



ELSEVIER

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Diet and trophic structure of fishes in the Barents Sea: The Norwegian-Russian program “Year of stomachs” 2015 – Establishing a baseline

Elena Eriksen^{a,*}, Aleksander N. Benzik^b, Andrey V. Dolgov^b, Hein Rune Skjoldal^a, Mikko Vihtakari^a, Edda Johannesen^a, Tatiana A. Prokhorova^b, Felicia Keulder-Stenevik^a, Irina Prokopchuk^b, Espen Strand^a

^a Institute of Marine Research, Bergen, Norway

^b Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography (PINRO), Murmansk, Russia

ARTICLE INFO

Keywords:

Fish diet

The Barents Sea

Trophic interactions

Food-web

Warming

ABSTRACT

There is a long history of investigations of fish diet in the Barents Sea. The focus has been on commercially important fish species and their food consumption, while diet and interactions of other fishes have been studied only sporadically. In 2015, a large-scale stomach sampling program was carried out for fish species caught on routine monitoring surveys in the Barents Sea during different seasons of the year, supplemented with samples collected from Russian commercial fisheries. A total of 27,657 stomachs from 70 fish species (including two genera) were analysed, providing a baseline on fish diet in the Barents Sea which can serve as a reference for future studies related to climate change. We summarize methodological aspects and diet composition for the studied species. Cluster analysis grouped the fishes in nine trophic groups based on similarities in diet among fish species, while principal component analyses revealed the position of the species and trophic groups along axes reflecting degrees of piscivory, planktivory, and benthivory. The three most distinctly separated groups were piscivores, a group of benthivores feeding on polychaetes, and planktivores feeding on small crustaceans. The latter could be further split into two groups: fishes of Atlantic origin feeding on copepods and euphausiids, and fishes of Arctic origin feeding on hyperiid amphipods. Warming in the Barents Sea were associated with redistribution of water masses, species and increasing biomass of krill and jellyfish. A boreal *Meganyctiphanes norvegica*, not observed in the northern Barents Sea before, were found in diet of three Arctic fishes (2% of stomachs only). Gelatinous plankton, mainly Ctenophora, were observed in the diet of 1430 individuals from 15 fish species, including two species which have not been reported to eat gelatinous plankton in the Barents Sea before. This work updates our knowledge about trophic structure and interactions in the Barents Sea, providing a baseline for further investigations.

1. Introduction

The Barents Sea food web is often considered to be rather simple and dominated by interactions between a few very abundant species. However, there are more than 3000 species of benthos, hundreds of species of zooplankton, more than 200 species of fish, many species (25–30) of sea birds and marine mammals, as well as a many other coastal and marine birds (ducks, geese, and shorebirds) (Jakobsen and Ozhigin, 2011). The high diversity of species represents complexity, which poses a challenge when representing the food webs of the Barents Sea ecosystem in conceptual or other types of models.

The Barents Sea ecosystem is located at high latitudes but is yet productive and supports important fisheries with an annual catch of

1.5–3 million tonnes in recent decades (Hunt et al., 2013; ICES 2019). Fish biomass is dominated by 10–12 species, among them are the most important commercially exploited species such as Atlantic cod *Gadus morhua*, capelin *Mallotus villosus*, haddock *Melanogrammus aeglefinus*, and herring *Clupea harengus*. Because of its importance for fisheries, there have been extensive scientific studies of fish stocks and the environment of the Barents Sea ecosystem for more than 100 years, including joint Norwegian-Russian investigations for now more than 60 years (Jakobsen and Ozhigin, 2011). Monitoring changes in fish stocks and collecting information needed for stock assessments and advice for fisheries management have been the driving forces for the large effort spent on monitoring and research in the Barents Sea (Eriksen et al., 2018).

* Corresponding author at: Postboks 1870 Nordnes, 5817 Bergen, Norway.

E-mail address: elena.eriksen@hi.no (E. Eriksen).

<https://doi.org/10.1016/j.pocean.2019.102262>

Received 22 March 2019; Received in revised form 22 November 2019; Accepted 30 December 2019

Available online 03 January 2020

0079-6611/ © 2020 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Diet investigations of commercially important fishes in the Barents Sea were initiated in the 1920's-30's by Soviet scientists (e.g. Idelson, 1929; Zenkevich and Brotskaya, 1931; Zatsepin, 1939; Zatsepin and Petrova, 1939) and others (Brown and Cheng, 1946), and continued during the 1950–60s (e.g. Grinkevich, 1957; Sysoeva, 1958; Ponomarenko, 1958). Details on Russian/Soviet publications on fish diet in the Barents Sea are provided in Dolgov et al. (2007) and Dolgov (2016). Great Britain also had stomach sampling as part of their monitoring when they had substantial fishing activity in the Barents Sea during the period 1930–1960 (Townhill et al., 2015). For some time after the 1960s, studies of fish feeding in the Barents Sea were less intensive and mainly concerned qualitative diet analyses (e.g. Ponomarenko et al., 1978; Ponomarenko and Yaragina, 1985, 1990; Yaragina and Dolgov, 2011). In addition, some occasional investigations of diet of non-target fishes were conducted in the 1930s and 40s (e.g. Briskina, 1939; Bulycheva, 1948) and in the 1970s and 80s (e.g. Falk-Petersen et al., 2018; Chernova, 1989; Berestovsky, 1989). Trophic investigations demonstrated the complexity of species interactions, with considerable local, seasonal and inter-annual feeding variation in most fish species (Dolgov, 2016).

A broad-scale and long-term sampling program of quantitative diet data from cod in the Barents Sea was initiated in 1984 by the Institute of Marine Research (IMR, Norway) and extended as a joint program with the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia) in 1986. The main aims were to support stock assessments by providing input data for estimating the consumption of, and predation mortality on, capelin, haddock, and cod, and to develop mathematical models of the Barents Sea fisheries and marine ecosystem (e.g. Tjelmeland and Bogstad, 1989; ICES, 2018). Also, the data has been used to identify changes in cod diet, reflecting underlying changes in the ecosystem (e.g. Mehl and Yaragina, 1992; Bogstad et al., 2000; Dolgov et al., 2007; Johannesen et al., 2012a, 2015). Alongside the quantitative cod stomach sampling program, PINRO has continued to sample diet data from other commercial and non-commercial fishes. This broad-scale and long-term sampling has provided a unique insight into the composition, structure and dynamics of pelagic and demersal fish communities in the Barents Sea (Dolgov, 2016). Stomach sampling was extended to capelin (in 2006) and polar cod (in 2007) and since carried out annually during the joint Barents Sea ecosystem survey (BESS) (Eriksen et al., 2018; Eriksen and Gjørseter, 2013).

Dolgov et al. (2007, 2011a, 2011b, 2011c, 2011d) described the joint investigations of fish diet and presented results on diet composition for many fish species and trophic groups. Important messages from this work were that: (1) the diets for the various fish species are generally diverse with many different types of food (species or groups) eaten as an aggregated average for a species, (2) there are considerable ontogenetic shifts in diet composition as fish grow from small to large individuals; and (3) there are considerable interannual variation and changes in diet over time (years and decades), reflecting changes in the ecosystem.

Planque et al. (2014) published a food web topology based on previously published studies. This was a data paper which provides both an overview (as a bibliography) and a detailed compilation of information on diet of fish species and other organisms from the large body of published and other sources of information. The information is qualitative in the sense that it records the presence of taxa in the diet of other species but not the quantitative diet composition (which is difficult to compare across studies).

The work presented here is part of the project “Trophic interactions in the Barents Sea - steps towards an Integrated Ecosystem Assessment (TIBIA)” aimed at increasing the knowledge of trophic interactions, food web structure and function, and energy flow in the Barents Sea ecosystem. The project has included studies of spatial and temporal patterns of primary production (using satellite-based information) and zooplankton biomass (Dalpadado et al., this volume), patterns of stable isotopes (C and N) across a wide range of species from the pelagic and

benthic realms with a focus on pelagic-benthic coupling in fish diet studies (reported here), and a special study on trophic relationships for Atlantic cod as a key species in the ecosystem (Johannesen et al., 2015).

The motivation for the study on fish diet which we report here, was to obtain updated and extended information on trophic relationships for fish communities in the Barents Sea including both commercially important and other non-commercial species. The work is based on data collected during an extensive fish stomach sampling program carried out by IMR and PINRO in 2015, in what we have dubbed ‘Year of the stomach’ (the notion stems from a sampling program in the North Sea in the 1980s; <http://ecosystemdata.ices.dk>). This is a snapshot in time, although a very extensive one with a total of 27,627 stomachs sampled from 70 fish species (including 2 genera) representing 24 families. The samples have been collected and processed according to standardized protocols by trained scientific personal. The data set is therefore internally consistent and comparable.

The 2015 ‘snapshot’ serves two main purposes which are also our main objectives for this study. The first is to provide a baseline on fish diet in the Barents Sea ecosystem. The Barents Sea is an ecosystem undergoing substantial changes due to warming and the associated processes referred to as ‘atlantification’ (Johannesen et al., 2012a) and ‘borealization’ (Fossheim et al., 2015). The 2015 baseline data set can therefore serve as a reference in time for future changes in fish communities and fish diets, as well as for evaluating changes in the past leading up to the 2015-situation.

The second objective is to construct a conceptual model of the trophic structure of the fish component of the Barents Sea ecosystem. The ‘snapshot’ character and the standardised nature of the data set is in one respect an advantage by providing a ‘frozen’ picture of the situation in one given year, 2015, reflecting a warm period in the Barents Sea. It must be recognized that this is not a sharp and ‘high-pixel’ resolution picture but rather a blurred and coarse picture by its nature. There are several reasons for this. While the data set is large, it is still limited with few stomach samples for many of the fish species (as we describe in the Material and methods). We also know that there are clear ontogenetic shifts in diet over the life span of species, as well as substantial seasonal changes. These aspects are partly resolved in the 2015 data set, but the results are treated elsewhere (seasonal and spatial patterns in this volume). Here, we use data at the species level, averaged over the size range of individuals and seasons included in the sampling for each species. The average diet and trophic position of a species are integrated and thereby hiding the considerable variability among individuals within a species. This is a drawback, but nevertheless a common and often necessary practice in ecosystem synthesis and modelling work.

In this paper we describe general patterns based on quantitative analysis of diet for 55 fish species (including two genera) which are classified using multivariate statistics in order to identify and characterize the main trophic groups across the species. We discuss the species diet and trophic structure of the fish community in light of earlier findings. The warming in the Barents Sea in recent decades was associated with changes in distribution of water masses and species, and the increased biomass of krill and jellyfish (Eriksen et al., 2016, 2017). We, therefore, studied (1) diet of nine Arctic species in the arctic part of the Barents Sea in terms of the occurrence of new boreal prey species in the diet and (2) occurrence of gelatinous plankton in the fish diet. We discuss some methodological aspects related to the data set and provide general description of our data set and the 2015 baseline as reference for future investigations of changes in the Barents Sea ecosystem. Through this paper we make the data set available to the scientific community ([data link](#)).

Table 1

Total number of individual fish stomachs collected, number of fish species sampled, and number of sampling stations by survey for the 2015 fish diet sampling program. The species number includes two genera for which fish could not be identified to the species level.

Survey	Sampling stations	Species sampled	Individuals sampled
NO-RU winter survey	216	30	5010
IESNS	31	14	1201
TIBIA	15	19	319
BESS	347	63	9356
RU-BOT	240	42	10,450
RU-COM	42	5	1291
Total	891	70	27,627

2. Material and methods

2.1. Fish sampling

Data on fish diet were collected during six research surveys in the Barents Sea in 2015, supplemented by samples from catches of Russian commercial vessels (Table 1, Fig. 1). Stomach samples were taken from catches of fish with pelagic and bottom trawls, based on the availability of species, and processed by trained and experienced scientific personnel.

A Norwegian-Russian (NO-RU) winter survey is run in January–March and is a combined acoustic and bottom trawl survey to obtain data on abundance, and length and weight at age for demersal fish species. The survey has been carried out each year since 1981, with a duration of 4–6 weeks and with a typical effort of the combined survey of 10–14 vessel-weeks. About 350 hauls with a “Campelen” shrimp bottom trawl have been made each year (Mehl et al., 2016).

The summer international ecosystem survey for the Nordic Seas (IESNS) is run in April–June each year and is an international multi-ship survey which includes the southern part of the Barents Sea to estimate the total biomass of the Norwegian spring-spawning herring stock (Eriksen et al., 2018). Additionally, data on plankton and hydrographical conditions in the area have been recorded. The southern Barents Sea was covered by a Russian vessel in 2015.

A summer TIBIA survey (TIBIA) was conducted in the period 27 May–6 June 2015 with the research vessel “Johan Hjort”. During the survey both pelagic “Harstad” and “Campelen” bottom trawls were used to collect fish samples. The survey report is available at https://www.hi.no/hi/publikasjoner/toktrapporter/2015/survey_report_tibia_2015.

The Barents Sea ecosystem survey (BESS) has been carried out in August–September (starting in 2004) jointly by IMR and PINRO. BESS provides simultaneous observations of hydrography, plankton, benthos, fish, seabirds and marine mammals (Michalsen et al., 2013; Eriksen and Gjørseter, 2013; Michalsen et al., 2011). The timing of BESS allows widest possible coverage of the whole Barents Sea shelf by research vessels, since sea-ice is at its seasonal minimum. Pelagic and demersal fish have been sampled with pelagic “Harstad” trawl and “Campelen” bottom trawl, respectively (Prozorkevich and Sunnanå, 2016).

A Russian bottom survey (RU-BOT) has been run in October–December since the 1980s as a trawl-acoustic survey for the assessment of juvenile fish and estimating of abundance indices of the main commercial Barents Sea fish stocks. The survey has covered a large part of the Barents Sea excluding the north-eastern areas. Trawling is carried out on regular stations and on echo registration by using the Russian bottom trawl type 2283-02.

Russian commercial vessels (RU-COM) were used for sampling biological data on commercially important demersal fishes by PINRO scientific observers. Stomach contents were analysed onboard (usually 25 fish of different length groups were randomly chosen from the

catch). In addition, some stomachs (usually 25 stomachs from one station) were frozen and transferred to PINRO for further laboratory analysis. Stomachs were sampled between June and October in rather restricted local fishery areas in the western, central and southeastern Barents Sea.

2.2. Sample processing

During the BESS and the NO-RU-winter surveys, fish samples were taken with pelagic and bottom trawls. They were processed quickly after retrieval, and stomachs were generally analysed immediately after the trawl samples were sorted. Fish samples for investigation of trophic interactions were taken based on availability of fish species in the trawl catch, and 10 individuals per fish species were selected, representing the length distribution in the catch. To be able to analyse many stomachs, samples from fish larger than 12 cm were processed on board, while smaller fish were frozen and stomach analyses were done in the laboratory. Length (down to nearest ½ cm), weight (down to nearest 1 g) and sex were recorded for all specimens. Stomachs were analysed individually for all samples. Sampling of cod on Joint IMR-PINRO surveys followed the standard sampling protocol (see Johannesen et al., 2015). The total content of a sampled stomach was weighed, and the content was split according to prey species or groups when identifiable. The weight and the degree of digestion (from 1: newly eaten to 5: digested and not identifiable) of the different prey items were recorded. Length measurements were taken of prey species that could be identified and when the length was unaltered due to a low degree of digestion.

Stomach data were also sampled onboard of Russian commercial vessels. 25 stomachs for each fish species were randomly selected and analysed from 1 trawl haul per 1–3 days (Dolgov et al., 2007). Additionally, fish length, weight, sex and maturity stage were recorded. Data from the commercial fisheries were more spatially and temporarily limited and related to commercial fleet locations. During the Russian commercial fishery, some cod stomachs were examined, and the prey were identified on board the ship immediately, while other stomachs were frozen and later examined in the lab. Data on total stomach content (g), prey composition (% from stomach content weight) and prey length and number were recorded.

2.3. The data set

Stomachs were collected from 68 species and 2 genera (*Iceland* and *Careproctus*) of fish from 24 families (Table 2). The most common families with 8 species each, were cods (Gadidae), righteye flounders (Pleuronectidae), and eelpouts (Zoarcidae). Nine families were represented by one species only (Supplementary material 1_1; SM1_1).

The number spans from a maximum of 11,557 stomachs for cod to only one stomach for 7 species (*Lampanyctus macdonaldi*, *Phycis blennoides*, *Lycodes polaris*, *Anisarchus medius*, *Lumpenus fabricii*, *Glyptocephalus cynoglossus*, *Hippoglossus hippoglossus*). Of these seven species, two had empty stomachs and provided no information on diet (*Lampenus fabricii*, and *Hippoglossus hippoglossus*), as did also not *Gasterosteus aculeatus*.

After cod, six species had the highest number of samples with more than 900 stomachs each: haddock, Greenland halibut *Reinhardtius hippoglossoides*, capelin, long-rough dab, deepwater redfish *Sebastes mentella*, and polar cod (Supplementary material 1_2; SM1_2). The 7 most common species together made up 83.5% of the stomach samples.

Size groups were defined based on fish length: 2 cm intervals up to 20 cm, 5 cm intervals from 20 to 40 cm, 10 cm intervals from 40 to 100 cm, and 30 cm intervals from 100 to 160 cm (Supplementary material 1_3; SM1_3). There were only two individuals (0-group saithe) in the smallest size group (0–2 cm), and 15 individuals (cod) in the largest group (130–160 cm). More than 30 fish species were represented in the size groups between 8 and 18 cm and 20–25 cm.

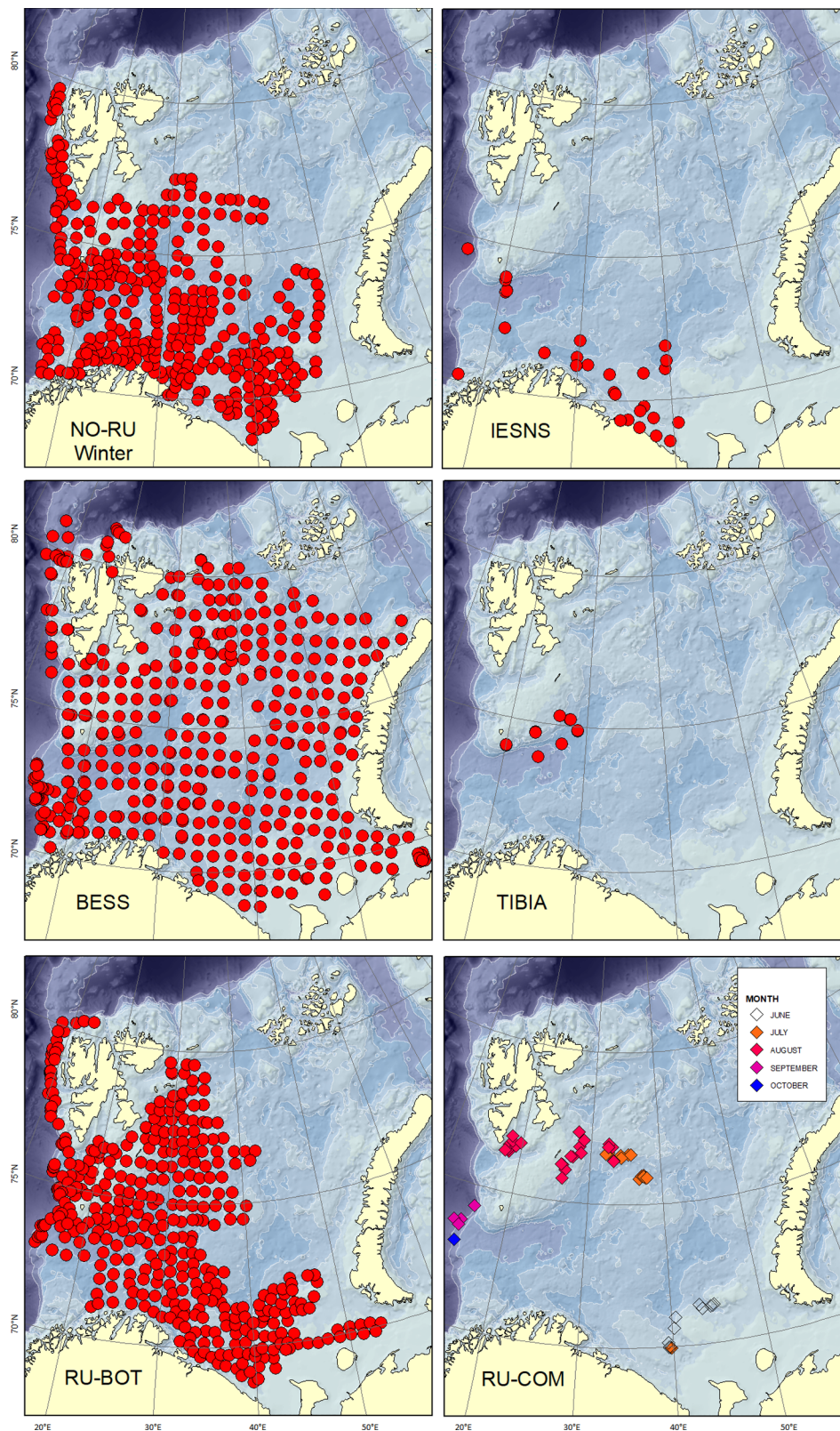


Fig. 1. Sampling stations for fish stomach data during the different surveys in 2015. The NO-RU Winter Survey was conducted in the first quarter of the year, the annual IESNS survey and the TIBIA survey were run in the 2nd quarter, the annual BESS in the 3rd quarter, and the RU winter survey (RU-BOT) was run in the 4th quarter. The Russian commercial data (RU-COM) was obtained during the 2nd, 3rd and 4th quarters.

The number of stomachs analysed and the number of fish species for six biogeographic groups (Arctic, mainly Arctic, Arcto-Boreal, boreal, mainly boreal, and widely distributed, see [Table 1](#)) are presented in [Supplementary material 1_4 \(SM1_4\)](#). The Arctic, mainly Arctic, and

Arcto-Boreal groups comprised a total of 31 species (13, 3, and 15, respectively). The boreal and mainly boreal groups comprised 35 species (16 and 19, respectively), while only two species were classified as widely distributed. The number of stomachs varied between the groups:

Table 2
List of 68 species and 2 genera of fish collected during the stomach sampling program in 2015. Length is maximum length taken from the literature and length for analysed fish is mean with range from minimum to maximum in parenthesis. Total number of stomachs and number and percentage of empty stomachs are presented. Biogeographical classification and habitat follow Mecklenburg et al. (2018). Species with < 5 stomachs with food (*) were excluded from further analysis.

Scientific name	English name	Family	Biogeography	Abbreviation	Habitat	Length (cm)	Fish length, mean (min;max)	Total N stomach	Total N empty stom.	% empty stom.
<i>Amblyraja hyperborea</i>	Arctic skate	Rajidae	Arctic	Amb_hypp	Benthic	106	54 (16; 71)	4	4	24
<i>Amblyraja radiata</i>	Thorny skate	Rajidae	Mainly boreal	Amb_rad	Epi-Mesobenthic	105	44 (11; 61)	59	59	20
<i>Bathyraja spinicauda</i>	Spintail ray	Rajidae	Mainly boreal	Bat_spi	Meso-benthic	182	77 (30; 149)	10	4	40
<i>Rajella fyllae</i>	Round ray	Rajidae	Boreal	Raj_fyl	Benthic	72	41 (11; 51)	15	2	13
<i>Clupea harengus</i>	Herring	Clupeidae	Mainly boreal	Clu_har	Pelagic	45	25 (9; 39)	415	313	75
<i>Clupea pallasi sworowi</i>	Chosa herring	Clupeidae	Arctic-boreal	Clu_swu	Pelagic	30	20 (17; 23)	35	13	37
<i>Argentina silus</i>	Greater argentine	Argentiniidae	Boreal	Arg_sil	Mesopelagic-Mesobenthopelagic	70	34 (16; 50)	105	41	39
<i>Mallotus villosus</i>	Capelin	Osmeridae	Arctic-boreal	Mal_vil	Pelagic	25/20	14 (5; 19)	2117	1039	49
<i>Osmerus dentex</i>	Arctic smelt	Osmeridae	Arctic-boreal	Osm_den	Benthic	34	18 (16; 22)	77	15	19
<i>Arctozenus risso</i>	White barracudina	Paralepididae	Widely distributed	Arc_ris	Pelagic	30	26 (19; 31)	9	2	22
<i>Lampanyctus macdonaldi*</i>	Rakery beaonlamp	Myctophidae	Widely distributed	Lam_mac	Mesopelagic	16	9 (9; 9)	1	0	0
<i>Macrourus berglax</i>	Rough-head grenadier	Macrouridae	Mainly boreal	Mac_ber	Benthopelagic	110	25 (12; 62)	13	4	31
<i>Brosme brosme</i>	Tusk	Lotidae	Boreal	Bro_bro	Benthopelagic	120	35 (10; 63)	22	13	59
<i>Enchelyopus cimbrius*</i>	Fourbeard rockling	Lotidae	Boreal	Enc_cim	Epi-mesobenthopelagic	42	23 (21; 27)	4	1	25
<i>Gaidropsarus argentatus*</i>	Arctic rockling	Lotidae	Arctic-boreal	Gai_arg	Benthopelagic	45	24 (13; 33)	4	0	0
<i>Physicis biennoides*</i>	Greater forkbeard	Physicidae	Boreal	Phy_dle	Benthopelagic	110	23 (23; 23)	1	0	0
<i>Boreogadus saida</i>	Polar cod	Gadidae	Arctic	Bor_sai	Cryopelagic	32	14 (4; 26)	902	293	32
<i>Eleginus nawaga</i>	Nawaga	Gadidae	Arctic	Ele_naw	Demersal	42	19 (14; 27)	175	68	39
<i>Gadialius argenteus thori</i>	Silvery pout	Gadidae	Boreal/temporate	Gad_arg	Benthopelagic	15	11 (7; 16)	9	9	16
<i>Gadus morhua</i>	Atlantic cod	Gadidae	Mainly boreal	Gad_mor	Demersal	200	58 (4; 143)	2587	22	22
<i>Melanogrammus aeglefinus</i>	Haddock	Gadidae	Mainly boreal	Mel_aeg	Epibenthopelagic	112	41 (6; 83)	3316	789	24
<i>Micromesistius poutassou</i>	Blue whiting	Gadidae	Mainly boreal	Mic_pou	Epi-mesobenthopelagic	50	24 (14; 42)	460	178	39
<i>Pollachius virens</i>	Saithe	Gadidae	Boreal	Pol_vir	Pelagic benthopelagic	130	56 (2; 112)	166	56	34
<i>Trisopterus esmarkii</i>	Norway pout	Gadidae	Boreal	Tri_esm	Benthopelagic pelagic	35	17 (10; 24)	119	12	10
<i>Gasterosteus aculeatus*</i>	Three-spined stickleback	Gasterosteidae	Mainly boreal	Gas_acu	Benthopelagic	11	8 (5; 10)	4	4	100
<i>Lophius piscatorius*</i>	Anglerfish	Lophidae	North Atlantic	Lop_pis	Benthic	200	15 (11; 19)	2	0	0
<i>Sebastes mentella</i>	Deepwater redfish	Sebastidae	Mainly boreal	Seb_men	Epi-mesobenthopelagic	55	26 (3; 46)	1044	719	69
<i>Sebastes norvegicus</i>	Golden redfish	Sebastidae	Mainly boreal	Seb_mar	Epi-mesobenthopelagic	122	32 (13; 56)	12	2	17
<i>Sebastes viviparus</i>	Norway redfish	Sebastidae	Boreal	Seb_viv	Epibenthopelagic	41	17 (10; 31)	19	4	21
<i>Eurigla gurnardus</i>	Grey gurnard	Triglidae	North Atlantic	Eur_gur	Benthic	60	37 (14; 41)	7	1	14
<i>Aredtillus atlanticus</i>	Atlantic hookear sculpin	Cottidae	Arctic-boreal	Art_atl	Mesobenthic	17	8 (4; 16)	457	128	28
<i>Gymnocyttus tricuspidis</i>	Arctic staghorn sculpin	Cottidae	Arctic	Gym_tri	Benthic	30	11 (8; 14)	5	0	0
<i>Icelus spp.</i>	Iceland sculpin	Cottidae	Arctic/Arctic-boreal	Ice_spp	Benthic	8 (6; 17)	8 (6; 17)	16	2	13
<i>Myoxocephalus scorpius*</i>	Shorthorn sculpin	Cottidae	Arctic-boreal	Myo_sco	Benthic	60	16 (15; 18)	2	1	50
<i>Triglops murrayi</i>	Moustache sculpin	Cottidae	Mainly boreal	Tri_mur	Benthic	20	10 (6; 16)	113	30	27
<i>Triglops nybelini</i>	Bigeys sculpin	Cottidae	Arctic	Tri_nyb	Mesobenthic	17	8 (4; 14)	137	17	12
<i>Triglops pingelli</i>	Ribbed sculpin	Cottidae	Arctic-boreal	Tri_pin	Benthic	23	12 (7; 16)	54	11	20
<i>Cottunculus microps</i>	Polar sculpin	Psychrolutidae	Arctic-boreal	Cot_mic	Mesobenthic	33	13 (6; 25)	35	0	0
<i>Aspidophoroides olrikii</i>	Northern alligatorfish	Agonidae	Mainly Arctic	Asp_olr	Benthic	10	6 (5; 7)	15	6	40
<i>Lepagionus decagonus</i>	Atlantic poacher	Agonidae	Arctic-boreal	Lep_dec	Benthic	25	14 (6; 19)	219	10	5
<i>Cyclopterus lumpus</i>	Lumpsucker	Cyclopteridae	Mainly boreal	Cyc_lum	Epibenthopelagic	63	24 (7; 51)	105	5	5
<i>Eumicrotremus derjugini</i>	Leatherfin lumpsucker	Cyclopteridae	Arctic	Eum_der	Benthic	13	7 (5; 10)	11	0	0
<i>Eumicrotremus spinosus</i>	Atlantic spiny lumpsucker	Cyclopteridae	Mainly Arctic	Eum_spi	Benthic	14	8 (4; 13)	115	25	22
<i>Careproctus spp.</i>	Snailfish/tadpole	Liparidae	Arctic	Car_spp	Mesobenthic	44	11 (4; 20)	44	7	16
<i>Liparis bathyartcticus</i>	Arctic snailfish	Liparidae	Mainly Arctic	Lip_bat	Benthic	27	4 (5; 23)	14	1	7
<i>Liparis fabricii</i>	Gelatinous snailfish	Liparidae	Arctic	Lip_fab	Demersal	21	8 (3; 18)	139	31	22
<i>Lycodes esmarkii</i>	Greater eelpout	Zoaridae	Mainly boreal	Lyc_esm	Mesobenthic	100	38 (18; 64)	32	5	16

(continued on next page)

Table 2 (continued)

Scientific name	English name	Family	Biogeography	Abbreviation	Habitat	Length (cm)	Fish length, mean (min,max)	Total N stomach	Total N empty stom.	% empty stom.
<i>Lycodes eudipleurostictus</i>	Doubleline eelpout	Zoarctidae	Arctic	Lyc_eud	Benthic	45	19 (8;31.5)	7	6	86
<i>Lycodes gracilis</i>	Gracile eelpout	Zoarctidae	Mainly boreal	Lyc_gra	Epi-mesobenthic	56	25 (17; 31)	241	101	42
<i>Lycodes pallidus</i>	Pale eelpout	Zoarctidae	Arctic	Lyc_pal	Epi-meso-bathybenthic	29	14 (18; 21)	43	29	67
<i>Lycodes polaris</i> *	Canadian eelpout	Zoarctidae	Arctic	Lyc_pol	Benthic	33	24 (24; 24)	1	0	0
<i>Lycodes reticulatus</i>	Arctic eelpout	Zoarctidae	Arctic	Lyc_ret	Epi-mesopelagic	65	20 (6; 41)	34	21	62
<i>Lycodes rossi</i>	Threespot eelpout	Zoarctidae	Arctic	Lyc_ros	Benthic	31/38	15 (9; 29)	43	19	44
<i>Lycodes seminudus</i>	Longear eelpout	Zoarctidae	Arctic	Lyc_sem	Benthic	57	17 (11; 24)	6	1	17
<i>Anisarchus medius</i> *	Stout eelblenny	Stichaeidae	Arctic-boreal	Ani_med	Benthic	29/20	21 (21; 21)	1	0	0
<i>Lepocottus maculatus</i>	Daubed shanny	Stichaeidae	Arctic-boreal	Lep_mac	Benthic	22	12 (8; 16)	128	46	36
<i>Lumpenus fabricii</i> *	Slender eelblenny	Stichaeidae	Arctic-boreal	Lum_fab	Benthic	37	21 (21; 21)	1	1	100
<i>Lumpenus lampretaeformis</i>	Snakeblenny	Stichaeidae	Mainly boreal	Lum_lam	Benthic	64	20 (6; 32)	74	25	34
<i>Anarhichas denticulatus</i>	Northern wolffish	Anarhichadidae	Arctic-boreal	Ana_den	Demersal	180/144	68 (3; 121)	52	23	44
<i>Anarhichas lupus</i>	Atlantic wolffish	Anarhichadidae	Mainly boreal	Ana_lup	Demersal	152/120	27 (3; 84)	54	13	24
<i>Anarhichas minor</i>	Spotted wolffish	Anarhichadidae	Mainly boreal	Ana_min	Demersal	180/144	78 (3; 130)	59	19	32
<i>Anmodytes marinus</i>	Lesser sandeel	Ammodytidae	Boreal	Amm_mar	Demersal	25	18 (8; 23)	19	1	5
<i>Glyptocephalus cynoglossus</i> *	Witch flounder	Pleuronectidae	Boreal	Gly_cyn	Benthic	78/62	34 (34; 34)	1	0	0
<i>Hippoglossoides platessoides</i>	Long rough dab	Pleuronectidae	Arctic-boreal	Hip_pla	Benthic	83/54	28 (4; 51)	1553	898	58
<i>Hippoglossus hippoglossus</i> *	Atlantic halibut	Pleuronectidae	Mainly boreal	Hip_hip	Benthopelagic	266	74 (74; 74)	1	1	100
<i>Limanda limanda</i>	Common dab	Pleuronectidae	Mainly boreal	Lim_lim	Benthic	42	19 (11; 34)	79	53	67
<i>Microstomus kitt</i>	Lemon sole	Pleuronectidae	Boreal	Mic_kit	Benthic	66/46	28 (14; 37)	10	3	30
<i>Pleuronectes platessa</i>	European plaice	Pleuronectidae	Boreal	Ple_pla	Benthic	100/50	38 (23; 70)	129	102	79
<i>Liopsetta glacialis</i>	Arctic flounder	Pleuronectidae	Boreal	Lio_gla	Benthic	35	16 (12; 19)	22	7	32
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	Pleuronectidae	Arctic-boreal	Rei_hip	Mesobenthic	130	49 (10; 108)	2583	1871	72

17,878 (mainly boreal; including cod and haddock), 7318 (Arcto-Boreal; including capelin, long-rough dab, and Greenland halibut), 1,520 (Arctic), 697 (boreal), 144 (mainly Arctic), and 10 (widely distributed).

Seasons were defined based on biological seasons in the Barents Sea: winter (January-March), spring (April-June), summer (July-September) and autumn (October-December). Sampling effort was largest in autumn (11,852 stomachs from 47 fish species) and summer (9004 stomach from 58 fish species), and lowest in spring (1761 stomachs from 23 fish species). For more information see [Supplementary material 1_5 \(SM1_5\)](#).

2.4. Data treatment

The more than 350 prey types recorded in the stomachs are presented in the [Supplementary material \(data link\)](#). The prey types included a wide range of taxonomic resolution, from phylum to species. To describe diet composition and variability among the fish species, we combined prey items into 12 larger groups: copepods (dominated by *Calanus* species); euphausiids (dominated by *Meganctiphanes norvegica* and *Thysanoessa* species); hyperiids (dominated by *Themisto* species); gelatinous plankton (dominated by ctenophores); small demersal crustaceans (SD_crustacea, dominated by gammarid amphipods and isopods); large demersal crustaceans (LD_crustacea, dominated by shrimps and crabs); other plankton (dominated by chaetognaths and pteropods); fish (dominated by capelin, polar cod *Boreogadus saida*, cod, long rough dab and daubed shanny *Leptoclinius maculatus*); echinoderms (dominated by brittle stars Ophiuroidea and sea cucumbers Holothuroidea); worms (dominated by polychaetes); molluscs (dominated by bivalves and gastropods), and other food (including cephalopods dominated by Oegopsida and Octopoda; unidentified items). Unidentified crustaceans were distributed proportionally (by weigh) among available crustacean categories for each predator fish. Digested food was not used as a separate prey category in the analyses, and total weight of stomach content was therefore reduced by the weight of digested food to calculate the percentage prey composition for the prey categories. This is based on an assumption that digested food was evenly distributed among the identified prey categories for each predator species.

We decided to use a cut-off of minimum of 5 stomachs with positive content (excluding empty stomachs) for the quantitative analysis. This reduced the number of taxa from 70 to 55 for the quantitative description of trophic groups and trophic structure. The choice of 5 was somewhat arbitrary, but the intended effect was to exclude species with only one or a few stomachs sampled where random (individual) variation could have a large influence on results.

We calculated two different indices as quantitative expressions of the diet composition: (1) Average (summed) wet weight percentage, % W = 100% × ΣWi/ΣWt, where Wi is weight of prey group i in a stomach, while Wt is the total weight stomach content (Anon, 1974). The sums are taken over all individuals for a given predator (fish) species. This index has been named “aggregate volume” in seminal literature (Martin et al., 1946; Swanson et al., 1974), and the way it is constructed by summation across individuals, it is biased towards large individuals by giving more weight (literally) to their stomachs than to stomachs from smaller individuals. (2) Frequency of occurrence, % F = 100% × Ni/N, where Ni is the number of stomachs with specific prey items, while N is the total number of non-empty stomachs (Anon, 1974). Both diet indices were used as proportions in statistical calculations.

Hierarchical clustering with unweighted pair-group average (UPGMA) agglomeration method was used to identify similarities in diet among fish species. A Bray-Curtis dissimilarity matrix was calculated from the species-averaged weight percentage (%W) stomach content data and used in the analysis. The number of clusters was defined using Gap statistics (Tibshirani et al., 2001) and the silhouette method (Rousseeuw, 1987), as well as an ecological understanding of

the fish species and their diet (Supplementary material SM_2). The different methods produced the same result with 9 clusters identified. Principal component analyses (PCA) using the square-root transformed species-averaged weight proportion data ($\sqrt{\%W}$; $\%W \in [0,1]$) were further used to examine the trophic structure in the fish community. Principal component analysis (PCA) is the most widely used method to derive dietary patterns. Spearman correlations using the mean weight diet data were calculated to examine the PCA and clustering results in further detail. Statistical analyses were performed using PAST 3.14 (Hammer et al., 2001) and R (R Core Team, 2019).

3. Results

We processed a total of 27,627 stomachs from 70 fish species (including two genera) from 24 fish families in the Barents Sea (Table 2). During the BESS, 63 fish species were collected, while during the Russian and Joint winter surveys 42 and 30 species were collected, respectively. More than 30 fish species were collected during at least two seasons and in different part of the Barents Sea.

3.1. Empty stomachs and digested food

Out of the total number, 17,876 stomachs contained food while 9751 (35%) were empty (Table 2). More than half of the analysed stomachs were empty for several species, including some commercial species that were extensively sampled: plaice *Pleuronectes platessa* (79%), Atlantic herring (75%), Greenland halibut (72%), deepwater redfish (69%), common dab *Limanda limanda* (67%), tusk *Brosme brosme* (59%) and long rough dab (58%) (Table 1).

The diet composition by prey categories for the 67 fish species with food in the stomach is given as wet weight and frequency of occurrence in the data set (data link). Digested food (which could not be identified to other prey categories) was not included in the quantitative analyses of diet composition described in the following sections. The average weight proportion of digested food (%W) was 3.6% for all species. The highest proportions of digested food were found for Atlantic wolffish and navaga with 16%, daubed shanny with 20%, and doubleline eelpout with 100% (only one stomach; 6 out of 7 stomachs were empty). The average weight proportion of digested food was below 10% for 36 species, with 29 of them having no digested food (data link).

3.2. Importance of prey groups

The two metrics used to quantify importance of prey groups in the fish diet, average % wet weight (%W) and frequency of occurrence (% F), were positively and significantly correlated for each of the prey categories (Pearson $r = 0.82$ – 0.94 , except for ‘other prey’ with $r = 0.61$; $p < 0.001$ in all cases) (Fig. 3)). Thus, fish species which ate a prey category more frequently also ate more of that prey in terms of weight. Fish species located in the upper right corner of the plots in Fig. 2 had those prey categories as the most important in their diets, both in terms of frequency and amount. There is general agreement between the species for which prey categories show up as important in Fig. 2, and the main prey composition for different clusters of fish species which we describe in the next section.

There are some differences in the importance of frequency versus amount of prey for some of the prey categories. Thus, the amount eaten tended to be high relative to frequency for fish as prey (positioned to the upper left in the plot), whereas the amount eaten tended to be low relative to frequency for euphausiids and small demersal crustaceans (positioned to the lower right) (Fig. 2). A species such as deepwater redfish *Sebastes mentella* (Seb_men) ate a large amount of fish but with low frequency, while it ate a lower amount of euphausiids but with higher frequency. Northern wolffish (Ana_den) and white barracudina (Arc_ris) had both eaten a large amount of gelatinous plankton, although with low frequency of occurrence. Rough-head grenadier

(Mac_ber) in contrast ate gelatinous plankton frequently but in low amount. Likewise, this species ate small demersal crustaceans frequently but also in this case in low amount.

3.3. Diet composition of fish species and groups

The results from the cluster analysis performed on the species-averaged weight percentages from the selected 55 species/genera are shown in Fig. 3, where the mean diet composition for the species has been arranged according to the outcome of the cluster analysis. Results from Spearman correlation, using the mean weight diet data, indicated significant correlations ($r = 0.40$ – 0.95) between species within the clusters (SM2_1).

The number of clusters was determined both by using statistical plots (gap statistics and silhouette plot, SM2_2) and ecological understanding of the species. We identified nine clusters (some of them with sub-clusters), as summarized in Table 3.

Thirteen of the species were grouped into a ‘fish’ cluster with over half of the average stomach weight consisting of fish (cluster I). Three of the clusters had primarily pelagic food, while the remaining five were associated with benthic foraging. There was a cluster of 7 fish species that preyed primarily on euphausiids and copepods (cluster II). Eight species formed a ‘hyperiid’ cluster (III), while four species made up a ‘gelatinous plankton’ cluster (IV). Of the benthic foraging groups, nine species had ‘worms’ (mainly polychaetes) as the main food (cluster V). Three clusters had a more mixed diet: mainly large demersal crustaceans and fish (VI), small demersal crustaceans and hyperiids (VII), and worms, molluscs and echinoderms (VIII). Two fish species fed mainly on echinoderms (cluster IX).

The size of fish varied among the clusters, with small species in the pelagic clusters II and III of planktivorous fish, in the ‘worms’ cluster V, and in the ‘small demersal crustacea’ cluster VII (Fig. 4). The largest species were in the groups of piscivores (cluster I), benthivores that ate various demersal invertebrates and echinoderms (clusters VIII and IX), and the mixed benthic- and piscivores in cluster VI. The species that ate gelatinous plankton (cluster IV) were also relatively large. The proportion of fish in the diet increased with increased predator size ($R^2 = 0.19$), as did the proportion of gelatinous plankton ($R^2 = 0.16$).

3.4. Trophic structure

Principal component analyses were performed on the species-averaged proportional data (%W). Analyses indicated three large distinct groups: species feeding on fish, crustaceans, and worms. The PC1 indicated that species feeding on fish had little or no overlap in averaged diet with species feeding on worms or hyperiids (Fig. 5A, C), while the PC2 separated these two latter groups (Fig. 5A, D). PC3 separated the crustacean feeders that fed on copepods and euphausiids from those feeding on hyperiid amphipods (Fig. 5B, E). The three axes explained 60% of the total diet variance.

The nine clusters from Fig. 3 were complementary to the PCA results, where species aligned close to each other along the same axis are correlated (Fig. 5). The piscivore cluster I, hyperiid cluster III, and benthic worms cluster V were the most clearly distinct and separated groups, whereas the other benthivore clusters VI to IX were positioned in the centre part of the PCA plots. The relative positions of the groups, and the relative positions of the species within each group, reflect the trophic positions of the species and groups based on prey composition in the diet.

3.5. Diet in relation to warming

Two dietary aspects that we investigated in relation to warming were: (1) occurrence of a new boreal prey species *Meganyctiphanes norvegica*, which was not observed in the northern Barents Sea before, in the diet of arctic fish species, and (2) occurrence of gelatinous

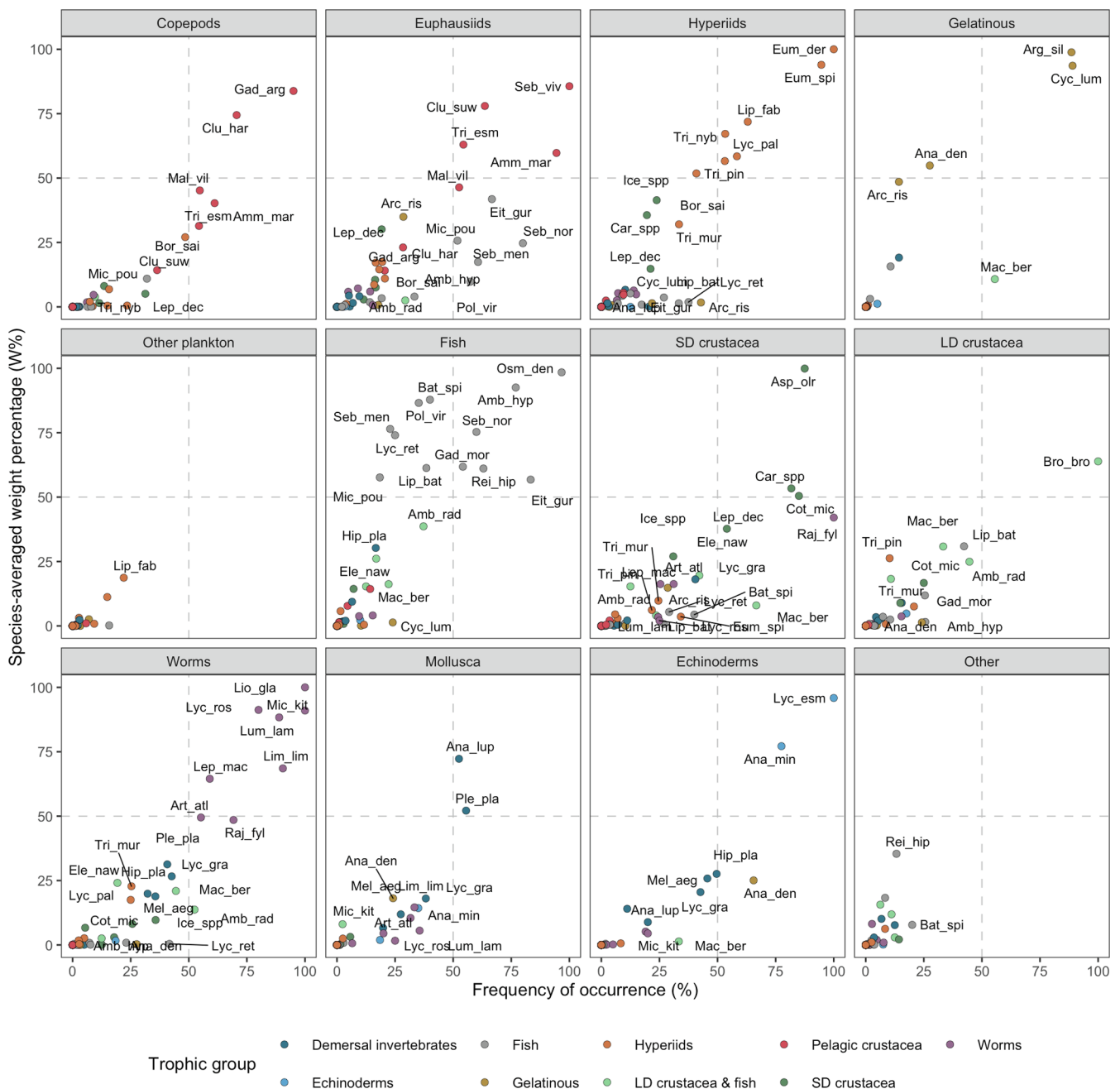


Fig. 2. Species averaged weight percentage (%W) versus frequency of occurrence (%F) of prey-groups (panels) in the diet of fish (dots with text – see Table 1 for species abbreviations). The color of the dots refers to the trophic groups identified by cluster analysis (Fig. 3 and Table 3). A prey category is both frequent and contributes a high mass to the diet of fish species positioned in the right top quarter, while the situation is the opposite (rare and low mass contribution) for species in the bottom left quarter.

plankton in the fish diet.

Among the planktivore groups, Arctic fishes tended to feed on hyperiids while boreal and Arcto-Boreal fishes tended to feed on euphausiids (Table 3). A total of 722 stomachs from nine arctic fish species captured in the arctic part of the Barents Sea (north of 77°N and east of 30°E) were analysed and *M. norvegica* were found in 19 stomachs from three species (*Lycodes pallidus*, *Boreogadus saida* and *Triglops nybelini*). This corresponds to only 2.4% of the analysed stomachs but demonstrates nevertheless that Arctic fishes were able to prey on this relatively large boreal krill species.

Gelatinous plankton was observed in the diet of 1430 individuals from 15 fish species. Gelatinous plankton was mainly found in cod (931) and haddock (344), which dominated stomach samples (SM1_1),

and lumpfish (97). Results also showed unusual dominance (%W) of gelatinous plankton in the diet of greater argentine and white barracudina. Almost all greater argentine (54 of 64) and one out of seven white barracudina had jellyfish in the diet (Fig. 2).

4. Discussion

The fish stomach sampling program in 2015 is the most comprehensive single study of diet and trophic structure of fishes in the Barents Sea since the beginning of trophic investigations early last century. It covered the entire Barents Sea and the majority of common or regularly occurring fish species, with sampling at different seasons throughout the year. The data set and the results we present here provide a baseline

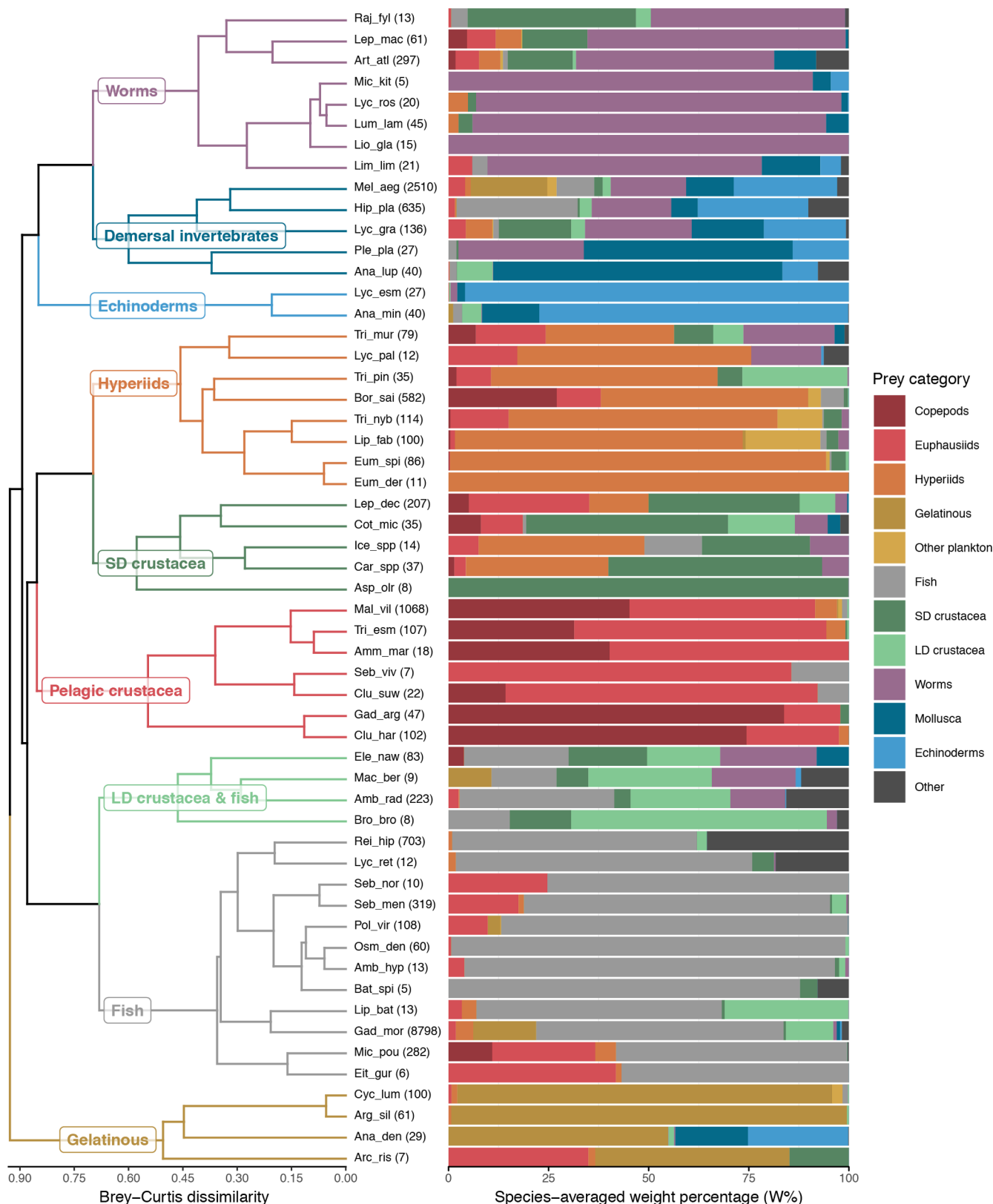


Fig. 3. Hierarchical cluster analysis based on diet composition of 55 fish species (including two genera). The right panel shows the average weight proportions (% wet weight) of each prey category relative to the total stomach content for the fish species. The dendrogram on the left side shows the identified group of species from the cluster analysis as summarized in Table 3. Fish name abbreviations are explained in Table 1, while the number in parenthesis are numbers of individual stomachs for each species of fish.

Table 3
Clusters of fish species based on diet composition from stomach analysis. Results from cluster analysis of mean weight of stomach content of 12 prey categories (see Fig. 3).

Cluster	Sub-cluster	Fish species	Prey composition	
I. Fish	A	<i>Bathyraxa spinicauda</i>	Fish (Sebastes)	
		<i>Osmerus dentax</i>	Fish (Agonidae, Stichaeidae, Cottidae and Ammodytidae)	
		<i>Amblyraja hyperborea</i>	Fish (herring, capelin and polar cod)	
		<i>Pollachius virens</i>	Fish (cod, haddock, herring, capelin and polar cod)	
		<i>Sebastes mentella</i>	Fish (capelin, cod, haddock, <i>Careproctus</i> spp.), euphausiids (<i>Meganyctiphanes norvegica</i>)	
		<i>Sebastes norvegicus</i>	Fish (capelin), euphausiids	
	B	<i>Lycodes reticulatus</i>	Fish (capelin, gelatinousnaillfish and Agonidae)	
		<i>Eutrigla gurnardus</i>	Fish (cod, <i>Sebastes</i> , lemon sole), euphausiids	
		<i>Micromesistius poutassou</i>	Fish (capelin, daubed shanny, <i>Sebastes</i>), euphausiids (Euphausiidae and <i>M. norvegica</i>)	
	C	<i>Gadus morhua</i>	Fish (haddock, herring, capelin, polar cod, Greenland halibut, <i>Sebastes</i> and other), LD crustacea (snow crab, <i>Hyas</i>)	
		<i>Liparis bathyartcticus</i>	Fish (polar cod, <i>Liparis</i>), LD crustacea (<i>Sclerocrangon boreas</i>)	
	D	<i>Reinhardtius hippoglossoides</i>	Fish (cod, haddock, herring, capelin, polar cod, Greenland halibut and other), euphausiids and other food	
II. Pelagic crustaceans (euphausiids and copepods)	A	<i>Ammodytes marinus</i>	Euphausiids (<i>T. inermis</i>), copepods	
		<i>Trisopterus esmarkii</i>	Euphausiids (<i>M. norvegica</i>), copepods	
		<i>Mallotus villosus</i>	Euphausiids (<i>T. inermis</i>), copepods	
	B	<i>Clupea pallasii suworowi</i>	Euphausiids	
		<i>Sebastes viviparus</i>	Euphausiids	
	C	<i>Clupea harengus</i>	Copepods, euphausiids	
		<i>Gadiculus argenteus thori</i>	Copepods, euphausiids	
	III. Hyperiid	A	<i>Boreogadus saida</i>	Hyperiid (<i>Themisto libellula</i>), copepods (<i>C. glacialis</i> , <i>M. longa</i>), euphausiids (<i>M. norvegica</i> , <i>T. inermis</i>)
			<i>Triglops pingelii</i>	Hyperiid (<i>T. libellula</i>), LD crustacea (<i>Lebbeus polaris</i>), euphausiids (<i>T. inermis</i>)
B		<i>Eumicrotremus derjugini</i>	Hyperiid (<i>T. libellula</i>)	
		<i>Eumicrotremus spinosus</i>	Hyperiid (<i>T. libellula</i> , <i>T. abyssorum</i>)	
C		<i>Liparis fabricii</i>	Hyperiid (<i>T. libellula</i>), other plankton (<i>Limacina helicina</i>)	
		<i>Triglops nybelini</i>	Hyperiid (<i>T. libellula</i>), euphausiids (<i>M. norvegica</i>), other plankton (<i>Limacina helicina</i>)	
D		<i>Lycodes pallidus</i>	Hyperiid (<i>T. libellula</i>), Euphausiids (<i>M. norvegica</i>), worms (Polychaeta)	
		<i>Triglops murrayi</i>	Hyperiid (<i>T. libellula</i> , <i>T. abyssorum</i>), worms (Polychaeta)	
IV. Gelatinous plankton	A	<i>Cyclopterus lumpus</i>	Gelatinous plankton (Ctenophora, <i>Hydrozoa/Scyphozoa</i>)	
		<i>Argentina silus</i>	Gelatinous plankton (Ctenophora)	
	B	<i>Arctozenus risso</i>	Gelatinous plankton (Ctenophora), euphausiids (<i>M. norvegica</i>)	
V. Worms	A	<i>Microstomus kitt</i>	Worms (Polychaeta)	
		<i>Lycodes rossi</i>	Worms (Polychaeta)	
		<i>Lumpenus lampretaeformis</i>	Worms (Polychaeta)	
		<i>Liopsetta glacialis</i>	Worms (Polychaeta)	
		<i>Limanda limanda</i>	Worms (Polychaeta), molluscs (Bivalvia)	
	B	<i>Artediellus atlanticus</i>	Worms (Polychaeta), SD crustacea (Gammaridea), other food	
		<i>Leptoclinus maculatus</i>	Worms (Polychaeta), other crustaceans, other	
		<i>Rajella fjyllae</i>	Worms (Polychaeta), SD crustacea (Gammaridea)	
VI. LD_crustaceans + Fish		<i>Eleginus nawaga</i>	Fish (Ammodytes, <i>H. platessoides</i>), Worms (Polychaeta), SD crustacea (Gammaridea), LD crustacea (Paguridae)	
		<i>Amblyraja radiata</i>	Fish (capelin, cod, long rough dab), LD crustacea (Paguridae), worms (Polychaeta)	
		<i>Macrourus berglax</i>	LD crustacea (<i>Pandalus</i>), worms (Polychaeta), fish (polar sculpin)	
		<i>Brosme brosme</i>	LD crustacea (<i>Munida sarsi</i> , <i>Pandalus borealis</i>), fish (moustache sculpin), SD crustacea (<i>Aega psora</i>)	
VII. SD_crustaceans		<i>Aspidophoroides olrikii</i>	SD crustacea (Gammaridea)	
		<i>Careproctus spp.</i>	SD crustacea (Gammaridea), hyperiid (<i>T. libellula</i>)	
+ Hyperiid		<i>Icelus spp.</i>	Hyperiid (<i>T. libellula</i> , <i>T. abyssorum</i>), SD crustacea (Gammaridea), other crustaceans	
		<i>Cottunculus microps</i>	SD crustacea (Gammaridea), other crustaceans	
		<i>Leptagonus decagonus</i>	SD crustacea (Gammaridea), hyperiid (<i>T. libellula</i> , <i>Amphipoda</i>), euphausiids (<i>T. inermis</i> , <i>M. norvegica</i>)	
VIII. Demersal invertebrates (Worms, mollusca, echinoderms)	A	<i>Hippoglossoides platessoides</i>	Echinoderms (brittle stars), Fish (capelin, cod), worms (Polychaeta)	
		<i>Lycodes gracilis</i>	Worms (Polychaeta), echinoderms (brittle stars), SD crustacea (Gammaridea)	
		<i>Melanogrammus aeglefinus</i>	Echinoderms (brittle stars), worms (Polychaeta), molluscs (Gastropoda, Bivalvia)	
	B	<i>Anarhichas lupus</i>	Molluscs (Gastropoda, Bivalvia), other food	
		<i>Pleuronectes platessa</i>	Molluscs (Gastropoda, Bivalvia), worms (Polychaeta)	
IX. Echinoderms		<i>Anarhichas minor</i>	Echinoderms	
		<i>Lycodes esmarkii</i>	Echinoderms	

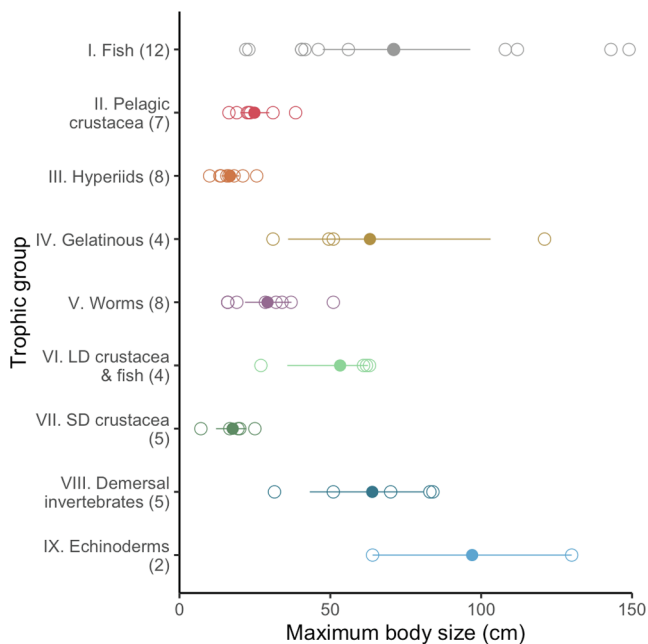


Fig. 4. Maximum body length (cm) for the species of fish in the nine trophic groups (Fig. 3 and Table 3). Open circles indicate maximum body lengths among all studied fish for a species. Closed circles and error bars indicate the mean values and bootstrapped 95% confidence intervals for the means. Numbers in parentheses behind group names indicate the number of species per group.

for fish diet and trophic structure at a time when the Barents Sea ecosystem is undergoing substantial warming and change (Fossheim et al., 2015; Eriksen et al., 2017; Lind, 2018). We provide a brief review of fish diet studies which puts our results in the context of earlier findings in the Barents Sea. We also identified some changes in fish diet that could be reflecting ongoing changes in the ecosystem. These aspects are discussed in more detail in following sections.

4.1. The 2015 ‘Year of the stomach’ data set – establishing a baseline

Bogstad et al. (2000), Dommasnes et al. (2001), Bodini et al. (2009), Planque et al. (2014) and Dolgov (2016) summarized information on diet of fish species and other organisms in the Barents Sea food web. The first three works developed a comprehensive documentation of the food web based on available literature, mainly from the last century, while Dolgov (2016) published fish diet results for the period 1990–2010. The present work provides updated information on trophic interactions in the Barents Sea for one year (2015) during a record warm period (2012–2016; ICES 2018). We will come back to the specific results, but first we consider some methodological aspects related to our 2015 data set.

The data set is comprehensive although heterogenous in many respects. It is standardized through the use of standard protocols to collect and analyse fish stomachs. The sampling design, however, was opportunistic, using available sampling platforms where the joint Norwegian-Russian autumn and winter surveys provided much of the data. Sampling of fish stomachs was based on two principles: (1) availability of species in the catches, aimed to evaluate spatial variation in fish diet, and (2) availability of fish of different size, aimed to evaluate ontogenetic changes in the fish diet. The main motivation for these criteria was that the sampling should represent the geographical and length distributions of species. Sampling effort was limited by time and manpower and was spent to cover as many species as possible by keeping track of which species had already been sampled and which had not.

During the autumn ecosystem survey (BESS), which covered the entire Barents Sea with sampling by both pelagic and bottom trawls, 63 fish species were collected. During the Russian and Joint winter surveys, which do not cover the northern parts of the Barents Sea due to ice, 42 and 30 species were collected, respectively. A total of about 200 species of fish have been recorded from the Barents Sea, with around 100 species being regularly collected during the BESS (Jakobsen and Ozhigin, 2011, Wienerroither et al., 2011). Thus, our sampling of 70 species (including two genera) from 24 families included the majority of the common fish species in the Barents Sea. Most species live at or associate with the bottom (Dolgov 2016), and the 2015 sampling represented the general pattern of the Barents Sea fish community dominated by demersal and benthic species.

The 2015 fish stomach data set was strongly heterogenous in sample size across species, and dominated by abundant and commercially important species such as cod and haddock due to their wide distribution and routine size-stratified sampling at IMR and PINRO, in contrast to limited sampling of non-abundant species with restricted geographical distribution. The uneven number of individual stomachs sampled across the species, and the low number of stomachs for some of the species, must be kept in mind when interpreting the results.

The sampling was also heterogenous in sample size across fish length. High number of size groups was generally obtained for larger fish species such as cod, haddock, Greenland halibut, Atlantic wolffish, deepwater redfish, long rough dab, and saithe. More than 30 fish species were observed in the size group between 8 and 30 cm, and this most likely reflects that the Barents Sea is dominated by smaller and medium sized species. This is in agreement with Dolgov (2016) who studied the Barents Sea fish community between 1998 and 2010 and concluded that it was dominated by small and medium sized fish (almost 80 fish species had body size between 6 and 20 cm and 40–60 species had body size between 26 and 40 cm). A bottom trawl captures small individuals and species less effectively than larger ones (since they escape through the net), and sampling therefore biased against the small fishes.

The opportunistic sampling design with the allocation of effort based on the two criteria of availability of species and size groups in trawl catches is likely to have affected our results. We have in this study calculated average diet composition for each species, and one important question is how representative these values are as annual average values. This translates into the bigger question of how representative our data set is as a baseline for the year 2015. The questions of representativity are related to sources of error which are of both random and systematic (biased) nature. The random error relates to variability among individuals which determines the accuracy of an average value. Our data are based on analysis of individual stomachs, and our full data set contains information on individual variability. We have not yet done a formal analysis of the individual variability, but we note that its effect would generally be largest for species with small sample sizes (few stomachs) and of low or negligible importance for the species with large sample sizes (e.g. the species with over 1000 stomachs).

Systematic error or bias could stem from an imbalance in the data in terms of geography, seasons, and size groups. The two main sources of the data are the joint ecosystem survey (BESS) in early autumn (we have denoted these as summer data from a biological perspective) and the joint and Russian winter surveys. For more than 30 species, we have data for the contrasting summer and winter situations (SM1_5). Most of the species are classified biogeographically as boreal (or mostly boreal) and Arcto-Boreal (35 plus 15 species), with fewer species classified as Arctic (13 species) (SM1_4). The geographical coverage of the cruises is such that boreal and Arcto-Boreal species would be generally covered both summer and winter, whereas Arctic species only and sampled in summer due to ice coverage during winter.

In summary, most of the 55 fish species included in the quantitative analyses have broad spatial coverage and seasonal resolution with samples from both summer and winter. We are addressing spatial and

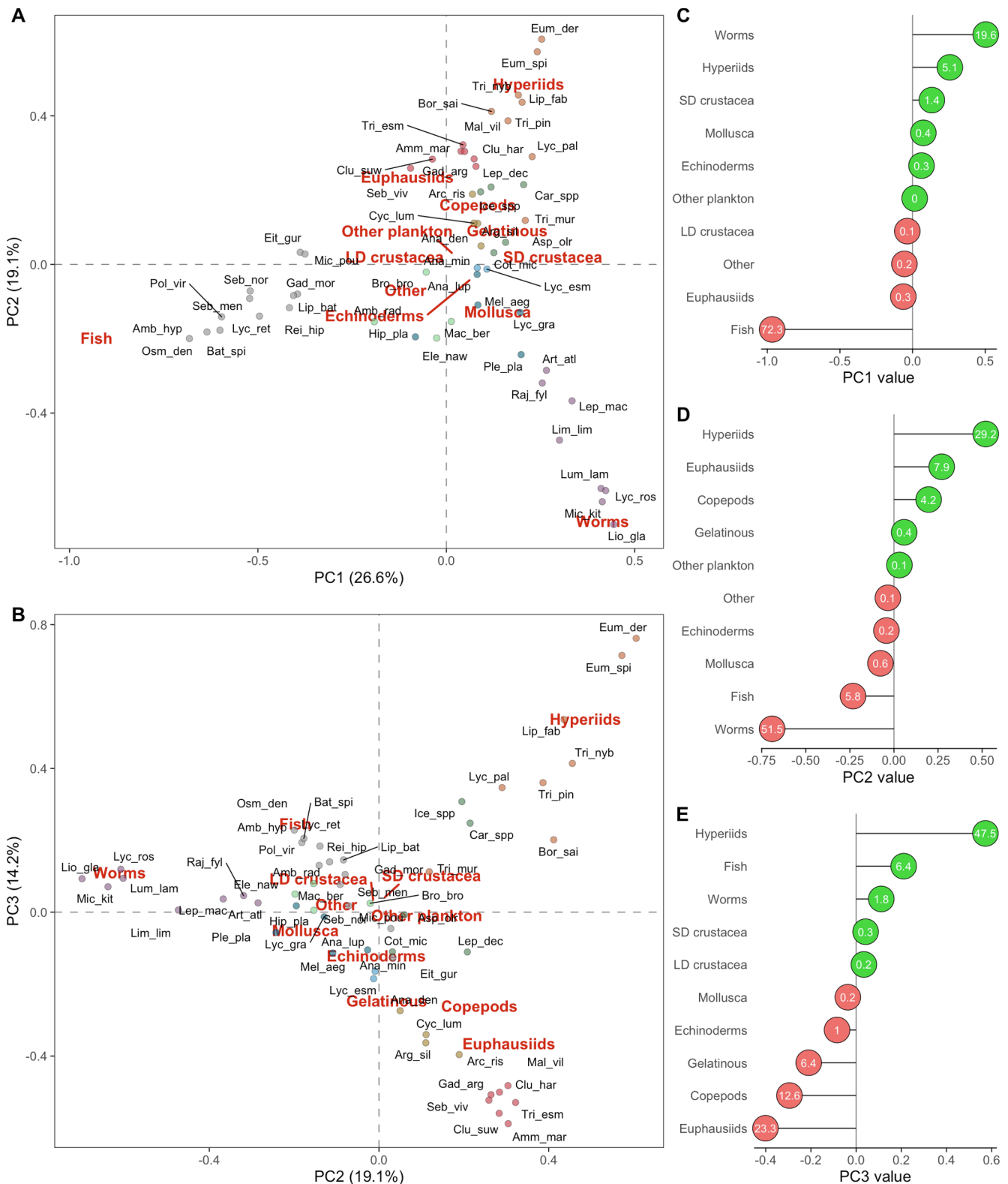


Fig. 5. Principal component analysis (PCA) of species-averaged weight proportion (%W) data. (A) Principal axes 1 and 2, and (B) Principal axes 2 and 3. Dots with text indicate the average values for each species. Colors of dots indicate the 9 trophic groups from cluster analysis (see Fig. 3). Red text indicates the principal component scores for the 12 prey categories. (C–E) Prey-group contributions to principal axes 1 to 3. The percentage contribution is given inside the circles.

seasonal patterns in fish diet in our data set in another paper (this volume). The size range covered is generally quite extensive for most species and is not expected to cause much bias due to lack of representativity. The metric (%W) we have been using is biased towards large individuals (due to the summed weights used in calculation),

while trawl sampling is biased against small individuals. The average diet composition of a species is therefore expected to reflect disproportionately the larger individuals in the sampled population. The fact that percentage weight of a prey component in the diet was strongly correlated with its frequency of occurrence suggests that any

bias towards large individuals did not materially shift the patterns in diet composition among the species. All in all, we believe that the sampling program is adequate to update information on trophic interactions in the Barents Sea and describe the food web in the current period of large changes in the ecosystem, where comprehensive sampling (spatially, temporally, number of species collected simultaneously) is needed.

4.2. Comparison of fish species by diet composition

The grouping of fish species by cluster analysis is in broad agreement with a general division into piscivores (cluster I), planktivores (clusters II–IV), and benthivores (clusters V–IX, Table 3) (Dolgov et al., 2011a, 2011b, 2011c, 2011d). The two most clearly distinct groups were species feeding on fish (cluster I) and on polychaetes (worms, cluster V), which had little or no overlap in diet. The fish eaters (cluster I) in our study contain species which are known to be piscivores from previous studies (Dolgov et al., 2011d): Atlantic cod, saithe, spinytail skate, Arctic skate, deep water redfish, Norway redfish, and Greenland halibut. The two redfish species and blue whiting clustered as piscivores with euphausiids as additional food. Blue whiting is known to shift diet from plankton to small fish as it grows (Monstad, 2004; Dolgov et al., 2010, 2011c; Langøy et al., 2012). Deepwater and golden redfish are known to feed both on fish and plankton (Dolgov et al., 2011d). In our study, they fed more frequently on euphausiids although in lower amounts than on fish. Arctic eelpout, which grouped as a piscivore in our study, also included benthic invertebrates in the diet (cephalopods and crustaceans). This eelpout is previously known to feed on fish and bottom invertebrates (Andriyashev, 1986).

The planktivores in cluster II such as capelin, Atlantic and Pacific herring and lesser sandeel, which are well-known plankton feeders in the Barents Sea, fed on various proportions of euphausiids and copepods (Orlova et al., 2010; Dolgov et al., 2011c, Hop and Gjøsaeter, 2013). The hyperiid eaters (cluster III) were comprised mainly of Arctic species. The most prominent is polar cod which is known to feed on *Themisto* but also to take copepods, euphausiids and some other prey (Orlova et al., 2005, 2009; Dolgov et al., 2011c, Hop and Gjøsaeter, 2013). The three species of the genus *Triglops* (moustache, bigeye, and ribbed sculpins) had all eaten hyperiid amphipods as the dominant prey, supplemented with various benthic invertebrates and some euphausiids. Our results are in general agreement with what was known previously in that these sculpins were said to feed on small crustaceans, polychaetes and fish (Fedorov, 1986; Dolgov, 2016), although we found no fish in their diet.

Lumpsucker in cluster IV is known to feed mainly on gelatinous zooplankton (Bjelland and Holst, 2004), while northern wolffish has been found to consume gelatinous prey to varying degree (Shevelev and Kuzmichev, 1990; Shevelev and Johannessen, 2011). In agreement with this, we found northern wolffish to have fed on a large amount of gelatinous plankton but with low frequency, while other prey for this species were molluscs and echinoderms. The dominance of gelatinous plankton in the diet of greater argentine and white barracudina was somewhat unusual. Greater argentine is known to feed on zooplankton including copepods and krill, small pelagic fishes, and squid (Dolgov, 2016). White barracudina were found to feed extensively on euphausiids in both the Barents Sea (Dolgov, 2016) and the Norwegian Sea where it was found to take small mesopelagic fishes (Salvanes, 2004). Euphausiids were a major additional food source (~35% by weight) for this species in our study.

The distinct group of worm eaters in cluster V included eight species, all of them benthic – three flounders, one sculpin, two pricklebacks, one skate, and one eelpout. The three righteye flounders (Pleuronectidae) are all known to feed on polychaetes and other small benthic invertebrates (Dolgov et al., 2011b). Round skate is known to feed on various benthic and benthopelagic invertebrates and also some fish (Berestovsky, 1989; Dolgov, 2005; Dolgov et al., 2011b). Similarly,

in our study demersal crustaceans were an important component of the diet in addition to polychaetes. Atlantic hooker sculpin is known to feed on small benthic invertebrates (Fedorov, 1986; Atkinson and Percy, 1992; Dolgov, 1994; Dolgov et al., 2011b). We found that this species had eaten small demersal crustaceans, and some euphausiids and hyperiids as additional diet to polychaetes. The two pricklebacks (Stichaeidae), daubed shanny and snakeblenny, are also known to eat polychaetes and other small invertebrates (Makushok, 1986; Dolgov, 1994; Dolgov et al., 2011b). Our results are in general agreement with this and also giving a higher taxonomic resolution. Threespot eelpout had eaten polychaetes almost exclusively, with small amounts of hyperiids and other crustaceans in addition. This species has been difficult to identify and is very similar to Arctic eelpout, which we found to be a piscivore.

A group of benthivores (cluster VI) had a relatively mixed diet dominated by various crustaceans (predominantly larger forms such as shrimps and crabs, but also smaller forms, such as gammarid amphipods) and in addition some fish and polychaete worms. The largest contribution of fish in the diet was for thorny skate, which is known to prey typically on fish and large benthic crustaceans (Berestovsky, 1989; Dolgov, 2005, 2016; Dolgov et al., 2011b, 2011d). Navaga and roughhead grenadier had eaten a mixture of demersal crustaceans, fish, and polychaetes. Roughhead grenadier is known as a benthivorous predator with northern shrimp *Pandalus borealis* found as a main prey species in previous studies (Dolgov et al., 2008, 2011b). Tusk was the most dissimilar of the species in this cluster with diet made up largely of demersal crustaceans. Information about the diet of tusk in the Barents Sea is limited and it has been described as a crustacean feeder (Dolgov, 2016).

A group of small benthic fish species (cluster VII) had a mixed diet dominated by small demersal crustaceans, predominantly gammarid amphipods. Atlantic poacher and polar sculpin are known previously to feed on gammarid amphipods, as are sea tadpole *Careproctus reinhardtii* (Dolgov, 1994, 2016; Dolgov et al., 2011b). We found that the species in this group fed additionally on hyperiid amphipods (mainly *Themisto libellula*) and euphausiids (particularly for Atlantic poacher). We have labelled the group as being primarily benthivores, although we note that they also take pelagic prey.

A group of five species made up cluster VIII characterized by a mixed diet of various benthic invertebrates. Haddock had a mixed diet of polychaetes, echinoderms, molluscs, some fish, smaller amounts of crustaceans, and jellyfish in our material. This is similar to what is typically found for haddock, which is considered primarily a benthivore in the Barents Sea (Dolgov et al., 2011b). Long rough dab is also considered a benthivore, although large individuals take a considerable fraction of fish (Dolgov et al., 2011b). This is also the case in our data where long rough dab is positioned close to haddock, but with larger proportion of fish in the diet. Plaice and Atlantic wolffish had eaten a considerable fraction of molluscs along with some echinoderms and also polychaetes in case of plaice. This is in agreement with earlier results where plaice in the Barents Sea has been found to feed predominantly on bivalves and polychaetes (Antipova and Kovtsova, 1982; Dolgov et al., 2011b), and Atlantic wolffish has been found to feed mainly on molluscs, crabs, and echinoderms (Dolgov et al., 2011b).

Spotted wolffish and greater eelpout formed a separate cluster (IX) where they had eaten echinoderms as the main food. Spotted wolffish also eat some molluscs and crustaceans, which is in agreement with what has been found earlier (Dolgov et al., 2011b). Greater eelpout had eaten echinoderms almost exclusively, while in other studies, this species has been found also to consume crustaceans and bivalves, as well as fish and fish offal (Andriyashev, 1986; Bjelland et al., 2000; Dolgov, 2016).

4.3. Trophic structure

Our analyses identified 9 clusters or trophic groups based on the

average quantitative diet composition of 55 species (including two genera) of fish in the Barents Sea. A key feature of the clusters is that they are relatively homogenous and distinct, typically dominated by one diet category. Thus, one diet category made up 50% or more of the total diet for 43 out of the 55 species (78% of the species). The species of piscivores in cluster I and the planktivores in clusters II, III and IV ate predominantly one type of prey, either fish, copepods, euphausiids, hyperiid amphipods, or gelatinous plankton. In contrast, three of the benthivore groups (clusters VI, VII and VIII) had larger dietary diversity, feeding on various mixtures of benthic invertebrates.

There is an obvious caveat associated with these observations related to the taxonomic resolution of the prey categories. We have grouped prey by aggregating over 300 prey types to a relatively high taxonomic level (10 prey categories). These categories vary in terms of taxonomic level and diversity. The category “Hyperiid” is at the family level (Hyperiididae) dominated by two species, *Themisto libellula* and *T. abyssorum*, which are particularly important species in the Barents Sea (Dalpadado et al., 2002). ‘Small demersal’ and ‘Large demersal’ crustaceans combine species from groups at taxonomic subclass level or order levels, distinguishing between amphipods, cumaceans and a few other groups as “small”, and shrimp and crabs as “large” forms of crustaceans. It is worth noting that crustaceans are split into 5 prey categories (copepods, euphausiids, hyperiids, and small and large demersal crustaceans), reflecting their general importance in both pelagic and benthic food-webs (and for the couplings between them).

Fish, in contrast to crustaceans, is treated as one prey group (at the class or super-class level). It is obvious, therefore, that the piscivores in our cluster I were feeding on only one prey category which was fish. The results of previous studies have demonstrated a high degree of temporal change and dynamics in diet composition of many species of fish from the Barents Sea, reflecting underlying dynamics of the ecosystem and its components (Johannesen et al., 2012a, 2015). Earlier results have also suggested a relatively high diversity in prey types for several species of piscivore fish (Dolgov et al., 2011; Dolgov 2016). Our result that piscivores ate predominantly one prey category (fish) hides the fact that many different types and species of fish were consumed (a total of 141 fish species were observed in fish stomachs). Thus cod alone preyed on 33 fish species, with dominance of capelin, haddock, herring, polar cod, Greenland halibut and redfish species (data link), which is very similar to earlier aggregated and averaged results (Johannesen et al., 2012a, 2015; Dolgov, 2016). This illustrates very clearly the importance of taxonomic resolution for descriptions of trophic relationships.

The nine clusters or trophic groups retained their distinctness in the PCA representation where fish-eaters in cluster I, hyperiid-feeders in cluster III, and worm-feeders in cluster V were the most distinctly separated groups. We interpret the PCA axes as PC1 representing fish versus other prey, PC2 as an axis which distinguish between pelagic and benthic prey, and PC3 as an axis which splits groups of pelagic crustaceans with hyperiid amphipods on one side and euphausiids and copepods on the other. The positions of species and groups in the PCA plots (which are projections and therefore can be somewhat distorted) reflects the similarities and differences in their trophic positions relative to degrees of piscivory, planktivory, and benthivory.

The nine clusters are trophic groups or feeding guilds by similarity of their diet composition (Simberloff and Dayan, 1991). At the scale of the whole Barents Sea, without spatial resolution, the clusters may also be considered as functional groups. In line with this, we have synthesised our results into a conceptual model shown in Fig. 6, which illustrates the links between the 9 functional groups of fish and the 10 categories of prey. The similarity between species will, however, diminish along three axes of resolution. The first is the taxonomic resolution of prey types which we have already addressed. At lower taxonomic level, e.g. species rather than class, the similarity may disappear if fishes in the same cluster are feeding on different species within a category of prey. Secondly, different biogeographical and habitat associations may

separate species in a functional ecological sense even if they otherwise are feeding on similar type of prey. Examples from the group of piscivores are separation by geography, with grey gurnard found in the southwestern corner and nebulous snailfish found in the cold waters of the northern Barents Sea, and by habitat, with Arctic skate being benthic, blue whiting mesopelagic, and Arctic smelt coastal. Thirdly, different morphology and behaviour may contribute to niche separation of species which coinhabit the same geographical area and habitat.

One important aspect of morphology is the size of fish. In aquatic communities, body size of predators has been linked directly to foraging success, and larger predators become more successful due to factors such as increased swimming speed and better visual acuity (Webb, 1976; Beamish 1978; Blaxter 1986) and increased gape and thus increased range of prey size (Keast and Webb 1966; Popova 1978; Nielsen 1980; Persson 1990; Juanes and Conover, 1994). In this study, the largest species belonged to piscivores (cluster I), the mixed benthic- and piscivores in cluster VI and fish feeding on echinoderms in cluster IX. Scharf et al. (2000) studied 18 species of marine fish predators from continental shelf off the northeast US coast and found the range of prey size expanded with increasing predator body size, however trophic-niche breadths generally did not expand with predator ontogeny. We plan to study ontogenetic variation of diet and trophic niche breadth in separate works.

4.4. Diet according to warming

Climatic change in the Barents Sea has resulted in considerable changes in distributions of water masses (atlantification, Johannesen et al., 2012b; Lind, 2018) fish species, and fish communities (borealization of the Barents Sea, Fossheim et al., 2015) and in increased biomass of krill, jellyfish and some pelagic and demersal fish stocks (Eriksen et al., 2012, 2017; Kjesbu et al., 2014; ICES 2019). These changes have resulted in changes in food webs in fish communities (Kortsch et al., 2015). Under these new conditions we can expect changes in diet composition of all fish species.

A clear difference in species by biogeography was seen for the hyperiid cluster (III), mainly Arctic species and in euphausiids and copepods cluster II, mainly Arctic-Boreal and boreal fish species. This reflects a difference in distribution of prey organisms, with *Themisto libellula* being an Arctic species, while *Meganyctiphanes norvegica* is boreal or *Thysanoessa inermis* is Arctic-boreal species (Dalpadado et al., 2002, 2008). With warming and redistribution of plankton and fish (ICES, 2019), we expected changes in the diet of Arcto-Boreal and Arctic species, especially fish belong to cluster III and some fish in cluster II-A, which feed on hyperiids and copepod of Arctic origin. Abundance and biomass of large copepod species (*Calanus finmarchicus* and *C. glacialis*) decreased, while the abundance of small copepods (*Pseudocalanus minutus*), which are not important prey, has increased in the northern area in recent years (ICES, 2019). Thus, Hyperiid-eaters, most likely this is partly explained by geography since the dominant hyperiid species *Themisto libellula* is mostly an Arctic species eaten by Arctic fish species. Thus, this group could be negatively affected by warming due to prey redistribution and/or decline of prey biomass (ICES, 2019).

M. norvegica is the largest euphausiids species and being advected from the Norwegian Sea into the western Barents Sea in 1990s-early 2000s (Drobysheva 1994; Zhukova et al., 2009; Orlova et al., 2013) and into the central and eastern Barents Sea in recent years (Eriksen et al., 2017; ICES, 2018). *M. norvegica* has not observed yet during the routine monitoring in the arctic part of the Barents Sea (ICES 2018), although we identified *M. norvegica* in fish diet. We selected nine arctic species, which were captured in the arctic part of the Barents Sea (north of 77°N and east of 30°E), and observed *M. norvegica* in diet of three species (*Lycodes pallidus*, *Boreogadus saida* and *Triglops nybelini*). The proportion of *M. norvegica* in diet consisted on average 2% only, and therefore their importance was negligible. However, this finding is important in terms

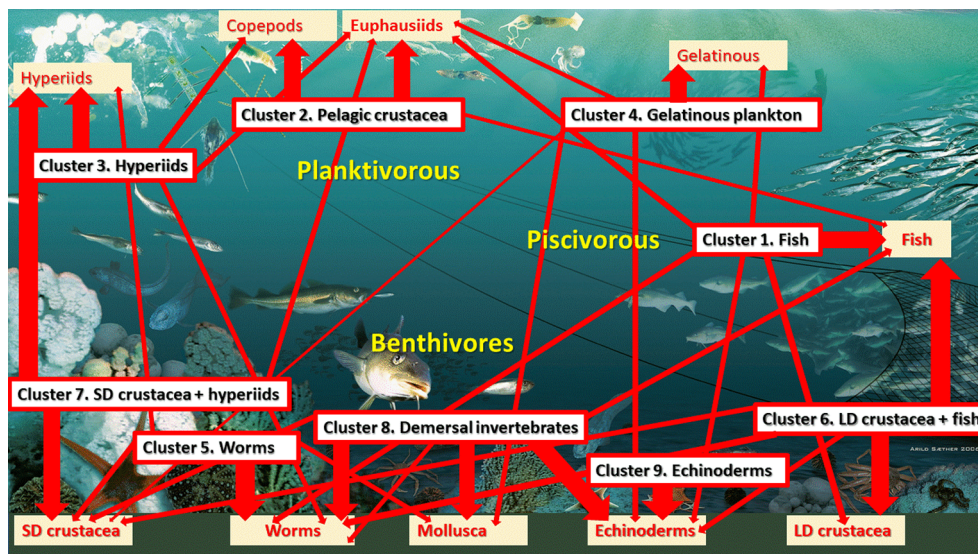


Fig. 6. Conceptual model for the Barents Sea trophic structure and interactions. The nine clusters or trophic groups of fish species (see Fig. 3) are linked to ten categories of prey with thick and thin arrows representing main and secondary prey groups, respectively.

of observation of further shift of *M. norvegica* and ability of arctic fish species to respond to changes in redistribution of boreal prey species.

Our results showed unusual dominance of gelatinous plankton in diet of northern wolffish, greater argentine and white barracudina. Ctenophora dominated of in the northern wolffish diet in the North-Atlantic (Albikovskaya, 1983, Torres et al., 2000, Román et al., 2004), and consisted 12% (%W) in the diet the Barents Sea (2000–2010, Dolgov, 2016). In 2015, each third northern wolffish consumed gelatinous (mainly Ctenophora) and > 50% of averaged diet (%W) contained Ctenophora. Ctenophores were seldom found in the diet of greater argentine in the Rockall Trough, a deep-water bathymetric feature to the northwest of Scotland and Ireland (Mauchline and Gordon 1983), while not observed in the Barents Sea (Dolgov, 2016). Gelatinous were not reported earlier in the diet of white barracudina (Salvanes, 2004, Dolgov 2016), but we found Ctenophors in one of seven stomachs with food. Increase of gelatinous plankton in the Barents Sea was associated with warming of during 1930–1950 (Zelickman 1970) and 2000s (Eriksen et al., 2012, 2015) and their increase in cod diet were also associated with increasing of fish size and the numbers (Eriksen et al., 2017). Results from 2015 showed that gelatinous were found in 200 stomachs (excluding 941 cod and 344 haddock stomachs) from 13 fish species, and their proportion increased with increasing of predator size. Mianzan et al. (1996) examined 69 species from the Argentine continental shelf and 35% of the fish species included some ctenophores during the spring bloom, while 15 to 23% of the fish species included some ctenophores during other seasons. Therefore, the increase proportion and frequency of occurrence of gelatinous plankton in the Barents fish diet could be linked to increased biomass and distribution of gelatinous due to warming, but could also reflect ontogenetic changes with fish grow, such as cod, or seasonal changes in the fish diet.

5. Conclusions

This paper has updated our knowledge about trophic interactions in the Barents Sea and supported earlier findings about the main functional groups across the species. Additionally, we provided a baseline, which could be useful in future investigation to identify changes in the diet.

The occurrence of new boreal krill species in the diet of arctic fish and occurrence of gelatinous plankton in diet of 15 fishes could be linked to increased biomass and distribution of these species in the Barents Sea due to warming.

The large material presented here is a first step to quantifying the production and energy flow through the Barents Sea food web and explore variation in time and space. We plan therefore, to work further with the data and investigate in detail ontogenetic changes in fish diet and diet similarity between size groups within and between species, that are needed to better understand feeding strategy and intra- and interspecies interactions. Furthermore, seasonal and spatial variation in the diet of 30 fishes in the Barents Sea will be send in this issue.

Synthesis of the TIBIA accumulated data will improve the knowledge base for food web dynamics in the Barents Sea to strengthen the input to Integrated Ecosystem Assessment through ecosystem and food-web models.

Acknowledgement

We would like to acknowledge economical support provided by the TIBIA project (Trophic Interactions in the Barents Sea – steps towards Integrated Assessment) funded by The Research Council of Norway (pr. nr 228880) and by IMR founded the WGIBAR project (Integrated Ecosystem Assessment for the Barents Sea, Nr15178).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2019.102262>.

References

- Albikovskaya, L.K., 1983. Feeding characteristics of wolffishes in the Labrador-Newfoundland region. NAFO Sci. Coun. Studies 6, 35–38.
- Andriyashev, A.P., 1986. Zoarcidae. In: Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the Northeastern Atlantic and the Mediterranean. Unesco, Paris, pp. 1130–1150.
- Anon, 1974. Methodical Manual on Investigations of Feeding and Trophic Relations of Fish Under Natural Conditions. Nauka Publishing, Moscow, pp. 254 (in Russian).
- Antipova, T.V., M.V. Kovtsova, 1982. Diurnal, seasonal and annual variations in feeding and condition of plaice of the Barents Sea. In: Ecology and fishery for demersal fish of the North-European basin, Selected Papers, PINRO, Murmansk, pp. 43–56. (in Russian).
- Atkinson, E.G., Percy, J.A., 1992. Diet comparison among demersal marine fish from the Canadian Arctic. Polar Biol. 11 (8), 567–573.
- Beamish, F.W.H., 1978. Swimming capacity. In: Hoar, W.S., Randall, D.J. (Eds.), Fish physiology. Academic Press, New York, pp. 101–187.
- Berestovsky, E.G., 1989. Feeding of skates *Raja radiata* Donovan and *Raja fyllae* Lutken (Rajidae) in the Barents and Norwegian Seas. J. Ichthyol. 29 (6), 994–1002 (in Russian).

- Bjelland, Holst, 2004. Other fish species and fish communities. In: Skjoldal, H.R. (Ed.), *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp. 357–370.
- Blaxter, J.H.S., 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc.* 115, 98–114.
- Bodini, A., Bellingeri, M., Allesina, S., Bondavalli, C., 2009. Using food web dominator trees to catch secondary extinctions in action. *Philosophical Transactions of the Royal Society of London. Series B: Biol. Sci.* 364, 1725–1731.
- Bogstad, B., Haug, T., Mehl, S., 2000. Who eats whom in the Barents Sea? *NAMMCO Sci. Publ.* 2, 98–119. <https://doi.org/10.7557/3.2975>.
- Briskina, M.M. 1939. Feeding of non-target fishes. *Proceedings of the Institute of Marine Fisheries and Oceanography of the USSR*, vol. 4, pp. 339–354 (in Russian).
- Brown, W.W., Cheng, C., 1946. Investigations into the food of the cod (*Gadus callarias* L.) off Bear Island, and of the cod and haddock (*G. aeglefinus* L.) off Iceland and the Murman coast. *Hull Bull. Marine Ecol.* 3 (18), 35–71.
- Bulycheva, A.I., 1948. Materials on feeding of flatfishes in Eastern Murman. *Proc. Marine Biol. Station USSR Acad. Sci.* 1 (C), 261–275 (in Russian).
- Chernova, N.V. 1989. Materials on feeding of *Liparis gibbus* (Scorpaeniformes: Liparidae). In: Podrazhanskaya, S.G. (Ed.). *Daily Diurnal Rhythms and Feeding Rations of Commercial Fishes of the in the World Oceans*, pp. 89–96. , VNIRO Press, Moscow, 215 pp. (in Russian).
- Dalpadado et al., this volume.
- Dalpadado, P., Bogstad, B., Gjøsæter, H., Mehl, S., Skjoldal, H.R., 2002. Zooplankton-fish interactions in the Barents Sea. In: Sherman, K., Skjoldal, H.R. (Eds.), *Large Marine Ecosystems of the North Atlantic*. Elsevier, pp. 269–291.
- Dalpadado, P., Yamaguchi, A., Ellertsen, B., Johannessen, S., 2008. Trophic interactions of macro-zooplankton (krill and amphipods) in the marginal ice zone of the Barents Sea. *Deep Sea Res. Part II* 55, 2266–2274.
- Dolgov, 1994. Some aspects of biology of non-target fish species in the Barents Sea. *ICES CM* 1994/O:12.
- Dolgov, A.V., 2005. Feeding and food consumption by the Barents Sea skates. *J. Northw. Atl. Fish. Sci.* 35, 495–503.
- Dolgov, A.V., 2016. Composition, formation and trophic structure of the Barents Sea communities. In: Sokolov, K.M. (Ed.), *Murmansk. PINRO Press, Murmansk*, pp. 336 (in Russian).
- Dolgov, A.V., Bogstad, B., Johannessen, E., Skern-Mauritzen, M., 2011a. An overview of trophic interactions in the Barents Sea. Chapter 8.1 (p. 431–437) in Jakobsen, T., Ozhigin, V.K. (Eds.) 2011. *The Barents Sea. Ecosystem, resources, management, Half a century of Russian-Norwegian cooperation*. Tapir Academic Press.
- Dolgov, A.V., Johannessen, E., Bogstad, B., 2011c. Benthivorous fish. Chapter 8.3 (pp. 455–465) In: Jakobsen, T., Ozhigin, V.K., (Eds.) 2011. *The Barents Sea. Ecosystem, resources, management. Half a century of Russian-Norwegian cooperation*. Tapir Academic Press.
- Dolgov, A.V., Johannessen, E., Heino, M., Olsen, E., 2010. Trophic ecology of blue whiting in the Barents Sea. *ICES J. Mar. Sci.* 67, 483–493.
- Dolgov, A.V., Orlova, E.L., Johannessen, E., Bogstad, B., Rudneva, G.B., Dalpadado, P., Mukhina, N.V., 2011b. Planktivorous fish. In: T. Jakobsen, K. Ozhigin (Eds.), *The Barents Sea Ecosystem, Resources, Management, Half a Century of Russian Norwegian Cooperation* (2011), pp. 438–454.
- Dolgov, A.V., Orlova, E.L., Johannessen, E., Bogstad, B. 2011d. Piscivorous fish. Chapter 8.4 (pp. 466–484). In: Jakobsen, T., Ozhigin, V.K., (Eds.) 2011. *The Barents Sea. Ecosystem, resources, management. Half a century of Russian-Norwegian cooperation*. Tapir Academic Press.
- Dolgov, A.V., Yaragina, N.A., Orlova, E.L., Bogstad, B., Johannessen, E., Mehl, S., 2007. 20th anniversary of the PINRO-IMR cooperation in the investigation of fish feeding in the Barents Sea- results and perspectives. In: Haug, T., Misund, O.A., Gjøsæter, H., Røttingen, I., (Eds.). *Long term bilateral Russian-Norwegian scientific co-operation as a basis for sustainable management of living marine resources in the Barents Sea. Proceedings of the 12th Norwegian Russian Symposium. IMR/PINRO Joint Report Series. Institute of Marine Research, Bergen, Norway*, vol. 5, pp. 44–78. 212 pp.
- Dommasnes, A., Christensen, V., Ellertsen, B., Kvamme, C., Melle, W., Nøttestad, L., Pedersen, T., et al., 2001. An Ecopath model for the Norwegian Sea and Barents Sea In *Fisheries impacts on North Atlantic ecosystems: models and analyses*. In: Guénette, S., Christensen, V., Pauly, D., (Eds.), *Fisheries Centre Research Reports*, vol. 9, no. 4, pp. 213–239.
- Drobysheva, S.S., 1994. *Euphausiids of the Barents Sea and their role for productivity* 139 (in Russian).
- Eriksen, E., Prozorkevich, D., Trofimov, A., Howell, D., 2012. Biomass of scyphozoan jellyfish, and its spatial association with 0-group fish in the barents sea. *PLoS One* 7 (3), e33050. <https://doi.org/10.1371/journal.pone.0033050>.
- Eriksen, E., Skjoldal, H.R., Dolgov, A.V., Dalpadado, D., Orlova, E.L., Prozorkevich, D.V., 2016. The Barents Sea euphausiids: methodological aspects of monitoring and estimation of abundance and biomass. *ICES J. Mar. Sci.* 73 (6), 1533–1544. <https://doi.org/10.1093/icesjms/fsw022>.
- Eriksen, E., and Gjøsæter, H., (Eds.), 2013. A monitoring strategy for the Barents Sea. Report from project no 14256 “Survey strategy for the Barents Sea”, vol. 2013, no. 28. Institute of Marine Research, Bergen. 73 pp.
- Eriksen, E., 2015. Do scyphozoan jellyfish limit the habitat of pelagic species in the Barents Sea during the late feeding period? *ICES J. Mar. Sci.* 73 (2), 217–226. <https://doi.org/10.1093/icesjms/fsv183>.
- Eriksen, E., Skjoldal, H.R., Gjøsæter, H., Primicerio, R., 2017. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Prog. Oceanogr.* 151, 206–226.
- Eriksen, E., Gjøsæter, H., Prozorkevich, D., Shamray, E., Dolgov, A., Skern-Mauritzen, M., Stiansen, J.E., Kovalev, Yu, Sunnanaa, K., 2018. From single species surveys towards monitoring of the Barents Sea ecosystem. *Prog. Oceanogr.* 166, 4–14. <https://doi.org/10.1016/j.pocan.2017.09.007>.
- Falk-Petersen, I.B., Frivoll, V., Gulliksen, B., Haug, T., Vader, W., 1988. Age/size relations of two snailfishes, *Liparis gibbus* and *Careproctus reinhardtii* (Teleostei, Liparidae) from Spitsbergen coastal waters. *Polar Biol.* 8 (5), 353–358.
- Fedorov, V.V., 1986. Cottidae. In: Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds.), *Fishes of the Northeastern Atlantic and the Mediterranean*. Unesco, Paris, pp 1243–1260.
- Fossheim, M., Primicerio, R., Johannessen, E., Ingvaldsen, R.B., Aschan, M.M., Dolgov, A.V., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* 5, 673–677.
- Griukovich, N.S., 1957. Year-to-year changes in feeding of the Barents Sea cod. *Trudy PINRO* 10, 88–105 (in Russian).
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Paleontol. Electronica* 4 (1), 9 pp.
- Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Mar. Biol. Res.* 9 (9), 878–894.
- Hunt Jr., G.L., Blanchard, A.L., Boveng, P., Dalpadado, P., Drinkwater, K.F., et al., 2013. The Barents and Chukchi Seas: comparison of two Arctic shelf ecosystems. *J. Mar. Syst.* 109–110 (2013), 43–68.
- ICES, 2018. Report of the Arctic Fisheries Working Group (AFWG), 18–24 April 2018, Ispra, Italy. *ICES CM* 2018/ACOM:06. 534 pp.
- ICES, 2019. The Working Group on the Integrated Assessments of the Barents Sea (WGBAR). *ICES Scientific Reports*. 1:42. 157 pp. <http://doi.org/10.17895/ices.pub.5536>.
- Iedson, M.R., 1929. On the nourishment of the food fishes in the Barents Sea. *Russian Hydrobiol. J.* 8 (10–12), 269–285.
- Jakobsen, T., Ozhigin, V.K., (Eds.), 2011. *The Barents Sea ecosystem, resources and management. Half a century of Russian-Norwegian cooperation*. Tapir Academic Press, Trondheim, Norway. 825 pp.
- Johannessen, E., Lindstrøm, U., Michalsen, K., Skern-Mauritzen, M., Fauchald, P., Bogstad, B., Dolgov, A.V., 2012a. Feeding in a heterogeneous environment: spatial dynamics in foraging Barents Sea cod. *Mar. Ecol. Prog. Ser.* 458, 181–197.
- Johannessen, E., Ingvaldsen, R., Dalpadado, P., Skern-Mauritzen, M., Stiansen, J.E., Eriksen, E., Gjøsæter, H., Bogstad, B., Knutsen, T., 2012b. Barents Sea ecosystem state: climate fluctuations, human impact and trophic interactions. *ICES J. Mar. Sci.* 69 (5), 880–889. <https://doi.org/10.1093/icesjms/fss046>.
- Johannessen, E., Johansen, G.O., Korsbrekke, K., 2015. Seasonal variation in cod consumption and growth in a changing sea. *Can. J. Fish. Aquat. Sci.* 2016 (73), 235–245.
- Juanes, F., Conover, D.O., 1994. Piscivory and prey size selection in young-of-the-year bluefish: predator preference or sizedependent capture success? *Mar. Ecol. Prog. Ser.* 114, 59–69.
- Keast, A., Webb, D., 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *J. Fish. Res. Board Can.* 23, 1845–1874.
- Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Ingvaldsen, R., Nash, R.D.M., Stiansen, J.E., 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. *PNAS* 111, 3478–3483. <https://doi.org/10.1073/pnas.1316342111>.
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V., Aschan, M., 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc. R. Soc. B* 282, 20151546. <https://doi.org/10.1098/rspb.2015.1546>.
- Langoy, H., Nøttestad, L., Skaret, G., Broms, C., Fernø, A., 2012. Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Mar. Biol. Res.* 8, 442–460.
- Lind, S., 2018. Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import. *Nat. Clim. Change*. <https://doi.org/10.1038/s41558-018-0205-y>.
- Makushok, V.M., 1986. Stichaeidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielse, J., Tortonese, E. (Eds.), *Fishes of the North-eastern Atlantic and the Mediterranean*, vol. 3. UNESCO, Paris, pp. 1122–1123.
- Martin, A., Gensch, R., Brown, C., 1946. Alternative methods in upland gamebird food analysis. *J. Wildl. Manag.* 10, 8–12. <http://www.jstor.org/stable/10.2307/3795806>.
- Mauchline, J., Gordon, J.D.M., 1983. Diets of clupeoid, stomiatoid and salmonoid fish of the Rockall Trough, northeastern Atlantic Ocean. *Mar. Biol.* 1983 (77), 67–78.
- Mecklenburg, C.W., Lynghammer, A., Johannessen, E., Byrkjedal, I., Christiansen, J.S., Dolgov, A.V., Karamushko, O.V., Mecklenburg, T.A., Møller, P.R., Steinke, D., Wienerroither, R.M., 2018. Marine Fishes of the Arctic Region. *Conservation of Arctic Flora and Fauna, Akureyri, Iceland*. ISBN: ISBN 978-9935-431-70-7.
- Mehl, S., Yaragina, N.A., 1992. Methods and results in the joint PINRO-IMR stomach sampling program. In: Bogstad, B., Tjelmeland, S. (Eds.), *Interrelations between fish populations in the Barents Sea, Proceedings of the Fifth PINRO-IMR Symposium, Murmansk, 12–16 August 1991*. pp. 5–16.
- Mianzan, H.W., Prenske, M.N., Sanchez, F., 1996. Fish predation on neritic ctenophores from the Argentine continental shelf: a neglected food resource? *Fish. Res.* 27, 69–79.
- Michalsen, K., Dalpadado, P., Eriksen, E., Gjøsæter, H., Ingvaldsen, R., et al., 2011. The joint Norwegian-Russian ecosystem survey: overview and lessons learned. In: *Proceeding of the 15th Norwegian-Russian Symposium Svalbard Climate change and effects on the Barents Sea marine living resources. 7–8 September August 2011. IMR/PINRO Joint Report Series* pp. 247–272.
- Michalsen, K., Dalpadado, P., Eriksen, E., Gjøsæter, H., Ingvaldsen, R.B., Johannessen, E., Jørgensen, L.L., Knutsen, T., Prozorkevich, D., Skern-Mauritzen, M., et al., 2013. Eight years of ecosystem surveys in the Barents Sea – Review and recommendations. *Mar. Biol. Res.* 9, 32–947.
- Monstad, T., 2004. Blue whiting. In: Skoldal, H.R. (Ed.), *The Norwegian Sea ecosystem*. Tapir, Trondheim, pp. 263–288.

- Nielsen, L.A., 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* 37, 11–19.
- Orlova, E.L., Boitsov, V.D., Dolgov, A.V., Rudneva, G.B., Nesterova, V.N., 2005. The relationship between plankton, capelin, and cod under different temperature conditions. *ICES J. Mar. Sci.* 62, 1281–1292.
- Orlova, E.L., Boitsov, V.D., Nesterova, V.N., 2010. The influence of hydrographic conditions on the structure and functioning of the trophic complex plankton – pelagic fishes – cod. *Murmansk Print. Comp., Murmansk*, pp. 190.
- Orlova, E.L., Dolgov, A.V., Rudneva, G.B., Oganin, I.A., Konstantinova, L.L., Orlova, E.L., Prokopchuk, I.P., Rudneva, G.B., Nesterova, V.N., Gabova, O.V., 2009. Trophic relations of capelin *Mallotus villosus* and polar cod *Boreogadus saida* in the Barents Sea as a factor of impact on the ecosystem. Results of comparative analysis of zooplankton catchability by Juday and WP2 nets. *Deep-Sea Research II Bulletin of MOIP. Biological department*, vol. 56114, no. 21–225, pp. 205459–206768 (in Russian).
- Orlova, E.L., Dolgov, A.V., Renaud, P.E., Boitsov, V.D., Prokopchuk, I.P., Zashihina, M.V., 2013. Structural changes in the macroplankton–pelagic fish–cod trophic complex caused by climatic effects. *Mar. Biol. Res.* 9 (89), 851–866.
- Persson, L., 1990. Predicting ontogenetic niche shifts in the field: what can be gained by foraging theory? In: Hughes, R.N. (Ed.), *Behavioural Mechanisms of Food Selection*. Springer-Verlag, Berlin, pp. 303–321.
- Planque, B., Primiticchio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjøsaeter, H., et al., 2014. Who eats whom in the Barents Sea: a food web topology from plankton to whales (Data paper). *Ecology* 95, 1430.
- Ponomarenko, I.Ya., 1958. Feeding of juvenile cod in the southern Barents Sea during winter 1956/57. *Sci.-tech. Bull. PINRO* 3 (7), 28–32 (in Russian).
- Ponomarenko, V.P., Ponomarenko, I.Ya., Yaragina, N.A., 1978. Consumption of the Barents Sea capelin by cod and haddock in 1974–1976. *Trudy PINRO* 41, 53–66 (in Russian).
- Ponomarenko, I.Ya., Yaragina, N.A., 1985. Seasonal and year-to-year dynamics of frequency of occurrence of capelin (*Mallotus villosus villosus*) in the feeding of the Barents Sea cod. In: *Feeding and Food Supply of Fishes on Early Ontogenetic Stages as a Factor of Formation of its Abundance, Growth and Concentrations*, pp. 3–19. VNIRO Press, Moscow. (in Russian).
- Ponomarenko, I.Ya., Yaragina, N.A., 1990. Year-to-year dynamics of the Barents Sea cod on capelin, euphausiids and shrimp and yearly consumption of these prey. *Food resources and trophic relations of fish in the North Atlantic*. PINRO Press, Murmansk (in Russian).
- Popova, O.A., 1978. The role of predaceous fish in ecosystems. In: Gerking, S.D. (Ed.), *Ecology of Freshwater Fish Production*. John Wiley & Sons, New York, pp. 215–249.
- Prozorkevich, D., Sunnanå, K., (Eds.), 2016. Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea and adjacent waters, August–October 2015. *IMR/PINRO Joint Report Series*, No. 1/2016, 77 pp.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>.
- Román, E., González, C., Ceballos, E., 2004. Food and feeding of most abundant fish species in Flemish Cap. *NAFO SCR Doc.* 04/58 Serial No. N5018. 17 pp.
- Rousseeuw, P.J., 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *J. Comput. Appl. Math.* 20, 53–65.
- Salvanes, A.G.V., 2004. Mesopelagic fish. In: Skoldal, H.R. (Ed.), *The Norwegian Sea Ecosystem*. Tapir, Trondheim, pp. 301–314.
- Scharf, F.S., Juanes, F., Rountree, R.A., 2000. 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.* 208, 229–248. <https://doi.org/10.3354/meps208229>.
- Shevelev, M.S., Kuz'michev, A.P., 1990. New biological data about the northern wolffish *Anarhichas latifrons*. *Vopr. Ikhtiol.* 30 (3), 386–391 (in Russian).
- Shevelev, Johannessen, 2011. Wolffish. Chapter 5.10. In: Jakobsen, T., Ozhigin, V.K., (Eds.), *The Barents Sea. Ecosystem, Resources, Management. Half a Century of Russian-Norwegian Cooperation*. Tapir Academic Press, pp. 329–338.
- Simberloff, D., Dayan, T., 1991. The Guild Concept and the Structure of Ecological Communities. *Annu. Rev. Ecol. Evol. Syst.* 22, 115–143. <https://doi.org/10.1146/annurev.es.22.110191.000555>.
- Syssoeva, T.K., 1958. Feeding of the Barents Sea cod in 1957. *Sci.-Tech. Bull. PINRO* 3 (7), 17–22 (in Russian).
- Swanson, G.A., Krapu, G.L., Bartonek, J.C., Serie, J.R., Johnson, D.H., 1974. Advantages in mathematically weighting waterfowl food-habits data. *J. Wildl. Manage.* 38, 302–307.
- Tibshirani, R., Walther, G., Hastie, T., 2001. Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society. Series B: Statist. Methodol.* 63, 411–423.
- Tjelmeland, S., Bogstad, B., 1989. MULTSPEC-A review of a multispecies modelling project of the Barents Sea. *Fish. Res.* 38, 127–142.
- Torres, P., Rodríguez-Marín, E., Loureiro, I., 2000. Preliminary results from feeding analysis for the most abundant demersal fishes in Flemish Cap during summer (1993–2000). *NAFO SCR Doc.* 00/60 Serial No. 4302.
- Townhill, B.L., Maxwell, D., Engelhard, G.H., Simpson, S.D., Pinnegar, J.K., 2015. Historical arctic logbooks provide insights into past diets and climatic responses of cod. *PLoS One* 10, e0135418. <https://doi.org/10.1371/journal.pone.0135418>.
- Webb, P.W., 1976. The effect of size on the fast-start performance of rainbow trout, *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. *J. Exp. Biol.* 65, 157–177.
- Wienerroither, R., Johannesen, E., Dolgov, A., Byrkjedal, I., Bjelland, O., Drevetnyak, K., Eriksen, K.B., Høines, Å., Langhelle, G., Langøy, H., Prokhorova, T., Prozorkevich, D., Wenneck, T., et al., 2011. Atlas of the Barents Sea Fishes. *IMR/PINRO Joint Report Series* 1–2011, 274 pp.
- Yaragina, N.A., Dolgov, A.V., 2011. Long-term variations in the importance of prey species for demersal fishes in the Barents Sea under climate change. In: Haug, T., Dolgov, A.V., Drevetnyak, K., Røttingen, I., Sunnanå, K., Titov, O. (Eds.), *Climate Change and Effects on the Barents Sea Marine Living Resources*. 15th Russian-Norwegian Symposium Longyearbyen, 7–8 September 2011, *IMR/PINRO Joint Report Series* 2–2011, pp. 160–180. Institute of Marine Research, Bergen, 290 pp.
- Zatsepin, V.I., 1939. Feeding of haddock (*Melanogrammus aeglefinus* L.) in the area off the Murman Coast relative to bottom fauna. *Trudy PINRO* 3, 39–96 (in Russian).
- Zatsepin, V.I., Petrova, N.S., 1939. Feeding of cod in the southern part of the Barents Sea (by observations in 1934–1938). *Proc. PINRO* 5, 1–170 (in Russian).
- Zenkevich, L.A., Brotskaya, V.A., 1931. Materials on the feeding of the Barents Sea fishes. *Proc. 1st ses. GOIN* 4, 1–35 (in Russian).
- Zhukova, N.G., Nesterova, V.N., Prokopchuk, I.P., Rudneva, G.B., 2009. Winter distributions of euphausiids (Euphausiacea) in the Barents Sea (2000–2005). *Deep Sea Res.* 56, 1959–1967.