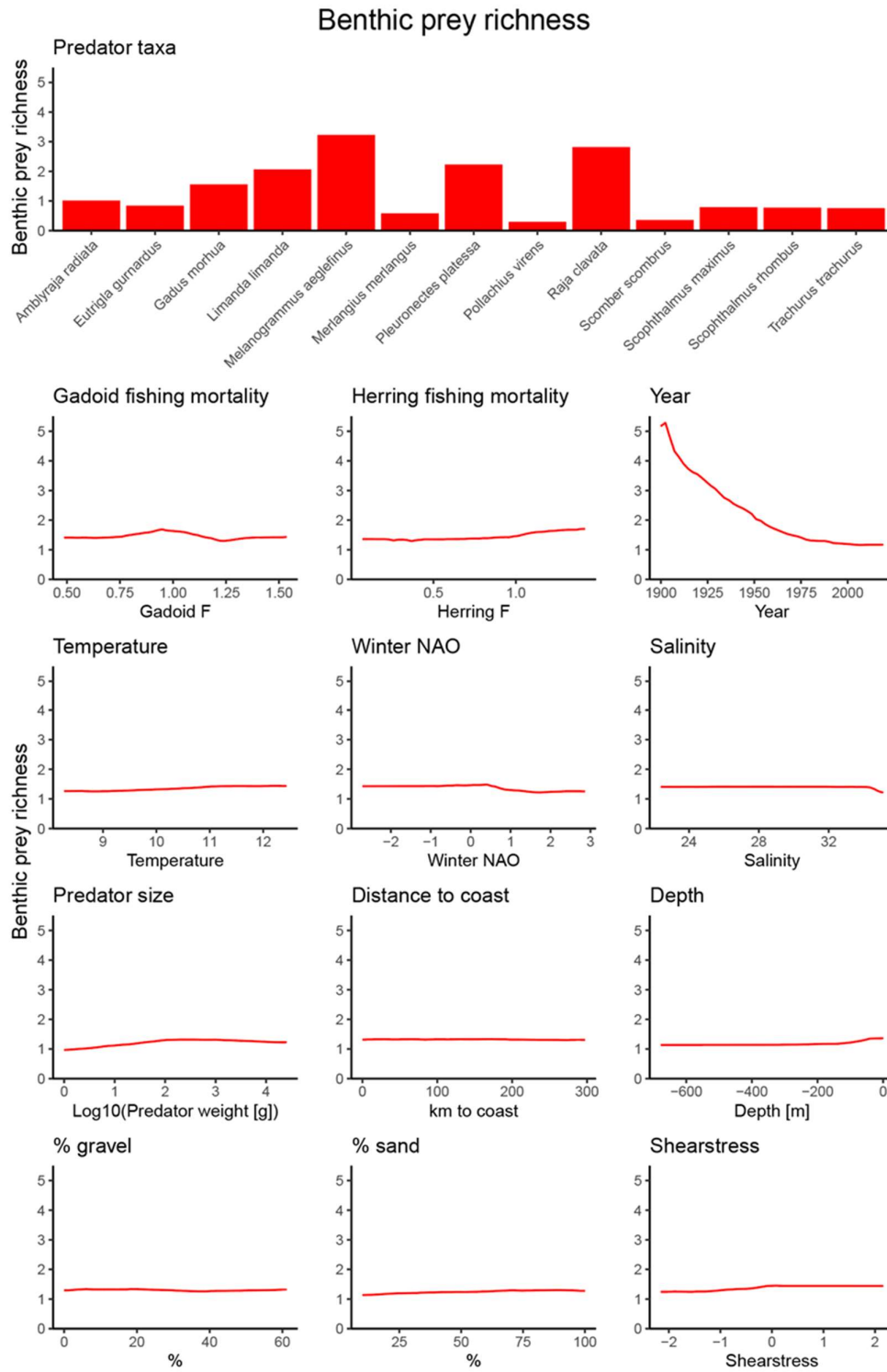
Figure 36. Partial dependence plots showing model predictions in red for the influence of predictor variables on the richness of benthic prey to fish stomach contents while keeping other variables fixed at their average values.
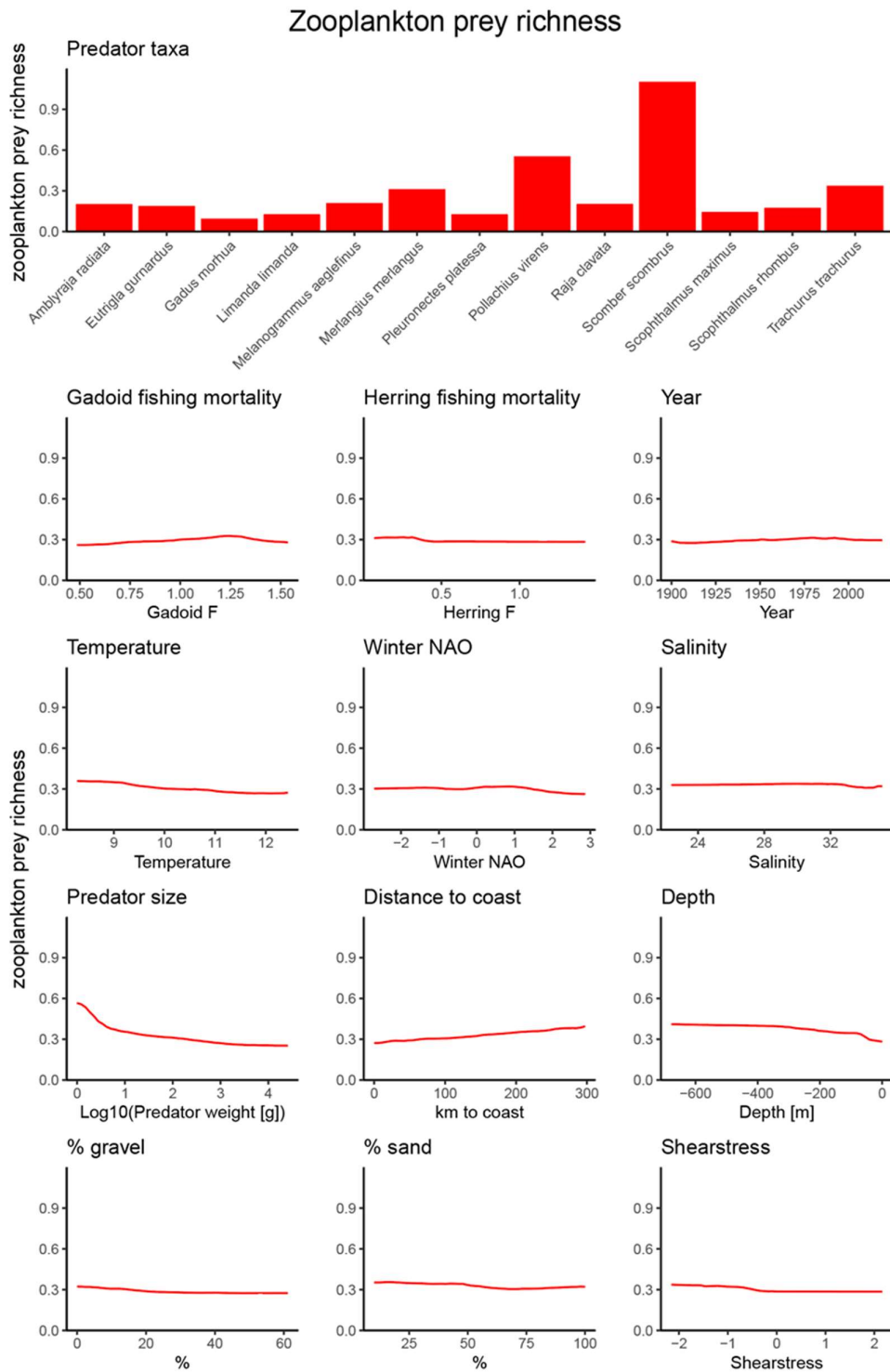
Figure 37. Partial dependence plots showing model predictions in red for the influence of predictor variables on the richness of zooplankton prey to fish stomach contents while keeping other variables fixed at their average values.
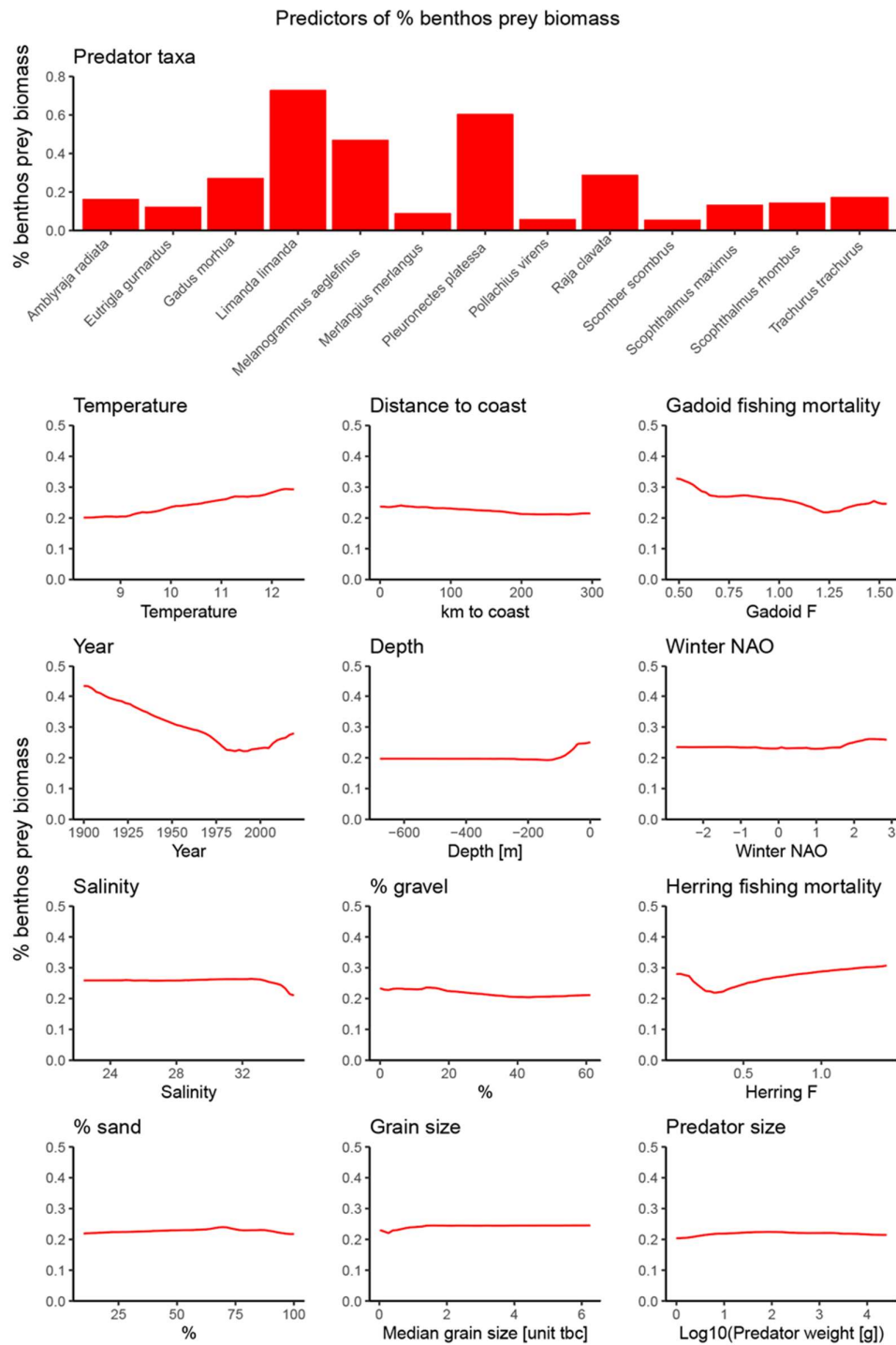
Figure 38. Partial dependence plots showing model predictions in red for the influence of predictor variables on the % benthic prey biomass contribution to fish stomach contents while keeping other variables fixed at their average values.

This study represents the most comprehensive empirical assessment of fish feeding behaviour in the North Sea to date. Many marine ecosystem studies have shown how fishing and climate change, among other human pressures, can affect community composition (11,90–93) but there is limited empirical information on how species interactions and the quantity of different prey have changed or why. Here, we use changes in fish feeding behaviour to provide simultaneous observations across plankton, benthic and fish assemblages to reveal how changes in fishing and temperature have affected the

structure and functioning of the North Sea food web. We also reveal substantial temporal declines in the importance of benthic prey over the 120-year study period that could not be explained with the variables in our models.

Predator species selection and body size were key given their importance as predictors across our models, which is unsurprising and has been well described in studies categorising fish into functional feeding groups (5,51,74). However, predator species and body size were included as predictors in our models to account for their effect and thus reveal general trends in fish feeding behaviour in response to human pressure gradients which are useful for gauging how ecosystem structure and functioning has changed more broadly. The negative relationship between gadoid fishing mortality and both percentage benthic prey biomass and benthic prey taxonomic richness provides empirical evidence for the negative effects of demersal fishing on the benthic prey assemblage (94,95) note that flatfish fishing mortality was positively correlated with gadoid fishing mortality and excluded from our models, but could also be impacting benthic prey assemblages. In some cases, important predictors in our models appeared to have little effect on the responses based on partial dependence plots, such as distance to coast when predicting piscivory and benthivory (Figure 31). This appearance of little effect could mean that there are important interactions between predictors, e.g., different predatory species had contrasting responses to the predictor. Further interrogation will be necessary to get a deeper understanding of the effect of important predictors whose relationship to the responses across fish species remains unclear.

This analysis showcases machine learning's ability to discern subtle trends from large noisy datasets (65). We also assess and tackle overfitting, which has been a key criticism levelled at machine learning, by using variable importance plots, partial dependence plots and adding a 'dummy variable' of random noise (69,96). Our variable importance plots show that the dummy variable was unimportant, and our partial dependence plots show smooth response curves (i.e., not jittery, highly variable, response curves indicative of overfitting) for each of the other predictors, adding further evidence that overfitting has not occurred.

By exploiting the vast information contained within fish stomach data and using cutting-edge analytical techniques, we have been able to quantitatively link changes in fish behaviour to a host of human pressure and environmental change gradients. Our models could be used to make predictions useful to understand how the North Sea might change under different management scenarios and also help refine information used in multispecies fisheries models on the quantities of different prey exploited by predators under a range of fishing pressures and climate scenarios.

Conclusion

Machine learning has produced new insights out of a noisy and large stomach content dataset and highlights how fish feeding behaviour changes in response to increasing fishing pressure and temperature, among other environmental change drivers. The patterns we document provide a completely unique long-term and spatially extensive perspective of change in the North Sea ecosystem, with simultaneous observations across plankton, benthic and fish assemblages that could not be explored using conventional biodiversity sampling programmes. Moving forward, we advocate the collection of predator stomachs both to establish biodiversity baselines in data deficient areas and as a means of gleaning additional insight from ongoing fisheries monitoring.

5 CONCLUSIONS AND SCIENTIFIC RECOMMENDATIONS

During this study, we have re-established the stomach content database from ICES and populated it with a range of new data points, which scientists can use in ecological and fisheries research for years to come. Old data from the 'Year of the Stomach' as well as previous tenders still need to be added to the database, which is an ongoing process that will take place as the database becomes common knowledge and functional across the scientific community. There is already work going on in the RCGs to update the database with stomach samples collected in other projects, to widen the scope of the dataset, as well as opening for more scientific endeavours. For large scale meta-studies of feeding across a large spatiotemporal scale it is now possible to combine the ICES and the DAPSTOM database for an incredibly large dataset spanning several decades. While all data is not made equal in the two databases, many potential studies can be conceived from the combined data.

Despite the short time frame of the study, some modelling efforts have been realised, and some interesting results have been shown for both the North Sea and the Baltic Sea. We have shown the temporal changes in Baltic cod diet, in light of the changes cod has experienced in physiology, prey availability and distribution. We have also explored how the diet and feeding behaviour of various species have changed through time in the North Sea. In particular, we have found that the consumption of benthic prey has changed through time and can be linked to both fishing and temperature. We also note a clear and mechanistic link between population abundance and predation. These three case studies have all applied advanced methodologies (often novel in their own right) to the new stomach content database, clearly highlighting the value of such data and what inference can be gained in terms of food web structure and function. The analysis on the new data presented here is far from exhaustive, with many future studies expected to come from the database.

The project was conducted in less than a year (from beginning of the tender to submission date of last report). This short time period has caused some complications in terms of having adequate time to 1) compile available data, 2) analyse data in lab, 3) construct the database and 4) scientifically analyse the data. However, despite these challenges, this report provides an overview of all the new data analysed uploaded to the database, how the database has been developed to promote a user-friendly experience when working with complex data and three interesting case studies that showcase how stomach data can be used for scientific analysis of food webs and predator-prey interactions.

For the coming years, we support an ongoing protocol to continuously collect and analyse new stomach samples, to keep the database up to date and be able to identify ecological changes happening due to fisheries, climate change, pollution etc. An organised protocol across ICES nations to collect and review stomach samples would also encourage more research into usability of both old and new data through novel modelling methods (such as the one applied for Baltic cod here), to formally integrate this valuable data source into the management of exploited marine resources. The geographical standards of these protocols need to be improved over the somewhat erratic sampling over the last couple of years. This erratic sampling is of course complicated by the fact that not all survey hauls contain predators of the correct species and size classes that we are looking for when creating food web models.

We conclude that predation and food web interactions have changed over time based on the three case studies presented in this document. Implementation of these results into management marine ecosystems becomes an important task for the foreseeable future, and we hope that the results are considered when making management plans for (and in) marine ecosystems.

6   REFERENCES

1. Reum JCP, Essington TE. Seasonal variation in guild structure of the Puget Sound demersal fish community. Estuaries Coasts. september 2008;31(4):790–801.

2. Deroba JJ. Sources of variation in stomach contents of predators of Atlantic herring in the Northwest Atlantic during 1973-2014. ICES J Mar Sci. juli 2018;75(4):1439–50.

3. Ainsworth CH, Kaplan IC, Levin PS, Mangel M. A statistical approach for estimating fish diet compositions from multiple data sources: Gulf of California case study. Ecol Appl. 2010;20(8):2188–202.

4. Lewy P, Vinther M. A stochastic age-length-structued multispecies model applied to North Sea stocks. Bd. ICES docum. 2004 s. p.-33.

5. Garrison LP, Link JS. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Mar Ecol Prog Ser. 28. august 2000;202:231–40.

6. Baker R, Buckland A, Sheaves M. Fish gut content analysis: robust measures of diet composition. Fish Fish. marts 2014;15(1):170–7.

7. Andersen NG, Beyer JE. How are prey fishes of multiple meals evacuated from the stomach of a piscivorous fish? J Fish Biol. 2007;71(1):219–34.

8. Tender No MARE/2012/02 Study on stomach content of fish to support the assessment of good environmental status of marine food webs and the prediction of MSY after stock restoration https://www.thuenen.de/media/institute/sf/Projektdateien/1321/Final_Report_Tender_No_MA RE-2012-02.pdf

9. Pinnegar JK, Cooper KM, Thompson MSA. DAPSTOM (integrated database and portal for fish stomach records) [Internet]. 2023. Tilgængelig hos: Cefas, UK. V1. doi: https://doi.org/10.14466/CefasDataHub.144

10. Moriarty R, Buitenhuis ET, Le Quéré C, Gosselin MP. Distribution of known macrozooplankton abundance and biomass in the global ocean. Earth Syst Sci Data. 2013;5(2):241–57.

11. Pitois SG, Fox CJ. Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. ICES J Mar Sci. juni 2006;63(5):785–98.

12. Studier EH, Sevick SH. Live mass, water content, nitrogen and mineral levels in some insects from south-central lower michigan. Comp Biochem Physiol A Physiol. 1992;103(3):579–95.

13. CHOWN SL, MARAIS E, TERBLANCHE JS, KLOK CJ, LIGHTON JRB, BLACKBURN TM. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. Funct Ecol. april 2007;21(2):282–90.

14. Silva JF, Ellis JR, Ayers RA. Length-weight relationships of marine fish collected from around the British Isles. Sci Ser Tech Rep. 2013;150:1–109.

15. Pinnegar JK, Trenkel VM, Tidd AN, Dawson WA, Du buit MH. Does diet in Celtic Sea fishes reflect prey availability? J Fish Biol. december 2003;63(s1):197–212.

16. Scharf FS, Juanes F, Rountree RA. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser. 2000;208:229–48.

17. Merella P, Quetglas A, Alemany F, Carbonell A. Length-weight relationship of fishes and cephalopods from the Balearic Islands (western Mediterranean). Naga. 1997;20:66–8.

18. Kastelein R, Battum R. The relationship between body weight and morphological measurements in harbour porpoises (Phocoena phocoena) from the North Sea. Aquat Mamm. januar 1990;16:48–52.

19. Victoria O, Fayeye T, Ayorinde K, Olojede H. Relationship between Body Weight and Linear Body Measurements in Japanese Quail (Coturnix coturnix japonica). J Sci Res. december 2013;6.

20. Markussen NH, Bjørge A, ØRitsland NA. Growth in harbour seals (Phoca vitulina) on the Norwegian coast. J Zool. november 1989;219(3):433–40.

21. Pisanu B, Chapuis JL, Périn R. Syphacia obvelata infections and reproduction of male domestic mice Mus musculus domesticus on a sub-Antarctic Island. J Helminthol. 2007/02/22 udg. 2003;77(3):247–53.

22. Hunt GL, Cobain MRD, McGill RAR, Pinnegar JK, Engelhard GH, Wigham BD, m.fl. Quantifying spatio-temporal consistency in the trophic ecology of two sympatric flatfishes. J Fish Biol. august 2023;103(2):378–92.

23. Rijnsdorp AD, Vingerhoed B. Feeding of plaice Pleuronectes platessa L. and sole Solea solea (L.) in relation to the effects of bottom trawling. J Sea Res. juni 2001;45(3–4):219–29.

24. Patel R, Roy S, Capuzzo E, J van der K. Seasonality of diet overlap among small pelagic fish in the waters southwest of the UK. Mar Ecol Prog Ser. 2023;708:101–23.

25. Macer CT. Some aspects of the biology of the horse mackerel [Trachurus trachurus (L.)] in waters around Britain. J Fish Biol. januar 1977;10(1):51–62.

26. Townhill BL, Maxwell D, Engelhard GH, Simpson SD, Pinnegar JK. Historical Arctic Logbooks Provide Insights into Past Diets and Climatic Responses of Cod. PLOS ONE. 2. september 2015;10(9):e0135418.

27. Thompson W. XXXVIII - On fishes new to Ireland. Ann Nat Hist. 1838;1:348–59.

28. Bentley JW, Hines D, Borrett S, Serpetti N, Fox C, Reid DG, m.fl. Diet uncertainty analysis strengthens model-derived indicators of food web structure and function. Ecol Indic. marts 2019;98:239–50.

29. Ogilvie H. Observations on the food of post-larval herring from the Scottih coast [Internet]. 1927. Tilgængelig hos: Scientific Investigations of the Fishery Board for Scotland, 1927(1), 11pp

30. Ogilvie H. The food of post-larval haddock with reference to the annual fluctuations in the haddock broods [Internet]. 1938. Tilgængelig hos: Rapports et procès-verbaux des réunions (1903–1991). Volume 107. https://doi.org/10.17895/ices.pub.9289

31. ICES. Cod (Gadus morhua) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). In the Report of the ICES Advisory Committee. ICES Advice 2023 [Internet]. 2023; Tilgængelig hos: https://doi.org/10.17895/ices.advice.21820497

32. Casini M, Hansson M, Orio A, Limburg K. Changes in population depth distribution and oxygen stratification are involved in the current low condition of the eastern Baltic Sea cod (Gadus morhua). Biogeosciences. februar 2021;18(4):1321–31.

33. Lindmark M, Anderson SC, Gogina M. Evaluating drivers of spatiotemporal variability in individual condition of a bottom-associated marine fish , Atlantic cod (Gadus morhua). ICES J Mar Sci. 2023;2019(October 2022):1–12.

34. Mion M, Haase S, Hemmer-Hansen J, Hilvarsson A, Hüssy K, Krüger-Johnsen M, m.fl. Multidecadal changes in fish growth rates estimated from tagging data: A case study from the Eastern Baltic cod (Gadus morhua, Gadidae). Fish Fish. marts 2021;22(2):413–27.

35. Casini M, Käll F, Hansson M, Plikshs M, Baranova T, Karlsson O, m.fl. Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. R Soc Open Sci. oktober 2016;3(10).

36. Kulatska N, Neuenfeldt S, Beier U, Elvarsson BÞ, Wennhage H, Stefansson G, m.fl. Understanding ontogenetic and temporal variability of Eastern Baltic cod diet using a multispecies model and stomach data. Fish Res. marts 2019;211:338–49.

37. Kulatska N, Woods PJ, Elvarsson BÞ, Bartolino V. Size-selective competition between cod and pelagic fisheries for prey. ICES J Mar Sci. august 2021;78(5):1900–8.

38. Neuenfeldt S, Bartolino V, Orio A, Andersen KH, Andersen NG, Niiranen S, m.fl. Feeding and growth of Atlantic cod (Gadus morhua L.) in the eastern Baltic Sea under environmental change. ICES J Mar Sci. marts 2020;77(2):624–32.

39. ICES. Report of the Workshop on Spatial Analyses for the Baltic Sea (WKSPATIAL). ICES CM 2015SSGIEA. november 2016;13:1–37.

40. Lindgren F, Rue H, Lindström J. An Explicit Link between Gaussian Fields and Gaussian Markov Random Fields: The Stochastic Partial Differential Equation Approach. J R Stat Soc Ser B Stat Methodol. 1. september 2011;73(4):423–98.

41. Anderson SC, Ward EJ, English PA, Barnett LAK. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. bioRxiv. 2022;2003–22.

42. Kristensen K, Nielsen A, Berg CW, Skaug H, Bell BM. TMB: Automatic Differentiation and Laplace Approximation. J Stat Softw. 2016;70(5):1–21.

43. Lindgren F, Rue H. Bayesian spatial modelling with R-INLA. J Stat Softw. 2015;63:1–25.

44. Goodman MC, Carroll G, Brodie S, Grüss A, Thorson JT, Kotwicki S, m.fl. Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem. Ecography. 2022;2022(9):e06084–e06084.

45. Carroll G, Holsman KK, Brodie S, Thorson JT, Hazen EL, Bograd SJ, m.fl. A review of methods for quantifying spatial predator–prey overlap. Glob Ecol Biogeogr. 2019;28(11):1561–77.

46. Gogina M, Zettler ML, Wåhlström I, Andersson H, Radtke H, Kuznetsov I, m.fl. A combination of species distribution and ocean-biogeochemical models suggests that climate change overrides eutrophication as the driver of future distributions of a key benthic crustacean in the estuarine ecosystem of the baltic sea. ICES J Mar Sci. 2021;77(6):2089–105.

47. Woodward. G, Warren PH. Body size and predatory interactions in freshwaters: scaling from individuals to communities. I: Hildrew AG, Raffaelli D, Edmonds-Brown R, redaktører. Body size: the structure and function of aquatic ecosystems. Cambridge: Cambridge University Press; 2007. s. 98–117.

48. Jennings S, Blanchard JL. Fish abundance with no fishing : predictions based on macroecological theory. 2004;(Pauly 1995):632–42.

49. Jennings S, Warr KJ. Smaller predator-prey body size ratios in longer food chains. Proc R Soc B Biol Sci. juli 2003;270(1522):1413–7.

50. ICES. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG), 29 March-7 April 2016. Copenhagen, Denmark; 2016 s. 867–867.

51. Thompson MSA, Pontalier H, Spence MA, Pinnegar JK, Greenstreet SPR, Moriarty M, m.fl. A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning. J Appl Ecol. 2020;0–2.

52. ICES. Working Group on Multispecies Assessment Methods (WGSAM; outputs from 2022 meeting) [Internet]. ICES Scientific Reports; 2023 feb [henvist 19. oktober 2023]. Tilgængelig hos: https://ices-library.figshare.com/articles/report/Working_Group_on_Multispecies_Assessment_Methods_WGSAM_outputs_from_2022_meeting_/22087292/1

53. Collie JS, Gislason H. Biological reference points for fish stocks in a multispecies context. Can J Fish Aquat Sci. 2001;58(11):2167–76.

54. Pikitch E, Santora E, Babcock A, Bakun A, Bonfil R, Conover D, m.fl. Ecosystem-based fishery management. Science. september 2004;305(5682):346–7.

55. Andersen KH, Pedersen M. Damped trophic cascades driven by fishing in model marine ecosystems. Proc R Soc B Biol Sci. marts 2010;277(1682):795–802.

56. Daskalov GM, Grishin AN, Rodionov S, Mihneva V. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proc Natl Acad Sci U S A. juni 2007;104(25):10518–23.

57. Frank KT, Petrie B, Choi JS, Leggett WC. Trophic cascades in a formerly cod-dominated ecosystem. Science. juni 2005;308(5728):1621–3.

58. du Pontavice H, Gascuel D, Reygondeau G, Maureaud A, Cheung WWL. Climate change undermines the global functioning of marine food webs. Glob Change Biol. marts 2020;26(3):1306–18.

59. Link JS, Watson RA. Global ecosystem overfishing: Clear delineation within real limits to production. Sci Adv. 2019;5:eaav0474–eaav0474.

60. Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, m.fl. Global imprint of climate change on marine life. Nat Clim Change. oktober 2013;3(10):919–25.

61. Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, m.fl. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science. marts 2017;355(6332).

62. Rooney N, McCann KS. Integrating food web diversity, structure and stability. Trends Ecol Evol. 2012;27(1):40–6.

63. Svenning JC, Ejrnaes R, Faurby S, Galetti M. Science for a wilder Anthropocene-synthesis and future directions for rewilding research. PNAS. 2016;113:898–906.

64. Gilbey J, Carvalho G, Castilho R, Coscia I, Coulson MW, Dahle G, m.fl. Life in a drop: Sampling environmental DNA for marine fishery management and ecosystem monitoring. Mar Policy. februar 2021;124.

65. Cordier T, Lanzén A, Apothéloz-Perret-Gentil L, Stoeck T, Pawlowski J. Embracing Environmental Genomics and Machine Learning for Routine Biomonitoring. Trends Microbiol. maj 2019;27(5):387–97.

66. Siegenthaler A, Wangensteen OS, Soto AZ, Benvenuto C, Corrigan L, Mariani S. Metabarcoding of shrimp stomach content: Harnessing a natural sampler for fish biodiversity monitoring. Mol Ecol Resour. januar 2019;19(1):206–20.

67. Trenkel VM, Vaz S, Albouy C, Amour AB, Duhamel E, Laffargue P, m.fl. We can reduce the impact of scientific trawling on marine ecosystems. Mar Ecol Prog Ser. januar 2019;609:277–82.

68. Traugott M, Thalinger B, Wallinger C, Sint D. Fish as predators and prey: DNA-based assessment of their role in food webs. J Fish Biol. februar 2021;98(2):367–82.

69. Yu Q, Ji W, Prihodko L, Ross CW, Anchang JY, Hanan NP. Study becomes insight: Ecological learning from machine learning. Methods Ecol Evol. november 2021;12(11):2117–28.

70. Crisci C, Ghattas B, Perera G. A review of supervised machine learning algorithms and their applications to ecological data. Ecol Model. august 2012;240:113–22.

71. Daan N. Data base report of the stomach sampling project 1981. ICES Coop Res Rep. 1981;164:1–150.

72. ICES. Database report of the stomach sampling project, 1991. ICES Coop Res Rep. 1997;219:1–426.

73. Pinnegar JK. DAPSTOM–An Integrated Database & Portal for Fish Stomach Records, Version 5.5. Lowestoft, UK; 2019 s. 1–34.

74. Thompson MSA, Lynam CP, Preciado I. Pilot Assessment of Feeding Guilds. In: OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic. 2023.

75. Chamberlain S. worrms: World Register of Marine Species (WoRMS) Client (R package version 0.4.0.). 2019;

76. Webb TJ, Vanhoorne B. Linking dimensions of data on global marine animal diversity: Dimensions of global marine diversity. Philos Trans R Soc B Biol Sci. december 2020;375(1814).

77. Enfield DB, Mestas-Nuñez AM, Trimble PJ. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U.S. Geophys Res Lett. maj 2001;28(10):2077–80.

78. Hurrell JW. Decadal trends in the North Atlantic oscillation: Regional temperatures and precipitation. Science. 1995;269(5224):676–9.

79. Jones PD, Jonsson T, Wheeler D. Extension to the North Atlantic oscillation using early instrumental pressure observations from Gibraltar and south-west Iceland. Int J Climatol. november 1997;17(13):1433–50.

80. Edwards M, Beaugrand G, Helaouët P, Alheit J, Coombs S. Marine Ecosystem Response to the Atlantic Multidecadal Oscillation. PLoS ONE. februar 2013;8(2).

81. Nye JA, Baker MR, Bell R, Kenny A, Kilbourne KH, Friedland KD, m.fl. Ecosystem effects of the Atlantic Multidecadal Oscillation. J Mar Syst. 2014;133:103–16.

82. Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC. Ecological effects of the North Atlantic Oscillation. Oecologia. 2001;128(1):1–14.

83. Rijnsdorp AD, Millner RS. Trends in population dynamics and exploitation of North Sea plaice (Pleuronectes platessa L.) since the late 1800s. ICES J Mar Sci. december 1996;53(6):1170–84.

84. Millner RS, Whiting CL. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES J Mar Sci. 1996;53:1185–95.

85. Pope JG, Macer CT. An evaluation of the stock structure of North Sea cod, haddock, and whiting since 1920, together with a consideration of the impacts of fisheries and predation effects on their biomass and recruitment [Internet]. 1996 s. 1157–69. (ICES Journal of Marine Science; bd. 53). Tilgængelig hos: https://academic.oup.com/icesjms/article/53/6/1157/592491

86. Loh J, Green RE, Ricketts T, Lamoreux J, Jenkins M, Kapos V, m.fl. The Living Planet Index: Using species population time series to track trends in biodiversity. I Royal Society; 2005. s. 289–95.

87. Wright MN, Ziegler A. Ranger: A fast implementation of random forests for high dimensional data in C++ and R. J Stat Softw. 2017;77(1).

88. Kuhn M. caret: Classification and Regression Training (6.0.86). 2020;

89. R Core Team. R: A language and environment for statistical computing. 2020.

90. Hiddink JG, Burrows MT, García Molinos J. Temperature tracking by North Sea benthic invertebrates in response to climate change. Glob Change Biol. januar 2015;21(1):117–29.

91. Hiddink JG, ter Hofstede R. Climate induced increases in species richness of marine fishes. Glob Change Biol. marts 2008;14(3):453–60.

92. Holland MM, Louchart A, Artigas LF, Ostle C, Atkinson A, Rombouts I, m.fl. Major declines in NE Atlantic plankton contrast with more stable populations in the rapidly warming North Sea. Sci Total Environ. november 2023;898.

93. Kenny AJ, Jenkins C, Wood D, Bolam SG, Mitchell P, Scougal C, m.fl. Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. ICES J Mar Sci. maj 2018;75(3):1080–92.

94. Collie J, Hiddink JG, van Kooten T, Rijnsdorp AD, Kaiser MJ, Jennings S, m.fl. Indirect effects of bottom fishing on the productivity of marine fish. Fish Fish. juli 2017;18(4):619–37.

95. Hiddink JG, Johnson AF, Kingham R, Hinz H. Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. J Appl Ecol. december 2011;48(6):1441–9.

96. Cordier T, Esling P, Lejzerowicz F, Visco J, Ouadahi A, Martins C, m.fl. Predicting the Ecological Quality Status of Marine Environments from eDNA Metabarcoding Data Using Supervised Machine Learning. Environ Sci Technol. august 2017;51(16):9118–26.

ANNEX 1 INVENTORY AND SELECTION OF STOMACH SAMPLES

Table 6. Baltic Sea. Inventory of available samples.

Country	Partner	Fish species of collected stomachs (predator)	Year of sampling	Number of stomachs
Latvia	BIOR	Cod	2017	432
Latvia	BIOR	Cod	2017	404
Latvia	BIOR	Cod	2018	209
Latvia	BIOR	Cod	2018	352
Latvia	BIOR	Cod	2019	240
Latvia	BIOR	Cod	2019	186
Latvia	BIOR	Cod	2020	101
Latvia	BIOR	Cod	2020	224
Latvia	BIOR	Cod	2021	321
Latvia	BIOR	Cod	2021	125
Latvia	BIOR	Cod	2022	155
Sweden	SLU	Cod	2021	624
Sweden	SLU	Flounder	2021	1 421
Poland	NMFRI	Cod	2021	384
Poland	NMFRI	Cod	2021	318
Denmark	DTU	Cod	2018	901
Denmark	DTU	Cod	2021	919
Germany	TI	Whiting	2020	400
Germany	TI	Whiting	2021	
Total				**7 716**
*Latvia	BIOR	Cod	1963-2013	27 663
Grand total				**35 379**

Table 7. North Sea. Inventory of available samples.

Country	Institute	Fish species of collected stomachs (predator)	Year of sampling	Number of stomachs
Netherlands	WMR	Mackerel	2013/2014	140
Netherlands	WMR	Mackerel	2013/2014	164
Netherlands	WMR	Mackerel	2013/2014	353
Netherlands	WMR	Grey gurnard	2013/2014	54
Netherlands	WMR	Grey gurnard	2012	24
Netherlands	WMR	Whiting	2022	412
Netherlands	WMR	Cod	2023	175
Netherlands	WMR	Whiting	2023	300
Netherlands	WMR	Monkfish	2022	5
Netherlands	WMR	Horse mackerel	2023	22
Netherlands	WMR	Spiny dogfish	2023	10
Netherlands	WMR	Turbot	2023	10
Netherlands	WMR	Cuckoo ray	2023	1
Netherlands	WMR	Thornback ray	2023	4
Netherlands	WMR	Common ling	2023	1
Netherlands	WMR	Brill	2023	2
Denmark	DTU	Whiting	2022	185
Denmark	DTU	Monkfish	2022	18
Denmark	DTU	Whiting	2022	213
Denmark	DTU	Mackerel	2022	1 172
Denmark	DTU	Cod	2023	89
Denmark	DTU	Atlantic halibut	2023	2
Denmark	DTU	Brill	2023	2
Denmark	DTU	Common ling	2023	3
Denmark	DTU	Pollack	2023	4
Denmark	DTU	Tub gurnard	2023	3
Denmark	DTU	Turbot	2023	3
Belgium	ILVO	Whiting	2022	58
Belgium	ILVO	Grey gurnard	2022	17
Belgium	ILVO	Whiting	2023	25
Belgium	ILVO	Grey gurnard	2023	4
Belgium	ILVO	Whiting	2023	150
Belgium	ILVO	Grey gurnard	2023	4
Belgium	ILVO	Whiting	2023	163
Total				**3 792**

Table 8. Baltic Sea. Samples selected for fish stomach content analysis.

Some additional samples were analysed by Denmark, adding to the samples selected in comparison with the inventory.

Country	Partner	Fish species of collected stomachs (predator)	Year of sampling	Number of selected stomachs
Latvia	BIOR	Cod	2017	432
Latvia	BIOR	Cod	2017	404
Latvia	BIOR	Cod	2018	209
Latvia	BIOR	Cod	2018	352
Latvia	BIOR	Cod	2019	240
Latvia	BIOR	Cod	2019	186
Latvia	BIOR	Cod	2020	101
Latvia	BIOR	Cod	2020	224
Latvia	BIOR	Cod	2021	321
Latvia	BIOR	Cod	2021	125
Latvia	BIOR	Cod	2022	155
Sweden	SLU	Cod	2021	624
Poland	NMFRI	Cod	2021	384
Poland	NMFRI	Cod	2021	318
Denmark	DTU	Cod	2018	901
Denmark	DTU	Cod	2021	919
Germany	TI	Whiting	2020	400
Germany	TI	Whiting	2021	
Total				**6295**
*Latvia	BIOR	Cod	1963-2013	27663
Grand total				**33958**

Table 9 North Sea. Samples selected for fish stomach content.

Country	Institute	Fish species of collected stomachs (predator)	Year of sampling	Number of selected stomachs
Netherlands	WMR	Mackerel	2013/2014	140
Netherlands	WMR	Mackerel	2013/2014	164
Netherlands	WMR	Mackerel	2013/2014	353
Netherlands	WMR	Grey gurnard	2013/2014	54
Netherlands	WMR	Grey gurnard	2012	24
Netherlands	WMR	Whiting	2022	412
Netherlands	WMR	Cod	2023	175
Netherlands	WMR	Whiting	2023	300
Netherlands	WMR	Monkfish	2022	5
Netherlands	WMR	Horse mackerel	2023	22
Netherlands	WMR	Spiny dogfish	2023	10
Netherlands	WMR	Turbot	2023	10
Netherlands	WMR	Cuckoo ray	2023	1
Netherlands	WMR	Thornback ray	2023	4
Netherlands	WMR	Common ling	2023	1
Netherlands	WMR	Brill	2023	2
Denmark	DTU	Whiting	2022	185
Denmark	DTU	Monkfish	2022	18
Denmark	DTU	Whiting	2022	213
Denmark	DTU	Mackerel	2022	1 172
Denmark	DTU	Cod	2023	89
Denmark	DTU	Atlantic halibut	2023	2
Denmark	DTU	Brill	2023	2
Denmark	DTU	Common ling	2023	3
Denmark	DTU	Pollack	2023	4
Denmark	DTU	Tub gurnard	2023	3
Denmark	DTU	Turbot	2023	3
Belgium	ILVO	Whiting	2022	58
Belgium	ILVO	Grey gurnard	2022	17
Belgium	ILVO	Whiting	2023	25
Belgium	ILVO	Grey gurnard	2023	4
Belgium	ILVO	Whiting	2023	150
Belgium	ILVO	Grey gurnard	2023	4
Belgium	ILVO	Whiting	2023	163
Total				**3 792**

ANNEX 2 ICES STOMACH DATABASE PROTOCOL AND DATABASE FORMAT

The stomach database protocol is a comprehensive guide for the scientific community in stomach sampling for biological studies. The protocol describes four parts (FI – File information; HH – Haul information; PI – predator information; PP – prey information) of the exchange format, and the latest version is available on the ICES homepage http://datsu.ices.dk/web/selRep.aspx?Dataset=157.

This annex is a short description of the datatypes, format and information potential uploaders need to populate the ICES stomach content database.

The database is available at

https://www.ices.dk/data/data-portals/Pages/Stomach-content.aspx

and uploaders need to have a login from their institution to be able to contribute to the database.

The uploaders need to prepare their data in four exchange files, which are thoroughly described in the section 'View File Format' (Figure 2, and link shown above) in the database and here in Table 10-13. The meta data required for some of these entries are online listed as 'mandatory' while others are optional.

Each field has an associated 'Datatype' which has a range categories (common to other SQL databases:

1. char (character of fixed length),
2. int (integer)
3. decimal (precise decimals)
4. float (scientific numbering)
5. varchar (character of variable length).

And also has a description of the datatype. Additionally, some character entries has a "Code List", where the uploader can chose options to enter from a dropdown menu (options shown in interactive link).

After preparing the exchange files, uploaders can use the datsu tool (https://datsu.ices.dk/web/screen.aspx) to screen the files for errors or bugs, and get an email sent which highlights fixes that need to be made.

Table 10. File information in the exchange format file.

Start	FieldCode	Datatype	Code List	Description
1	RecordType	char(2)		Record type
2	Country	char(2)	ISO_3166	Country code based on the ISO 3166 standard - Country of the organisation responsible for data collection and storage
3	Reporting_organisation	char(6)	EDMO	EDMO code of the reporting organisation
4	CruiseID	char(20)		CruiseID - Unique cruise ID in the format: Country + EDMO code + Ship code+ year (DA219526D42021)

Table 11. Haul information required for the exchange format.

Start	FieldCode	Datatype	Code List	Description
1	RecordType	char(2)		Record type
2	Ship	char(4)	SHIPC	SeaDataNet ship code
3	Gear	char(8)	SMTYP	Sampling gear used
4	HaulNo	int(6)		Haul number - sequential numbering by cruise
5	StationNumber	char(6)		Station number by national coding system
6	Year	char(4)		Year of the cruise
7	Month	int(2)		Month of the cruise
8	Day	int(2)		Day of the haul
9	Time	char(4)		Shooting time (UTC) (HHMM), 4 digits. E.g. 10:15=1015
10	ShootLat	decimal4(8)		Shoot of gear latitude
11	ShootLong	decimal4(9)		Shoot of gear longitude
12	HaulLat	decimal4(8)		Haul latitude
13	HaulLong	decimal4(9)		Haul longitude
14	ICESrectangle	char(4)	StatRec	ICES statistical rectangle of the sampling location
15	Depth	int(4)		Average depth during trawling
16	Survey	char(20)		Survey code (ICES survey codes) or project name
17	ICESDatabase	char(1)	YesNoFields	Catch and biological data available in other ICES databases, e.g. DATRAS or Acoustic - Yes or No field
18	Notes	char(100)		Any additional information

Table 12. Predator information in the exchange format file.

Start	FieldCode	Datatype	Code List	Description
1	RecordType	char(2)		Record type
2	Ship	char(4)	SHIPC	SeaDataNet ship code
3	Gear	char(8)	SMTYP	Sampling gear used
4	HaulNo	int(6)		Haul number - sequential numbering by cruise
5	StationNumber	char(6)		Station number by national coding system
6	Year	char(4)		Year of the cruise
7	Month	int(2)		Month of the cruise
8	Day	int(2)		Day of the haul
9	Time	char(4)		Shooting time (UTC) (HHMM), 4 digits. E.g. 10:15=1015
10	FishID	char(20)		Unique fish identification number for predator
11	AphiaIDPredator	int(10)		WoRMS AphiaID Species reference code of predator
12	IndWgt	decimal1(5)		Weight of predator in grams
13	Number	int(2)		Number of species taken for stomach analyses (pooled samples)
14	MeasurementIncrement	float(2)		Measurement increment in cm
15	Length	float(10)		Length of species
16	AgeSource	char(10)	AGDET	Age reading source material
17	Age	int(2)		Age of predator
18	Sex	char(1)	SEXCO	Sex of predator
19	MaturityScale	char(6)	AC_MaturityScale	Maturity scale
20	MaturityStage	char(4)	AC_MaturityCode	Maturity stage within chosen maturity scale
21	PreservationMethod	char(8)		Storage/preservation method at the time of sampling - Insert the storage/preservation method used according to ICES vocabulary METST/METFP
22	Regurgitated	int(4)		Number of stomachs regurgitated
23	StomachFullness	char(1)	StomachFullness	Stomach fullness scale
24	FullStomWgt	float(6)		Weight of stomach with prey
25	EmptyStomWgt	float(6)		Weight of stomach without prey
26	StomachEmpty	int(6)		Number of empty stomachs in the sample
27	GenSamp	char(1)	YesNoFields	Stomach content analysed using genetics - Yes or No
28	Notes	char(100)		Any additional information

Table 13. Prey information in the exchange format file.

Start	FieldCode	Datatype	Code List	Description
1	RecordType	char(2)		Record type
2	Ship	char(4)	SHIPC	SeaDataNet ship code
3	Gear	char(8)	SMTYP	Sampling gear used
4	HaulNo	int(6)		Haul number - sequential numbering by cruise
5	StationNumber	char(6)		Station number by national coding system
6	Year	char(4)		Year of the cruise
7	Month	int(2)		Month of the cruise
8	Day	int(2)		Day of the haul
9	Time	char(4)		Shooting time (UTC) (HHMM), 4 digits. E.g. 10:15=1015
10	FishID	char(20)		Unique fish identification number for predator
11	AphiaIDPredator	int(10)		WoRMS AphiaID Species reference code of predator
12	AphiaIDPrey	int(10)		WoRMS AphiaID Species reference code of prey
13	IdentMet	char(10)		Prey species identification method - Insert the identification method used according to ICES vocabulary METOA/SampleType
14	DigestionStage	int(1)	DigestionStage	Stage of digestion of prey items
15	GravMethod	char(5)	PARAM	Gravemetric method used
16	SubFactor	decimal4(9)		Subsampling factor - report 1 if the whole catch was analysed, or report a raising factor if only a part of the catch was analysed
17	PreySequence	int(10)		Unique prey sequence ID number
18	Count	int(8)		Number of prey
19	UnitWgt	char(6)	MUNIT	Unit of weight measurement
20	Weight	float(8)		Weight, individual or grouped
21	UnitLngt	char(6)	MUNIT	Unit of length measurement
22	Length	float(10)		Length of species
23	OtherItems	char(100)		Other items descriptor
24	OtherCount	int(10)		Number of other items
25	OtherWgt	float(6)		Weight of other items in grams
26	AnalysingOrg	varchar(6)	EDMO	EDMO code of the organisation in charge of analysing stomach samples
27	Notes	char(100)		Any additional information

ANNEX 3 DAPSTOM DATABASE

Table 14. Prey qualifier codes, used to differentiate different life stages.

Qualifier code	Qualifier description
Q1	None
Q2	Larvae
Q3	Elvers
Q4	Eggs
Q5	Adult
Q6	Adult-female
Q7	Adult-male
Q8	Copepodite
Q9	Copepodite 1-3
Q10	Copepodite 4-5
Q11	Nauplii
Q12	Pupae
Q13	Siphons (mollusc)
Q14	Ephyra
Q15	Nymphs
Q16	Imago
Q17	Megalopae
Q18	Juvenile
Q19	Cypris (barnacle)
Q20	Zoea
Q21	Parasite

Table 15. Assigned Taxonomic Serial Number (TSN) codes for prey items in the DAPSTOM database that were not available via the Integrated Taxonomic Information System (ITIS).

TSN code	Description
-99901	Empty
-99902	Regurgitated/everted
-99903	Unreadable
-99904	Unidentifiable/digested remains
-99905	Wood
-99906	Stones/rock
-99907	Sand/grit
-99908	Mud

TSN code	Description
-99909	Metal
-99910	Paper rubbish
-99911	Plastic rubbish
-99912	Fish-hooks
-99913	Unidentified benthic invertebrates
-99914	Other (unidentified) invertebrates
-99915	Unidentified invertebrate eggs

New datasets added to DAPSTOM in version 6.3

Data from 127 additional sampling campaigns were added to the database as part of this most recent update. Full details can be obtained by consulting the 'PROVENENCE' table within the database. Some datasets were derived from scientists logbooks or reports contained within the CEFAS archive, others were donated by 'partners' or were digitised from published peer-reviewed papers, with specific relevance to the British Isles.

Donated datasets include those provided by Adriaan Rijnsdorp (Wageningen Marine Research) as part of EU BENTHIS project (see Rijnsdorp & Vingerhoed 2001) and including cruises TRIDENS-01-1996, ISIS-01-1996, ISIS-02-1996, ISIS-03-1996 and U383-01-1996. An electronic dataset from the French EVHOE survey in the Celtic Sea (cruises THALASSA-2014 and THALASSA-2015) was made available by colleagues from the IFREMER laboratory in Lorient (see supplementary material in Marianne et al. 2022).

Recent datasets (2017-2023) include those collected as part of the annual Clean Seas Environmental Monitoring Programme (CSEMP), provided by Manuel Nicolaus and Freya Goodsir (CEFAS). These comprise data on dab stomach contents, collected at specific trawl localities around the North Sea coast (2017, 2019, 2021) or English Channel, Bristol Channel and Irish Sea (2018, 2020, 2023). In addition, stomach datasets for the northeast coast of England (dab and plaice) were provided by Georgina Hunt and resulted from a joint PhD between University of Newcastle and CEFAS (see cruise 'HUNT-2019') (Hunt 2021; Hunt et al. 2023). Data concerning pelagic fish species (anchovy, horse mackerel, sprat and sardine) were provided by Roweena Patel at University of Reading (cruise 'END15-19'), based on samples from CEFAS' PELTIC survey in October 2019 (Patel et al. 2023).

Historical datasets identified in the CEFAS archive and subsequently digitised include the following:

- Data digitised from spring-bound internal report found at Pinbush: Bellwood, D.R. (1978) The ecology of 1-group sole with particular reference to food and feeding. Industrial Training Report. Ministry of Agriculture, Fisheries & Food (MAFF), Directorate of Fisheries. 17pp.
- Data digitised from: Garrod, C. and Harding, D. (1981) Predation by fish on the pelagic eggs and larvae of fishes spawning in the west central North Sea in 1976. ICES CM 1981/L:11.
- Data digitised from: Last, J.M. (1979) The food of larval turbot Scophthalmus maximus L. from the west central North Sea. J. Cons. int. Explor. Mer, 38(3): 308-313.
- Data digitised from a folder full of raw data located during rationalisation of Pinbush. Also see: Macer, C.T. (1977) Some aspects of the biology of the horse mackerel [Trachurus trachurus (L.)] in waters around Britain. Journal of Fish Biology, 10: 51-62.
- Data digitised from: Pentelow, F.T.K., Southgate, B.A., Bassindale, R. (1933) II The proportion of the sexes and the food of smolts of salmon and sea trout in the Tees Estuary. Fishery Investigations, Series I., Vol III, Number 4, 11-14.

- Summary data digitised from a folder of Irish Sea records provided by Mike Armstrong (raw data lost; partially digitised in DAPSTOM 1.5 and 3.6).

Datasets digitised directly from published papers and reports included:

- Information on commercial fish species in the Norwegian Trench (Albert 1993; Albert 1994a,b; Albert 1995).
- Information on fish species from the Norwegian fjords and Skagerrak coast, both adults and larval fish (Bjorke 1976; Hop et al. 1992; Mattson 1981; Mattson 1990; Mattson 1992; Nedreaas 1985; dos Santos & Falk-Petersen 1989; Fjøsne & Gjøsæter 1996; Sunnana 1984).
- Information on commercial fish species around the Faroe Islands (Magnussen 2011; Jacobsen & Hansen 1996; Rae 1967b; Hislop & Youngson 1984).
- Information on fish species around Scotland – mostly taken from reports of the Department of Agriculture and Fisheries for Scotland (Ogilvie 1927; Ogilvie 1938; Rae 1956; Rae 1967; Rae & Shelton 1982; Daly et al. 2001; Mendonca et al. 2007; Sarno et al. 1994; Sayer et al. 1995; Robb & Hislop 1980; Robb 1981; Economou 1991; Klimpel et al. 2003).
- Information on freshwater fish species in Scotland, Wales, Ireland and England (Adams & Maitland 1998; Ferguson & Mason 1981; Pentelow 1932; Arawomo 1981; Garner 1996; Garner 1996; Hutchinson 1983; Mann et al. 1997; Pentelow 1933; Maitland 1965; Sinha, & Jones 1967; McGoran et al. 2016; Carpenter 1940; Jones 1951; Dunn 1954; Ball 1961; Graham & Jones 1962; Weatherly 1987; Hellawell (1971, 1972, 1974)).
- Flatfish and inshore species in the North Sea, especially off the Netherlands and French coast (Thijssen et al. 1974; Wetsteijn 1981; Beyst 1999; Daan 1973; De Grooy 1971; Lagardere 1987; Maes & Ollevier 2002).
- Elasmobranchs in the Irish Sea and North Sea (Ajayi 1982; Holden 1966; Holden & Tucker 1974; Lyle 1983).
- Miscellaneous inshore coastal fish in Wales, SW England, Scotland and Ireland (Seisay 2001; Rogers, 1991; Berg 1979; Badsha & Sainsbury 1978; Daly et al. 2001; Deady & Fives 1995a,b; Tully & O Ceidigh 1989; Liao 1999; Menon 1950).
- Stomach contents of immature bluefin tuna in the Bay of Biscay (Ortiz de Zärate & Cort 1986).

New predator species added in this iteration include four freshwater fish species that are endemic to the British Isles, namely: the Gwyniad (*Coregonus pennantii*), Ferox trout (*Salmo ferox*), Sonaghen (*Salmo nigripinnis*) and Gillaroo (*Salmo stomachicus*), as well as Vahl's eelpout (*Lycodes vahlii*) and chub (*Squalius cephalus*). The primary source materials for these new additions were the following:

- Gwyniad [WALES-1951, WALES-1952, WALES-1961, WALES-1962] from Dunn (1954) and Haram & Jones (1971), Llyn Tegid (Bala Lake), Merionethshire, Wales.
- Ferox trout, Sonaghen and Gillaroo [FERGUSON-1981] from Ferguson & Mason (1981), Lough Melvin, Ireland.
- Vahl's eelpout [ALBERT-1987A] from Alber (1993) in the Norwegian Deep.
- Chub [GARNER-1993, GARNER-1994, HELLAWELL-1964], from Garner (1996) and Hellawell (1971, 1972, 1974), River Great Ouse, England.

Table 16. Number of records and stomachs examined, by geographic area.

Sea	ICES Sub-Areas	Records	% Records	Stomachs	% Stomachs
Baltic	IIId (22, 24, 25, 26, 28)	628	0.2	3683	0.8
Barents Sea	Ib	3127	1.1	2662	0.6
Biscay	VIIIa-d	2067	0.7	1690	0.4
Bristol Channel	VIIf	2887	1.0	6959	1.4
Celtic Sea	VIIg-j	24796	8.8	21095	4.4
Channel	VIId,e	11654	4.1	30982	6.43
E Greenland	XIVa,b	3154	1.1	1288	0.3
Faroes	Vb	3106	1.1	7452	1.5
Freshwater	NA	7370	2.6	31567	6.5
Iceland	Va	2253	0.8	1474	0.3
Irish Sea	VIIa	30353	10.7	45703	9.5
Skagerak & Kattegat	IIIa + IIIb (21, 23)	2436	0.9	7638	1.6
North Atlantic	XII	18	0.0	9	0.0
North Sea	IVa,b,c	149545	52.8	253679	52.6
Norwegian Sea	IIa	7155	2.5	15376	3.2
Spitzbergen	IIb	25582	9.0	19229	4.0
W Ireland	VIIb,c	2791	1.0	15541	3.2
W Scotland	VIa	3782	1.3	16373	3.4
Labrador	NAFO 2 (2H, 2J)	417	0.1	298	0.1

ANNEX 4 BALTIC COD DIET - MODEL

The spatiotemporal models are predictive-process generalised-linear mixed models with spatial and spatiotemporal random effects. These random effects are assumed to be drawn from a Gaussian random field, constrained by a Matérn covariance function. The random fields are approximated using a triangulated mesh and the SPDE approach. Specifically, the random effects are estimated at the vertices ('knots') of this mesh and bilinearly interpolated to the data locations. We set up the mesh to have a minimum allowed distance between points in the mesh of 6 km for the diet model and 15 km for the biomass density model.

The spatiotemporal diet model can be written as follows:

$$\mathbb{E}[y_{s,t}] = \mu_{s,t},$$
$$\mu_{s,t} = f^{-1}\left(X_{s,t}^{\mathrm{main}}\beta + X_{s,t}^{\mathrm{tvc}}\gamma_t + \omega_s\right) \quad \text{(A1)}$$

where $y_{s,t}$ is the feeding ratio of cod (weight of prey divided by weight of cod) in unit kg/kg at point s and time t; μ is the mean and f is a link function; X^{main} and X^{tvc} are design matrices for main (*main*) and temporally varying coefficients (*tvc*); β is vector of fixed-effect coefficients; γ_t is a vector of time-varying intercepts; ω_s is a spatiotemporal random field, $\omega_s\sim$MVN($\mathbf{0},\mathbf{\Sigma}_\omega$); and we use a Tweedie distribution with a log link function.

The species distribution model of Baltic cod follows a similar structure:

$$\mathbb{E}[y_{s,t}] = \mu_{s,t},$$
$$\mu_{s,t} = f^{-1}\left(X_{s,t}^{\mathrm{main}}\beta + X_{s,t}^{\mathrm{svc}}\zeta_s + \epsilon_{s,t}\right) \quad \text{(A2)}$$

where $y_{s,t}$ is the biomass density of cod in unit kg/km^2 at point s and time t; μ is the mean and f is a link function; X^{main} and X^{svc} are design matrices for main (*main*) and spatially varying coefficients (*svc*); β is vector of fixed-effect coefficients; ζ_s is a spatially varying coefficient (a random field), $\zeta_s\sim$MVN($\mathbf{0},\mathbf{\Sigma}_\zeta$); $\epsilon_{s,t}$ is a spatiotemporal random field, $\epsilon_{s,t}\sim$MVN($\mathbf{0},\mathbf{\Sigma}_\epsilon$); and we use a delta-model approach (binomial, gamma) with a logit and log link function.
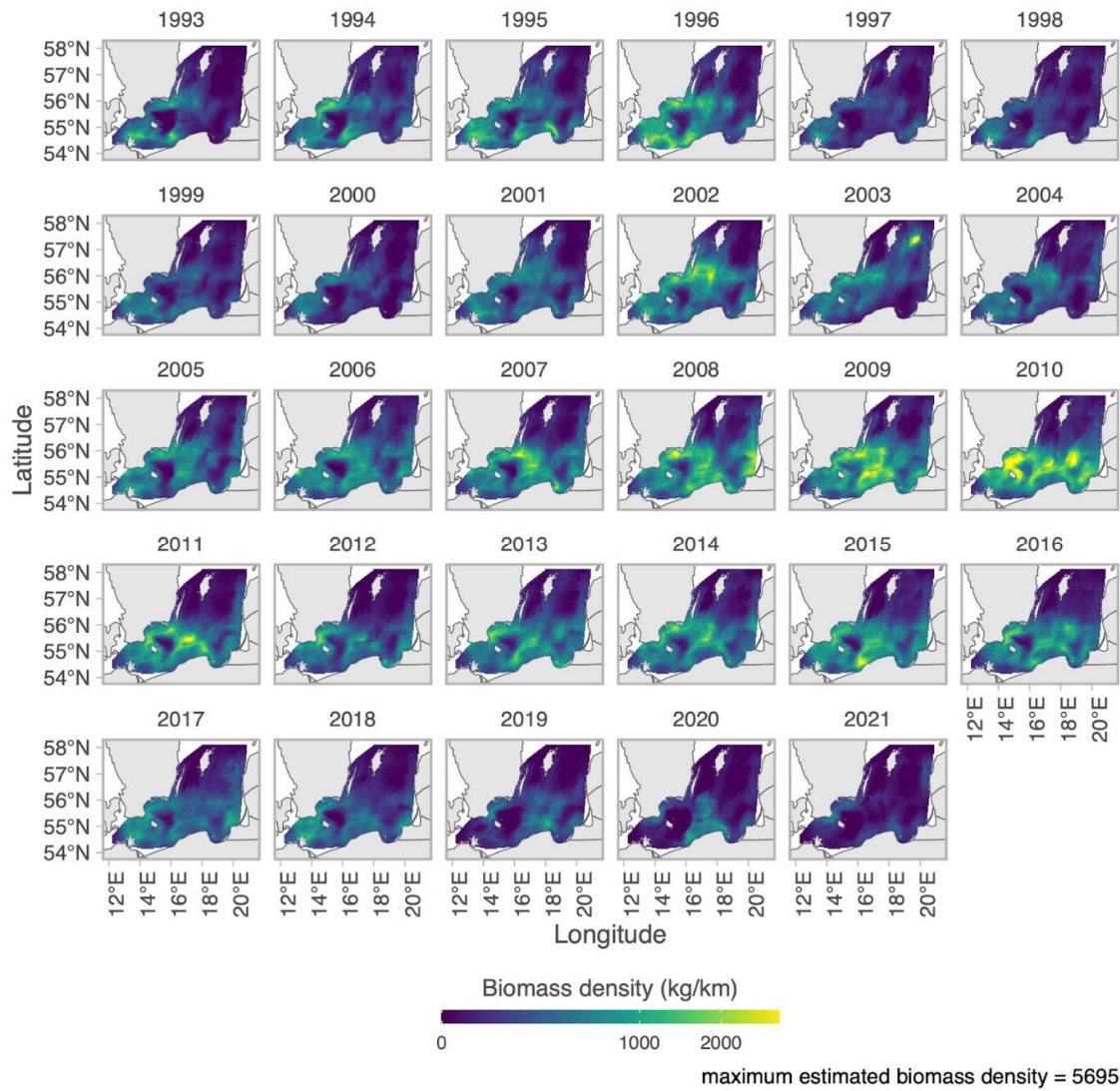
Figure 39. Predicted biomass density of cod in the Baltic Sea from the spatiotemporal species distribution model, by year.
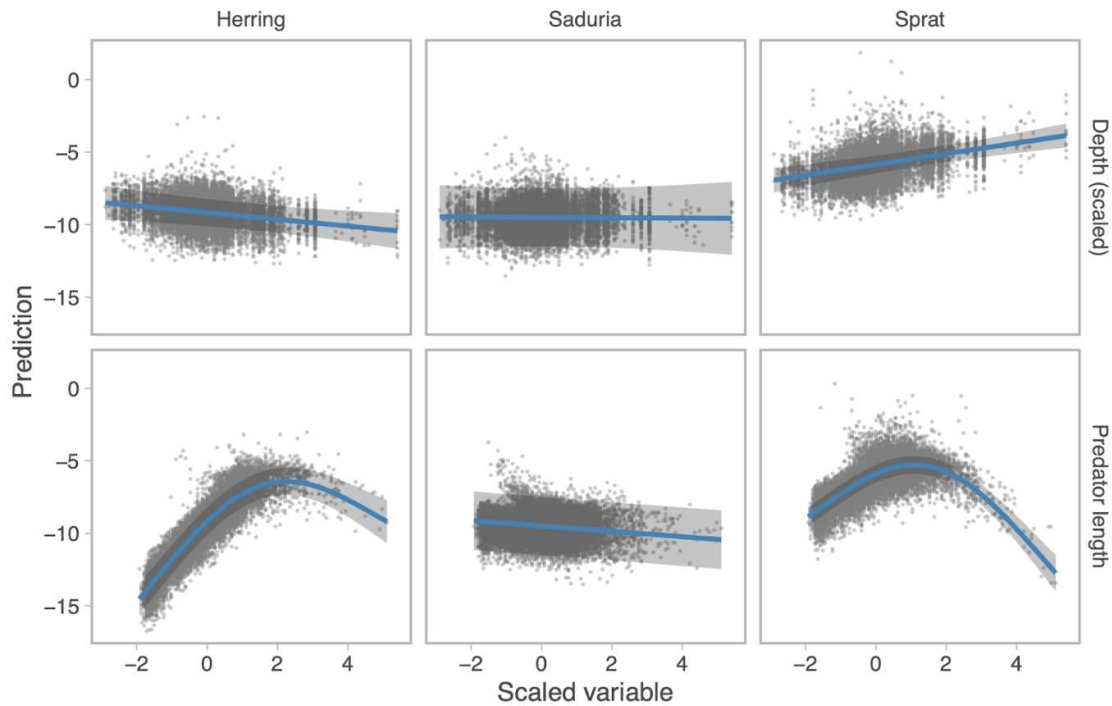
Figure 40. Conditional effects of covariates depth (linear) and predator length (spline) on the feeding ratio (per capita) on the log link scale.
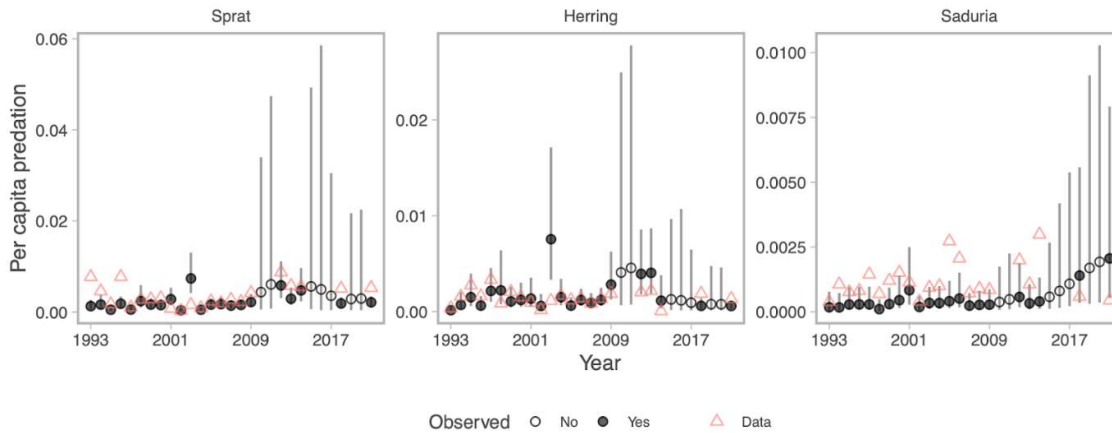

Figure 41. Spatially-averaged per capita predation by cod on sprat, herring and *saduria,* by year. Black circles depict the predicted per capita predation, red open triangles are data means (calculated after removing values larger than the 99th percentile) and the vertical lines depict the 95% confidence interval. Open circles are years without data, where the prediction is interpolated from the spatially varying intercepts following a random walk. The discrepancy between data and prediction that is evident mainly in *saduria* is due to the model's inability to capture the extreme values.
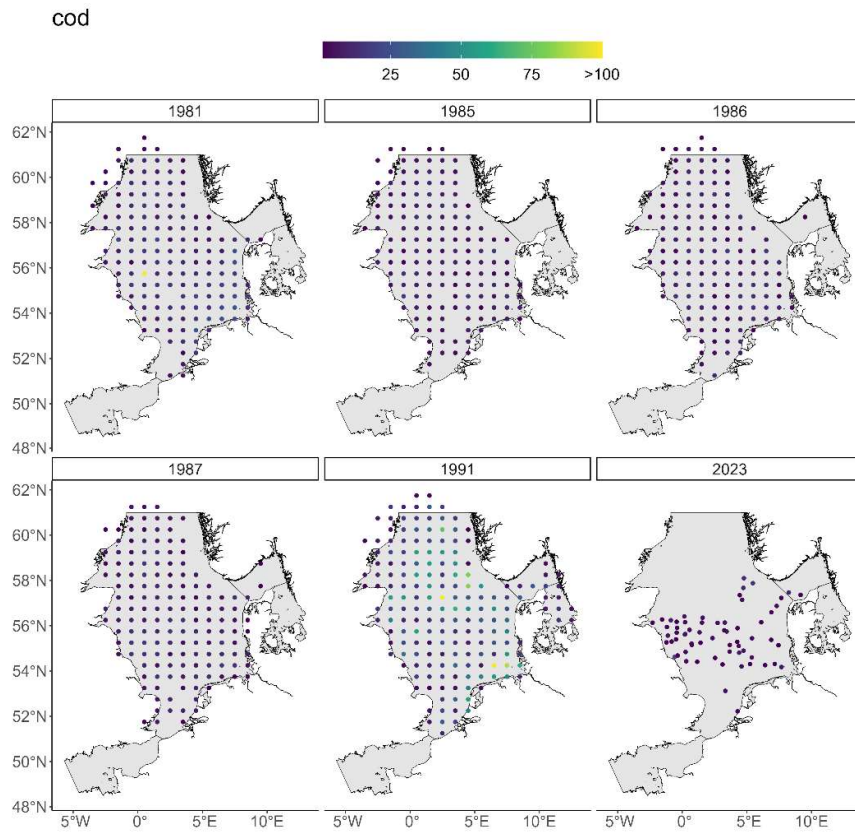
Distribution of samples from SMS predators.

cod

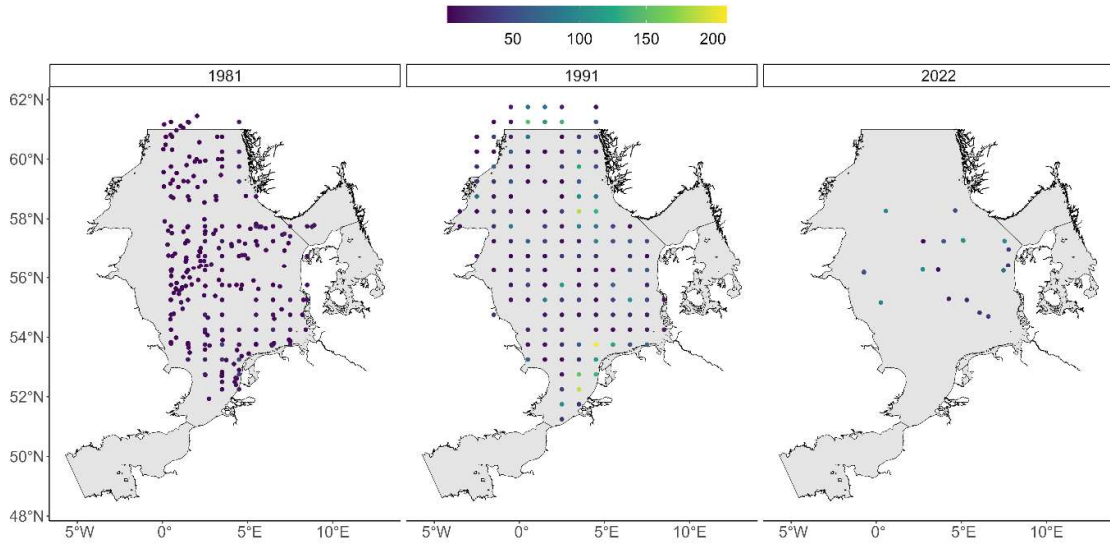**Figure 42. Distribution of cod stomach samples in SMS and the newly analysed data (2023).**

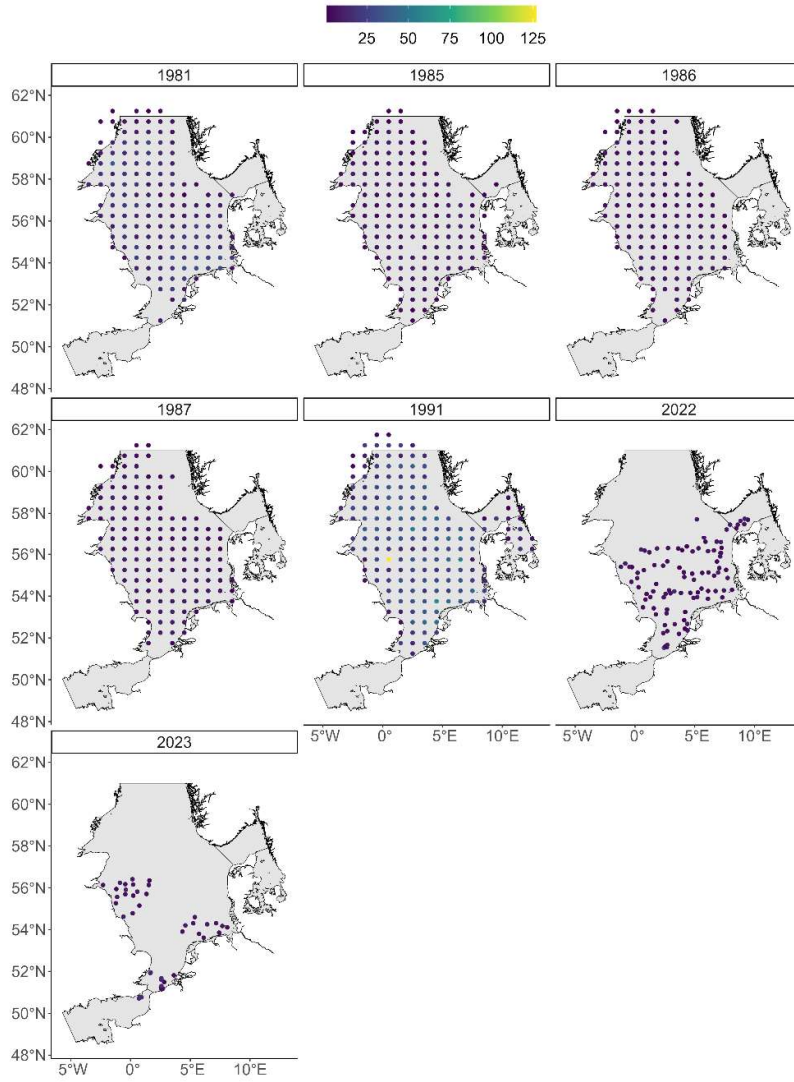**Figure 43. Distribution of mackerel samples from SMS (1981, 1991) and the new samples (2022).**

Figure 44. Distribution of whiting samples from SMS and the newly collected samples (2022 and 2023).

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