Vol. 747: 117–132, 2024
https://doi.org/10.3354/meps14700

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 17

Summer and polar night diets of polar cod *Boreogadus saida* and Atlantic cod *Gadus morhua* in Kongsfjorden, Svalbard, Norway

Olof Bengtsson[1,2], Christian Lydersen[1], Jan Marcin Węsławski[3], Jørgen Berge[2], Kit M. Kovacs[1,*]

[1]The Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway
[2]Department of Arctic and Marine Biology, UiT The Arctic University of Norway, 9037 Tromsø, Norway
[3]Institute of Oceanology, Polish Academy of Sciences, 81-712 Sopot, Poland

---

ABSTRACT: Rapid Atlantification of marine ecosystems in the Svalbard Archipelago (Norway) is posing a threat to the local polar cod (*Boreogadus saida*) population. In Kongsfjorden, the decreasing population of polar cod is experiencing a shift in their prey community from Arctic to Atlantic zooplankton and fish. Simultaneously, the abundance of Atlantic cod *Gadus morhua* is increasing. In this study, we explore seasonal dietary patterns, foraging strategies, and potential competition between these 2 gadids in Kongsfjorden via stomach content analyses. Polar cod diet by proportion biomass (B) was dominated by pricklebacks (family Stichaeidae) and conspecifics during polar night ($B = 72.7\%$) and by *Calanus* spp. ($B = 52.4\%$) and *Themisto* spp. during summer ($B = 31.2\%$). Atlantic cod diet was dominated by polar cod in both seasons (polar night: $B = 37.4\%$; summer: $B = 93.6\%$). Despite high dietary overlap (Schoener's $D = 0.67$) between similarly sized polar cod and Atlantic cod (9–25 cm) during polar night, competition for food between these species is likely relatively low due to polar cod having high individual specialization in their foraging strategies. However, continued Atlantification, and increased abundance of the now established population of Atlantic cod, is a threat to polar cod because of direct consumption of the smaller species by the larger. The high predation rates by Atlantic cod on polar cod also make it a potential competitor with other top predators in the region, which could have negative consequences for local sea birds and marine mammals.

KEY WORDS: Atlantification · Arctic · Barents Sea · Climate change · Dietary overlap · Gadid · Seasonal variation · Stomach contents

---

1. INTRODUCTION

Arctic marine ecosystems are experiencing rapid changes due to global warming (Deb & Bailey 2023), with especially pronounced effects in the northwestern Barents Sea due to the large influence of Atlantic Water (AW) in the region (Lind et al. 2018). AW is transported to the region through the West Spitsbergen Current (Fig. 1), which has experienced a warming of 0.045°C yr^{-1} in the surface layer and 0.021°C yr^{-1} in the intermediate layer during the last 2 decades (Merchel & Walczowski 2020). As a consequence of the increasing ocean temperatures in the area, there is an ongoing northward expansion of the distribution of boreal marine species and a reduction in the abundance of Arctic species, which is particularly noticeable in shelf waters and fjords along the western and northern coasts of the Svalbard Archipelago (Weydmann et al. 2014, Fossheim et al. 2015, Misund et al. 2016, Weydmann-Zwolicka et al. 2021).

---

*Corresponding author: kit.kovacs@npolar.no

Publisher: Inter-Research · www.int-res.com

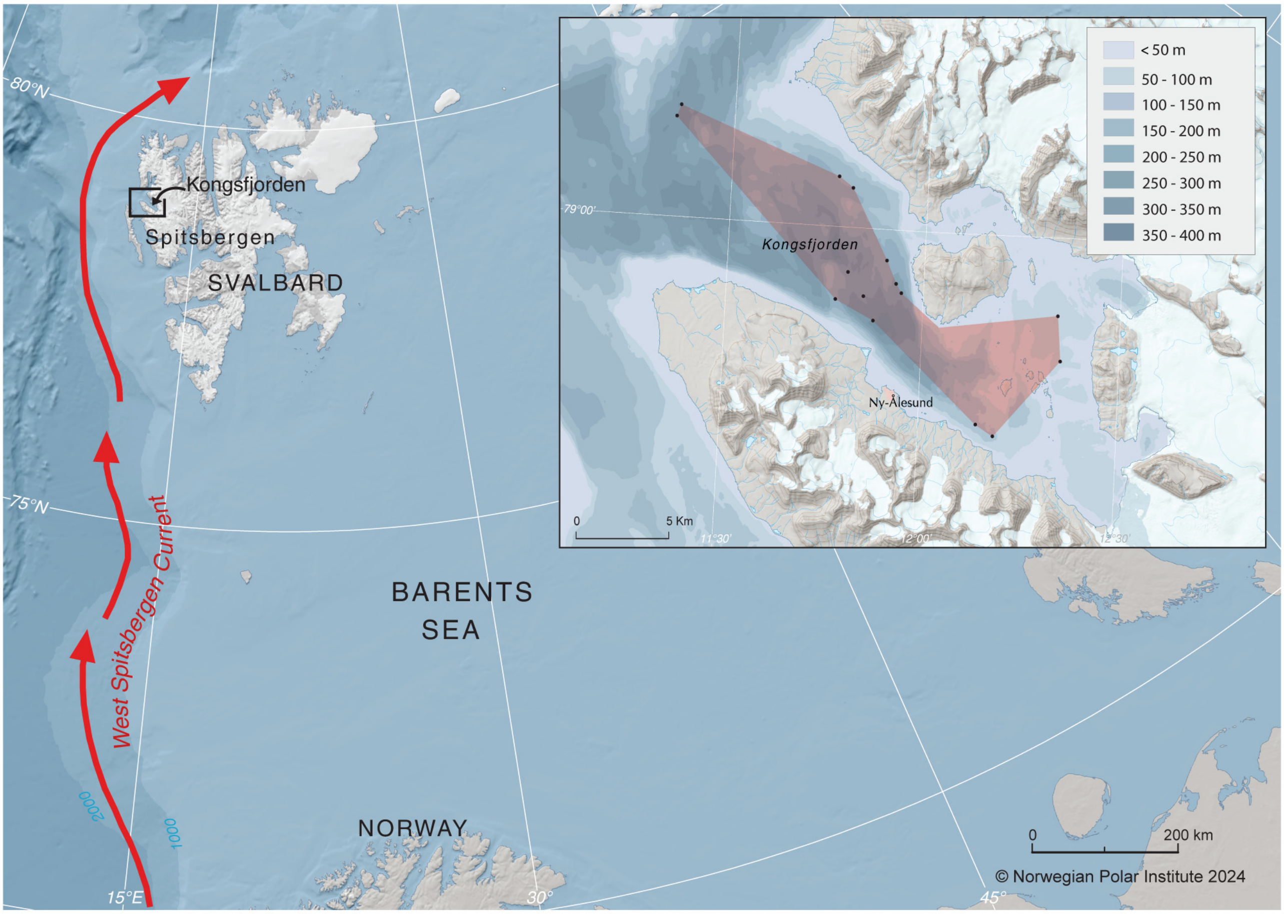

Fig. 1. Barents Sea region and Kongsfjorden (inset), Norway. Red transparent polygon marks the area where trawling for polar cod and Atlantic cod was conducted during polar night and summer 2022, and black dots represent trawling stations

This process is often referred to as borealization or the more geographically specific Atlantification. A clear example of the ongoing Atlantification is the increased presence of the Barents Sea stock of Atlantic cod *Gadus morhua* and establishment of the species in coastal waters in Svalbard (Drinkwater 2009, Johansen et al. 2013, Spotowitz et al. 2022, Brand et al. 2023). Concurrently, serious concern is being raised for the Arctic endemic polar cod *Boreogadus saida* in the Barents Sea, and the species is thought to be in jeopardy in the region (ICES 2018, Huserbråten et al. 2019, Geoffroy et al. 2023). Among polar cod populations in the circumpolar Arctic, the Barents Sea population is considered to be one of the most vulnerable to climate change-induced ecosystem shifts, e.g. sea ice decline, ocean warming and shifts in the predator and prey communities (Eriksen et al. 2015, Huserbråten et al. 2019, Geoffroy et al. 2023). The abundance of polar cod in the Barents Sea shows high interannual variability, and while trends in total stock size are uncertain, there are negative trends for local populations in areas with especially high influences from AW, such as Kongsfjorden on the west coast of Spitsbergen, Svalbard (Fig. 1; Institute of Marine Research 2022a, Gorska et al. 2023).

Polar cod is a relatively small (generally <30 cm, but individuals over 40 cm have been recorded, Pethon 1994) species in the family Gadidae, with a circumpolar Arctic distribution (Falk-Petersen et al. 1986, Mueter et al. 2016, Aune et al. 2021). It is regarded as a key species in Arctic marine food webs (Craig et al. 1982, Hop & Gjøsæter 2013, Johannesen et al. 2017, Kohlbach et al. 2017, Marsh et al. 2020). In some regions, polar cod is estimated to account for more than 70% of the energy transfer from pelagic zooplankton to piscivorous vertebrates (Bradstreet & Cross 1982, Benoit et al. 2010, Steiner et al. 2019). The diet of adult polar cod in Svalbard is generally dominated by hyperiid amphipods, mainly *Themisto libellula*, which is especially abundant in fjords dominated by Arctic water masses (Lønne & Gulliksen 1989, Dalpadado et al. 2016, Cusa et al. 2019). There are, however, regional and seasonal variations, and prey such as krill (Euphausiidae), copepods, sympagic amphipods and fish can be more important in some areas or seasons (Dalpadado et al. 2016, Kohlbach et al. 2017, Cusa et al. 2019, Larsen et al. 2023). In Svalbard, polar cod is important prey for many species of seabirds, marine mammals and predatory fish, including Brünnich's guillemot *Uria lomvia*, black-legged kittiwakes *Rissa tridactyla*, ringed seals *Pusa hispida*, white whales *Delphinapterus leucas*, Greenland halibut *Reinhardtius hippoglossoides* and Atlantic cod (Mehlum et al. 1996, Dahl et al. 2000, 2003, Vollen et al. 2004, Wold et al. 2011, Bengtsson et al. 2020, Larsen et al. 2023).

Atlantic cod is a large (<160 cm) boreal gadid with a wide distribution. There are several populations of Atlantic cod in the North Atlantic, of which the largest is the Barents Sea cod stock (Link et al. 2009, Ottersen et al. 2014, Institute of Marine Research 2022b). This species plays a central role in the Barents Sea ecosystem as a key prey species and a top predator, simultaneously serving as both prey to and a major competitor for resources with marine mammals (Link et al. 2009, Bogstad et al. 2015, Solvang et al. 2022). The diet of the Barents Sea cod stock has been extensively studied in its native range but has only been the subject of a handful of studies in Svalbard fjords. It is known to be a generalist, mostly demersal, partly pelagic predator that feeds on large quantities of different invertebrate species during its first years and then shifts to a more fish-dominated diet as it grows larger (Bogstad et al. 1994, Ingvaldsen et al. 2017, Holt et al. 2019, Solvang et al. 2021, Brand et al. 2023, Larsen et al. 2023). Capelin *Mallotus vilosus* is generally considered the main prey of Barents Sea Atlantic cod, but several other fish species can be important locally, seasonally and during years with low abundance of capelin, e.g. redfish *Sebastes* spp., haddock *Melanogrammus aeglefinus* and Atlantic herring *Clupea harengus*, while the largest individuals of the stock shift their dietary focus towards conspecifics (Holt et al. 2019, Townhill et al. 2021).

Few comparative dietary studies have been done on co-existing polar cod and Atlantic cod in Svalbard, and existing studies have focused on individuals occurring in shallow waters, or have been seasonally restricted. Renaud et al. (2012) found that there was little dietary overlap (<40%) between co-occurring juvenile polar cod and Atlantic cod (<13 and <10 cm, respectively) from different habitats (fjords, open water and sea ice) in Svalbard. While juvenile polar cod fed mainly on calanoid copepods and hyperiid amphipods (mostly *T. libellula*), the diet of juvenile Atlantic cod was dominated by krill. However, Larsen et al. (2023) documented a relatively high dietary overlap (>50%) on krill or similar fish species between co-occurring polar cod and Atlantic cod (<25 cm) during polar night in Kongsfjorden.

Since the early 2000s, more research focus has been directed toward marine ecosystems during polar night, the period during winter where the sun never rises above the horizon (Berge et al. 2020b). In Kongsfjorden, this period lasts from the end of October until the middle of February. Previous assumptions of little biological activity during this season of low, but not absent, light have been discarded, as a growing body of studies have revealed high levels of intricate biological interactions (Berge et al. 2015, Cottier & Porter 2020). Still, knowledge gaps concerning this period, especially regarding Arctic fish communities, remain.

Kongsfjorden is one of the most studied marine ecosystems in Svalbard and arguably in the whole Arctic. It is a good location to study the effects of climate change on Arctic ecosystems because this open fjord is heavily influenced by AW (Søreide et al. 2021, De Rovere et al. 2022). The fish community in Kongsfjorden is not well studied, but it is known to be diverse, with both endemic Arctic species and species of sub-Arctic and Atlantic origin. The shallow water fish community is mostly dominated by sculpins (*Myoxocephalus scorpius* and *Gymnocanthus tricuspis*) and Atlantic cod (Brand & Fischer 2016). Atlantic cod in the shallow water in Kongsfjorden are primarily juveniles (0–2 yr old), indicating that this zone functions as a nursery ground for this species (Brand et al. 2023). In the deeper parts of the fjord, a shift in the fish community has taken place during the last decade, with a higher proportional abundance of large fish — likely of Atlantic origin, e.g. Atlantic cod and haddock — at the expense of the smaller Arctic endemic polar cod (Szczucka et al. 2017, Gorska et al. 2023). The pelagic macro-zooplankton (>20 mm) community in Kongsfjorden is characterized by high abundances of krill and amphipods, where Arctic species such as *Thysanoessa inermis* and *T. libellula* occur in high abundances in the inner parts of the fjord, close to the tidewater glacier fronts, while species more associated with AW, such as *Thysanoessa longicaudata, Meganyctiphanes norvegica* and *Themisto abyssorum*, are dominant in the central and outer parts of the fjord (Dalpadado et al. 2016).

The present study investigated the dietary patterns of 2 key fish species in the central deep parts of Kongsfjorden: the native resident polar cod and the boreal partly resident Atlantic cod. The primary objectives were to (1) analyze stomach contents to identify important prey species/classes in the diets of polar cod and Atlantic cod during both summer and polar night, (2) assess potential dietary overlap and competition between polar cod and Atlantic cod by comparing their diet compositions, and (3) examine the extent of predation by Atlantic cod on polar cod. This research will provide valuable insights into the ecological dynamics within an Arctic marine ecosystem, shedding light on the foraging behavior and diet of 2 important fish species during a time of increasing Atlantification due to global warming.

2. MATERIALS AND METHODS

2.1. Fieldwork and laboratory analysis

Polar cod and Atlantic cod were collected in central Kongsfjorden, Svalbard, Norway, from the RV 'Helmer Hanssen' during polar night (mid-January) and late summer (early September), 2022 (Fig. 1). The fish were caught using a Campelen 1800 bottom trawl (mesh size 9.8 mm at the cod end) at depths between 114 and 349 m, and a Harstadtrål pelagic trawl (mesh size 5.5 mm at the cod end) between 30 and 183 m. Depths of pelagic trawling were chosen by identifying dense concentrations of organisms using a multibeam echosounder at 18 and 38 kHz. Speed was kept at ca. 3 knots during all trawls. Total length (±0.1 mm) and weight (±0.01 g) were measured for all fishes. All polar cod and Atlantic cod <1 kg were frozen whole and stored at −20°C to avoid degradation of stomach contents. For logistical reasons, stomachs of Atlantic cod >1 kg were excised before being frozen and stored in the same manner as the whole fish. Polar cod were thawed at room temperature to the point that stomachs could be excised while their contents remained frozen. The contents were then stored in 70% ethanol. Sex and maturity of the fish of both species were determined by the state of the gonads. In cases where gonads could not be inspected due to damage, polar cod and Atlantic cod were considered mature if they were >10 and >25 cm, respectively, based on the length distributions of the fish which could be classified based on their gonads (Table 1). Otoliths of polar cod were collected and measured (±0.1 mm) under a Leica MZ6 stereomicroscope with an ocular micrometer. The stomachs of Atlantic cod were opened, and contents were removed. The stomach contents from both species were washed gently on sieves with a mesh size of 0.25 mm, and remaining contents were analyzed under a stereomicroscope. Prey items were identified to species (or lowest possible taxonomic level) using Härkönen (1986), Klekowski & Węsławski (1992), Vassilenko & Petryashov (2009) and Mecklenburg et al. (2018) as identification guides, along with a reference otolith collection provided by the Norwegian Institute of Marine Research. When prey items were intact (digestion state ~1–3 in Table A1 from Buckland et al. 2017), they were measured (±0.1 mm) under the stereomicroscope or simply on measuring tape when items were over ca. 5 cm and weighed (±0.1 mg) using a Mettler-Toledo ME403 or a Soehnle kitchen scale when items were over 400 g. Contents preserved in ethanol were not weighed due to expected biomass loss from the preservation (Wetzel et al. 2005). In these cases, and in cases where prey items were too digested for meaningful size assessments, prey biomass and

Table 1. Sex/maturity, length and body mass of polar cod and Atlantic cod collected during polar night and summer in Kongsfjorden, Svalbard, Norway, 2022. F: sexually mature female; M: sexually mature male

Sex	Polar night			Summer		
	n	Length (cm) Mean ± SD (min–max)	Body mass (g) Mean ± SD (min–max)	*n*	Length (cm) Mean ± SD (min–max)	Body mass (g) Mean ± SD (min–max)
Polar cod						
Mature	599[a]	15.40 ± 1.66 (8.60–24.20)	21.90 ± 8.62 (3.19–101)	377	13.30 ± 1.99 (10.10–20.20)	14 ± 7.48 (5.64–49.50)
F	313	15.50 ± 1.87 (8.60–24.20)	22.90 ± 10.30 (3.19–101)	189	13.30 ± 1.95 (10.20–19)	14 ± 7.26 (6.11–40.20)
M	282	15.30 ± 1.39 (11.60–21)	20.80 ± 6.15 (8.05–53.30)	188	13.30 ± 2.02 (10.10–20.20)	14 ± 7.72 (5.64–49.50)
Juvenile	14	8.38 ± 0.82 (7–10)	3.04 ± 0.70 (2.23–4.26)	3	7.73 ± 2.06 (5.60–9.70)	3 ± 1.76 (1.16–4.66)
Atlantic cod						
Mature	197[b]	39 ± 10.30 (21.50–88.50)	632 ± 789 (82–6635)	33	67 ± 12.80 (38.50–88)	2711 ± 1272 (460–5560)
F	62	35.20 ± 6.05 (22–50)	395 ± 198 (82–1044)	25	66.20 ± 13.40 (38.50–88)	2641 ± 1346 (460–5560)
M	46	35.30 ± 5.70 (21.50–48.50)	396 ± 186 (94–900)	8	69.60 ± 11 (51.50–81)	2930 ± 1053 (1260–4000)
Juvenile	14	17.80 ± 7.73 (9.20–36)	67.80 ± 90.20 (5.1–346)	6	11.20 ± 2.26 (9.40–15.60)	12.30 ± 8.85 (5.47–29.90)

[a] Includes 4 individuals assumed to be mature based on length (>10 cm)
[b] Includes 89 individuals assumed to be mature based on length (>25 cm)

polar cod length were reconstructed using otolith length or body length for back calculation or by using species body mass averages from relevant prey species collected along the west coast of Svalbard (1990—2000) by the Institute of Oceanology of the Polish Academy of Sciences (IO PAS; Table S1 in the Supplement at www.int-res.com/articles/suppl/m747p117_supp.pdf).

2.2. Statistical analysis

Statistical analyses were conducted using R version 4.3.1 with RStudio (R Development Core Team 2023). A significance level of $\alpha = 0.05$ was used for all analyses. For dietary analyses, individuals with empty stomachs were excluded, and only dietary items were considered (non-food items, e.g. parasites and stones, were excluded).

A Student's *t*-test or Mann-Whitney *U*-test (Mann & Whitney 1947) was used to determine potential differences in length and weight of juvenile and sexually mature gadids between seasons. The former was used if the data fulfilled assumptions of homogeneity of variance, tested by Levene's test (Levene 1960), and normal distribution, tested by Shapiro-Wilk's normality test (Shapiro & Wilk 1965).

Diet compositions were assessed using 3 dietary indices: (1) frequency of occurrence (FO_i), the percentage of all individuals of a given species which had consumed prey species i; (2) relative numerical frequency (NF_i), the percentage of the total number of individual prey made up by species i; and (3) the relative proportion of biomass (B_i), the percentage of the total prey biomass made up by species i. To explore and visualize sources of the consumed prey (pelagic, demersal, benthic, as described in Klekowski & Węsławski 1992, Vassilenko & Petryashov 2009, Mecklenburg et al. 2018 and IO PAS unpubl. data), only prey with either FO or $B > 5\%$ during either season were included. The 5% cutoff point was arbitrarily chosen to include only the most influential prey species. Year classes (YCs) of polar cod consumed by Atlantic cod were estimated using total length or reconstructed total length from otolith length when the state of digestion was too high. Length intervals (cm) for the different YCs were <11.5 (YC 1), <13.95 (YC 2), <15.66 (YC 3), <16.9 (YC 4), <18.5 (YC 5) and >18.5 (YC 6) (Falk-Petersen et al. 1986).

To determine whether the average size of polar cod eaten by Atlantic cod was influenced by the size of the Atlantic cod or by the season, linear mixed-effects models were used. The total length of polar cod (cm) was used as the response variable in the model, and the total length of Atlantic cod (cm) and the season (polar night/summer) were set to be independent predictors. Additionally, the individual ID of the Atlantic cod was included as a random effect to account for cases where 1 individual had eaten more than 1 polar cod. The model was formulated as:

$$\begin{gathered}\text{Polar cod length} \sim \text{Atlantic cod length} + \\ \text{Season} + (1 \mid \text{ID})\end{gathered} \quad (1)$$

The lmer function from the lme4 package in R (Bates et al. 2009), along with the lmerTest package, was employed to obtain p-values and degrees of freedom based on the Satterthwaite's approximation (Kuznetsova et al. 2017). Assumption of normality of residuals was diagnosed using a quantile-quantile plot, and linearity of residuals was assessed by examining Pearson residual plots versus fitted values on the response scale.

For visualizations and further analyses, prey species were grouped into 8 different functional/taxonomic classes; large fish (>5 g), small fish (⩽5 g), amphipods, copepods, decapods, krill, worms (Polychaeta, Sipunculidea and Nematoda) and 'other'. The 'other' class consisted of different invertebrate species which comprised only small parts of the diet in terms of both numbers and biomass (e.g. Mysida, Cumacea and Echinodermata).

Dietary overlap between polar cod and Atlantic cod during polar night and summer was estimated using Schoener's niche overlap index (D; Schoener 1968):

$$D = 1 - 0.5 \times \left(\sum_{i=1}^{n} \left| p_{xi} - p_{yi} \right| \right) \quad (2)$$

where p is the biomass proportion of prey type i in species x and y, and n is the total number of prey types. D takes on a value between 0 and 1, and overlap was considered high for values >0.6, intermediate for values between 0.4 and 0.6 and low for values <0.4 (Grossman 1986).

Feeding strategies of polar cod and Atlantic cod, and the relative importance of the different prey classes in their respective diets during summer and polar night, were evaluated by plotting FO_i and prey-specific abundance (P_i) of the different prey classes in modified Costello plots (Costello 1990, Amundsen et al. 1996). P_i was calculated as:

$$P_i\ (\%) = 100 \times \sum_{i=1}^{n_i} \left(\frac{S}{S_t} \right)_i \quad (3)$$

where S is the biomass of prey type i, S_t is the total biomass of all prey types in stomachs containing prey type i, and n_i is the number of stomachs containing prey type *i*. In the Costello plot, feeding strategy is determined on the *y*-axis (specialization high vs. generalization low), and prey importance varies from the lower left to upper right diagonal (rare vs. dominant; for further explanations and examples see Amundsen et al. 1996).

The influence of predator (fish) size on diet composition was explored by dividing both polar cod and Atlantic cod into 3 length groups. Polar cod length groups were designated to correspond with YC divisions based on length (Falk-Petersen et al. 1986): 7–11.5 cm (YC 1), 11.5–16.9 cm (YC 2–4) and 16.9–25 cm (YC >5). For Atlantic cod, fish 9 to 25 cm were grouped as juveniles, and fish 25 to 60 and 60 to 90 cm were grouped to correspond with a size-dependent shift in diet of the Barents Sea cod from capelin based to gadid based as described by Holt et al. (2019). Nonmetric multidimensional scaling (NMDS) was applied on a matrix consisting of log-transformed biomasses of 7 of the prey classes per individual fish (excluding the 'other' class), using the metaMDS function from the vegan R package (Oksanen et al. 2013) with Bray-Curtis distance, 3 dimensions, 999 maximum number of iterations per NMDS run and 500 maximum numbers of random starts. The number of dimensions retained in the ordination was chosen by inspection of scree plots using stress as the *y*-axis and identifying the elbow of the curve. Results were visualized in biplots with 40% CI ellipses of the mean position for each species length group. Differences in diet composition between length groups were tested by applying permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) on the Bray-Curtis distances of the log-transformed diet composition data, using the adonis2 function from the vegan R package (Oksanen et al. 2013) with 1000 permutations, followed by pairwise comparisons with Holm's adjusted p-values.

3. RESULTS

In total, 613 polar cod and 211 Atlantic cod were collected during polar night, and 380 polar cod and 39 Atlantic cod were collected during summer (Table 1). Pelagic trawls were only conducted during polar night; only 12 polar cod and 17 Atlantic cod were collected using this method. For analytical purposes, these were pooled together with fish collected from benthic trawls conducted during polar night. No differences were observed in average total length and body mass between sexually mature males and females caught during the same season in either species. Sexually mature polar cod collected during polar night had significantly longer total length (Mann-Whitney: U = 184555, $p < 0.001$) and larger body mass (Mann-Whitney: U = 185412, $p < 0.001$) than those caught during summer. The opposite was true for Atlantic cod, where sexually mature fish had significantly shorter total length (Mann-Whitney: U = 324.5, $p < 0.001$) and smaller body mass (Mann-Whitney: U = 326, $p < 0.001$) during polar night than during summer. There were no significant differences in total length and body mass between seasons for juveniles of either species.

In total, 475 (77.5%) of the polar cod and 207 (98.1%) of the Atlantic cod had identifiable stomach contents during polar night, and 363 (95.6%) of the polar cod and 39 (100%) of the Atlantic cod had identifiable stomach contents during summer. All further dietary analyses focused only on these fishes.

Fish, predominantly small (<5 g) polar cod and pricklebacks, dominated the diet of polar cod in terms of biomass during polar night (B = 72.7%; Fig. 2a). Copepods, mainly *Calanus* spp., were the most numerous prey (NF = 62.7%) and were found in almost half of the stomachs (FO > 48%). Krill of the genus *Thysanoessa* were also a relatively important part of the polar night diet of polar cod, being found in 16% of the stomachs and contributing 14.3% of the prey biomass (Fig. 2a). Calanoid copepods dominated the summer diet of polar cod in terms of biomass (B = 52.4%; Fig. 2a) and numbers (NF = 94.4%) and were found in 84% of the stomachs. Pelagic amphipods of the genus *Themisto* (mainly *T. abyssorum*) also played

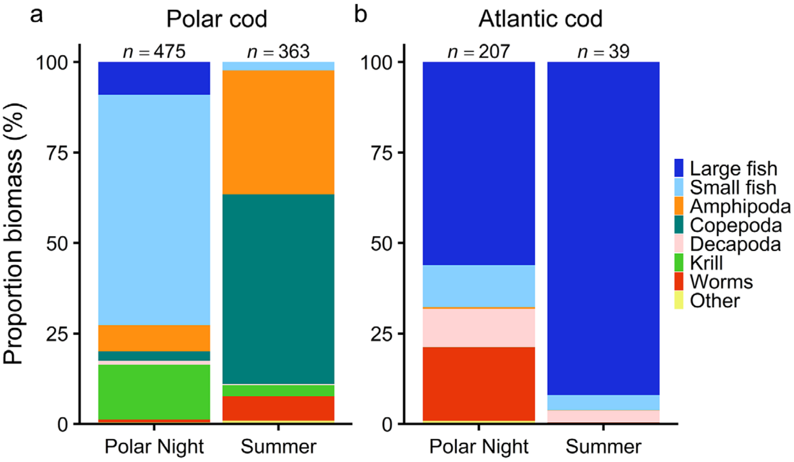

Fig. 2. Proportion of biomass of different prey groups in the diet of (a) polar cod and (b) Atlantic cod collected during polar night and summer in Kongsfjorden, Svalbard, Norway, 2022

an important role in the summer diet of polar cod, contributing 31.2% of the prey biomass (Fig. 2a). See Table S2 for a detailed list and dietary indices for polar cod prey.

The diet of Atlantic cod during polar night comprised mainly fish (>5 g), in particular polar cod (B = 37.4%) and Atlantic cod (B = 17.1%; Fig. 2b). However, the Atlantic cod in the diet were only found in 2.4% of the stomachs. Sipunculid worms of the family Golfingiidae also made up a large proportion of the polar night diet of Atlantic cod in terms of biomass (B = 18.9%; Fig. 2b). The caridean shrimp *Pandalus borealis* (NF = 24.5%) and the benthic amphipod *Arrhis phyllonyx* (NF = 11.7%) were the species with the highest relative contributions in terms of numbers and were the species found in the largest percentages of stomachs ($FO_{P.\ borealis}$ = 41.4% and $FO_{A.\ phyllonyx}$ = 31.7%) during polar night. During summer, large (>5 g) polar cod dominated the diet of Atlantic cod in terms of biomass (B = 93.6%; Fig. 2b) and were found in 69.2% of the stomachs. The pelagic amphipod *T. abyssorum* was the most numerous prey (NF = 46.7%) and was found in 64.4% of the stomachs, though it comprised little in terms of biomass (B = 0.1%). See Table S3 for a detailed list and dietary indices of Atlantic cod prey.

Parasitic nematodes were found in 34.6% of the Atlantic cod stomachs during polar night and in 66.7% during summer. Small (<0.5 mm) plastic fragments were found in 1.9% of the Atlantic cod stomachs during polar night (Table S3). No parasites or plastic fragments were found in the polar cod stomachs.

Seven of the polar cod prey types had FO or $B > 5\%$ during at least 1 season. Two of these prey types were benthic (polychaetes and the cumacean *Eudorella emarginata*), and these prey types had FO or $B > 5\%$ only during summer (Fig. 3). Pelagic *Calanus* spp. and *Themisto* spp. had FO or $B > 5\%$ during both seasons for polar cod, while pelagic fish and *Thysanoessa* spp. had FO or $B > 5\%$ only during polar night (Fig. 3).

Atlantic cod had 16 prey types with FO or $B > 5\%$. Eleven types were benthic or demersal prey, while 5 were pelagic. Among pelagic prey, 3 (polar cod, Atlantic herring and *Thysanoessa* spp.) had FO or $B > 5\%$ during both seasons (Fig. 3). Atlantic cod had predominantly consumed polar cod of YC 1 (44%) and YC 2 (30.9%), while the older YCs (3–6) constituted 25.1% of the polar cod consumed. The total length

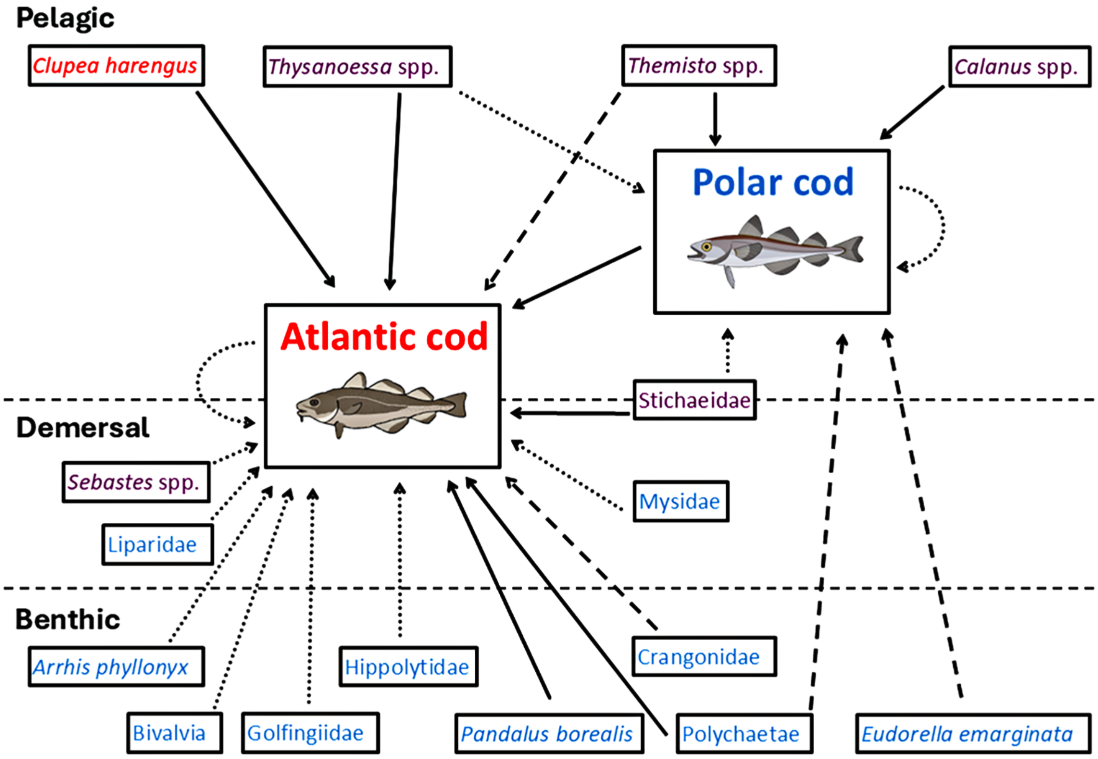

Fig. 3. Prey with frequency of occurrence (FO) or relative proportion of biomass (B) > 5% in the diet of polar cod or Atlantic cod collected during polar night and summer in Kongsfjorden, Svalbard, 2022. Arrows with solid lines denote taxa with FO or B > 5% during both seasons, dotted lines denote those only during polar night, and dashed lines denote those only during summer. Red coloration shows species associated with Atlantic Water (AW), purple shows families with species present in Svalbard associated with both AW and local Arctic water masses, and blue shows species associated with only local Arctic water masses

(cm) of the polar cod eaten by Atlantic cod increased significantly with the total length of the Atlantic cod (linear mixed-effects model: $\beta = 0.11 \pm 0.024$, $t_{20.089} = 4.632$, $p = 0.0002$). Season had no significant effect, and the random effect (ID) accounted for 15.4% of the total variance in the model.

Dietary niche overlap between polar cod and Atlantic cod was low during both polar night (*D* = 0.24) and summer (*D* = 0.03). Polar cod displayed a high level of individual specialization on either small fish, krill or amphipods during polar night (Fig. 4a). Atlantic cod had a more mixed feeding strategy during polar night, with some few individual specialization on large fish and worms, but most Atlantic cod demonstrated a general foraging strategy, feeding on small fish, decapods, amphipods and 'other' (Fig. 4b). During summer, polar cod had a somewhat mixed feeding strategy, largely specializing on copepods or amphipods, while Atlantic cod specialized on large fish (Fig. 4d,e).

Looking closer at only polar cod and Atlantic cod of similar size (9–25 cm), dietary niche overlap was high during polar night (*D* = 0.67), and small fish made up most of the biomass in the diet of both species. However, this size class of Atlantic cod did show some specialization for small polar cod during polar night (Fig. 4c). During summer, the dietary niche overlap was low (*D* = 0.13) between similarly sized gadids, and the small Atlantic cod maintained a specialized diet of small fish while also showing an increased utilization of amphipods (Fig. 4f).

There were significant differences in diet composition between the different length groups of polar cod and Atlantic cod, both during polar night (PERMANOVA: pseudo-$F_{5,570} = 22.18$, $p = 0.001$) and during summer (PERMANOVA: pseudo-$F_{5,389} = 31.754$, $p = 0.001$). Pairwise comparisons of the polar night samples revealed that all length groups of polar cod had significantly different diet composition compared with each length group of Atlantic cod (Table 2). The differences between the smallest length group of Atlantic cod (9–25 cm) and the 2 other length groups were also significant (Table 2). During summer, significant differences in diet composition were found between each length group of polar cod and each

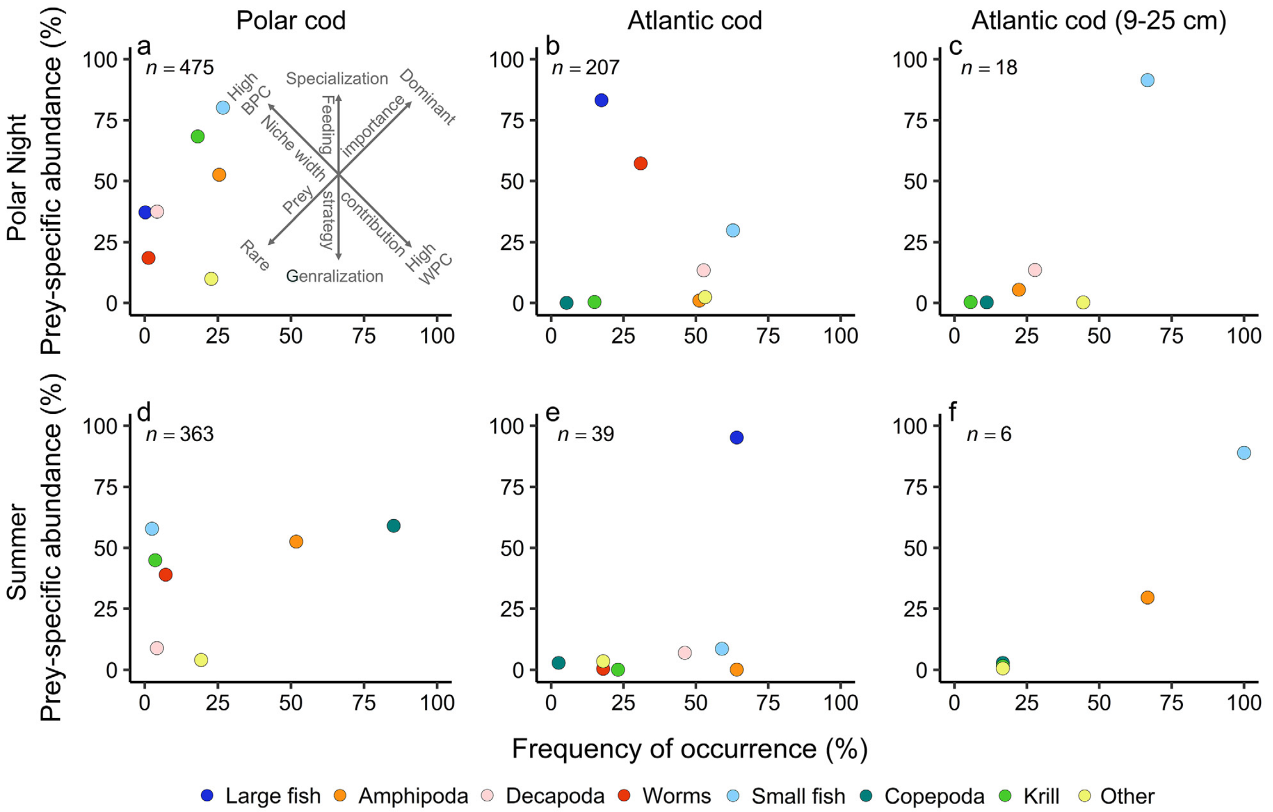

Fig. 4. Amundsen modified Costello plots showing frequency of occurrence and prey-specific abundance in terms of biomass for different prey classes in the diets of polar cod (7–25 cm) and Atlantic cod (9–90 cm) collected in Kongsfjorden, Svalbard, 2022; (a,d) polar cod, (b,e) Atlantic cod, (c,f) only Atlantic cod 9–25 cm during (a–c) polar night and (d–f) summer. Descriptive plot reproduced from Amundsen et al. (1996) is presented in (a) to aid with interpretation of graphs. BPC: between-phenotype component; WPC: within-phenotype component

Table 2. Pairwise PERMANOVA comparisons for Bray-Curtis distances of log-transformed biomass data of 7 prey classes (small fish, large fish, amphipods, copepods, decapods, krill and worms) found in the stomachs of polar cod (PC) and Atlantic cod (AC) collected during polar night (below diagonal) and summer (above diagonal) in Kongsfjorden, Svalbard, 2022. Length intervals (cm) are as follows: for PC, small = 7–11.5, intermediate (int) = 11.5–16.9, large = 16.9–25; for AC, small = 9–25, int = 25–60, large = 60–90. **Bold**: significant results ($\alpha = 0.05$). p_{adj}: adjusted p-value

	$\mathrm{PC}_{\mathrm{small}}$	$\mathrm{PC}_{\mathrm{int}}$	$\mathrm{PC}_{\mathrm{large}}$	$\mathrm{AC}_{\mathrm{small}}$	$\mathrm{AC}_{\mathrm{int}}$	$\mathrm{AC}_{\mathrm{large}}$
$\mathrm{PC}_{\mathrm{small}}$		$F = 3.39$ $p_{adj} = 0.188$	$F = 3.26$ $p_{adj} = 0.188$	**$F = 34.00$** **$p_{adj} = 0.015$**	**$F = 47.25$** **$p_{adj} = 0.015$**	**$F = 128.61$** **$p_{adj} = 0.015$**
$\mathrm{PC}_{\mathrm{int}}$	$F = 2.31$ $p_{adj} = 0.240$		$F = 0.29$ $p_{adj} = 0.649$	**$F = 18.56$** **$p_{adj} = 0.015$**	**$F = 29.08$** **$p_{adj} = 0.015$**	**$F = 94.48$** **$p_{adj} = 0.015$**
$\mathrm{PC}_{\mathrm{large}}$	$F = 3.39$ $p_{adj} = 0.108$	$F = 1.70$ $p_{adj} = 0.376$		**$F = 23.52$** **$p_{adj} = 0.015$**	**$F = 28.73$** **$p_{adj} = 0.015$**	**$F = 87.98$** **$p_{adj} = 0.015$**
$\mathrm{AC}_{\mathrm{small}}$	**$F = 13.95$** **$p_{adj} = 0.015$**	**$F = 8.70$** **$p_{adj} = 0.015$**	**$F = 4.57$** **$p_{adj} = 0.045$**		$F = 3.32$ $p_{adj} = 0.188$	**$F = 22.06$** **$p_{adj} = 0.015$**
$\mathrm{AC}_{\mathrm{int}}$	**$F = 16.77$** **$p_{adj} = 0.015$**	**$F = 93.28$** **$p_{adj} = 0.015$**	**$F = 27.07$** **$p_{adj} = 0.015$**	**$F = 4.27$** **$p_{adj} = 0.036$**		**$F = 8.05$** **$p_{adj} = 0.015$**
$\mathrm{AC}_{\mathrm{large}}$	**$F = 11.11$** **$p_{adj} = 0.015$**	**$F = 7.84$** **$p_{adj} = 0.018$**	**$F = 5.91$** **$p_{adj} = 0.018$**	**$F = 7.67$** **$p_{adj} = 0.021$**	$F = 1.18$ $p_{adj} = 0.376$	

length group of Atlantic cod as well as between the largest length group of Atlantic cod (60–90 cm) and the 2 smaller length groups of Atlantic cod (Table 2).

NMDS of the diet composition of the various length classes of the 2 gadoids showed that most of the polar cod clustered around amphipods, copepods, krill and small fish during polar night (Fig. 5a). Atlantic cod were more loosely scattered with diets that included large and small fish, decapods, amphipods and worms, and the smallest length group was separated from the other 2 length groups by being more associated with small fish (Fig. 5a; see Figs. S1 & S2 for biplots including the third NMDS axis). During summer, the polar cod length groups overlapped greatly with each other, and most individuals clustered around amphipods and copepods (Fig. 5b). Atlantic cod were again more loosely scattered around amphipods, decapods and small and large fish, with the largest length group separating from the other 2 and having a tighter association with large fish (Fig. 5b, see Figs. S1 & S2 for biplots including the third NMDS axis). Diet compositions (proportion biomass) of the different length classes of polar cod and Atlantic cod are presented in Fig. S3.

4. DISCUSSION

4.1. Proportion of empty stomachs during polar night and summer

The proportion of polar cod with prey in their stomachs was noticeably lower during polar night (77.5%) than during summer (95.6%) in the present study, which is consistent with current knowledge of the foraging behavior of polar cod in Svalbard (Geoffroy & Priou 2020, Larsen et al. 2023). Reduced feeding by polar cod during polar night likely has several causes related to prey availability (Kraft et al. 2013, Berge et al. 2020a), predator avoidance (Benoit et al. 2010), light conditions (Varpe et al. 2015, Geoffroy & Priou 2020) and gonad development (Hop et al. 1995). Polar cod in this study fed on a higher proportion of fish during winter than during summer, and a shift in diet towards relatively larger and faster swimming prey could potentially lead to a lower success rate when foraging and thus explain the larger number of empty stomachs during polar night. There was a negligible difference in the proportion of empty stomachs between polar night and summer for Atlantic cod in this study. This is in contrast to previous studies on the polar night/winter diet of Atlantic cod in Svalbard and the Barents Sea, which have reported a marked increase in empty stomachs during polar night/winter (Johannesen et al. 2016, Geoffroy & Priou 2020, Larsen et al. 2023). However, it does confirm that Atlantic cod can forage successfully in Kongsfjorden on a year-round basis and that there is year-round availability of prey for Atlantic cod in Kongsfjorden. Polar cod had a higher proportion of empty stomachs (22.5%) during polar night than Atlantic cod (1.9%) in this study, which is similar to what was found by Larsen et al. (2023) but in contrast to Geoffroy & Priou (2020). The reason for this discrepancy between the 2 gadids is not certain, but it might be linked to their preferred prey. The abundance of fish, which was the dominating prey group for Atlantic cod, likely fluctu-

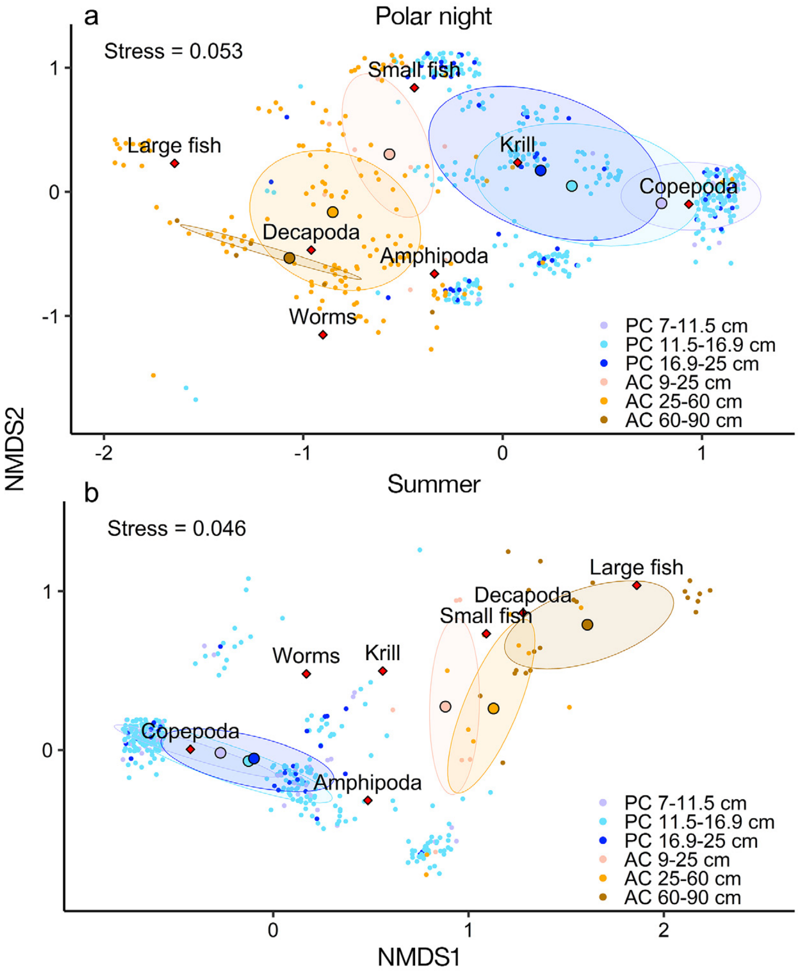

Fig. 5. First 2 axes of non-metric multidimensional scaling (NMDS) of diet composition (biomass of 7 prey classes) of different length classes of polar cod (PC) and Atlantic cod (AC) collected during (a) polar night and (b) summer in Kongsfjorden, Svalbard, 2022. Individual fish are represented by small points. Large points are group centroids, and ellipses cover 40% confidence areas for the mean position of each group. Red rhombi denote prey groups

ates to a much lower degree between seasons than zooplankton (Dalpadado et al. 2016, Wold et al. 2023), which polar cod consumes more commonly.

4.2. Polar cod diet and seasonal patterns

In the present study, the diet of polar cod varied between seasons, with small fish being the most important prey in terms of biomass during polar night, while the summer diet was dominated by amphipods and copepods. Copepods were present in almost half of the polar cod stomachs (*FO* > 48%) during polar night but contributed little in terms of biomass. The polar cod population in Svalbard is known to express some level of dietary specialization, where pelagic amphipods often have a central role. However, it has been documented that polar cod are able to opportunistically shift their diet to whatever prey are available in their habitat (Cusa et al. 2019, Schaafsma et al. 2024). Whereas the Arctic amphipod *Themisto libellula* often dominates the polar cod diet in regions dominated by Arctic water masses, polar cod in regions with a higher influence of AW display higher levels of individual specialization on different pelagic invertebrates, e.g. krill, copepods and the AW-associated amphipod *Themisto abyssorum* (Nahrgang et al. 2014, Dalpadado et al. 2016, Cusa et al. 2019). The present study was conducted in Kongsfjorden, which is undergoing Atlantification and has largely transitioned to an Atlantic-type fjord during the last 2 decades (De Rovere et al. 2022). The high proportion of biomass of *T. abyssorum* and *Calanus* spp. and low proportion of *T. libellula* in the summer diet of polar cod in this study must be seen in this context. It reflects the high influx of Atlantic zooplankton, transported with AW to Svalbard during the summer months (Willis et al. 2006, Wold et al. 2023). Similar patterns are also seen in other parts of the Arctic, where large proportions of copepods (and other boreal or sub-Arctic species) are found in the polar cod diet in regions affected by inflowing non-Arctic water masses (Nakano et al. 2016, Buckley & Whitehouse 2017, Prokopchuk 2017). Extended periods of phytoplankton blooms in the Arctic are predicted to promote increased reproduction and faster development of calanoid copepods, which consequently will lead to smaller individuals but increased overall calanoid abundance and overall amount of lipids stored in the calanoid community (Renaud et al. 2018, Møller & Nielsen 2020, Hatlebakk et al. 2022). This development could be beneficial for polar cod, which are able to feed on small prey en masse through pump filter feeding (Carlig et al. 2021), as opposed to predators that target individual copepods, e.g. the little auk *Alle alle* (Renaud et al. 2018). Further, the small fish dominating the polar night diet of the polar cod were mainly juvenile pricklebacks and conspecifics, which are both pelagic during this life stage (Falk-Petersen et al. 1986, Meyer Ottesen et al. 2011, Eriksen et al.

2012). This is in line with previous studies which have shown that the proportion of fish in the polar cod diet in Svalbard is larger, and sometimes dominating, during the winter months (Cusa et al. 2019, Larsen et al. 2023). The dominance of pelagic prey in the polar cod diet during both summer and polar night implies that polar cod in Kongsfjorden mainly forage on pelagic prey, regardless of season. The average length and weight of polar cod in this study was significantly higher during polar night than during summer, which could have exaggerated the seasonal dietary differences. Increased size of polar cod has been shown to be correlated with increased size and trophic position of their prey (Gray et al. 2016, Buckley & Whitehouse 2017, Marsh et al. 2017). However, there were no significant differences in diet composition between the length classes of polar cod during either season in the present study, indicating a relatively low size-dependent effect on diet composition for polar cod.

4.3. Atlantic cod and seasonal patterns

Atlantic cod fed predominantly on polar cod in this study. Seasonal variation was observed, with invertebrates and other species of fish being consumed to a higher degree during polar night. Atlantic cod of the Barents Sea stock feed predominantly on capelin, but polar cod become more prevalent as prey in the northern, more Arctic parts of their range (Johannesen et al. 2012, Holt et al. 2019). In Kongsfjorden, polar cod are relatively abundant and are a common prey for juvenile Atlantic cod (Brand et al. 2023, Larsen et al. 2023). The present study shows that polar cod are also important prey for mature Atlantic cod in Kongsfjorden. In contrast, capelin were not important as prey for the Atlantic cod in this study, either in terms of biomass (B < 1.2%) or FO (<2.6%), which likely reflects the fact that there is generally low capelin abundance in waters in western Svalbard compared to the central Barents Sea (Eriksen et al. 2017). The seasonal pattern documented for Atlantic cod in this study is different than the broader Barents Sea Atlantic cod stock, in which capelin usually dominate during winter, followed by a more varied diet during summer (Johannesen et al. 2016, Holt et al. 2019). It is possible that the seasonal pattern observed in this study is exaggerated to some degree because Atlantic cod sampled during summer were significantly larger than the ones sampled during polar night. Atlantic cod tend to become more strictly piscivorous with size (Holt et al. 2019), which would explain the low contribution of different invertebrates during summer. Some size-related tendencies on diet composition were also observed in this study. The diet of the largest length class of Atlantic cod (60–90 cm) was significantly different from the 2 smaller ones during summer, being more associated with large fish, whereas the smallest length class (9–25 cm) was more associated with small fish and had a significantly different diet composition than the 2 larger length classes during polar night. While polar cod was still the most important prey during polar night in the present study, other fish (most importantly conspecifics, redfish, and to some degree Atlantic herring), decapods (mainly *Pandalus borealis*) and sipunculid worms (Golfingiidae) also constituted substantial proportions of the ingested prey biomass. Cannibalism is relatively high for the Barents Sea cod compared to other cod populations and occurs when small and large cod overlap. Cannibals tend to be 2 to 3 times larger than their prey, and larger fish are more commonly cannibalistic (Bogstad et al. 1994, Yaragina et al. 2009, Holt et al. 2019). The occurrence of cannibalism during polar night but not during summer (when the Atlantic cod were on average larger) in the present study may be due to seasonal spatial division between large and small Atlantic cod, as demonstrated by Gorska et al. (2023). However, it should be noted that while constituting a large proportion of the ingested prey biomass during polar night, conspecifics were not a common prey type (FO = 2.4%) for Atlantic cod. Gorska et al. (2023) also showed that polar cod separate vertically from Atlantic cod during summer in Kongsfjorden, residing closer to the surface. However, in the present study, polar cod were caught in deep bottom trawls (114–349 m) together with Atlantic cod. Sipunculids are found in relatively high densities in the central and outer parts of Kongsfjorden, and the community is mostly dominated by 2 species, *Golfinga vulgaris* and *G. margaritacea* (Kędra & Murina 2007, Kędra & Włodarska-Kowalczuk 2008). They are benthic deposit feeders, and their relatively high occurrence in the polar night diet of Atlantic cod, along with other benthic/demersal prey with little or no presence in the summer diet in the present study (e.g. *Arrhis phyllonyx*, redfish, mysids, and bivalves), indicates a more demersal foraging strategy during polar night than during summer for Atlantic cod in Kongsfjorden. A positive relationship between the length of the Atlantic cod and the average length of the consumed polar cod was observed in this study. This is a well-documented phenomenon for Atlantic cod and is a natural consequence of an increasing gape size as they grow, allowing them to feed on larger prey (Bogstad et al. 1994, Scharf et al. 2000, Holt et al. 2019).

Still, most of the ingested polar cod belonged to the 2 youngest YCs, which makes Atlantic cod potential competitors with the local population of ringed seals in Svalbard, who also target these YCs of polar cod as their main prey (Labansen et al. 2007, Bengtsson et al. 2020). However, the dietary and spatial overlap between Atlantic cod and ringed seals in Kongsfjorden, or Svalbard as a whole, is currently not known and should be the subject of further studies. Furthermore, the youngest YCs of polar cod tend to reside more sympagically and pelagically in shallow parts of fjords compared to older age classes (Falk-Petersen et al. 1986, Benoit et al. 2010). The dominance of polar cod in the summer diet of Atlantic cod in the present study supports the suggestion that Atlantic cod forage more pelagically and higher up in the water column during summer than during polar night.

4.4. Dietary comparison, foraging strategies and niche overlap

Polar cod and Atlantic cod had similar seasonal foraging strategy patterns in this study, with a high level of individual specialization on different prey classes during polar night shifting toward a more general shift by all individuals to 1 or 2 prey classes during summer. However, dietary niche overlap between the 2 species was low during both seasons, suggesting limited potential for competition. Renaud et al. (2012) had similar conclusions for the summer feeding of these 2 gadids in west Spitsbergen fjords, although krill were more important overall in their study, and the Atlantic cod in the study by Renaud et al. (2012) were on average shorter than 7.4 cm (caudal length), which could explain the absence of fish in the diet. Fish of the 2 species of similar size (9–25 cm) showed high dietary niche overlap during polar night, though it remained low during summer. This is similar to findings of previous studies from Kongsfjorden (Renaud et al. 2012, Larsen et al. 2023) and suggests that potential competition could occur between the 2 species, although the feeding strategies of the similar-sized polar cod and Atlantic cod did differ in this study. Small fish dominated the overall diet of polar cod in terms of biomass but were only preyed on by about a quarter of the population, while other parts of the population specialized on other prey types, e.g. krill and amphipods. In comparison, the similar-sized Atlantic cod consistently specialized on small fish, which indicates that the potential for interspecific dietary competition during polar night might only be relevant for part of the polar cod population. The seasonal pattern of the polar cod foraging strategy, going from individual specialization during polar night to a more similar population mode during summer, was also observed by Cusa et al. (2019). This shift is probably linked to higher abundances of preferred prey during summer. The similar-sized Atlantic cod in this study maintained a diet specialized on small fish throughout both seasons, but the importance of amphipods (*Themisto* spp.) did increase during summer. The low sample size in our study for this season dictates caution in overinterpreting the findings, but it seems that *Themisto* spp. were relatively important for both gadid species.

4.5. Study limitations

This study is not without limitations, and as with all stomach analyses, the diet is estimated by extrapolating from a snapshot of what the fish have been eating in the most recent hours/days. Prey community composition and diet of the 2 studied gadids vary interannually, and the present study was only conducted during a single year; important interseasonal dietary patterns were, however, documented. Not having fish caught with a pelagic trawl during summer could have introduced a bias, as the diet of the fish may be different depending on where in the water column they are caught (e.g. Renaud et al. 2012). This bias was considered to be relatively small in the present study, however, as the proportion of fish collected pelagically versus benthically during polar night was relatively small. Analyzing stomach contents also comes with inherent biases — evacuation rates may differ depending on a number of factors, such as ambient temperature and prey species (Macdonald et al. 1982, Sæther et al. 1999). Digestibility of prey also differs depending on species, body tissue composition, size, etc. (Hyslop 1980, Legler et al. 2010, Baker et al. 2014). This may have led to an overestimation of prey species with bones or thick chitinous exoskeletons, which take longer to degrade and stay longer in the stomach, e.g. fish, decapods and amphipods, which were found in large numbers in the present study. Similarly, it is also possible that the contributions of soft-bodied prey, such as polychaetes, sipunculids and different gelatinous zooplankton, were underestimated. Other soft-bodied species such as chaetognaths, pteropods and appendicularians were absent in the stomachs from the present study, despite being relatively abundant in Svalbard and common prey for polar cod in other parts of the Arctic (Weydmann et al. 2014, Gluchowska et al. 2016, Buckley & Whitehouse 2017, Prokopchuk 2017). Reconstructing the biomass of prey from length measurements, which was done when prey items were deemed too digested for direct weighing in this study, is also potentially biased toward species that break down more slowly and maintain their structure longer in the stomachs (Baker et al. 2014, Amundsen & Sánchez-Hernández 2019). Despite these shortcomings, this study provides valuable insights into an ecosystem strongly affected by climate change and compliments previous studies with important knowledge about the dietary dynamics of 2 key fish species in a hotspot for Atlantification.

5. CONCLUSIONS

In conclusion, polar cod in Kongsfjorden are pelagic foragers with a diet that varies between seasons. Fish, mainly pricklebacks and conspecifics, are important prey during polar night, while AW-associated zooplankton dominate the diet during summer, e.g. *T. abyssorum* and *Calanus* spp. (*C. finmarchicus* and *C. glacialis*). Atlantic cod feed on polar cod throughout the year but also incorporate other fish species and benthic/demersal invertebrates in their diet during polar night. The relatively large biomass contribution of sipunculid worms in the present study stood out, as it has not been reported previously as a particularly important prey type for Atlantic cod. Dietary niche overlap between polar cod and Atlantic cod is low regardless of season when all length classes are combined. However, the overlap is high during polar night when only looking at individuals of similar size (while overlap remains low during summer). However, this study further revealed that the species' foraging strategies differed between the similar-sized gadids, which implies a relatively low potential for competition between Atlantic cod and polar cod, even during polar night. The heavy predation of Atlantic cod on polar cod in Kongsfjorden is a cause for concern for the already diminishing local population of polar cod (Gorska et al. 2023). Furthermore, Atlantic cod is potentially competing with the local ringed seal population year-round, as they predominantly feed on the same YCs of polar cod and with seabirds in summer. With further Atlantification, it is likely that the ecosystem in Kongsfjorden and other areas in Svalbard with high influence of AW will resemble the current ecosystem in the Barents Sea, where Atlantic cod is the most abundant top predator, having significant effects on prey abundances and body condition of marine mammals (Durant et al. 2014, Solvang et al. 2021, 2022).

Acknowledgements. This study was funded by the Norwegian Research Council (NFR) ARK project (no. 313678). Fieldwork for O.B. was partly funded by The Arctic Field Grant, granted by NFR. Polar night sampling was made possible thanks to UiT The Arctic University of Norway, project Deep Impact (NFR project no. 300333). Summer samples were collected during a scientific cruise organized by the University Center in Svalbard for the course AB-320 Arctic Marine Zooplankton; we thank Malin Daase for her cooperation. Sławomir Kwaśniewski assisted in prey identification. The map of the study region was made by Oddveig Øien Ørvoll from the mapping division of the Norwegian Polar Institute. Lotta Lindblom from the Norwegian Institute of Marine Research provided us with a reference collection of fish otoliths.

LITERATURE CITED

Amundsen PA, Sánchez-Hernández J (2019) Feeding studies take guts — critical review and recommendations of methods for stomach contents analysis in fish. J Fish Biol 95:1364–1373

Amundsen PA, Gabler HM, Staldvik F (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

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Aune M, Raskhozheva E, Andrade H, Augustine S and others (2021) Distribution and ecology of polar cod (*Boreogadus saida*) in the eastern Barents Sea: a review of historical literature. Mar Environ Res 166:105262

Baker R, Buckland A, Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. Fish Fish 15:170–177

Bates D, Maechler M, Bolker B, Walker S and others (2009) Package 'lme4'. http://lme4.r-forge.r-project.org

Bengtsson O, Lydersen C, Kovacs KM, Lindstrøm U (2020) Ringed seal (*Pusa hispida*) diet on the west coast of Spitsbergen, Svalbard, Norway: during a time of ecosystem change. Polar Biol 43:773–788

Benoit D, Simard Y, Gagné J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. Polar Biol 33:1505–1520

Berge J, Renaud PE, Darnis G, Cottier F and others (2015) In the dark: a review of ecosystem processes during the Arctic polar night. Prog Oceanogr 139:258–271

Berge J, Daase M, Hobbs L, Falk-Petersen S, Darnis G, Søreide JE (2020a) Zooplankton in the polar night. In: Berge J, Johnsen G, Cohen JH (eds) Polar night marine ecology: life and light in the dead of night, Vol 4. Springer, Cham, p 113–159

Berge J, Johnsen G, Cohen JH (2020b) Introduction. In: Berge J, Johnsen G, Cohen JH (eds) Polar night marine ecology: life and light in the dead of night, Vol 4. Springer, Cham, p 1–15

Bogstad B, Lilly GR, Mehl S, Palsson OK, Stefánsson G (1994) Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Mar Sci Symp 198:579–599

Bogstad B, Gjøsæter 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

Bradstreet MSW, Cross WE (1982) Trophic relationships at high Arctic ice edges. Arctic 35:1–12

Brand M, Fischer P (2016) Species composition and abundance of the shallow water fish community of Kongsfjorden, Svalbard. Polar Biol 39:2155–2167

Brand M, Spotowitz L, Mark FC, Berge J and others (2023) Age class composition and growth of Atlantic cod (*Gadus morhua*) in the shallow water zone of Kongsfjorden, Svalbard. Polar Biol 46:53–65

Buckland A, Baker R, Loneragan N, Sheaves M (2017) Standardising fish stomach content analysis: the importance of prey condition. Fish Res 196:126–140

Buckley TW, Whitehouse GA (2017) Variation in the diet of Arctic cod (*Boreogadus saida*) in the Pacific Arctic and Bering Sea. Environ Biol Fishes 100:421–442

Carlig E, Christiansen JS, Di Blasi D, Ferrando S and others (2021) Midtrophic fish feeding modes at the poles: an ecomorphological comparison of polar cod (*Boreogadus saida*) and Antarctic silverfish (*Pleuragramma antarctica*). Polar Biol 44:1629–1642

Costello M (1990) Predator feeding strategy and prey importance: a new graphical analysis. J Fish Biol 36:261–263

Cottier F, Porter M (2020) The marine physical environment during the polar night. In: Berge J, Johnsen G, Cohen JH (eds) Polar night marine ecology: life and light in the dead of night, Vol 4. Springer, Cham, p 17–36

Craig P, Griffiths W, Haldorson L, McElderry H (1982) Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can J Fish Aquat Sci 39: 395–406

Cusa M, Berge J, Varpe Ø (2019) Seasonal shifts in feeding patterns: individual and population realized specialization in a high Arctic fish. Ecol Evol 9:11112–11121

Dahl TM, Lydersen C, Kovacs KM, Falk-Petersen S, Sargent J, Gjertz I, Gulliksen B (2000) Fatty acid composition of the blubber in white whales (*Delphinapterus leucas*). Polar Biol 23:401–409

Dahl TM, Falk-Petersen S, Gabrielsen GW, Sargent JR, Hop H, Millar RM (2003) Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord. Mar Ecol Prog Ser 256: 257–269

Dalpadado P, Hop H, Rønning J, Pavlov V and others (2016) Distribution and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard) and changes in their relative importance as key prey in a warming marine ecosystem. Polar Biol 39: 1765–1784

De Rovere F, Langone L, Schroeder K, Miserocchi S, Giglio F, Aliani S, Chiggiato J (2022) Water masses variability in inner Kongsfjorden (Svalbard) during 2010–2020. Front Mar Sci 9:741075

Deb JC, Bailey SA (2023) Arctic marine ecosystems face increasing climate stress. Environ Rev 31:403–451

Drinkwater K (2009) Comparison of the response of Atlantic cod (*Gadus morhua*) in the high-latitude regions of the North Atlantic during the warm periods of the 1920s–1960s and the 1990s–2000s. Deep Sea Res II 56: 2087–2096

Durant JM, Skern-Mauritzen M, Krasnov YV, Nikolaeva NG, Lindstrøm U, Dolgov A (2014) Temporal dynamics of top predators interactions in the Barents Sea. PLOS ONE 9:e110933

Eriksen E, Prokhorova T, Johannesen E (2012) Long term changes in abundance and spatial distribution of pelagic Agonidae, Ammodytidae, Liparidae, Cottidae, Myctophidae and Stichaeidae in the Barents Sea. In: Ali M (ed) Diversity of ecosystems. IntechOpen, Rijeka, p 109–126

Eriksen E, Ingvaldsen R, Nedreaas K, Prozorkevich D (2015) The effect of recent warming on polar cod and beaked redfish juveniles in the Barents Sea. Reg Stud Mar Sci 2: 105–112

Eriksen E, Skjoldal HR, Gjøsæter H, Primicerio R (2017) Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. Prog Oceanogr 151:206–226

Falk-Petersen IB, Frivoll V, Gulliksen B, Haug T (1986) Occurrence and size/age relations of polar cod, *Boreogadus saida* (Lepechin), in Spitsbergen coastal waters. Sarsia 71:235–245

Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Chang 5:673–677

Geoffroy M, Priou P (2020) Fish ecology during the polar night. In: Berge J, Johnsen G, Cohen JH (eds) Polar night marine ecology: life and light in the dead of night, Vol 4. Springer, Cham, p 181–216

Geoffroy M, Bouchard C, Flores H, Robert D and others (2023) The circumpolar impacts of climate change and anthropogenic stressors on Arctic cod (*Boreogadus saida*) and its ecosystem. Elementa Sci Anthrop 11:00097

Gluchowska M, Kwasniewski S, Prominska A, Olszewska A and others (2016) Zooplankton in Svalbard fjords on the Atlantic–Arctic boundary. Polar Biol 39:1785–1802

Gorska N, Schmidt B, Węsławski JM, Grabowski M, Dragan-Górska A, Szczucka J, Beszczynska-Möller A (2023) Fish in Kongsfjorden under the influence of climate warming. Front Mar Sci 10:1213081

Gray BP, Norcross BL, Blanchard AL, Beaudreau AH, Seitz AC (2016) Variability in the summer diets of juvenile polar cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas. Polar Biol 39:1069–1080

Grossman GD (1986) Food resource partitioning in a rocky intertidal fish assemblage. J Zool 1:317–355

Härkönen T (1986) Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu ApS, Hellerup

Hatlebakk M, Kosobokova K, Daase M, Søreide JE (2022) Contrasting life traits of sympatric *Calanus glacialis* and *C. finmarchicus* in a warming Arctic revealed by a year-round study in Isfjorden, Svalbard. Front Mar Sci 9:877910

Holt RE, Bogstad B, Durant JM, Dolgov AV, Ottersen G (2019) Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. ICES J Mar Sci 76:1641–1652

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: 878–894

Hop H, Trudeau VL, Graham M (1995) Spawning energetics of Arctic cod (*Boreogadus saida*) in relation to seasonal development of the ovary and plasma sex steroid levels. Can J Fish Aquat Sci 52:541–550

Huserbråten MBO, Eriksen E, Gjøsæter H, Vikebø F (2019) Polar cod in jeopardy under the retreating Arctic sea ice. Commun Biol 2:407

Hyslop E (1980) Stomach contents analysis — a review of methods and their application. J Fish Biol 17:411–429

ICES (2018) Interim report of the Working Group on the Integrated Assessments of the Barents Sea (WGIBAR). ICES CM 2018/IEASG:04. ICES, Copenhagen, p 210

Ingvaldsen RB, Gjøsæter H, Ona E, Michalsen K (2017) Atlantic cod (*Gadus morhua*) feeding over deep water in the high Arctic. Polar Biol 40:2105−2111

Institute of Marine Research (2022a) Biomass of polar cod in the Barents Sea. Environmental monitoring of Svalbard and Jan Mayen (MOSJ). https://mosj.no/en/indikator/fauna/marine-fauna/biomass-of-polar-cod-in-the-barents-sea/ (accessed 26 Feb 2024)

Institute of Marine Research (2022b) Stock of Northeast Arctic cod in the Barents Sea. Environmental monitoring of Svalbard and Jan Mayen (MOSJ). https://mosj.no/en/indikator/fauna/marine-fauna/stock-of-northeast-arctic-cod/ (accessed 26 Feb 2024)

Johannesen E, Lindstrøm U, Michalsen K, Skern-Mauritzen M, Fauchald P, Bogstad B, Dolgov A (2012) Feeding in a heterogeneous environment: spatial dynamics in summer foraging Barents Sea cod. Mar Ecol Prog Ser 458:181−197

Johannesen E, Johansen GO, Korsbrekke K (2016) Seasonal variation in cod feeding and growth in a changing sea. Can J Fish Aquat Sci 73:235−245

Johannesen E, Mørk HL, Korsbrekke K, Wienerroither R and others (2017) Arctic fishes in the Barents Sea 2004−2015: changes in abundance and distribution. IMR/PINRO Joint Report Series, No. 1/2017. Institute of Marine Research, Bergen, and Polar Research Institute of Marine Fisheries and Oceanography, Murmansk

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

Kędra M, Murina GV (2007) The sipunculan fauna of Svalbard. Polar Res 26:37−47

Kędra M, Włodarska-Kowalczuk M (2008) Distribution and diversity of sipunculan fauna in high Arctic fjords (west Svalbard). Polar Biol 31:1181−1190

Klekowski RZ, Węsławski JM (1992) Atlas of the marine fauna of southern Spitsbergen: invertebrates, Vol 2. Ossolineum, Gdansk

Kohlbach D, Schaafsma FL, Graeve M, Lebreton B and others (2017) Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: evidence from stomach content, fatty acid and stable isotope analyses. Prog Oceanogr 152:62−74

Kraft A, Berge J, Varpe Ø, Falk-Petersen S (2013) Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula.* Mar Biol 160:241−248

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82:1−26

Labansen AL, Lydersen C, Haug T, Kovacs KM (2007) Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. ICES J Mar Sci 64:1246−1256

Larsen LH, Cusa M, Eglund-Newby S, Berge J and others (2023) Diets of gadoid fish in Arctic waters of Svalbard fjords during the polar night. Polar Biol 46:783−799

Legler ND, Johnson TB, Heath DD, Ludsin SA (2010) Water temperature and prey size effects on the rate of digestion of larval and early juvenile fish. Trans Am Fish Soc 139:868−875

Levene H (1960) Robust tests for equality of variances. In: Olkin I (ed) Contributions to probability and statistics. Essays in honor of Harold Hotelling. Stanford University Press, Stanford, CA, p 279−292

Lind S, Ingvaldsen RB, Furevik T (2018) Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import. Nat Clim Chang 8:634−639

Link JS, Bogstad B, Sparholt H, Lilly GR (2009) Trophic role of Atlantic cod in the ecosystem. Fish Fish 10:58−87

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biol 9:187−191

Macdonald JS, Waiwood KG, Green RH (1982) Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*). Can J Fish Aquat Sci 39:651−659

Mann HB, Whitney DR (1947) On a test of whether one of two random variables is stochastically larger than the other. Ann Math Stat 18:50−60

Marsh JM, Mueter FJ, Iken K, Danielson S (2017) Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes. Deep Sea Res II 135:78−94

Marsh JM, Mueter FJ, Quinn TJ (2020) Environmental and biological influences on the distribution and population dynamics of polar cod (*Boreogadus saida*) in the US Chukchi Sea. Polar Biol 43:1055−1072

Mecklenburg CW, Johannesen E, Byrkjedal I, Christiansen J and others (2018) Marine fishes of the Arctic region, Vols 1 & 2. Conservation of Arctic Flora and Fauna, Akureyri

Mehlum F, Hunt GL, Klusek Z, Decker MB, Nordlund N (1996) The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. Polar Biol 16:537−547

Merchel M, Walczowski W (2020) Increases in the temperature and salinity of deep and intermediate waters in the West Spitsbergen Current region in 1997−2016. Oceanologia 62:501−510

Meyer Ottesen C, Hop H, Christiansen JS, Falk-Petersen S (2011) Early life history of the daubed shanny (Teleostei: *Leptoclinus maculatus*) in Svalbard waters. Mar Biodivers 41:383−394

Misund OA, Heggland K, Skogseth R, Falck E and others (2016) Norwegian fisheries in the Svalbard zone since 1980. Regulations, profitability and warming waters affect landings. Polar Sci 10:312−322

Møller EF, Nielsen TG (2020) Borealization of Arctic zooplankton — smaller and less fat zooplankton species in Disko Bay, western Greenland. Limnol Oceanogr 65:1175−1188

Mueter FJ, Nahrgang J, Nelson RJ, Berge J (2016) The ecology of gadid fishes in the circumpolar Arctic with a special emphasis on the polar cod (*Boreogadus saida*). Polar Biol 39:961−967

Nahrgang J, Varpe Ø, Korshunova E, Murzina S, Hallanger IG, Vieweg I, Berge J (2014) Gender specific reproductive strategies of an Arctic key species (*Boreogadus saida*) and implications of climate change. PLOS ONE 9:e98452

Nakano T, Matsuno K, Nishizawa B, Iwahara Y and others (2016) Diets and body condition of polar cod (*Boreogadus saida*) in the northern Bering Sea and Chukchi Sea. Polar Biol 39:1081−1086

Oksanen J, Blanchet FG, Kindt R, Legendre P and others (2013) Package 'vegan': community ecology package, version 2.6-2. http://vegan.r-forge.r-project.org

Ottersen G, Bogstad B, Yaragina NA, Stige LC, Vikebø FB, Dalpadado P (2014) A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). ICES J Mar Sci 71: 2064–2087

Pethon P (1994) Aschehougs store fiskebok: alle norske fisker i farger. Aschehoug, Oslo

Prokopchuk I (2017) Feeding of polar cod *Boreogadus saida* in the Kara Sea. J Ichthyol 57:591–602

R Development Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Renaud PE, Berge J, Varpe Ø, Lønne OJ, Nahrgang J, Ottesen C, Hallanger I (2012) Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? Polar Biol 35:401–412

Renaud PE, Daase M, Banas NS, Gabrielsen TM and others (2018) Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of resilience. ICES J Mar Sci 75:1871–1881

Sæther BS, Christiansen JS, Jobling M (1999) Gastrointestinal evacuation of particulate matter in polar cod *Boreogadus saida.* Mar Ecol Prog Ser 188:201–205

Schaafsma FL, Flores H, David CL, Castellani G and others (2024) Insights into the diet and feeding behavior of immature polar cod (*Boreogadus saida*) from the under-ice habitat of the central Arctic Ocean. J Fish Biol 105:907–930

Scharf FS, Juanes F, Rountree RA (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

Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52:591–611

Solvang HK, Haug T, Knutsen T, Gjøsæter H and others (2021) Distribution of rorquals and Atlantic cod in relation to their prey in the Norwegian high Arctic. Polar Biol 44:761–782

Solvang HK, Haug T, Øien N (2022) Recent trends in temporal and geographical variation in blubber thickness of common minke whales (*Balaenoptera acutorostrata acutorostrata*) in the Northeast Atlantic. NAMMCO Sci Publ 12. https://doi.org/10.7557/3.6308

Søreide JE, Pitusi V, Vader A, Damsgård B and others (2021) Environmental status of Svalbard coastal waters: coastscapes and focal ecosystem components (SvalCoast, Chapter 6). In: Moreno-Ibáñez et al. (eds) SESS report 2020. Svalbard Integrated Arctic Earth Observing System, Longyearbyen, p 142–174. https://doi.org/10.5281/zenodo.4293849

Spotowitz L, Johansen T, Hansen A, Berg E, Stransky C, Fischer P (2022) New evidence for the establishment of coastal cod *Gadus morhua* in Svalbard fjords. Mar Ecol Prog Ser 696:119–133

Steiner NS, Cheung WW, Cisneros-Montemayor AM, Drost H and others (2019) Impacts of the changing ocean–sea ice system on the key forage fish Arctic cod (*Boreogadus saida*) and subsistence fisheries in the western Canadian Arctic—evaluating linked climate, ecosystem and economic (CEE) models. Front Mar Sci 6:179

Szczucka J, Hoppe Ł, Schmidt B, Fey DP (2017) Acoustical estimation of fish distribution and abundance in two Spitsbergen fjords. Oceanologia 59:585–591

Townhill BL, Holt RE, Bogstad B, Durant JM and others (2021) Diets of the Barents Sea cod *Gadus morhua* from the 1930s to 2018. Earth Syst Sci Data 13:1361–1370

Varpe Ø, Daase M, Kristiansen T (2015) A fish-eye view on the new Arctic lightscape. ICES J Mar Sci 72: 2532–2538

Vassilenko SV, Petryashov VV (eds) (2009) Illustrated keys to free-living invertebrates of Eurasian Arctic seas and adjacent deep waters, Vol 1. University of Alaska Fairbanks, Fairbanks, AK

Vollen T, Albert OT, Nilssen EM (2004) Diet composition and feeding behaviour of juvenile Greenland halibut (*Reinhardtius hippoglossoides*) in the Svalbard area. J Sea Res 51:251–259

Wetzel MA, Leuchs H, Koop JH (2005) Preservation effects on wet weight, dry weight, and ash-free dry weight biomass estimates of four common estuarine macro-invertebrates: no difference between ethanol and formalin. Helgol Mar Res 59:206–213

Weydmann A, Carstensen J, Goszczko I, Dmoch K, Olszewska A, Kwasniewski S (2014) Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current. Mar Ecol Prog Ser 501:41–52

Weydmann-Zwolicka A, Prątnicka P, Łącka M, Majaneva S, Cottier F, Berge J (2021) Zooplankton and sediment fluxes in two contrasting fjords reveal atlantification of the Arctic. Sci Total Environ 773:145599

Willis K, Cottier F, Kwasniewski S, Wold A, Falk-Petersen S (2006) The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). J Mar Syst 61:39–54

Wold A, Jæger I, Hop H, Gabrielsen GW, Falk-Petersen S (2011) Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. Polar Biol 34:1147–1155

Wold A, Hop H, Svensen C, Søreide JE, Assmann KM, Ormanczyk M, Kwasniewski S (2023) Atlantification influences zooplankton communities seasonally in the northern Barents Sea and Arctic Ocean. Prog Oceanogr 219: 103133

Yaragina NA, Bogstad B, Kovalev YA (2009) Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947–2006. Mar Biol Res 5:75–85

Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA
Reviewed by: C. Bouchard, B. Gray and 1 anonymous referee

Submitted: May 27, 2024
Accepted: September 5, 2024
Proofs received from author(s): October 10, 2024