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The Effect of Seasonality on Polar Cod (*Boreogadus saida*) Dietary Habits and Temporal Feeding Strategies in Svalbard Waters.

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The Effect of Seasonality on Polar Cod (*Boreogadus saida*) Dietary Habits and Temporal Feeding Strategies in Svalbard Waters.
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Abstract

Climate change in polar regions will likely disrupt the fine-tuned trophic interactions among organisms in Arctic marine ecosystems. Modifications in prey phenology and composition as well as increased competition and predation from boreal species expanding their range northward are expected to affect the key Arctic fish species polar cod (*Boreogadus saida*) and thus have important repercussions on the Arctic marine food web. Aside from climate, the extreme seasonal light variations at high latitudes are important for phenology and foraging. Endemic Arctic organisms such as polar cod may be adapted to these drastic light variations whereas, non-endemic species may be confronted with a new set of environmental variables that could limit their northward range expansion in the context of a warming Arctic climate. In order to assess the ability of polar cod to cope with future changes in marine Arctic ecosystems, it remains important to understand their dietary plasticity. The main goal of this study was to investigate the flexibility of polar cod feeding strategies across seasons by documenting its temporal position on the generalist-specialist spectrum. Polar cod were harvested on the western and northern coast of Svalbard in September, October, January, and May in fjords influenced by Arctic water masses and fjords influenced by Atlantic water masses. The organisms' stomach contents were extracted and analysed and prey species were identified to the lowest taxonomic level possible. Specimens were expected to experience marked seasonal variability in their feeding success and foraging strategy. Polar cod feeding success was observed to be seasonally heterogenous, with winter specimens dispalying a higher probability of having empty stomachs compared to specimens from the fall or the spring. Seasonality affected polar cod diet in terms of ingested prey composition with fall specimen from Arctic domains feeding primarily on the hyperiid amphipod *Themisto libellula*. This suggests that larger demersal polar cod ascended in the water column in the fall to forage on this pelagic prey. The important contribution of fish prey throughout sites in the winter highlighted a flexible size-biased diet and the potential ability to switch diet to a temporarily abundant resource. Polar cod adopted a population specialist strategy in the fall and an individual specialist strategy in the winter. Therefore, the opportunistic feeding strategy adopted by polar cod is affected by seasonality insofar as diet is limited to a few preferred prey in the fall and diversified during the polar night likely as a results of visual constraints on selectivity of preferred prey.

Keywords: Feeding strategy, *Boreogadus saida*, diet, seasonality, Svalbard.

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Prologue

This project saw quite a number of modifications with time as the initial question: "how does seasonality affect polar cod diet?" became increasingly difficult to address due to a lack of adequate samples. As the project went forward the question changed to "how does seasonality affect gadoids diet?" and later to "how does seasonality affect fish community composition?". Only after samples were collected in January 2016 was I able to get back to my initial question. Therefore, a relatively large Appendix follows the thesis and is regularly referred to, and Appendix C holds material that goes beyond the scope of the objectives stated in this thesis but that are still relevant to the interpretation of the results.

Part of the diet analysis results from this thesis were incorporated in the following publication:

Berge J., Daase M., Renaud P.E., Ambrose Jr. W.G., Darnis G., Last K.S., Leu E., Cohen J.H., Johnsen G., Moline M.A., Cottier F., Varpe Ø., Shunatova N., Bałazy P., Morata N., Massabuau J-C., Falk-Petersen S., Kosobokova K., Hoppe C.J.M., Węsławski J.M., Kukliński P., Legeżyńska J., Nikishina D., Cusa M., Kędra M., Włodarska-Kowalczuk M., Vogedes D., Camus L., Tran D., Michaud E., Gabrielsen T.M., Granovitch A., Gonchar A., Krapp R., Callesen T.A. (2015). Unexpected Levels of Biological Activity during the Polar Night Offer New Perspectives on a Warming Arctic. *Current Biology*, 25(19), 2555-2561.

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À l' équipage d'Ainhara

1

Introduction

Climate warming is expected to be particularly amplified in northern regions above 60 ºN with some model projections suggesting increases in temperatures of 5-7 ºC by the end of the 21st century (ACIA, 2005; IPCC, 2013). Rising water temperatures and a resulting decline in sea ice in the Arctic are expected to affect the Arctic marine ecosystem and disrupt the fine-tuned trophic interactions among organisms (Edwards & Richardson, 2004; Both et al., 2009). Pelagic primary production blooms may be affected, possibly creating a mismatch between phytoplankton peak and herbivorous zooplankton which could have repercussions higher up the food web (Hansen et al., 2003; Drinkwater et al., 2010). Furthermore, increasing temperatures could directly affect the reproduction and growth of Arctic species (Huntley and Lopez, 1992; Nahrgang et al., 2014; Swalethorp et al., 2014). Changes in biotic factors such as competition and predation triggered by the northward expansion of Atlantic boreal species will also likely lead to complex changes in the community structure (Aschan et al., 2013). Possible alterations in Arctic marine ecosystems are expected to affect polar cod (*Boreogadus saida*) and thus have important repercussions on the Arctic marine food web (Hop & Gjøsæter, 2013). The ability of polar cod to cope with modifications in prey composition and with increased competition will partly depend on their seasonal dietary plasticity. This Arctic gadoid is often described as a zooplankton generalist feeder (Renaud et al., 2012; Mueter et al., 2016), yet little is known about the dynamics of its temporal feeding strategies and diet analysis often remain purely descriptive and constrained to a single season. Considering the extreme seasonal variations in the high Arctic, particularly in terms of light regime (Varpe et al., 2015), seasonality must be considered in order to better understand the effect of climate change on trophic interactions (Varpe & Fiksen, 2010). In this study, I investigated polar cod seasonal feeding strategies in Svalbard waters to provide information that could help elucidate polar cod vulnerability to a changing trophic system.

1.1. The Arctic Ocean

1.1.1. Geographical and bathymetric characteristics

Given that alternative definitions exist, the term Arctic is used in this paper to describe the region north of the polar circle at 66° 33'N. The Arctic comprises of land masses shared among eight countries and of an ocean of about 14,056,000 km^2 that is partly covered by sea ice all year round (Jakobsson et al. 2004). Arctic surface waters form a dynamic cryosphere at and around the North pole (Petty et al., 2016). The Arctic Ocean's border as defined by the International Hydrographic Organization (IHO), goes beyond that of the polar circle and varies in latitude as it expands down to 57°N in the Hudson Bay region and up to 70°N by the westernmost side of the European continent (Jakobsson, 2002). The Arctic Ocean's bathymetry still remains to be fully mapped but it is now well established that the Lomonosov Ridge separates two main basins, the Eurasian basin and the Amerasian basin, and that 53% of its area is comprised of a continental shelf (Aagaard et al., 1985; Jakobsson et al., 2012; Bluhm et al. 2015). The 2600 meters deep Fram Strait situated between Greenland and Svalbard is the deepest avenue for water to flow in and out of the Arctic Ocean (Bluhm et al. 2015). Due to its northern location, the Arctic Ocean is exposed to extreme seasonal light variations including periods of 24h darkness and 24h light above the Arctic Circle.

1.1.2. Water masses in Arctic Ocean

The current hydrographic features of the Arctic Ocean date back from the early Holocene roughly 10 thousand years ago and are therefore relatively recent. The ocean is stratified into four main water masses, an Arctic relatively fresh surface water and ice that is largely affected by wind circulation, a halocline complex with denser modified Pacific-origin waters and even denser modified Atlantic-origin waters, the Arctic Circumpolar Boundary current circulating Atlantic water through the basins, and Arctic deep waters (Bluhm et al. 2015). Water flows in and out of the Arctic Ocean thanks to four important gateways. These are, the Fram Strait, the Barents Sea Opening, the Bering Strait, and the Davis Strait. An inflow of relatively warm and saline Atlantic water occurs west of the Norwegian coast and via the West Spitsbergen Current west of Svalbard and via the Norwegian Atlantic Current through the Barents Sea Opening. Less saline Pacific-origin water enters the Arctic Ocean through the shallow Bering Strait. Arctic water exits via the East Greenland Current and the

Fram Strait, and to a lesser extent through the Davis Strait and the Canadian Archipelago (Bluhm et al., 2015). The peculiarity of Arctic bathymetry largely determines the circulation patterns (Aagaard et al., 1985). Over the last few decades, the Arctic Ocean's sea ice has diminished both in extent and in thickness (Kwok et al., 2009; Cavalieri and Parkinson, 2012) possibly due to an increase of Atlantic water heat advection (Polyakov et al., 2010; Stroeve et al., 2012). Perhaps one of the most dramatic changes in the sea ice is the reduction of multi-year Arctic sea ice and a rapidly declining average summer sea ice minimum (Kinnard et al., 2008; Comiso, 2012).

1.1.3. Arctic marine ecosystems and trophic web

Life in the Arctic requires adaptations to extreme environmental conditions including cold temperatures and the polar seasonal light regime. Some organisms, including polar cod, produce anti-freeze proteins (Chen et al., 1997) which allow them to survive sub-zero temperatures and exploit the cryosphere (Gradinger & Bluhm, 2004). Many species accumulate large lipid reserves in the spring (Scott et al., 2000; Falk-Petersen et al., 2009) and other adaptations include the ability to slow their metabolism (Hop et al., 1997a), undergo diapause (Darnis & Fortier, 2014), and adopt different life history strategies depending on yearly environmental conditions (Daase et al., 2013).

Together with ice algal primary production, the spring phytoplankton bloom is a primordial event that is essential for sustaining annual phenological events within Arctic communities (Gosselin et al., 1997; Arrigo and van Dijken, 2004; Arrigo et al., 2012). The relatively short and intense Arctic growing season means that, the timing of these photosynthetic events is crucial for determining the degree of success or failure of the life strategies adopted by local zooplankton grazers (Daase et al., 2013). Herbivorous mesozooplankton are preyed upon by carnivorous macrozooplankton such as the hyperiid amphipods *Themisto* spp. (Auel & Werner, 2003; Kraft et al., 2013) and by vertebrate organisms such as polar cod (Renaud et al., 2012). Larger vertebrates such as seabirds and marine mammals feed extensively on polar cod making it an important link in the Arctic marine food web (Bradstreet et al., 1986; Węsławski et al., 1994; Melnikov and Chernova 2013).

Seasonality is particularly extreme at high latitudes with a narrow time window allowing for the acquisition and accumulation of energy (McNamara & Houston, 2008; Varpe, 2012). If temperature is responsible to some degree for triggering important phenological episodes, then an increase in temperatures induced by climate change could lead to a mismatch between trophic levels and impede energy transfer (Edwards & Richardson, 2004). Such changes in marine trophodynamics could have important repercussions on pelagic vertebrates such as polar cod. In the face of climate change, an organism's seasonal dietary plasticity will largely influence its ability to cope with disruptions in phenological events.

1.2. Svalbard fjords

1.2.1. Oceanography in Svalbard

Svalbard is situated right at the border between Arctic and Atlantic domains (Narayanaswamy et al., 2010; Nahrgang et al., 2014). The west coast of the archipelago is warmed by the West Spitsbergen Current (WSC) which brings in Atlantic water into the Arctic through the Fram Strait and infiltrates Svalbard waters through fjord troughs (Streuff, 2013). This WSC current is highly variable (Saloranta and Haugan, 2001; Walczowski and Piechura, 2006) and the west Spitzbergen shelf water is modified not only by the WSC but also by glacial melt, and by an Arctic water current coming down the east coast of the Svalbard archipelago and back up along the shelf on the west coast (Cottier et al. 2005).

1.3. Polar cod, *Boreogadus saida* (Lepechin, 1774)

1.3.1. Distribution and abundance

Throughout the Arctic Ocean, polar cod (*Boreogadus saida*), a species ubiquitous both in open water and below the pack-ice (Lønne and Gulliksen 1989; Gradinger and Bluhm 2004), is believed to be the most abundant Arctic fish species in ocean zones at depths from 0-500m at high latitudes (Benoit et al. 2008; Fortier et al. 2015). Large schools of polar cod have regularly been reported in the literature in the Beaufort Sea (Geoffroy et al. 2011) (with an estimated total biomass of 250 thousand tonnes in the Amundsen Gulf alone (Benoit et al. 2014)), and under the pack-ice of the Amerasian Basin (Melnikov & Chernova, 2013) and of the Eurasian Basin (with an estimated median abundance of 5000 individuals per square kilometer (David et al. 2016)). Polar cod high abundance and circumpolar distribution render distribution boundaries difficult to assess. Thus, Rajasakaren (2013) noted that assessing polar cod distribution in the Barents Sea and around Svalbard is a challenging endeavour because of a lack of consistent monitoring, because this distribution appears to differ widely depending on the age-group, and because it displays important inter-annual variabilities. The author suggests that temperatures and salinity associated with Arctic Waters are important factors affecting the distribution of age-1+ polar cod and further state that predation avoidance and prey availability must not be neglected when attempting to identify the causes of distribution. Finally, the author points out that distribution will likely change seasonally due to spawning migrations.

Although it is difficult to establish clear-cut boundaries describing polar cod distribution in the inflow shelf, regular surveys conducted by the Institute of Marine Research reveal the presence of adult polar cod in the north and north east Barents sea (Skaret et al., 2015). Other irregular sampling on the west and northern coasts of Svalbard consistently show the presence of polar cod (Falk-Petersen et al., 1986; Nahrgang et al., 2014, Renaud et al., 2012). This Arctic cryo-pelagic gadoid occurs in environments that are associated with Arctic Waters (Rajasakaren, 2013), but they are regularly observed in Svalbard in domains that were recently described by Nahrgang et al. (2014) as both «Arctic» and «Atlantic» (Falk-Petersen et al., 1986; Renaud et al., 2012; Nahrgang et al., 2014). The presence of polar cod in both the Atlantic and Arctic domains in Svalbard suggests that this species has important adaptive capacities and can tolerate a wide range of temperatures and salinity. A combination of factors dictate the distribution of polar cod (Kessel et al., 2016) rather than temperature and salinity alone. This is in accordance with the observation that polar cod can tolerate much warmer temperatures than the ones that it is usually exposed to in its realized habitats (Drost et al., 2014). Thus, the strong association of polar cod with the cryosphere is more likely due to reproduction, prey availability, and predator avoidance (Crawford & Jorgenson, 1993; Gradiner & Bluhm, 2004; Bouchard & Fortier, 2011; Crawford et al., 2012) rather than temperature (Drost et al., 2014). In open waters however, it is likely that local distribution is determined by a quest for balance between predator avoidance, prey availability, and physiological acclimation to rapidly and seasonally changing temperatures and salinity (Kessel et al., 2016). If resource availability has the potential to balance out predation risk, this means that prey distribution and abundance, but also prey type are important factors in determining the level of risk that a school of polar cod will take in temporarily establishing in a given region.

1.3.2. Diet of age-1+ polar cod

1.3.2.1. The status of diet studies in the Arctic

A number of studies have focused on adult polar cod diet throughout the Arctic. Most of these studies were conducted on the outflow, North American interior, and Pacific inflow shelves, off the coast of Canada and Alaska. Few studies were conducted on the Atlantic inflow shelf in the Barents Sea and only a handful in the Svalbard archipelago. The most complete and recent circumpolar review of polar cod diet dates back from 2012 (Renaud et al., 2012) and testifies the lack of adult polar cod diet studies in Svalbard and on the Atlantic inflow shelf in general. Some of these studies were undoubtedly conducted by Russian colleagues, but enduring language barriers with the Russian scientific literature renders this work inaccessible to non-Russian speaking researchers and serious mistranslations and misuse of Russian work remain problematic (E.g. Girsa 1961, a study conducted on saithe (*Pollachius virens* [Russian: saida/saidoi]) and often misused in the polar cod literature (*Boreogadus saida* [Russian: saika]) (personal communication with J. S. Christiansen)). The majority of adult polar cod diet studies throughout the Arctic were conducted in the late winter in May, in the summer between June and August, or in the fall in September and October, and to date there is only sparse and very descriptive early or mid-winter diet studies conducted at high latitudes (i.e. ≥79°N) during the polar night (Melnikov & Chernova, 2013). The lack of winter studies makes any kind of seasonal approach difficult to undertake. That being said, thorough literature reviews can give preliminary understandings of polar cod diet in general and can provide insights on its feeding strategy during diurnally illuminated seasons.

1.3.2.2. Diet studies in the North American Arctic

The wide array of prey species in polar cod diet has sometimes made it difficult to forge meaningful conclusions on dietary preferences when comparing studies. Specimens caught in various regions of the Beaufort Sea in July and August have had diets predominantly composed of calanoid copepod and amphipods (Cui et al., 2012; Walkusz et al., 2013; Majewski et al., 2016). Even if calanoid copepods may not form the bulk of food items, they often have a high frequency of occurrence in polar cod stomachs from a given sample (Benoit et al., 2010; Rand et al., 2013). On the Pacific inflow and North American interior shelves, in the northern Bering Sea and southern Chukchi Sea, Nakano et al. (2016) report an important dietary contribution of gelatinous appendicularians, an unusual prey item, in spite of high abundance and thus availability of the expected preferred copepod prey in the water column. This rather intriguing finding contrasts with the observations of Cui et al. (2012) and Lowry and Frost (1981) and illustrates the difficulty to make attempts at identifying polar cod preferred prey. Though calanoid copepods are frequently reported as being an important prey item in polar cod diet, other copepods such as harpacticoid or cyclopoid copepods have also dominated stomach contents (Matley et al., 2013). Similarly, a variety of amphipods have been reported in polar cod diet with the predominance of set families or suborders depending on the region. Thus, Hyperiidea amphipods, *Themisto* spp. dominate the amphipod composition in polar cod diet in the Canadian Beaufort Sea (Majewski et al., 2016) along with the Senticaudata amphipod, *Apherusa glacialis* (Walkusz et al., 2013), whereas Ampeliscidae amphipods, a family of the suborder, Gammaridea, were reported to be particularly dominant in the diet of polar cod in the northern Bering Sea (Cui et al., 2012). Although juvenile teleost are regularly observed in polar cod diet (Craig et al., 1982; Cui et al., 2012; Rand et al., 2013; Majewski et al., 2016), they singularly bring an important contribution to polar cod dietary composition (Rand et al., 2013). Other prey species occasionally dominate polar cod diet such as Mysiids (Craig et al., 1982) or euphausiids (Rand et al., 2013) and the underlying factors explaining these abrupt changes in the observed ingested prey species compositions are suspected to be the outcome of seasonality, local (pelagic versus benthic) and regional habitat heterogeneity, and of the resulting prey availability. These observations have led an important body of specialists on polar cod to conclude that polar cod are largely opportunistic feeders (Lowry & Frost, 1981; Bradstreet et al., 1986; Ajiad & Gjøsæter, 1990; Christiansen et al., 2012) and will feed on which ever prey is available and most abundant at a given moment.

1.3.2.3. Diet studies in Svalbard and the Barents Sea

Calanoid copepod, whether *Calanus hyperboreus*, *Calanus glacialis*, or *Calanus finmarchicus* have been an important part of the diet of polar cod from the Atlantic inflow shelf along with the hyperiid amphipod *Themisto* spp. (Lønne & Gulliksen, 1989; Ajiad & Gjøsæter 1990; Nahrgang et al., 2014). The majority of studies from the Atlantic inflow shelf were conducted in the Barents Sea (Lønne & Gulliksen, 1989; Ajiad & Gjøsæter, 1990), and a few studies on juvenile polar cod diet were conducted in Svalbard (Falk-Petersen et al., 2008; Renaud et al., 2012). Nahrgang et al. (2014) investigated the diet of adult polar cod on the western and northern coast of Svalbard in September

2013, and Master students have brought important contributions in developing our understanding of adult polar cod diet in Svalbard (Hovinen, 2007 cited in Renaud et al., 2012; Johannessen, 2007; Eglund Newby, 2015).

In a first attempt to investigate the diet of polar cod in Arctic versus Atlantic domains, Nahrgang et al. (2014) have collected specimen in regions of Svalbard that are affected by different water masses, and have noted a much more diverse diet in polar cod from the Atlantic domain whereas polar cod from the Arctic domain fed strictly on the hyperiid amphipod, *Themisto libellula*. Johannessen (2007) noted a difference in species richness between seasons with diet from the fall being more diverse than diet form the spring in Kongsfjorden. They further observed that polar cod from both Kongsfjorden and Billefjorden seemed to forage on a majority of calanoid copepod in the spring and the fall. In Kongsfjorden, krill was also consumed in the spring and mostly replaced by *Themisto* spp. in the fall. Frequency of occurrence of calanoid copepod did not seem related to size whereas the frequency of occurrence of *Themisto* spp. and krill increased with size. It must be noted here that the samples included in this project were collected in 2006, a year of important transition in Kongfjorden (Willis et al., 2008). In January 2014 in Kongsfjorden, Eglund Newby (2015) reported that, though the diet was different between demersal and pelagic caught polar cod, prey taxa were generally pelagic with higher abundance of copepod and fish in stomachs of demersal caught specimen and higher abundance of euphausiids in pelagic caught specimen. The author did not note the presence of the typically Arctic amphipod *Themisto libellula* which is in accordance with the results from Nahrgang et al. (2014) on Atlantic domains and is coherent with observations indicating a rapid warming of this fjord (J. Berge personal communication). Because of the important environmental changes that have recently risen in Kongsfjorden, it is difficult to justify the comparison of a diet study conducted in 2006 with one conducted in 2014. Furthermore, Johannessen (2007) looked at prey abundance for pooled polar cod of 4 cm to 18+ cm length which renders the interpretation of the result difficult. The scarcity of polar cod diet studies in Svalbard calls for more contribution in this region. Svalbard is at the meeting point of cold Arctic domains and warmer Atlantic domains (Nahrgang et al., 2014) and its relatively accessible environment offers unique opportunities to investigate the impacts of a rapidly changing climate on Arctic endemic species such as the polar cod.

1.4. Feeding strategies

1.4.1. A theoretical concept

In an attempt to classify and describe feeding variability among species, various grouping and conceptual approaches have been proposed. Prey selectivity and the adoption of a generalist or specialist feeding strategy have been the focus of optimal diet models. Generalist feeding describes the behaviour of an organism that will feed on a wide spectra of available foods without displaying any particular preferences. In contrast, specialist feeding describes the behaviour of an organism that has a marked preference for given food types (Gerking, 1994a). Authors often describe the generalist-opportunist strategies as operating on a continuum both at the species level (Panzacchi et al., 2008) and at the community level (Poisot et al., 2015). Generalist and specialist feeding are sometimes used to describe temporal strategies rather than static feeding groups categorizing species (Gerking, 1994a). Thus, many species can shift from one strategy to another over the course of their life. Such a shift in feeding strategy or in diet can be linked to ontogenesis or phenology, but can also be triggered by the sudden abundance or scarcity of a given prey or by an increase or decrease in competition. In ichthyology, diet switching is observed intermittently yet frequently and was described by Gerking (1994a) as an opportunist behaviour. Thus, opportunist fish may fall anywhere on the specialist-generalist spectrum and may temporally switch to a more profitable food source either because it is temporarily more abundant or because their usual food source is in decline. It was argued that practically all fish species are opportunists, although some narrow specialist species may have physiological adaptations that do not allow for changes in their diet. Ultimately, the ability to opportunistically shift from one diet to a more profitable diet is also referred to as trophic adaptability (Gerking, 1994a).

In 1996, Amundsen and colleagues published a review of Costello's method for assessing feeding strategy and proposed a diagram that allows for the exploration of feeding strategies, prey importance, and inter- and intra- individual components of niche width using mere stomach content analysis (Amundsen et al, 1996). A narrow niche width is representative of a temporal specialist feeding whereas a broad niche width is representative of a temporal generalist feeding. Optimal foraging theory asserts that an organism can be described as specialist when it feeds on a specific prey as a result of high abundance of that preferred prey item. Generalisation may therefore come as a response to low abundance of preferred prey or of any prey item (MacArthur & Pianka, 1966).

However, according to the general niche theory, individual specialization is expected as a response to low abundance of preferred prey when intraspecific competition is high and triggers resource partitioning within the population (Putman, 1994). Indeed, specialist individuals can occur within a generalist population thereby increasing the population dietary niche width. Amundsen and colleagues's diagram allows to identify whether the generalisation or specialisation operates at the population or at the individual level.

1.4.2. Polar cod feeding strategy

Because of their broad prey spectrum, polar cod are often referred to as opportunist (Ajiad & Gjøsæter, 1990; Walkusz et al., 2013; Majewski et al., 2016) or generalist (Renaud et al., 2012; Mueter et al., 2016) feeders. There is, however, no consensus over the characterization of these terms, and opportunism is often used interchangeably with generalism. Unless an unambiguous definition of the terms is established prior to adopting them, describing polar cod as either opportunists or generalists offers little insight on their dietary plasticity and their trophic adaptability. For the purpose of this paper, I will use the terms specialism and generalism on a continuum to describe a temporal feeding event rather than to classify a species feeding habit. Opportunism will be used to describe a species trophic adaptability or the ability to shift from one diet to another.

1.5. Objectives

The main goal of this study was to investigate the temporal feeding strategies adopted by polar cod across seasons by documenting its position on the generalist-specialist spectrum. I hypothesize that the feeding strategy of polar cod is seasonally plastic, thereby qualifying polar cod as opportunist. However, I suspect that this plasticity does not ensure uniform feeding success between season inasmuch as other physiological and physical factors are at play. To test this hypothesis, I document: (1) if polar cod feeding success varied seasonally; (2) if polar cod diet varied seasonally in terms of prey taxa composition, and (3) how polar cod diet varied seasonally in terms of ingested prey taxa composition. I put the results of these objectives in context with the literature and with concomitant data on prey community composition to investigate if ingested prey taxa composition corresponds to available prey taxa in the water column. Finally, some possible factors at play in explaining my results, such as reproductive phenology and high latitude light regime, are adressed in the Discussion.

2

Materials and methods

2.1. Sampling

Fish were collected on a seasonal basis around the archipelago of Svalbard (Fig. 1). The areas of interest for this study were Billefjorden, Kongsfjorden, and Smeerenburg on the west coast of Spitsbergen as well as Rijpfjorden located on the north east of Svalbard. Characteristics of the sites are described below.

The fish were caught using a Campelen 1800 bottom trawl with a 22 mm cod end mesh size and a Harstad pelagic trawl with an 8 mm mesh size aboard the R/V *Helmer Hanssen*. Out of 45 trawls only 15 were retained for the diet analysis (Table 1) as this study focuses on adult polar cod and the other trawls contained either too few or no polar cod, or only juvenile (<10cm) polar cod. These trawls were performed in September and October 2014, January 2015, May 2015, September 2015, and January 2016. A Sea-Bird Electronics conductivity, temperature, and depth (CTD) instrument was used at some sites to measure salinity and water temperature at trawling depth (See Table A1 in Appendix A for details on CTD stations).

Table 1 Trawling stations information for sites and seasons from which polar cod stomachs were harvested and analyzed for ingested prey composition. Coordinates are in decimal degrees.

Trawl ID	Site	Season	Date	Trawl type	Latitude	Longitude	Trawling Depth (m)	Total stomach processed
RA	Rijpfjorden	September	28/09/2014	Bottom	80.31	22.27	249	29
RD	Rijpfjorden	September	29/09/2014	Bottom	80.33	22.16	220	15
RC	Rijpfjorden	September	29/09/2014	Bottom	80.34	22.08	253	10
BA	Billefjorden	October	04/10/2014	Bottom	78.66	16.72	163	51
KE	Kongsfjorden	January	17/01/2015	Bottom	78.91	12.18	300	51
KF	Kongsfjorden	May	08/05/2015	Bottom	78.92	12.12	122	20
BE	Billefjorden	May	13/05/2015	Bottom	78.59	16.50	161	20
SA	Smeerenburg	September	13/09/2015	Bottom	79.72	11.10	208	40
RF	Rijpfjorden	September	17/09/2015	Bottom	80.32	22.25	267	40
BF	Billefjorden	January	11/01/2016	Bottom	78.60	16.51	158	40
SB	Smeerenburg	January	13/01/2016	Bottom	79.76	11.09	189	40
RG	Rijpfjorden	January	14/01/2016	Bottom	80.38	22.06	260	40
RI	Rijpfjorden	January	14/01/2016	Bottom	80.38	22.09	251	39
RH	Rijpfjorden	January	14/01/2016	Pelagic	80.34	22.06	220	20
KQ	Kongsfjorden	January	22/01/2016	Bottom	78.91	12.21	88	19

2.2. Particularities of the fjords in this study

The trawls conducted for this study were performed along the west and northern coast of the Svalbard archipelago and display a variety of bathymetric and oceanographic characteristics. Rijpfjorden is a northern fjord roughly situated at 80°N that is largely influenced by Arctic water and to a lesser but non-negligible extent by Atlantic water (Błachowiak-Samołyk et al., 2015). The Atlantic water mass overlaying that Arctic water is illustrated by the CTD profile from September 2015 (Fig. A5 in Appendix A). Rijpfjorden is relatively shallow (240 meters maximum), and usually ice covered by January or February (Søreide et al., 2010) for a duration of 6-8 months (Wallace et al., 2010). The zooplankton community of this fjord is largely composed of Arctic species but species often associated with the Atlantic water mass can also be advected in high abundance through the WSC (Wallace et al., 2010). Kongsfjorden is situated on the west coast of Svalbard at 79°N and is largely influenced by the inflow of relatively warm and saline Atlantic water (Cottier et al., 2005) due to a lack of sill and to a large trough, Kongsfjordrenna, reaching up to the shelf-break. In Kongsfjorden, the Atlantic water mass is at its highest proportion in the fall (Wlodarska-Kowalczuk et al., 2005) and its importance compared to that observed in Rijpfjorden is reflected in the CTD profile from the fall 2015 (Fig. A6 in Appendix A). Kongsfjorden also harbors cold fresh water by its glaciers Blomstrandbreen, Conwaybreen, Kongsbreen, Kronebreen, and Kongsvegen (Svendsen et al., 2002; Streuff, 2013). Until recently, Kongsfjorden was covered by ice during the winter. 2006 marks the first ice free winter in the fjord which hasn't seen winter ice formation since then (Willis et al., 2008) and has undergone rapid borealization (Kortsch et al., 2012). Zooplankton species and abundance in Kongsfjorden undergo strong variations in terms of abundance and biomass and both Atlantic species that are advected in the fjord and Arctic species co-occur (Hop et al., 2002). Advection of Atlantic species is stronger in the fall and more recently Atlantic species have been reported in the inner glacial bay (Walkusz et al., 2009). Billefjorden is a silled fjord that is situated in the inner Isfjorden (Berge et al. 2014). Whereas Isfjorden is largely influenced by the inflow of Atlantic water due to a lack of sill and a large trough connecting it to the shelf break, Billefjorden's sill isolates it from Atlantic water and it displays Arctic characteristics such as frozen waters in the winter (Arnkværn et al., 2005; Nilsen et al., 2008). For that reason, it has been described as an Arctic domain by Nahrgang et al. (2014). Because of limited water mass exchange, Arctic zooplankton seems to be favored in Billefjorden though Atlantic species are also found but in lower abundance than in Kongsfjorden (Walkusz et al., 2003). Samples were also taken in Smeerenburg Bay west of Svalbard and at a latitude of 79°N. The influence of Atlantic water in Smeerenburg Bay is quite striking and well illustrated on the CTD taken in the fall 2015 (Fig. A7 in Appendix A) and the zooplankton community of the area is likely to be influenced by the inflow of Atlantic water (personal communication with M. Daase).

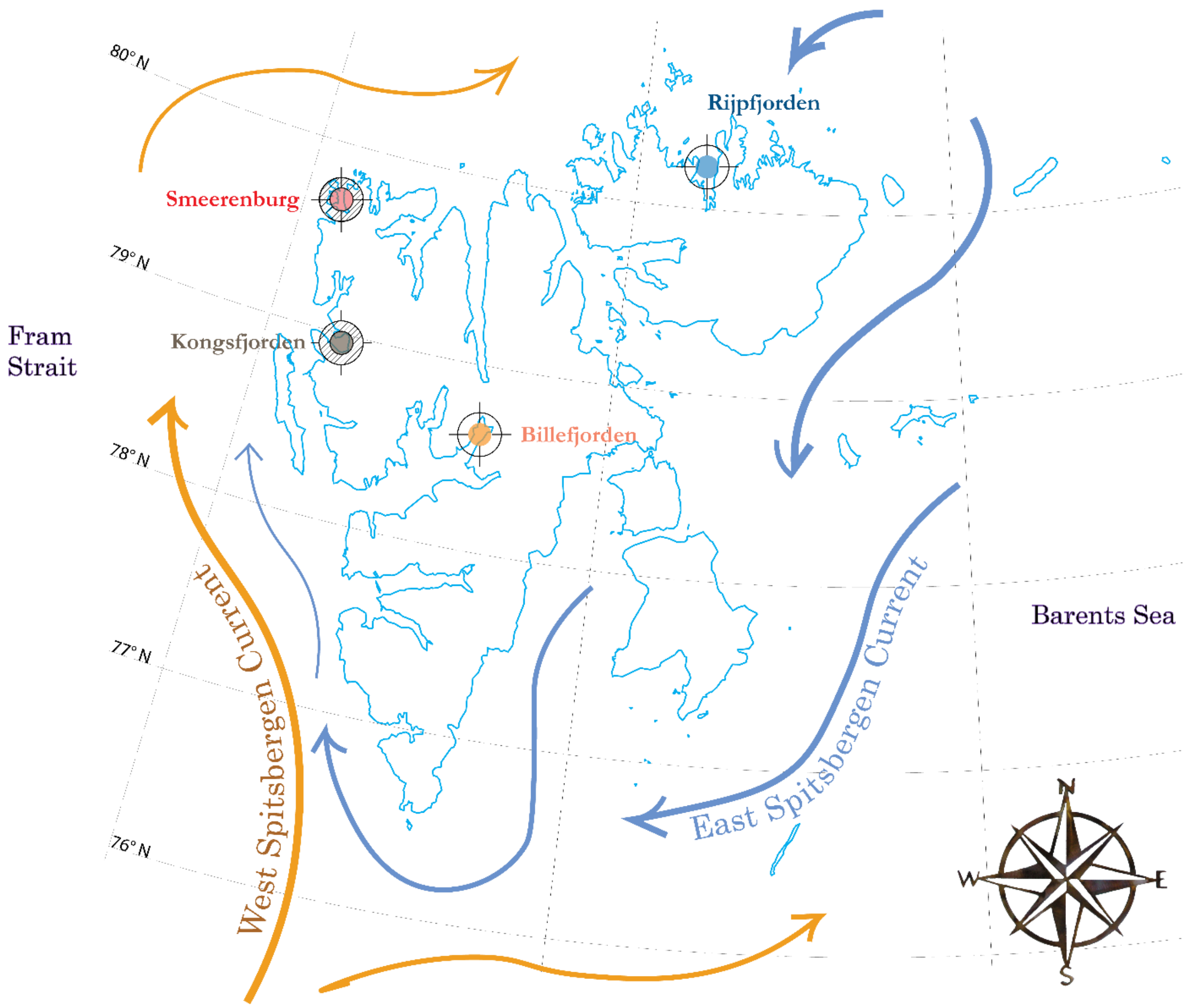


Fig. 1 Map of Svalbard currents and sampling sites. Empty circles represent domains that are more typically Arctic and dashed circles represent domains that are more typically Atlantic. Close up maps for each site can be found in the Appendix A (Fig. A1, A2, A3, & A4).

2.3. Morpho-biological measurements and dietary data

Polar cod were weighed and measured. Based on Falk Petersen et al. (1986a) polar cod were divided into three size categories: <10 cm, 10-15 cm, and >15 cm. Only stomachs from bottom trawl were included in the analysis. Stomachs of polar cod were systematically extracted for adult polar cod (above 10 cm) for up to 50 individuals when available and stomach content was analysed in the laboratory. Stomach weight, gonad weight, and liver weight were measured on site and sex was estimated when possible. The dissected stomachs were kept in ethanol. Stomach content of polar cod was examined with a dissecting microscope, stomach fullness was estimated using a subjective method on a scale from 0 (completely empty) to 5 (distended) as suggested by Haram and Jones (1971), and prey taxa were identified to the lowest possible taxonomic level. Individuals of each prey taxa identified were counted for numerical analysis and weighed for gravimetric analysis for each stomach. Non identified material was recorded as "unknown" and weighed. Initial dietary categories (IDC) were grouped into broader dietary categories (BDC) for the analysis. All weights were measured in grams at two digits after decimal point.

2.4. Modelling seasonal variations in feeding success

The fullness data set is a factorial study with fullness ranging from 0 = "completely empty" to 5 = "distended" with two environmental factors, season and site, which have three, and four levels respectively (season = fall, winter, spring; sites = Billefjorden, Kongsfjorden, Smeerenburg, and Rijpfjorden). Due to the ordinal nature of our fullness response variable, we fitted a cumulative link model (clm) to the data. This model is appropriate for ordinal dependent variables and categorical independent variables as it treats categorical (or ordinal) variables as such and is free of linear regression assumptions such as the normal distribution of residuals (Christensen, 2015). Predictions were denoted by extracting the fitted values and using the resulting fitted probabilities to estimate the probability that a given stomach observation will fall within a given fullness response category. Because of the small sample size of polar cod > 15 cm in the Spring, predictions for that size category at that season were not performed. The clm was performed using the "ordinal" package (Christensen, 2015) in R (R Core Team, 2013).

2.5. Seasonal dietary similarities and diet relationship with environmental variables

Two data sets were generated for the multivariate analysis: Dataset A, where the gravimetric contribution of BDC in percent (%W) was calculated for each stomach by dividing prey taxa weight by total prey weight for each stomach and multiplying the result by 100; and dataset B, in which the average BDC weight was calculated for each trawl trawl by adding total prey taxa weight for each trawl, dividing total prey taxa weight by total prey weight for each trawl, and multiplying the result by 100. Dataset B calculation were performed separately for each polar cod size category.

Dataset B was used to measure the Bray-Curtis similarity index and generate a dendrogram based on a group average hierarchical agglomerative cluster analysis. The validity of the dendrogram groups were evaluated by performing similarity profile (SIMPROF) permutation tests. As advised by Clarke and Warwick (2001) I then performed an ordination to see whether the group clusters generated by the cluster analysis were also visible in the ordination. Here, I preferred the use of a non-metric multi-dimensional scaling method (nMDS) since it has often been referred to as an excellent method for visualizing (dis)similarity matrices (Everitt, 1978). The stress calculated along with the plotting of the nMDS measures the amount of error. We ran one-way analysis of similarities (ANOSIM) on the similarity matrices of the two size categories to test the null hypothesis that there are no differences between seasons in dietary composition (in terms of food item similarity or similar food item variability).

Dataset A was used to compute the Bray-Curtis similarity index on the non-transformed percentage of prey importance for specific sites. Here, we produced nMDS where each stomach was treated as an individual sample for each of the four sites. For the purpose of the nMDS and due to the high number of stomachs, empty stomachs were removed and prey species that occurred in less than 5% of the stomachs were removed for each site as suggested by Clarke and Gorley (2006) (See Appendix A for specifications on SIMPROF tests, nMDS analysis, and ANOSIM).

In order to identify relationships and patterns between environmental variables and prey species composition in polar cod stomach, we performed a canonical correspondence analysis (CCA) using the compositional dataset A. Since there is a divergence in the literature when it comes to the inclusion or exclusion of rare species in this type of gradient analysis (Jackson & Harvey, 1989), we performed a CCA with the full data set and displayed it with a contribution biplot (Greenacre, 2013). Seasons were coded as dummy variables.

The hierarchical clustering and nMDS were performed using PRIMER v6 (Clarke & Gorley, 2006). The CCA and contribution biplot were performed using the "vegan" package (Oksanen et al., 2013) in R (R Core Team, 2013).

2.6. Seasonal ingested prey importance, richness, and diversity

The frequency of occurrence (%FO) and both numerical (%N) and gravimetric (%W) percentages were calculated for each site using the broad prey category and separating polar cod into two size classes (10-15 cm and >15 cm) and pooling trawl data from a given site and season together. The gravimetric method has recently been described as the most robust and accurate fish diet analysis method (Ahlbeck et al., 2012), and the numerical method is best suited for estimating foraging effort and prey selection (Ball 1961). Hyslop (1980) suggested the combination of amount and bulk measurements, here numerical and gravimetric, as a more representative measure of the dietary importance of food categories. Thus, we used %N, %W, and %FO to measure the index of relative importance (IRI), a standardized measure of prey importance allowing for cross-study comparisons. %FO and IRI were calculated as followed:

$$\%FO = (N_p / N_d)\ 100$$

$$IRI = (\%N + \%W)\ \%FO$$

where N*p* is the number of stomach with a given prey in their stomach and where N*d* is the total number of stomachs excluding empty stomachs.

In order to reduce the complex multivariate nature of our dietary data, we measured species richness (S) (i.e. the number of species), and niche width with the Shannon-Wiener (H') diversity index (Spellerberg & Fedor, 2003) on our %IRI data.

2.7. Assessing seasonal feeding strategies

Polar cod feeding strategy was directly assessed using the percent prey-specific abundance ($\%P_i$) versus percent frequency of occurrence (*%FO*) diagram described by Amundsen et al. (1996) as an alternative to Costello (1990). $\%P_i$ was measured using the following equation:

$$P_i = (\Sigma S_i / \Sigma St_i) \text{ x } 100$$

where P_i is the prey-specific abundance of prey *i*, S_i is the total weight of prey *i* from stomach *i*, and S_t is the total prey weight of all stomachs containing prey *i*. Empty stomachs were excluded from the calculations along with unidentified material which would bias the results. Given the small number of samples for some sites and seasons, I also removed any prey species that occurred in less than two stomachs otherwise they would be over-represented and subject to misinterpretation in the diagram (personal communication with P.A. Amundsen). Diagrams were generated separately for each four sites, three seasons, and two size classes. The distribution of points gives information about prey importance and predator feeding strategy as illustrated in Fig. 2. Prey points positioned in the upper right corner of the diagram indicate a specialization from the predator in those preys, whereas prey points positioned in the lower left corner of the diagram indicate a generalization from the predators on those preys (Amundsen et al., 1996). In the context of dietary analysis, high between-phenotype component (High BPC) describes a population in which different individuals specialize on different prey categories, and high within-phenotype component (High WPC) describes populations in which most individuals will all feed on many prey species (Amundsen, 1995).

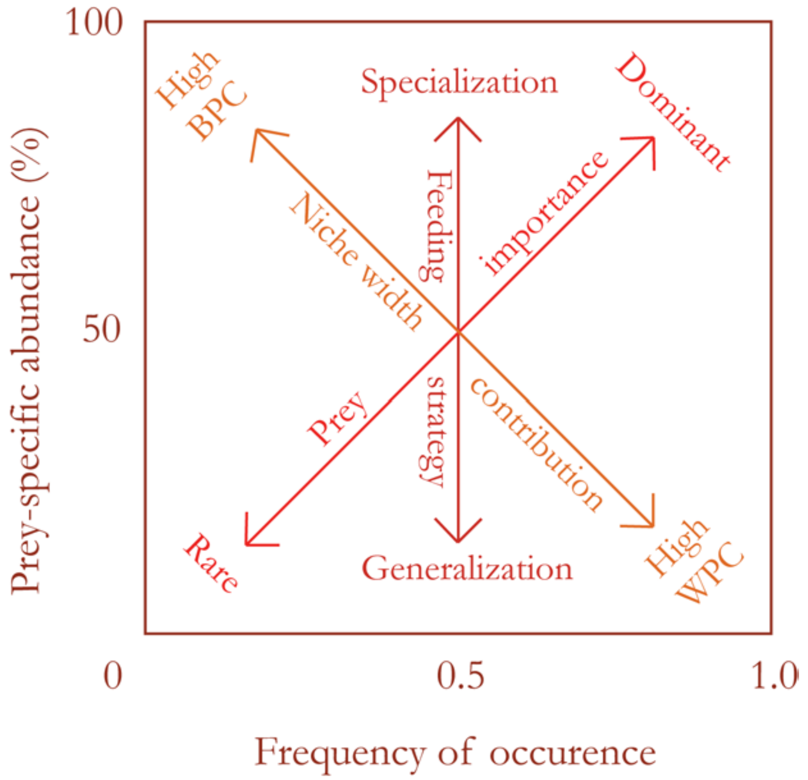


Fig. 2 Illustration of feeding strategy diagram interpretation based on Amundsen et al. (1996) diagram and method. The feeding strategies are represented by the positioning of prey points in the diagram.

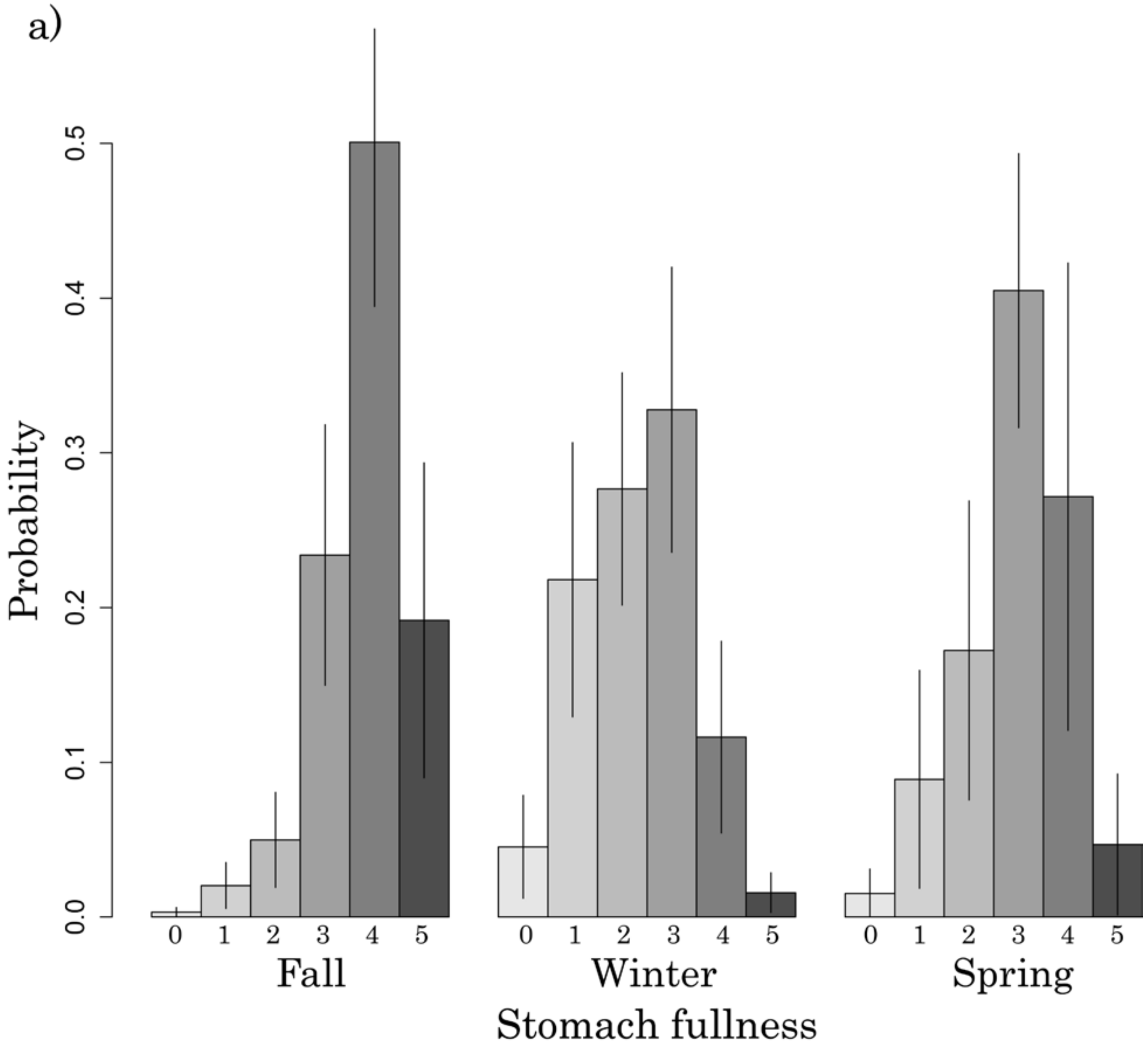
3

Results

Polar cod from 15 trawls across the months of September, October, January, and May spanning over the years of 2014 to 2016 were retained for the analysis. For the diet analysis, only stomachs from bottom trawls were kept as too few pelagic trawls were taken, any stomach from polar cod smaller than 10 cm were removed from the analysis, and the remaining stomachs were divided into two size categories which resulted in 200 stomachs for polar cod over 15 cm in length, and 230 stomachs for polar cod from 10-15 cm (See Table B1 in Appendix B for details on morpho-biological measurements).

3.1. Seasonal variations in feeding success

The probability of a polar cod above 10 cm to have an high stomach fullness (full: 4, on a scale from 0-5) is highest in September-October when all sites are combined, and the highest probability of stomach fullness being at its maximum (full: 5) is during the fall. In the January, stomach fullness has a higher probability of being lower (full: 2 or 3) and the highest probability of stomach fullness to be empty or practically empty (full: 0 or 1) is during the winter. In May, stomach fullness will have a higher probability of being important (full: 3 or 4) (Fig. 3). The stomach fullness was slightly lower for May compared to September-October and significantly lower for January (Table 2 & 3).


a)
Probability
0.0
0.1
0.2
0.3
0.4
0.5
0 1 2 3 4 5
Fall
0 1 2 3 4 5
Winter
0 1 2 3 4 5
Spring
Stomach fullness

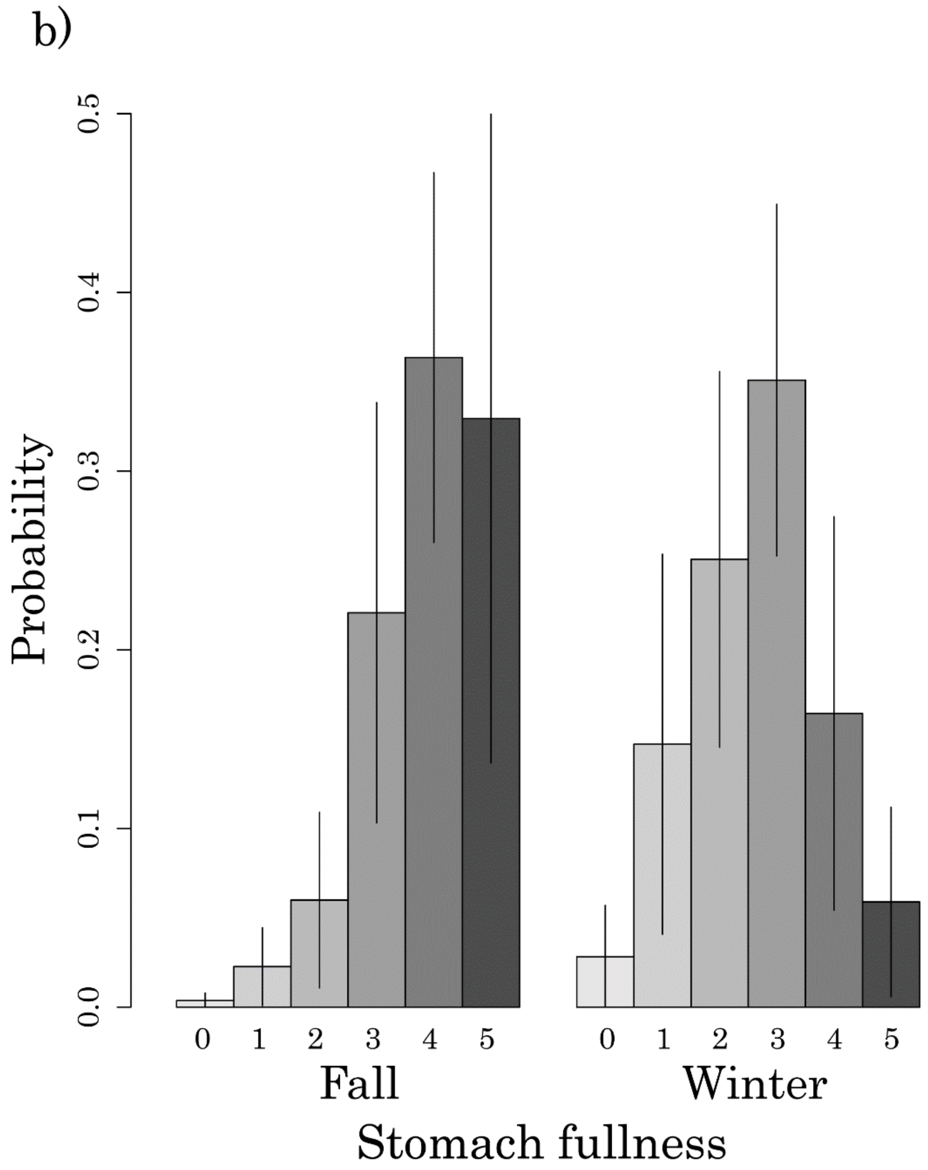


Fig. 3 Probability of an individual to be categorized into fullness 0-5 depending on season predicted from a cumulative link model (clm) fitted values for (a) 10-15 cm individuals and (b) >15 cm individuals. The error bars correspond to the ±1.96 standard error for the mean prediction.

Table 2 Ordinal regression analysis (a.k.a. cumulative link modelling) between polar cod stomach fullness (for polar cod of 10-15 cm) and the location and season at which they were caught with September in Billefjorden as the first level.

Predictor variable	Estimate	Standard error	z value	p-value
Kongsfjorden	-0.65	0.35	-1.83	0.067 .
Rijpfjorden	-0.55	0.32	-1.73	0.084 .
Smeerenburg	-0.98	0.42	-2.33	0.019 *
Spring	-1.57	0.49	-3.21	0.001 **
Winter	-2.69	0.35	-7.69	1.45e-14 ***

Table 3 Ordinal regression analysis (a.k.a. cumulative link modelling) between polar cod stomach fullness (for polar cod of >15 cm) and the location and season at which they were caught with September in Billefjorden as the first level.

Predictor variable	Estimate	Standard error	z value	p-value
Kongsfjorden	-1.80	0.66	-2.73	0.006 **
Rijpfjorden	-0.92	0.44	-2.10	0.036 *
Smeerenburg	-2.28	0.52	-4.40	1.08e-05 ***
Spring	0.62	1.02	0.61	0.542
Winter	-2.06	0.32	-6.52	6.86e-11 ***

3.2. Diet seasonal clusters and relationship with environmental variables

The ANOSIM allowed us to reject the null hypothesis that there are no differences between seasons in dietary composition for both size categories of polar cod between the fall and the winter (ANOSIM polar cod >15 cm (999 permutations): R=0.63, $p<0.005$; ANOSIM polar cod 10-15 cm (999 permutations): R=0.32, $p<0.05$). For both size categories however we could not reject the null hypothesis between the fall and spring and between the spring and winter. Both the nMDS and the dendrogram illustrated distinct seasonal clusters of dietary similarities for both size categories of polar cod and were more pronounced for large polar cod over 15 cm and particularly for the months of January and September-October (Fig. 4 & 5). There were 4 diet groups identified by the SIMPROF permutation test ($p<0.05$) for polar cod over 15 cm and a stress of 0.06 on the associated ordination plot, and 3 diet groups identified by the SIMPROF permutation test ($p<0.05$) for polar cod from 10-15 cm and a stress of 0.10 on the associated ordination plot (Fig. 4 & 5). As tested by SIMPROF, the four groups were determined at a 45% similarity level for polar cod over 15 cm and the three groups were determined at a 20% similarity level for polar cod from 10-15 cm. The seasonal partitioning is well illustrated by nMDS on individual stomachs for all four sites (Fig. B1 in Appendix B).

Results from the Canonical Correspondence Analysis using temperature, salinity, latitude, depth, and season to constrain the diet data showed that teleostei prey were associated with higher latitudes and with the month of January whereas *Themisto* spp. were associated with the month of September and with lower temperatures (Fig. 6). Euphausiids, were associated with higher temperatures, higher salinity, lower latitudes, and the month of May (Fig. 6).

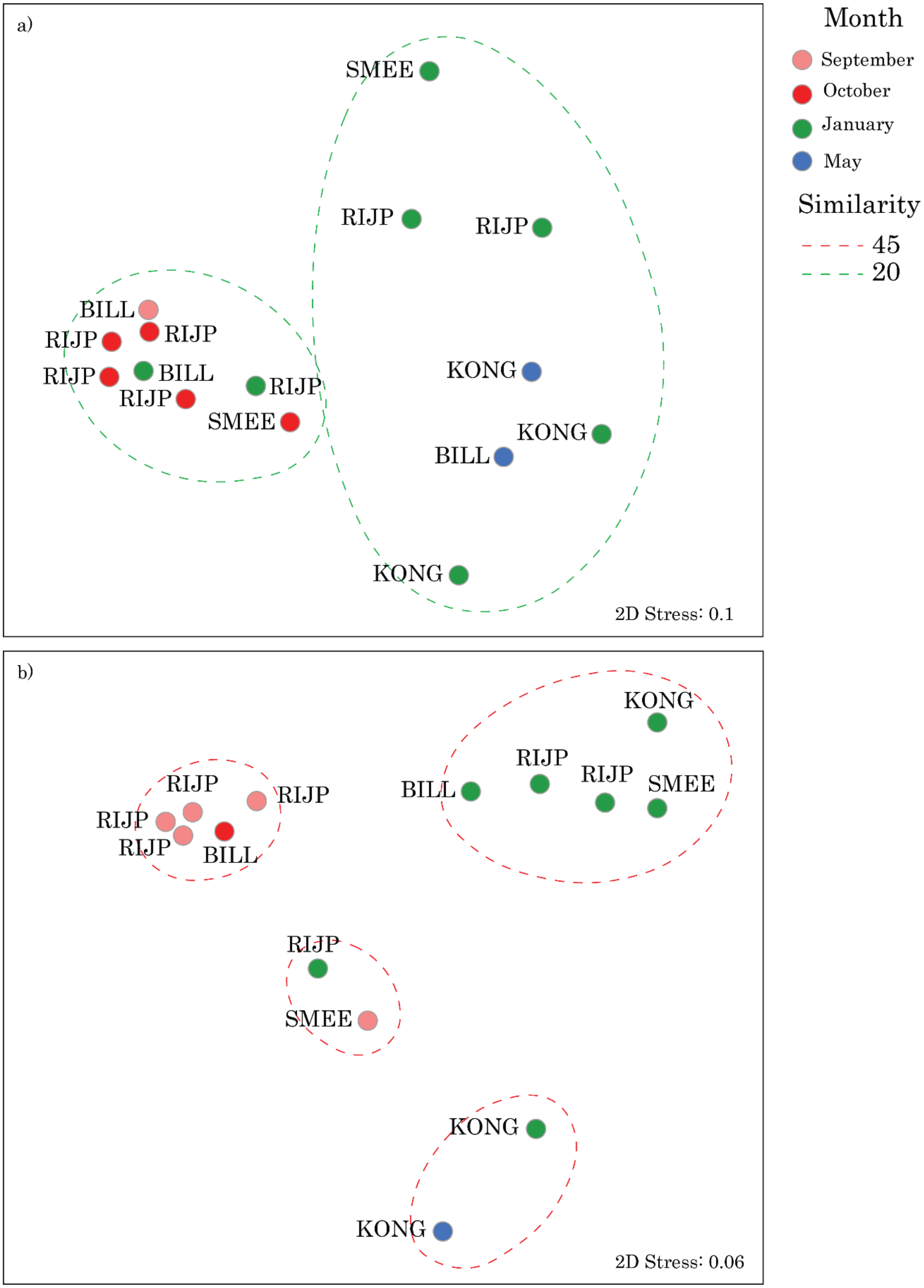


Fig. 4 Non-metric multidimensional scaling (nMDS) ordination of gut content from stomachs of polar cod from (a) 10-15 cm (b) and >15 cm based on Bray-Curtis similarity. RIJP = Rijpfjorden, BILL = Billefjorden, KONG = Kongsfjorden, SMEE = Smeerenburg

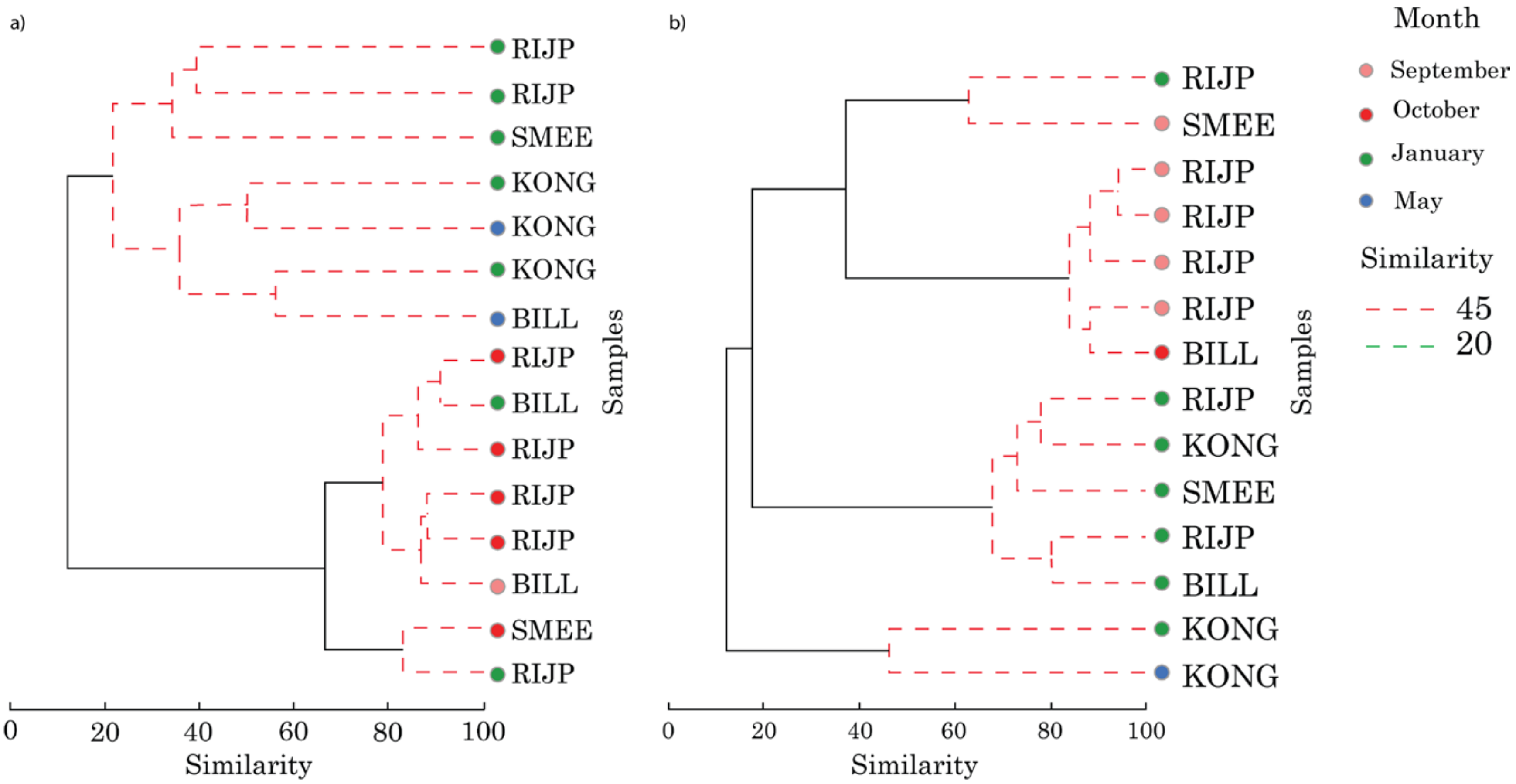


Fig. 5 Dendrogram with dietary clusters identified by similarity profile permutation tests (in red) for (a) polar cod from 10-15 cm and (b) polar cod above 15 cm.

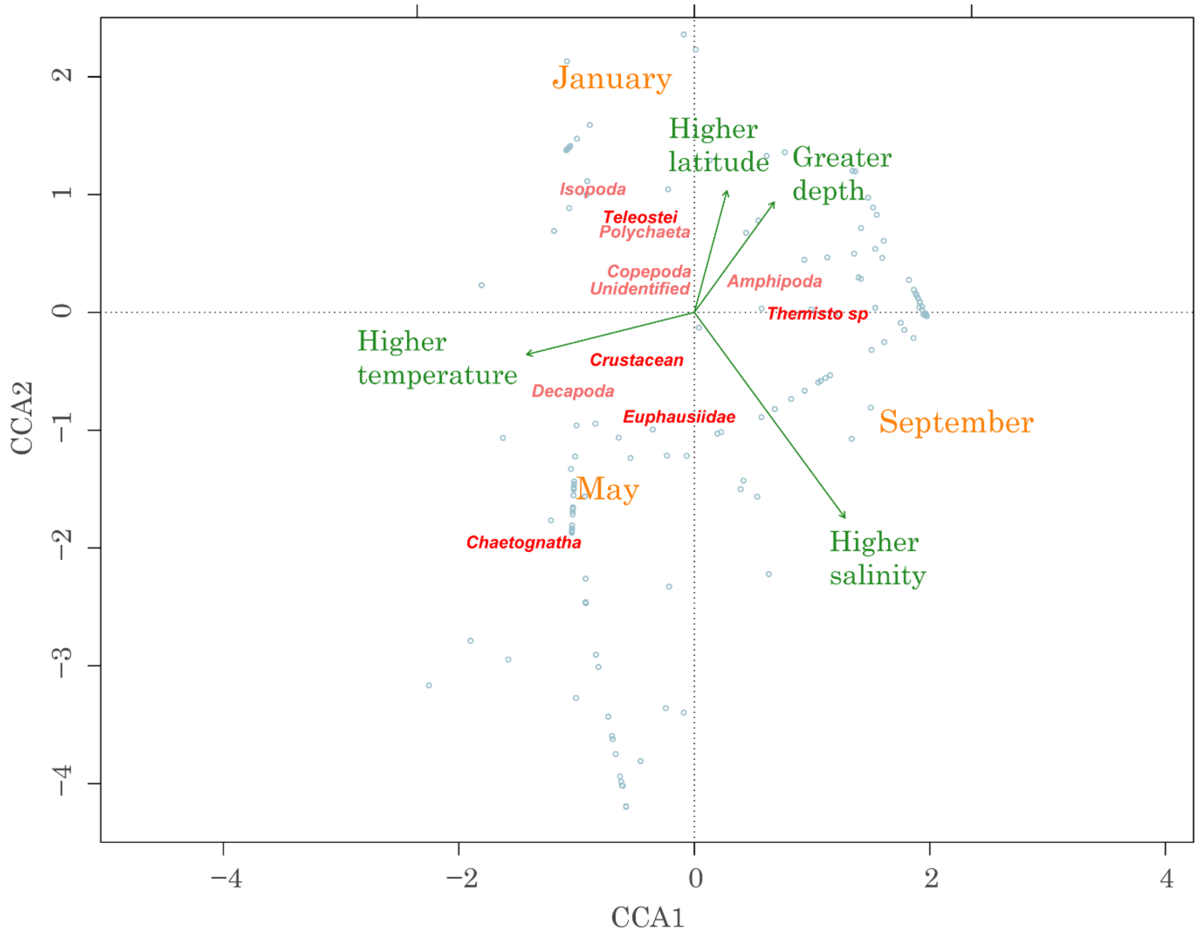


Fig. 6 Canonical correspondence ordination plot of *Boreogadus saida* prey species pooled in broad dietary groups showing association between ingested prey occurrence likelihood based on environmental variables. Only the above average contributing prey species are represented here. Eigenvalues (Axis I = 0.47, Axis II = 0.21, and sum of all constrained = 0.82) indicate that the CCA axis I and II explain 82.9% of the explained variance.

3.4. Dietary composition of prey among sites, seasons, and polar cod size classes

In terms of relative importance (IRI) and frequency of occurrence (FO) the dominant prey species differed between season and to a lesser extent between sites given a specific season. During the months of September and October and for both polar cod size categories, the dominant prey taxa was were *Themisto* spp. (Fig. 7 & 8; Table 4 & 5). At these months, *Themisto* spp. occurred frequently in the stomachs irrespective of the two size categories (10-15cm and >15cm) (Table B2 & B3 in Appendix B). Both euphausiids and copepods occurred relatively frequently in the fall (Table B2 & B3 in Appendix B), but had much lower IRI than *Themisto* spp. except in Smeerenburg (Table 4 & 5). A shift in diet occurred between September-October and January in terms of percent weight abundance (Fig. 7 & 8) and relative importance (Table 4 & 5). In all sites except for Kongsfjorden, teleostei contributed to the bulk of stomach content (Fig. 8) and occurred relatively frequently (>33.33 %FO) (Table B3 in Appendix B) in stomachs of polar cod over 15 cm. Polar cod from 10-15 cm also had an important contribution of teleostei for Rijpfjorden and Smeerenburg (Fig. 7). Teleostei were particularly important in the diet of both size categories from Smeerenburg (10-15cm = 57.32 %IRI; >15cm = 92.97 %IRI) (Table 6). In Billefjorden in January, *Themisto* spp. were also important with a clear partitioning between size categories (10-15cm = 82.40 %IRI; >15cm = 29.64 %IRI) (Table 4 & 5). In January, copepod were important to a greater extent than in the fall in terms of %FO (Appendix) and %IRI (Table 4 & 5) for both size categories but were still negligible in terms of %weight (Fig. 7 & 8). At this month, euphausiids occurred very frequently in polar cod stomachs from both size categories in Kongsfjorden (Table B2 & B3 in Appendix B). In May, 10-15 cm individuals from Billefjorden and Kongsfjorden were frequently feeding on euphausiids and copepods, and an important number of individuals had crustacean remains too digested to identify (Table B2 in Appendix B). Only two larger (>15 cm) individuals were caught in May and thus are likely not representative of the population of polar cod. Niche width was higher within sites in January compared to September-October, particularly for the larger size class of polar cod (Table 6).

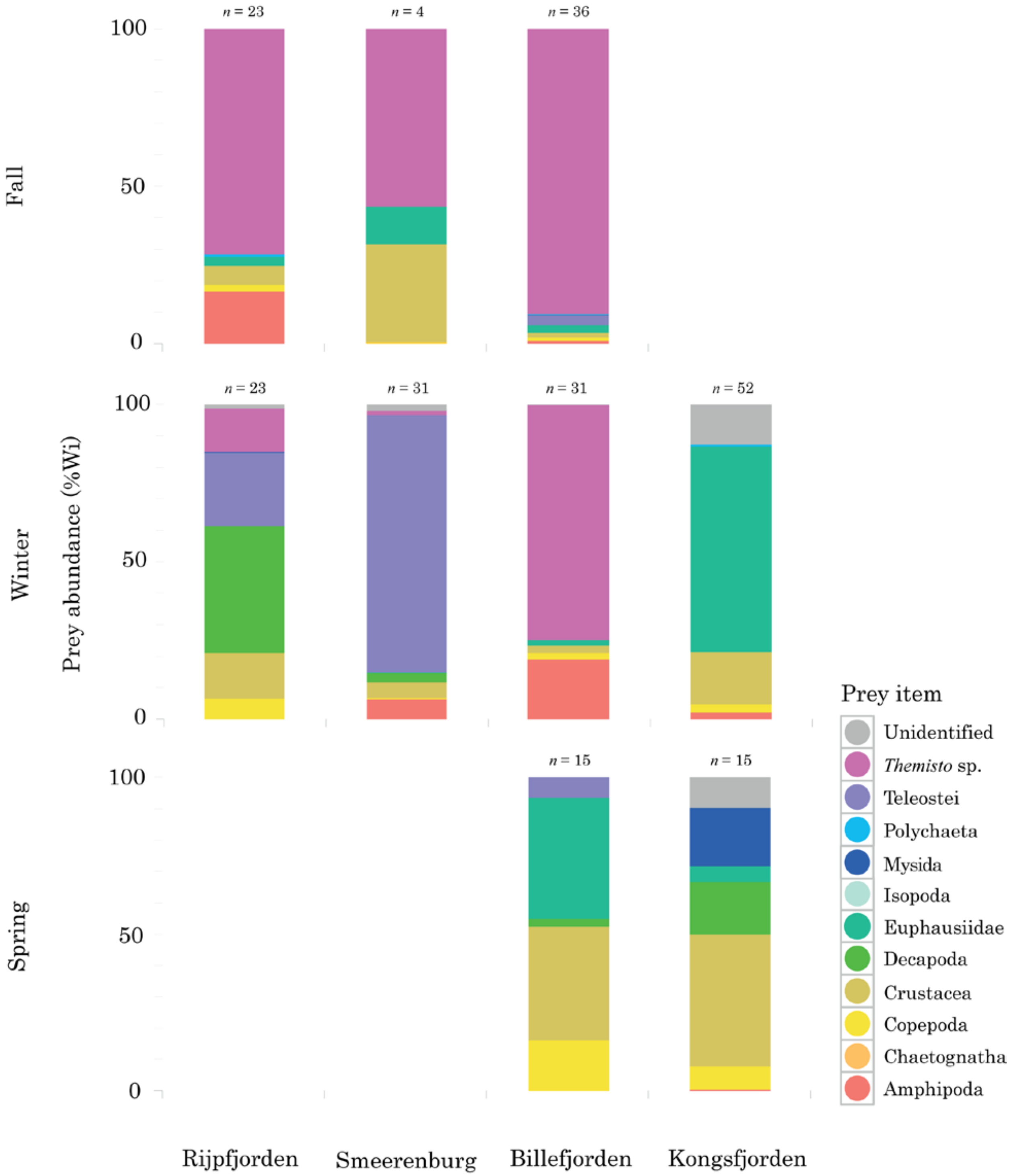


Fig. 7 Proportion of ingested prey based on percent prey weight (in grams) for different sites and seasons for polar cod of 10-15 cm.

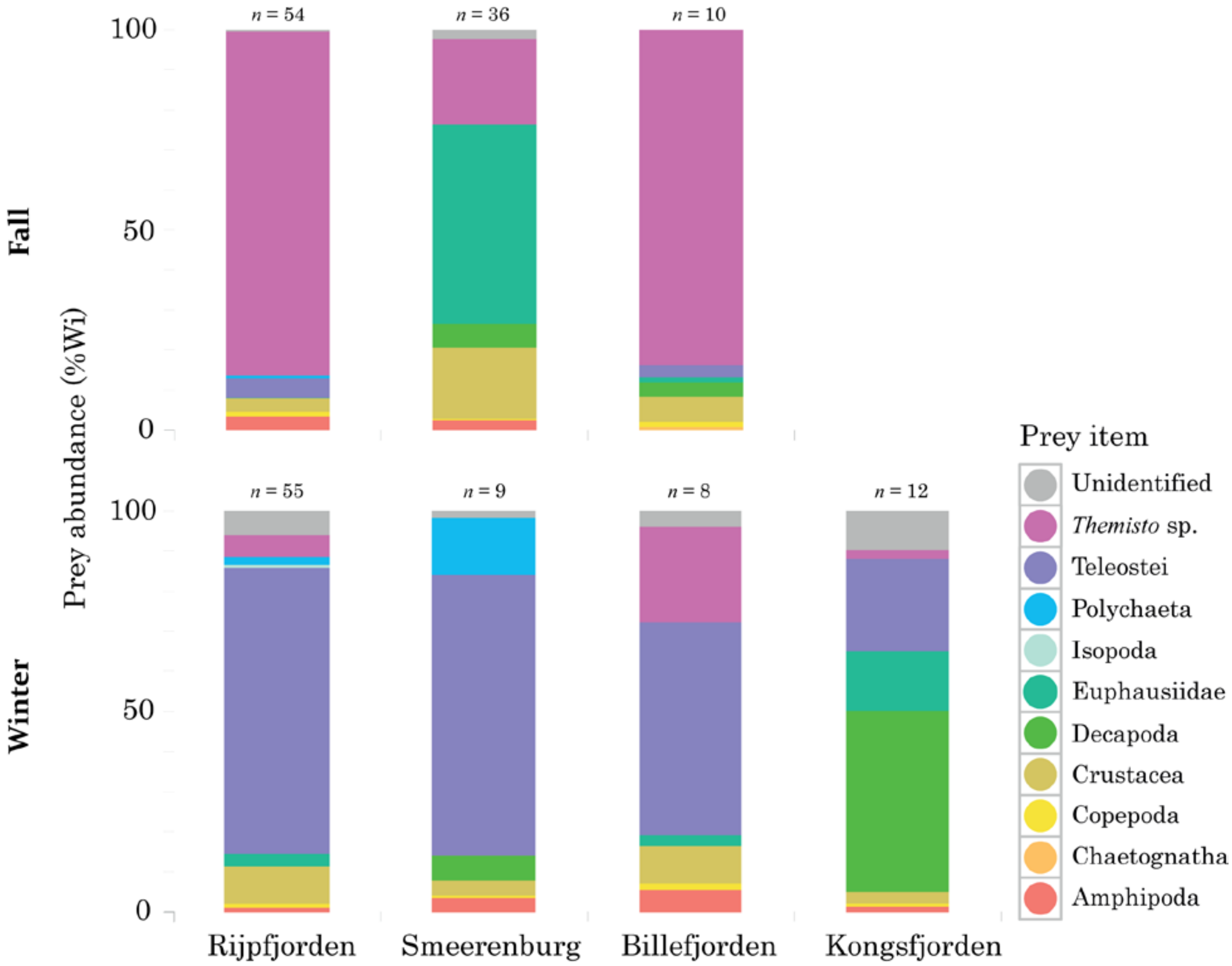


Fig. 8 Proportion of ingested prey based on percent prey weight (in grams) for different sites and seasons for polar cod >15 cm.

Table 4 Index of relative importance for each prey item, from adult polar cod of >15 cm in length caught during the fall, winter, and spring at given sites. (Appendix)

%IRI

Prey	**September - October**			**January**				**May**
	Rijpfjorden	Smeerenburg	Billefjorden	Rijpfjorden	Smeerenburg	Billefjorden	Kongsfjorden	Kongsfjorden
Amphipoda	3.16	0.91	0.00	0.25	2.18	5.85	0.85	0.00
Chaetognatha	0.00	0.00	0.04	0.00	0.00	0.00	0.00	35.94
Copepoda	4.17	7.56	4.53	40.30	14.08	30.52	17.04	0.00
Crustacea	0.62	23.39	1.81	5.66	7.16	1.83	3.50	44.08
Decapoda	0.00	0.25	0.32	0.00	2.78	0.00	8.66	19.98
Euphausiidae	0.02	37.00	0.81	1.00	0.00	2.26	52.81	0.00
Teleostei	0.26	0.00	0.78	44.03	62.97	28.55	5.33	0.00
Isopoda	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00
Mysida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.07	0.00	0.00	0.09	4.53	0.00	0.00	0.00
Themisto spp.	91.69	28.67	91.69	2.13	0.00	29.64	1.00	0.00
Unidentified	0.02	2.21	0.00	6.49	6.31	1.34	10.81	0.00

Table 5 Index of relative importance for each prey item from adult polar cod of 10-15 cm in length caught during the fall, winter, and spring at given sites. (Appendix)

%IRI

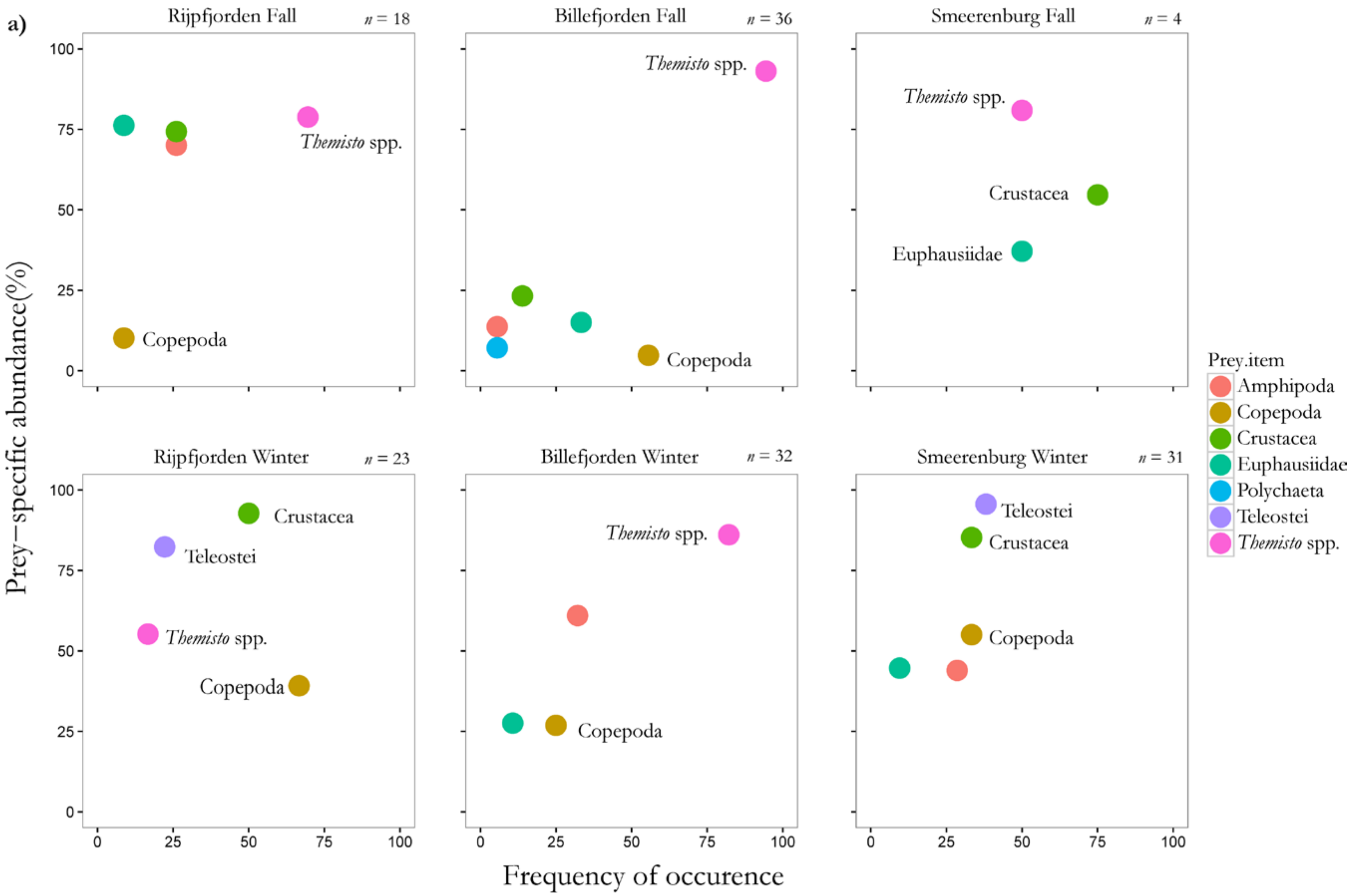
Prey	**September - October**			**January**				**May**	
	Rijpfjorden	Smeerenburg	Billefjorden	Rijpfjorden	Smeerenburg	Billefjorden	Kongsfjorden	Billefjorden	Kongsfjorden
Amphipoda	15.51	0.00	0.06	0.00	6.98	9.77	0.49	0.00	0.16
Chaetognatha	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	3.17	7.80	15.84	70.49	16.46	6.98	12.53	33.43	25.55
Crustacea	2.98	30.49	0.21	15.29	7.60	0.11	10.81	34.06	58.34
Decapoda	0.00	0.00	0.00	2.85	0.35	0.00	0.00	0.19	3.82
Euphausiidae	0.46	13.55	1.34	0.00	0.61	0.55	71.60	31.85	1.82
Teleostei	0.00	0.00	0.06	7.66	57.32	0.00	0.00	0.47	0.00
Isopoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mysida	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.00	5.17
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.07	0.00	0.04	0.00	0.00	0.00	0.03	0.00	0.00
Themisto spp.	77.82	48.16	82.43	3.53	0.24	82.40	0.00	0.00	0.00
Unidentified	0.00	0.00	0.00	0.17	10.44	0.18	4.53	0.00	5.14

3.5. Feeding strategies among sites, seasons, and polar cod size classes

Generally, both size category individuals had a narrow niche width in September-October (Table 6) particularly in Arctic fjords with a temporal population specialization on *Themisto* spp (Fig. 9). In the Atlantic influenced fjord of Smeerenburg, euphausiid prey were relatively important in the diet of polar cod (Table 4 & 5) with individual specialization shared between euphausiids and *Themisto* spp (Fig. 9). The positioning of other prey points in the lower left of the diagram indicates prey that occurred occasionally in the diet and that are representative of a generalist diet. Thus, copepods were eaten occasionally in all sites and always had a low prey-specific abundance indicating that this prey species was consumed in response to a more generalist feeding strategy. The feeding strategy switched from a population specialization in the fall to more of an individual specialization in the winter month of January with a contrasting emphasis on teleostei, particularly exacerbated for the larger size category (Fig. 9b). In the winter, Billefjorden retained a high population specialization on *Themisto* spp. for both size categories (Fig. 9). Broader categories such as crustacean and amphipods are hard to interpret as they could be digested copepods, euphausiids, *Themisto* spp., or other prey taxa.

Table 6 Species richness and dietary niche width calculated with Shannon-Wiener diversity index separated for size classes, seasons, and sites.

Size	Season	Site	S	H'
10-15 cm	September	Rijpfjorden	6	0.73
		Smeerenburg	4	1.18
		Billefjorden	9	0.54
	January	Rijpfjorden	7	0.96
		Smeerenburg	8	1.30
		Billefjorden	6	0.62
		Kongsfjorden	7	0.91
	May	Billefjorden	5	1.13
		Kongsfjorden	7	1.18
> 15 cm	September	Rijpfjorden	8	0.38
		Smeerenburg	7	1.40
		Billefjorden	7	0.39
	January	Rijpfjorden	9	1.22
		Smeerenburg	7	1.25
		Billefjorden	7	1.46
		Kongsfjorden	8	1.45
	May	Kongsfjorden	3	1.05


a)
Rijpfjorden Fall
n = 18
Billefjorden Fall
n = 36
Smeerenburg Fall
n = 4
Rijpfjorden Winter
n = 23
Billefjorden Winter
n = 32
Smeerenburg Winter
n = 31
Prey−specific abundance(%)
Frequency of occurence
0
25
50
75
100
Themisto spp.
Copepoda
Crustacea
Euphausiidae
Teleostei
Prey.item
Amphipoda
Copepoda
Crustacea
Euphausiidae
Polychaeta
Teleostei
Themisto spp.

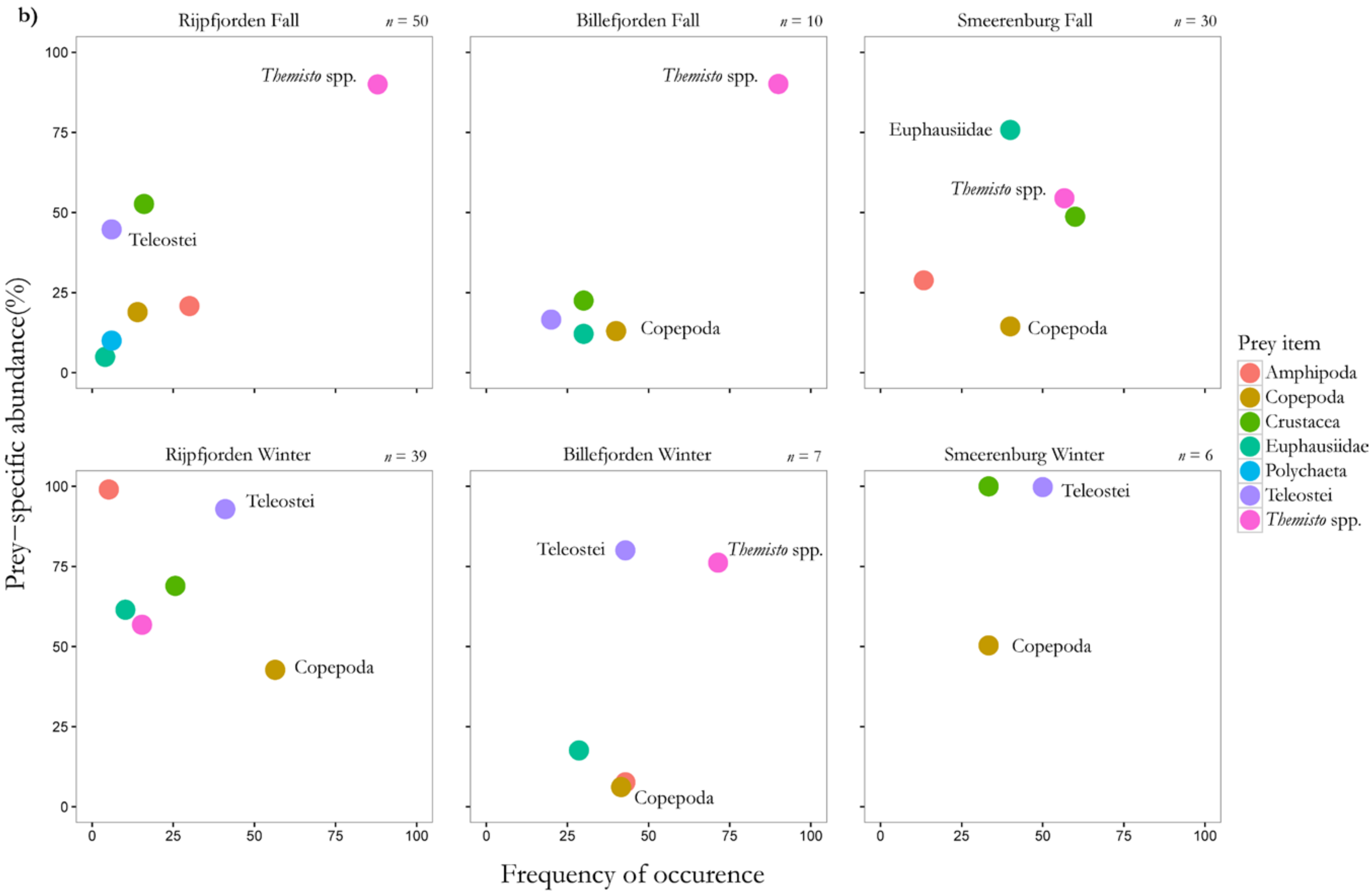


Fig. 9 Prey-specific abundance in percentage (Pi) versus frequency of occurrence in percentage (FO) for (a) polar cod from 10 to 15 cm and (b) polar cod over 15 cm.

4

DISCUSSION

Before the environmental changes brought by a rapidly warming climate, endemic Arctic species are likely to face what has sometimes been referred to as the "Arctic squeeze" (Baltensperger & Huettmann, 2015). This phenomenon can be described as a gradual loss of climatically suitable habitat for high latitude endemic species whereby boreal species will expand northward, and Arctic species will see their distribution potential constrained by latitude. Thus, the vulnerability of endemic Arctic species to stressful factors brought by climate change will depend on their phenotypic plasticity and on their ability to undergo evolutionary adaptation (Hoffmann & Sgro, 2011). Dietary plasticity and trophic adaptability are likely to be important determinants in safeguarding successful adaptation to changes in community composition and the resulting unstable trophic dynamic that may be brought upon Arctic food webs by climate change. If species believed to be ecologically important such as the polar cod are unable to cope with disruptions in prey phenology and in seasonal prey distribution, they may be more vulnerable to intermittent interspecific competition and predation from sub-arctic species. Thus, the main goal of this study was to determine polar cod seasonal ingested prey composition and feeding strategy in Svalbard fjords deemed "Atlantic" and "Arctic". Here I described specialist and generalist feeding strategies as temporal events operating on a continuum, and I defined the opportunistic feeding strategy as the ability of an organism to switch from its usual diet to another temporarily more convenient diet. In comparing diet from September-October, January, and May, I observed that polar cod diet varied seasonally and though it was quite diverse, I noted a strong predation over *Themisto* spp. in the fall for both size categories (10-15 cm and >15 cm) that was particularly pronounced for Arctic domains (i.e. Rijpfjorden and Billefjorden). In contrast, I noted a strong predation on teleostei (hereafter fish prey) in January particularly for polar cod over 15 cm (hereafter larger polar cod) for both Atlantic and Arctic domains. In accordance with methods proposed by Amundsen et al. (1996), there was a strong seasonal population specialization for *Themisto* spp. in the fall for both size categories and an individual specialization on fish prey in January.

4.1. Seasonal feeding success

Seasonal stomach fullness may reflect seasonal changes in feeding activity or in feeding success (Hyslop, 1980) and this information can be used to make inferences about the factors that are responsible for seasonal changes in feeding behavior. I hypothesized that stomach fullness would vary seasonally and would be lower during the polar night. Based on my assessment of feeding success, I observed that polar cod from both size categories are more likely to have a full stomach (full: 4-5) in the fall than in the spring or winter. The probability of a polar cod to have an empty (full: 0) or nearly empty stomach (full: 1-2) is much higher in the winter than it is in the fall. Though the feeding success of another gadoid, the subArctic Atlantic cod (*Gadus morhua*), does not seem to be affected by seasonality (Hop et al., 1992) even at high latitudes (Eglund Newby, 2015), the present study reveals that stomach fullness of polar cod varies both with season and with location. Indeed, stomach fullness counts illustrate a striking difference in fullness in the winter depending on the site with higher counts of high fullness in Billefjorden and higher counts of low fullness in Rijpfjorden (Fig. B2 in Appendix B). In the following section, possible causes for lower fullness and fullness heterogeneity in the winter are addressed with a focus on prey abundance and reproduction.

Local prey availability and patchiness is believed to explain seasonal, geographical, and depth-related variability in polar cod diet (Renaud et al., 2012). Thus, the extent to which polar cod have fed successfully could be the product of seasonal prey availability. Mesozooplankton prey availability fluctuates seasonally with a marked mortality in January (Daase et al., 2014). The importance of mesozooplankton carcasses in nets during the winter could be tied to a variety of factors including low productivity and reproductive phenology (Daase et al., 2014). Though their abundance decreases during the polar night, mesozooplankton remain active in the water column in Atlantic (Berge et al., 2015) and Arctic (Błachowiak-Samołyk, 2015) domains. Research on the abundance and distribution of macrozooplankton during the winter months remains elusive but we know that their abundance and biomass does not change significantly between the end of the winter and the spring (Søreide et al., 2003). No study points towards an important decline of both overall mesozooplankton and overall macrozooplankton taxa, and unless such decline occurs, some prey taxa should remain sufficiently abundant to provide food for an opportunistic feeder such as polar cod (Bradstreet et al., 1986; Ajiad & Gjøsæter, 1990; Christiansen et al., 2012). If polar cod is truly opportunistic, one would expect a shift in diet that would secure feeding success throughout seasons. Instead, disparity in fullness between locations is observed and is difficult to explain in the light of overall prey availability. Acoustic methods conducted in January 2016 by the trawling locations revealed a similar backscatter in two Arctic domains (personal communication with M. Geoffroy; Fig. C1 in Appendix C) and both fjords appeared to hold potential prey, yet fullness proportions were different. This illustrates the need to examine the abundance of each prey taxa individually if inferences about feeding success are to be made.

A likely factor influencing polar cod foraging success is polar cod reproductive phenology. Polar cod is an iteroparous breeder (Graham & Hop, 1995), which is reported to reproduce commonly between November and March in the Barents Sea (Nahrgang et al., 2016). The fall is an important season for energy storage prior to gonadal maturation and the energy invested by polar cod into reproduction is important as the fish loses about 50% of its body mass to reproduction (Hop et al., 1995). This phenomenon is particularly striking in Arctic domains where the energy reserve as illustrated by the HSI is significantly lower in January than it is in September and October (Fig. D2 in Appendix D). Different seasonal energy requirements could therefore perhaps explain higher fullness in the fall and lower fullness in the winter. Moreover, the mature gonads occupy a substantial amount of space in polar cod body cavity possibly reducing the available space for stomach swelling due to prey ingestion (Hop et al., 1995). Polar cod are not observed to fast during reproduction, and though they may feed in lesser quantities prior to spawning, they continue to feed actively until and right after spawning (Graham & Hop, 1995). Some of the variation in polar cod stomach fullness might be explained by the level of maturation and contrasting seasonal energy requirements though this does not seem to explain spatial variability in fullness within the winter month of January (i.e. similar levels of maturation and different fullness between sites – Fig. D1 in Appendix D).

No one factor mentioned above seems to fully explain the variability in stomach fullness among seasons and among sites. Visual constraints induced by low irradiance levels during the polar night have also been suspected to affect feeding success of visual predators (Kaartvedt 2008) though studies have led to the conclusion that many Arctic and subArctic or boreal fish species continue to feed throughout the winter (Eglund Newby, 2015; Berge et al., 2015). The role of light in marine fish foraging ecology at high latitudes has only recently begun to be the focus of studies and remains elusive, ergo I will return to this topic to address both feeding success and foraging strategy in later paragraphs.

4.2. Seasonal prey composition and the effect of prey availability on polar cod diet

The present study confirms the hypothesis that ingested prey taxa composition changes seasonally as is commonly observed in seasonal fish diet studies (Greenstreet et al., 1998; Schafer et al., 2002). The majority of polar cod diet studies refer to this species as being opportunistic (Ajiad & Gjøsæter, 1990; Christiansen et al., 2012; Walkusz et al., 2013; Majewski et al., 2016) and recent literature reviews have described it as a zooplankton generalist (Renaud et al., 2012; Mueter et al., 2016). If this is the case, it should be expected that polar cod diet fluctuates in concordance with prey availability in the water column. Here, I reviewed some of the literature and unpublished data on prey abundance as an attempt to discern if the observed changes in diet could have been driven by prey availability. In order to interpret the results, I deemed it necessary to provide some background information on the most frequently consumed prey.

4.2.1. The case of *Themisto libellula*

4.2.1.1. Background of an ingested prey - *Themisto libellula*

Themisto libellula is a pelagic amphipod that is more readily available in Arctic domains rather than in Atlantic domains (Dunbar, 1957; Kraft et al., 2013) and which accounts for most of the *Themisto* spp. found in the guts of Arctic domain polar cod. The life-span of *T. libellula* varies between a year to two years depending on location and this species was described as being semelparous, dying off right after reproduction (Wing, 1976). Important variations seem to exist in population abundances throughout the water column. In Frobisher Bay, Canada, Percy (1993) noted that the population sampled in the upper 30 meters of the water column displayed a peak in abundance in late August and an abundance minimum in the mid-winter. It was suggested that a descent towards deeper layers during the fall and winter could explain such variation in abundance (Wing, 1976) though *T. libellula* seem to remain active throughout the winter (Kraft et al., 2013). The small size of the subArctic-boreal species *T. abyssorum* and its smaller content of wax ester compared to its Arctic congener *T.*

libellula (Kraft et al., 2013) potentially makes it a prey of lesser value which could explain the less pronounced population specialization on *T. abyssorum* observed in the present study. Majewski et al. (2016) did note the prevalence of *T. abyssorum* in polar cod guts though with somewhat limited importance compared to that of *T. libellula*, and concluded that both *Themisto* spp. are key prey taxa in polar cod diet. *T. libellula* is frequently reported in polar cod diet (Lønne & Gulliksen, 1989; Ajiad & Gjøsaeter, 1990; Renaud et al., 2012; Walkusz et al., 2013; Majewski et al., 2016) and the extent to which it is actually considered an important prey item varies. Some discrepancies have been recognized regarding the importance of *T. libellula* in polar cod when comparing stomach content analysis with carbon isotope analysis, the latter revealing the importance of *T. libellula* in polar cod diet despite their absence in stomach content analysis (Matley et al., 2013).

4.2.1.2. Availability of *Themisto libellula* and polar cod diet

In September and October, when polar cod's feeding success was at its highest compared to May and January, feeding strategy was spatially distinct with the population adopting a specialist feeding mode on *T. libellula* in Arctic domains and an individual specialist strategy on euphausiids and *T. abyssorum* in Atlantic domains. These results are in concordance with observations from Nahrgang et al. (2014) who observed high frequency of occurrence of *T. libellula* in Arctic domains and higher prey diversity in Atlantic domains. This is further illustrated by the present study which exposes a narrow dietary niche width in Arctic domains and a wider dietary niche width in the Atlantic domain. According to the optimal foraging theory, feeding strategy becomes specialized when resources are abundant (MacArthur & Pianka, 1966), thereupon, polar cod from Arctic domains could be responding to an increased abundance of prey types in the fall by temporarily specializing on *Themisto* spp.

The lack of systematic simultaneous zooplankton sampling impedes on the interpretation of the results. As part of the AB320 course offered by the University Centre in Svalbard, zooplankton data were collected in the fall 2014 at Rijpfjorden, and allowed for an observation of macrozooplankton abundance and biomass. In Rijpfjorden during the fall 2014, the Arctic associated amphipod *T. libellula* were abundant in the water column both at night and during the day along with other potential prey such as euphausiids and the boreal associated amphipod *T. abyssorum* (Fig. C2 in Appendix C). A high abundance of potential prey in the pelagic zone was also recorded in Billefjorden in early October, when euphausiids were caught in great numbers (>90,000) along with *T. libellula*, juvenile *Leptoclinus* spp., and juvenile polar cod (<6 cm) using a single pelagic trawl (personal observations). The absence of either *Themisto* spp. or euphausiids in the epibenthic sled (EBS) performed in Rijpfjorden both at night and during the day at 200 meters depth (personal observations; unpublished data from the AB320 cruise report) could be an artefact of the EBS sampling itself (time of sampling, net avoidance, invertebrate patchiness, etc…) or could reflect the absence of these taxa in the demersal zone. These results are supported by Percy (1993) and could indicate that polar cod caught in the bottom trawl and feeding on *T. libellula* ventured in the pelagic zone to forage. This is in concordance with observations from Geoffroy et al. (2016) who noted that the important size-based niche partitioning occurring between February and September tempers down in September when large polar cod start ascending up in the mesopelagic layer possibly as a response to declining irradiance. This behavior is believed to be caused by predation pressure and occurs throughout the Arctic (Geoffroy et al., 2016; Benoit et al., 2010). Larger vertebrate species mainly piscivorous seabirds and marine mammals feed extensively on polar cod (Welch et al, 1993; Weslawski et al. 1994). Ringed seal (*Phoca hispida*), an important polar cod predator, is widely distributed around Svalbard (Lydersen, 1998; Reeves, 1998; Labansen et al., 2007). Predation pressure could therefore induce settling of large polar cod in the demersal zone and restrict their diet to a limited number of prey type until the fall when the light conditions become darker and more favourable for predator avoidance in the pelagic zone.

Polar cod seem to selectively forage on *T. libellula* when this prey is abundant in the fall in Svalbard Arctic domains and will dismiss other abundant potential prey in favour of this pelagic amphipod. The temporal specialization of polar cod, whether it be an individual or a population specialization, could potentially follow a ranked prey preference where, if one prey type is absent or present in very low abundance, the predators will redirect their specialization towards another prey type. Though such assumption cannot be validated here, they have been observed on a limited number of specimen by Hop and colleagues (personal communication with H. Hop) who noted that polar cod had a preference for *T. libellula* over large *Calanus* spp. which was itself preferred over small *Mysis* sp. The results from the present study confirm the optimal foraging theory whereby, if prey taxa are abundant, predators will display preferences for and specialize on a superior prey type (Murdoch, 1969). However, in order to encounter high abundance of potential prey, polar cod may ostensibly have to move up the water column.

4.2.2. The case of Teleostei

4.2.2.1. Background of ingested prey – Teleostei

Juvenile of three fish prey taxa were identified in polar cod stomachs: *sebastes* sp. (hereafter redfish), *leptoclinus* sp., and polar cod. Juvenile redfish are extremely difficult to identify to species level (Wienerroither et al., 2011) and, based on their distribution, could have been juvenile of *Sebastes marinus* or *Sebastes mentella*. I therefore refer to either one of these two species when talking about juvenile redfish. These species of *Sebastes* are long lived, can reach the age of 75 years old, and begin to be sexually mature at 11 years old. Their recruitment varies importantly between years and is episodic (once every 5 to 30 years) (COSEWIC, 2010). Whereas the year 2013 had very low abundance of 0-group redfish, the year 2014 and 2015 mark the strongest recruitment years of *Sebastes mentella* since 2008 in the western Barents sea (Eriksen et al., 2014). Redfish are usually described as pelagic to benthopelagic (Wienerroither et al., 2011) and 0-year group are often found in deep areas (Eriksen et al., 2014).

Leptoclinus maculatus is a typical Arctic species and can occur in sub-zero degree Celsius waters. It has a lipid sac that is believed to be a particularly important energy storage for winter conditions (Falk-Petersen et al., 1986b). It's body flesh is also high in lipid content (40% of dry weight) (Falk-Petersen et al., 1986b). *L. maculatus* has previously been stated as being an important prey items for polar cod though the data was not published (Ottesen et al., 2011). This potential polar cod prey is a demersal species though postlarval juvenile occur in the pelagic zone and begin to descend at depth between age 2-5 before they reach maturity.

Polar cod hatching is influenced by environmental conditions and occurs between January and July (Bouchard & Fortier, 2011). Juvenile polar cod are often associated with sea ice and occur in cryo-pelagic habitats. They turn form a larval stage to a juvenile pelagic stage at 27-35 mm in the month of August (Ponomarenko, 2000). For the last several years, recruitment of polar cod in Svalbard has been quite low and this is associated to unfavorable living conditions or reduced spawning compared to the 1980s and the 1990s (Eriksen et al., 2014; Prokhorova et al., 2015).

4.2.2.2. Availability of Telostei and polar cod diet

Polar cod are typically described as zooplankton consumers (Renaud et al., 2012; but see Rand et al., 2013) and fish prey are rarely reported in diet studies but when they are, they often account for an important proportion of the diet in terms of weight (Rand et al., 2013). In the present study, and in contrast to the fall diet, some strong individual specialization on fish prey was observed in January in Rijpfjorden, Billefjorden, and Smeerenburg with a remaining population specialisation on *T. libellula* in Billefjorden. The general niche theory predicts that individual specialization will happen when food resources are low and intra-specific competition triggers stronger niche partitioning (Amundsen, 1995). Therefore, the phenomenon observed in the present study could be a functional response to lower abundance of preferred prey in the winter. Unfortunately, macrozooplankton data is not available for January 2016 but available fish prey data can be extracted from the trawl community composition (See Appendix D for details on the methods). The high recruitment of redfish in August 2015 (Prokhorova et al., 2015) and their strong association with the month of January in demersal trawls (Fig. D4 in Appendix D) presumably explain part of the diet of polar cod in the winter. That being said, the absence of ingested fish prey in the fall and the presence of several ingested fish species in the winter suggest that the January fish oriented diet cannot solely be attributed to a higher abundance of juvenile redfish, but also to additional factors favoring individual specialization on fish prey in the winter. One of these factors could be the effect of extreme seasonal light regime on the selective ability of polar cod and is addressed in a later paragraph.

Notwithstanding these observations on a fish prey oriented winter diet, diet partitioning occurred in Rijpfjorden between pelagic caught specimen and similar size demersal caught specimen (personal observations) with a smaller proportion of fish prey and a larger proportion of *T. libellula* prey in pelagic specimen. Similar observations between a demersal diet oriented on fish and a pelagic diet oriented on euphausiids were noted by Rand et al. (2013) in August in the Beaufort sea. Likewise, in a study conducted in January 2014 in Kongsfjorden, Eglund Newby (2015) observed a 24% frequency of occurrence of fish prey in the guts of demersal caught polar cod compared to no occurrence of fish prey in the guts of pelagic caught polar cod. The author observed that the main fish prey consumed by polar cod were *L. maculatus*, which could indicate that demersal caught polar cod had fed in the demersal zone. Though movement between habitats likely occurs and diet may overlap between pelagic caught specimen and demersal caught specimen (Renaud et al., 2012), results from these studies and from the present study point toward exacerbated dietary niche partitioning of similar size polar cod in the winter. In Rijpfjorden, the lower contribution by weight of *T. libellula* in stomachs of pelagic specimen when compared to the fall suggests a lower abundance of that preferred prey in the pelagic zone in January. As proposed by the general niche theory, lower abundance of superior prey items in the pelagic zone may have prompted obligate intra-specific food partitioning and individual specialization. Therefore, it is possible that the ascent of the larger polar cod in the mesopelagic zone in the fall (Geoffroy et al., 2016) is not uniform throughout the population in the winter months due to intra-specific competition.

In Billefjorden, diet partitioning seemingly occurred in the winter but between demersal caught specimen of different size categories, with smaller polar cod feeding practically solely on *T. libellula*, and larger polar cod feeding predominantly on both *T. libellula* and fish prey. Size-based food partitioning is commonly reported in the fish literature (Gerking, 1994b) though the extent of diet overlap may vary seasonally (Sandheinrich & Hubert, 1984). Physiological limitations due to predator size could affect the ability of smaller polar cod to forage on fish prey (Ajiad and Gjøsæter 1990; Wainwright & Richard, 1995; Dalpadado et al., 2009) and could account for the individual specialization leaning towards a population specialization on fish prey among the larger size class. If this held true, these physiological limitations should hinder the ability of smaller polar cod to feed on fish prey at all sites, which is not the case. Therefore, the observed size-based food partitioning in Billefjorden seems more likely to be a response of lower abundance of the preferred prey *T. libellula* though it is not excluded that limitations induced by size affect the frequency of occurrence of ingested fish prey throughout sites. Such partitioning induces that smaller polar cod fed in the mesopelagic layer and moved between habitats.

The absence of fish prey in polar cod stomachs from Rijpfjorden in January 2013 and the predominance of ingested *T. libellula* (personal communication with J. Berge) in a year of low redfish recruitment (Eriksen et al., 2014) and despite a low abundance of *T. libellula* (personal communication with J. Cornelius Grenvald) suggest active selection towards larger prey (size-biased feeding; Gerking, 1994c) even if abundances of larger prey are low. The predominance of fish in the diet in January 2016 is likely related to the high recruitment of redfish and suggest that polar cod have a flexible diet and are capable of taking advantage of temporarily abundant resources.

4.2.3. The case of copepod

Copepod prey are frequently reported in polar cod diet studies (Renaud et al., 2012) and they have been described by Majewski and colleagues (2016) as a key prey species in the Canadian Beaufort Sea. Their importance in polar cod diet depends on predator size (Renaud et al., 2012) and varies greatly depending on whether the authors focused on gravimetric or numerical methods. Here I observe that in adult polar cod the importance of copepod was not a function of predator size, and that though copepod were relatively important in terms of numbers, they were much less important in terms of weight. Numerical methods have been criticized mainly as they increase the risk of overestimating the importance of small prey such as copepods (Hyslop, 1980) though they are perhaps best suited than a gravimetric method when attempting to estimate foraging effort (Ball, 1961). The results from the present study indicate that copepod are frequently present in the diet of polar cod but represent a small proportion of the total bulk of prey-specific stomach content and that their presence in polar cod guts illustrates a generalized feeding strategy on these prey. Though the lipid rich calanoid copepod represent a high energy source for predators (Scott et al., 2000), they seem particularly important for the metabolic development of juvenile polar cod (Hop et al., 1997) and are not specialized on by adult polar cod if larger prey are available. These observations once more confirm the optimal foraging theory according to which size-biased feeding is more advantageous for visual particulate feeding predators (Gerking, 1994c). The relative unimportance in terms of weight of copepod throughout seasons and sites in Svalbard suggests that the shift in abundance of more lipid rich Arctic species in Arctic domains to a more lipid poor Atlantic species such as *C. finmarchicus* in Atlantic domain will have little repercussions on adult polar cod.

4.3. Seasonality and polar cod temporal feeding strategy: light as a determining factor

The previous chapters have illustrated that in Arctic domains, polar cod undergo a drastic shift in feeding strategies between the fall and the winter, switching from an important population specialization on *T. libellula* in the fall to an individual specialization in the winter. Based on information regarding prey availability, it seems fair to assume that adult polar cod feed selectively on *T. libellula* though it should be emphasized that these remain mere speculations. In the winter, a more diverse diet and a shift to individual specialization illustrate that polar cod display the capacity to forage year round (Graham & Hop, 1995) and that some external environmental factors must dictate their feeding behavior. One of these factors is undoubtedly the variation in prey availability as discussed above. The morphology of polar cod (Wainwright & Richard, 1995; personal observations) along with its ability to behave as a size-biased specialist feeder on zooplankton as proposed by this study suggest that this species uses particulate suction feeding as foraging means and thus vision plays an important role in the detection, pursuits, and capture of prey (Gerking, 1994c). The lack of solar illumination in the winter at high latitudes (Berge et al., 2015) could therefore play an important role in the foraging behavior of pelagic suction feeders such as polar cod and could explain specific adaptations to a low light environment (Jönsson et al., 2014).

The role of light in shaping fish sensory biology has often been the focus of deep-sea (Helfman et al., 2009a; Landgren et al., 2014) and Antarctic (Montgomery & Macdonal, 1998) research, but has rarely been at the center of fish foraging behavior in the Arctic. Just like the Antarctic however, the light regime at high latitudes hugely fluctuates with season (Clark et al., 2013) and the winter photic environment is exceptionally dark (Berge et al., 2015; Last et al., 2016). This has lead Kaartvedt (2008) to hypothesize that the northward expansion of mesopelagic fish will be hindered by extreme light regimes in the high Arctic. Notwithstanding this assumption, boreal fish species have been reported to forage successfully during the polar night at high latitudes (Berge et al., 2015; Eglund-Newby, 2015). Indeed, aside from using other senses such as tactioception and mechanoreception, visual feeders can forage in extremely dim environments (Warrent, 2004; Landgren et al., 2014). Thus, it is possible that, as for the krill species *Thysanoessa inermis* (Cohen et al., 2015), polar cod lens plasticity (Jönsson et al., 2014) and visual spectral sensitivity allows it to utilize the atmospheric light available in the epipelagic zone during the polar night. Furthermore, other light sources such as those provided by bioluminescent zooplankton may provide significant background illumination against which target prey may become visible (Nilsson et al., 2014). Therefore, the suggestion that polar cod feeding success could be heavily impaired by the local photic environment hardly prevails over the possibility that polar cod are capable of visually exploiting the low light levels of the polar night. It is possible however that, though polar cod feeding success might not be significantly affected by a low light environment, their selective ability might be impaired as important visual cues such as pigmentation (Gerking, 1994c) become harder to distinguish in dim light. Thus, larger prey species such as fish may cast a larger silhouette than typical zooplankton prey and may therefore be easier target for particulate predators which would explain the shift to a fish prey oriented diet in the winter. Interestingly, the presence of *T. libellula* in the stomach of polar cod from Billefjorden indicate an ability to feed on this pelagic amphipod at low light levels and lower latitudes in Svalbard. This could be done intermittently during the polar night when light levels become more elevated because of moonlight and clear sky or it could be the product of a more exploitable light environment at the these lower latitudes (Berge et al., 2015; Last et al., 2016; personal communication with J. Cohen).

If irradiance levels during the polar night indeed impair polar cod vision and prevents them from being selective, polar cod might adjust their foraging behavior to keep feeding successfully at low light levels. In fact, fish species for which vision is expected to be an important sense for feeding such as polar cod, may feed more successfully in the pelagic zone when light is available but may require other senses to orient themselves in space and feed successfully in a dark environment (Eiane et al. 1997; Helfman, 2009b). Some salmonids which are often thought of as pelagic visual predators can feed successfully in the dark when given access to a bottom surface (Jørgensen & Jobling, 1990). Like most gadoid, polar cod are equipped with a chin barbel which could, along with other sensory appendages enable it to forage successfully in the benthic zone when vision is severely impaired by low light levels. In fact, if this was the case, one would expect a decrease in pelagic feeding success (Jørgensen & Jobling, 1990) and an increase of ingested benthic prey under restricted light environments. We do not observe a clear shift in ingested species guild from pelagic in the fall to benthic in the winter though juvenile *Sebastes* and *L. maculatus* which are ingested at all sites in the winter could occur in the demersal zone, and copepod which are ingested more frequently in the winter may be overwintering at depth (Clarke et al., 2012; Darnis & Fortier, 2014; Berge et al., 2015) (Fig. B3 in Appendix B). Furthermore, there is an obvious decrease in the frequency of occurrence of the pelagic *T. libellula*, euphausiids, and *T. abyssorum* in the winter diet, and the presence of some hyperbenthic organisms such as *Lebbeus polaris*. Due to a lack of knowledge on the spatial segregation of species in the water column during the polar night, it remains difficult to assess whether polar cod fed in the demersal or pelagic zone in January. The apparent reduction of ingested pelagic prey however points toward the possibility that larger adult polar cod feed in the demersal zone during the polar night possibly using other senses than vision to forage. The hypothesis that polar cod have the ability to switch from a selective pelagic feeding in adequate light conditions to a demersal feeding mode in low light conditions should also be valid for near-glacier environments where visibility is severly decreased due to high sedimentation (Davies-

Colley, 2001). Results from Carbon-13 isotope analysis suggest that polar cod caught by a glacier had a more benthic diet than polar cod caught elsewhere (McGovern, 2016). Thus we cannot either confirm or dismiss, the possibility that polar cod use the bottom surface as a way to orient themselves in space and to forage during the polar night.

Though extreme seasonal light variations may not drastically affect foraging success, they are likely to have an effect on the selective ability of particulate predators. Several personal observations seem to confirm such statement. Indeed, the switch to an individual specialization on fish prey in the winter is not necessarily synonymous with individual preferences for fish but rather individual disparities in the ability to successfully forage on fish. This seems to be the case as polar cod rarely fed on more than a single fish, and if ingested, a fish prey would usually fill the entire stomach, accounting for most if not all of the fullness recorded for that particular stomach. The switch in diet and feeding strategy is likely due to a combination of factors amongst which the variability in prey abundance and in the light regime seem critical.

4.4. Implications in the context of a warming climate

The North Atlantic Current is responsible for carrying warm saline Atlantic Water (AW) in the Arctic Ocean through the Fram strait and since the beginning of the 20th century both the water temperature and the inflow of warm water of AW have increased (Spielhagen et al., 2011). Evidences suggest that polar cod might have expanded their range southward in colder eras (Christiansen & Fevolden, 2000) whereas they are now displaced northwards in Greenland waters (Drost et al., 2014). Polar cod is a eurythermal species capable of withstanding a wide range of temperature variations, and changes in temperature are therefore unlikely to be the sole factors determining their distribution and fitness (Drost et al., 2014). Variations in water temperatures will however have an important impact on species assemblages (Murawski, 1993). Climate change induced changes in the abundance and distribution of copepod (Daase et al., 2013) and other pelagic zooplankton favoring the establishment of smaller plankton species in the Arctic Ocean (Pomerleau et al., 2014) are often stated as factors that will have an impact on polar cod foraging and competitive ability (McNicholl et al., 2016). Indeed, the displacement of large copepod to the profit of smaller species will likely be in the disfavor of juvenile planktonic polar cod and will benefit expanding competitive species (Falardeau et al., 2014). This study suggests however that adult polar cod will not specialize on copepod prey if larger prey are available. The effects of changes in prey availability on adult polar cod remain elusive, and though it was argued that prey associated with Atlantic domains may represent an energetic drop for polar cod (Nahrgang et al., 2014), this was never directly measured. Based on diet overlap of adult specimen, studies have argued that sub-Arctic species such as Capelin (*Mallotus villosus*) may exacerbate inter-specific competition with polar cod (McNicholl et al., 2016) and will displace them in the future (Hop & Gjøsæter, 2013). Despite potential overlap in prey species, polar cod plastic diet and size-biased particulate feeding suggests that this predator is capable of switching dietary niches in the face of competition or predation. That being said, polar cod display a marked preference for specific larger Arctic preys in adopting a population dietary specialization. The larger niche width and the less exacerbated population specialization in Atlantic domains indicate that no one-prey taxa is favored over others in these warmer waters. Therefore, polar cod preference for *T. libellula* might be an adaptation to Arctic domains and might be an illustration of optimal foraging conditions for this predator.

4.5. Personal reflections

The seasonal aspect of this project has been a real challenge to overcome. I would not have been able to answer any of the questions that I presented here if it wasn't for the five cruises that I boarded and particularly for the last one in January 2016 that enabled me to get samples from Rijpfjorden, Billefjorden, and Smeerenburg in the winter. Unfortunately, Rijpfjorden is unaccessible in May because of sea ice conditions which impede on a seasonality study for this fjord. In May 2016, I had the chance to board the Helmer Hanssen once more and to collect data from Smeerenburg and Billefjorden but, for obvious time constraints, these data were not incorporated in this thesis. The polar cod population of Kongsfjorden has been unstable and patchy and thus, it has been extremely difficult to obtain seasonal diet data from adult specimen in this location. The very nature of such seasonal study assumes regular sampling at a given site. However, due to the isolation factor and associated expenses, this remains difficult to achieve and therefore, such studies will likely continue to be conducted opportunistically.

As this study moved forward, it became clear to me that it would be challenging to go beyond a mere descriptive study unless I had data on prey availability. The vast majority of polar cod diet studies are based on stomach content analysis and in order to move forward in our understanding of ecological systems, diet analysis should systematically be conducted alongside zooplankton community studies. Therefore, if time allowed, this study would have greatly benefited from regular macro- and meso-zooplankton sampling using Methot Isaac Kidd (MIK) and Working Party No 2 (WP2) nets, as well as an Epibenthic sledge (EBS). Fortunately, I was able to retrieve some macro-zooplankton data from colleagues which allowed for some extrapolation of the results.

A topic that has sprouted my curiosity in the process of writing this thesis and that was addressed in the Discussion concerns visual constraints during the polar night. A growing body of literature bases itself on the assumption that low irradiance levels might impede on the foraging efficacy of fish at high latitudes, yet little is known about light detection abilities of these organisms. The present study demonstrates that polar cod are feeding during the polar night but the drastic changes in diet and feeding strategies raise questions regarding their ability to use the ambient light to forage. Experiments are being conducted by Jonathan Cohen from the University of Delaware on the spectral sensitivity of krill and such knowledge on polar cod would be an important step towards understanding the factors that may have an impact on polar cod seasonal diet.

4.6. Conclusion

Polar cod, an endemic Arctic fish species and key link in the Arctic trophic food web is often referred to as generalist and an opportunist plankton feeder. Here, I wanted to see whether this definition holds true on a seasonal basis and wanted to elaborate on the possible causes for the observed results. I first observed a significant difference in seasonal stomach fullness with a higher probability of empty stomachs in the winter and a higher probability of full stomachs in the fall which suggests that polar cod temporal feeding intensity is affected by some physiological or environmental factor. Here, I assumed that this disparity in fullness was likely related to reproductive phenology and energetic requirements though this is merely a speculation. Secondly, I noted a significant seasonal difference in diet taxa assemblages with between-sites diet from a single season having an important level of similarity which suggests that polar cod diet is not seasonally homogeneous. Thirdly, I observed that polar cod diet was composed mainly of pelagic zooplankton in the fall (*T. libellula* in Arctic domains, and euphausiids and *T. abyssorum* in the Atlantic domain) and of a combination of pelagic and demersal prey in the winter with a large proportion of fish prey at all sites which confirms that polar cod diet is seasonally plastic. Finally, I observed an important population specialization of adult polar on *T. libellula* in the fall in Arctic domains despite the presence of other prey taxa in the water column which suggests a strong preference for this prey and movement of larger polar cod up in the mesopelagic zone. The individual specialization on fish prey in the winter is likely a function of high recruitment rate of redfish, size-biased feeding, and visual constraints making larger prey a more visible target. These results underline the potential seasonal importance of fish prey in the diet of polar cod. Polar cod are opportunists in that they are capable of switching from one diet type to another and in that their feeding strategy is seasonally plastic. The importance of defining terms such as opportunism and generalism is highlighted here however since, though polar cod can be considered opportunists, this study disproves the assumption that they are zooplankton generalists. In fact, this study illustrates the propensity of polar cod to adopt a specialist strategy whether it be at the population level or the individual level.

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Appendices

Appendix A: An elaboration on methods

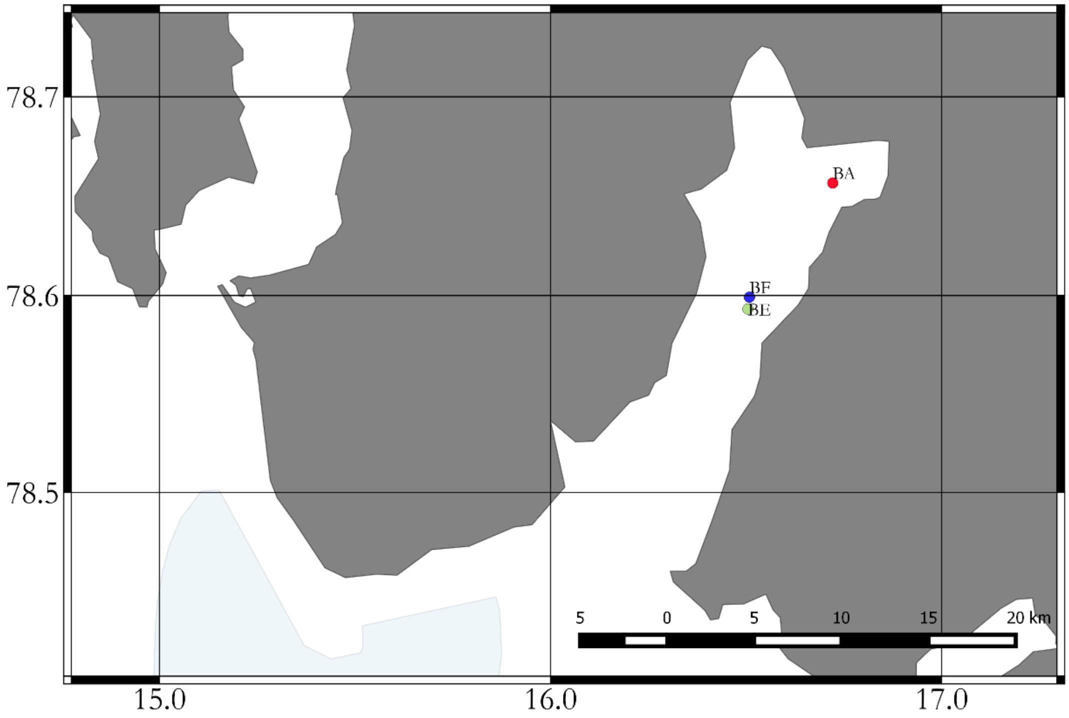


Fig. A1 Sampling sites in Billefjorden. Blue dots represent samples taken in January, red dots represent sites taken in September and October, and green dots represent samples taken in May.

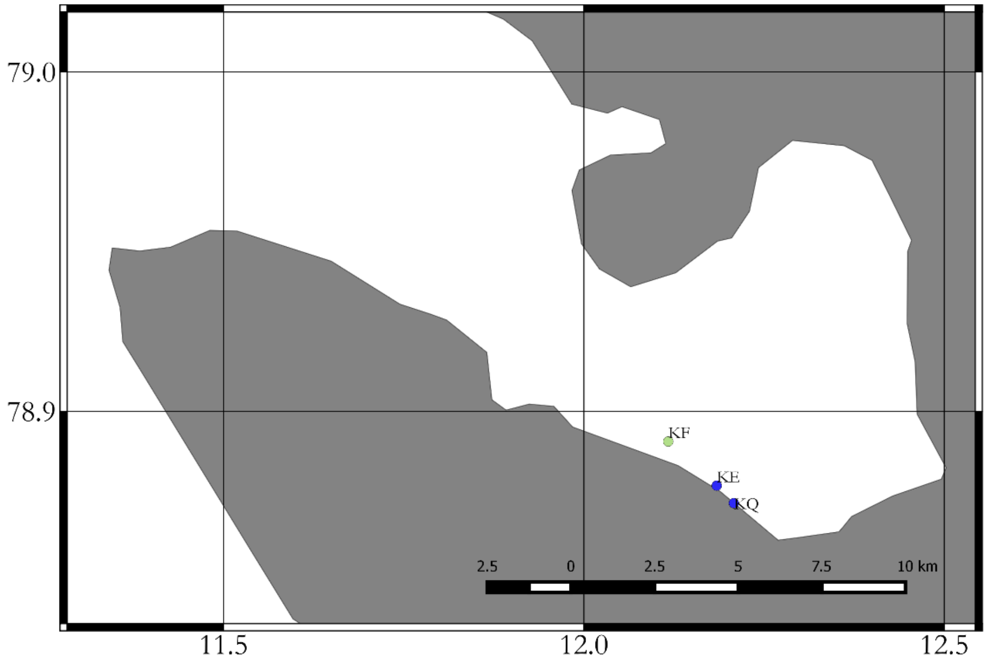


Fig. A2 Sampling sites in Kongsfjorden. Blue dots represent samples taken in January, red dots represent sites taken in September and October, and green dots represent samples taken in May.

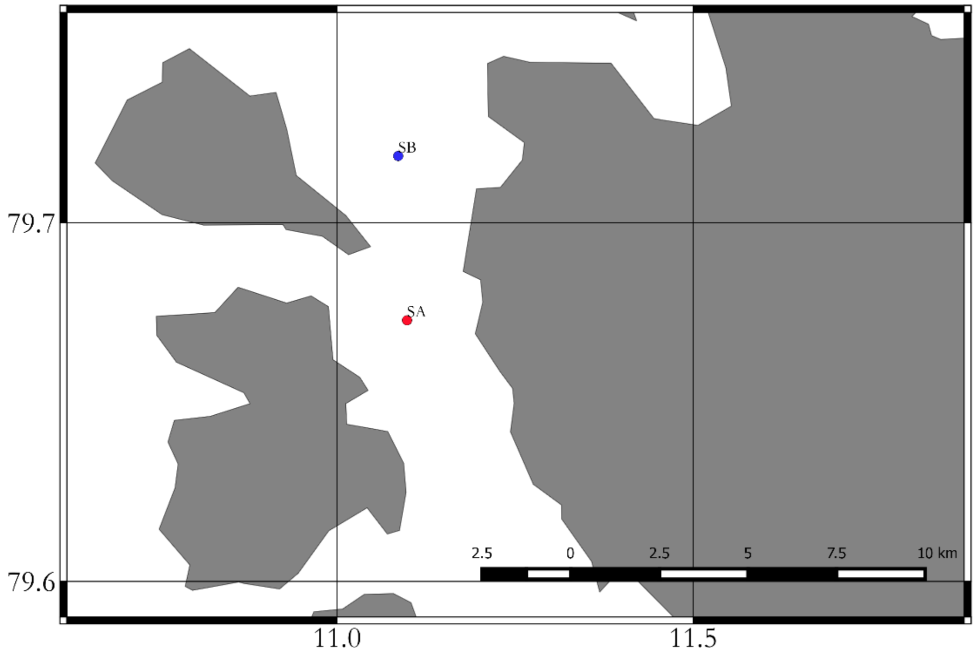


Fig. A3 Sampling sites in Smeerenburg. Blue dots represent samples taken in January, red dots represent sites taken in September and October, and green dots represent samples taken in May.

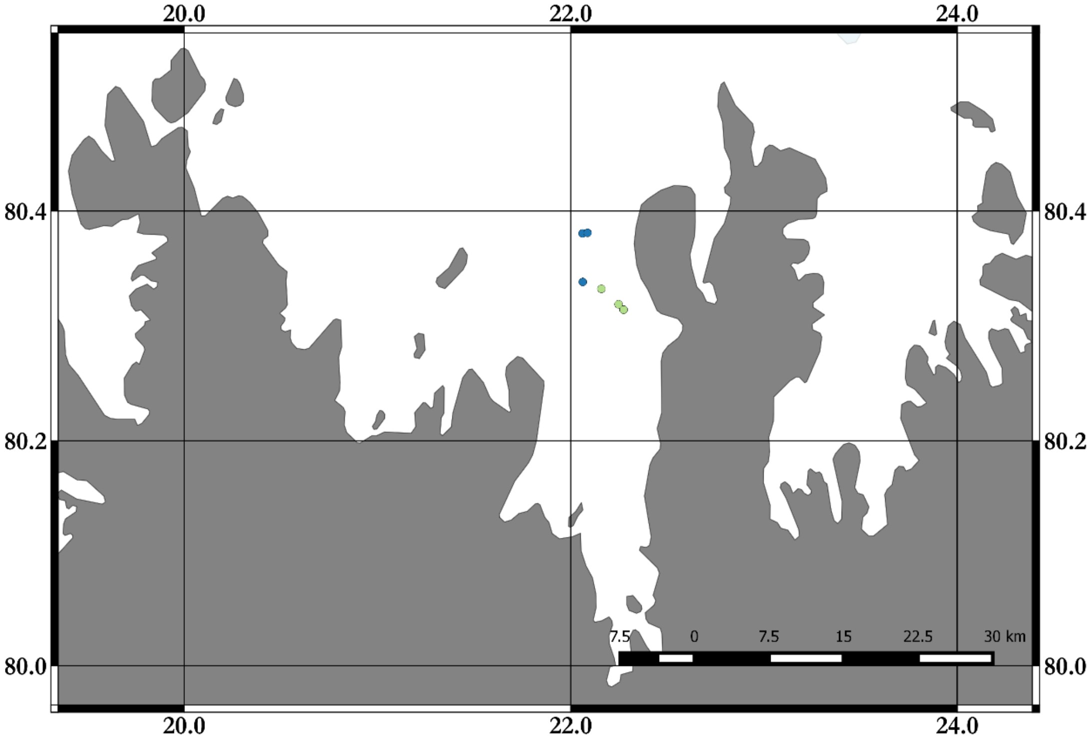


Fig. A4 Sampling sites in Rijpfjorden. Blue dots represent samples taken in January, red dots represent sites taken in September and October, and green dots represent samples taken in May.

Table A1 CTD stations information

Station Number	Site	Date	Latitude	Longitude	Depth (m)
631	Rijpfjorden	28/09/2014	80.30	22.29	271
1360	Kongsfjorden	10/09/2015	78.98	11.72	313
1364	Kongsfjorden	10/09/2015	78.96	11.95	342
1366	Kongsfjorden	10/09/2015	78.92	12.23	110
1368	Kongsfjorden	10/09/2015	78.96	11.83	245
1411	Smeerenburg	14/09/2015	79.69	11.11	217
1425	Rijpfjorden	16/09/2015	80.54	22.17	248
1424	Rijpfjorden	16/09/2015	80.30	22.20	249
1420	Rijpfjorden	16/09/2015	80.10	22.21	175
1428	Rijpfjorden	17/09/2015	80.29	22.29	258
769	Kongsfjorden	08/05/2015	78.94	11.97	298
830	Billefjorden	13/05/2015	78.59	16.50	158
833	Billefjorden	13/05/2015	78.59	16.50	160
0014	Billefjorden	11/01/2016	78.66	16.73	192
0026	Smeerenbug	12/01/2016	79.70	11.10	227
0038	Rijpfjorden	14/01/2016	80.31	22.27	280
0117	Kongsfjorden	20/01/2016	78.96	11.95	342
0117	Kongsfjorden	20/01/2016	78.96	11.95	342
0104	Kongsfjorden	20/01/2016	78.95	11.96	341
0131	Kongsfjorden	21/01/2016	78.90	12.44	71
0145	Kongsfjorden	22/01/2016	78.91	12.20	71
0158	Kongsfjorden	23/01/2016	78.92	12.21	62
0160	Kongsfjorden	23/01/2016	78.91	12.23	79

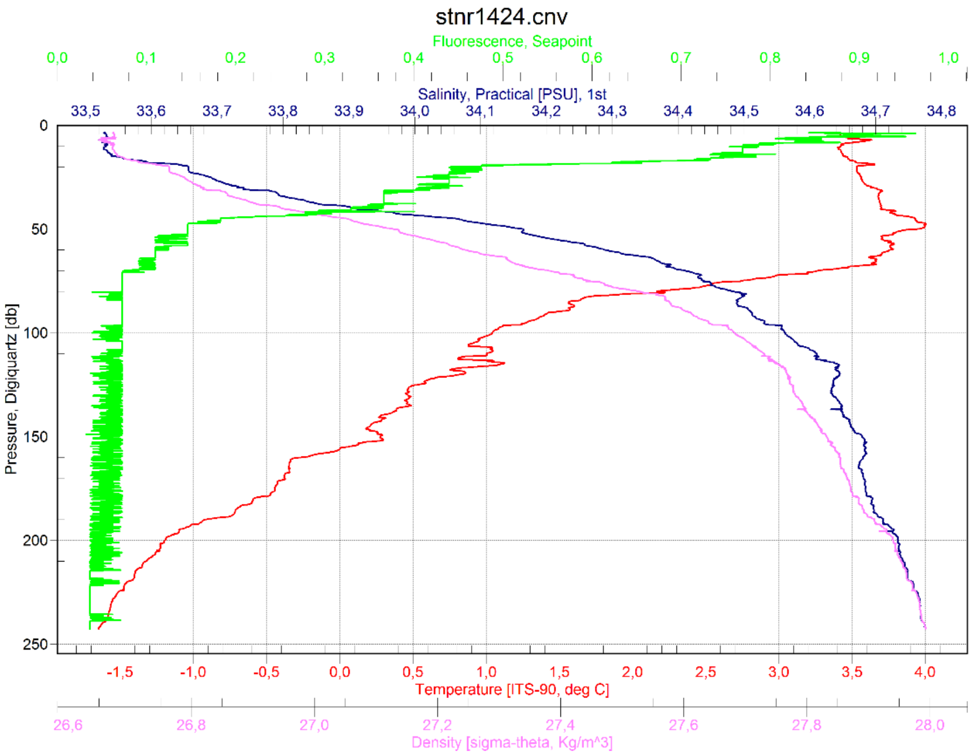


Fig. A5 Rijpfjorden CTD profile in the September 2015

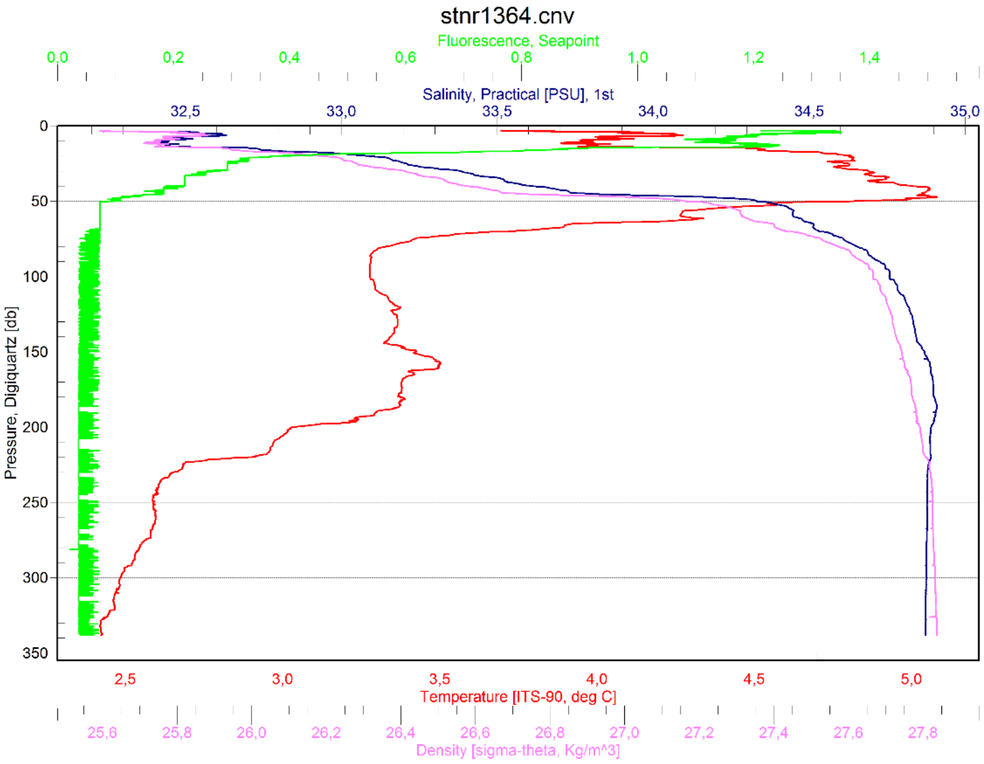


Fig. A6 Kongsfjorden CTD profile in September 2015

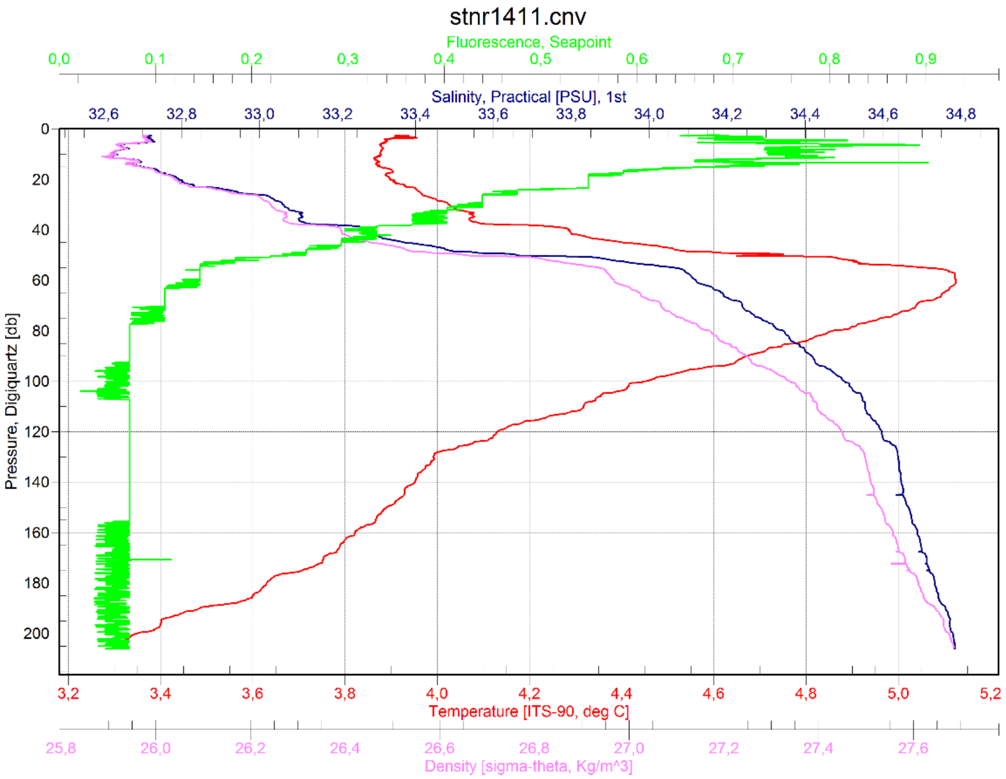


Fig. A7 Smeerenburg CTD profile in September 2015

Similarity profile analysis (SIMPROF)

SIMPROF is used to identify assemblage patterns in community ecology by using a null hypothesis. The SIMPROF is performed on a similarity matrix such as the Bray-Curtis metric used here. A profile plot is created using the similarity matrix by ranking similarities in order of magnitude. The original data is then randomly shuffled through an iterative permutation technique to generate the null hypothesis profile. The two profiles are compared and statistical significance of the difference between null and observed profile is tested via pi (prediction interval) statistic. SIMPROF is used to identify objectively genuine groups within a cluster analysis and thus tests are performed at every node of the dendrograms.

Nonmetric multidimensional scaling (nMDS) and Shepard stress

An MDS is a two or three dimensional diagram that helps to visualize the outcome of a similarity (or dissimilarity) matrix such as Bray-Curtis index. Rather than depicting the original distances generated by the dissimilarity or similarity matrix, the nMDS depicts the ranked dissimilarities or similarities. The output reads as follows: depicted samples that are close together are similar in terms of community composition and depicted samples that are far apart are more dissimilar. The nMDS algorithm is iterative in nature and must be run several times before finding an optimal depiction.

The Shepard stress plot is a scatter plot that illustrates the similarity matrix values against the ordination distances. High correlation indicates that the nMDS is trustworthy. A high stress value (above 0.2 should be interpreted with caution) while a low stress value (0.1 or lower) indicates a good fit.

Analysis of similarities (ANOSIM)

ANOSIM will test the null hypothesis that there are no differences between groups by using a similarity matrix, here Bray-Curtis coefficients. ANOSIM is a permutation test and should not be used to assess the significance of groups generated by a cluster analysis but rather should be used to test the null hypothesis that there are no differences between hypothetical groups. Whereas SIMPER will test if dendrogram clusters are significantly different from each other, ANOSIM will test if there is a significant difference in community composition between hypothetical groups. ANOSIM generates an R value between 0 and +1, and the closer the value is to 1 the stronger is the effect of the factor (here: season) on the variable (here: dietary similarity).

Appendix B : An elaboration results

Table B1 Mean (± SD) values for length, gonado-somatic index, and hepato-somatic index, and range values for length of polar cod caught in Svalbard fjords at different seasons.

Month	Site	Centimeters (cm)				Grams (g)		Grams (g)	
		Length	Length min	Length max	*n*	GSI	*n*	HSI	*n*
Sept-Oct	Rijpfjorden	14.9 ± 3.3	8.5	24.0	94	5.30 ± 3.48	91	14.23 ± 3.13	94
	Billefjorden	13.5 ± 2.3	6.6	17.7	51	6.57 ± 5.02	46	13.63 ± 2.72	51
	Smeerenburg	17.6 ± 2.3	12.0	26.6	40	3.67 ± 1.99	40	11.51 ± 3.45	40
January	Rijpfjorden	16.1 ± 2.5	9.4	21.3	99	16.78 ± 11.15	96	8.84 ± 3.04	98
	Billefjorden	14.0 ± 2.2	9.2	21.0	40	16.94 ± 8.68	40	9.17 ± 2.84	40
	Smeerenburg	14.1 ± 1.5	12.4	19.5	40	3.08 ± 6.77	37	8.30 ± 3.08	40
	Kongsfjorden	12.9 ± 3.0	8.5	21.0	70	5.30 ± 9.32	58	5.53 ± 2.28	70
May	Billefjorden	11.3 ± 2.4	9.3	20.5	20	1.29 ± 1.54	12	3.38 ± 1.88	18
	Kongsfjorden	12.1 ± 1.8	8.6	15.4	21	1.18 ± 0.83	19	4.92 ± 1.06	20
Total		**14.5 ± 3.0**	**6.6**	**26.6**	**475**	**8.6 ± 9.46**	**439**	**10.22 ± 4.23**	**471**

Table B2 Frequency of occurrence of prey based presence/absence of each prey item for *n* stomachs of adult polar cod of 10-15 cm in length caught during the fall, winter, and spring at given sites.

Prey	**September - October**			**January**				**May**	
	Rijpfjorden	Smeerenburg	Billefjorden	Rijpfjorden	Smeerenburg	Billefjorden	Kongsfjorden	Billefjorden	Kongsfjorden
Amphipoda	26.1	0.0	5.6	0.0	22.2	30.0	9.1	0.0	6.7
Chaetognatha	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda	8.7	25.0	55.6	57.1	25.9	23.3	40.9	40.0	20.0
Crustacea	26.1	75.0	13.9	42.9	25.9	3.3	38.6	80.0	66.7
Decapoda	0.0	0.0	0.0	4.8	3.7	0.0	0.0	6.7	13.3
Euphausiidae	8.7	50.0	33.3	0.0	7.4	10.0	61.4	46.7	13.3
Teleostei	0.0	0.0	2.8	19.0	29.6	0.0	0.0	6.7	0.0
Isopoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mysida	0.0	0.0	2.8	4.8	0.0	0.0	2.3	0.0	13.3
Ophiuroidea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaeta	4.3	0.0	5.6	0.0	0.0	0.0	2.3	0.0	0.0
Themisto spp.	69.6	50.0	94.4	14.3	3.7	76.7	0.0	0.0	0.0
Unidentified	0.0	0.0	0.0	4.8	29.6	6.7	25.0	0.0	26.7
(n) polar cod	*23*	*4*	*36*	*21*	*30*	*27*	*44*	*15*	*15*

Table B3 Frequency of occurrence of prey based presence/absence of each prey item for *n* stomachs of adult polar cod >15 cm in length caught during the fall, winter, and spring at given sites.

Prey	**September - October**			**January**				**May**
	Rijpfjorden	Smeerenburg	Billefjorden	Rijpfjorden	Smeerenburg	Billefjorden	Kongsfjorden	Kongsfjorden
Amphipoda	28.8	11.8	0.0	4.2	12.5	42.9	10.0	0.0
Chaetognatha	0.0	0.0	10.0	0.0	0.0	0.0	0.0	50.0
Copepoda	13.5	35.3	40.0	45.8	25.0	42.9	30.0	0.0
Crustacea	15.4	52.9	30.0	20.8	25.0	14.3	20.0	100.0
Decapoda	0.0	2.9	10.0	0.0	12.5	0.0	10.0	50.0
Euphausiidae	3.8	35.3	30.0	8.3	0.0	28.6	60.0	0.0
Teleostei	5.8	0.0	20.0	33.3	37.5	42.9	10.0	0.0
Isopoda	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Mysida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ophiuroidea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaeta	5.8	0.0	0.0	2.1	12.5	0.0	0.0	0.0
Themisto spp.	84.6	50.0	90.0	12.5	0.0	71.4	10.0	0.0
Unidentified	3.8	23.5	0.0	29.2	25.0	14.3	30.0	0.0
(n) polar cod	*52*	*34*	*10*	*48*	*7*	*8*	*10*	*2*

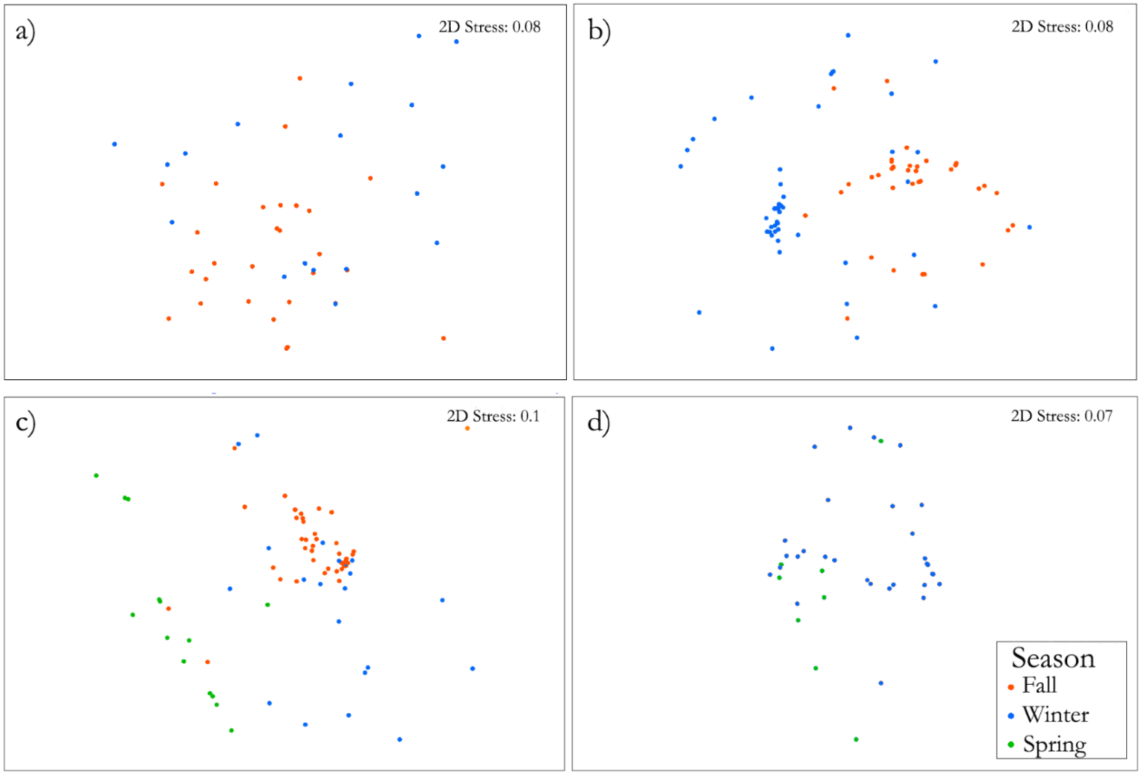


Fig. B1 Non-metric multidimensional scaling (nMDS) ordinations of gut content from stomachs of both size categories of polar cod based on Bray-Curtis similarity for (a) Smeerenburg, (b) Rijpfjorden, (c) Billefjorden, and (d) Kongsfjorden. Stomachs are treated as individual samples.

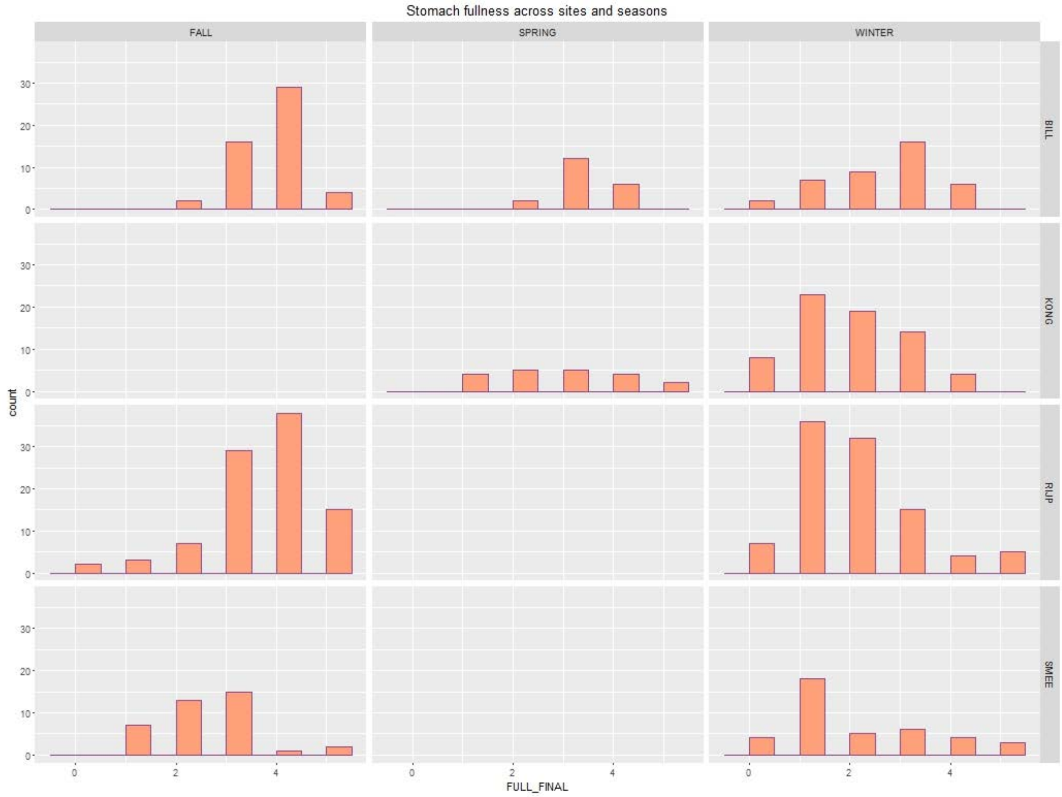
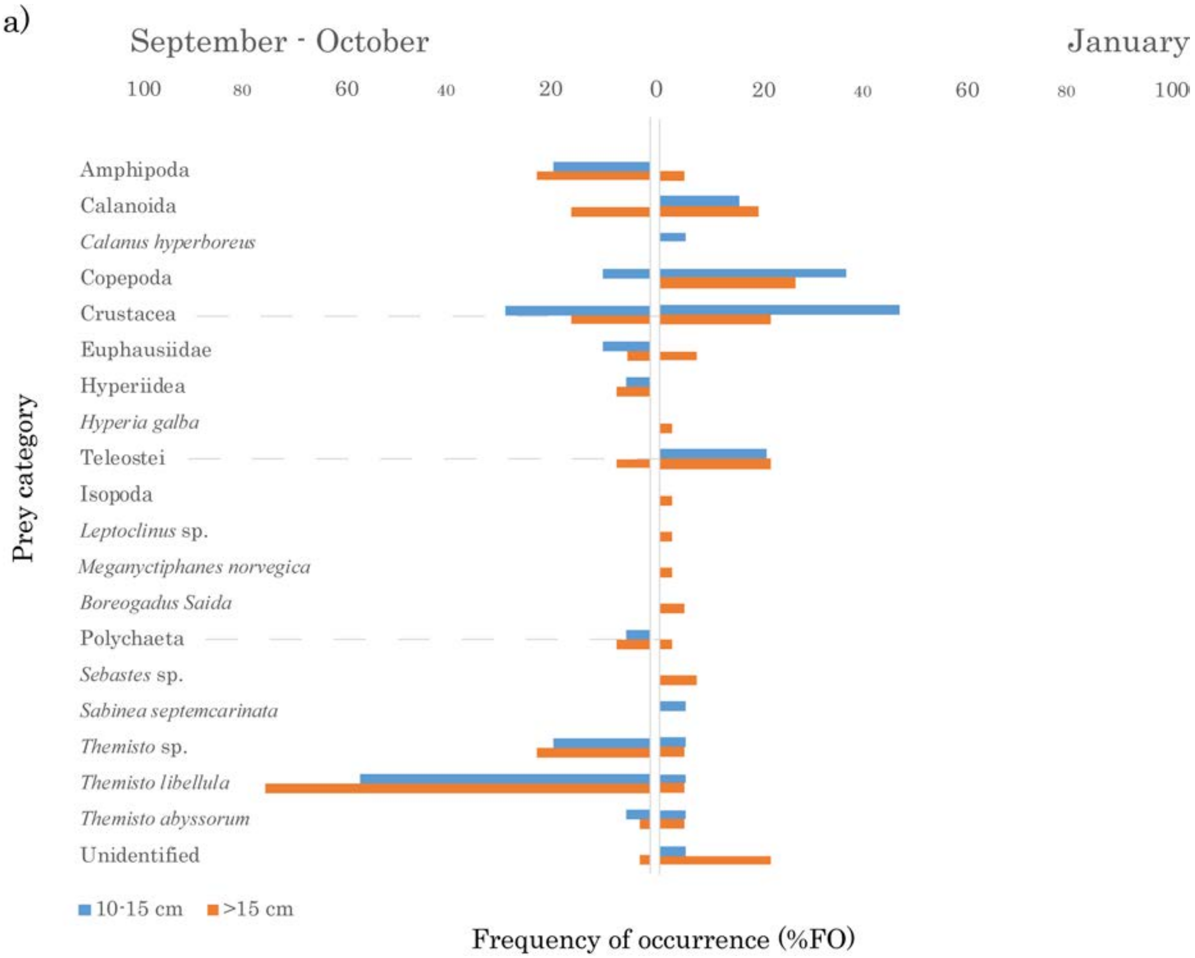


Fig. B2 Stomach fullness counts across sites and seasons.

a)


September - October
January
100
80
60
40
20
0
20
40
60
80
100
Prey category
Amphipoda
Calanoida
Calanus hyperboreus
Copepoda
Crustacea
Euphausiidae
Hyperiidea
Hyperia galba
Teleostei
Isopoda
Leptoclinus sp.
Meganyctiphanes norvegica
Boreogadus Saida
Polychaeta
Sebastes sp.
Sabinea septemcarinata
Themisto sp.
Themisto libellula
Themisto abyssorum
Unidentified
10-15 cm
>15 cm
Frequency of occurrence (%FO)

b)

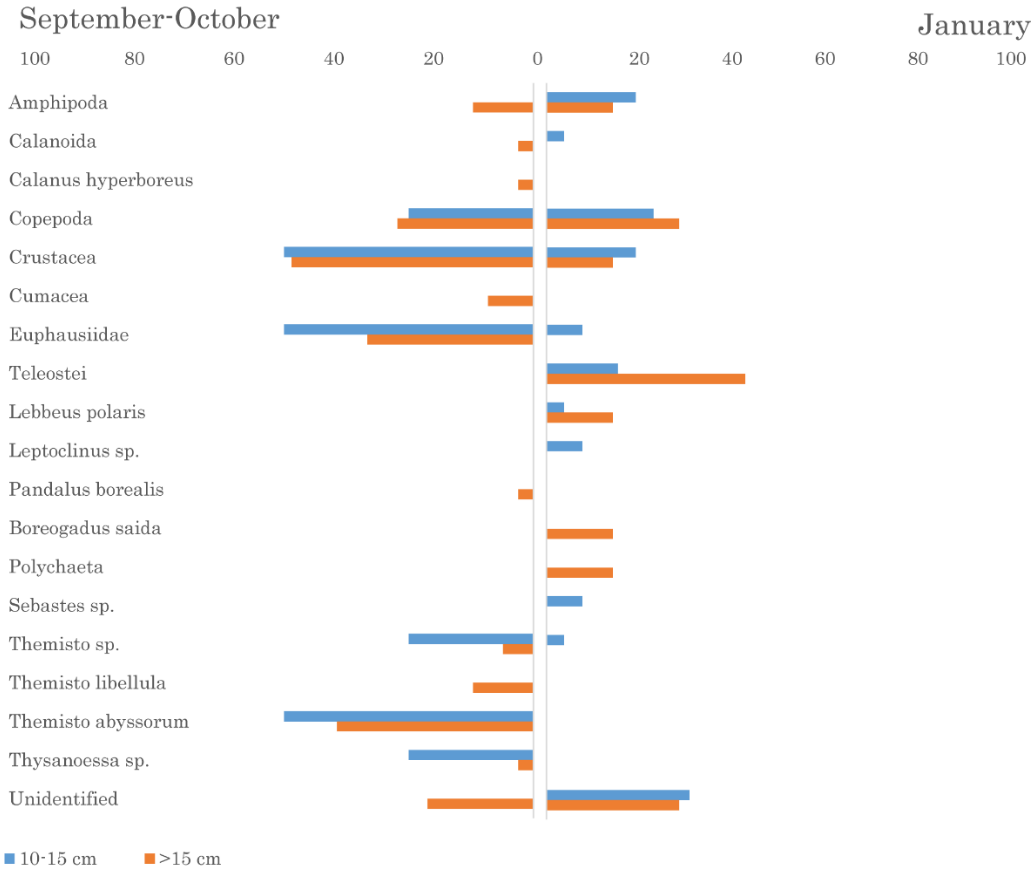


Fig. B3 Frequency of occurrence of ingested prey species in (a) Rijpfjorden, and (b) Smeerenburg based on IDC (initial dietary categories).

Table B4. Percent abundance of prey based on numerical stomach content (%N_i) for *n* stomachs of adult polar cod >15cm in length caught during the fall, winter, and spring at given sites.

Prey	**September - October**			**January**				**May**
	Rijpfjorden	Smeerenburg	Billefjorden	Rijpfjorden	Smeerenburg	Billefjorden	Kongsfjorden	Kongsfjorden
Amphipoda	10.21	3.73	0.00	2.73	6.25	6.67	3.45	6.90
Chaetognatha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	55.17
Copepoda	37.29	16.42	16.18	55.45	31.25	62.22	31.03	3.45
Crustacea	1.66	17.16	2.94	8.18	12.50	2.22	6.90	20.69
Decapoda	0.00	0.75	1.47	0.00	6.25	0.00	3.45	3.45
Euphausiidae	0.48	32.84	2.94	4.55	0.00	4.44	34.48	10.34
Teleostei	0.71	0.00	2.94	13.64	25.00	6.67	6.90	0.00
Isopoda	0.00	0.00	0.00	0.91	0.00	0.00	0.00	0.00
Mysida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.71	0.00	0.00	0.91	6.25	0.00	0.00	0.00
Themisto spp.	48.69	23.88	73.53	5.45	0.00	13.33	3.45	0.00
Unidentified	0.24	5.22	0.00	8.18	12.50	4.44	10.34	0.00

Table B5. Percent abundance of prey based on numerical stomach content ($\%N_i$) for *n* stomachs of adult polar cod of 10-15cm in length caught during the fall, winter, and spring at given sites.

Prey	**September - October**			**January**				**May**	
	Rijpfjorden	Smeerenburg	Billefjorden	Rijpfjorden	Smeerenburg	Billefjorden	Kongsfjorden	Billefjorden	Kongsfjorden
Amphipoda	36.05	0.00	0.98	0.00	10.42	16.90	3.33	0.00	1.18
Chaetognatha	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda	30.23	31.58	44.26	79.31	33.33	30.99	28.00	65.78	72.94
Crustacea	4.07	10.53	0.98	10.34	10.42	1.41	11.33	5.32	12.94
Decapoda	0.00	0.00	0.00	1.15	2.08	0.00	0.00	0.33	1.18
Euphausiidae	1.74	15.79	3.93	0.00	4.17	4.23	51.33	28.24	3.53
Teleostei	0.00	0.00	0.33	4.60	20.83	0.00	0.00	0.33	0.00
Isopoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mysida	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	5.88
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaeta	0.58	0.00	0.66	0.00	0.00	0.00	0.67	0.00	0.00
Themisto spp.	27.33	42.11	48.20	3.45	2.08	43.66	0.00	0.00	0.00
Unidentified	0.00	0.00	0.00	1.15	16.67	2.82	5.33	0.00	2.35

Appendix C : Data from external sources (methods not included)

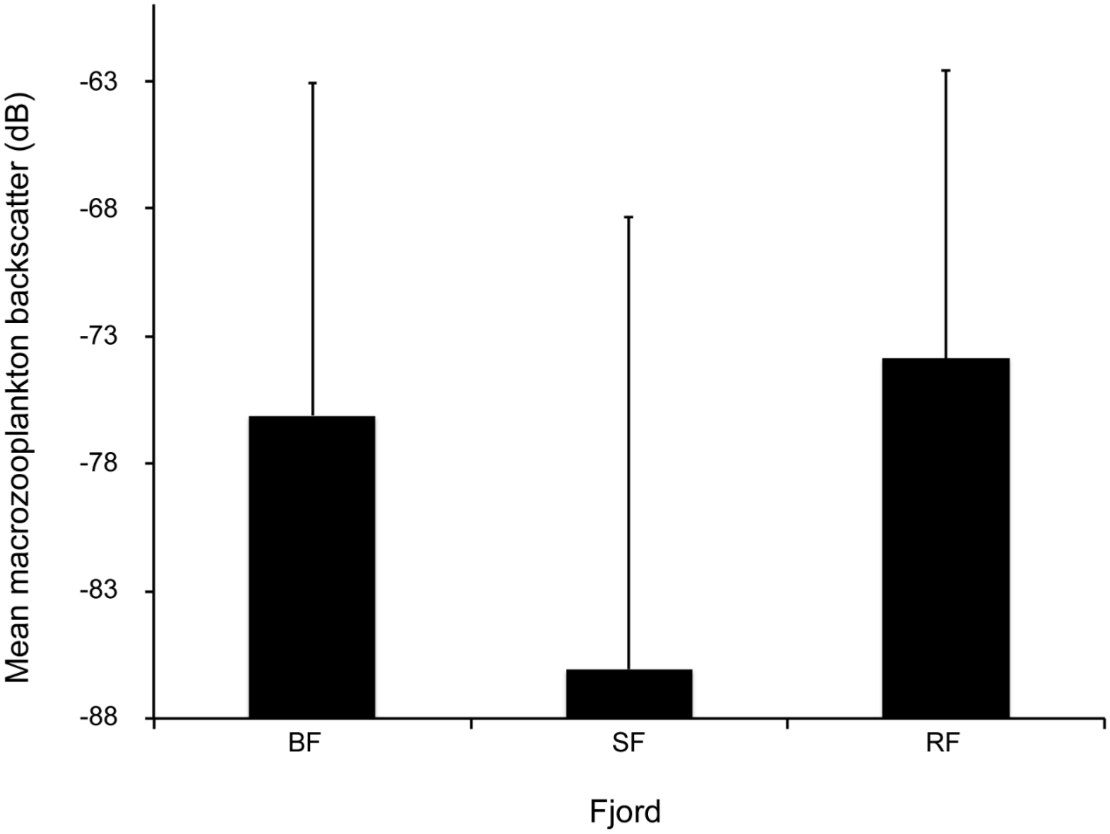


Fig. C1 Mean macrozooplankton volume backscattering strength (Sv) at 120 kHz in Billefjorden (BF); Smeerenburgfjorden (SF); and Rijpfjorden during the Polar Night Cruise in January 2016. Error bars represent one standard deviation. *Data collected and analyzed by Maxime Geoffroy.*

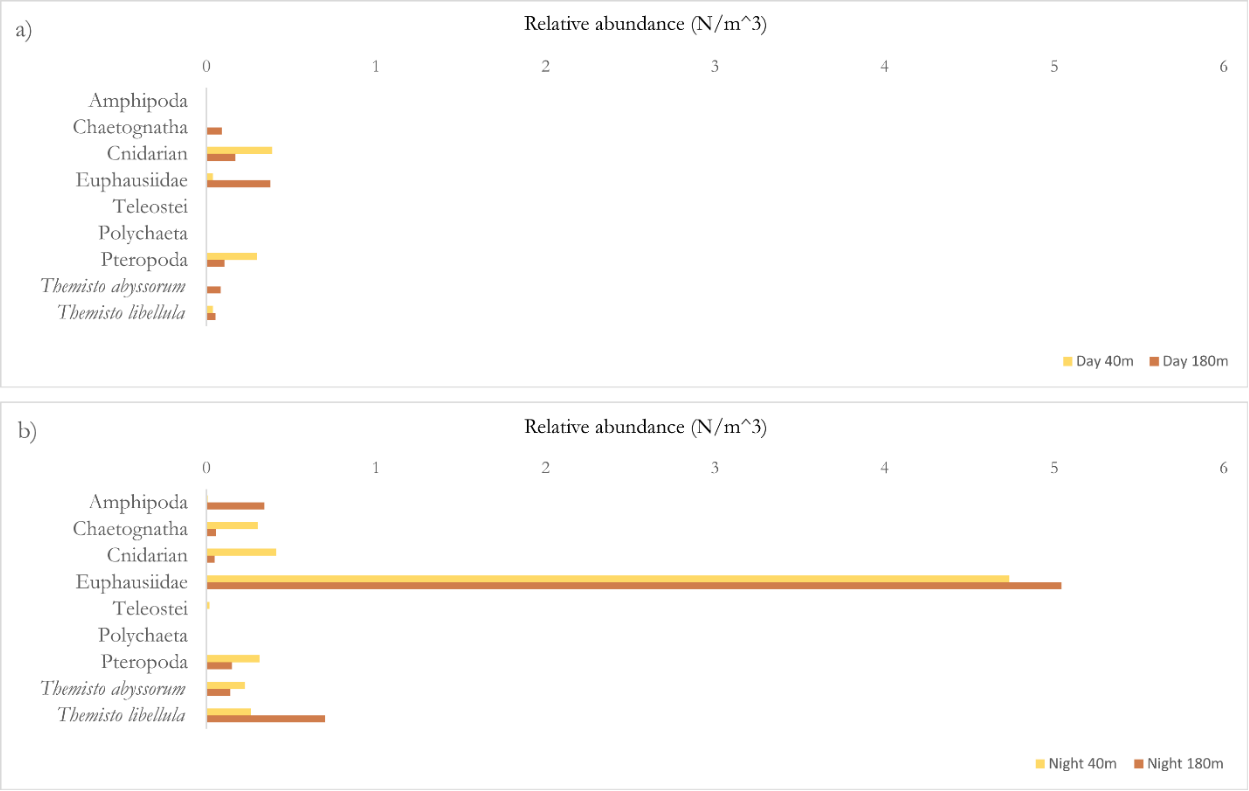


Fig. C2 Relative macro-zooplankton abundance (number of individuals / a cubic meter of water) caught in MIK net in Rijpfjorden in September 2014 as part of the AB320 cruise.

Appendix D : Additional analysis for side objectives

D.1. Morphobiological measurements

Gonado-somatic index (GSI) and hepato-somatic index (HSI) were calculated using the following formulas:

GSI = (Gonad weight (g) / Fish weight (g)) × 100
HSI = (Liver weight (g) / Fish weight (g)) × 100

The GSI is calculated in order to get a measure of the maturity level of an organism while the HSI is calculated to get a measure of the energy reserve in an organism. GSI was used for an inter-seasonal comparison of the gonado-somatic index of polar cod. The p value is from an inter-seasonal comparison using a kruskal-wallis test. The HIS was used for an inter-site comparison of the hepato-somatic index of polar cod. The p value is from an inter-site comparison using a kruskal-wallis test.

D.2. Fish community composition sampling and data

All catch from a total of 45 trawls performed between September 2014 and January 2016 and were sorted into species. The number of individuals and total weight were recorded for each identified species of fish and invertebrates. A random subsample of polar cod and Atlantic cod was selected and the length and weight were measured for up to 50 specimen for each species. This measurement allowed to identify size categories for polar cod and Atlantic cod. Size categories were chosen based on the literature and their relevance in the context of this project. Based on Falk Petersen et al. (1986) polar cod were divided into three size categories: <10 cm, 10-15 cm, and >15 cm. Atlantic cod were divided into two size categories: ≤20 cm labelled as Atlantic cod juvenile, and >20 cm labelled as Atlantic cod. This division was based on the observation that up to age 1 Atlantic cod can reach 20 cm (Armstrong et al. 2004) and on the consideration that large adult polar cod will reach a size of ~ 20 cm on average. Therefore, Atlantic cod juvenile (≤20 cm) are treated here as potential competitors of polar cod, whereas Atlantic cod (>20 cm) are treated as potential predators.

Since the question of interest here pertains to polar cod in a fish community, all invertebrates were removed from the data for the analysis. Furthermore, all deep sea trawls below 900 meters were removed since none of them contained polar cod and since most fish species co-occurring with polar cod were also absent from these trawls. Pelagic trawls could be inaccurately representing fish abundance because of net avoidance, therefore we've only retained benthic trawls for the community composition analysis. Not all fish taxa were identified to the species level and some remain in separate categories from that of the species (E.g. three categories of *Liparis* genus were included in the analysis: *Liparis gibbus*, *Liparis fabricii*, and *Liparis* sp.).

Considering trawl duration is often slightly longer or shorter than the planned 15 minutes, I measured the standardized number of individuals for a given volume of water and in doing so generated an individual/m^3 standardized unit for each trawl. I divided the recorded individual fish species abundance for each trawl by the filtered volume of water (m^3) which is equal to the net opening in m^2 (17m x 4.5m) x the speed in m/sec (~3 knots = 1.543 m/sec) x the time trawled in seconds.

D.3. Fish community composition analysis (nMDS & CCA)

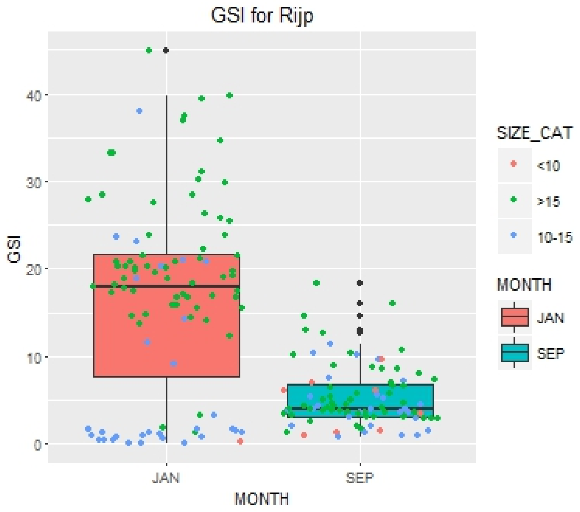
Following the aforementioned standardization of fish community abundance to individual per m^3, the data were square root transformed in order to reduce the weight brought by abundant species in a similarity matrix and to allow less abundant species to have some effect in the matrix. I measured the Bray-Curtis similarity index, or dissimilarity coefficient subtracted from 100, on the standardized and transformed fish community data. A dendrogram based on a group average hierarchical agglomerative cluster analysis from the triangular similarity matrix was produced in order to better visualize similarities between trawls in terms of species community composition. In order to evaluate the validity of the dendrogram groups we performed similarity profile (SIMPROF) permutation tests. A SIMPROF test was performed at every node of the dendrogram and evaluated whether the observed similarities in the dendrogram are significantly different from similarities randomly generated by an iterative permutation procedure. I then performed a non-metric multi-dimensional scaling method (nMDS) and the stress calculated along with the plotting of the nMDS measures the amount of error.

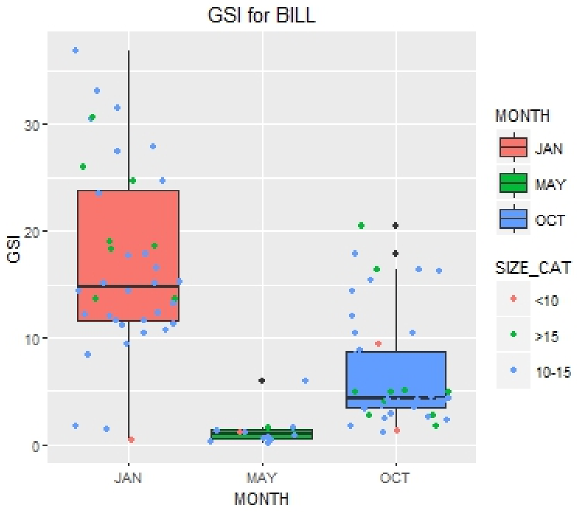
In order to identify relationships and patterns between environmental variables and fish species composition, I performed a canonical correspondence analysis (CCA). We performed the CCA with the full data set and displayed it with a contribution biplot.

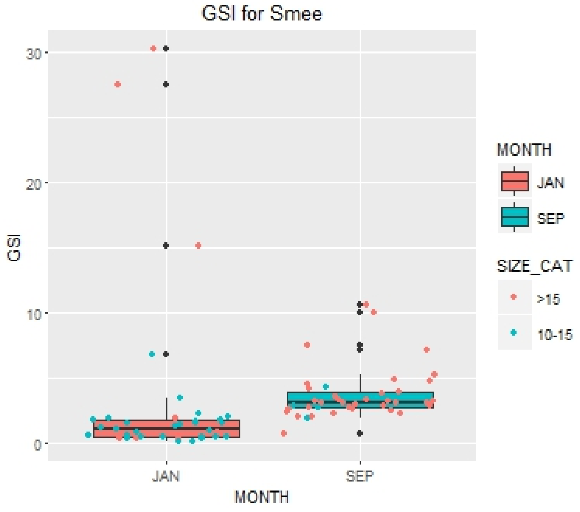
The hierarchical clustering and nMDS were performed using PRIMER v6 (PRIMER-E Ltd, Plymouth, UK). The CCA and contribution biplot were performed using the "vegan" package (Oksanen et al. 2013) in R (R Core Team 2013).

D.4. General biology - Results

The general biology (GSI & HSI) was measured for 475 polar cod. The individuals selected were mostly all above 10 cm except for 29 individuals evenly distributed between Rijpfjorden, Kongsfjorden, and Billefjorden. Overall the mean length was 14.51 ± 3.03 and the length ranged from 6.6cm to 26.6cm. During the month of January, the GSI values were significantly different between Rijpfjorden and Smeerenburg ($p<0.001$) and Rijpfjorden and Kongsfjorden ($p<0.001$), and between Billefjorden and Smeerenburg ($p<0.001$) and Billefjorden and Kongsfjorden ($p<0.001$) with Rijpfjorden and Billefjorden having high GSI values and Kongsfjorden and Smeerenburg having low GSI values. During the month of January, the HSI were only significantly different between Rijpfjorden and Kongsfjorden and between Billefjorden and Kongsfjorden with Kongsfjorden HSI values being relatively slow compared to the other sites. GSI were also significantly different between Billefjorden and Smeerenburg ($p<0.001$) and between Rijpfjorden and Smeerenburg ($p<0.001$) with Smeerenburg having a slightly lower GSI compared to the other two sites. Some difference in GSI is observed between Billefjorden and Kongsfjorden in May ($p=0.005$). In the fall, the HSI between Billefjorden and Kongsfjorden ($p=0.005$), Billefjorden and Smeerenburg ($p<0.001$) and Rijpfjorden and Smeerenburg ($p<0.001$) are significantly different, Smeerenburg having a lower HSI. Some difference in HSI is observed between Billefjorden and Kongsfjorden in May ($p=0.005$). The difference between male and female GSI is not significant for January ($p=0.07$) but is significant for the September-October ($p<0.001$) and for May ($p<0.01$). At any given site except for Kongsfjorden, there was a significant difference between January and October, with GSI being higher in January for both Rijpfjorden and Billefjorden and slightly higher in September in Smeerenburg. Individual measurements indicate that larger individuals over 15cm tend to have higher GSI than individuals of 10-15cm in Rijpfjorden, Smeerenburg, and Kongsfjorden during the month of January. The HSI was significantly higher in September-October compared to January for all sites except for Kongsfjorden, and lower in May for Billefjorden. The size categories do not seem to affect the HSI within sites.







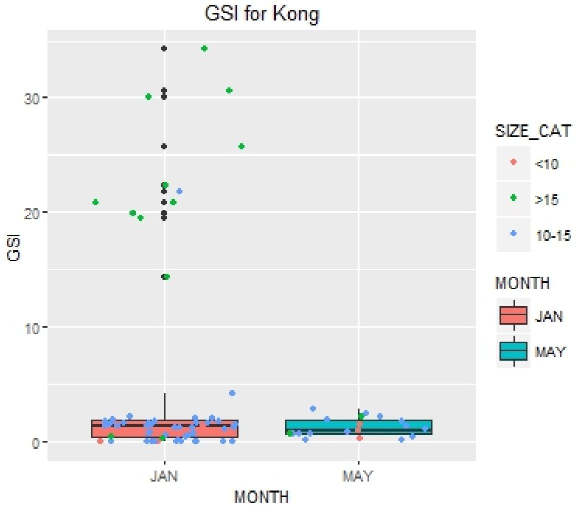


Fig. D1 GSI for polar cod across sites and seasons (Smee = Smeerenburg, Kong = Kongsfjorden, Rijp = Rijpfjorden, and Bill = Billefjorden).

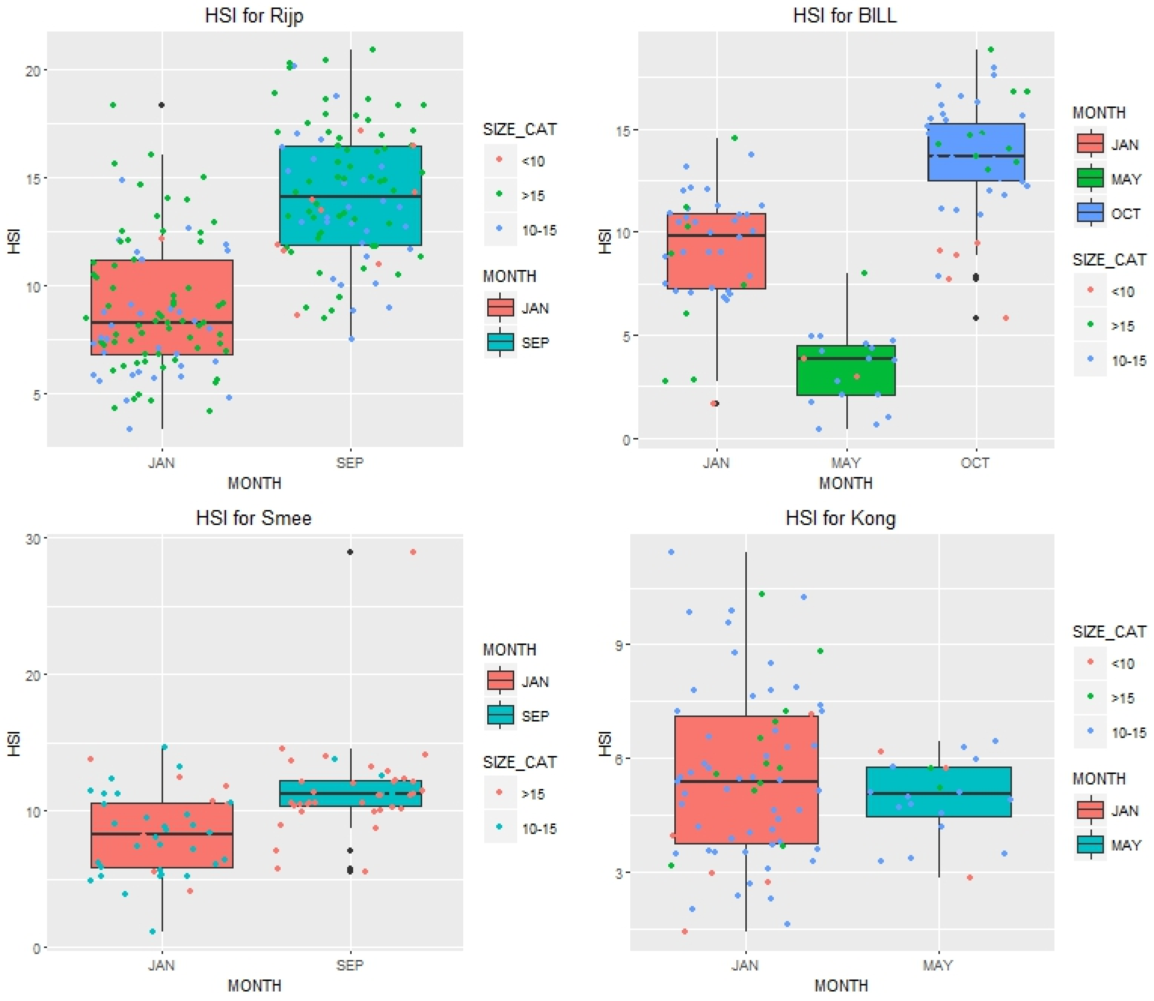


Fig. D2 HSI for polar cod across sites and seasons (Smee = Smeerenburg, Kong = Kongsfjorden, Rijp = Rijpfjorden, and Bill = Billefjorden).

D.5. Fish community compositon - Results

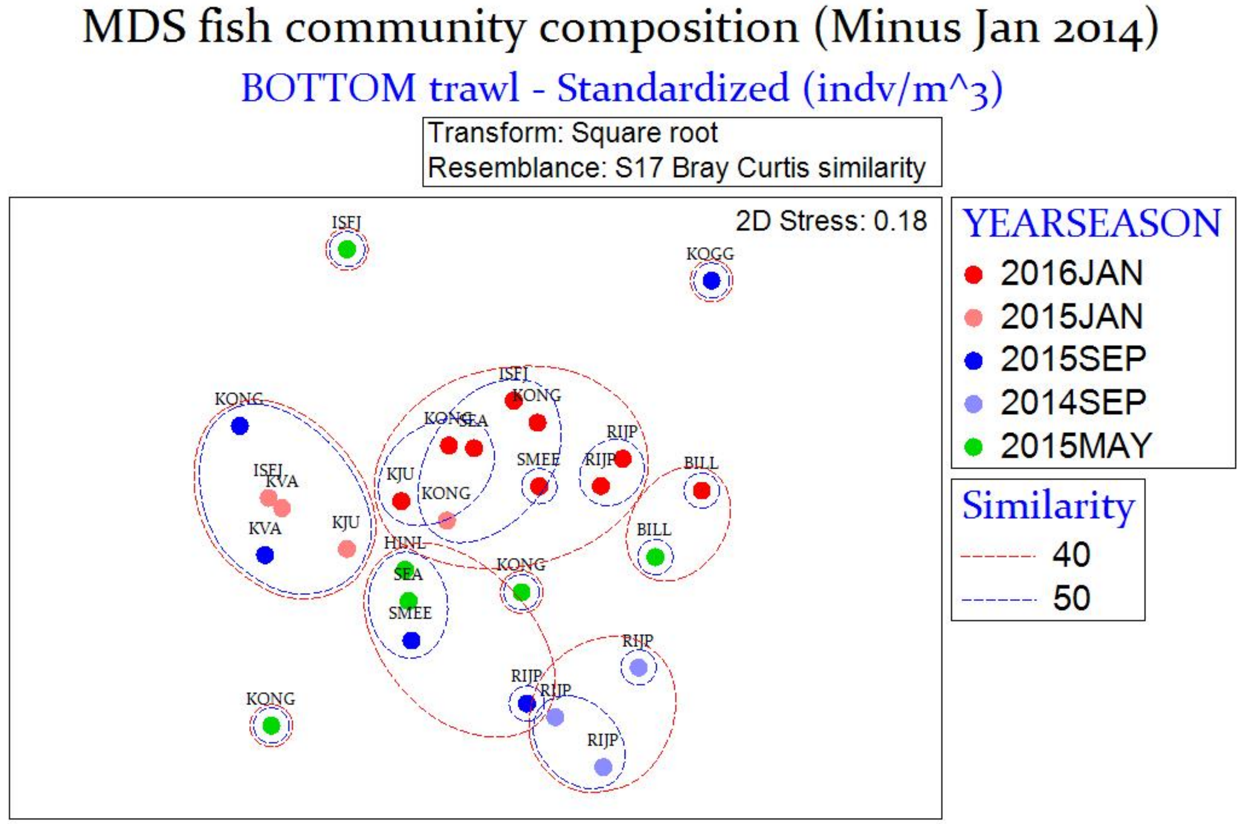


Fig. D3 nMDS based on fish species community composition illustrating a seasonal cluster.

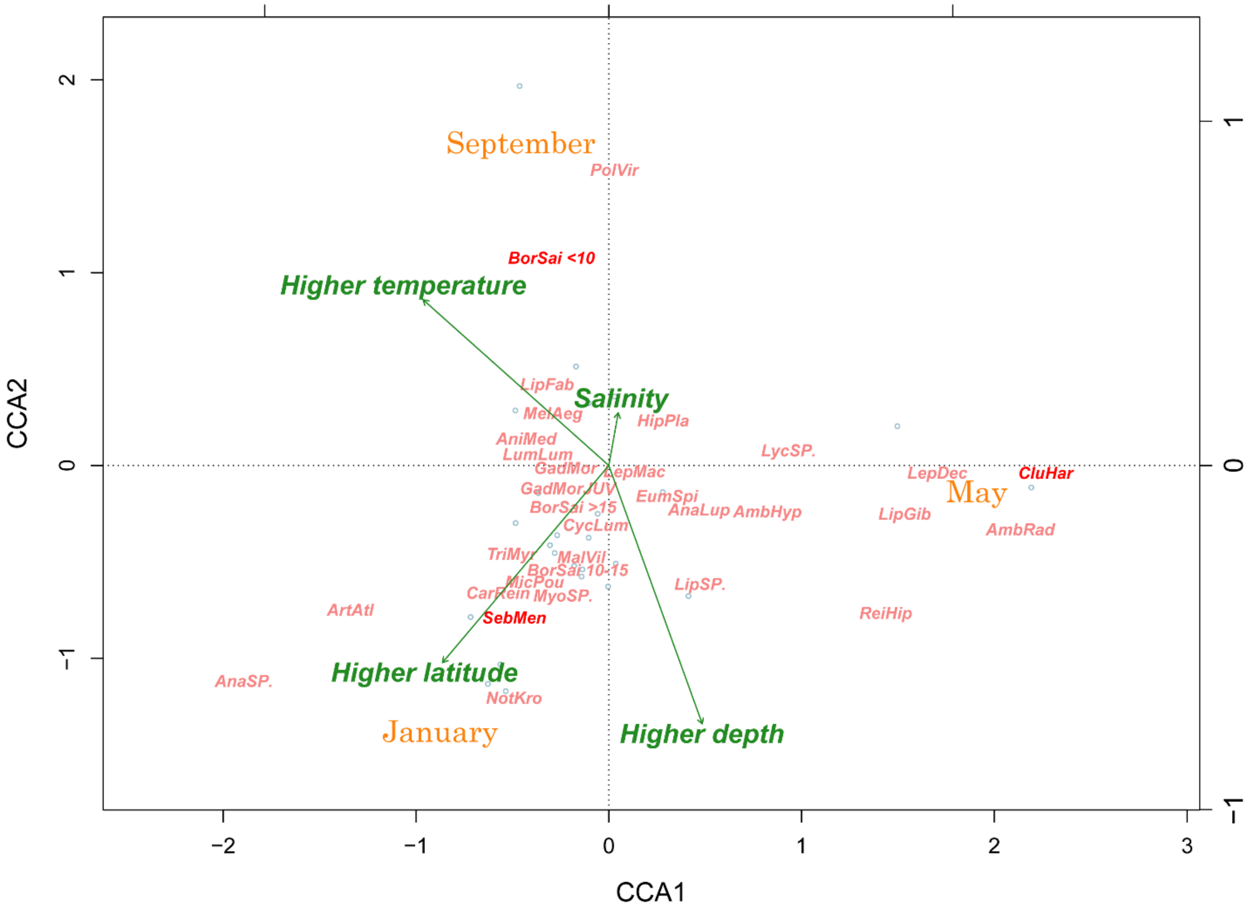


Fig. D4 Canonical correspondence analysis of fish community composition (BorSai = *Boreogadus saida*, GadMor = *Gadus morhua*, SebMen = *Sebastes mentella*, CluHar = *Clupea Harrengus*).