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Feeding ecology of age-0 polar cod (*Boreogadus saida*) in the Greenland Sea

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Abstract

Polar cod (*Boreogadus saida*) play a crucial role as a key species in Arctic marine ecosystems. The importance of successful feeding of particularly their sensitive early life stages for survival and later recruitment into the adult population is known. This study investigated the diets of age-0 polar cod in the Greenland Sea (Northeast Greenland) during the summer and fall of 2017, focusing on regional feeding patterns and prey preferences. Stomach contents were analyzed in conjunction with environmental data, including oceanographic conditions and zooplankton distributions, to identify and quantify prey taxa, estimate ingested carbon contents, and assess prey selectivity. The findings revealed two regional groups characterized by differing oceanographic conditions and dietary patterns. Consistent with findings from other regions, Calanoid copepods were the predominant and preferred prey across both groups. Age-0 polar cod in the shelf group consumed a higher number of prey items with lower overall carbon contents, showing a preference for *Calanus spp.* nauplii. The basin group ingested fewer, but higher carbon content prey items, with a preference for *Pseudocalanus spp.* nauplii. These results illustrate the differences in polar cod diets at a regional scale. Investigating the feeding ecology of early life stages in East Greenland is an important tool to understand their role in a changing Arctic.

1 Introduction

1.1 Arctic marine ecosystems in the context of climate change

Out of all regions on Earth, Arctic regions are undergoing the most rapid changes due to effects of anthropogenic climate change. Global surface temperatures have increased by about 1.1°C since the late 19th century (IPCC, 2023a), and mean temperatures in the Arctic are accelerating four times faster than the global average due to Arctic amplification (Rantanen et al., 2022). While global temperatures are expected to rise by at least 1.5°C by the end of the century due to past and current emissions alone (IPCC, 2023a), the Arctic regions will experience a more dramatic rise, with mean annual surface temperatures increasing by 3.3-10°C above the average levels recorded from 1985 to 2014 (AMAP, 2021). As humanity is currently failing to adequately reduce global greenhouse gas emissions to limit further warming (IPCC, 2023a), sea-ice free Arctic summers can be expected before 2050 (AMAP, 2021). The Arctic of the future may be quite different from the ecosystems we know today, as there have already been numerous documented changes compared to pre-industrial times. Arctic marine species adapted to cold temperatures and distinct seasonal cycles are confronted with drastic environmental changes: higher sea surface temperatures, ocean acidification, decreases in sea-ice extent and volume as well as increased input of freshwater and nutrients from melting glaciers and rivers (AMAP, 2021; IPCC, 2023a). Previously rare extreme events such as marine heatwaves have increased in frequency and intensity (AMAP, 2021; IPCC, 2023a). Seasonal events are diverging from historical patterns and becoming more irregular. A prominent example is the shortened period of complete ice coverage in Arctic seas. The sea ice cover is breaking up increasingly early in the spring, while winter freeze-up is starting later (Vaughan et al., 2013). Reproductive cycles of endemic species in the Arctic are closely tied to the timing of these seasonal phenomena, most prominently due to the onset of primary production when light becomes available in spring and summer. In an environment with extreme light seasonality and low temperatures, timing is crucial for offspring to utilize periods of high productivity and build up lipid reserves to survive winter months despite limited food availability. While shifts in the seasonal timing of organisms allow for some level of adaptation to changing environments, limitations in these biological responses oftentimes mean they are not sufficient to cope with escalating effects of climate

change (IPCC, 2023b). The wide array of changes in both abiotic and biotic factors are expected to negatively impact fitness and the survival of offspring of Arctic species. Boreal species from temperate regions such as the Norwegian Sea are increasingly expanding into Arctic waters and are competing for resources with endemic inhabitants (Darnis et al., 2012; Wassmann et al., 2011). Increased anthropogenic activity in the Arctic is furthermore leading to higher pollution levels from various sources (AMAP, 2021; Wassmann et al., 2011). Climate change has caused substantial damages and irreversible losses to Arctic ecosystems which will impact the structure and function of Arctic marine food-webs, and threaten the biodiversity of the region (Darnis et al., 2012; IPCC, 2023a; Wassmann et al., 2011). Some aspects of Arctic warming may be favorable for single species in the short-term (source on increased production advantages). Food production in Arctic regions in the current century could potentially increase due to higher expected fisheries yields in the North, although those projections have low confidence (IPCC). However, most research indicates that the fast rate of environmental changes will negatively affect endemic Arctic species over the long-term (sources) and result in adverse outcomes for human communities living and working in the Arctic. Investigating Arctic food webs, trophic relations, and dynamics can offer an insight on how the combination of environmental changes may affect the ecosystem as a whole.

1.2 Arctic marine food-webs

Arctic marine ecosystems are characterized by low temperatures and strong light seasonality (Wassmann (Edt.) et al., 2018). Characteristics for organisms of Arctic marine ecosystems are the specialized adaptation to these conditions, one result of which is that Arctic organisms generally store a big amount of energy in form of lipids to survive in the highly fluctuating environment. Arctic marine foodwebs are interconnected webs with different trophic levels

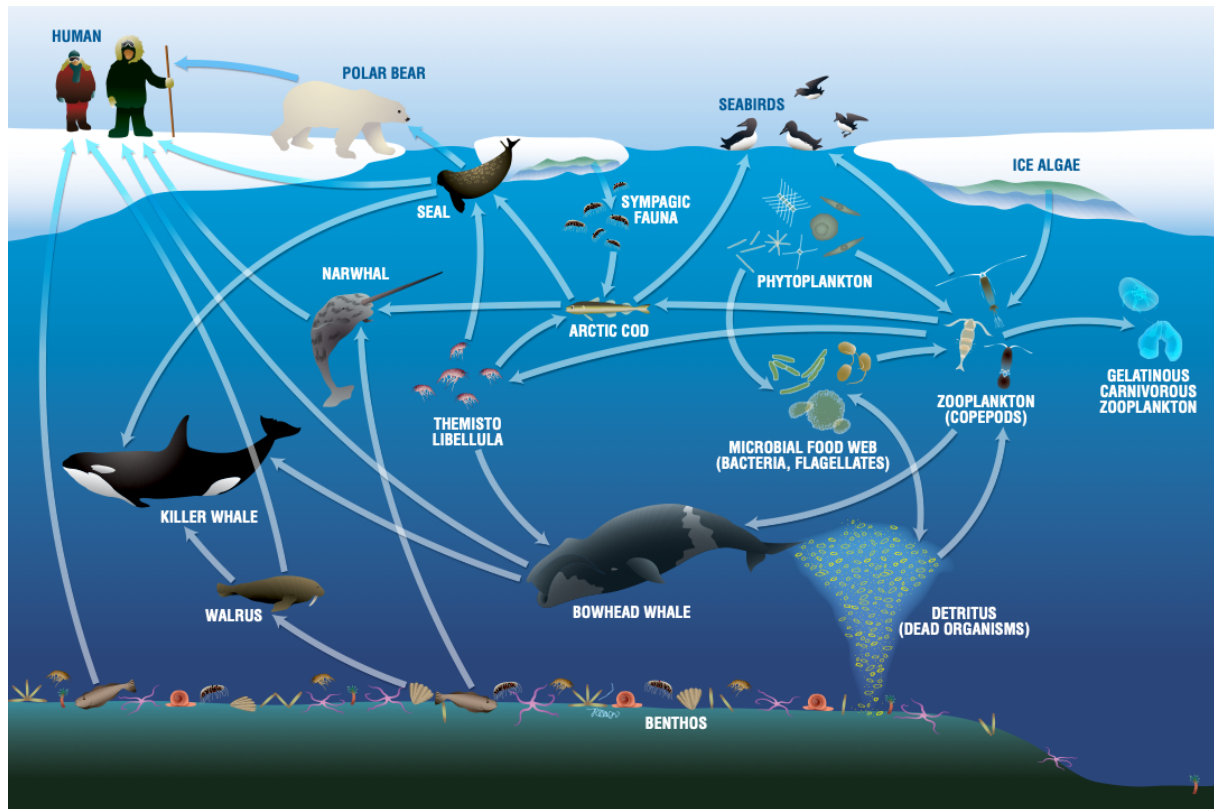


Fig. 1 Illustration of an Arctic marine food-web with *Boreogadus saida* (commonly referred to as both Polar cod and Arctic cod) in the center and a left-to-right transition from coastal to oceanic environment. Source: (Darnis et al., 2012)

(Fig. 1). The lowest level of Arctic marine foodwebs consists of phytoplankton production based on inorganic resources by small algae, diatoms, and ice algae. The microbial foodweb consists of bacteria and flagellates and ciliates feeding on organic compounds produced by phytoplankton as well as on detritus and dissolved organic matter (Darnis et al., 2012; Seuthe, Bratbak & Larsen in Wassmann (Edt.) et al., 2018). These are subject to seasonal changes, since only the summer months offer light exposure and therefore opportunity for increased production by photosynthesis. Primary production by phytoplankton is only possible in the limited time window when light is available (Reigstad & Berge in Wassmann (Edt.) et al., 2018). Zooplankton and sympagic (ice-associated) fauna both rely on primary production of phytoplankton, microbial production, and detritus as a food source. Zooplankton are important secondary producers and serve as a major food source to both other carnivorous zooplankton and ichthyoplankton, as well as many higher-level organisms. Marine mammals, seabirds, fish, and benthic organisms all feed on zooplankton. While zooplankton can be a direct food source, the nutrients produced by this trophic level also indirectly reach the higher trophic levels. Since the food-web involves dynamic, interconnected relationships, trophic

levels are neither static nor separate. Higher trophic levels in the Arctic consist of larger fish, seabirds, marine mammals such as seals, whales and polar bears, and humans. Polar bears (*Ursus maritimus*), bowhead whales (*Balaena mysticetus*), Greenland sharks (*Somniosus microcephalus*), little auks (*Alle alle*) and humans are among the most important apex predators in Arctic marine ecosystems and at the highest trophic level (Karnovsky et al., 2011; Laidre et al., 2007; Nielsen et al., 2014).

1.3 The Greenland Sea

The Greenland Sea is a High-Arctic region undergoing significant warming in the past two decades (de Steur et al., 2023). It is located between Greenland and the Spitsbergen archipelago and is part of the Nordic Seas (**Error! Reference source not found.**). The East Greenland Current flows southward through Fram Strait along the entire East coast of Greenland, transporting a large fraction of Arctic sea ice and water masses into the Greenland Sea and the North Atlantic (Rudels et al., 2002; Willcox et al., 2023). The region therefore plays a large role in thermohaline circulation (Buch, 2007). The shallow Northeast Greenland Shelf is not only a major Arctic outflow area, but also increasingly influenced by meltwater and run-

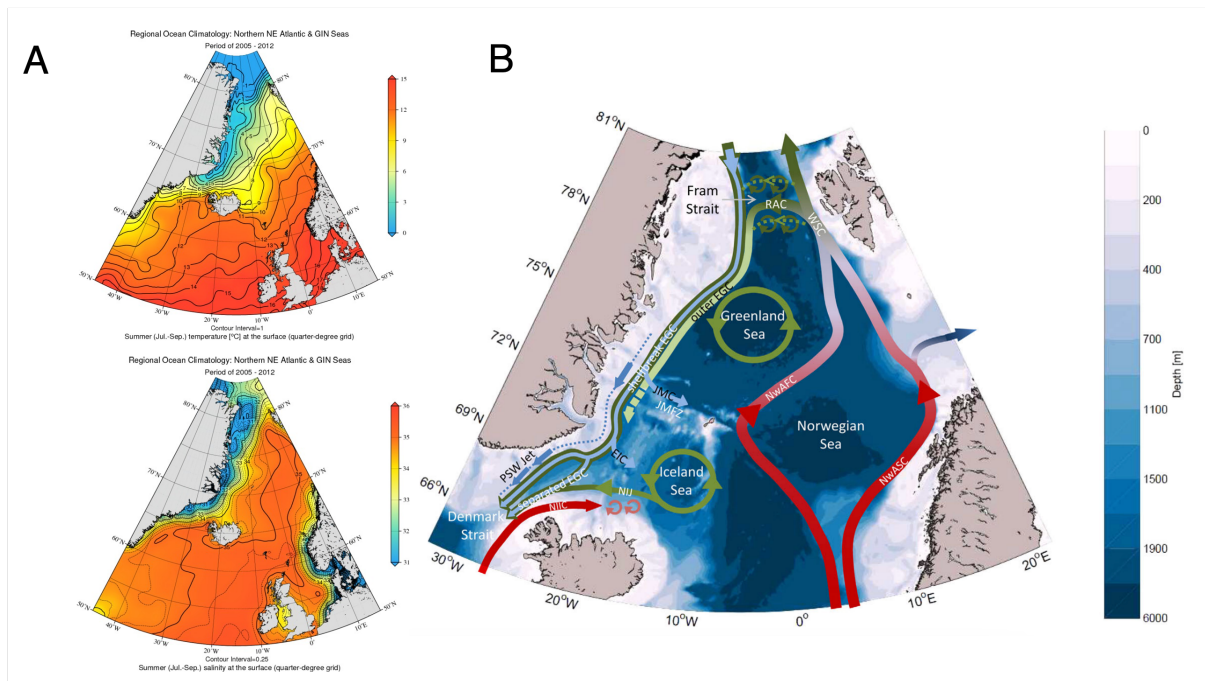


Fig. 2 Greenland Sea oceanography. a) average sea-surface temperatures and salinities in the summer in the GIN seas between 2005-2012 (objectively analyzed means from Jul-Sep.), b) Currents in the Greenland Sea. Sources: (Håvik et al., 2017), National Oceanic and Atmospheric Administration (NOAA).

off from the Greenland Ice Sheet (Hopkins, 1991; Mattingly et al., 2023; Willcox et al., 2023). It is separated from the deep waters of the open Greenland Sea by a steep continental slope (Boertmann et al., 2020; Buch, 2007). While sea ice and icebergs are present year-round (Boertmann et al., 2020), a combination of warming polar waters and greater presence of warm Atlantic water has led to a reduction in sea ice cover in the Greenland Sea (de Steur et al., 2023). The Greenland Sea has experienced significant Atlantification in the past decades (Gjelstrup et al., 2022). Polynyas (ice-free areas within the sea ice) are important sites of biological production in the Greenland Sea (Hirche et al., 1994), just like in other Arctic regions (Bouchard & Fortier, 2008; Holst et al., 2001; Møller et al., 2018). The Northeast Water Polynya is located to the north and the Sirius Water Polynya to the South of the Northeast Greenland shelf (Boertmann et al., 2020; Schneider & Budéus, 1994).

1.4 Polar cod - an Arctic key species

General lifecycle and characteristics

The polar cod (*Boreogadus saida*) is a highly abundant Gadid fish with a pan-Arctic distribution (Geoffroy et al., 2023; Mueter et al., 2016). It is known as Arctic cod in North America (not to be confused with the European Arctic cod *Arctogadus glacialis*) and as eqalugaq in Greenland.

The forage fish is a prime example of an endemic inhabitant of the Arctic. It is physiologically highly adapted to Arctic conditions (Ewart & Hew, 2022) and therefore thrives in cold waters (Graham & Hop, 1995). Part of its life cycle can be spent in association with sea-ice (David et al., 2016) and other sympagic organisms are a staple in

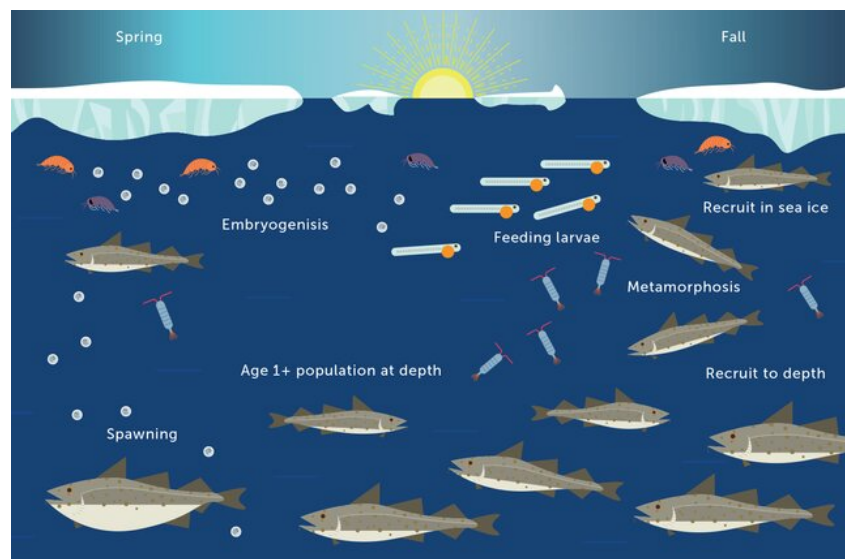


Fig. 3 Illustration of the lifecycle of polar cod (*Boreogadus saida*). Depicted are five lifestages: 1) planktonic, positively buoyant eggs in surface waters in the spring; 2) epipelagic, opportunistically sympagic larvae and juveniles in the fall; 3) pelagic, immature age-1 fish; 4) mature adults stratified by size in deeper and near-bottom waters, spawning eggs during springtime. Source: (Geoffroy et al., 2023)

their diet (Kohlbach et al., 2016, 2017; Schaafsma, 2018; Schaafsma et al., 2024). Polar cod are involved in the transport of energy from lower trophic levels to higher trophic levels and in the cycling of carbon in Arctic marine systems (Walkusz et al., 2011, 2013; Welch et al., 1993). At the foundational level, polar cod themselves are a major consumer of zooplankton (Welch et al., 1993). At the upper levels, Polar cod are preyed on by various larger fish species, such as Atlantic cod (*Gadus morhua*), Atlantic haddock (*Melanogrammus aeglefinus*) and Greenland halibut (*Reinhardtius hippoglossoides*) (Marsh & Mueter, 2020). Marine mammals such as ringed and harp seals, narwhals and belugas utilize them as a major food source (Labansen et al., 2011; Welch et al., 1993). They are also commonly found in the diet of seabirds, such as thick-billed murre, fulmars and black-legged kittiwakes (Welch et al., 1993). Due to their ecological importance abundance and trophic connectivity, they are one of the most highlighted and well-researched Arctic fishes. The life cycle of polar cod is commonly described in five stages (**Fig. 3**) and plays out across different levels of the water column (Geoffroy et al., 2023). Adult polar cod have a demersal lifestyle and inhabit both open water and ice-covered areas. They are occasionally found in large schools in shallow waters, fjords and at the bottom of basin (Welch et al., 1993). Adults can reach a size of up to 30 cm and different sizes and ages are often stratified by depth, with the largest individuals furthest at the bottom (Geoffroy et al., 2016). Polar cod do not show sexual dimorphism but have been reported to show different phenotypes in coastal vs. open water conditions (Bouchard et al., 2023). The fish reach their reproductive stage within 3 years. They are mass spawners and release their eggs in the period from September to April, with a peak in February. After spawning, the positively buoyant eggs are found in surface waters. Since polar cod often spawn in ice-covered areas, sea ice may protect the eggs from predation of larger fish (Geoffroy et al., 2023). Hatching occurs from March to April at the start of the productive season. Newly hatched polar cod larvae are less than 1cm in standard length and subject to water currents (Graham & Hop, 1995). Juvenile polar cod are pelagic and mostly limited to the upper 100 m of the water column. When sea ice is present, age-0 polar cod are found hiding in crevices on the underside of the sea ice. This protective behavior is another facet of their adaptation to cold regions. Polar cod are especially at risk of predation due to their small size and slow swimming speed. Age-1 and mature polar cod migrate to the bottom of the ocean and join the older individuals in their demersal lifestyle.

Feeding ecology of polar cod early life stages

When age-0 polar cod start exogenous feeding, there is a limited time window during which the larvae can utilize abundant food sources before the onset of the dark winter months with lower biological productivity. It is important for them to be in a favorable feeding environment with abundant and nutritious prey, as high prey densities reduce energetic costs of foraging (David et al., 2022). Sufficient feeding of age-0 polar cod is required for the survival through their first winter, which in turn is crucial to later recruit into the mature population. Polar cod populations are an important food source for many species across all Arctic regions and play a key role in the transport of carbon from lower to higher trophic levels. Therefore, understanding the foundations of early life stage diet and feeding ecology is necessary to assess how changing dynamics in a warming Arctic might affect polar cod populations in the future, on both a pan-Arctic and regional level. Immatures and adult polar cod are opportunistic feeders utilizing a wide variety of prey types depending on region, body size, season, and habitat. Polar cod larvae and juveniles showcase a very narrow prey spectrum compared to older individuals (Geoffroy et al., 2023). They are also more limited in their prey selection than immatures and adults due to their habitat, as they exclusively inhabit upper water levels. After hatching, the larvae rely at first on their comparatively large yolk sac for nutrition. Resorption of the yolk sac may take between 18 up to 40 days after hatching (Geoffroy et al., 2023; Graham & Hop, 1995) and occurs more quickly in higher temperatures. Some papers distinguish between yolk sac larvae and feeding larvae. The larvae can already start exogenous feeding before their yolk sac is completely absorbed and have under laboratory conditions been observed to do so within a day of hatching. However, as the size of the yolk sac impedes the larvae's swimming ability, feeding success may be higher after yolk sac absorption. Feeding success in polar cod larvae may also be related to depth, with larvae close to the water surface showing highest growth rates under laboratory conditions (Graham & Hop, 1995). Mouth gape size and larval length have been named as the main limitations for marine fish larvae at the beginning of exogenous feeding, as they restrict particle size, swimming ability and hunting success. Predation therefore becomes more effective with larval growth. (Yúfera & Darias, 2007). Calanoid copepods of the genus *Calanus* spp. constitute the main food source of polar cod larvae, with early-stage larvae primarily feeding on eggs and nauplius stages (Bouchard & Fortier, 2020). Early-stage larvae have also

been observed to feed on rotifera and other prey to a lesser degree (Walkusz et al., 2011). Late-stage polar cod larvae mainly consume the larger developmental stages of *Calanus* spp. (copepodite stages I-VI, including adults). *Pseudocalanus* spp. is another calanoid copepod genus commonly found in the diet of age-0 polar cod. Various other zooplankton prey such as appendicularians, ... have been occasionally found in late-stage larvae. With larval growth, there is not only a shift in prey types; it has also been observed that the number of prey items per fish decreases, while the size of individual prey items increases (Walkusz et al., 2011). Metamorphosis occurs when the larvae reach a size of about 30 mm standard length. Calanoid copepods continue to be a major food source for juvenile polar cod after metamorphosis, with several studies showing this life stage positively selecting the copepodites of *Calanus* spp. over eggs or nauplii. The larger copepodite stages of *Calanus* spp. have a higher lipid content than eggs and nauplii and constitute the main source of carbon for juveniles. Bioenergetic modeling suggested that the quantity and quality of ingested prey is the biggest factor influencing the growth rate of polar cod larvae (David et al., 2022). The feeding ecology of polar cod larvae is furthermore affected by temperature changes, as spawning and hatching likely evolved to be timed with the most favorable feeding environments. Hatching times of larvae have been shown to be directly affected by changing temperatures, with hatching occurring earlier after a temperature increase (Graham & Hop, 1995). In terms of prey preference, Arctic copepod species such as *Calanus glacialis* are a favorable prey for Polar cod. These species contain a higher amount of lipids and are larger in size compared to their boreal relatives such as *Calanus finmarchicus*. However, due to warming temperatures, smaller boreal species are gaining ground in waters formerly dominated by Arctic species (Møller & Nielsen, 2020). Boreal zooplankton species generally have shorter lifestages than Arctic species. This may lead to mismatch dynamics with the lifecycles of polar cod. Temperature changes, apart from affecting lifecycle timing, also show effects on the ontogenesis of polar cod early life stages, as they are highly sensitive to environmental conditions. Low temperatures are considered one of the crucial factors of successful early life in polar cod (Graham 1995). The temperature tolerance between polar cod adults and larvae greatly differs, as larvae show high mortality rates after temperature changes which do not seem to affect adults (Graham & Hop, 1995). Warming temperatures also lead to higher metabolic stress. How these impacts may affect the hunting success, nutritional needs of polar cod larvae is still under investigation. Polar cod of all lifestages are visual hunters and their hunting success is assumed to be limited by light

conditions and visibility. This can be affected by increased particle discharge into Arctic waters, as is expected to occur in a warming Arctic. While polar cod are central in the Arctic marine foodwebs of today, their future fate is unclear. While some studies show that they could profit of warming effects such as melting of glaciers to a limited extent (Bouchard et al., 2021), they are expected to struggle in a warming Arctic (Geoffroy et al., 2023). The biggest competitors for their ecological niche are expected to be sand lance and capelin who feed on similar prey but as boreal species are better adapted to warmer temperatures. Other competition for polar cod include Atlantic haddock and Atlantic cod.

1.5 Study aim

The overall aim of this study was to describe the diet of age-0 polar cod in the southern Greenland Sea shelf and slope region. Based on previous diet studies of polar cod larvae and juveniles in other Arctic regions, *Calanus* spp. and potentially other calanoid copepods were expected to constitute a main food source of age-0 polar cod in the Greenland Sea, both regarding the number of ingested prey items and carbon contributions. Larger and lipid-rich prey such as *Calanus* spp. were expected to be preferred by young polar cod over other copepod taxa and smaller prey items with a lower lipid-content. There was reason to assume regionally different feeding conditions may exist between polar cod located on the Greenland Sea shelf and polar cod sampled closer to the Greenland Sea basin. The oceanography of the region suggests that the East Greenland Current may influence environmental conditions and spatial distribution of both polar cod larvae and prey to different degrees. Research in other Arctic regions has shown that localized, habitat-specific feeding conditions can be described for demersal adult polar cod between shelf and slope samples and for ice-associated age-1 polar cod. Therefore, the question emerged if pelagic age-0 polar cod sampled in upper water layers may show localized feeding patterns within the southern Greenland Sea shelf region.

The first objective of this study was to identify which prey taxa were consumed by age-0 polar cod and how much energy the different prey types provided. This was approached by visually analyzing the stomach contents and estimating Carbon contributions of identified prey through length-based allometric relationships. The second objective was to assess if age-0 polar cod in the Greenland Sea prefer specific prey taxa over other available prey. A prey selectivity index determining positive or negative prey selection was applied, which was based

on the ratio of prey types found in the stomachs compared to ratio in the environment. As potential localized feeding patterns between shelf and basin stations within the study area were of special interest, the third objective was to compare the results between those region groups and assess if different feeding patterns could be detected.

This study investigated the following research questions:

- 1) Do Age-0 polar cod sampled on the Greenland Sea shelf and close to the basin show measurable differences in feeding, which may be reflected in prey composition, carbon intake and prey selectivity?
- 2) Do age-0 polar cod in the Greenland Sea show a general preference for energy-rich *Calanus* spp. copepodites and nauplii, and positively select them over other types of prey available in the environment?

2 Methods

2.1 Sampling

This study was part of a larger sampling effort in the region (Boertmann et al., 2020; Bouchard et al., 2022). Oceanographic data, zooplankton data and ichthyoplankton samples were provided for this thesis by the Greenland Institute of Natural Resources and Aarhus University.

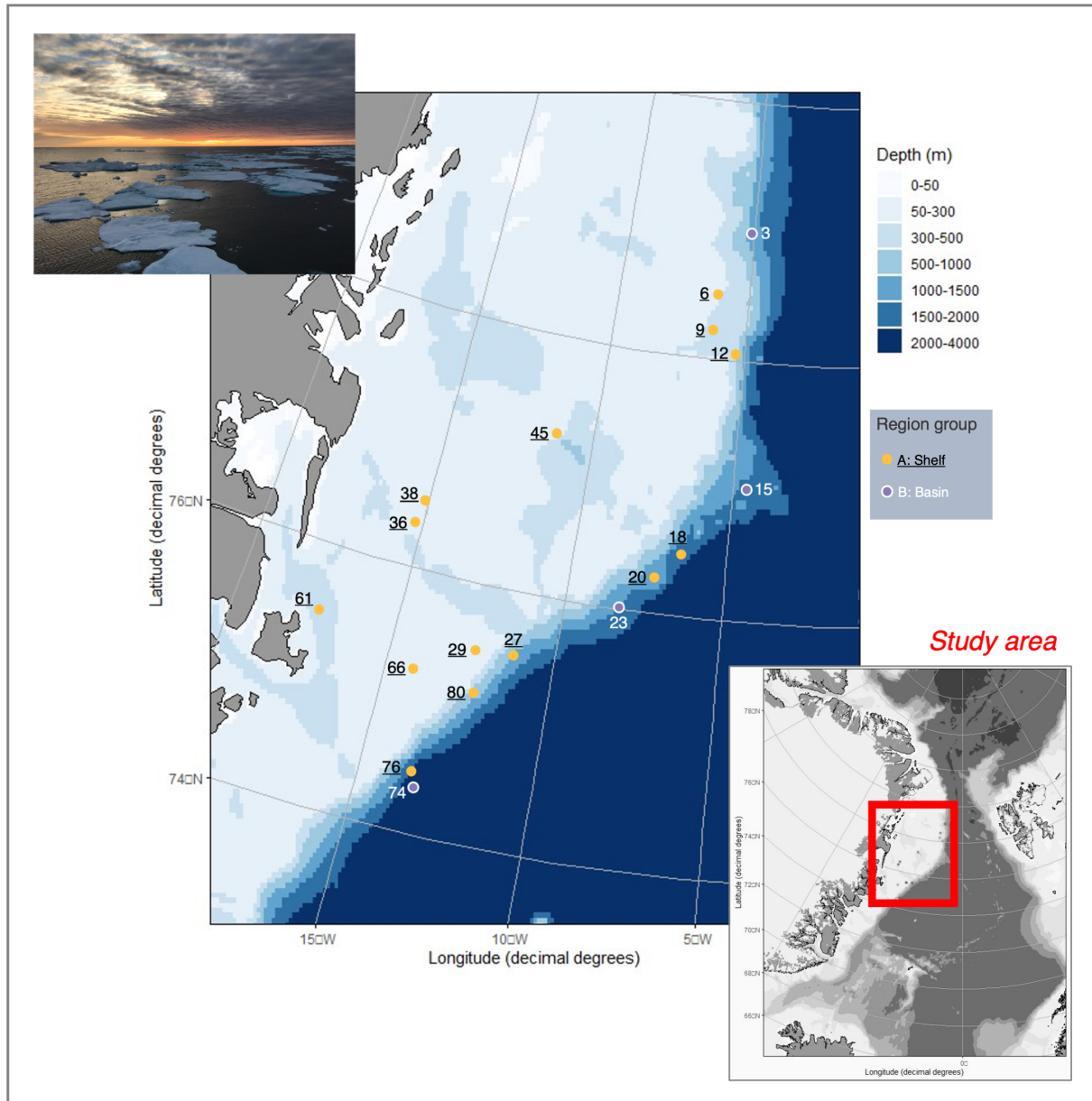


Fig. 4 Station map of cruise NEG-2017 in the Greenland Sea (number of stations = 18), illustrating the two region groups A: Shelf (yellow dots, $n = 14$) and B: Basin (purple dots with white outer circle, $n = 4$), separated by k-means clustering of CTD-data (see Methods 2.3). Photo: Thomas Juul Pedersen.

Samples were taken in the Greenland Sea during late summer and autumn of 2017 (Aug 23rd – Sep 11th) on cruise NEG 2017 aboard R/V Dana. The surveyed area extended between 2° W to 20° W and 74.5° N to 79° N, both on the Greenland Sea shelf (at 100 – 400 m bottom depth) and along the slope. The cruise track and sampling stations were based on local ice conditions (**Fig. 4**, appendix **Tab. 1**). Conductivity, temperature and depth (CTD) were measured at all 18 stations of this study, using a 24 Hz Seabird SBE 911 plus CTD-system mounted on a bottle carousel water sampler. The sampling range was limited to 1000 m water depth due to the depth rating of the sensors attached to the device. The CTD-profiles were post-processed using the Seabird Seasave software for data acquisition and processing (Bouchard et al., 2022). Additionally, information about water mass identification was referenced from Bouchard 2023 (C. Mohn) to further characterize the environmental conditions in the region.

Biological sampling

The zooplankton assemblage in the water column of every station was examined using a Hydrobios Multinet[®] (referred to as multinet) with a 0.25-m² aperture and 5 nets of 50 µm mesh size. The multinet was deployed separately from the MIK-net and hauled vertically from about 10 m above the seafloor up to surface level at each station. Sampled depth intervals were from the bottom up to 200 m, 200 to 100 m, 100 to 50 m as well as 50 m to surface level at ship speed of 0.5 m s⁻¹. All samples were preserved in a 4% formaldehyde borax-buffered seawater solution. Subsamples were split from the total sample of each station using a Folsom splitter to provide a manageable number of zooplankton that could be identified and counted during the cruise while staying representative of the total assemblage. Subsamples contained

between 400 to 600 individuals and were identified to the lowest taxonomic level, counted, and measured in length.

Ichthyoplankton (**Fig. 5**) were sampled using a Methot-Isaac-Kidd-net (MIK-net) on the East Greenland shelf and along the slope down near the Greenland basin (**Fig. 4**). The MIK-net with a 2 m-diameter frame and mesh size of 1500 μm was used after determining this mesh size to be adequate for the size range of ichthyoplankton present in the area (Bouchard et al., 2022). The large aperture of this net is advantageous to maximize ichthyoplankton yield at stations with low abundances. Towing speed and sampling depth were measured using a General Oceanics® flowmeter and Scanmar® real-time depth sensor attached to the MIK-net. The



Fig. 5 *Ichthyoplankton assemblage on cruise NEG-2017 including various fish species*

depth sensor was used to detect optimal sampling depth. Upper water layers between 144 to 20 m depth were sampled by towing the net at ship speed of 3.01 ± 0.25 kn (Bouchard et al., 2022). Standard lengths were measured in mm in freshly caught individuals, followed by preservation of individual larvae in 95% EtOH in singular glass vials. At station 6, 9, 15 and 20, about 20-25 individuals were measured fresh and then preserved individually, while the rest was preserved in bulk in 125 ml polypropylene bottles due to high catch numbers. For the same reason, fresh measurements were conducted of 9 individuals at station 3, while the rest of the sample was preserved individually.

2.2 Regional grouping

While the geographical locations of sampling stations seemed to suggest a possible regional separation of coastal, shelf, slope and/or basin stations, further investigation showed such grouping was not supported by the collected CTD-data. A Principal Component Analysis (PCA) was conducted in R (R version 4.3.0 “Already Tomorrow”) to investigate potential regional clusters using oceanographical parameters recorded for each station, that is mean

temperature (°C) and mean salinity (psu) in the upper 30 m of the water column, as well as bottom depth (m) at each station (appendix **Tab. 1**). PC1 accounted for 64.2% of variance between stations and was mainly driven by mean salinity (loading scores: mean salinity 0.66, mean temperature 0.55, bottom depth 0.51). Station 3, 15, 23 and 74 showed the largest variance from the rest of the stations (appendix **Fig. 12**). While PC1 and PC2 combined accounted for 90.5% of variance, it was not possible to visually identify distinct clusters of stations. Therefore, stations were separated into groups by applying K-means clustering to the same dataset as for the PCA (Kodinariya & Makwana, 2013). Using the elbow method (appendix **Fig. 11A**) and silhouette width (appendix **Fig. 11B**), a separation into $k = 2$ region groups was most plausible. The K-means clustering was conducted in R (using `kmeans()`, `iter.max = 100`). Station 3, 15, 23 and 74 were assigned into one group by the k-means algorithm, reflecting the variance from the rest of the sample indicated in the PCA. The two final region groups A (Greenland Sea shelf and slope) and B (basin) are illustrated in the station map (**Fig. 4**) and station list (appendix **Tab. 1**).

2.3 Processing of Polar cod larvae

Identification and morphometrics

Gadid larvae were first identified as either *Boreogadus saida* (**Fig. 6**) or *Arctogadus glacialis* based on external morphology. Since both species look very similar in their early life stages and cannot be safely distinguished using only external morphology, a subsample of 119 gadid larvae of 13 stations were further identified genetically. The subsample contained all 8 gadid larvae sampled on the cruise considered to be *Arctogadus glacialis*, as well as 111 gadid larvae considered to be *Boreogadus saida*. Muscle tissue preserved in 97% EtOH was sent to the Laboratory of Biodiversity and Evolutionary Genomics of University of Leuven, Belgium. The analysis was performed by Sarah Maes and following DNA barcoding methods for polar cod (Bouchard 2020). Of the genetic samples, all *Arctogadus glacialis* larvae as well as 104 *Boreogadus saida* larvae were confirmed to be identified correctly. 7 individuals were not analysed successfully and therefore excluded from the results. In total, 440 polar cod larvae were identified in the MIK-net samples. For 3 polar cod from the basin group considered in later analysis, standard lengths were only measured in preserved condition. Fresh standard

lengths (SL_f) were therefore calculated based on a linear model (Equation 1) fitted to the existing data points of fresh and preserved standard lengths (SL_p).

$$\text{Equation 1 } SL_f (\text{mm}) = -0.23 + 1.09 SL_p (\text{mm}); r^2 = 0.9779, \text{Std. Error} = 0.584$$

Stomach content analysis

Stomachs and intestines were transferred to glycerol to examine ingested contents (Fig. 7a). Larval gut contents were examined using stereomicroscopes with integrated camera systems (Leica S9i with APO 1.6x objective and Zeiss Discovery.V20 with Plan S 1.0x objective). Prey items were found in varying degrees of digestion. While the majority of



Fig. 6 Age-0 polar cod sample from NEG-2017

prey items could be assigned to at least class level (Fig. 7c), heavily digested items as shown in Fig. 7b were not identifiable and therefore excluded from the analysis. Especially higher copepodite life stages were sometimes found in pieces due to digestion. Upper body parts of copepodites were originally counted and measured but excluded from later analysis, while lower parts of the prosome or urosomes were ignored, as they were more likely to detach from the animal and break off into small fragments. For identification of copepodites and nauplii down to species level and life stage, length measurements as well as the number of segments and legs were considered. Length ranges for different nauplii and copepodite life stages as well as adults of copepod species present in the sampling area during cruise NEG-2017 were provided by the zooplankton group, based on multinet data. The length ranges were used as reference when analyzing digested copepoda in the stomachs to avoid misidentification. Copepodites which could not be identified to the species level due to digestion and a size that corresponded to overlapping size ranges of two or more species were recorded as unidentified copepodites. Prey items that were not copepods were also identified based on references from the multinet data. Stomach contents were disposed of after analysis. All prey items were recorded and measured in length and width in μm using affiliated stereomicroscope measurement softwares (LAS X V.3.0.14.23224 with LAS X Measurements for Leica and ZEN Pro 2.3 for Zeiss). Copepod body length was measured from the anterior to

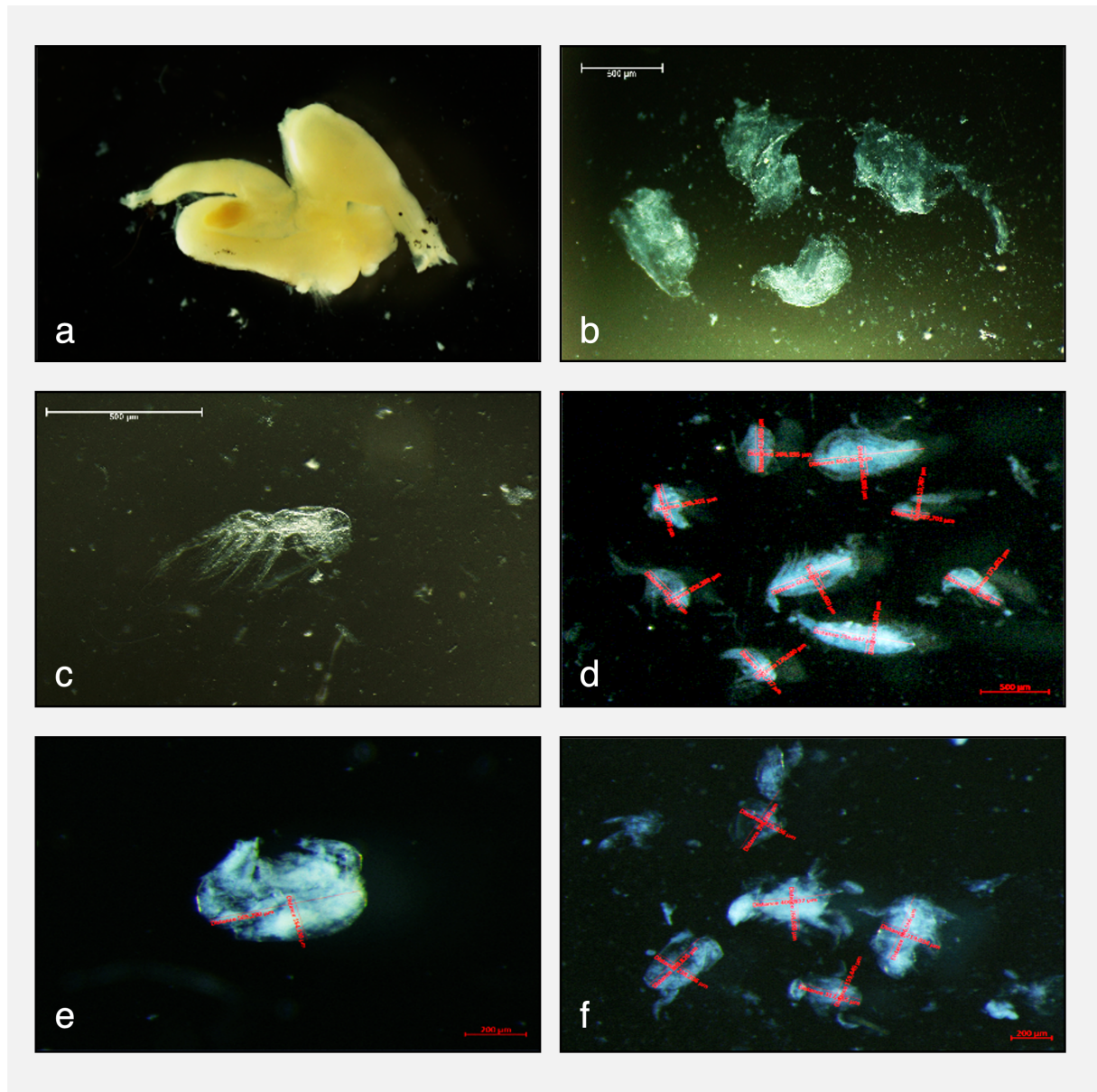


Fig. 7 Stomach content analysis of age-0 polar cod. (a) *Boreogadus saida* gut; (b) highly digested prey items; (c) digested copepodite; (d) Copepod copepodite length and width measurements; (e), (f) Copepod nauplii length and width measurements. Measurements conducted with ZEN Pro software (red).

the posterior tip of the prosome and width was recorded at the widest part of the prosome in copepodite stages C1-C5 as well as adult individuals (**Fig. 7d**). For copepod nauplii life stages N1-NVI, body length and width were measured excluding antennules and setae (**Fig. 7e**, **Fig. 7f**). Copepod eggs were measured in diameter and counted. When possible, egg abundance per egg sack was determined. While copepoda made up most of the sample, other prey taxa such as amphipoda, appendicularia, euphausiacea and gastropoda were found in the stomachs occasionally. Amphipoda and euphausiacea length was measured from the anterior tip of the cephalothorax to the posterior tip of the urosome. Appendicularia size

measurements were made of only the trunk, excluding the tail. Gastropoda shells were measured in width.

Estimation of carbon content

Allometric relationships are commonly used as a simple way to estimate dry weight and carbon content in zooplankton based on the length of an organism (Schaafsma et al., 2022). Length and dry weights of zooplankton are measured to create length-weight-regressions. Carbon contents can be estimated from the dry weights by using conversion factors for general zooplankton or specific taxa such as calanoid copepods (Falardeau et al., 2014; Legendre & Michaud, 1998; Mauchline, 1998). Based on the size measurements of prey items described above, carbon contents of each stomach sample were estimated based on allometric relationship equations used in previous studies on polar cod diet, listed in appendix Tab.x (Bouchard et al., 2016; Falardeau et al., 2014). Whenever possible, species-specific equations based on data collected during summer and autumn were used. Species-specific data was not available for all taxa, and not all prey items could be identified down to species level, therefore more general equations have been used when necessary.

Prey selectivity analysis

In order to assess which prey types were positively selected from the environment by the larvae, a prey selectivity analysis was conducted following Manly-Chesson's selectivity index (Chesson, 1978). This index compares the relative frequencies of prey types in the environment to the prey found in a predator's diet. A difference in the proportion of available vs. ingested prey indicates the occurrence of selective predation. Five prey types were selected to conduct the prey selectivity calculation: *Calanus* spp. copepodites and nauplii, *Pseudocalanus* spp. copepodites and nauplii, as well as *Oithona similis* copepodites. These prey types contributed most to counts and/or carbon contents. Unidentified prey items or prey items with low abundances were excluded from the analysis. One polar cod from group A/shelf was therefore omitted from the selectivity analysis, due to ingesting only 4 unidentified copepods. Abundances of each prey type in both region groups (in abundance per m², based on multinet data of each station) were compared to abundances within the stomach of each individual fish (in counts ind⁻¹). Chesson's alpha values for each prey type in each individual were calculated. With five prey types, the alpha-value indicating perfectly

neutral selection was $\frac{1}{n} = \frac{1}{5} = 0.2$. A Chesson's alpha > 0.2 indicated a preferential selection of a prey type (positive selectivity), while alpha < 0.2 indicated a negative selection. Prey selectivity was calculated for each individual larva and results illustrated in comparative boxplots to show the mean prey selectivity in the two region groups A/shelf and B/basin. To assess the statistical significance of differences in the prey selectivity between the region groups, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed in R (vegan package, `adonis()`).

3 Results

3.1 Environmental conditions in the Greenland Sea

Two region groups were identified in the study area (**Fig. 4**). Group A/Shelf was comprised of 14 stations located in relatively shallow waters on the Greenland Sea shelf, including both coastal and slope stations with a mean bottom depth of 317 m (SD = 122). Group B/Basin consisted of 4 stations located on the slope close to the Greenland Sea basin, with a mean bottom depth of 1201 m (SD = 188). While CTD-profiles were recorded across the entire water column for each station (appendix **Fig. 15**), the regional grouping was based on mean salinities and temperatures between 0-30m where age-0 polar cod were located, as well as bottom depth as a proxy for location on or off the shelf (appendix **Tab. 1**). The overall mean salinity in the shelf group was 30 psu (SD = 0.32), while the basin group showed a slightly higher mean salinity of 31 psu (SD = 1.03) with the southernmost station 74 reaching the highest value of 32.6 psu. Basin station 74 furthermore recorded the highest mean temperature of 2.15 °C, while the overall mean temperature of the basin group was 0.4 °C (SD = 1.19). Temperatures at the shelf group stations were lower, with an overall mean of 0.14 °C (SD = 0.49). The shelf region therefore was shallower, fresher, and colder compared to the basin region. Water masses in the study area were identified by Bouchard (2022) and summarized in an overview table for this study (appendix **Tab. 2**). The water layer in the upper 0-100 m consisted of cold and fresh Polar Surface Water (PSW) originating from the Arctic Ocean in both regions, which was transported onto the Greenland Sea shelf by the East Greenland Current (EGC). More saline Arctic Atlantic Water (AAW) was present at 100-200 m depth along the continental slope where the basin group stations were located. The warmest and most saline water in the study area, Return Atlantic Water (RAW), was also present along the continental slope at 100-300 m depths. However, temperature and salinity ranges of this water mass did not show any overlap with the oceanographical data of the 0-30 m water layer considered in the regional grouping. Upper Polar Deep Water (UPDW) was present at depths >400 m. Water masses and CTD-profiles are illustrated in appendix **Fig. 14**.

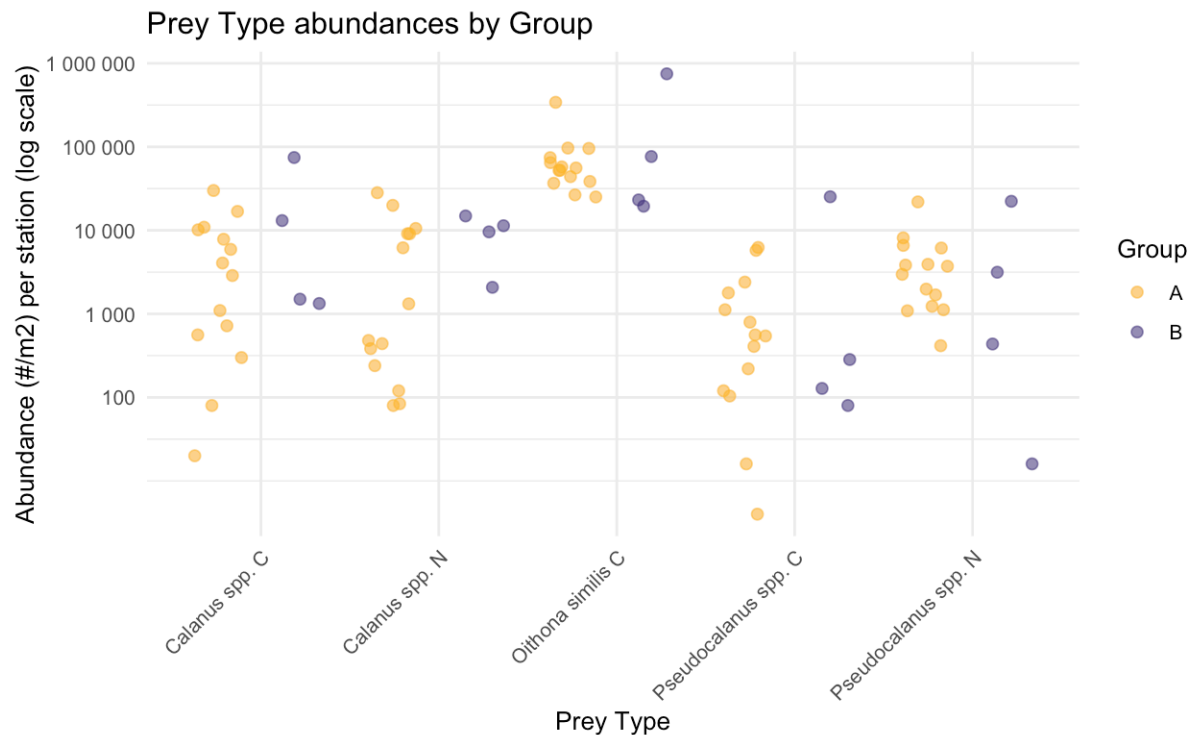


Fig. 8 Prey type abundances (in counts per m² for each station), separated by region group A/shelf (n = 14) and B/basin (n = 4) with y-axis on a logarithmic scale.

The zooplankton assemblages in both region groups (**Fig. 8**) were quite similar regarding the five prey types considered in the selectivity analysis. Extremely high abundance values for *Oithona similis* are contrasted by comparatively low values of Calanoid copepods. While the shelf group (A) has a higher number of stations, the distribution of prey abundances at the four basin group (B) stations lies mostly within a similar range, except for a singular notable maximum outlier for copepodites of *Calanus* spp. and *Pseudocalanus* spp., and minimum outlier for *Pseudocalanus* spp. nauplii.

3.2 Distribution and morphometrics of age-0 polar cod

Polar cod (*Boreogadus saida*) larvae were found in the ichthyoplankton assemblages at 18 out of the 25 stations, with *Arctogadus glacialis*, *Triglops nybelini*, *Liparis fabricii* and *Gymnocanthus tricuspis* making up the rest of the assemblages. In total, 451 polar cod larvae were caught, with high abundances in the slope and offshore regions. Lower abundances were recorded on the shelf (appendix **Tab. 1**). Other fish species caught during ichthyoplankton surveys were *Arctogadus glacialis*, *Triglops nybelini*, *Liparis fabricii* and *Gymnocanthus tricuspis*. Polar cod standard lengths ranged from 12 to 31.2 mm (appendix **Fig. 13**).

3.3 Diet of age-0 polar cod

Prey abundances and carbon contents

Copepods dominated the diet of *B. saida* larvae in the Greenland Sea, both in terms of abundance and carbon contents. Copepod species *Oithona similis* and calanoid copepods *Calanus* spp. and *Pseudocalanus* spp. were the most abundant prey taxa in both region groups, constituting on average more than 70 % of all ingested prey items for each group (**Fig. 9c**). The mean total prey count for fish on the shelf (group A) was 69 counts ind⁻¹ (SD = 62), with values ranging from 4 to 285 counts per individual larva (appendix **Fig. 16 (1)**). In the basin (group B), the mean total prey count of 52 (SD = 25) was considerably lower, with values ranging from 11 to 116 counts ind⁻¹. Both groups show a large range regarding the number of ingested prey items, with lower variability in the basin group. In terms of carbon contents, fish in the basin group ingested a higher amount of carbon than fish in the shelf group, despite ingesting fewer prey items on average (appendix **Fig. 16 (2)**). The mean carbon content in the shelf group was 60.8 µg C per individual (SD = 55), while the mean carbon content in the basin group was considerably higher with 82 µg C ind⁻¹ with higher variability (SD = 64). Carbon contents showed a range of 5 to 223 µg C ind⁻¹ on the shelf and 13 to 235 µg C ind⁻¹ in the basin group. About 25 % of copepodites and nauplius larvae could not be identified further due to limitations in the visual identification of small copepod taxa and heavily digested items (**Fig. 9c**). Using a general copepoda equation for these unidentified copepodites and nauplii led to an estimated average carbon contribution of 30 % in the shelf group and 15 % in the basin group (**Fig. 9d**).

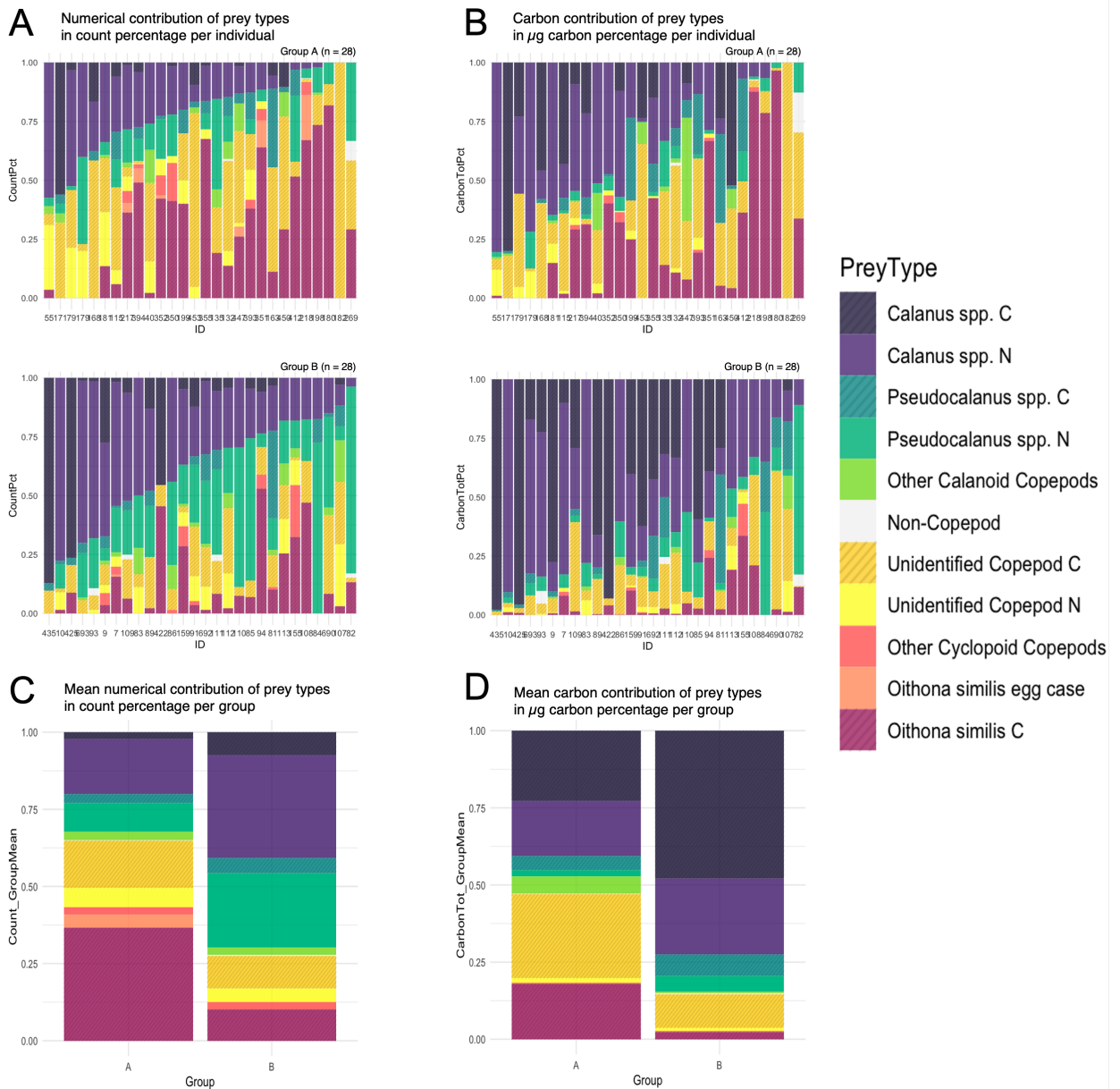


Fig. 9 Comparisons of the relative numerical and carbon contributions of prey types in stomach contents of age-0 polar cod (total $n = 56$), split by region groups A: shelf, and B: basin ($n = 28$ per group). Panel a) Numerical contribution of prey types in % of counts per individual (each bar representing one larva). b) Carbon contribution of prey types in % of μg C per individual. c) Mean numerical contribution of prey types in % of counts per group. d) Mean carbon contribution of prey types in % of μg C per group. Shared prey type legend for all panels with 11 prey types. Copepods are separated into C: copepodite stages/adults & N: nauplius larvae. Highly abundant taxa depicted individually, taxa with low abundances summarized as follows: Other Calanoid Copepods (Metridia longa C & N, Microcalanus spp. C & N), Other Cyclopid Copepods (Triconia borealis C, cyclopid copepod N), Non-Copepods (amphipod, appendicularian, Limacina helicina, furcilia larva, gastropod). Oithona similis egg cases were not considered in carbon content estimations.

In the shelf group (A), *Oithona similis* copepodites were the most abundant prey species with a mean of 36 % of counts per individual, followed by nauplius stages of *Calanus spp.* with 18 % and *Pseudocalanus spp.* nauplii with 11 % counts ind⁻¹ (**Fig. 9c**). The mean relative carbon contribution of *Oithona similis* copepodites with 18 % and *Pseudocalanus spp.* nauplii with 4 % is comparatively lower, while *Calanus spp.* nauplii contributed about the same percentage to carbon as to abundances in the shelf group (**Fig. 9d**). While *Calanus spp.* copepodites contributed just over 2 % to the diet in terms of abundance, the mean relative carbon contribution of 23 % $\mu\text{g C ind}^{-1}$ was considerably higher, exceeding the carbon contribution of the more abundant nauplius stages (**Fig. 9c, d**). *Pseudocalanus spp.* copepodites and other calanoid copepods made up about 6 % of prey counts combined (**Fig. 9c**) but showed higher carbon contributions with 5 % and 6 % $\mu\text{g C ind}^{-1}$, respectively (**Fig. 9d**). The mean total number of identified prey items found in shelf group samples was 69 counts ind⁻¹ (appendix **Fig. 16** (1a)), ranging from 4 to 285 prey items per stomach. Each sample contained 61 μg carbon on average (appendix **Fig. 16** (2a)), ranging from 5 to 222 $\mu\text{g C ind}^{-1}$. The mean standard length of polar cod larvae in this region group was 1.96 mm (appendix **Fig. 13**).

In the basin group (B), *Calanus spp.* and *Pseudocalanus spp.* nauplius stages dominated prey counts with mean contributions of 35 % and 27 % counts ind⁻¹. The third most abundant prey types were *Oithona similis* copepodites with 10 % (**Fig. 9c**). In terms of carbon contributions, *Calanus spp.* nauplii showed a similar relative percentage (25 % $\mu\text{g C ind}^{-1}$), while *Pseudocalanus spp.* and *Oithona similis* contributed comparatively little (6 % and 3 %, respectively) just as in the shelf group. The majority of carbon in the basin group samples was sourced from *Calanus spp.*, with copepodites alone contributing close to half of the mean carbon content (**Fig. 9d**). The strong influence of *Calanus spp.* in the basin group became especially clear when comparing carbon contents in absolute values, with copepodite and nauplius stages combined reaching nearly 60 $\mu\text{g C ind}^{-1}$ while values of all other prey types remained substantially below 20 $\mu\text{g C ind}^{-1}$ (appendix **Fig. 16** (2b)). The mean total number of prey items found in basin group samples of 51 counts ind⁻¹ was lower than on the shelf and ranged from 11 to 116 prey items per sample (appendix **Fig. 16** (1a)). Each sample contained an average amount of 82 $\mu\text{g C ind}^{-1}$ ranging from 12 to 235 $\mu\text{g C ind}^{-1}$ (appendix **Fig. 16** (2b)). Relative to the shelf group, mean carbon contents in the basin group are 21 μg higher, or about 34 % greater. The mean standard length of basin group polar cod was 19.9 mm (appendix **Fig. 13A**).

Other calanoid copepod taxa identified in the stomachs of both region groups were *Metridia longa* and *Microcalanus* spp., while *Triconia borealis* was the only other identified cyclopoid copepod. These prey taxa occurred in very low numbers in the stomachs (< 20 counts ind⁻¹) and consistently contributed low percentages to abundances (**Fig. 9a**) and carbon contents (**Fig. 9b**).

Prey selectivity

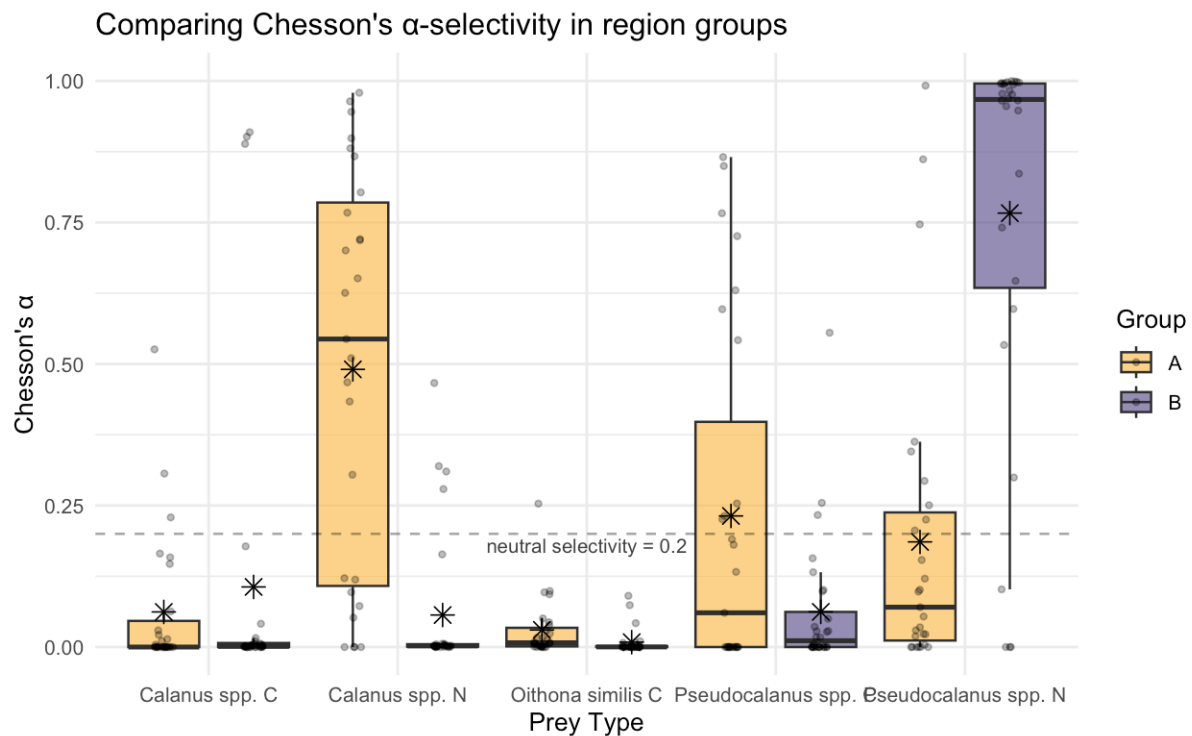


Fig. 10 Chesson's α -selectivity index of top five prey types in *B. saida* stomach contents, comparing two region groups (A: shelf, $n = 27$; B: basin, $n = 28$). α -values indicate positive or negative selection of prey types from the environment: $\alpha = 0.2$ (Neutral selectivity, dashed line), $\alpha < 0.2$ (Negative), $\alpha > 0.2$ (Positive). Mean Chesson's α -values marked (*). Boxplots display the median (center bar), interquartile range IQR between 1st and 3rd quartile (lower and upper hinges) and data points within $1.5 * IQR$ (whiskers). Distribution of individual data points shows outliers outside the whiskers.

The prey selectivity boxplots (**Fig. 10**) show an overall strong positive selection of nauplius larvae on average, while copepodites on average were mostly negatively selected. In the shelf group (A), polar cod larvae showed a strong positive selection of the nauplius larvae of *Calanus* spp. with alpha-values of up to 0.9 and mean and median alpha around 0.5. Nauplius larvae of *Pseudocalanus* spp. also were strongly positively selected by three larvae in this region as the outliers between 0.75 and 1 show. However, the mean alpha-value of this prey type was around the 0.2 neutral selectivity mark and the median indicated a negative selection for most of the 28 larvae in this region group. The second highest mean alpha-value in the shelf group was found for copepodites of *Pseudocalanus* spp.. Maximum alpha-values were just below 0.9 and there were no outliers for this prey type. Copepodites of *Calanus* spp. And *Oithona similis* were strongly negatively selected, with mean alpha values around 0.5 and median values at 0. Both prey types showed several outliers above the threshold for positive selection with

maximum values around 0.5. The prey type with the strongest positive selection in samples of the basin group (B) were nauplius larvae of *Pseudocalanus* spp., with a mean of 0.76 and median of 0.95. While some outliers showed alpha-values of 0, a clear majority of samples showed a strong positive selection of this prey type. This stands in contrast to the shelf group, which showed neutral to negative selection. All other prey types in the basin group were strongly negatively selected on average, with median values of 0 or close to zero. Several outliers showed positive selection of *Calanus* spp. copepodites and nauplius larvae, as well as *Pseudocalanus* spp. copepodites. Similar to the shelf group, fish in the basin group showcased strong negative selection of *Oithona similis* copepodites. The PERMANOVA indicated a highly significant difference in mean Chesson's alpha values between the two regions, with a p-value of 0.001.

4 Discussion

4.1 Environmental conditions and prey abundance

The observed differences in oceanographical conditions between the two region groups shelf (A) and basin (B) were due to a variety of factors. A stronger influence of mixed Arctic Atlantic Water transported by the EGC to the deeper basin group stations was the most plausible explanation for slightly warmer and more saline conditions in this region. As shown in appendix **Tab. 2**, water masses in both region groups were influenced by Polar Surface Water from the EGC. The shelf group with fresher and less saline conditions may also have been influenced by glacial melt and river outflow, especially at coastal stations. Different exposure to the EGC may have been an explanation for the different distribution of age-0 polar cod in the two region groups to some degree. As shown in Fig.3 in Bouchard et al. (2022), polar cod were found at higher densities close to the slope and in low densities on the shelf during the NEG-2017 cruise. As suggested in the paper, polar cod might have hatched in the Northeast Water Polynya and drifted southward through the EGC. Finding more favorable conditions in the basin region (B), they might therefore have survived and occurred at higher densities. Although the shelf group (A) also included stations located close to the slope, the mean standard length of all individuals measured from the basin group tended to be higher (appendix **Fig. 13A**). However, the significance of standard length differences was unclear due to an overrepresentation of polar cod sampled at one basin station (15) and might have been specific to this station. A higher number of samples per basin station would have been more representative of basin group conditions (appendix **Fig. 13B**). Body condition of polar cod, i.e. considering weight or body girth was not assessed in this study, which could have proved valuable to further assess how the fish in both regions differed. Separating the polar cod by size classes in addition to region groups would have been another possible approach (Michaud et al., 1996).

It was difficult to reliably assess differences in the zooplankton assemblages between the two regional groups analysed in this study ($n = 18$) due to the low number of stations included in the basin group (B). Møller et al. (2019) showed in their Fig. 6.12 that copepod biomasses at all zooplankton sampling stations of cruise NEG-2017 ($n = 27$) were highest on the slope and lowest on the shelf in the upper 50 m of the water column. Copepod biomass in this water

layer was also dominated by different species of the genus *Calanus* (Møller et al., 2019). The abundances of *Calanus* spp. nauplii and *Pseudocalanus* spp. nauplii were of special interest in this study, as those were the most selected prey types in the shelf group and in the basin group, respectively. Fig.8 in Bouchard et al. (2022) illustrated zooplankton abundances at all zooplankton sampling stations and showed a stark contrast between abundances of various *Calanus* spp. stages and *Pseudocalanus* copepodites on the shelf versus slope. While *Calanus* spp. showed high densities on the slope and low densities on the shelf, *Pseudocalanus* spp. copepodites were abundant also in coastal areas. Copepod nauplii have previously been found to be less abundant in shallow waters in Northeast Greenland in the summer (Michaud et al., 1996). Considering the basin group location in deeper waters, feeding patterns might have been linked to processes at depths below 100 m, for example regarding prey availability. Diel vertical migration of zooplankton might have influenced prey abundances determined in upper water layers, which means the prey field available to age-0 polar cod might have been larger if measured over an extended period (Bandara et al., 2021). However, as visual predators and with limited swimming ability, age-0 polar cod might not have been able to hunt all potential prey.

4.2 Regional differences in polar cod feeding patterns

Regarding prey type abundances and carbon contents, polar cod showed clear differences in their diet depending on the region. While higher numbers of prey items were counted in stomachs of the shelf group, higher amounts of carbon were found in the basin group (appendix **Fig. 16**). This was due to the prominence of *Oithona similis* copepodites in the shelf group diet, which were highly abundant and made up almost half of the ingested prey items in an average stomach yet contributed less than 25 % to carbon contents. In the basin group, more than half of identified prey items in an average stomach were calanoid copepods (*Calanus* spp. and *Pseudocalanus* spp. copepodites and nauplii), while *Oithona similis* copepodite abundances and carbon contents were low (**Fig. 9**). High carbon contents in the basin group were due to the presence of energy-rich *Calanus* spp. nauplii and copepodites. As illustrated in **Fig. 9A**, **Fig. 9B** and appendix **Fig. 16** (1, 2), there was large intra-group variability in terms of absolute and relative numerical contributions and carbon contents. A general trend was the higher proportion of copepod nauplius stages compared to larger copepodite stages in the samples. *Oithona similis* and *Calanus* spp. were the prey types lowest and highest

in carbon contents in both groups in the present study. A previous feeding study on age-0 polar cod in Northeast Greenland showed different results in terms of prey abundance (Michaud et al., 1996). While *Oithona similis* similarly dominated copepod abundances in the water, it was rarely found in the stomachs of analyzed polar cod sized >10 mm. Copepod nauplii dominated the diet of all analyzed fish regardless of size, while larger copepodites such as *Calanus* spp. and *Pseudocalanus* spp. occurred only in low numbers overall. Copepod eggs were shown to become less relevant as a prey with increasing size, which mirrors the low numbers of copepod eggs found in polar cod of the present study (Michaud et al., 1996; Tab.1).

The prey selectivity analysis clearly showed that *Oithona similis* copepodites were negatively selected in both region groups. While some polar cod in the basin group showed a strong positive selection for *Calanus* spp. copepodites, the mean Chesson's alpha values clearly indicated both shelf and basin polar cod negatively selected the larger life stages. Polar cod in the shelf group strongly selected for *Calanus* nauplii and furthermore showed a mean positive preference for *Pseudocalanus* copepodites and nauplii (**Fig. 10**). On the shelf, fewer *Calanus* spp. were present than on the slope and basin, meaning that the alpha value of nauplii in the shelf group indicated a very high positive selection for this particular prey type. The preference for *Pseudocalanus* spp. was possibly due to several factors. The very low abundances of *Pseudocalanus* spp. nauplii at station 15 in the basin group resulted in the high mean Chesson's alpha value for this prey type, as 20 polar cod were analysed at this station. *Pseudocalanus* copepodite abundances in **Fig. 8** showed a similar pattern in both region groups, except for the maximum value at station 74 in the basin group. (Møller et al., 2019) however showed that *Pseudocalanus* spp. copepodites were present in higher numbers on the shelf than *Calanus* spp., especially at coastal stations.

Copepod nauplii were considered the most important and most preferred prey in previous studies on polar cod early life stage diets, especially in sizes <15 mm (Falardeau et al., 2014; Michaud et al., 1996). Results in these studies were split by polar cod size classes and showed that polar cod >15 mm started to select for copepodite stages with increasing size. However, *Pseudocalanus* spp. nauplii and copepodite stages were not as clearly positively selected for in Michaud et al., 1996. Copepod eggs, specifically of *Calanus glacialis*, were positively selected in the other studies, while only *Oithona similis* eggs were occasionally found in the

present study and not considered in the selectivity analysis due to low occurrence. Negative selection of *Oithona similis* copepodites was also observed in both Northeast Greenland as well as the other regions (Bouchard & Fortier, 2020; Falardeau et al., 2014; Michaud et al., 1996). The negative selection of *Oithona similis* despite high abundances in both regions was likely due to increased energy expenditure in relation to energy content provided by the prey. To achieve the energy content of just one *Calanus* nauplius stage, a polar cod would need to catch several *Oithona similis* copepodites.

The low number of stations in the basin group with most analyzed stomachs from station 15 limited the geographical range represented in this study. Despite this, differences in shelf and basin group diets were statistically significant, supporting the existence of different feeding patterns in the two regions as suggested in the first research question. Since prey type abundances were similar in the environments of both region groups, the findings from the zooplankton samples did not clearly answer research question 1 regarding different feeding patterns between regions due to environmental conditions. The abundances and carbon contents of prey items inside polar cod stomachs showed that there clearly were differences in feeding patterns between the shelf and basin group. These differences were possibly connected to prey availability. However, physiological factors such as polar cod size and developmental stage could have been considered for a broader investigation. The selection for *Calanus* spp. nauplius larvae rather than copepodites in the shelf group, and the preference of *Pseudocalanus* spp. over *Calanus* spp. in the basin group was possibly due to polar cod size. However, as mean standard lengths only differed by 1 mm between the two regions, it was unclear if size differences were large enough to be the main reason the two groups selected different-sized prey. Low copepodite abundances in stomachs of Michaud et al. (1996) were probably due to sampled polar cod being smaller and therefore selecting smaller nauplius stages. Comparing mean prey width and length between the two studies, or additional measurements such as polar cod mouth gape size, could have been an interesting approach to further explore diet composition results.

Referring to the second research question, these findings of the present study supported polar cod in the Greenland Sea preferring energy-rich prey types, which similar studies have shown in other regions (Bouchard & Fortier, 2020). The question was also supported by the maximum alpha values for Calanoid copepods, which were higher than for cyclopoid copepod *Oithona*

similis. However, the strong positive selection for *Pseudocalanus* spp. nauplii in the basin group did not seem to support a preference for *Calanus* spp. exclusively. Another important aspect regarding research question 2 was that *Calanus* spp. copepodites were negatively selected in both region groups, despite this prey type having contributed most to average carbon contents.

4.3 Outlook

The fate of polar cod in a warming Arctic

Since polar cod is a prominent pan-Arctic key species, research efforts have been made to understand its general ecology and specifically impacts that climate change may have on this species. Warming temperatures have numerous effects on the feeding and development of this species. As shown in this study, the relative carbon contribution of prey types to a polar cod's diet can be quite different and unrelated to its abundance. It has been shown in this study and other feeding studies that lipid-rich Calanoid copepods, especially Arctic species such as *Calanus glacialis*, are an attractive prey to polar cod, providing a high amount of energy per capture. Prey species like *Oithona similis*, which may be very abundant and have high numerical contributions to the stomach contents do not always provide a lot of energy. With increased borealisation, it is expected that Arctic species such as *Calanus glacialis* will retreat further north, potentially shifting the zooplankton assemblage towards a dominance of boreal species. This might lead to polar cod spending more energy and time on capturing prey, limiting resources available for reproduction. The physiological development of early life stages is furthermore heavily affected by water temperatures. Polar cod exposed to warming waters may not develop optimally, which can impact hunting abilities and increase predation, negatively affecting recruitment to the adult population.

Polar cod in the Greenland Sea

Northeast Greenland has historically not been a focus in Arctic research due to limited accessibility. Compared to other Arctic areas, there has been very little research on climate change impacts (Wassmann et al., 2011). Due to its position as a major Arctic outflow area, it would be of interest to investigate how the effects of anthropogenic climate change manifest in this region. While a snapshot of the diet of age-0 polar cod can provide valuable insights,

continuous surveys would be necessary to confidently assess polar cod feeding ecology in the area. A shift towards a dominance of Atlantic prey species is expected in the Greenland Sea in the next decades due to warming temperatures, which will affect the diet of polar cod. The Greenland Sea has experienced an increase in marine heat events, like other Arctic regions. These changes may affect not only the prey available for polar cod, but also the physiological development and survival of age-0 polar cod through their first winter. Allometric relationships of zooplankton dry weights based on data from the Greenland Sea were not available for this study but would provide a useful tool in assessing the carbon flux in the region. Changes in the ichthyoplankton assemblage may increase inter-specific competition pressure on polar cod and may have wide-reaching consequences for higher trophic levels if fewer polar cod are available. Summary reports such as Møller et al. (2019) provide valuable information about the Northeast Greenland ecosystem. While there have been studies on the use of polar cod by humans in West Greenland (Bouchard et al., 2023) and predation on polar cod in East Greenland by predators such as ringed seals (Labansen et al., 2011; Siegstad et al., 2014), establishing a larger knowledge base would be helpful to understand the extent of how large-scale environmental changes will impact the region's ecosystems and communities depending on them.

5 Conclusion

While oceanographical conditions differed between shelf group (A) and basin group (B), zooplankton abundances and composition in the water were similar in both regions. The same prey types were available in both regions, however group B stations showed higher maximum abundances for copepodites. *Oithona similis* copepodites showed much higher abundances in the water column compared to calanoid copepods in both regions. Age-0 polar cod of the shelf group had a higher average number of prey items in their stomachs due to the presence of *Oithona similis*. Basin group polar cod had higher average carbon contents due to the presence of *Calanus* spp. in the stomachs. Both regional groups positively selected for Calanoid copepods, with the shelf group showing the strongest preference for more energy-rich *Calanus* spp. nauplii and the basin group strongly selecting for *Pseudocalanus* spp. nauplii. *Oithona similis* was negatively selected by both groups. Since the regional differences in feeding patterns did not seem to be driven by prey availability, salinity and water mass influence were the most plausible explanation behind the stomach content observations. Different conditions for the physiological development of age-0 polar cod in the two regions, such as varying influence of the East Greenland Current on transport of eggs and ichthyoplankton, should be considered in further analysis.

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Appendix

Tab. 1 Station list ($n = 18$ stations) including sampling date and location, oceanographic data used in PCA and k-means clustering, number of caught and analyzed polar cod, and region group.

Station	Sampling date	Latitude	Longitude	Mean temperature (°C) 0-30 m	Mean salinity (psu) 0-30 m	Bottom depth (m)	Number of polar cod caught	Number of polar cod analyzed	Region group
3	2017-08-25	79.02.116 N	005.15.880 W	0,53	30,4	1050	51	3	B (Basin)
6	2017-08-25	78.50.951 N	006.20.668 W	0,47	30,4	293	81	1	A (Shelf)
9	2017-08-26	78.22.090 N	006.30.380 W	0,78	30,2	300	137	1	A (Shelf)
12	2017-08-26	78.05.419 N	005.37.528 W	-0,24	30,3	338	3	1	A (Shelf)
15	2017-08-28	77.03.916 N	004.55.121 W	-0,33	30,5	1438	44	20	B (Basin)
18	2017-08-28	76.47.897 N	006.53.971 W	0,48	29,7	375	14	1	A (Shelf)
20	2017-08-28	76.29.531 N	007.39.065 W	-0,33	30,4	641	34	2	A (Shelf)
23	2017-08-29	76.01.794 N	008.36.117 W	-0,42	30,7	1269	10	2	B (Basin)
27	2017-08-29	75.53.481 N	011.24.131 W	0,17	30,1	298	14	3	A (Shelf)
29	2017-08-30	75.49.920 N	012.45.378 W	-0,66	29,9	396	6	6	A (Shelf)
36	2017-08-31	76.34.997 N	015.26.588 W	-0,51	30,1	268	2	2	A (Shelf)
38	2017-09-01	76.52.919 N	015.07.044 W	-0,02	29,5	247	1	1	A (Shelf)
45	2017-09-02	77.26.012 N	011.32.323 W	-0,95	29,8	444	4	4	A (Shelf)
61	2017-09-04	75.50.810 N	017.42.109 W	-0,16	29,9	171	2	2	A (Shelf)
66	2017-09-05	75.25.109 N	014.14.828 W	0,09	29,8	193	1	1	A (Shelf)
74	2017-09-06	74.38.915 N	013.32.449 W	2,16	32,6	1049	26	3	B (Basin)
76	2017-09-07	74.48.896 N	013.53.640 W	-0,46	30,7	188	5	2	A (Shelf)
80	2017-09-08	75.16.452 N	012.26.870 W	-0,63	30,4	291	5	1	A (Shelf)

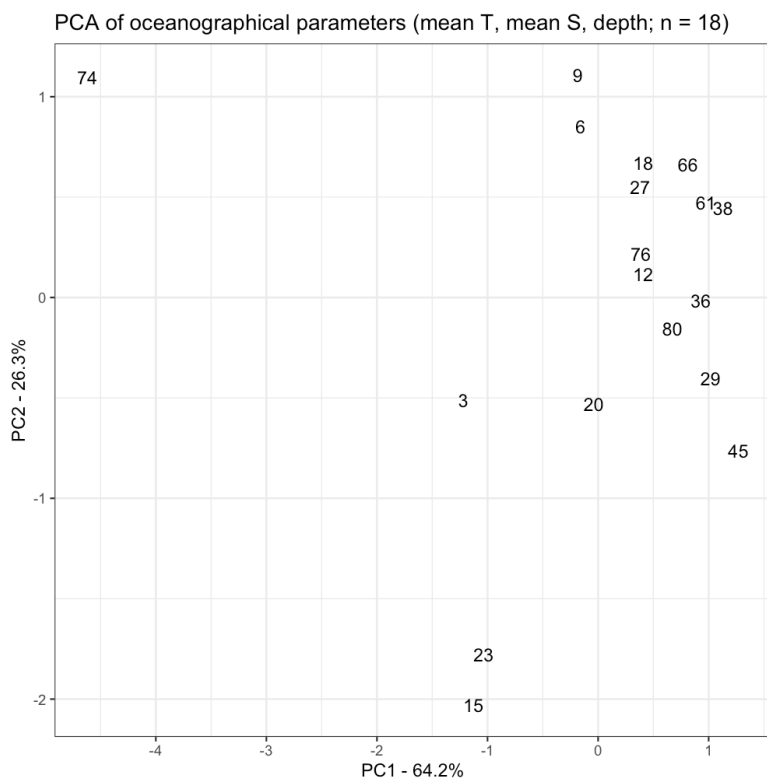


Fig. 12 PCA of 18 stations considering three oceanographical parameters at each station: mean T (°C) and mean S (psu) between 0-30 m as well as bottom depth (m). Values plotted with station numbers.

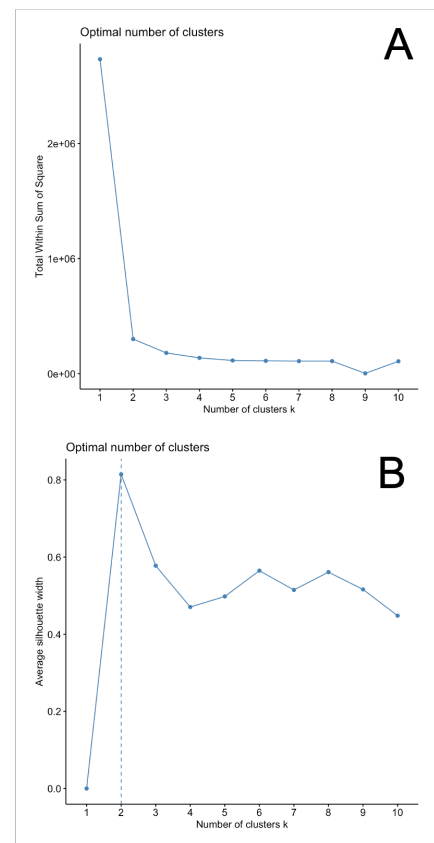


Fig. 11 Determining the optimal number of clusters k for CTD-data of 18 stations. A) Elbow plot of the total within sum of squares, B) Silhouette plot of the average silhouette width.

Tab. 2 Water masses present in the Greenland Sea during cruise NEG 2017.

Water layer	Water mass	Main characteristics	Properties			Origin, location and remarks
			Depth [m]	Potential Temperature θ [°C]	Salinity [PSU]	
near-surface waters*	Polar Surface Water (PSW)* [▲]	cold, fresh* (warmer and least saline at <50m)	< 100*	$-1.73 < \theta < 2$ *	< 33*	transported from cold and fresh Arctic Ocean (AO) [▲] via East Greenland Current (EGC) onto Greenland sea shelf *; surface waters (<50m) influenced by seasonal heating and ice melt *
epipelagic	Arctic Atlantic Water (AAW)* [▲]	cold, more saline than PSW	100-200*	$-1.73 < \theta < 2$ *	34 - 34.8*	transported from cold and fresh AO [▲] via EGC southward along continental slope of the Greenland Sea shelf*; injections of saline Atlantic water *
epipelagic/upper mesopelagic	Return Atlantic Water (RAW)* [▲]	warmest and most saline*	100-300*	$2 < \theta < 4$ [♦]	$34.9 < S < 35.1$ [♦] (core at > 35)	re-circulating warm and saline Atlantic water of the West Spitsbergen Current (WSC) [▲] , incorporated into EGC at 78°N and transported along Greenland Sea shelf break *
mesopelagic	Upper Polar Deep Water (UPDW)* [▲]	less warm, saline	> 400*	$-0.5 < \theta < 2$ [♦]	$34.85 < S < 34.95$ [♦]	transported from AO via EGC [▲] ; waters between 1-2 °C likely influenced by RAW [♦]

* water mass properties in the Greenland Sea during cruise NEG-2017 described in Bouchard et al., 2022 (Figure 2, Results)
[♦] personal communication with Christian Mohn
[▲] water mass classification and origin based on Rudels et al., 2002 (Table 1, Observations)

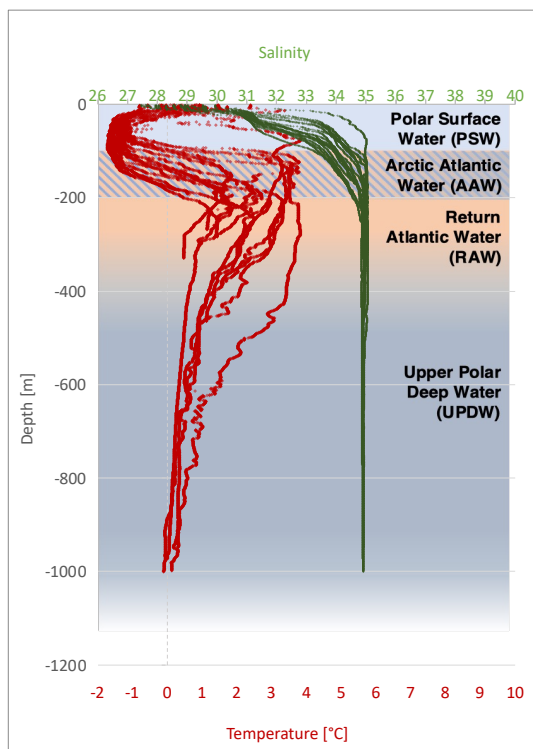


Fig. 14 Temperature and salinity data for 0-1000m depth for all stations with illustration of water masses.

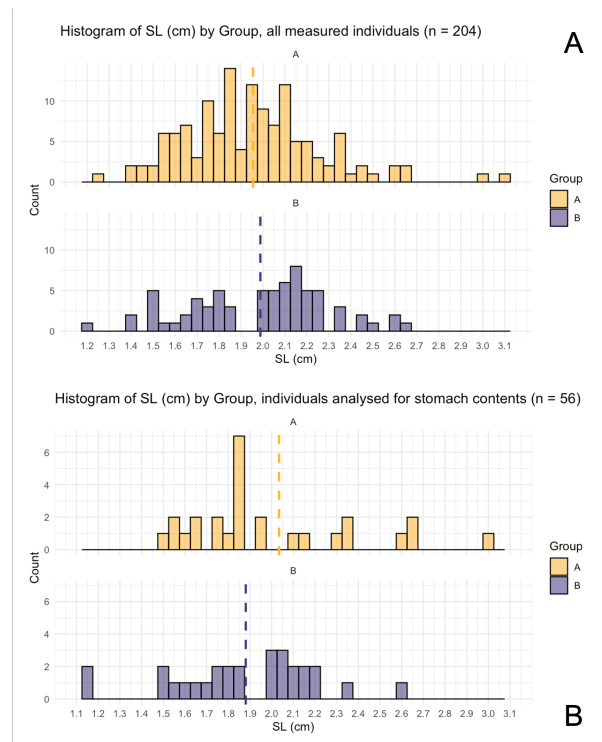


Fig. 13 Distribution of polar cod standard lengths (cm) for two region groups (group A: shelf, group B: basin), of A) all measured polar cod and B) polar cod analysed in this study.

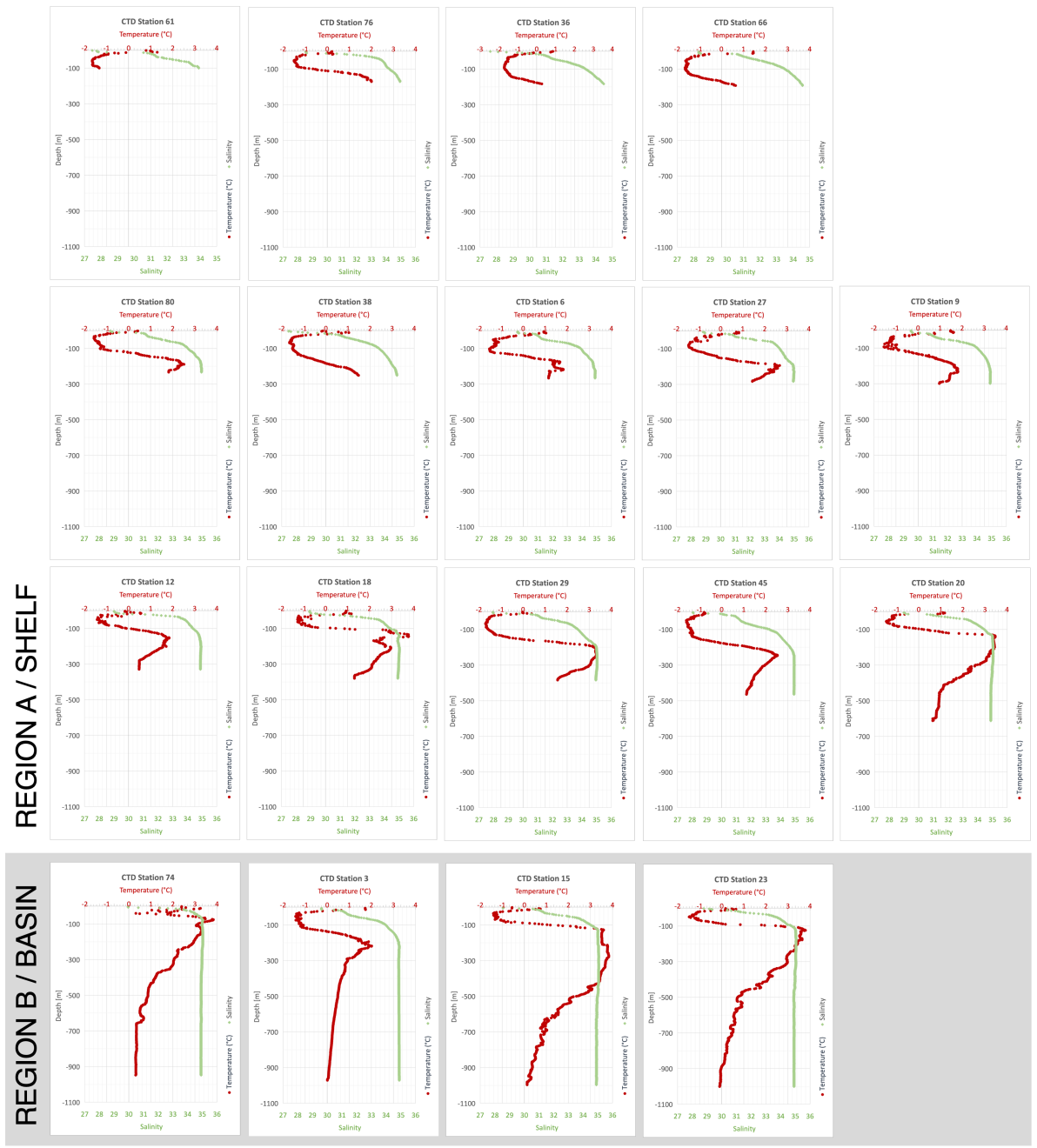


Fig. 15 Temperature, salinity and depth profiles for all stations ($n = 18$) in region group A/shelf and group B/basin, ordered by descending bottom depth.

Tab. 3 Allometric relationship equations for calculating dry weights and carbon contents based on zooplankton length measurements. Table based on Falardeau (2014), Table 1, and Bouchard (2016), Table 3. Abbreviations: *L* = length, *PL* = prosome length, *TL* = total length, *D* = diameter. Length measurements in mm, carbon contents in μg .

Prey taxa (stomach content)	Equation taxa	Equations	References
<i>Calanus</i> spp. copepodites	Copepoda	$C = 10^{(3.07 \cdot \log(PL \cdot 1000) - 8.37)}$	Uye (1982), Table 1
<i>Calanus</i> spp. nauplii	<i>Calanus finmarchicus</i> nauplii	$C = 4.29 \cdot 10^{-6} \cdot (L \cdot 1000)^{2.05}$	Hygum et al. (2000), Fig. 4 (high food resources)
<i>Oithona similis</i> copepodites	<i>Oithona similis</i>	$C = 9.4676 \cdot 10^{-7} \cdot (PL \cdot 1000)^{2.16}$	Sabatini & Kjørboe (1994), Fig. 1
<i>Triconia borealis</i> copepodites	<i>Oithona similis</i>	$C = 9.4676 \cdot 10^{-7} \cdot (PL \cdot 1000)^{2.16}$	Sabatini & Kjørboe (1994), Fig. 1
<i>Cyclopoidea</i> nauplii	<i>Oithona similis</i> nauplii	$C = 5.545 \cdot 10^{-8} \cdot (PL \cdot 1000)^{2.71}$	Sabatini & Kjørboe (1994), Fig. 1
<i>Microcalanus</i> spp. copepodites	Copepoda	$C = 10^{(3.07 \cdot \log(PL \cdot 1000) - 8.37)}$	Uye (1982), Table 1
<i>Microcalanus</i> spp. nauplii	<i>Pseudocalanus newmani</i> nauplii	$C = (10^{(2.515 \cdot \log L + 0.975)} \cdot 0.447)$	Lee et al. (2003), Fig. 3, (1)
<i>Pseudocalanus</i> spp. copepodites	<i>Pseudocalanus</i> spp.	$C = 10^{(2.85 \cdot \log(PL \cdot 1000) - 7.62)} \cdot 0.447$	Liu & Hopcroft (2008), Fig. 1.
<i>Pseudocalanus</i> spp. nauplii	<i>Pseudocalanus newmani</i> nauplii	$C = (10^{(2.515 \cdot \log L + 0.975)} \cdot 0.447)$	Lee et al. (2003), Fig. 3, (1)
<i>Metridia longa</i> copepodites	<i>Metridia longa</i>	$C = 7.498 \cdot PL^{3.225}$	Forest et al. (2011) Fig 4c (summer)
<i>Metridia longa</i> nauplii	<i>Acartia tonsa</i> nauplii	$C = 3.18 \cdot 10^{-9} \cdot (PL \cdot 1000)^{3.31}$	Berggreen et al. (1988), Fig. 3
unidentified copepodites	Copepoda	$C = 10^{(3.07 \cdot \log(PL \cdot 1000) - 8.37)}$	Uye (1982), Table 1
unidentified copepod nauplii	<i>Pseudocalanus newmani</i> nauplii	$C = (10^{(2.515 \cdot \log L + 0.975)} \cdot 0.447)$	Lee et al. (2003), Fig. 3, (1)
Appendicularia	<i>Oikopleura rufescens</i> , <i>Oikopleura vanhaeffeni</i>	$C = 8.2 \cdot 10^{-8} \cdot (L \cdot 1000)^{2.7}$	Sato et al. (2003), Eq. 7
Amphipoda	<i>Scina crassicornis</i> , <i>Phrosina semilunata</i> , <i>Phronima sedentaria</i>	$C = 10^{\frac{\log L - 0.063}{0.272}} \cdot 0.285$	Gorsky et al. (1988), Tables 1 & 2
<i>Limacina helicina</i>	<i>Limacina retroversa</i>	$C = 10^{(3.102 \cdot \log D + 1.469)}$	Conover and Lalli (1974), Fig. 1
Furcilia larvae	<i>Thysanoessa longicaudata</i>	$C = (0.0003 \cdot (TL^{3.499} \cdot 1000) + 0.4)$	Schaafsma et al. (2022), Table 3
Proportion of carbon to dry weight:	Copepoda	0,447	Mauchline (1998)
	Zooplankton	0,4	Legendre & Michaud (1998)

(Berggreen et al., 1988; Conover & Lalli, 1974; Forest et al., 2011; Gorsky et al., 1988; Hygum et al., 2000; Lee et al., 2003; Legendre & Michaud, 1998; Liu & Hopcroft, 2008; Mauchline, 1998; Sabatini & Kjørboe, 1994; Sato et al., 2003; Schaafsma et al., 2022; Uye, 1982)

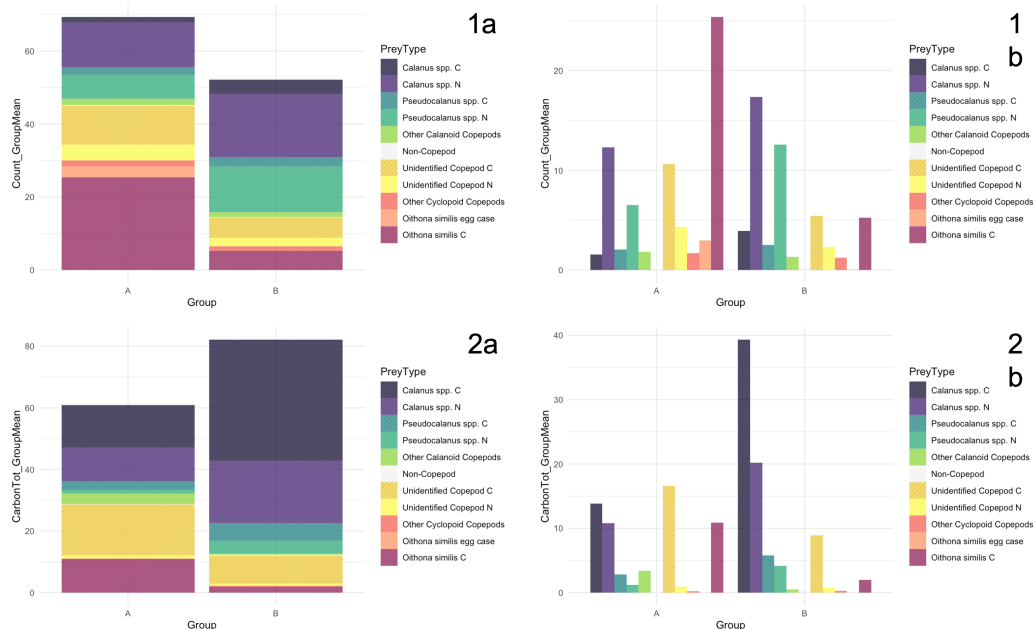


Fig. 16: 1) Mean prey type abundances (counts ind^{-1}) and 2) mean prey type carbon contents ($\mu\text{g C ind}^{-1}$) for region group A/shelf and group B/basin in absolute values, depicted as a) stacked barplot to illustrate total values per group and b) grouped barplot to compare values of each individual prey type. *Oithona similis* egg cases were excluded from the carbon content estimation.

