Feeding activity and diet of Arctic and boreal fish species during the Polar night

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Fish feeding during the Polar night

Abstract

The Arctic is warming, enabling a northwards shift and increasing dominance of boreal species at the expense of native Arctic species. Despite this, sustained darkness during the polar night may still provide a barrier to survival and long-term establishment in the region, thus constraining the effect of global warming. However, the paradigm that there is little biological activity during the polar night has recently been challenged. High population densities and bioluminescent activity of zooplankton and active foraging by visually feeding predators have been observed. In addition, some Arctic organisms have been found to have extremely sensitive vision, adapted perhaps for using the wavelengths of light associated with bioluminescence. Such discoveries have challenged the 'photoperiod constraint' hypothesis. Here, a comparison of the diet and winter feeding success of co-occurring native and invasive fish from 79° N in Kongsfjorden, Svalbard, found no clear differences in feeding success between Arctic and boreal species. Instead, three co-occurring gadoids, the Arctic polar cod (*Boreogadus saida*) and the boreal Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) had fed most successfully. There were indications that polar cod was the most adept at selectively feeding from pelagic prey, though it cannot be concluded from this study whether or not this was due to visual prey selection. Atlantic cod had fed the most successfully overall in both the pelagic and demersal habitats. The dominance of benthic prey items in the diet of demersal Atlantic cod, particularly in the largest fish, highlights the role of sensory predation for this fish species. The similar feeding success between the pelagic and benthic habitats indicates that their prey detection in the pelagic, by whatever means it occurs, is just as unconstrained by the extreme light environment as their sensory benthic prey detection. As Atlantic cod had consumed comparable amounts to individuals collected south of Svalbard in the Barents Sea such, for Atlantic

cod at least, the polar night may not provide a barrier to further Arctic expansion as the climate continues to warm.

Acknowledgements

I would like to thank Jørgen Berge for getting me involved in the Marine Night project and the crew of the R/V *Helmer Hanssen* for their great help during our polar night cruise. Additionally, I would like to thank Jørgen, Øystein Varpe and everyone else at UNIS for their involvement with this project and with Arctic science in general. Finally, I would like to thank Clive Trueman, and everyone else at the NOC for their help throughout this project and over the years.

Introduction

Borealisation of the Arctic

Long term warming in Arctic and Sub-Arctic regions is leading to large declines in sea ice extent and thickness and to the long predicted northward expansion of boreal species (Wassmann *et al*. 2011). The spawning areas of the well-studied stocks of Arcto-Norwegian Atlantic cod (*Gadus morhua)* have shifted northward along the coast (Sundby & Nakken 2008). The biomass of this commercially exploited stock has also increased, due to both favourable environmental conditions and the reduction in mortality as a result of fisheries management (Kjesbu *et al*. 2014). Cod, Atlantic Salmon, Mackerel and Haddock have all recently been caught either for the first time, or with increasing frequency in Svalbard, a Norwegian Arctic archipelago at 78°N, where they now co-occur with native species (Berge *et al*. 2015).

Fjords along the west coast of Spitsbergen, such as Kongsfjorden at 79°N, are heavily influenced by Atlantic water masses transported in the West Spitsbergen Current (WSC), as well as a coastal Arctic water current (Svendsen *et al.* 2002). Due to the increase in temperature of the WSC, Kongsfjorden and other West coast fjords have experienced an overall increase in temperature greater than in the Arctic as a whole (Pavlov *et al.* 2013), providing a natural environment to explore the impacts of climate changes before they occur in the Arctic as a whole (Hop *et al*. 2002).

These fjords experience large intra-annual variations in seawater conditions (Cottier *et al*. 2005), depending on local atmospheric conditions and the strength of the Spitsbergen current, which varies in step with the North Atlantic oscillation (NAO)(Schlichtholz & Goszczko, 2006). The Arctic and Atlantic water masses, and their associated zooplankton, follow seasonal cycles of dominance (Willis *et al*. 2006, Walkusz *et al.* 2009). In Kongsfjorden, the density barrier between cold, winter cooled water in the fjord and warmer water outside gradually breaks down during spring, allowing first coastal Arctic water, and then Atlantic water from the WSC to advect into the fjord (Cottier *et al*. 2005). Surface cooling serves to reinstate the dominance of arctic water masses and fauna over the course of the autumn and winter (Cottier *et al*. 2005).

Species invasion

There are also large inter-annual variations in the atmospheric and oceanographic conditions in these fjords, especially in winter conditions (Weslawski *et al.* 1987). Inter-annual fluctuations and extreme weather events have played an important role in the establishment of new species on Svalbard. In Kongsfjorden, sustained northerly winds during the winter of 2005/2006, as opposed to the usual south-westerly winds, led to the transport of surface waters out of the fjord by Ekman drift (Cottier *et al*. 2007). As a consequence, the density barrier at the fjord mouth was overcome and the warm waters of the North Atlantic current were transported into the fjord at depth (Cottier *et al*. 2007). With the cold fjord water lost, there was insufficient surface cooling for sea ice formation and, as a result, the density barrier at the fjord mouth was not re-established. The fjord has remained in a warmer state ever since dominated by both Atlantic water masses and fauna (Nilsen *et al*. 2008, Cottier *et al*. 2007). In another example, the migration and establishment of a colony of blue mussels, *Mytilus edulis*, found at the mouth of Isfjorden in 2004, was facilitated by the coincidence of a particularly strong year for the North Atlantic current, and prevailing winds which intensified the flow of Atlantic water into the fjord (Berge *et al*. 2004). The survival and increased abundance of boreal species in Svalbard waters, however, is evidence of a more prolonged and sustained change in conditions.

Changes that are benefiting boreal species can also have direct negative consequences for native Arctic species (Nahrgang *et al*. 2014). Polar cod, *Boreogadus saida*, is a key species in the Arctic food web, providing an important trophic link between zooplankton and piscivorous seals, birds and whales (Hop & Gjosæter 2013). The relatively high temperature of Atlantic dominated water masses, the different diet available to polar cod and the increased predation pressure, predominately from large Atlantic are combining to reduce reproductive success and growth rate of polar cod in the Atlantic (Nahrgang *et al*. 2014).

Ecological interactions

The increasing range overlap of closely related arctic and boreal species may also lead to other ecological interactions, including competition, which could exacerbate the negative effects already seen in Arctic species such as polar cod (Renaud *et al.* 2012, Nahrgang *et al.* 2014).

The northward expansion of Atlantic cod and haddock, *Melanogrammus aeglefinus*, has led to the co-occurrence of these boreal gadoids with *B. saida* (Renaud *et al.* 2012). However, fish collected in Svalbard fjords in August and September of 2006 were found to have little dietary overlap, suggesting that interspecific competition for food is in fact minimal (Renaud *et al*. 2012). This niche separation may be an indication of adaptation to exploit different food resources during past range overlap (Connell 1980).

Indeed, the presence of boreal species in Svalbard is not unprecedented. The aforementioned blue mussel was present in Svalbard up until 1000 years ago, during the medieval warm period, a period which also saw the westwards spread of the Viking civilisation from Scandinavia to both Iceland and Greenland (Berge *et al.* 2005). Also, nutrient rich upwelling in large areas devoid of sea ice, discovered North of Svalbard in January 2012, are similar to those conditions that once sustained large historical stocks of Bowhead, *Balaena mysticetus*, and other whales (Falk-Petersen *et al.* 2014). The 'whalers bay' area was largely ice-free during the 17th and 18th centuries, during which time the whale populations were decimated by whaling (Vinje *et al.* 1999). Current conditions, and increased sightings of bowhead and other whales mark a return to highly productive conditions following heavy winter ice cover in this region for most of the 19th and 20th Centuries (Falk-Petersen *et al*. 2014).

The photoperiod constraint hypothesis

With environmental conditions becoming increasingly inhospitable to native species, and increasingly favourable to boreal taxa, it has been proposed that the extreme light conditions of the Arctic polar night may provide a final barrier to invasion (Kaartvedt 2008). The 'photoperiod constraint hypothesis' proposes that the inability of boreal visual predators to feed during the sustained dark period may inhibit their establishment in the Arctic (Kaartvedt 2008). In contrast, native species are well adapted to the extreme seasonality of the Arctic, and have life cycles well adapted to the polar night. Krill of the genus *Thysanoessa* and calanoid copepods, such as *Calanus hyperboreus* build up stores of wax esters during the short period of intense primary production characteristic of the Arctic (Falk-Petersen *et al.* 1981, Falk-Petersen *et al.* 2009). Their reproductive cycles are also timed in order to make use of the early spring growth of ice-algae and the subsequent open water spring blooms (Falk-Petersen *et al.* 2009). Calanoid copepods undergo seasonal vertical migration and mature into reproductive adults at depth during winter using the energy stored in their wax esters (Visser & Jónasdóttir 1999). Fish are also well adapted to the polar night. The daubed shanny, *Leptoclinus maculatus*, contains liquid lipid droplets (Murzina *et al.* 2013), whilst polar cod has large energy stores in its liver (Nahrgang *et al*. 2010), polar cod has also been found to have a reduced growth rate and a 50% reduction in food intake despite an unlimited food supply (Jensen *et al.* 1991). In contrast, winter food scarcity can lead to a reduce condition in Atlantic cod, suggesting that they are not equally adapted to winter food shortage (Hawkins *et al.* 1985).

Recent insights into polar night marine biology

The long held assumption that the polar night is a period of little biological activity is being challenged by recent insights into the marine ecosystem (Lønne *et al.* 2014). Visual predators including birds, fish and zooplankton have been found to feed successfully (Kraft *et al.* 2012). High levels of bioluminescence, rivalling those of the deep sea, and the diurnal vertical migration of the bioluminescent and other zooplankton has also been observed in the water column both in the Arctic and Antarctic polar nights (Johnsen *et al.* 2014, Berge *et al.* 2009, Berge *et al.* 2012, Cisewski *et al*. 2010). The visual capabilities of Arctic species are also challenging our concept of dark. Copepods of the genus *Calanus* are highly important to the marine Arctic ecosystem (Conover 1988). They have been found to be sensitive to the light of a clear night's sky down to approximately 50m depth and to the light of the aurora borealis down to 60-100m (Båtnes *et al*. 2013). The eyes of polar cod are also thought to be well adapted to the sustained darkness of the polar night, and may even be adept for vision in the wavelengths emitted by the bioluminescence now known to be prevalent in the polar night (Jönsson *et al*. 2014). The eyes of Atlantic cod appear to be less well adapted to long periods of sustained darkness (Jönsson *et al.* 2014). However, in the more southerly, but still Arctic, Balsfjorden at 68°N in northern Norway, winter darkness was found to have no effect on the feeding of Atlantic cod (Klemetsen 1982), suggesting that at that latitude at least the photoperiod constraint hypothesis does not hold.

If boreal fish are able feed in the polar night, they will clearly negatively impact those species that they eat, and they may also compete with native Arctic species. The warming temperatures of Kongsfjorden, combined with the extreme light conditions of three months of continuous Arctic darkness at 79°N, provides a perfect setting in which to test the photoperiod constraint hypothesis. In the context of increased interest in the Arctic for fishing, hydrocarbon extraction and shipping, it is also important to fill in our knowledge gaps of this ecosystem so as to inform the responsible management of this vast and largely unexploited wilderness (Lønne *et al*. 2014).

Aims and objectives

This study aims to further expand the rapidly growing knowledge base of the functioning of marine ecosystems in the polar night, to assess the ability of 'invasive' boreal species to feed in the extreme light environment of the polar night and to explore the role of winter dietary competition in the growing dominance of boreal species.

Specifically, through study of the feeding success and diet of fish collected in the polar night, this paper aims to test the hypothesis that boreal species are less adapted than their Arctic counterparts to feed successfully during the polar night, and will answer the following questions:

- Do visually predating fish feed in the polar night?
- Are there differences in the feeding success and diet Arctic and non-native species?

- What is the role of visual predation for the fish community in the polar night?

Hypotheses

Null hypothesis 1:

H_0: Visually predating fish do not feed in the polar night.

H_1: Visually predating fish do feed in the polar night

Null hypothesis 2:

H_0: There are no differences in the feeding success of Arctic and boreal species.

H_1: Arctic species feed more successfully than boreal species

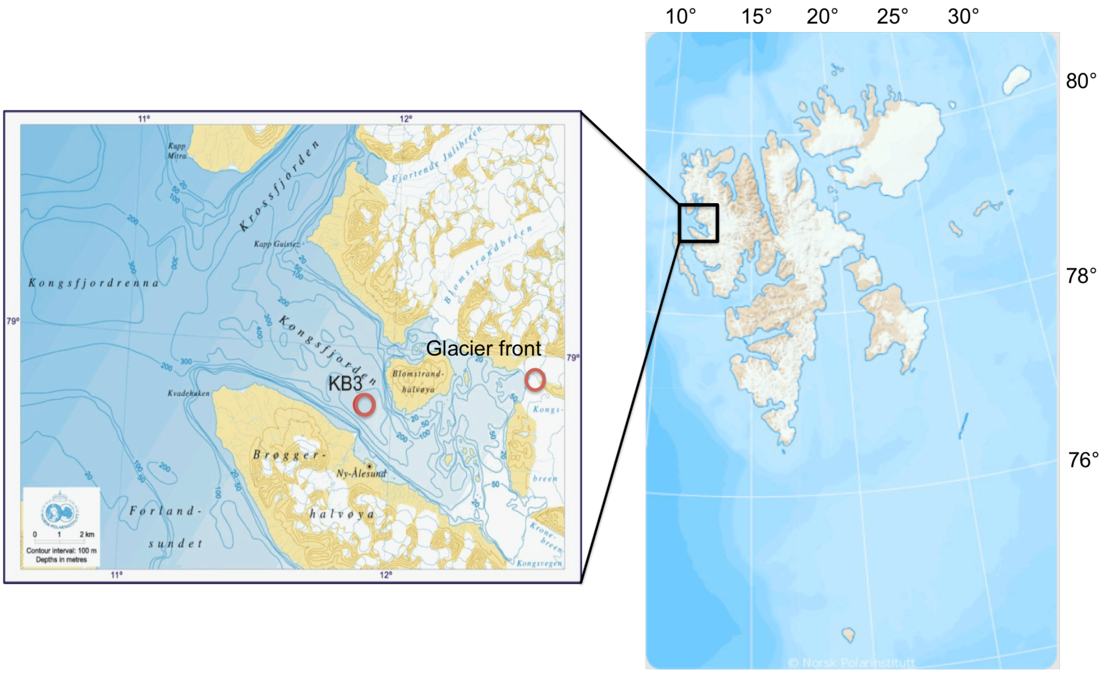


Figure 1 - The location of Kongsfjorden. Map adapted from the Norwegian Polar Institute.

Methods

Sample collection

All fish were collected in Kongsfjorden (78.5°N, 15° E) during the Polar Night cruise between the 16th and the 20th of January 2014, aboard the R/V *Helmer Hanssen*. During this time, and since the 22nd of November 2013, the solar altitude was constantly 9° or more below the horizon, a light climate characterised as *civil polar night* (Berge et al. in press). Six pelagic and two demersal trawl hauls were taken at the site KB3 in the central fjord basin (figure 1), with one further demersal trawl at the shared front of the Kongsbreen and Conwaybreen glaciers (figure 1). The pelagic trawls targeted the sound scattering layer identified by a ship based EK-60 multi-frequency hydro-acoustic profiler and varied in depth between 100 and 150m. The depths of the demersal trawls at KB3 were between 320 and 350m, and the depth of the demersal trawl at the glacier front was between 130 and 140m depth.

The pelagic trawls were taken with a Harstad pelagic trawl and a cod end with a mesh size of 20mm. The demersal trawls were taken with a Campelen 1800 shrimp trawl with rockhopper gear and a mesh size of 20mm. The date, duration and location of each trawl are presented in table 1, along with the total catch.

Table 1 - Total catch and stomachs sampled from Pelagic and demersal trawls in January 2014 in Kongsfjorden, Svalbard. All trawls were at a speed of 3 knots

Trawl	1	2	3	4	5	6	7	8	*9*	**Number of stomachs collected**	
Habitat	Pelagic	Pelagic	Demersal	Pelagic	Pelagic	Pelagic	Demersal	Pelagic	*Glacier*		
Depth (m)	125	125	330-350	130	125	100	300-355	100	*135-145*		
Date	16.01	17.01	17.01	18.01	18.01	19.01	19.01	19.01	*20.01*	**Pelagic**	**Demersal**
Time (UTC)	21:18	08:28	18:59	09:06	20:26	07:06	15:00	19:52	*12:32*		
Duration	19 min	16 min	17 min	15 min	15 min	17 min	15 min	16 min	*11min*		
Fish											
G. morhua	149	215	139	300	256	407	79	348	*20*	**133**	**46**
M. aeglefinus	78	160	30	210	70	204	6	101	*40*	**132**	**10**
B. saida	13	15	52	11	11	7	80	7	*4200*	**35**	**87**
C. harengus	289	145	10	70	146	344	7	406	*90*	**27**	**0**
M. villosus	3	10	30	6	31	23	72	37	*10*	**40**	**31**
H. platessoides			24				7			**0**	**26**
A. hyperborea			2							**0**	**2**
Sebastes spp.	2	3		4			25	1			
L. maculatus	N.C	NC	NC	215	NC	NC	13	432	*200*		
R. hippoglossoides	5	5	6	3	2		5	3			
Myoxocephalus spp		1	1				2				
Liparis spp	4	6	3				4				
Lycodes spp									*30*		
Crustaceans											
P. borealis	307	655	9000	59	29	80	4148	20	*450*		
Euphausida	63 800	59 400		76 800	56 400	61 200		129 900			
S. septemcarinata			35		5		20		*40*		
Amphipoda	< 20	< 10						8			
M. norvegicus						40					

Water conditions

During the cruise the water column at KB3 was well mixed, with temperatures of between 0.75 and 1.25°C and a salinity of 34.9 p.s.u. This was a mixture of transformed Atlantic water and local water by the definition of Cottier *et al.* (2005). At the glacier front, the water was colder, between -1°C and -1.5°C and slightly fresher at approximately 34.5 p.s.u.

Fish sorting

On board, the trawl catches were sorted into species and the total biomass and number of individuals of each species was recorded. In the case of *Pandalus borealis* and euphausids, the volume of the catch was recorded and the total number was estimated by counting a subsample. Of the total catch, 100 fish of each species were haphazardly selected, if there were less than 100 individuals, then all individuals were used. The weight and total length was recorded for each fish in the subsample. Large specimens of *G. morhua* and *M. aeglefinus* were specifically selected from some trawls to ensure coverage of the whole range of fish sizes. As these individuals were not sampled randomly, they were not included in calculations of the size distribution of each species. On the basis of the size distribution of all fish collected during the cruise, the following size categories were chosen: ≤9cm, 9.1-18cm, 18.1-28cm, ≥28.1cm. (See appendix for the detailed size distribution of each species.)

From each subsample of up to 100 individuals, a further stratified subsample of 30 individuals was selected to cover all size ranges present. If there were less than 30 individuals in the original sample, then all individuals were used. These fish were dissected, their stomachs, livers and gonads (if present) were removed and individually weighed, and the gender of each fish was determined. If no gonads were found, the fish was classified as a juvenile. In addition, the somatic weight of each fish (the weight after the removal of all internal organs) was measured. The stomachs were then placed in individual labelled jars of 70% ethanol. The ethanol was replaced with fresh 70% ethanol on returning to land. An overview of the number of stomachs collected for each species is presented in table 1.

Condition, hepato-somatic index and gonado-somatic index

The Fulton's condition factor was calculated for each fish that was subsampled for dietary analysis. The Fulton's condition factor (K) is calculated as

$$K=100 \times W/L^3$$

where, W is the wet weight of the fish and L is the total length (Fulton 1904).

The hepato-somatic index (HSI) is a measure of energy storage in a fish and is measured as the ratio of liver weight to somatic weight. The gonado-somatic index (GSI) is a measure of sexual maturity and is measured as the ratio of gonad weight to somatic weight.

For those species that occurred in both habitats, inter-habitat differences in condition and HSI were tested using the Kruskal-Wallace non-parametric analysis of variance. An inter-habitat comparison of GSI, again using the Kruskal-

Wallace test, was conducted for polar cod only, as it was the only species with a large proportion of mature individuals.

Prey identification

For diet analysis, stomachs were analysed in a random order. They were removed from the ethanol, dabbed on a paper towel to remove excess liquid and re-weighed (in order to assess if there had been any change in stomach weight during storage). The stomach contents were removed under a dissecting microscope. At this point it was necessary to differentiate between prey items and the stomach lining, which had a tendency to contract around prey material or in on itself to give the appearance of a prey item. The empty stomach and the stomach lining and were then re-weighed in order to calculate total contents weight.

The prey contents were identified under a dissecting microscope to the lowest possible taxonomic group and were enumerated. In some cases specific identification wasn't possible due to the level of digestion. A list of all identified taxa is presented in table 2.

Feeding success

'Feeding success' was determined as the percentage of fish of a given species that had successfully fed. The stomach fullness of those fish that had successfully fed was calculated using the total fullness index (TFI):

Table 2 - An overview of all prey items encountered in the stomachs of fish collected in Kongsfjorden, January 2014.

CRUSTACEANS

- Crustacean indet

Euphausids

- Euphausida indet
- *Thysanoessa* spp.
- *T. longicaudata*
- *T. inermis*
- *T. raschii*
- *Meganictyphanes norvegicus*
- Euphausid furcilla

Non-euphausid decapods

- Decapoda indet
- Decapoda larvae
- Caridae
- Crangonidae
- *Pandalus borealis*
- *Sabinea septemcarinata*
- Hyas

Copepods

- Copepoda indet.
- Calanoida indet.
- *Calanus* spp
- *C. hyperboreus*
- *C. glacialis/*
- *C. finmarchicus*
- *Paraeuchaeta norvegica*
- *Pseudocalanus* spp.
- *Microcalanus* spp.
- *Metridia longa*
- *Gaetanus* spp.
- *Chiridius obtusifrons*
- *Scaphocalanus magnus*

Amphipods

- Amphipoda indet
- Gammaridae spp.
- Oedicerotidae spp.
- Lysianassidae sp.
- *Stegocephalus inflatus*
- *Ampelisca* sp.
- *Themisto* spp.
- Hyperiidae spp.
- Mysida spp.
- Isopoda spp.
- Cumacea spp.
- Tanaidae sp.

FISH

- Fish indet
- Gadoidae indet
- *Gadus morhua*
- *Boreogadus saida*
- *Melanogrammus aeglefinus*
- *Reinhardtius hippoglossoides*
- *Leptoclinus maculatus*
- *Clupea harengus*
- *Mallotus villosus*

OTHERS

- Polychaeta spp.
- Bivalvia spp.
- *Limacina* spp.
- Foraminifera spp.

$$TFI=10^4W/L^3$$

where, W is the total wet weight of prey in the stomach, and L is the total length of the fish. Inter-species and inter-habitat differences in TFI were tested using Kruskal-Wallace non-parametric analysis of variance.

Stomachs that contained only ‘mush’, material that was digested beyond both identification and enumeration, were classified as having successfully fed and their TFI was calculated. However, as the abundance of mush could not be counted, fish containing only mush were not included in further dietary analysis.

Diet analysis

Percentage abundance was calculated as the numerical abundance of a given prey group as a proportion of the total number of prey items in a given group of fish. Percentage abundance was calculated for each size class of each species in each habitat. The demersal trawls at KB3 and the glacier front were grouped.

Percentage occurrence was calculated as the number of stomachs in which a prey item occurred as a proportion of the total number of stomachs that contained at least one prey item besides mush. Percentage occurrences were calculated for each species in each habitat.

Rarefaction curves were calculated to assess whether or not each species had been representatively sampled for diet in each habitat. The rarefaction curves indicated that the gadoids were more representatively sampled for diet than the other fish species. As such, comparative multivariate statistical analysis was focussed on the gadoids to give the statistical tests more power. (See appendix for rarefaction curves.)

Percentage abundance values for each individual were compared using multivariate analyses. A non-metric multidimensional scaling analysis (NMDS) was performed using the bray-curtis dissimilarity of square-root transformed percentage abundance data to visualise the diet of each individual fish. Percentage occurrence is less appropriate for such analysis as it requires the use of average values calculated from a larger group, hiding any within group variation. Using the percentage abundances of each individual sample meant that the NMDS could identify differences between species or habitats, which are identified through clustering on the NMDS plot.

The complementary similarity percentage (SIMPER) and analysis of similarity (ANOSIM) analyses quantify the intra-specific similarity of diet and quantify and assess the statistical significance of inter-specific dietary dissimilarity (Rees et al. 2005). SIMPER calculates the average similarity within, or the average dissimilarity between, grouped samples; in this case samples were grouped by species and habitat. Every individual sample is compared to every other sample, either within the group (in the case of similarity) or between groups (in the case of dissimilarity). ANOSIM, calculated from the bray-curtis dissimilarity matrix, takes into account both within group and between group variations to evaluate the overall significance of any dietary variation indicated by the SIMPER analysis.

The Schoener's index of dietary overlap was also calculated in order to compare the results of this study with that of Renaud et al. (2012).

$$\text{Schoener's index of overlap} = \left(\sum_{1=1}^{n} |Pxi - Pyi| \right)$$

where P_{xi} and P_{yi} are the proportions of food item i in species x and y respectively, and n is the total number of prey items identified.

The multivariate analysis and the Schoener's index of overlap were calculated using two different sets of prey categories, one with high taxonomic resolution, including 31 different prey categories, and the other with lower taxonomic resolution, including 11 different categories. This was to look for any variations in the patterns of dietary similarity, especially given the potentially overlapping prey categories which result from the inability to identify partially digested prey items. The high-resolution and low-resolution sets of prey categories will hereafter be referred to as 'narrow' and 'broad' respectively. Each category in the narrow group contained either a single species, or in the case of low abundance, a group of a few, very closely related species, such as *calanus* or hyperiidae. Prey categories were created so as to constitute >5% of the percentage abundance of at least one fish species. The broad categories contained a larger number of species in related groups, such as euphausids or fish. The results of the SIMPER and ANOSIM analyses and the Schoener's overlap values are presented in table 3.

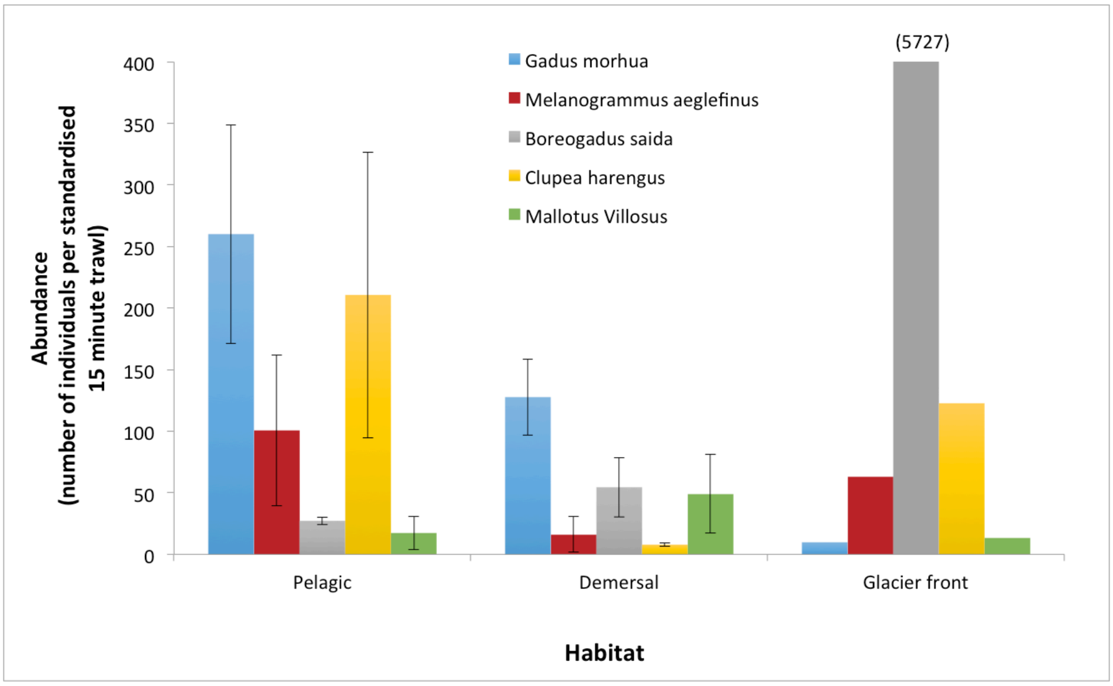


Figure 2 - The relative abundance in the different trawls of the most abundant fish in Kongsfjorden. All trawls were standardised to a 15 minute trawl at a speed of 3 knots. The number above *B. saida* in the glacier front trawls represents the total catch, which could not be displayed on the y-axis. Error bars show standard deviation.

Results

Trawl catch

Atlantic cod was numerically dominant in both the pelagic and the demersal trawls (table 1, figure 2). Polar cod was dominant in the cold waters of the glacier front.

There was considerable size overlap between the three gadoids and capelin, though there were also several large Atlantic cod, up to 110cm. In all species but polar cod, there was considerable size overlap between the demersal and the pelagic habitats. Polar cod showed considerable differences in total length between the pelagic, demersal and glacier front trawls. (see appendix for figures)

Inter-habitat comparison of condition, HSI and GSI

Individuals of Atlantic cod and capelin caught in the demersal trawls were in better condition than those caught in the pelagic trawls, whilst haddock were in a better condition in the pelagic (figure 3). Demersal Atlantic cod also had larger liver energy stores than pelagic Atlntic cod, whilst there was no inter-habitat difference in HSI for either capelin or haddock (figure 4).

Polar cod caught at the glacier were in the best condition, had the largest liver energy stores and were the most reproductively mature (figures 3,4,5). There were no differences in condition or GSI between pelagic and demersal caught polar cod, reflecting the fact that most of the fish caught in these trawls were juveniles. However, demersal caught polar cod had larger liver energy stores

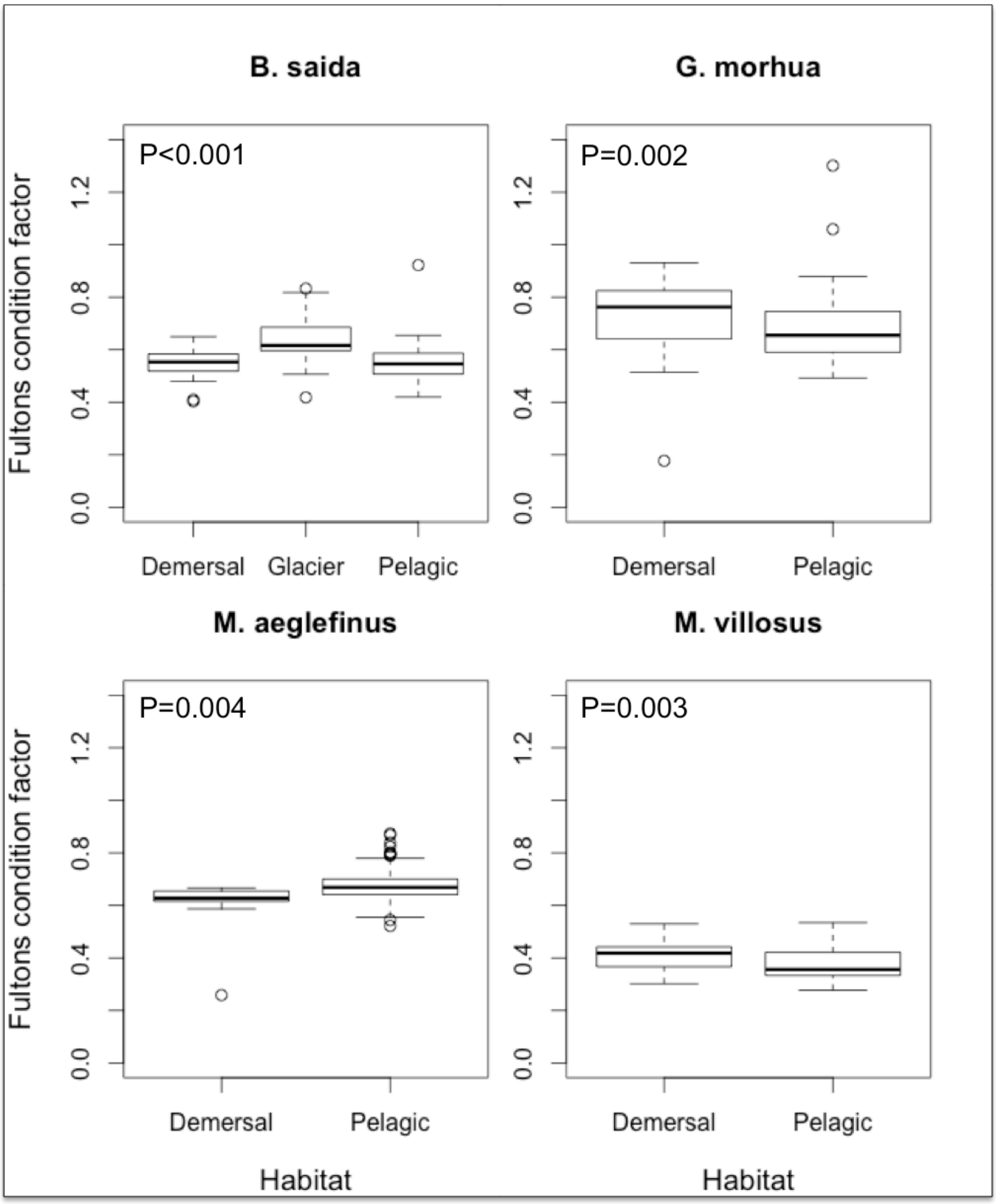


Figure 3 – Inter-habitat comparison of the Fulton's condition factor for the four fish species found in both demersal and pelagic trawls. Only polar cod from the glacier trawl were weighed and measured. The P values are from kruskal-wallace tests comparing the habitats for each species.

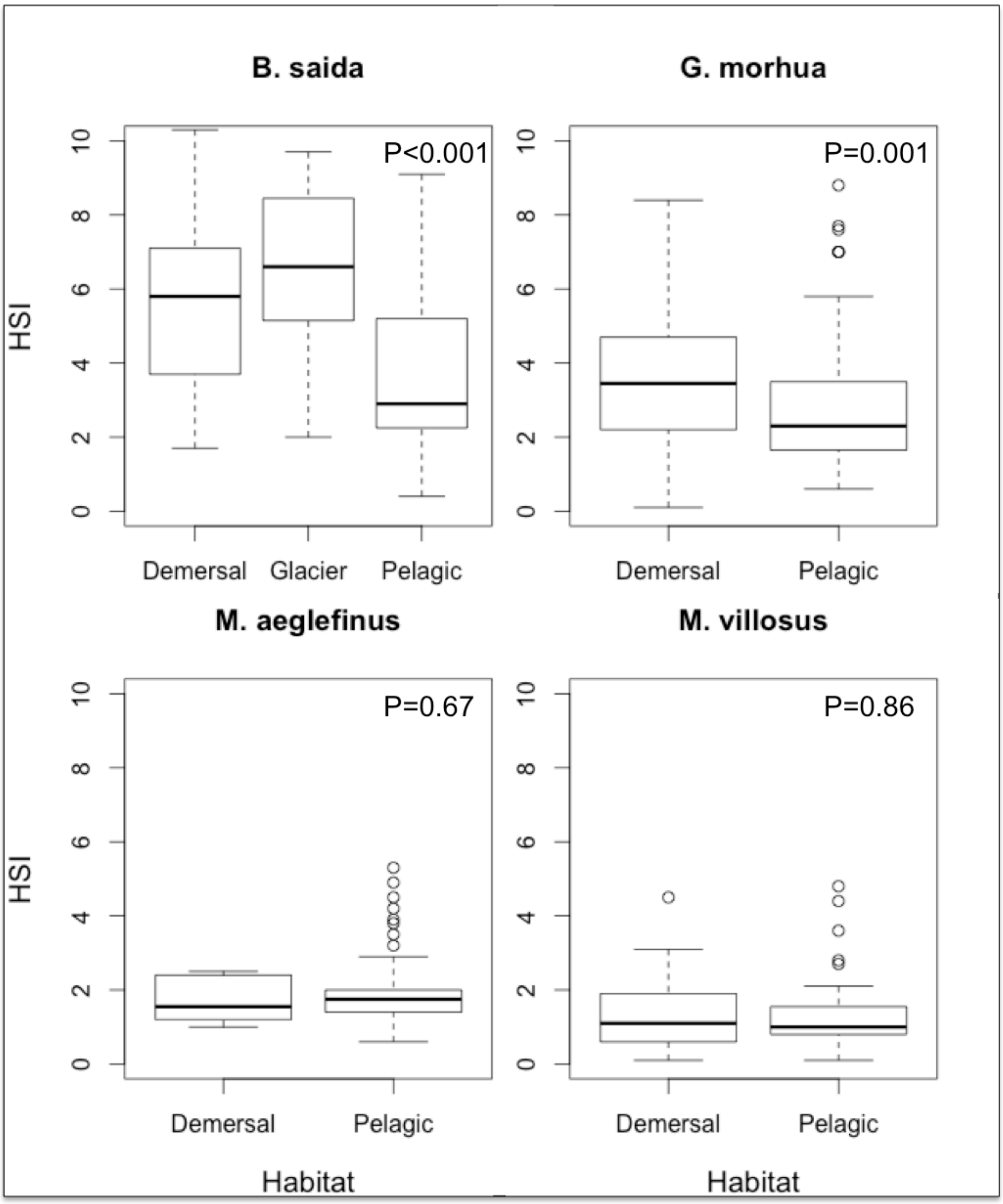


Figure 4 – Inter-habitat comparisons of the hepato-somatic index of the four fish species found in both demersal and pelagic trawls. Only polar cod livers were weighed from the glacier front trawl. The P values are from kruskal-wallace tests comparing the habitats for each species.

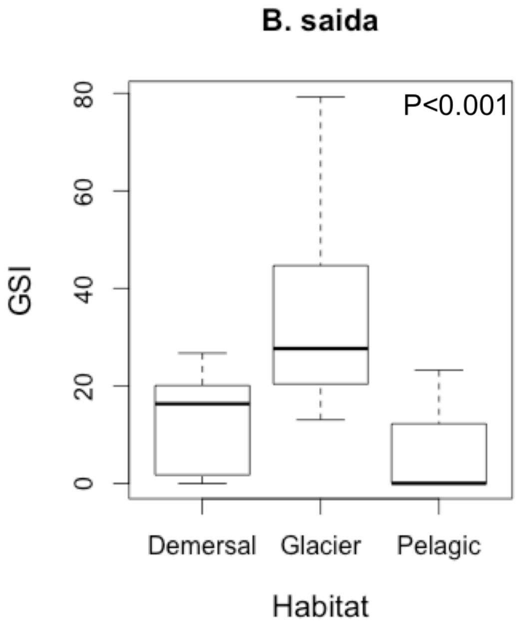


Figure 5 - Inter-habitat comparison of the gonado-somatic index of polar cod, *Boreogadus saida*. The P value is from a inter-habitat comparison using a kruskal-wallace test.

than pelagic fish. Very few fish of other species had mature gonads, though the largest female Atlantic cod had large ripening gonads.

Feeding success

Do fish feed?

All species for which stomachs were collected contained individuals that had prey in their stomach (figure 6).

Are there differences in feeding success between native and non-native species?

There were clear differences in the feeding success between species (figure 6), but no clear overall difference in feeding success between the more Arctic species (polar cod, Arctic skate (*Amblyraja hyperborea*) and capelin (*Mallotus villosus*)) and the more boreal species (Atlantic cod and haddock). Instead, the three gadoid species were found to have fed more successfully than all other species, with the exception of Arctic skate (figure 6). Though the three gadoids had comparable feeding success, the stomachs of Atlantic cod were more full than those of all other species in both the pelagic and the demersal, again with the exception of the two Arctic skates sampled (figure 7). The stomachs of haddock were the least full of all species in both habitats (figure 7).

Are there differences in feeding success between habitats?

Of those fish species collected in both demersal and pelagic trawls, polar cod had fed more successfully in the pelagic and haddock had fed more successfully in the

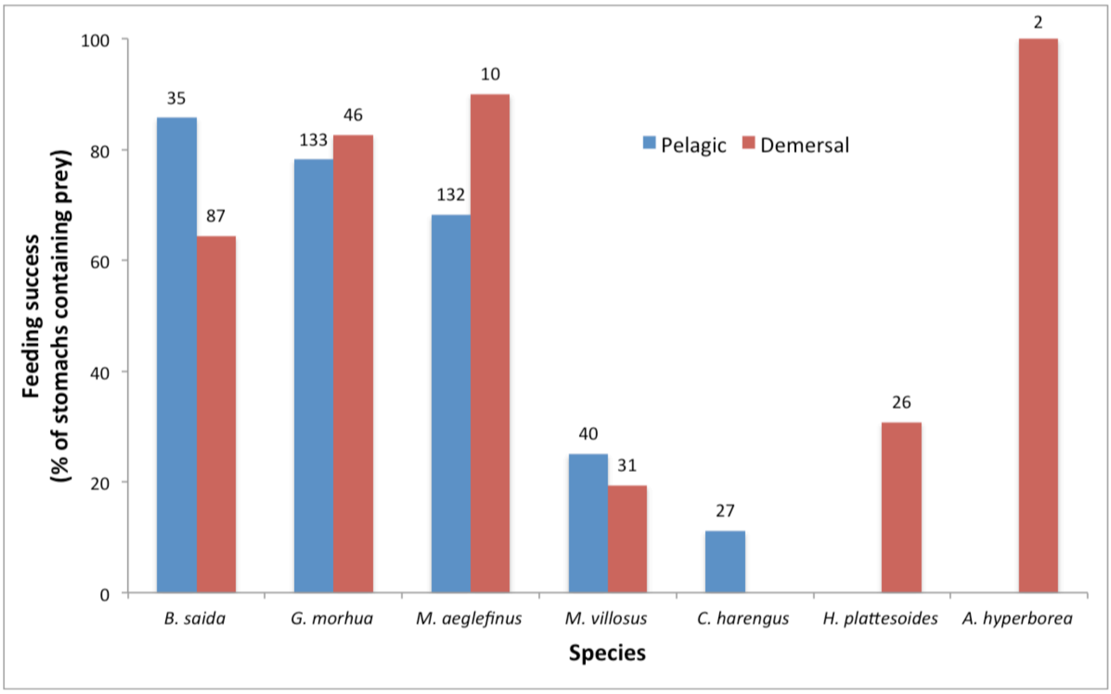


Figure 6 - The percentage feeding success of each species. The number above each bar is the number of individuals in each sample.

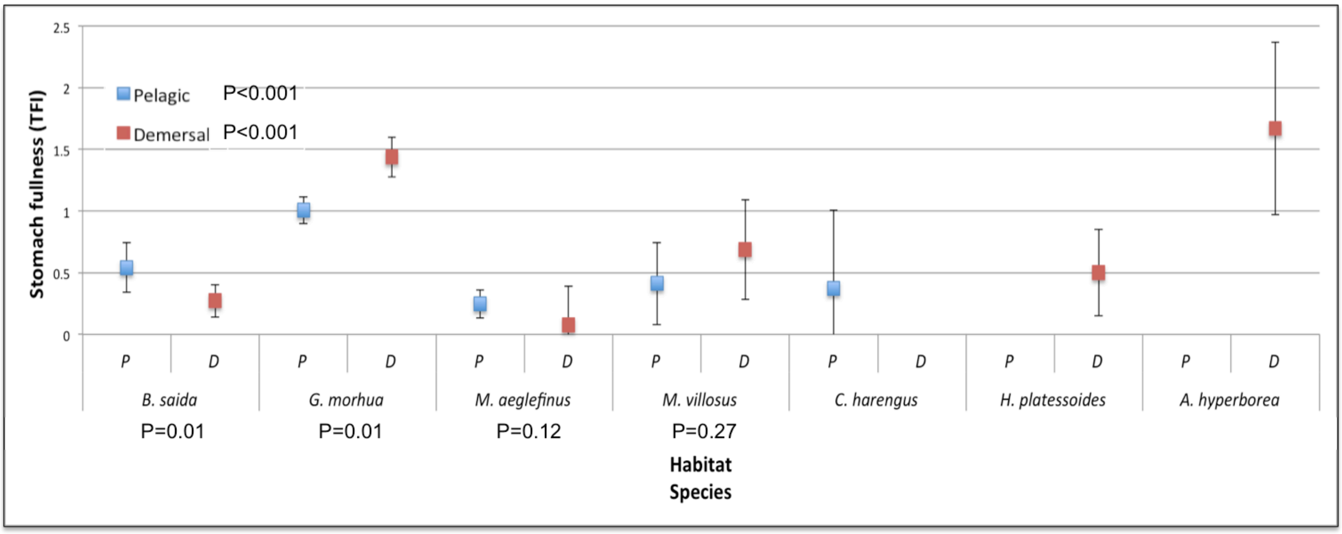


Figure 7 – Mean stomach fullness (TFI) of each species in each habitat. Error bars show standard error of the mean. P values are calculated from inter-species and inter-habitat comparisons using a Kruskal-Wallace test.

demersal whilst for capelin and Atlantic cod there was no difference in feeding success between the habitats (figure 6).

Taking into account both fullness and percentage feeding success, Atlantic cod and polar cod had clear inter-habitat differences in overall feeding success (figures 6&7). Atlantic cod were more full in the demersal (figure 7) whilst polar cod had both fed more successfully and were more full in the pelagic (figures 6&7a). Of the ten haddock caught in the demersal, all had fed(figure 6), but those haddock caught in the pelagic trawls appeared more full, though there was no significant difference (figure 7). Capelin appeared to have fed equally well in the pelagic and the demersal trawl (figures 6&7a).

Diet

Inter-habitat comparison

The overall diet of the fish community was different between the pelagic and demersal habitats (figure 8), as is indicated by the clustering of samples in the NMDS (figure 9).

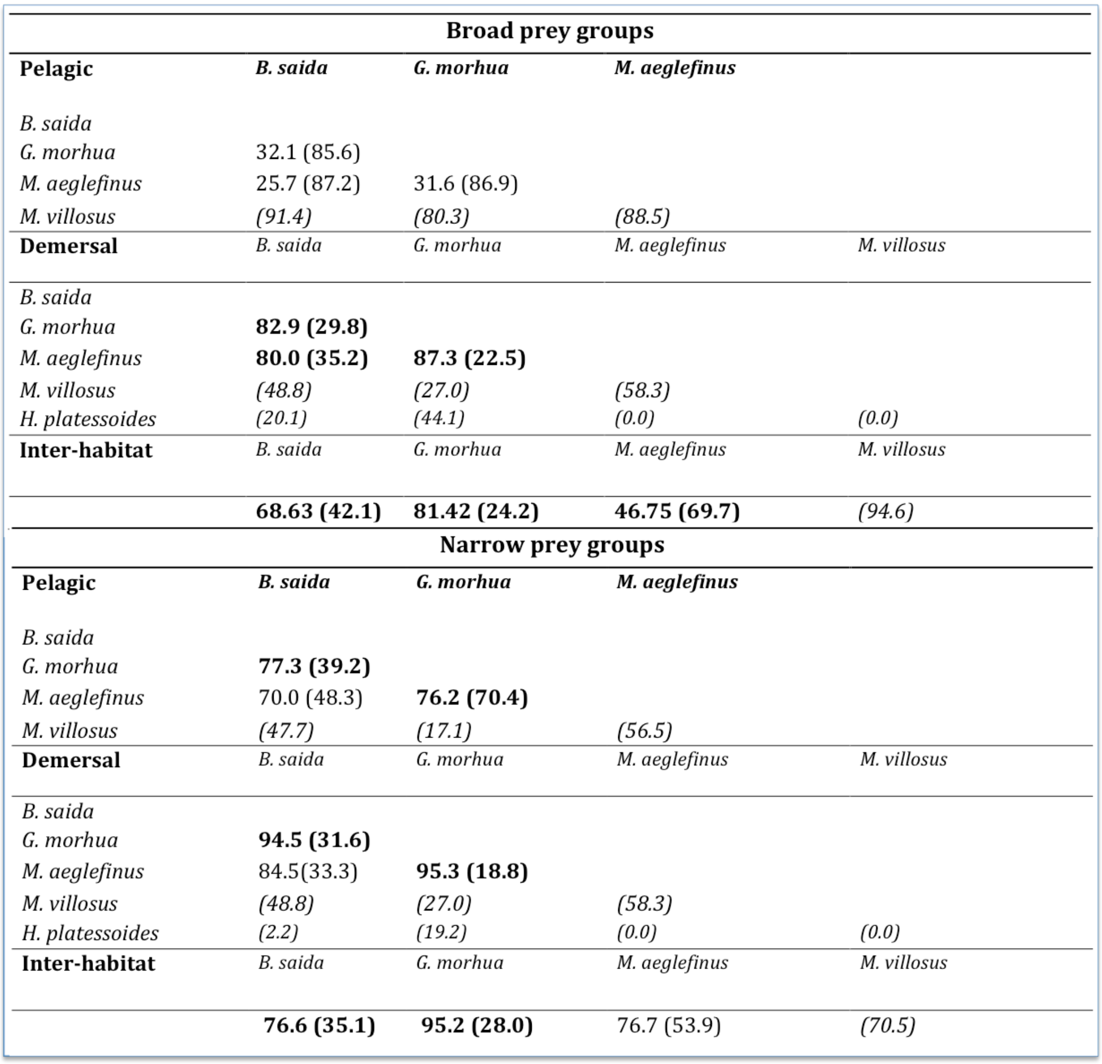
In the pelagic, diet was homogenous across all the different fish species (figure 8, tables 3 & 4). The dominant prey item in all species was krill, which occurred in 90% of stomachs overall. The only variation between individuals of different sizes was the increased importance of fish in the diet of larger fish and the increased importance of copepods in smaller fish (figure 8). However, when the higher resolution prey groups were compared, the diet of Atlantic cod was

Table 3 - The percentage occurrence of each prey item in the diets of fish caught in demersal and pelagic trawls. Fish caught in demersal trawls at KB3 and the glacier front were combined.

Pelagic					
Prey item	B. saida (n=26)	G. morhua (n=99)	M. aeglefinus (n=64)	M. villosus (n=10)	C. harengus (n=2)
Euphausids	92	88	92	90	100
Non-euphausid decapods	0	5	0	0	0
Calanoid copepods	15	3	3	10	0
Amphipods	4	4	5	10	0
Other crustaceans	4	1	2	0	0
Fish	0	33	2	0	0
Polychaetes	0	0	0	0	0
Bivalves	0	2	2	0	0
Limacina	0	0	8	0	0
Foraminifera	0	0	3	0	0

Demersal						
Prey item	B. saida (n=46)	G. morhua (n=34)	M. aeglefinus (n=6)	M. villosus (n=5)	H. platessoides (n=2)	A. hyperborea (n=2)
Euphausids	46	21	67	80	0	50
Non-euphausid decapods	2	44	0	0	50	100
Calanoid copepods	59	18	0	20	0	0
Amphipods	11	50	33	0	0	100
Other crustaceans	0	24	0	0	0	50
Fish	24	41	0	20	50	50
Polychaetes	2	21	0	0	0	0
Bivalves	0	0	0	0	0	50
Limacina	0	0	17	0	0	0
Foraminifera	0	3	17	0	0	50

Table 4 - Inter-species and inter-habitat dietary comparisons. The numbers outside of the brackets are the percentage dissimilarity between groups, calculated with SIMPER and the numbers in brackets are the Schoener's index of overlap between species/ habitats. Numbers in bold indicate a significant difference in diet, as indicated by ANOSIM.



		Broad prey groups		
Pelagic	***B. saida***	***G. morhua***	***M. aeglefinus***	
B. saida				
G. morhua	32.1 (85.6)			
M. aeglefinus	25.7 (87.2)	31.6 (86.9)		
M. villosus	*(91.4)*	*(80.3)*	*(88.5)*	
Demersal	*B. saida*	*G. morhua*	*M. aeglefinus*	*M. villosus*
B. saida				
G. morhua	**82.9 (29.8)**			
M. aeglefinus	**80.0 (35.2)**	**87.3 (22.5)**		
M. villosus	*(48.8)*	*(27.0)*	*(58.3)*	
H. platessoides	*(20.1)*	*(44.1)*	*(0.0)*	*(0.0)*
Inter-habitat	*B. saida*	*G. morhua*	*M. aeglefinus*	*M. villosus*
	68.63 (42.1)	**81.42 (24.2)**	**46.75 (69.7)**	*(94.6)*
		Narrow prey groups		
Pelagic	***B. saida***	***G. morhua***	***M. aeglefinus***	
B. saida				
G. morhua	**77.3 (39.2)**			
M. aeglefinus	70.0 (48.3)	**76.2 (70.4)**		
M. villosus	*(47.7)*	*(17.1)*	*(56.5)*	
Demersal	*B. saida*	*G. morhua*	*M. aeglefinus*	*M. villosus*
B. saida				
G. morhua	**94.5 (31.6)**			
M. aeglefinus	84.5(33.3)	**95.3 (18.8)**		
M. villosus	*(48.8)*	*(27.0)*	*(58.3)*	
H. platessoides	*(2.2)*	*(19.2)*	*(0.0)*	*(0.0)*
Inter-habitat	*B. saida*	*G. morhua*	*M. aeglefinus*	*M. villosus*
	76.6 (35.1)	**95.2 (28.0)**	76.7 (53.9)	*(70.5)*

significantly different to that of both haddock and polar cod (table 4). This was due to higher abundances of ‘unidentified euphausids’ as a proportion of the total number of euphausids.

In the demersal, there was clear dietary variation both between different size classes (figure 8) and between different species (figures 8&9, tables 3&4). The overall dietary diversity was also higher in the demersal than in the pelagic (figure 8). Krill, calanoid copepods, fish and non-euphausid decapods were all important prey items. Gammarid and hyperiid amphipods, mysids and polychaetes also all occurred in >5% of stomachs. The importance of euphausids and copepods decreased with size, whilst fish and non-euphausid decapods increased in importance with size(figure 8). As such, benthic prey items were more important in the largest demersal fish, predominately Atlantic cod, whilst the prey of smaller fish was largely pelagic in origin. Pelagic prey items were most important to capelin, haddock and polar cod, whilst benthic items dominated the diet of Atlantic cod, especially in the larger fish (figure 8).

Specific inter-habitat comparisons

Polar cod

The demersal diet of *B. saida* was significantly different to the pelagic diet, containing higher abundances of copepods and fish and lower abundances of euphausids (figure 8, tables 3 & 4). None of the food items were benthic in origin, and the higher occurrence of copepods and small fish, mainly *Leptoclinus maculatus*, reflect their higher abundances in the demersal.

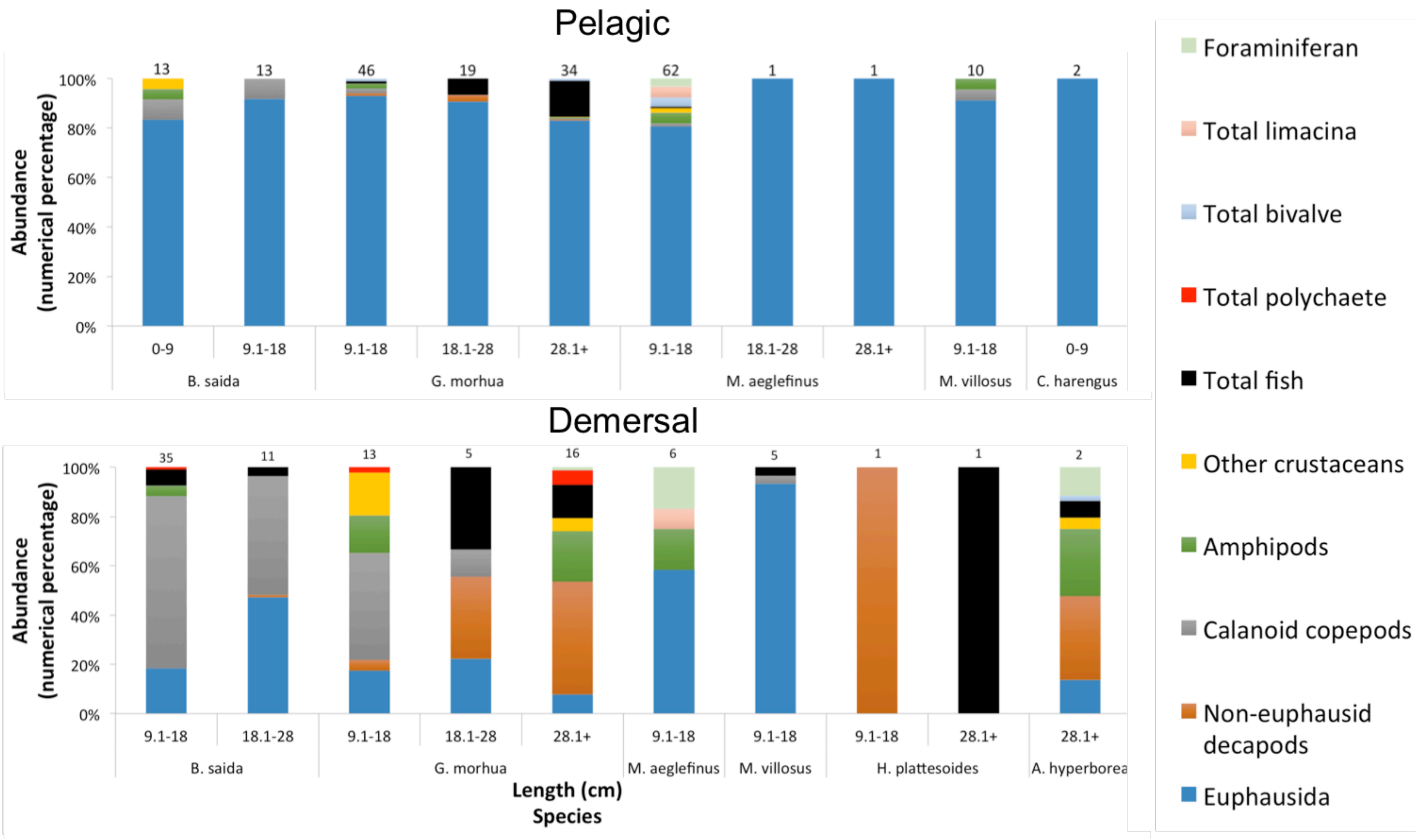


Figure 8 - The proportional abundance of each food item in the diet for the different species and size classes of fish. The number above each bar is n, the number of fish in each sample

Atlantic cod

The demersal diet of Atlantic cod was significantly different to its pelagic diet, containing more benthic food items such as gammarid amphipods, non-euphausid decapods as well as more copepods than in the pelagic. The pelagic Atlantic cod had a much higher abundance of euphausids in their diet (figure 8, tables 3 & 4).

Haddock

The diet of haddock was not significantly different between the two habitats, with euphausids the dominant prey items in both habitats (figure 8, tables3 & 4). There was a slightly higher abundance of euphausids in the pelagic, and higher abundances of amphipods, *limacina* spp. and foraminifera in the demersal. All prey items found in the diet of haddock were found in the stomachs of fish in both habitats.

Capelin

The diet of capelin was similar between the pelagic and the demersal caught fish, with similar contributions of euphausids and copepods (figure 8, tables 3 & 4).

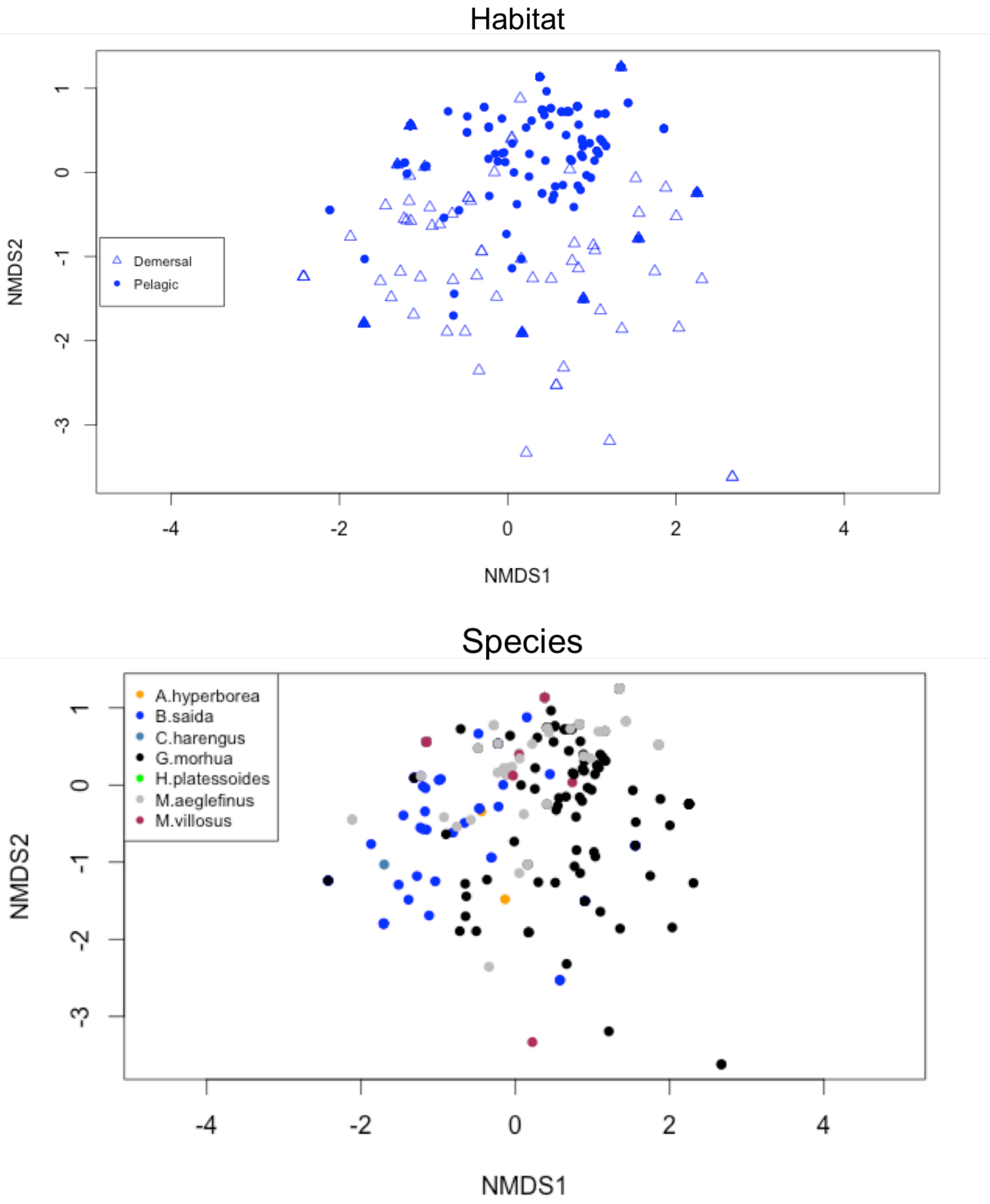


Figure 9 - NMDS plot of diet for all fish, using the narrow prey groups. The top plot shows the clustering of individuals from each habitat, whilst the bottom plot shows clustering by species.

Discussion

Boreal dominance

The relative abundance of the three gadoids observed here (figure 2, table 1) was different to that observed in 2006 and 2008 (Renaud *et al.* 2012). Atlantic cod and haddock had become more numerically dominant. In 2006, approximately twice as many polar cod were caught as haddock and Atlantic cod (Renaud *et al* . 2012), even though numbers where only reported by Renaud *et al*. (2012) for the 85%-100% of stomachs which were full, a conservative estimate would still indicate that polar cod were dominant. In 2008, only polar cod was caught in the pelagic trawls in Kongsfjorden and in both years neither haddock nor Atlantic cod were caught in demersal trawls (Renaud *et al.* 2012). In January 2014, both haddock and Atlantic cod were caught in demersal trawls, which they weren't in either 2006 or 2008. This shift in the fish community is evidence of the increasing borealisation of the Arctic.

The high abundance of euphausids observed in the fish stomachs and in the trawls is also in itself evidence of the borealisation of Kongsfjorden. In 1996, the Arctic species *Limacina helicina* and *Themisto* spp. were numerically dominant in the fjord, even in July when there would have been increased influence of Atlantic water (Weslawski & Pedersen 2000).

Visual predation and dietary overlap

Renaud *et al* (2012) found little dietary overlap between juvenile haddock, Atlantic cod and polar cod, and found that each species had high dietary fidelity between fjords. The high pelagic dietary overlap in this study contrasts with the consistent preferential selection of certain prey items found by Renaud *et al.* (2012). This may reflect an inability to selectively target prey in the darkness, or may also reflect the absence of preferred food items such as the pelagic amphipod *Themisto* spp for polar cod (Renaud *et al*. 2012, Nahrgang *et al.* 2014), and appendicularians for haddock (Renaud *et al.* 2012). The dominance of highly bioluminescent *Thysanoessa* in the diets of all pelagic fish could also suggest that all fish were somehow visually cued towards the same prey item.

The differences in patterns of dietary overlap between Renaud *et al.* (2012) and those seen here may also have been due to different sizes of the co-occurring fish. The fish collected in this study were generally larger than those collected by Renaud *et al.* (2012), perhaps as a result of the four months extra growth time since spawning as a result of being sampled in January rather than in September, when they were sampled by Renaud *et al.* (2012). This indicates that the degree of competition between co-occuring gadoids in the Arctic may vary over their life histories. However, due to the high abundance of euphausids in the sound-scattering layers (table 1), the high dietary overlap observed may not necessarily indicate high levels of competition.

Ultimately, the very high abundance of euphausids in Kongsfjorden during this study also made it impossible to conclusively test the hypothesis that fish were visually selecting prey. An ideal situation to test this would be in an environment with two or more zooplankton taxa in high abundance, for example *Themisto* and *Thysanoessa*. This would be especially interesting to test the role of bioluminescence in winter visual predation as *Thysanoessa* spp. are bioluminescent, whilst *Themisto* spp. are not (Berge *et al*. 2012). This would then provide a setting in which to test whether polar cod does indeed have a higher capacity than Atlantic cod to see in those wavelengths of light produced from bioluminescence (Jönnson *et al.* 2014).

Visual predation vs other methods of predation

The occurrence of a wide variety of benthic items highlights the use of tactile predation in Atlantic cod. The apparent selection of copepods by demersal polar cod, indicated by a higher occurrence of copepods than in the other fish species, may reflect a higher ability for visual predation in polar cod, perhaps indicating a higher capacity of polar cod eyes to detect those wavelengths of light produced by bioluminescent organisms (Jönsson *et al.* 2014), including the euphausids that were so abundant during our sampling effort. The absence of benthic prey items from the diet of polar cod offers no evidence of tactile predation in polar cod.

Feeding success and winter survival

Atlantic cod exploited benthic and pelagic food resources better than the other gadoids and capelin (figure 8). They consumed a higher weight of food than polar cod and haddock and had a threefold higher percentage feeding success than capelin. In the Barents Sea in winter 25% of Atlantic cod larger than 50cm were found to have empty stomachs (Michalsen *et al.* 2008). Of the 5 fish we caught over 50cm long, all had fed, and 4 of the 5 had a TFI equal to or exceeding the winter levels and similar to the summer levels of feeding reported by Michalsen *et al*. (2008). As such, the winter feeding success of large Atlantic cod does not appear limited by the extreme light environment despite the maladaptation of their eyes to sustained darkness (Jönsson *et al.* 2014).

The dark season has previously been found to have no effect on the feeding success of Atlantic cod at 69°N, but here is documented the first evidence of this at such high latitudes (Klemetsen 1982). This all suggests that, for Atlantic cod at least, the polar night is not a barrier to invasion. Their ability to feed on benthic prey items, and to predate on fish in the dense zooplankton aggregations of the pelagic, perhaps lit by bioluminescent euphausids, suggests that as more northerly areas of the Arctic become warm enough to support Atlantic cod, their expansion and potential establishment will not be limited by winter feeding success. The ripening gonads of the largest female caught also suggest that the northward expansion of spawning areas of Arcto-Norwegian cod (Sundby & Nakken 2008) may even extend to the fjords of the west coast of Svalbard, which would further enhance the northward flux of juveniles.

This is bad news for polar cod. The ability of *B. saida* to feed in winter may not be as important to their survival as to that of the boreal species, as lab based studies have found them to have reduced food intake and growth rates in winter, despite an unlimited food supply (Jensen *et al.* 1991). However, in the warmer water of Atlantic dominated fjords such as Kongsfjorden, a higher metabolic rate and, therefore a higher winter energy demand may be a factor in the low condition and liver energy store observed in this study. The different diet availability, devoid of their preferred *Themisto*, and year round predation by Atlantic cod, which unlike seals cannot be avoided through vertical migration (Benoit *et al.*

2010) are all combining to decrease the growth and reproductive success of polar cod (Nahrgang *et al*. 2014).

High abundances of polar cod may become restricted to cold refuges at glacier fronts, as observed in Kongsfjorden, where they appear to face a trade off between reduced predation pressure and a reduced ability to feed. However, the basal metabolic rate of polar cod caught in the cold water at the glacier front is likely to have been lower than in the warmer fjord basin. Glacier-front polar cod were larger (see appendix for details), and had a higher HSI and GSI, than fish caught at KB3 (figures 4 & 5). The length distribution, GSI and HSI of the glacier-front polar cod were in fact more characteristic of polar cod in areas dominated by Arctic water masses (Nahrgang *et al.* 2014). Their range may be severely restricted, but where they do occur in high abundance, they may be just as fit as in true Arctic water.

Limitation - digestion

'Unidentified euphausids' were those that had been digested beyond specific identification, but were still identifiable as krill, either from the body or from lone compound eyes. As such, a higher abundance of 'unidentified euphausids' in the stomachs of haddock and polar cod indicates that the euphausids in their stomachs were on average more digested than those in the stomachs of Atlantic cod. This in turn suggests that the krill had spent longer in the stomachs of polar cod and haddock than they had in *G. morhua,* and that as such it had been longer since they fed. This highlights the importance of taking into account digestion rates of different fish species when assessing percentage feeding success. For example, in the situation where 80% of the stomachs of one species contain highly digested prey items, and 70% of the stomachs of another species contain fresh undigested species which species has fed more successfully? As such the percentage feeding success of polar cod and haddock have been over-exaggerated compared to that of Atlantic cod.

Similarly the proportion of unidentified euphausids was higher in the demersal than in the pelagic in all species, indicating that on average it had been longer since the demersal fish had fed on euphausids.

The dietary similarity between demersal and pelagic haddock, and the presence of pelagic items (eg. *limacina*) in the stomachs of demersal fish, and the presence of benthic items, (eg. bivalves) in the stomachs of pelagic fish indicate that they migrate between habitats. However, hard-shelled organisms such as those may take a long time to digest (Macdonald *et al*. 1982), indicating that switching between habitats may not necessarily be a regular occurrence. The inter-habitat dietary dissimilarity of Atlantic cod and polar cod suggests that they remain in either the pelagic or demersal habitats, at least for long enough to have digested prey that they had consumed in the other habitat.

Conclusions

The fish community sampled from Kongsfjorden in January 2014 was found to prey on both pelagic and demersal zooplankton and on benthic organisms. The high proportion of fish found to have fed adds to the growing list of visual predators known to feed in the polar night (eg. Berge *et al.* 2009), and further challenges the paradigm of the polar night as a period of low biological activity.

There was no clear difference in the feeding success of Arctic and boreal species. However, the three species of co-occuring gadoids, the Arctic polar cod, and the boreal Atlantic cod and haddock were found to have fed more successfully than other species.

Ultimately, conditions were not ideal to assess the role of visual prey selection. The very high abundance of euphausids in the sound scattering layer targeted by the pelagic trawls did not provide a variety of prey items from which to select. There were however implications that demersal polar cod were more adept than any other species at feeding on pelagic copepods. Whether this is due to better adaptation to visual predation during periods of sustained darkness, or merely a reflection of morphology or behaviour is unknown.

Atlantic cod exploited both pelagic and benthic food sources and fed more successfully than any other species in both the demersal and pelagic habitats, with the largest individuals having fed as successfully as fish further south in the Barents Sea. Similar feeding success between habitats, albeit with higher fullness in the demersal, suggests that Atlantic cod were equally adept at catching pelagic and benthic prey. Whether pelagic predation was due to visual prey detection or to any other means of detection cannot be concluded from this study. What can be concluded is that the darkness of the polar night does not appear to inhibit the feeding success of Atlantic cod. For this species at least, photoperiod constraint may not provide a barrier to continued expansion into the Arctic.

The combination of environmental conditions and several ecological interactions, possibly including dietary competition, will determine the future success of Arctic and boreal fauna. Whilst the warm conditions of the fjord basin appear unfavourable for polar cod, the cold water at glacier fronts may provide a refuge from predation from Atlantic cod and a means to sustain populations in a warming Arctic.

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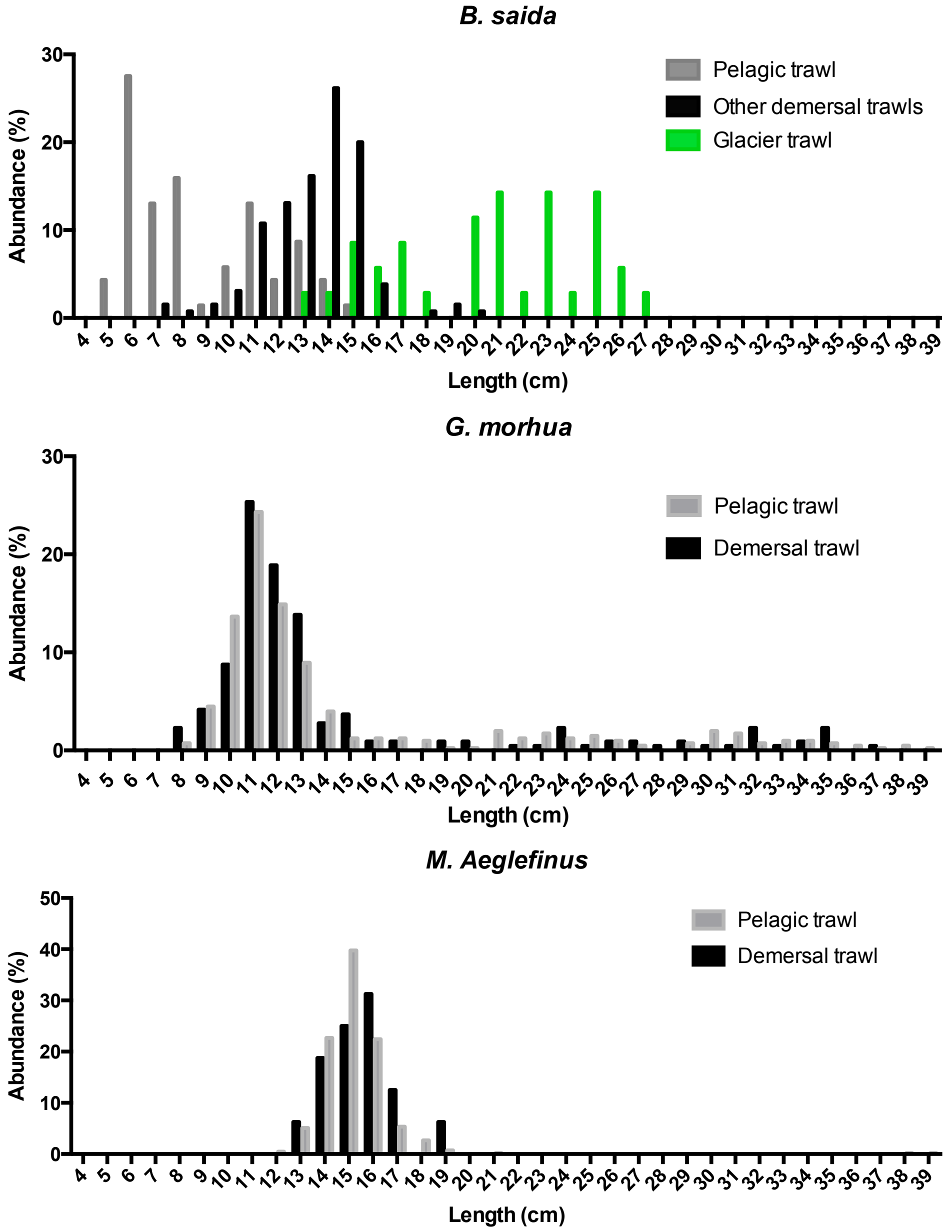
Appendix

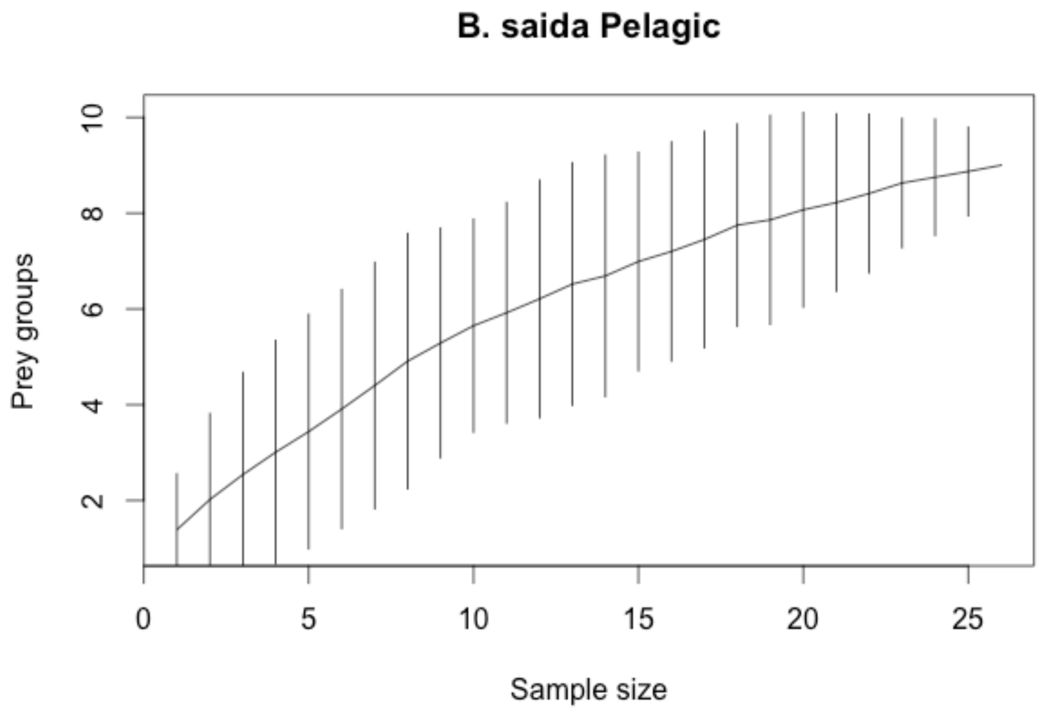


B. saida

G. morhua

M. Aeglefinus

Figure A1 – the sixe distributions of the three co-occurring gadoids



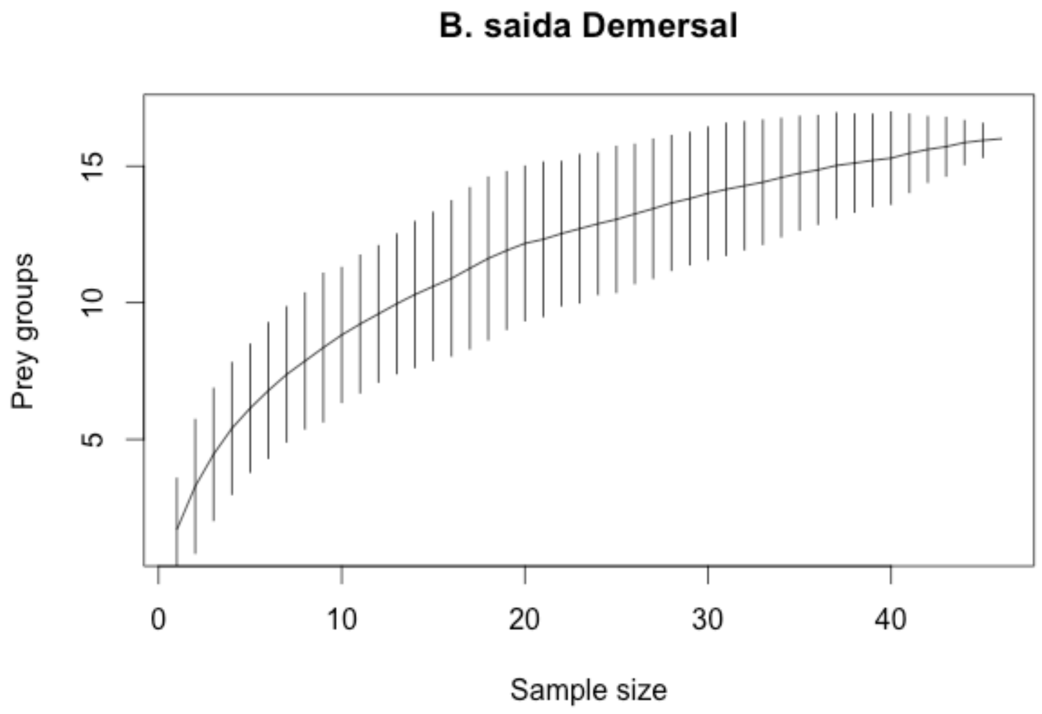
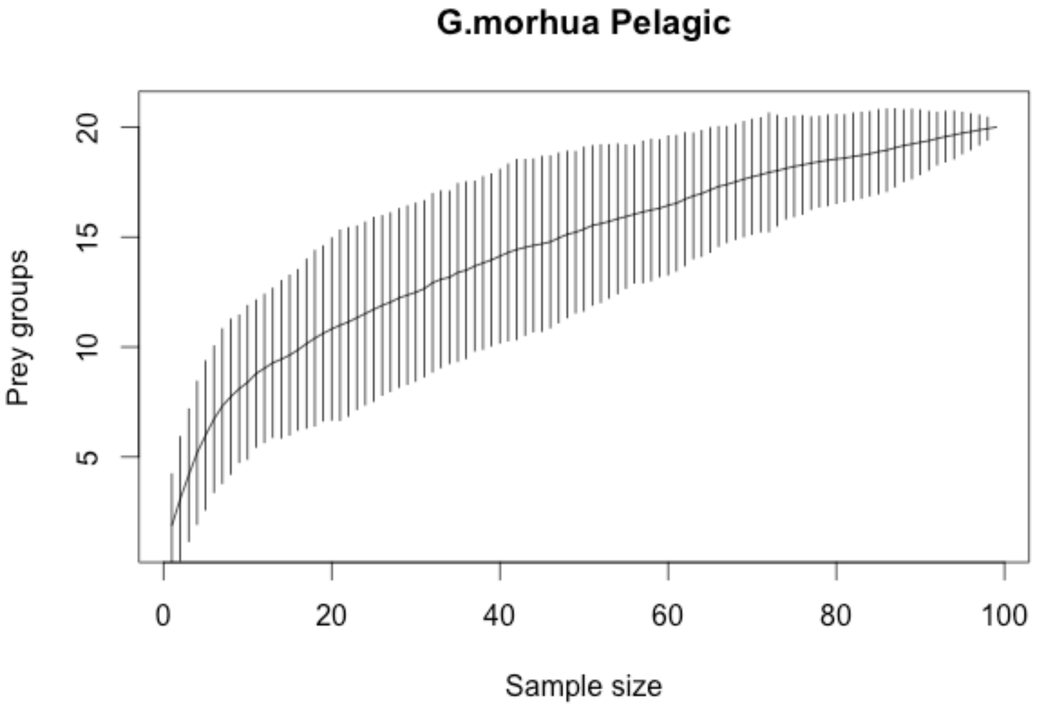
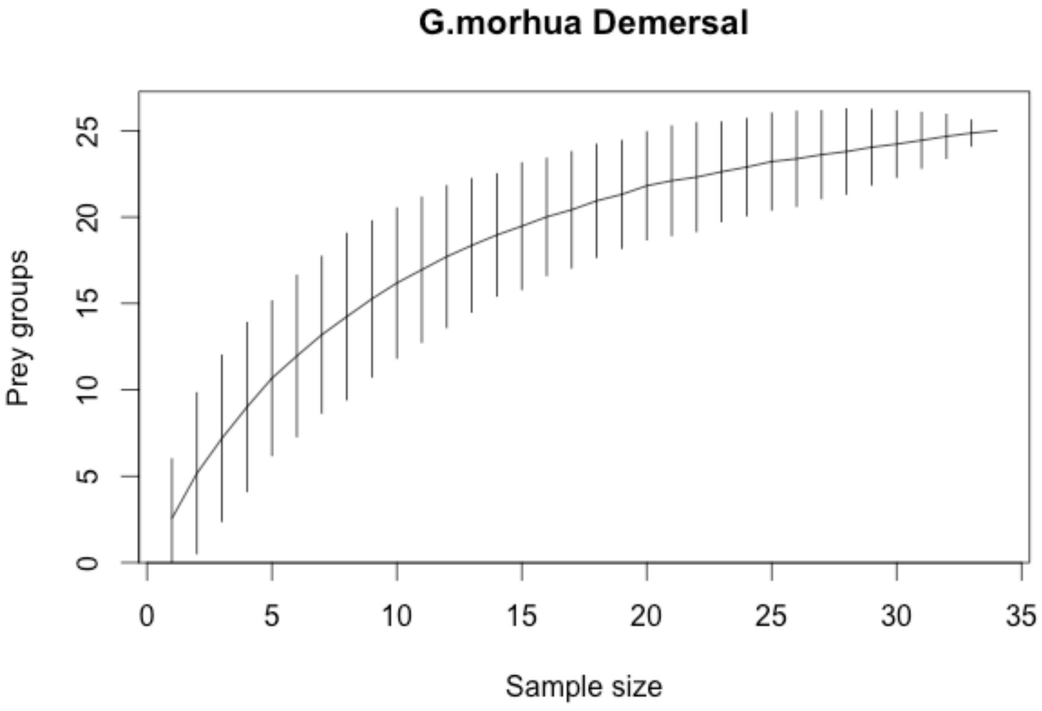


Figure A2 – rarefaction curves calculated for *B. saida*





Fi Figure A3 – rarefaction curves calculated for *G. morhua*

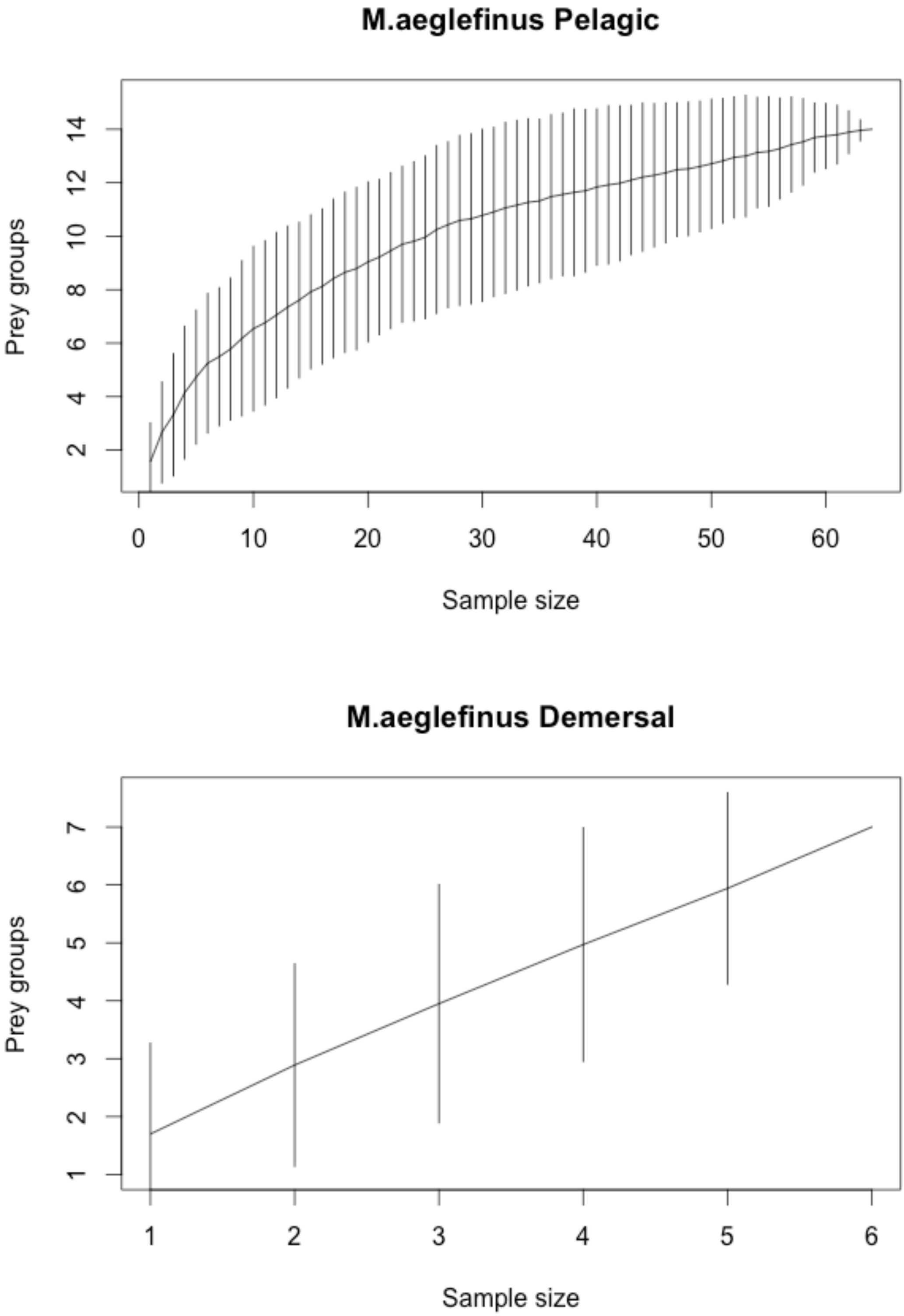


Figure A4 – rarefaction curves calculated for *M. aeglefinus*

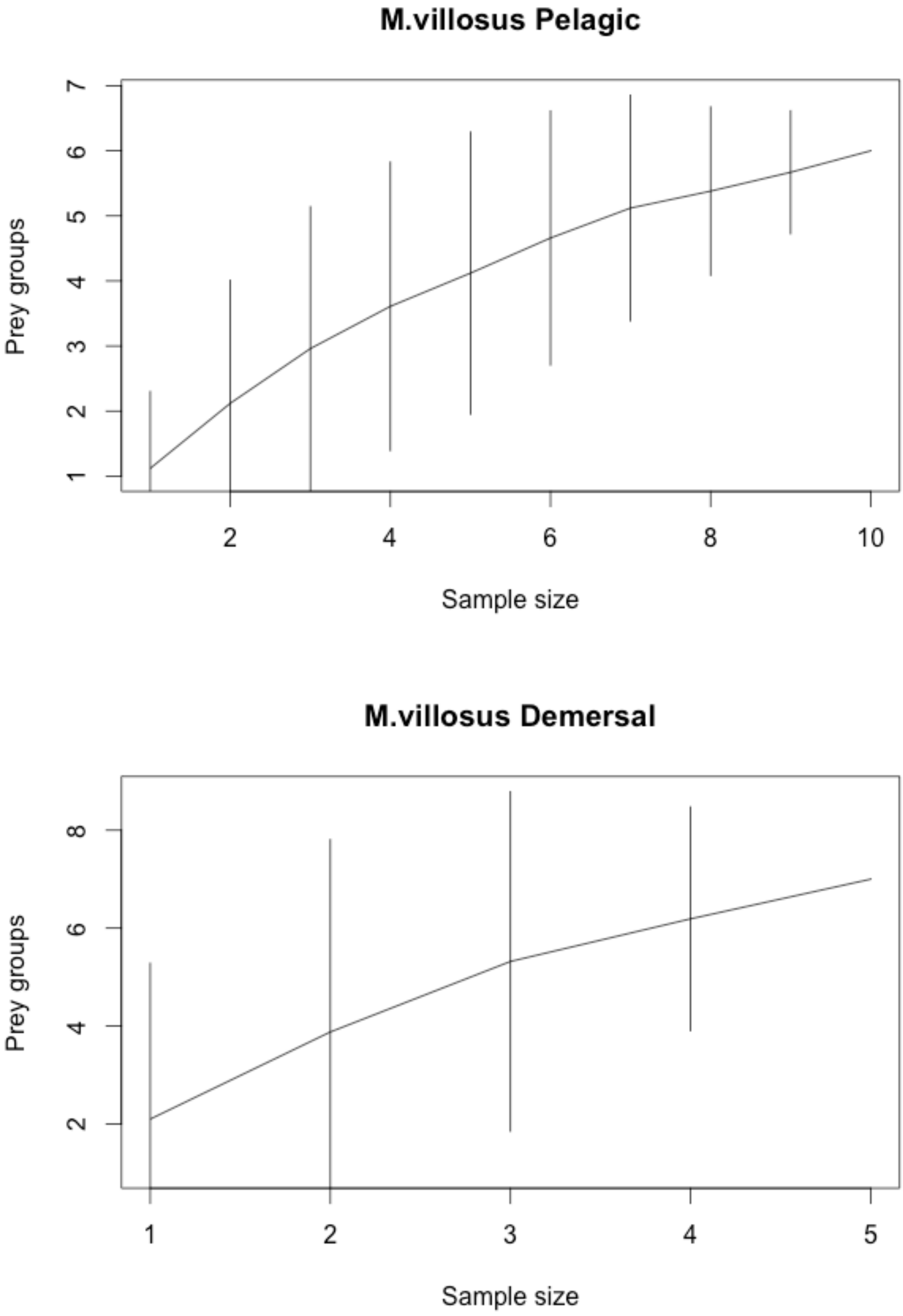


Figure A5 – rarefaction curves calculated for *M. villosus*