

# Cod diet as an indicator of Ctenophora abundance dynamics in the Barents Sea

E. Eriksen<sup>1,\*</sup>, B. Bogstad<sup>1</sup>, A. Dolgov<sup>2</sup>, I. M. Beck<sup>1</sup>

<sup>1</sup>Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway

<sup>2</sup>Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6 Knipovich Street, Murmansk 183038, Russia

**ABSTRACT:** There is growing scientific interest in gelatinous zooplankton, including Ctenophora, as prey and their role in the ecosystem. Ctenophora are difficult to sample using traditional methods. Fish stomach content data is one possible indicator of variations in the abundance of Ctenophora, although predation by fish on gelatinous zooplankton such as Ctenophora is generally low. We examined Atlantic cod *Gadus morhua* as epibenthic feeders that are distributed widely in the Barents Sea. More than 340 000 cod stomachs analysed for the period 1984–2014 were used to investigate the occurrence of Ctenophora in the cod diet. Ctenophora was found in about 5% of stomachs analysed, and generally low mass and low frequency of occurrence indicated that Ctenophora is not an important food item for cod. Cod mainly preyed on Ctenophora in the eastern and southern part of the Barents Sea in the autumn to early winter period. The proportion of Ctenophora in the cod diet increased with increasing cod size, especially in recent years, when the number of large cod in the stock increased considerably. An increased amount of Ctenophora in cod diet was observed during more recent years, with higher water temperature. The ongoing warming seems to be favourable for Ctenophora in the Barents Sea. This study showed that lack of data on the amount and distribution of Ctenophora could be partially solved by using predator diets.

**KEY WORDS:** Ctenophora · Distribution · Cod diet · Barents Sea · Climate

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

The abundance of gelatinous zooplankton, including medusae, ctenophores and pelagic tunicates, varies in many marine ecosystems around the globe (Condon et al. 2013). Seasonal increases ('blooms') and long-term, multiyear increases in ctenophores are documented in many of these ecosystems (Purcell & Arai 2001, Purcell et al. 2007). There has been a growing scientific interest in gelatinous zooplankton as prey in recent decades (Arai et al. 2003, 2005, Condon et al. 2013).

The Barents Sea ecosystem has undergone a rapid environmental change during the past few decades, with a warming trend with increasing peaks since the mid-1980s and the recent decades being the

warmest on record (Jakobsen & Ozhigin 2011). Climate warming can affect the distribution and biomass of marine species, reorganize ecological communities and influence ecosystem function (Fosheim et al. 2015, Kortsch et al. 2015, Quiñones et al. 2015, Eriksen 2016, Eriksen et al. 2017).

Sampling gelatinous zooplankton remains a major challenge (Hamner et al. 1975, Weisse et al. 2002, Purcell 2009). A range of methods and gear have been used during the Barents Sea monitoring surveys, from plankton nets to pelagic and demersal trawls (Michalson et al. 2011); however, there are still limitations regarding sampling gear and the vertical distribution of organisms. Small plankton nets underestimate ctenophores due to avoidance, while trawls underestimate them due to extrusion through the meshes or damage

to fragile ctenophores in the cod end. High densities of ctenophores have been observed near the bottom (e.g. Costello & Mianzan 2003) and are thus under-sampled by the trawls, which sample the upper 50 m (pelagic) and 5 to 10 m above the bottom (demersal). One way to overcome sampling difficulties for such organisms is to use fish stomachs as a sampling tool (Fahrig et al. 1993, Frid & Hall 1999, Link & Ford 2006). Despite some investigations on Ctenophora that were conducted in the Barents Sea (e.g. Kamshilov 1961, Zelikman 1972), there are no long-term data on abundance dynamics of this important plankton group. We examined whether Atlantic cod *Gadus morhua*, as epibenthic feeders, may be particularly good samplers for ctenophores, and whether changes in the frequency of occurrence and importance of ctenophores in the cod diet may reflect the dynamics of their abundance in the Barents Sea ecosystem, and likely also in other marine ecosystems.

The population of Atlantic cod in the Barents Sea (also called the Northeast Arctic cod) is the most important species in this ecosystem both in terms of fisheries and ecologically. The Barents Sea cod (BS cod) is currently the largest cod stock in the world by far and supports one of the largest fisheries globally, with a long-term (70 yr) average catch of 665 000 t and higher catches in recent years (ICES 2016). The biology of the BS cod stock is described e.g. by Yaragina et al. (2011). The stock has increased substantially over the past few decades, driven to a large extent by strong recruitment related to favourable climatic conditions combined with good management practices (meaning reduced fishing mortality) based on extensive monitoring and scientific advice (Bogstad et al. 2013, 2015, Kjesbu et al. 2014, ICES 2017).

During the past warm decade, the cod stock has covered most of the Barents Sea shelf in autumn (August–September), and it has also expanded northwards during winter (Johansen et al. 2013). The warming has allowed an expansion of cod distribution to include the northern and northeastern part of the Barents Sea, which was previously in the Arctic domain and not available for cod (Kjesbu et al. 2014, Fossheim et al. 2015) but with rather good food resources for cod (Dolgov & Benzik 2014). The Barents Sea capelin is a main prey for the BS cod, and consumption of alternative food increased during the capelin collapses (Link et al. 2009, Dolgov & Benzik 2016). Cod diet in the Barents Sea has been studied during the past 65 yr and is summarized in numerous publications (references in Dolgov et al. 2007). The diet of BS cod is relatively diverse, but is dominated by fish and crustaceans.

The objective of our study was to determine the importance of Ctenophora as prey for cod from the northeast Arctic. We used several indices to determine how important ctenophores are in the cod diet, and how often, where and when they are consumed as potential indicators of the relative abundance of these gelatinous organisms in the Barents Sea ecosystem. We also studied the spatial distribution of Ctenophora based on cod diet, and linked changes in the abundance and distribution of Ctenophora to dietary changes in cod (ctenophores vs. other food items) due to ongoing warming.

## MATERIALS AND METHODS

### Study area

The Barents Sea is a high-latitude, Arcto-boreal shallow shelf sea, where the circulation is dominated by the Norwegian Atlantic Current (partly as a continuation of the Gulf Stream) entering through Bear Island Trench to the west of the Barents Sea (Fig. 1). The heat content of the Atlantic water leads to relatively mild conditions in the western and southern regions, whereas cold Arctic water entering from the northeast causes Arctic conditions to prevail in the northern and eastern regions of the Barents Sea (Ozhigin et al. 2011). The Atlantic and Arctic water masses are separated by the Polar Front and the location of the Front is mainly defined by the Barents Sea bottom topography).

There are several hundred species of zooplankton in the Barents Sea including copepods, pteropods, chaetognaths, and a variety of gelatinous forms such as ctenophores, small hydromedusae and larger jellyfishes. The Barents Sea fish community is dominated by a few large commercially and ecologically important stocks, such as the Northeast Arctic cod *Gadus morhua*, Barents Sea capelin *Mallotus villosus*, Northeast Arctic haddock *Melanogrammus aeglefinus* and Norwegian spring-spawning herring *Clupea harengus*. The Barents Sea serves as a nursery area for the offspring of these fish stocks, which spawn along the Norwegian and Murman (Russia) coasts.

During the study period, the temperature conditions changed from cold in the 1980s to moderate in the 1990s and the warmest temperatures ever recorded in the 2000s (ICES 2017). Warmer temperature ( $T$ ) conditions in the Barents Sea are associated with an increased coverage of Atlantic ( $T > 3^{\circ}\text{C}$ ) and mixed ( $0 < T < 3^{\circ}\text{C}$ ) waters and reduced sea-ice cover (Ozhigin et al. 2011, Eriksen et al. 2017, ICES 2017).

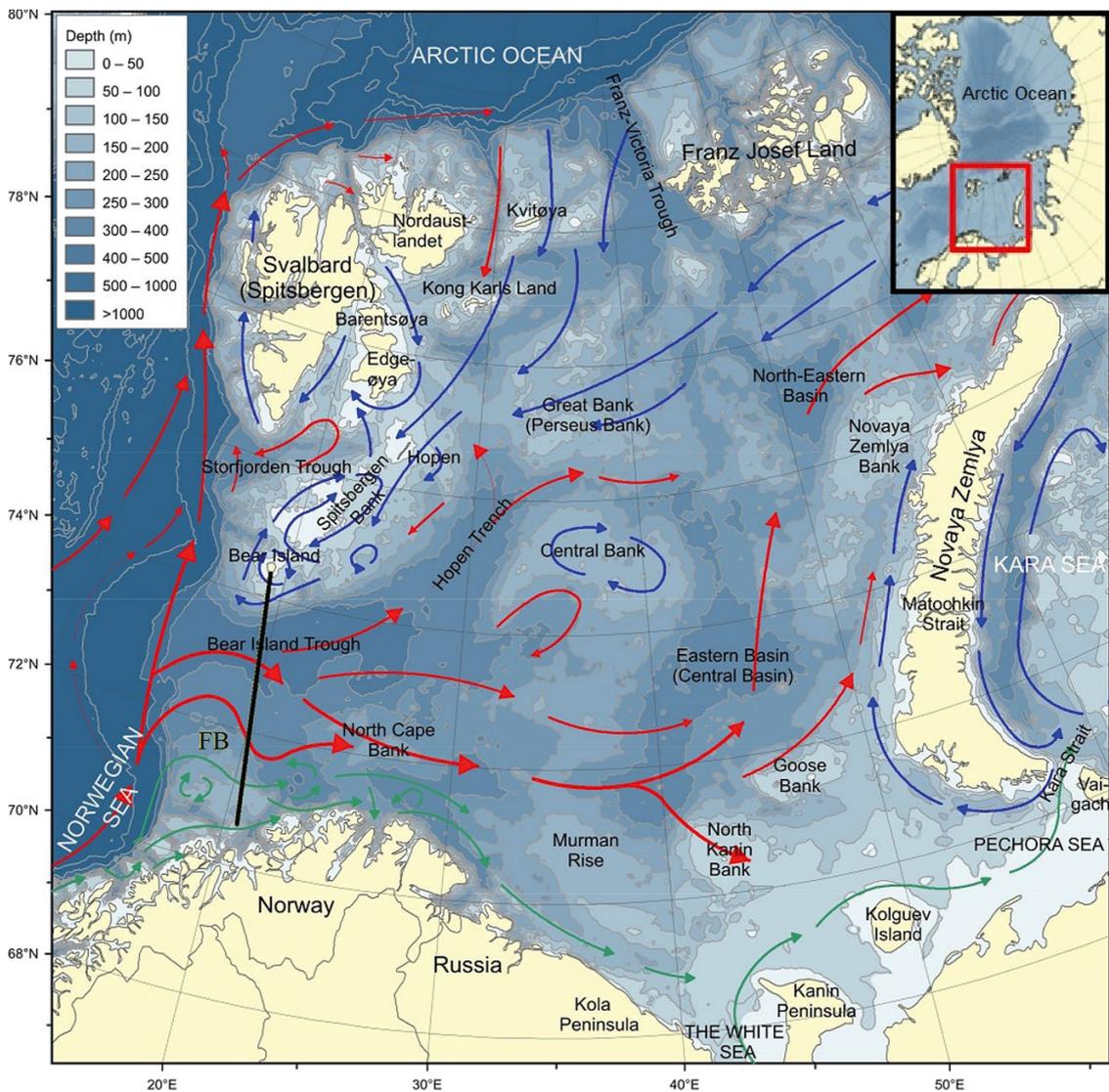


Fig. 1. The Barents Sea. Red arrows show Atlantic water currents, blue arrows show Arctic currents and green arrows show currents of coastal waters. The black line shows the position of the Fugløya-Bear Island oceanographic transect (FB)

### Stomach sampling programme

A broad-scale and long-term sampling programme of cod stomach contents from the Barents Sea conducted by the Institute of Marine Research (IMR, Norway) and the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia) aimed to identify changes in the fish diet and changes in the underlying ecosystem (Mehl & Yaragina 1992, Dolgov et al. 2007). Cod stomach data were collected from scientific surveys and commercial fisheries throughout the year in the Barents Sea. All Norwegian data were collected on research vessels. Russian data were mainly collected on research vessels dur-

ing Russian and joint Russian–Norwegian surveys, but a considerable part of the data was also collected onboard commercial vessels (from 10–25% during 1986–1995 and 2008–2014 to 46–58% during 1996–2007; mean = 33% in Russian data from commercial vessels). Data on the total stomach content (g) and the prey composition (g and % occurrence) and number were recorded. Additionally, cod length, weight and sex were recorded. Data on Ctenophora as prey for cod have been recorded during the whole period of stomach sampling starting in 1984, although this dataset has never been analysed with respect to trends in this taxon. Most of the data were collected during the scientific surveys, covering the ice-free

area of the Barents Sea (see more information about the surveys in Eriksen & Gjørseter 2013). Data from the commercial fisheries are more spatially and temporarily limited and related to commercial fleet locations, and thus not always representative for the whole stock. However, including the data from commercial vessels improves the spatial and temporal coverage, and also provides considerably more data for larger cod. Size-stratified sampling (1 fish in each 5 cm length interval) was used under Norwegian and joint Norwegian-Russian scientific surveys, while for data from commercial vessels and national Russian surveys usually 25 stomachs (random sample) are analysed from 1 to 3 trawls per day and each trawl station (Dolgov et al. 2007). During the commercial fishery and scientific surveys, some cod stomachs were examined and the prey were identified onboard the ship immediately, while other cod stomachs were fixed in formalin (in Russia up to the mid-1990s) or frozen immediately and later examined in the lab. Ctenophores have a special porridge-like consistency, structure and colour (which varies from pink to light yellow-red) in cod stomachs and thus could be easily identified. It was usually difficult or impossible to identify the ctenophores to the family or species level. Due to the large amount of data collected (more than 300 000 stomachs) and omnivorous diet of cod we limited the data by focusing on Ctenophora as prey, while all other prey taxa were combined into 1 group. An overview of stomach samples by year, month and cod length group is given in Figs. 2 & 3.

### Biological data

Costello (1990) and Amundsen et al. (1996) suggested different methods to calculate prey relative abundance (or contribution to the stomach contents). Costello (1990) defined relative abundance of prey as the percentage of total stomach contents (volume, weight or numbers) in all predators of a spe-

cies in which at least 1 individual's stomach contained that given prey. In contrast, Amundsen et al. (1996) proposed the calculation of the 'prey-specific abundance of prey', which takes into account only those predators in which the actual prey occurs. To

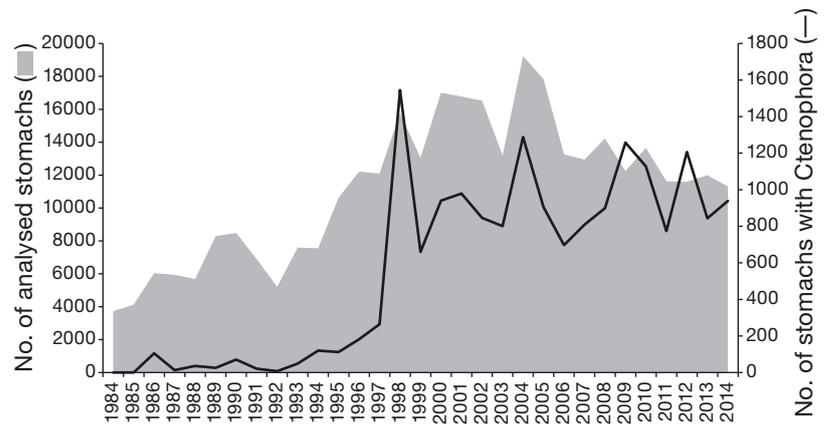


Fig. 2. Number of cod stomachs investigated in 1984–2014 (grey area) and number of stomachs with Ctenophora (black line). Note that no stomachs contained Ctenophora in 1984–1985

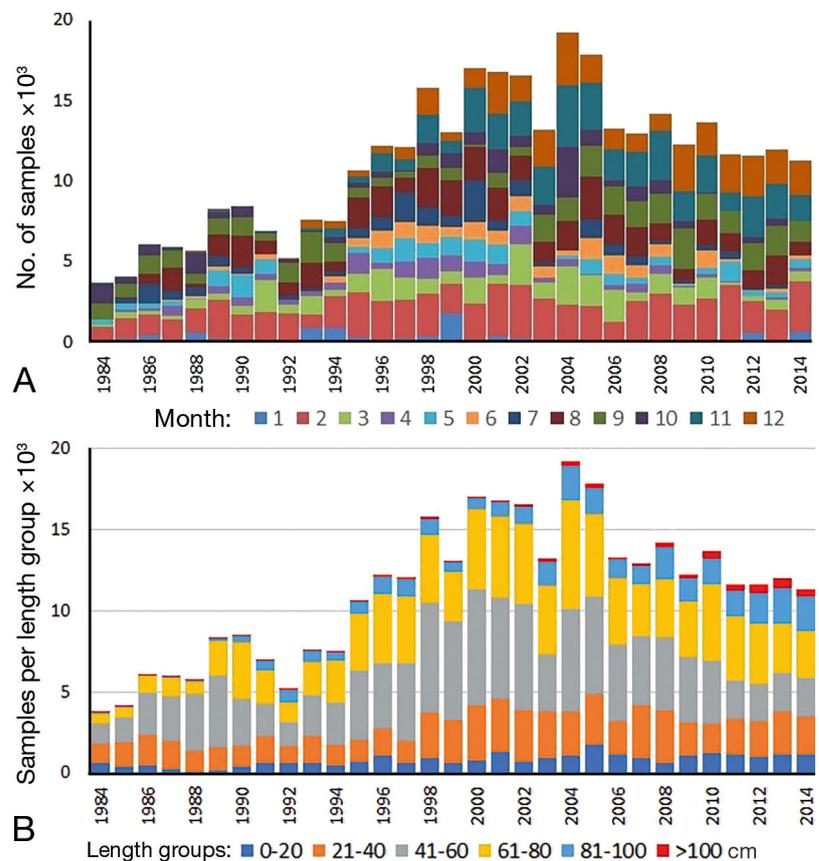


Fig. 3. Sampling extent. (A) Number of samples (in 1000s) collected during the year and month shown with different colour. Month numbers 1 to 12 correspond to months January to December. (B) Number of samples collected per length group (in 1000s), with length given in cm

evaluate the seasonal and annual variability of Ctenophora in cod diets we calculated the following indicators, which provide different insights into the feeding habits of the fish (Borutski 1974, Hyslop 1980): frequency of occurrence index (%FI =  $(N_i/N) \times 100$ , where  $N_i$  is the number of stomachs with Ctenophora, while  $N$  is the total number of non-empty stomachs); %W (%W =  $W_i \times 100/W_t$ , where  $W_i$  is the sum of weights of Ctenophora in stomach contents, while  $W_t$  is the sum of weights of other prey); and the partial fullness index (PFI, Lilly & Fleming 1981, for Ctenophora),  $PFI = 10\,000 \times W/L^3$ , where  $W$  is the wet weight of Ctenophora (in g) and  $L$  is the cod length (cm). PFI values were also estimated for males and females separately to test whether the amount of Ctenophora in the stomach differs between the sexes (using Welch's  $F$ -test). We calculated minimum length ( $L_{min}$ ), average length ( $L_{mean}$ ) and maximum length ( $L_{max}$ ) of cod for each year to study length distribution of cod feeding on Ctenophora. We tested for statistically significant trends in the data using the Mann-Kendall test and for correlations between different time series with Pearson correlations using the software PAST 3.14 (Hammer et al. 2001). We also studied the spatial distribution of the Ctenophora eaten by cod during the study period. The Ctenophora data (PFI) were gridded as average values for  $60 \times 60$  n mile grid cells covering the whole Barents Sea by the software Manifold 8.0. The size of the grid cells corresponds to  $1^\circ$  latitude but due to the Earth's curvature they do not align with either latitude or longitude lines. Distribution maps are presented for 3 periods (1986–1997, 1998–2008 and 2009–2014) and quarters of the years (the first 2 quarters are combined due to the low content of Ctenophora at this time of the year).

### Environmental data

Temperature of the Atlantic water in the Barents Sea was measured monthly in the standard oceanographic section Fugløya-Bear Island (FB,  $70^\circ 30' N$  and  $20^\circ 00' E$  to  $74^\circ 15' N$  and  $19^\circ 10' E$ ; Fig. 1) by the IMR. The water temperature (Temp FB) was measured by CTD at predetermined stations along the FB section. Time series of areas of Atlantic water (AW,  $T > 3^\circ C$ ) and mixed water (MW,  $0 < T < 3^\circ C$ ) were taken from the Working Group on the Integrated Assessments of the Barents Sea (WGIBAR) report (ICES 2017). Here, we use a time series of annual temperatures at 50–200 m depth taken from the part of Atlantic inflow and areas of AW and MW to evaluate the effect of recent warming on Ctenophora.

Canonical correlation analysis (CCA) was used to study the associations between groups of biological (%FI, %W, PFI,  $L_{min}$ ,  $L_{mean}$ ,  $L_{max}$ ) and environmental (Temp FB, AW and MW) quantities. CCA is a multivariate ordination technique, which is a form of linear regression between 2 sets of variables and these dimensions are established to maximize the correlation between biological and environmental variables. Stratigraphically constrained clustering (using the UPGMA algorithm) of years based on biological (%FI, %W, PFI,  $L_{min}$ ,  $L_{mean}$ ,  $L_{max}$ ) and environmental (Temp FB, AW and MW) variables for the period 1984–2014 were used to identify different periods within the study period. CCA and clustering analyses were performed using the software PAST 3.14 (Hammer et al. 2001). Data were standardized to zero mean and unit variance for CCA.

## RESULTS

Over the study period (1984–2014) approximately 347 000 cod stomachs were analysed, of which approximately 82 000 (24%) were empty, and Ctenophores were found in more than 17 000 (5%) (Fig. 2). Of the stomachs with Ctenophora, 5% also contained other food, indicating that some cod consume Ctenophora whether other prey are available or not. Note that no stomachs contained Ctenophora in 1984 to 1985.

### Temporal and size-related variation

Distinct trends of increasing abundance of Ctenophora in the cod diet were observed from 1984 to 2014. The %FI for Ctenophora showed an increasing trend ( $R^2 = 0.76$ ) from the 1980s to 2014: from 0–4% in 1984–1997 to 7–13% since 1998 (Fig. 4). Ctenophora have occurred in 3 waves, peaking in 1998, 2009 and 2012, with %FI values over 12%. A similar increasing trend ( $R^2 = 0.76$ ) was seen in the weight proportion of Ctenophora in the cod diet (%W; Fig. 4).

The PFI of Ctenophora in cod stomachs varied between seasons. The PFI was lowest during the first 2 quarters of the year, with an average of 0.01 (January–June; Fig. 5). The average increased to 0.03 during Quarter 3 and 0.08 in Quarter 4 (October–December; Fig. 5). The PFI of Ctenophora in cod stomachs reached the highest level in October–December, and values were around 0.15 in 2009–2014. The PFI showed a statistically significantly increasing trend (Mann-Kendall test  $R^2 = 0.74$ ) over the period.

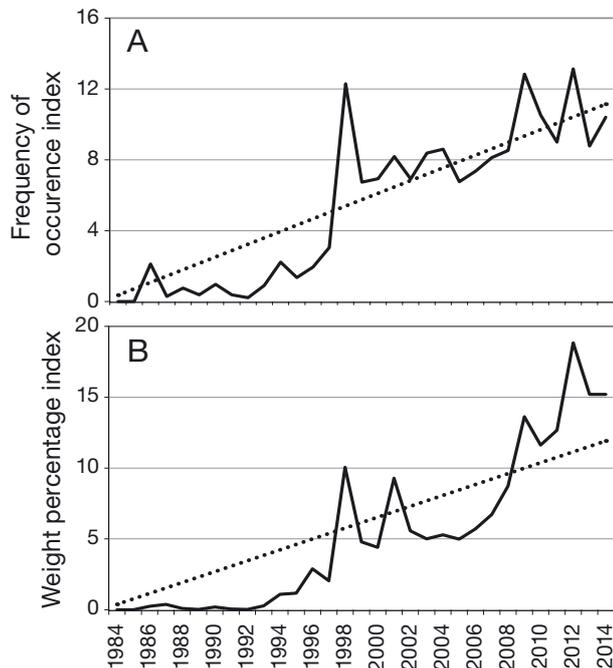


Fig. 4. (A) Frequency of occurrence index (%FI) and (B) weight percentage index (%W) of Ctenophora in cod diet (solid lines) and regression lines (dotted) showing an increasing trend for %FI and %W ( $R^2 = 0.76$  and  $0.71$ , respectively) over the period

Cod with lengths between 15 and 141 cm were observed to consume ctenophores. There was a significant increasing trend in the maximum ( $p < 0.001$ ,  $R^2 = 0.80$ ) and mean ( $p < 0.001$ ,  $R^2 = 0.58$ ) length of cod (Fig. 6), and this is related to the larger cod being more numerous during the last part of the period (Kjesbu et al. 2014, ICES 2016). The minimum ( $p <$

$0.001$ ,  $R^2 = 0.71$ ) length of cod decreased over the time series, which means that smaller cod were observed to consume ctenophores in the recent warm years.

The content of Ctenophora in cod stomachs, expressed as the PFI, also varied between fish of different length groups. Cod with a body length of  $\leq 60$  cm consumed Ctenophora sporadically, and the PFI of Ctenophora was low, with an average of 0.002 (1984–2014). Cod  $\geq 61$  cm consumed Ctenophora regularly, especially during the 2000s (Fig. 7). The highest feeding level was observed in cod of 81 to 100 cm, with an average PFI higher than 0.1 for the period 1984–2014. During the period of high Ctenophora consumption, PFI and %W increased to 0.3 and 19, respectively, and was highest in the last 6 yr.

Since 2000, the cod stock has increased and has been at a high level since 2009 (ICES 2016). An increased spawning stock biomass of cod, indicating mature fish (generally larger than 60 cm), was significantly correlated with increased feeding on Ctenophora (Pearson correlation for cod spawning stock biomass and %W:  $r = 0.79$ ,  $p < 0.001$ ). Since 2010, the proportion of large fish ( $> 100$  cm) in the cod stock has increased, and this increase of Ctenophora in cod diet indicates that cod stock may be able to switch to alternative food (see 'Discussion: Importance of Ctenophora in cod diet').

We also tested whether the Ctenophora content of stomachs differed between female and male cod. There was a statistically significant difference between the sexes, with males consuming more Ctenophora, especially in recent years (Welch's  $F$ -test,  $F = 3.2$ ,  $p = 0.001$ ).

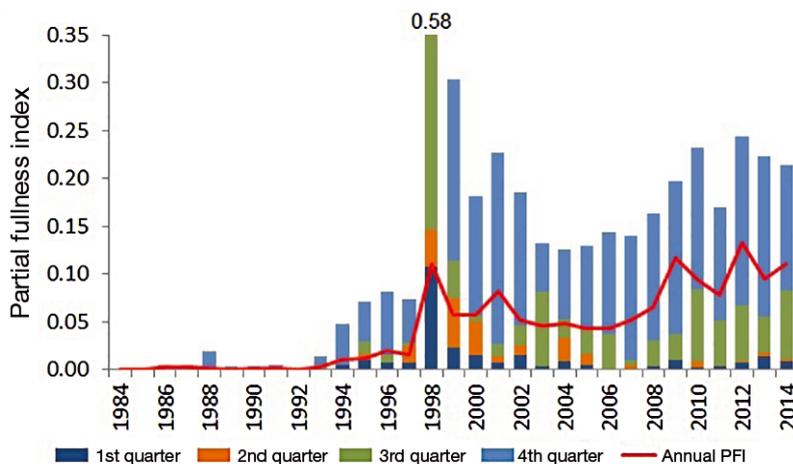


Fig. 5. Annual partial fullness index (PFI) of Ctenophora in cod diet in the Barents Sea during 1984–2014 (red line shows a statistically significant increasing trend). Ctenophora PFI in the cod diet were divided into quarters (1: January–March; 2: April–June; 3: July–September; and 4: October–December to show interseasonal variation in diet

## Environmental drivers

During the 1980s, lower temperatures were observed in the Fugløya-Bear Island section and a small area influenced by Atlantic water. During the 1990s, both temperature and the areas of warm Atlantic and mixed water masses increased. This was followed by a warm period, with record warm years in 2006 and 2007, and large areas of warm waters, decreasing somewhat during the last 4 yr of the study period. The study period can be broadly divided into 2 segments based on differences in the oceanographic and biological variables before and after 1998, as shown by hierarchical clustering (Fig. 8). Each of these

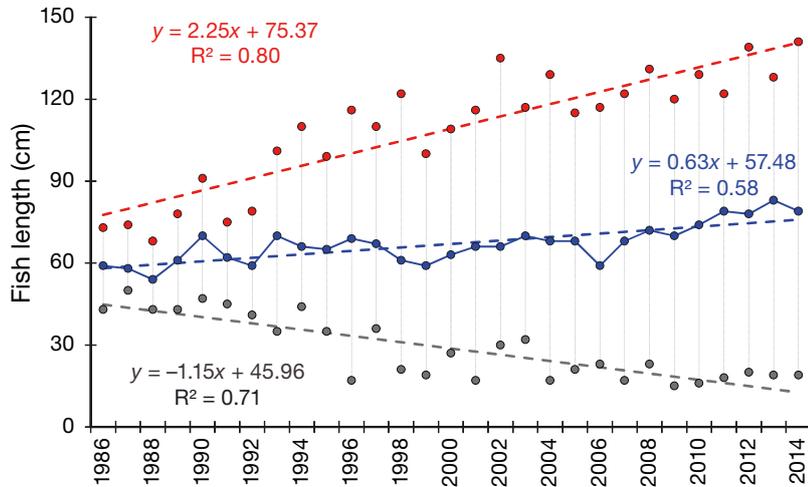


Fig. 6. Average (blue dots and solid blue line), minimum (dark grey dots) and maximum (red dots) length of cod consuming Ctenophora and regression lines showing a statistically significant trend for average (blue dashed line), minimum (dark grey dashed line) and maximum (red dashed line) length over the period

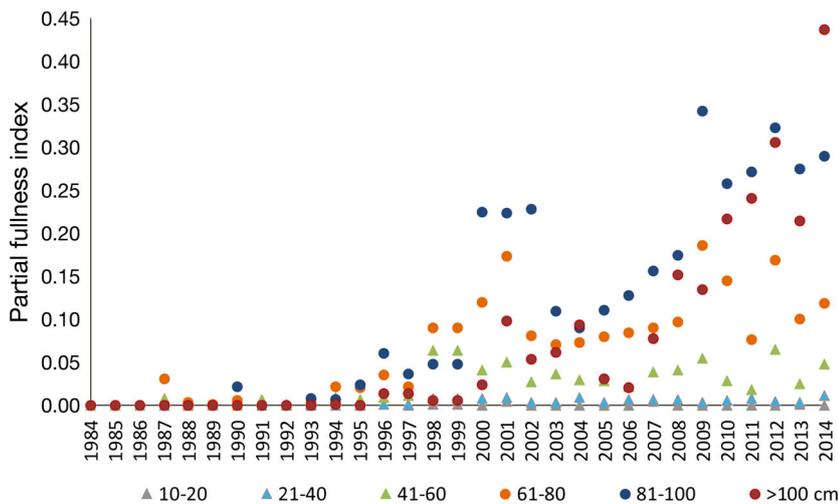


Fig. 7. PFI of Ctenophora in cod stomachs of different length groups

periods can also be divided into 2 additional segments. The period 1986–1992 was characterized by a very low content of Ctenophora in stomachs (%FI, %W, PFI) and a small area of AW and MW. During the next period (1993–1997), both the consumption of Ctenophora and area of relative warm water (AW and MW) slightly increased. The period 1998–2014 was characterized by the start of warming and an increase in consumption of Ctenophora. The last period (2009–2014) was characterized both by high content of Ctenophora in cod stomachs (%FI, %W, PFI) and a large area covered by relatively warm water masses. Also, an increase in the mean length of cod consuming Ctenophora was observed during the warm period (1998–2014).

The temporal dynamics of the abundance of Ctenophora and environmental conditions were characterized using integrated trend analysis, which is a CCA run on time series of the 6 biotic and 3 abiotic variables (CCA; Fig. 9). The first dimension is the most important, accounting for 92.4% of the variance explained for the 2-dimensional solution. The first dimension is principally temperature and area of mixed water masses (MW), and to a lesser extent area of Atlantic water masses (AW). Temperate (2001–2008) and warm years (2009–2014) and frequency of occurrence and weight of eaten Ctenophora were positively associated with the first dimension, while cold years and cod length were negatively associated. During the recent warming, a higher abundance of Ctenophora was distributed over a larger area of the Barents Sea, especially at the end of the year (Fig. 10). Increasing areas of mixed water masses and higher seawater temperatures during warm years were associated with an increased frequency of occurrence, while the amount and importance of Ctenophora in the cod diet were correlated with cod length.

The spatial distribution of cod consuming Ctenophora varied between the periods (1986–1997, 1998–2008 and 2009–2014) and seasons (Quarters 1+2, 3 and 4). Ctenophora in cod stomachs were found close to the coast during the first 2 periods, while a wider distribution was observed during the

third period. A wider distribution of ctenophores was also observed during the intensive feeding period during the 3rd quarter of the year (July–September), and Ctenophora were found throughout the Barents Sea during the last period (2009–2014; Fig. 10).

## DISCUSSION

### Observation uncertainty

The broad-scale and long-term Russian–Norwegian sampling programme of cod stomachs (Mehl & Yaragina 1992, Dolgov et al. 2007) allowed for the study of the spatial and temporal dynamics of Ctenophora in

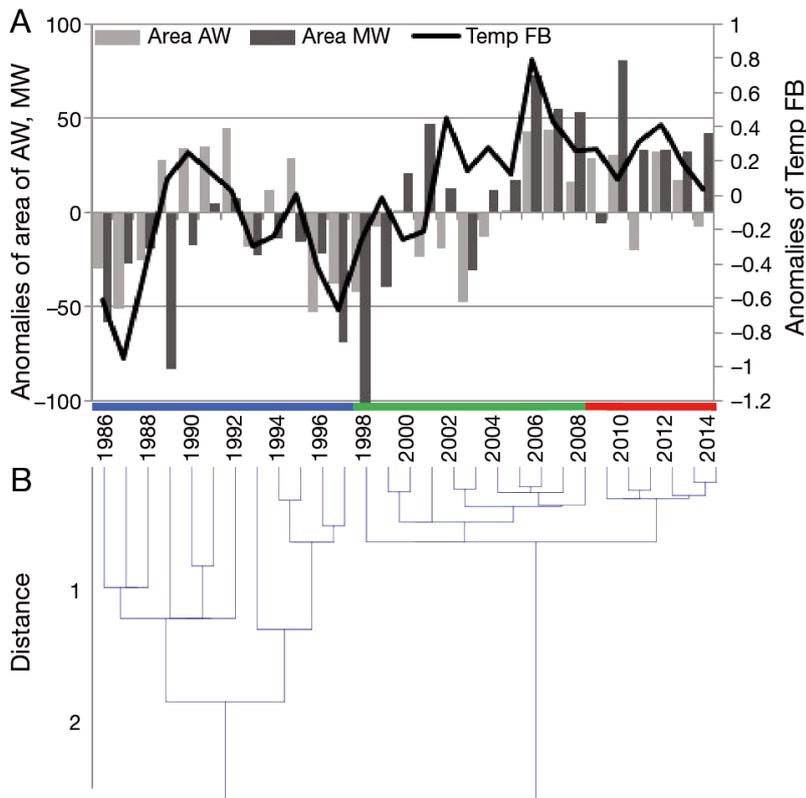


Fig. 8. (A) Oceanographic conditions in the Barents Sea: annual temperature anomalies ( $^{\circ}\text{C}$ ) at the Fugløy-Bear Island section (Temp FB) and anomalies of areas (square nautical miles) of Atlantic water (AW) and mixed waters (MW) in August–September 1986–2014. (B) Stratigraphically constrained clustering of years based on abiotic and biotic variables for the period 1986–2014. Lines show linkages of groups of years based on similarity from constrained cluster analysis (using the UPGMA algorithm), colour bars show the periods defined in Fig. 9

the Barents Sea. The special consistency and colour of Ctenophora allowed their identification in the cod stomachs, but it was still difficult to nearly impossible to identify them to family and species levels by visual identification. The pink colour (or sometimes light yellow-red) of the Ctenophora in the cod stomach contents most likely suggested *Beroe* spp., which have a slightly yellow-pink tint (Novikova 1965). Several studies have suggested that cod prey on *Beroe cucumis* in the Barents Sea (Zatsepin & Petrova 1939, Kamshilov 1961, Novikova 1963, 1965). Eventually, genetic analysis of the stomach content is needed to identify gelatinous prey in cod stomachs to species level.

The gastric evacuation rate of fish is affected by various factors such as water temperature, food size and type, and fish size (Suzuki 1993). Given the high rate of digestion of Ctenophora (Arai et al. 2003), fish that are frozen will already have lost much of their content and thus the measured mass of different organisms in the stomachs of predators should be

scaled by their relative rates of digestion (Arai et al. 2003). In our study, a large proportion of the stomachs were frozen and processed in the lab and thus some parts of Ctenophora were lost during the preserving process. Therefore, we think that our estimates are most likely underestimates and should be used as indicators of Ctenophora occurrence; however, their proportion in cod stomachs is most likely higher than we observed.

At present, traditional plankton nets are used to monitor mesoplankton in the Barents Sea, and very few and sporadic observations of Ctenophora in plankton nets indicate problems with sampling and/or sample processing (Ctenophora are neither identified nor recorded). Despite the lower overall dietary importance of Ctenophora for cod, the cod diet is likely to be the best available indicator for the dynamics in Ctenophora abundance in the Barents Sea.

### Importance of Ctenophora in cod diet

In our study, Ctenophora were found regularly in the cod diet, and their occurrence in the cod diet seemed to be season-dependent. The highest amount and frequency of Ctenophora were observed during August–December, especially in the last 2 mo (the season with low feeding intensity), while fewer Ctenophora were found during January–June, especially in the first 3 mo. Larger (and older) cod were generally observed to consume more Ctenophora than smaller (and younger) cod, especially during gonad development (late fall to winter). In recent decades, small cod (20 to 40 cm) were also observed to consume Ctenophora, and their proportion increased over the years. Cod consumed Ctenophora whether other food items were available or not. Thus, the seasonality indicates that feeding by cod on Ctenophora is a common, routine, non-selective, maintenance-feeding type of process that is primarily dependent upon the ambient abundance of Ctenophora and in effect depends on the cod encountering ctenophores. Novikova (1963, 1965) studied cod diet and the importance of different food items in the period 1957 to 1961, including Ctenophora, and con-

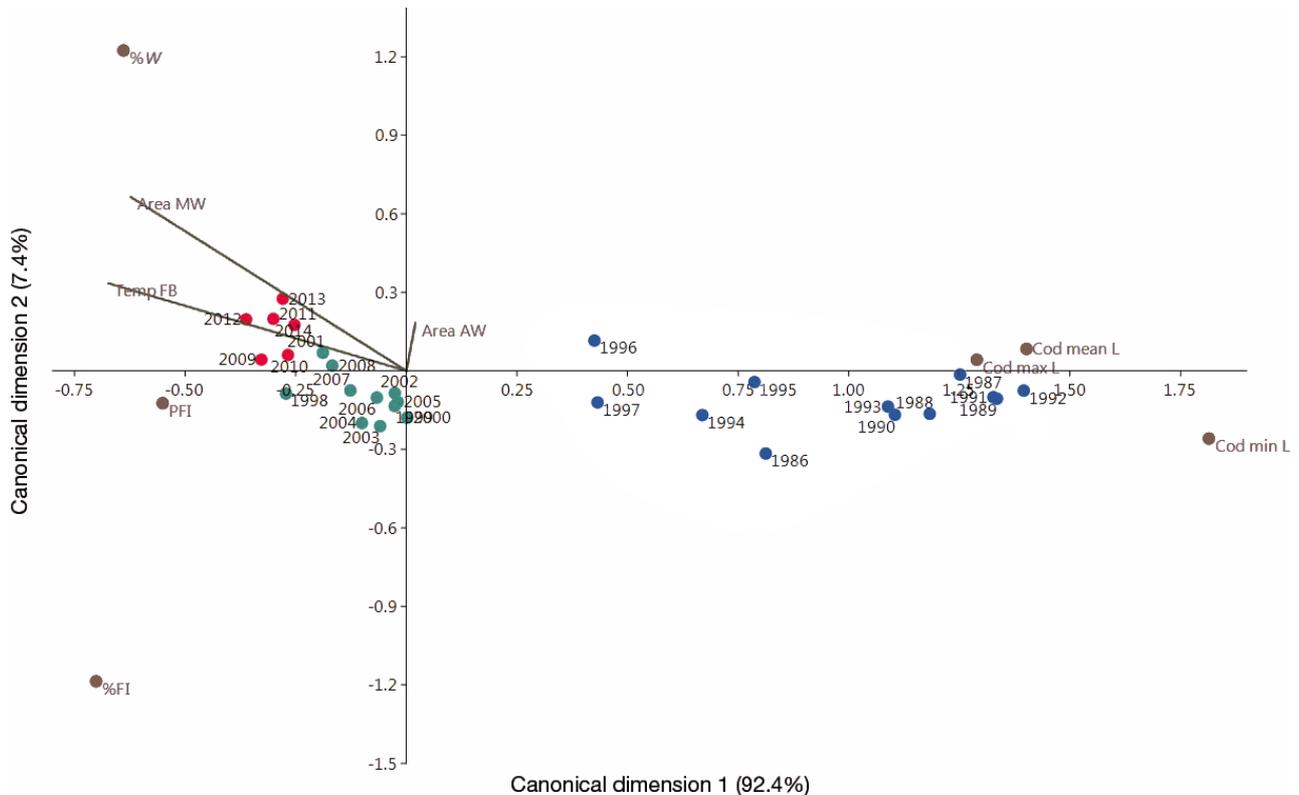


Fig. 9. Plot from CCA analyses of temporal variation (1986–2014) of biotic values (% FI, & % W, PFI, Lmin, Lmean, Lmax) and abiotic variables (Temp FB, AW, MW), where the first dimension (general warming trend from cold 1980s to moderate 1990s with low area of Atlantic waters to warm 2000s with large area of mixed water masses and higher temperature) explained 92% of variations, while the second dimension explained 7%. The data points (years) for the variables are shown with different colours for the periods: 1986–1997 (●); 1998–2008 (●); and 2009–2014 (●)

cluded that cod consumed Ctenophora regularly even when heavily feeding on capelin. Cod larger than 45 cm consumed more Ctenophora than cod of body length of 35 to 45 cm during the autumn, whereas both large and small cod consumed fewer Ctenophora during the feeding period on capelin in spring (Novikova 1965). Our results agree with earlier studies (Zatsepin & Petrova 1939, Novikova 1963, 1965) that showed that cod consumed less Ctenophora in the beginning of the year, indicating that cod mainly feed on capelin during the capelin spawning migration. However, in the years of 2 capelin collapses (1986–1989 and 1993–1997), cod consumed low number of ctenophores, most likely indicating a low abundance of Ctenophora during the 1980 to 1990s. The increase in Ctenophora in the cod diet in recent years indicates that the cod stock may be able to switch to alternative foods. Thus, the earlier and present results indicate that variation in Ctenophora in the cod diet depends on the feeding strategy and the availability of Ctenophora for cod.

In our study, Ctenophora were found in more than 5% of samples; however, their mass and low frequency of occurrence indicated that Ctenophora is

not an important food item for cod and this is in agreement with earlier studies (Zatsepin & Petrova 1939, Novikova 1965). Barents Sea capelin (and fish in general) is a main prey for BS cod, and consumption of alternative food increased during the capelin collapses (Link et al. 2009, Dolgov & Benzik 2016, our Fig. 11 taken from ICES 2016). Cod typically mostly consume capelin during their spawning migration in spring (Quarters 1 and 2), but especially in recent years the consumption has also been high in autumn (Quarters 3 and 4; Fig. 12 taken from ICES 2017). Amount of 'other' preys, including Ctenophora, increased since 2002 and was the highest in 2012 with a simultaneous increase of cod stock from 1.5 to 3.6 million t (Fig. 11 taken from ICES 2016). The proportion of Ctenophora in the cod diet was high (up to 30 to 45% of fish consumed Ctenophora and 40 to 70% of the diet [weight] consisted of Ctenophora) in some local areas. Novikova (1963, 1965) observed that in some local areas and months, up to 70% of cod consumed Ctenophora, comprising 20 to 40% of their diet. Ctenophora may not replace the key prey species, capelin, but it seems that cod intensify their

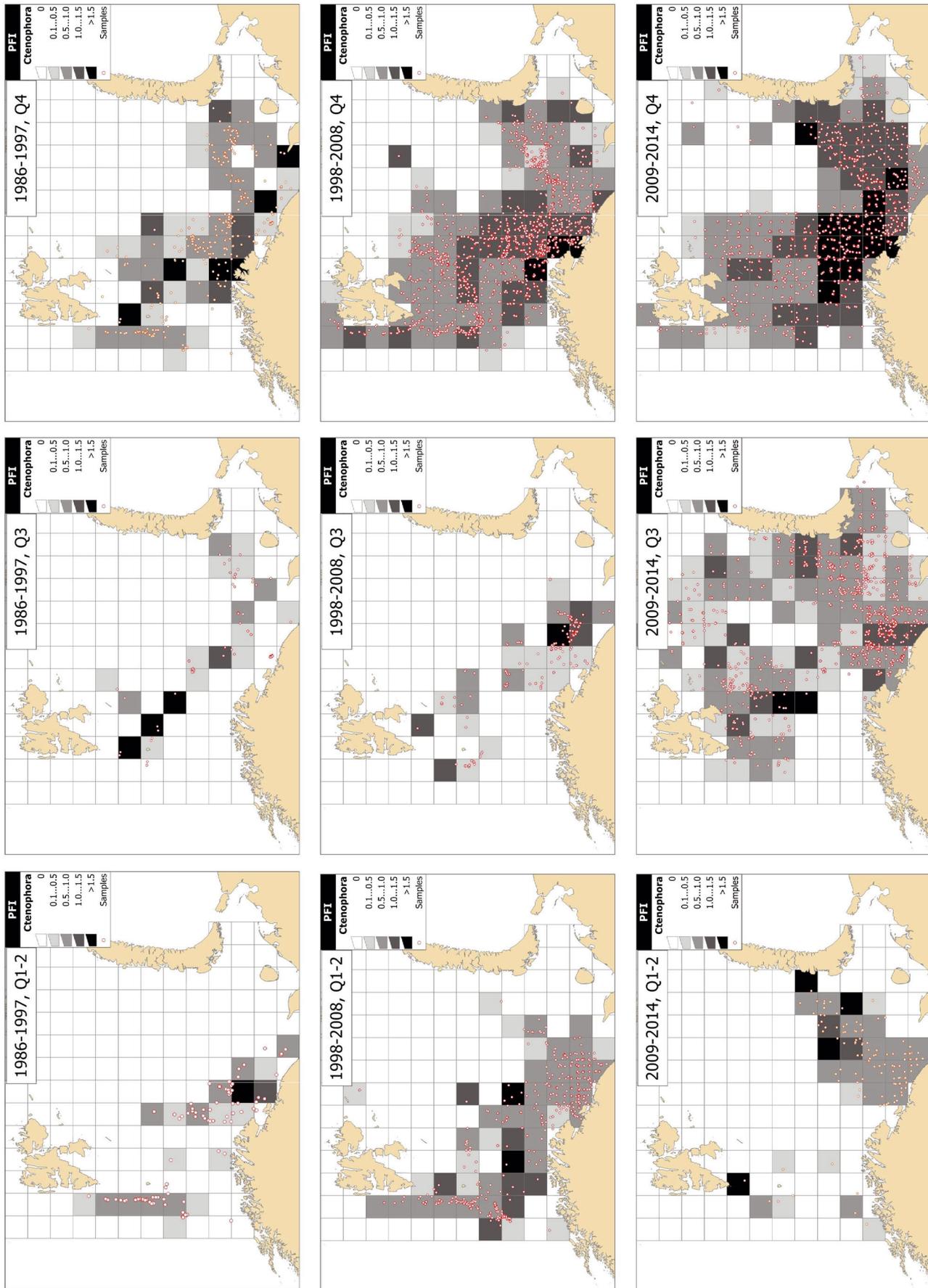


Fig. 10. Spatial distribution of Ctenophora in cod stomachs. Distribution maps for 3 periods (1986–1997, 1998–2008 and 2009–2014) and for quarters of the year for the whole period aggregated (Quarters 1 and 2 are combined due to low content of Ctenophora in these quarters). Intensive colouring indicates higher amount of Ctenophora in cod stomachs; capture location is shown (○)

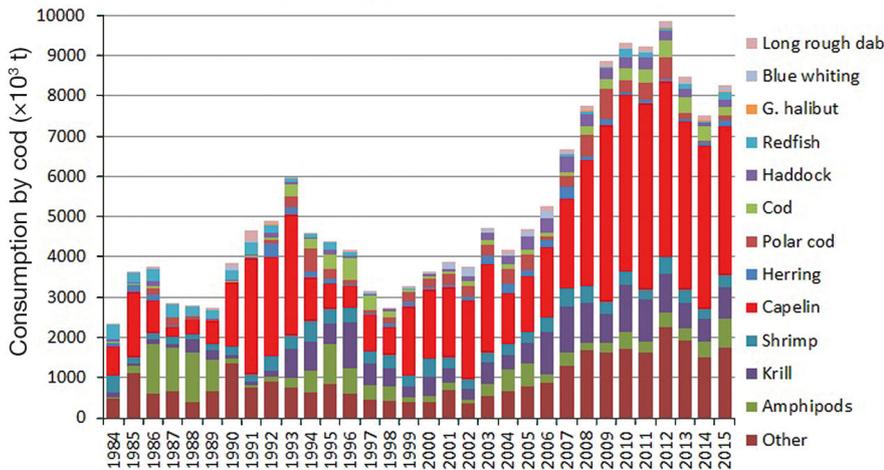


Fig. 11. Total consumption of prey by cod ( $\times 10^3$  t) 1984–2015. Consumption by mature cod outside the Barents Sea (3 mo during first half of year) not included. From ICES (2016)

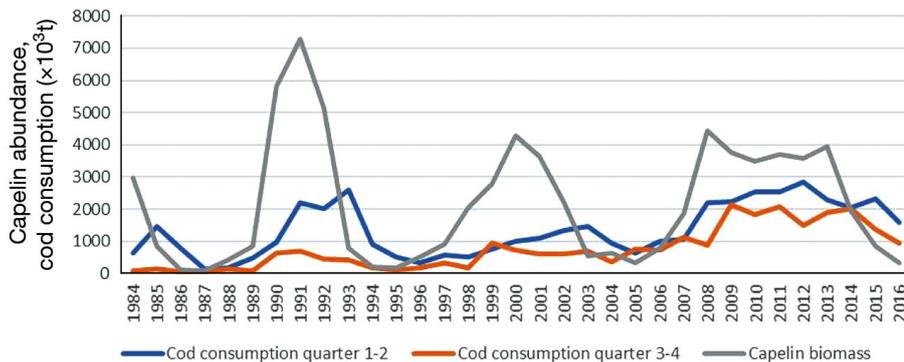


Fig. 12. Size of the capelin stock and estimated consumption of capelin by the Barents Sea cod. From ICES (2017)

search for additional prey when the capelin stock is low and the cod stock is high.

Even when cod consume large amounts of Ctenophora (up to 1 kg of Ctenophora in an individual stomach has been reported), it is difficult to believe that Ctenophora could be a beneficial source of energy for cod. The consumption of Ctenophora by cod can be explained as the instinctive reaction of cod, as a visual predator, to a moving object. It is difficult to answer the question of why the cod, even those that are small, consume Ctenophora, without additional investigations into the antimicrobial ‘qualities’ of Ctenophora. Cod consumption of *B. cucumis* is linked to antimicrobial and immunomodulatory activities in tissues of *B. cucumis* (Chentsov 1964). Aquatic invertebrate animals living in a microbe-laden environment are presumed to use an endogenous antimicrobial peptides (AMPs)-based system as principal defense against potential pathogens (Ovchinnikova et al. 2006). A

variety of AMPs have been discovered and characterized from jellyfish, such as *Chrysaora quinquecirrha*, *Linuche unguiculata*, *Aurelia aurita*, and Ctenophores (Ovchinnikova et al. 2006, Morales-Landa et al. 2007, Grant et al. 2010, Suganthi & Bragadeeswaran 2013).

### Other studies of predation on Ctenophora

Other fish such as haddock (Zatsepin & Petrova 1939, Novikova 1965), lumpfish *Cyclopterus lumpus* (Kamshilov 1961, Kudryavtseva 2008, Rusyaev & Orlov 2014), northern wolffish *Anarhichas denticulatus* (Barsukov & Nizovzev 1960) and saithe *Pollachius virens* (Mironova 1961) have also been observed to consume Ctenophora in the Barents Sea. The diet of lumpfish consists of 65 to 95% Ctenophora, and in the southern Barents Sea this species can consume up to 0.25 million tonnes, which is 10% of the total estimated Ctenophora biomass in the area (Rusyaev & Orlov 2014). Haddock are also observed to prey on Ctenophora, and larger (>40 cm) haddock prey on them more frequently (5 to 15%) than

smaller (<40 cm) haddock (2 to 7%). However, larger haddock mostly consume Ctenophora between 12:00 and 20:00 h, while smaller haddock show no variation during the day (Novikova 1965). The populations of pelagic Ctenophora are often seasonally reflected in the diets of the generalist predators (Arai 2005).

Mianzan et al. (1996) examined 69 fish species from the Argentine continental shelf, of which 35% included some ctenophores in their diet during the spring bloom of coelenterates, while 15 to 23% included some ctenophores during other seasons. Arkhipkin & Laptikhovskiy (2013) observed maximum occurrence of Ctenophora in the diet of *Patagonotothen ramsayi* and *Squalus acanthias* on Patagonian Shelf in late summer to autumn, which corresponds to our results. However, fish stomach contents do not always reflect seasonal prey abundance (Arai 2005). Off Oregon, Brodeur et al. (1987) found that Cnidaria were most common in *S. acanthias* stomachs in May

but in *Anoplopoma fimbria* stomachs in September. Anomalous seasonal differences in feeding may reflect changes in diet as fish grow; for example, chum salmon *Oncorhynchus keta* rarely eat gelatinous material in the first few weeks of life in salt water but begin to utilize coelenterates in later summer (King & Beamish 2000). However, lack of focus on gelatinous plankton in fish diet makes it difficult to understand the role of ctenophores in the Barents Sea ecosystem. Additionally, challenges with observation and sampling methods are needed to understand the role of Ctenophora in fish diet and in the ecosystem.

This study is based on long-term (and ongoing) monitoring of cod diet. It provides basic information about the spatial and temporal distributions of Ctenophora in the Barents Sea and suggests possible monitoring of Ctenophora by using their predators as samplers. To understand the role of Ctenophora in the Barents Sea ecosystem and the factors affecting their spatial and temporal fluctuations, it is essential to improve the monitoring of gelatinous plankton by implementation of additional methods (such as continuous plankton recorder and studies of stable isotope analyses and DNA).

**Acknowledgements.** The authors thank the Institute of Marine Research (IMR, Norway) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia) for their joint efforts in generating the cod stomach database. Also thanks to Edda Johannesen (IMR) for handling of the database. The authors gratefully acknowledge the support of the Norwegian Research Council for funding of the TIBIA project (22880, Trophic Interactions in the Barents Sea — steps towards an Integrated Assessment).

#### LITERATURE CITED

- Amundsen PA, Gabler HM, Staldvik J (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. *J Fish Biol* 48:607–614
- Barsukov VV, Nizovtsev GP (1960) On feeding of Barents Sea wolffishes (*Anarhichas latifrons* Steenstrup et Hallgrímsson, *A. minor* Olafsen, *A. lupus* L.). *Tr Murm Morsk Biol Inst* 2:203–206 (in Russian)
- Borutski EV (ed) (1974) Methodical manual on the investigations of feeding and food relationships in fish on natural conditions (Metodicheskoe posobie po izucheniyu pitaniya i pishchevykh otnoshenij ryb v estestvennykh usloviyakh). Nauka Publishing, Moscow (in Russian)
- ✦ Arai MN (2005) Predation on pelagic coelenterates: a review. *J Mar Biol Assoc UK* 85:523–536
- ✦ Arai MN, Welch DW, Dunsmuir AL, Jacobs MC, Ladouceur AR (2003) Digestion of pelagic Ctenophora and Cnidaria by fish. *Can J Fish Aquat Sci* 60:825–829
- ✦ Arkhipkin A, Laptikhovskiy V (2013) From gelatinous to muscle food chain: rock cod *Patagonotothen ramsayi* re-cycles coelenterate and tunicate resources on the Patagonian Shelf. *J Fish Biol* 83:1210–1220
- ✦ Bogstad B, Dingsør GE, Ingvaldsen RB, Gjørseter H (2013) Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea. *Mar Biol Res* 9:895–907
- ✦ Bogstad B, Gjørseter H, Haug T, Lindstrøm U (2015) A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Front Ecol Evol* 3:29
- Brodeur RD, Lorz HV, Pearcy WG (1987) Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. NOAA Technical Report NMFS 57
- Chentsov BV (1964) Antimicrobial action of the tissues and organs of the comb jelly *Beroe cucumis* Fabr. and the mollusc *Mytilus edulis* L. (Antimikrobnje deystvie tkanej I organov grebnevika *Beroe cucumis* Fabr. i mollyuska *Mytilus edulis* L.). *Tr Murm Morsk Biol Inst* 5:226–231 (in Russian)
- ✦ Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proc Natl Acad Sci USA* 110:1000–1005
- ✦ Costello MJ (1990) Predator feeding strategy and prey importance: a new graphical analysis. *J Fish Biol* 36:261–263
- ✦ Costello JH, Mianzan HW (2003) Sampling field distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): planktonic or benthic methods? *J Plankton Res* 25:455–459
- Dolgov AV, Benzik AN (2014) Feeding of cod in the northern Barents Sea. In: Karasev AB (ed) Peculiarities of biological productivity in the northern Barents Sea under warming period in Arctic. PINRO Press, Murmansk, p 126–137 (in Russian)
- Dolgov AV, Benzik AN (2016) Possible consequences of capelin abundance decreasing on feeding conditions of the Barents Sea cod. In: Matishov GG, Tarasov GA (eds) Complex investigations of nature of Spitsbergen archipelago and adjacent shelf, Vol 13. Proc All-Russian Sci Conf with an international component, Murmansk, 2–4 November 2016. Southern Scientific Center Press, Rostov-on-Don, p 108–112 (in Russian)
- Dolgov AV, Yaragina NA, Orlova EL, Bogstad B, Johannesen E, Mehl S (2007) 20th anniversary of the PINRO-IMR cooperation in the investigations of fish feeding in the Barents Sea—results and perspectives. In: Haug T, Misund OA, Gjørseter H, Røttingen I (eds) Long-term bilateral Russian-Norwegian scientific cooperation as a basis for sustainable management of living marine resources in the Barents Sea. Proc 12th Norwegian-Russian Symp, Tromsø, 21–22 August 2007. IMR, Bergen, p 44–78. [www.imr.no/publikasjoner/andre\\_publicasjoner/imr-pinro\\_samarbeidsrapporter/2007/nb-no](http://www.imr.no/publikasjoner/andre_publicasjoner/imr-pinro_samarbeidsrapporter/2007/nb-no)
- ✦ Eriksen E (2016) Do scyphozoan jellyfish limit the habitat of pelagic species in the Barents Sea during the late feeding period? *ICES J Mar Sci* 73:217–226
- Eriksen E, Gjørseter H (eds) (2013) A monitoring strategy for the Barents Sea. Report from Project nr.14256 Survey Strategy for the Barents Sea. Institute of Marine Research, Bergen
- ✦ Eriksen E, Skjoldal HR, Gjørseter H, Primicerio R (2017) Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Prog Oceanogr* 151:206–226
- ✦ Fahrig L, Lilly GR, Miller DS (1993) Predator stomachs as sampling tools for prey distribution: Atlantic cod (*Gadus*

- morhua*) and capelin (*Mallotus villosus*). Can J Fish Aquat Sci 50:1541–1547
- ✦ Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan M, Dolgov A (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Change 5:673–677
- ✦ Frid CLJ, Hall SJ (1999) Inferring changes in North Sea benthos from fish stomach analysis. Mar Ecol Prog Ser 184: 183–188
- Grant S, Gisondi A, Hortano W, Defilippo J, Beck G (2010) Isolation and preliminary characterization of antimicrobial proteins and peptides from Ctenophores and Cnidaria. In: Gupta VK, Taneja SC, Gupta BD (eds) Comprehensive bioactive natural products, Vol 6: extraction, isolation & characterization. Studium Press LLC, New Delhi, p 258–279
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electronica 1:art4
- ✦ Hamner WM, Madin LP, Alldredge AL, Gilmer RW, Hamner PP (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. Limnol Oceanogr 20:907–917
- ✦ Hyslop EJ (1980) Stomach content analysis: a review of methods and their applications. J Fish Biol 17:411–429
- ICES (2016) Report of the Arctic Fisheries Working Group (AFWG). ICES CM 2016/ACOM:06. International Council for the Exploration of the Sea, Copenhagen
- ICES (2017) Report of the working group on the integrated assessments of the Barents Sea. ICES CM 2017/SSGIEA: 04. International Council for the Exploration of the Sea, Copenhagen
- Jakobsen T, Ozhigin V (eds) (2011) The Barents Sea — ecosystem, resources, management. Half a century of Russian-Norwegian cooperation. Tapir Academic Press, Trondheim
- ✦ Johansen GO, Johannesen E, Michalsen K, Aglen A, Fotland Å (2013) Seasonal variation in geographic distribution of North East Arctic (NEA) cod-survey coverage in a warmer Barents Sea. Mar Biol Res 9:908–919
- Kamshilov MM (1961) The biology of comb jellies of the Murman coastal region (Biologiya grebnevika Murmana). Trudy Murman Biological Institute 3:36–49 (in Russian)
- King JB, Beamish RJ (2000) Diet comparisons indicate a competitive interaction between ocean age-0 chum and coho salmon. NPAFC Bull 2:65–74
- ✦ Kjesbu OS, Bogstad B, Devine JA, Gjørseter H and others (2014) Synergies between climate and management for Atlantic cod fisheries at high latitudes. Proc Natl Acad Sci USA 111:3478–3483
- ✦ Kortsch S, Primicerio R, Fossheim M, Dolgov A, 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
- Kudryavtseva O (2008) The lump sucker (*Cyclopterus lumpus*) in the Barents Sea and adjacent waters. (O. Karamushko, ed) Nauka, Moscow (in Russian)
- Lilly GR, Fleming AM (1981) Size relationships in predation by Atlantic cod, *Gadus morhua*, on capelin, *Mallotus villosus*, and sand lance, *Ammodytes dubius*, in the Newfoundland area. NAFO Sci Coun Stud 1:41–45
- ✦ Link JS, Ford MD (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Mar Ecol Prog Ser 320:153–159
- ✦ Link JS, Bogstad B, Sparholt H, Lilly GR (2009) Role of cod in the ecosystem. Fish Fish 10:58–87
- Mehl S, Yaragina NA (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. Proc 5th PINRO-IMR Symp, Murmansk, 12–16 August 1991. IMR/PINRO Joint Report Series, IMR, Bergen, p 5–16
- ✦ Mianzan HW, Prenski MN, 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, Gjørseter H and others (2011) The joint Norwegian-Russian ecosystem survey: overview and lessons learned. In: Haug T, Dolgov A, Drevetnyak K, Røttingen I, Sunnanå K, Titov O (eds) Climate change and effects on the Barents Sea marine living resources. Proc 15th Norwegian-Russian Symp, Svalbard, 7–8 September 2011. IMR/PINRO Joint Report Series, IMR, Bergen, p 247–272. www.imr.no/publikasjoner/andre\_publicasjoner/imr-pinro\_sam arbeidsrapporter/2011/nb-no
- Mironova NV (1961) Migrations, schools composition and feeding of saithe (*Pollachius virens* L.) in the Barents Sea. In: Kamshilov MM (ed) Hydrological and biological peculiarities of coastal waters of Murman. Murmansk Book Publishing, Murmansk, p 59–89 (in Russian)
- ✦ Morales-Landa JL, Zapata-Pérez O, Cedillo-Rivera R, Segura-Puertas L, Simá-Alvarez R, Sánchez-Rodríguez J (2007) Antimicrobial, antiprotozoal, and toxic activities of cnidarian extracts from the Mexican Caribbean Sea. Pharm Biol 45:37–43
- Novikova NS (1963) Some data on the fat content of cod and haddock in the Barents Sea. (Nekotorye dannye o shirnosti treski i pikshi Barentsevogo moraya). Trydu PINRO 15: 149–162 (in Russian)
- Novikova NS (1965) Role of comb jellies in the food of the Barents Sea cod and haddock. (O role grebnevikov v pitanii Barentsevomorskix treski i pikshi). Trydu PINRO 7:61–67 (in Russian)
- ✦ Ovchinnikova TV, Balandin SV, Aleshina GM, Tagaev AA and others (2006) Aurelin, a novel antimicrobial peptide from jellyfish *Aurelia aurita* with structural features of defensins and channel-blocking toxins. Biochem Biophys Res Commun 348:514–523
- Ozhigin VK, Ingvaldsen RB, Loeng H, Boitsov V, Karsakov A (2011) Introduction to the Barents Sea. In: Jakobsen T, Ozhigin V (eds) The Barents Sea ecosystem: Russian-Norwegian cooperation in science and management. Tapir Academic Press, Trondheim, p 315–328
- ✦ Purcell JE (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. Hydrobiologia 616:23–50
- ✦ Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27–44
- ✦ Purcell JE, Uye SI, Lo WT (2007) Anthropogenic causes of jellyfish blooms and direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174
- Quiñones J, Mianzan H, Purca S, Robinson KL, Adams GD, Acha EM (2015) Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru. Mar Biol 162:2339–2350
- Rusyaev S, Orlov A (2014) Lumpfish as main consumer of northern comb jelly and effective tool of its research. ICES CM 2014/3064 A:30

- Suganthi K, Bragadeeswaran S (2013) Antimicrobial and immunomodulatory activities of jellyfish (*Chrysaora quinquecirrha*) venom. In: Sabu A, Augustine A (eds) Prospects in bioscience: addressing the issues. Springer, New Delhi, p 283–292
- Suzuki T (1993) A review of gastric evacuation rate of salmonids (in Japanese with English summary). Sci Rep Hokkaido Salmon Hatchery 47:101–107
- ✦ Weisse T, Gomoiu MT, Scheffel U, Brodrecht F (2002) Biomass and size composition of the comb jelly *Mnemiopsis* sp. in the north-western Black Sea during spring 1997 and summer 1995. Estuar Coast Shelf Sci 54:423–437
- Yaragina NA, Aglen A, Sokolov KM (2011) Cod. In: Jakobsen T, Ozhigin VK (eds) The Barents Sea: ecosystem, resources, management: half a century of Russian-Norwegian cooperation. Tapir Academic Press, Trondheim, p 225–270
- Zatsepin VI, Petrova NS (1939) Diet of the commercial cod aggregations in the southern Barents Sea. (Pitanie promuslovux kosyakov treski v juzhnoj chaste Barentseva moray). Pischepromizdat, Moscow (in Russian)
- Zelikman EA (1972) Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea, based on perennial plankton collections. Mar Biol 17:256–264

Editorial responsibility: Jennifer Purcell (Guest Editor),  
Bellingham, Washington, USA

Submitted: September 21, 2016; Accepted: May 17, 2017  
Proofs received from author(s): July 14, 2017