

Comparative feeding ecology of the sympatric cod fishes *Arctogadus glacialis* and *Boreogadus saida* in North-East Greenland evaluated from diet and stable isotope analyses



John Joensen

Master of Science in Biology
- field of study: fisheries biology
(60 credits)



Department of Aquatic BioSciences
Norwegian College of Fishery Science
University of Tromsø

February 2008

Table of contents

Abstract	3
Introduction	4
Materials and Methods	6
Results	12
Discussion	23
Conclusion	30
Acknowledgements	31
References	32
Appendices	37

Photo on front page: *Boreogadus saida* and *Arctogadus glacialis*. Photo taken by H. Schurmann.

Abstract

The fish fauna was investigated in autumn 2003 during the TUNU-I Expedition to NE Greenland fjords. Two gadoids *Arctogadus glacialis* and *Boreogadus saida* were abundant in many trawl hauls. In this study, the stomach contents and the stable isotope composition were determined in 60 *Arctogadus glacialis* and 50 *Boreogadus saida* from Tyrolerfjord and Dove Bugt. The diets were examined by Stomach Contents Analysis (SCA) and compared with chi-square test and Schoener index. The diets were similar containing the same prey species, mostly crustaceans (copepods, mysids and amphipods). Significant differences were found, mainly in the proportions of two crustaceans, the mysid *Mysis oculata* and the copepod *Metridia longa*. Fish was found in the stomachs of large *Arctogadus glacialis*. The stable isotope composition was analyzed with Stable Isotope Analysis (SIA). Differences were discovered between species and fjords. *Arctogadus glacialis* had $\delta^{13}\text{C}$ mean of -20.81 and -21.33‰, $\delta^{15}\text{N}$ mean of 14.92 and 14.21‰, in Tyrolerfjord and Dove Bugt, respectively. *Boreogadus saida* had $\delta^{13}\text{C}$ mean of -21.25 and -21.52‰, $\delta^{15}\text{N}$ mean of 13.64 and 14.47‰ in the respective fjords. Trophic levels of the species were inferred from mean $\delta^{15}\text{N}$ -values. The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the predators corresponded well with those of the prey species from the literature, with an enrichment value of 3.8‰ for $\delta^{15}\text{N}$. This is the first study that examines the isotope signature and trophical position of *Arctogadus glacialis*.



Introduction

Little is known about the ecology in the fjords of North East Greenland. The fjords are not accessible the whole year and are covered by sea ice except for the period of August-October. Two gadoid fish species are abundant in the fjords: *Arctogadus glacialis* (Peters, 1874) and *Boreogadus saida* (Lepechin, 1774). Both are endemic to the Arctic and are assumed to be cryopelagic, i.e. to be basically pelagic species but associated with sea-ice biota for at least part of their life-cycles (Andriashev 1964; Lønne and Gulliksen 1989; Sűfke et al. 1998; Gradinger and Bluhm 2004). *Arctogadus* and *Boreogadus* are widely distributed in arctic and sub-arctic waters (Andriashev 1970).

Arctogadus glacialis occurs circumpolarly (Sűfke et al. 1998) and has been reported from both ice-free and ice-covered waters in the western Arctic (Svetovidov 1948; Nielsen and Jensen 1967; Frost 1981; Borkin and Mel'yantsev 1984; von Dorrien et al. 1991). Little is known about *Arctogadus glacialis* since only a few specimens have been caught for scientific analyses (Boulva 1972) prior to the ARKTIS VII Expedition into the North East Water (NEW) Polynya in 1990 (Krause 1991). Then, *Arctogadus glacialis* and *Boreogadus saida* were caught in many trawl hauls and specimens were subsequently analyzed (von Dorrien et al. 1991). Sűfke et al. (1998) examined size and diet of 796 specimens of *Arctogadus glacialis* from the NEW Polynya. Copepods were dominant in the diet of small fish, whereas amphipods and mysids were more important for larger fish.

Boreogadus saida is distributed in Arctic waters with and without drifting sea (Ponomarenko 1968; Christiansen and Fevolden 2000). It is probably one of the most abundant fishes of the Arctic (Moskalenko 1964; Ponomarenko 1968; Falk-Petersen et al. 1986), and it is generally accepted that *Boreogadus saida* functions as a key link in the transfer of energy from lower to higher trophic levels (Bain and Sekerak 1978; Bradstreet and Cross 1982; Welch et al. 1992). It is reported as an important food item and major fraction in the diet of a variety of marine birds, marine mammals and fishes in the Arctic (Bradstreet et al. 1986; Lønne and Gulliksen 1989; Lønne and Gabrielsen 1992). *Boreogadus saida* is reported occasionally to form very large and dense schools in the Canadian Arctic during the open water season (Welch et al. 1993; Hop et al. 1997), and large aggregations have been observed in the autumn in Russian coastal waters (Moskalenko 1964; Andriashev et al. 1980). Copepods and amphipods

dominate the diet of juvenile *Boreogadus saida*, when associated with ice (Bradstreet and Cross 1982; Lønne and Gulliksen 1989). Bain and Sekerak (1978) found copepods and amphipods, but also fish (including young-of-the-year *Boreogadus saida*) to be important to adult *Boreogadus saida* caught in open water during August and September.

The overall objective of this thesis is to examine the feeding ecology of sympatric, e.g. sharing the same habitat, *Arctogadus glacialis* and *Boreogadus saida* in Tyrolerfjord and Dove Bugt in North East Greenland. Two approaches have been adopted: 1) prey identification of stomach contents (SCA), and 2) trophic level inferred from stable isotope analysis (SIA). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values in muscle tissue from the two gadoid species were used to determine variations in trophic levels and correlations to their prey.

The fishes examined in this work were sampled during the TUNU-I Expedition as part of the TUNU-MAFIG programme of the International Polar Year (Christiansen 2003). In the literature, there is some confusion about the common names of *Arctogadus glacialis* and *Boreogadus saida*. In Europe, polar cod is *Boreogadus saida* and Arctic cod is *Arctogadus glacialis*, whereas in North America the common names are the opposite. The two species are the only representatives of their respective genera. Thus in this thesis, I will use the term *Arctogadus* for *Arctogadus glacialis* and *Boreogadus* for *Boreogadus saida* to avoid name confusion.

Materials and methods

Study area and fish samples

The IPY- (International Polar Year) Programme on the Arctic marine fish fauna – TUNU-MAFIG (website: http://www.ipy.org/index.php?/ipy/detail/tunu_mafig) consists of several expeditions to the fjords of NE Greenland. Hence, two arctic gadoid species *Arctogadus glacialis* (*Arctogadus*) and *Boreogadus saida* (*Boreogadus*) were sampled during the TUNU-I Expedition in autumn 2003 using the *R/V Jan Mayen* as the operational platform (Christiansen 2003).

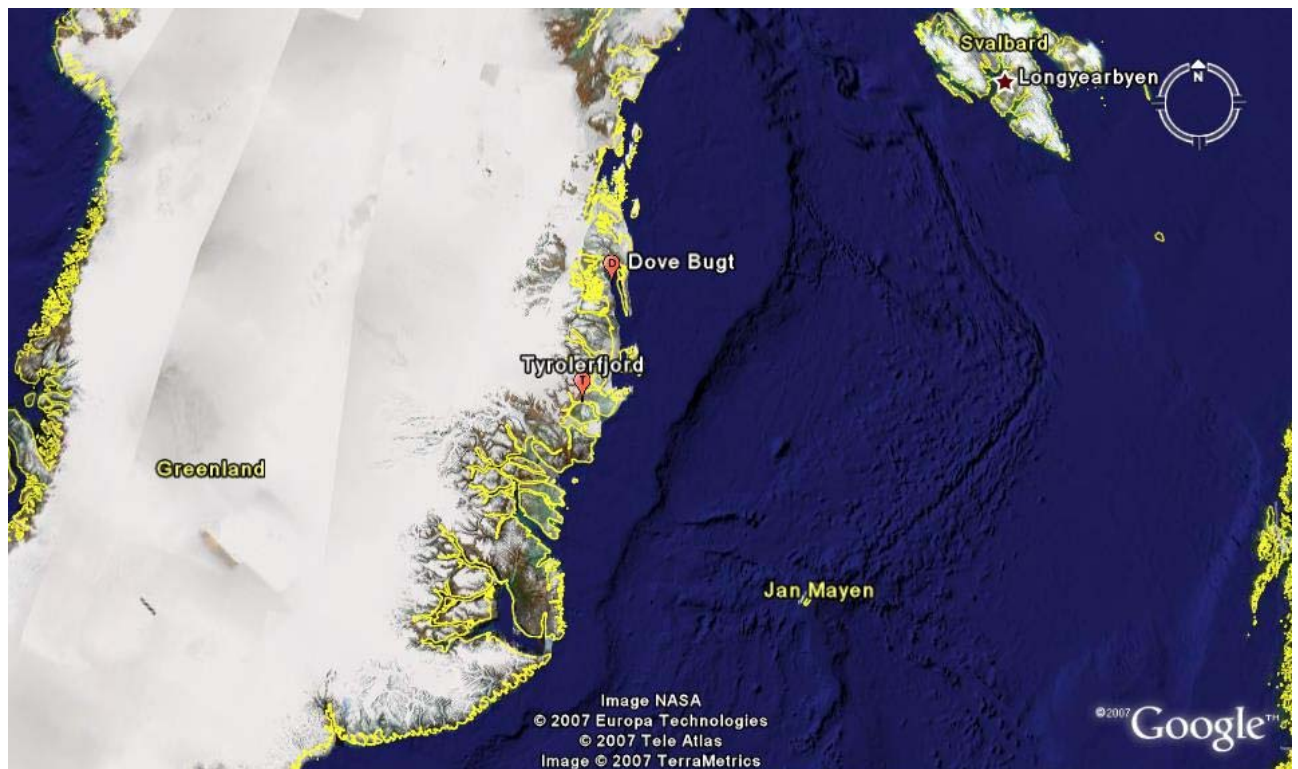


Fig. 1 A map showing the NE Greenland fjords investigated in the present study.

Arctogadus and *Boreogadus* were sampled in two fjords, a relatively warm fjord (Dove Bugt) and a subzero fjord (Tyrolerfjord) habitat, for comparative analyses of diet composition and the stable isotope values. The main physical properties of the fjords and the number of fishes analysed within each fjord are shown in Table 1.

The four fish groups in this study are a combination of the abbreviations for fjord and species: Tyrolerfjord (TF), Dove Bugt (DB), *Arctogadus* (AR) and *Boreogadus* (BO). Thus, *Arctogadus* from Tyrolerfjord = TFAR, *Boreogadus* from Tyrolerfjord = TFBO, *Arctogadus* from Dove Bugt = DBAR, and *Boreogadus* from Dove Bugt = DBBO.

The fishes were caught by a *Campelen Super 1800/96 NOFI* bottom trawl at a mean trawl speed of 3 nm h⁻¹ for 20 min. A *Scanmar* temperature sensor was deployed on the top bridle of the trawl for *in situ* registration of near bottom temperatures (0.1 °C). Immediately after catch, a random sub-sample of each fish species (Fig. 2) was labelled and stored frozen (-20 °C) for subsequent laboratory analyses.

Table 1 The NE Greenland fjords (Fig. 1) and the number of fishes investigated in 2003.

	Station ID	Position	Date of Sampling	Depth (m)	Sill	Temp. C	Number of fish	
							<i>Arctogadus</i>	<i>Boreogadus</i>
Dove Bugt	888	76 27N, 19 35W	7 October	420-426	No	0.8-1.1	30 (DBAR)	20 (DBBO)
Tyrolerfjord	895	74 27N, 21 11W	11 October	322-333	Yes	-1.7	30 (TFAR)	30 (TFBO)

Boreogadus saida



Arctogadus glacialis

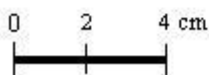


Fig. 2 The Arctic gadoid fishes investigated in the present study. Photo: H. Schurmann.

Laboratory analyses

Basic dissection

Single fish was thawed, drip dried and total weight (0.1 g) and total length (mm) measured. A few gill filaments were removed and stored in 96% ethanol for genetic analysis (not included in this study). The gut cavity was opened with scissors, and stomach, liver and gonads were removed and weighed (0.01 g). The gender was determined by macroscopical analysis of the gonads. Finally, the gutted fish (i.e. dressed out) was weighed (0.1 g), the otoliths (sagittae) removed, and a small piece (~1 g ww) of the epaxial muscle (no skin) was dissected and frozen (-20 °C) for subsequent analysis of stable carbon and nitrogen isotopes (Appendix 5).

Stomach contents analysis (SCA)

The stomach was dissected from the distal end of the oesophagus to the proximal end of the pylorus. The biomass of stomach contents (0.01 g) was estimated as the weight difference between the full and empty stomach. The stomach content was initially sorted into two broad prey categories, fish and invertebrates, and the digestion stage estimated semi-quantitatively (Appendices 1, 5). The fish prey were frozen or fixed in 70% ethanol and the invertebrates were fixed in 4% formaldehyde for subsequent identification. Fish remains were identified as fishes, ichthyoplankton, otoliths and fish bone. Invertebrates were washed in 96% ethanol, identified to the nearest taxon using a taxonomical key developed for northern marine invertebrates (Gaevskaia 1948), and the number of animals pertaining to each taxon were counted. A reference collection of prey species is deposited at the University of Tromsø, Department of Aquatic BioSciences.

Frequency of occurrence

Frequency of occurrence was used for the composition of the prey species in the stomachs of the different groups. If a certain prey species was present in a fish stomach it was accounted as 1 and if it was absent it was accounted as 0. The number of occurrences was then counted for all the species present in the stomachs of the whole group (TFAR, TFBO, DBAR, DBBO).

Division of fish groups

Each group of fish (TFAR, TFBO, DBAR, DBBO) (Table 1) were sub-divided into four size-classes to examine the diet in relation to body size. Division of the groups into size-classes was as follows: The fishes in the groups were ranged in size by length and the group divided into two equal halves, constituting small and large fish. If this resulted in an odd number, the half with the small fish gained the extra fish. Then the two groups were divided into two halves. If the number of fish was odd, the half nearer the median of the whole group got the extra fish. The resulting 4 size-classes of each group were numbered 1-4, with the small fish in size-class 1 and the large fish in size-class 4.

Percentage diet overlap (Renkonen-Schoener index)

Percentage diet overlap was calculated according to Martin (1984) using the equation:

$$\text{Schoener index} = 1 - 0.5 \left(\sum_{i=1}^n |P_{xi} - P_{yi}| \right) \quad (1)$$

P_{xi} is the proportion of food category i in the diet of species x , P_{yi} is the proportion of food category i in the diet of species y , and n is the number of food categories.

Stable isotope analysis (SIA)

The SIA was conducted at the Institute for Energy Technology, Kjeller, Norway. The epaxial muscle from individual fish was weighed and dried to constant weight (48–72 h) at 70 °C. Dried material was ground into fine powder in a glass mortar for subsequent analyses of stable ^{15}N and ^{13}C isotopes as described by Søreide et al. (2006). Lipids were removed by Soxhlet extraction with ca 100 ml of a solvent consisting of 7% methanol in dichloromethane by volume (Soxhlet 7% DCM) for ca 2 h, after which the samples were dried at 80 °C to constant weight. Dried samples were soaked in 2 N HCl for ca 5 min to remove carbonates and rinsed in distilled water to obtain a final pH of 6-7. The samples were dried again at 80 °C to constant weight.

Stable ^{15}N and ^{13}C isotope analyses were performed on ~ 1 mg of the residual material, which was packed into tin cups and analysed with a TermoQuest NCS 2500 elemental analyser coupled to a Micromass Optima IRMS. Stable isotope ratios were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (2)$$

Where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. International standards-USGS-24 calibrated against PeeDee Belemnite (Vienna) for ^{13}C , and IAEA-N-1 and IAEA-N-2 calibrated against atmospheric N_2 for ^{15}N , were used to determine R_{standard} . Measurement error is $\pm 0.2\text{‰}$ for ^{13}C and $\pm 0.3\text{‰}$ for ^{15}N , according to Søreide et al. (2006).

Trophic Level

Trophic Level (TL) was calculated from the $\delta^{15}\text{N}$ value using the formula:

$$\text{TL} = 1 + [(\delta^{15}\text{N} - \text{POM}) / \text{EV}] \quad (3)$$

Where Particulate Organic Material (POM) was 4.9‰ (Hobson et al. 1995) and the Enrichment Value (EV) from one trophic level to the next was 3.8‰ (Hobson and Welch 1992), which has also been applied to the North East Water Polynya marine food web, NE Greenland (Hobson et al. 1995).

Statistical analyses

Comparison of length

The software used to compare the mean length of fish groups was SYSTAT 11. Mean lengths were tested statistically with Analysis of Variance (ANOVA). Differences between groups (Fjord and Species) and within group (Males vs. Females) were tested.

Comparison of diet

The five most frequently occurring species (*Themisto abyssorum*, *Themisto libellula*, *Mysis oculata*, *Metridia longa* and *Euchaeta/Paraeuchaeta* spp.) in the stomachs of the four groups of fish were selected and a chi-square test applied on their relative proportions. The chi-square tests were performed in Microsoft Office Excel 2003.

Comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values

Mean length differed significantly among the fish groups. An ANOVA test was first used to compare the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, but since they were correlated with length, an ANCOVA test was used to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. The ANCOVA-test, with length as covariate, was performed in SYSTAT 11.

Regression analysis

Trophic levels were calculated for the 16 size classes and a regression analysis performed on trophic level vs. body length in Microsoft Office Excel 2003. Two outliers were removed from the calculations.

Results

Body size and sex

The body length and body mass of male and female *Arctogadus* and *Boreogadus* from Tyrolerfjord and Dove Bugt are shown in Table 2. Overall, the fishes from Tyrolerfjord were larger than those of Dove Bugt. Hence, *Arctogadus* (mean 235 mm, 99.9 g) significantly out-sized *Boreogadus* (mean 185 mm, 46.7 g) in Tyrolerfjord ($p < 0.001$), whereas *Boreogadus* (mean 141 mm, 18.0 g) displayed the larger body size compared to *Arctogadus* (mean 121 mm, 12.3 g) in Dove Bugt ($p < 0.001$). Male and female body size did not differ within species and habitats, except for *Boreogadus* in Tyrolerfjord where females (mean 206 mm, 56.3 g) were significantly larger than males (mean 147 mm, 30.0 g), ($p < 0.001$). Male and female fish were pooled in subsequent analysis.

Table 2 Mean body length and body mass with standard deviation (SD), Minimum (Min) and Maximum (Max). TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt. All = All fish from that location. F = Females. M = Males.

Group	n	Body length (mm)				Body mass (g)				
		Mean	SD	Min	Max	Mean	SD	Min	Max	
TFAR	All	30	235.4	63.0	140	389	99.9	97.3	14.0	487.1
	F	22	244.9	66.7	140	389	114.4	108.1	14.0	487.1
	M	8	209.4	45.4	142	274	59.9	40.8	14.0	117.2
TFBO	All	30	184.6	52.2	89	253	46.7	29.7	4.0	99.3
	F	19	206.3	39.9	99	253	56.3	25.5	5.2	99.3
	M	11	147.0	51.0	89	224	30.0	30.0	4.0	87.0
DBAR	All	30	121.3	21.4	93	211	12.3	9.9	5.4	59.7
	F	16	117.4	15.2	103	154	10.6	5.3	6.0	23.6
	M	14	125.9	26.7	93	211	14.2	13.4	5.4	59.7
DBBO	All	20	140.7	8.6	121	153	18.0	3.6	10.8	24.5
	F	13	139.9	9.5	121	153	17.2	3.9	10.8	23.6
	M	7	142.0	7.0	131	153	19.3	8.1	16.2	24.5

Table 3 The four groups of fish divided into four relative size-classes (1-4) by body length. TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt. n = number of individuals in the size-class. Mean, minimum, and maximum length (mm), with Standard Deviation, are indicated.

	Size class	n	Mean	Min	Max	SD
TFAR	1	7	163	140	186	20.9
	2	7	196	187	211	8.4
	3	7	251	226	280	21.2
	4	7	310	281	389	37.3
TFBO	1	7	106	89	126	12.6
	2	8	173	136	198	22.8
	3	8	218	206	224	5.9
	4	7	238	228	253	8.1
DBAR	1	7	103	93	109	5.2
	2	8	112	110	116	2.3
	3	7	123	118	126	2.9
	4	7	147	127	211	30.2
DBBO	1	5	129	121	132	4.5
	2	5	139	133	142	4.2
	3	5	145	143	148	2.2
	4	5	151	148	153	2.6

Stomach contents analysis and diet composition

A total of 25 prey items were identified from the stomach contents of *Arctogadus* and *Boreogadus*, and the frequency of prey occurrence (i.e. the presence or absence of a particular prey item) was determined for both gadoid predators in the two habitats (Table 4).

Overlap in frequency of occurrence

The five most frequent prey items were chosen for subsequent examination of the diet composition both for sympatric *Arctogadus* and *Boreogadus* and within species across habitats: *Themisto abyssorum* (42.1-56.7%), *Metridia longa* (14.3-73.7%), *Mysis oculata* (6.7-50.0%), *Euchaeta/Paraeuchaeta* (17.2-28.6%), *Themisto libellula* (3.4-26.7%)(Table 4). The diet composition differed significantly between *Arctogadus* and *Boreogadus* in Tyrolerfjord ($p = 0.019$). Similarly, in Dove Bugt, there was a tendency towards dietary

segregation between the two gadoid species, although not statistically significant ($p = 0.063$) (Table 5, Fig. 3).

The main difference in the diet between *Arctogadus* and *Boreogadus* could be ascribed to the prey species *Mysis oculata* and *Metridia longa*. In both habitats, *Mysis oculata* were eaten

Table 4 The frequency of occurrence and percent of the total diet of the gadoid species. The five most frequently occurring species that were selected for the chi-square test are in bold letters. TFAR= *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt. % occ. = frequency of occurrence (chi square test). % diet = Percent of total prey items found in the stomachs (Schoener index).

Species	TFAR		TFBO		DBAR		DBBO	
	% occ.	% diet	% occ.	% diet	% occ.	% diet	% occ.	% diet
ANNELIDA								
<i>Aglaophamus malmgreni</i>	3.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ophryotrocha</i> sp.	0.0	0.0	0.0	0.0	3.4	0.5	0.0	0.0
Polychaeta indet.	0.0	0.0	0.0	0.0	3.4	0.5	0.0	0.0
CRUSTACEA								
Copepoda								
<i>Calanus finmarchicus</i>	14.3	3.4	6.7	5.1	10.3	1.9	21.1	4.3
<i>Calanus hyperboreus</i>	0.0	0.0	10.0	3.4	3.4	0.5	5.3	0.9
<i>Calanus</i> sp.	0.0	0.0	16.7	4.3	0.0	0.0	10.5	1.7
<i>Euchaeta/Paraeuchaeta</i> sp.	28.6	3.1	23.3	10.3	17.2	3.3	21.1	4.3
<i>Metridia longa</i>	14.3	2.5	33.3	12.8	31.0	64.5	73.7	44.8
Calanoida indet.	0.0	0.0	10.0	3.4	10.3	1.4	0.0	0.0
Mysidacea								
<i>Mysis oculata</i>	50.0	28.4	6.7	1.7	37.9	9.5	15.8	2.6
Euphausiacea								
<i>Thysanoessa inermis</i>	0.0	0.0	0.0	0.0	0.0	0.0	15.8	2.6
<i>Thysanoessa</i> sp.	0.0	0.0	0.0	0.0	3.4	0.5	0.0	0.0
Amphipoda								
<i>Ampelisca</i> sp.	3.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Anonyx nugax/liljeborgi</i>	3.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stegocephalus inflatus</i>	14.3	1.2	0.0	0.0	0.0	0.0	5.3	0.9
<i>Gammarus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.9
Gammaridea indet.	0.0	0.0	0.0	0.0	3.4	0.5	0.0	0.0
<i>Themisto libellula</i>	25.0	7.4	26.7	12.0	3.4	0.5	21.1	7.8
<i>Themisto abyssorum</i>	50.0	50.3	56.7	46.2	51.7	16.1	42.1	26.7
Crustacea indet.	0.0	0.0	0.0	0.0	3.4	0.5	5.3	0.9
ECHINODERMATA								
Ophiuridea								
Ophiuroidea indet.	0.0	0.0	3.3	0.9	0.0	0.0	0.0	0.0
PISCES								
Fish bone	3.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Otolith	3.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Ichthyoplankton	7.1	1.9	0.0	0.0	0.0	0.0	10.5	1.7
Fish	3.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0

predominantly by *Arctogadus* (37.9–50.0%), whereas *Boreogadus* fed on *Metridia longa* (33.3–73.7%). Hence, in Tyrolerfjord *Mysis oculata* occurred in 50.0% of the *Arctogadus* stomachs but only in 6.7% of the *Boreogadus* stomachs. In Dove Bugt, on the other hand, 73.7% of the *Boreogadus* had eaten *Metridia longa* compared to 31.0% for *Arctogadus*. The amphipod *Themisto abyssorum* was a major and equally important prey species for *Arctogadus* and *Boreogadus* in both habitats with a frequency of occurrence ranging between 42.1 and 56.7% (Table 4, Fig. 3). The prey species that were specific for a particular predator (i.e. *Arctogadus* or *Boreogadus*) and habitat (Tyrolerfjord or Dove Bugt) are shown in Table 6.

To increase the resolution for qualitative size-specific analysis of the diet, *Arctogadus* and *Boreogadus* were sub-divided into four size-classes (Table 3). Marked differences in diet composition between size-classes were revealed. In both habitats, small *Arctogadus* tended to feed on *Themisto abyssorum*, whereas larger specimens preyed more on *Themisto libellula* and, in particular, *Mysis oculata* (Figs. 4, 5). On the other hand, small-sized *Boreogadus* tended to prey more on *Themisto libellula* whereas larger individuals fed on *T. abyssorum* and, in particular, *Metridia longa* (Figs. 4, 5). It is noteworthy that more benthic prey species (i.e. *Aglaophamus malmgreni*, *Ophrytrocha* sp., Polychaeta indet., *Ampelisca* sp., and *Anonyx nugax/liljeborgi*) were found in *Arctogadus* but not in *Boreogadus*. Two benthic species *Stegocephalus inflatus* and *Gammarus* sp. were found in both predators. Furthermore, fish remains, ichthyoplankton not included, were found only in the larger size-classes of both gadoid predators (Figs. 4, 5). In conclusion, based on the frequency of occurrence analysis, sympatric *Arctogadus* and *Boreogadus* displayed different diets, whereas the diet within species was the similar across habitats (Table 4).

Percentage diet overlap (Renkonen-Schoener index)

In contrast to the frequency of prey occurrence, the diet overlap analysis takes into account the numerical percentage of all the prey items eaten by *Arctogadus* and *Boreogadus* (Table 4). Hence, the diet overlap between the two gadoids was 0.64 in Tyrolerfjord and 0.70 in Dove Bugt. In Tyrolerfjord, the diets overlap was relatively high for *Themisto abyssorum* and *Themisto libellula* and low for *Mysis oculata*, *Euchaeta/Paraeuchaeta* and *Metridia longa*. In Dove Bugt, the diet overlap was relatively high for *Metridia longa*, *Themisto abyssorum* and *Paraeuchaeta* spp. and low for *Mysis oculata* and *Themisto libellula*. In conclusion, the diet overlap between the sympatric gadoids was relatively high (Table 7).

Table 5 p-values from the chi-square tests performed on the five most dominant prey-items in the stomachs of four fish groups: TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.

	TFAR	TFBO	DBAR	DBBO
TFAR				
TFBO	0.019			
DBAR	0.093	0.017		
DBBO	0.005	0.310	0.063	

Table 6 List of the species occurring in the stomach of the four groups of gadoid fish. A prey item (x) can be species specific (*Arctogadus* or *Boreogadus*) or location specific (Tyrolerfjord or Dove Bugt).

Species	Tyrolerfjord	Dove Bugt	<i>Arctogadus</i>	<i>Boreogadus</i>
Annelida				
<i>Aglaophamus malmgreni</i>	x		x	
<i>Ophryotrocha</i> sp.		x	x	
Polychaeta indet.		x	x	
Crustacea				
<i>Calanus</i> sp.				x
<i>Thysanoessa inermis</i>		x		x
<i>Thysanoessa</i> sp.		x	x	
<i>Ampelisca</i> sp.	x		x	
<i>Anonyx nugax/liljeborgi</i>	x		x	
<i>Gammarus</i> sp.		x		x
Gammaridea indet.		x	x	
Crustacea indet.		x		
Echinoderma				
Ophiuroidea indet.	x			x
Pisces				
Fish bone	x		x	
Otolith	x		x	
Fish	x		x	

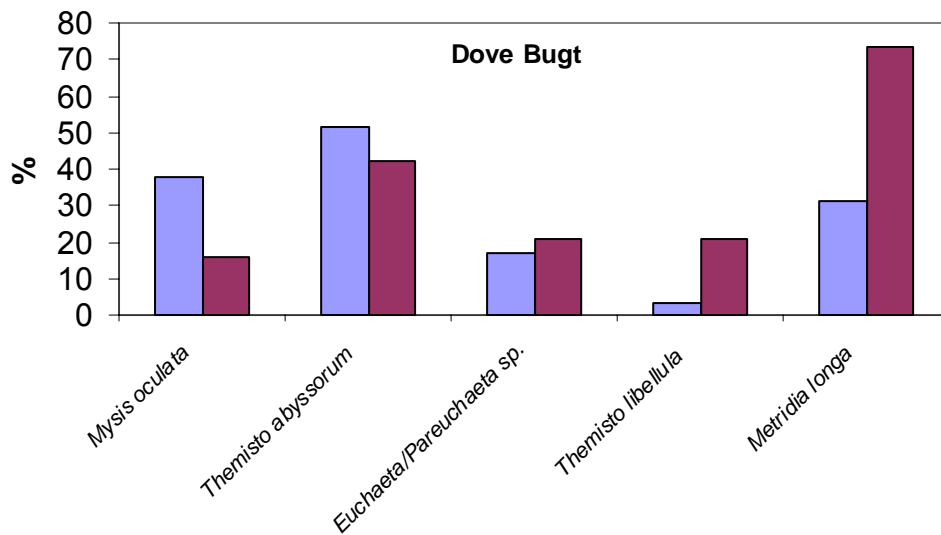
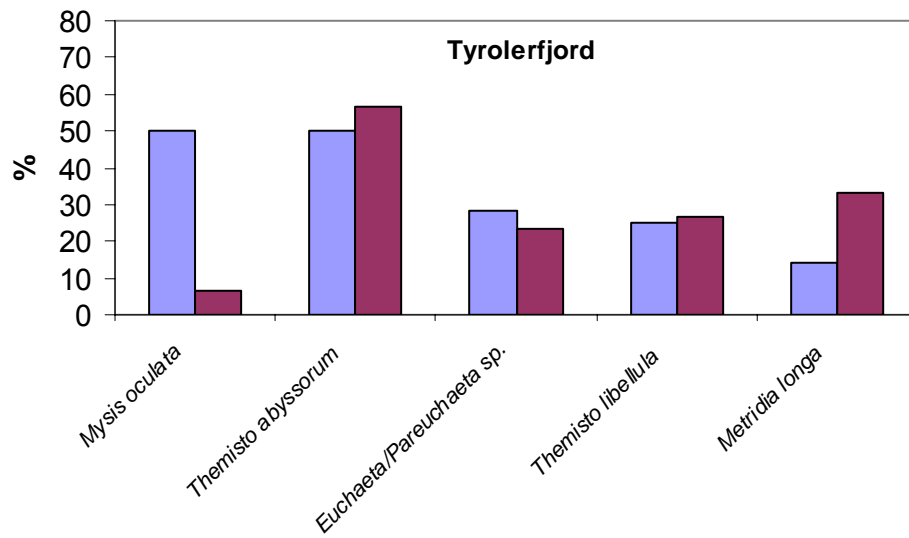


Fig. 3 The frequencies of occurrence of the five most frequent occurring prey species. Blue bars = *Arctogadus*. Red bars = *Boreogadus*.

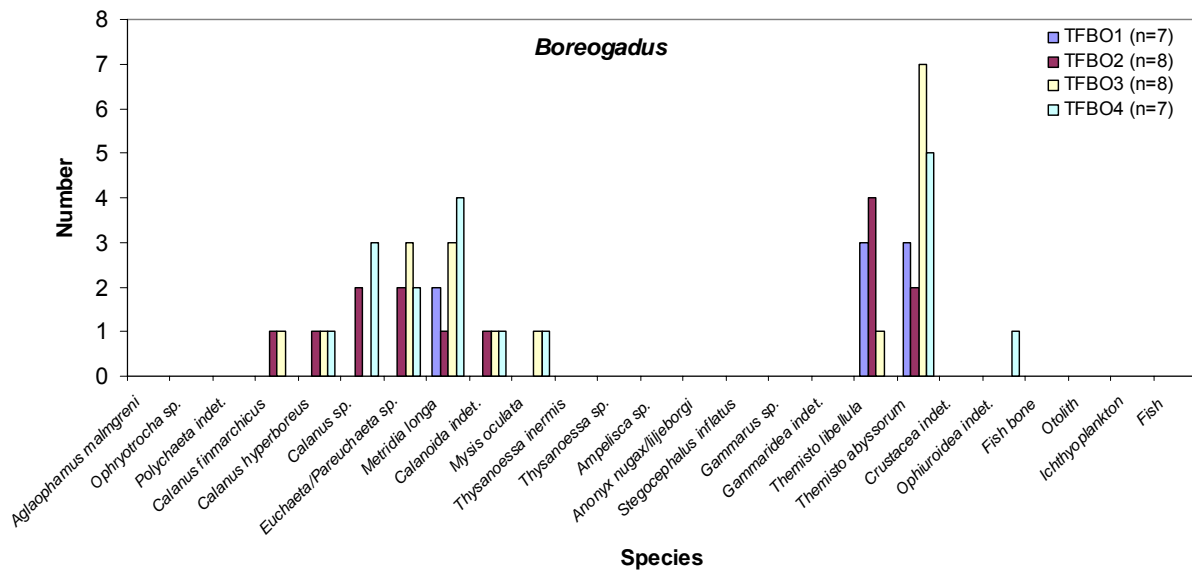
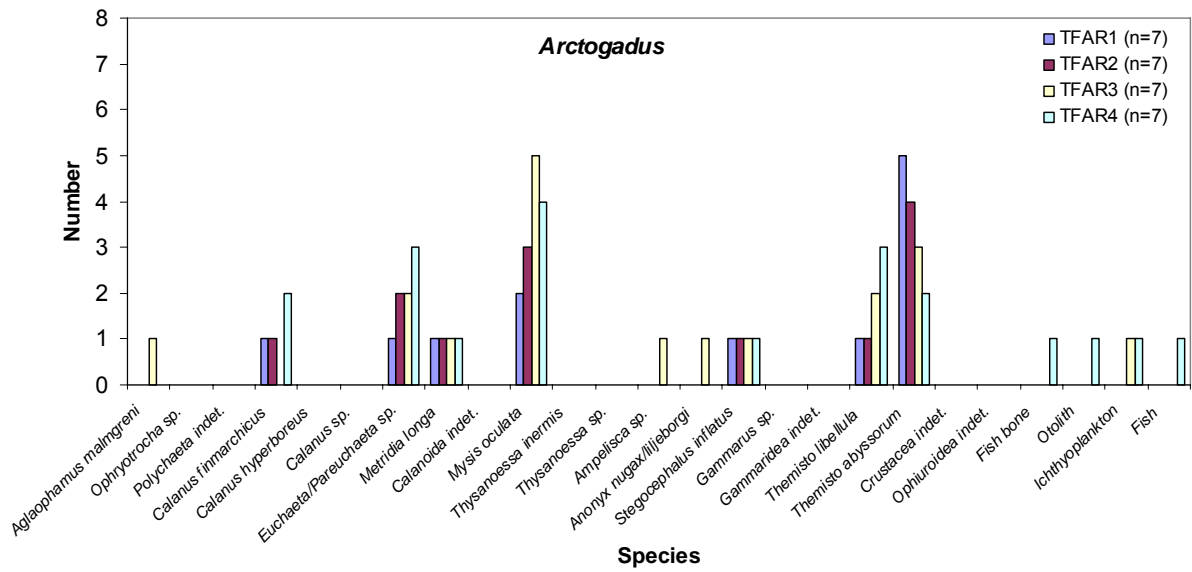


Fig. 4 The diets of *Arctogadus* and *Boreogadus* from Tyrolerfjord divided into four size-classes, from small (1) to large (4). TFAR 1-4 = *Arctogadus* from Tyrolerfjord. TFBO 1-4 = *Boreogadus* from Tyrolerfjord. Number = number of fish that have eaten a specific prey.

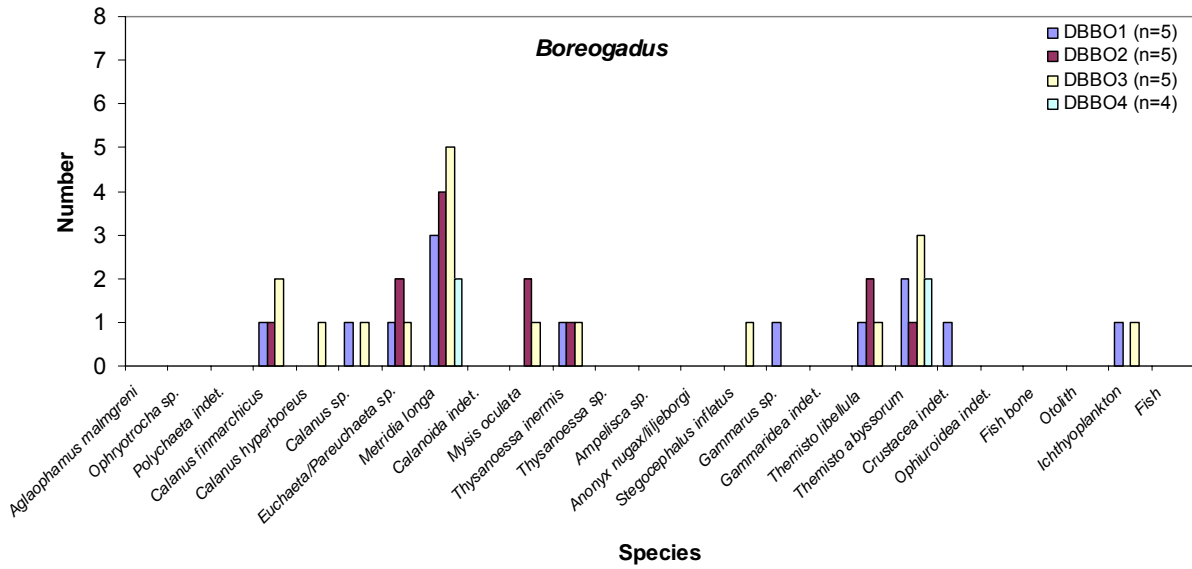
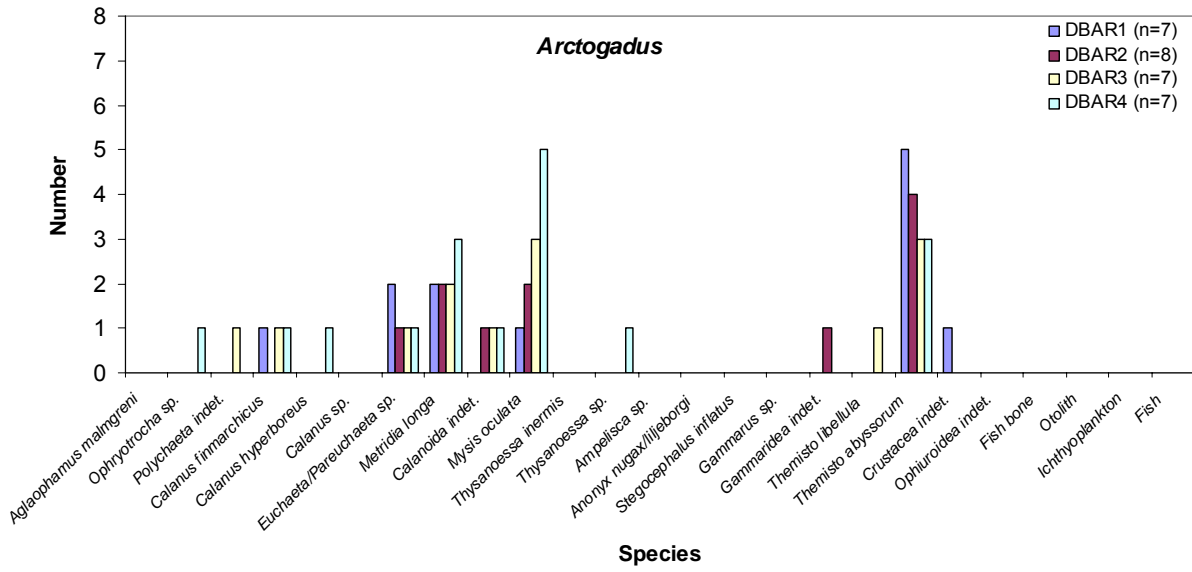


Fig. 5 The diet of *Arctogadus* and *Boreogadus* from Dove Bugt divided into four size-classes, from small (1) to large (4). DBAR 1-4 = *Arctogadus* from Dove Bugt. DBBO 1-4 = *Boreogadus* from Dove Bugt. Number = number of fish that have eaten a specific prey.

Table 7 Schoener index for *Arctogadus* and *Boreogadus* from Tyrolerfjord and Dove Bugt. The index was calculated from all prey species found in the stomachs of the four groups. A Schoener index of 1 is a complete overlap, whereas 0 is none. TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.

	TFAR	TFBO	DBAR	DBBO
TFAR				
TFBO	0.64			
DBAR	0.34	0.38		
DBBO	0.48	0.60	0.70	

Stable isotope analysis and trophic level

Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Preliminary analysis revealed that both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were positively correlated with body length (Appendix 3) and potential differences between habitats and species were examined by an ANCOVA-test to eliminate size effects. In Tyrolerfjord, *Arctogadus* had significantly higher mean values of both $\delta^{15}\text{N}$ (14.92‰) and $\delta^{13}\text{C}$ (-20.81‰) compared with *Boreogadus* ($\delta^{15}\text{N}$ = 13.64‰, $\delta^{13}\text{C}$ = -21.25‰; $p < 0.002$; Tables 8, 9). In Dove Bugt, on the other hand, the isotope values were similar for *Boreogadus* ($\delta^{15}\text{N}$ = 14.47‰, $\delta^{13}\text{C}$ = -21.52‰) and *Arctogadus* ($\delta^{15}\text{N}$ = 14.21‰, $\delta^{13}\text{C}$ = -21.33‰) (Table 8). Hence, the highest mean isotope values were displayed by *Arctogadus* in Tyrolerfjord (Fig. 6). Significantly higher $\delta^{15}\text{N}$ values for *Boreogadus* in Dove Bugt compared to conspecifics in Tyrolerfjord were found, whereas the $\delta^{15}\text{N}$ signal for *Arctogadus* did not differ between habitats. Furthermore, the $\delta^{13}\text{C}$ signal within species did not differ between habitats (Table 9).

Table 8 Mean values of stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from dorsal fish muscle and the corresponding trophic level calculated from the mean $\delta^{15}\text{N}$. TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Trophic Level
TFAR	-20.81	14.92	3.64
TFBO	-21.25	13.64	3.30
DBAR	-21.33	14.21	3.45
DBBO	-21.52	14.47	3.52

Table 9 ANOVA and ANCOVA results (p-values) from comparisons of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ means. Tyrolerfjord = Comparison of *Arctogadus* and *Boreogadus* from Tyrolerfjord. Dove Bugt = Comparison of *Arctogadus* and *Boreogadus* from Dove Bugt. *Arctogadus* = Comparison between *Arctogadus* from Tyrolerfjord and Dove Bugt. *Boreogadus* = Comparison between *Boreogadus* from Tyrolerfjord and Dove Bugt.

	Length as covariate		No covariate	
	$^{13}\text{C}/^{12}\text{C}$	$^{15}\text{N}/^{14}\text{N}$	$^{13}\text{C}/^{12}\text{C}$	$^{15}\text{N}/^{14}\text{N}$
Tyrolerfjord	0.002	<0.001	0.000	0.000
Dove Bugt	0.453	0.982	0.100	0.283
<i>Arctogadus</i>	0.116	0.230	<0.001	<0.001
<i>Boreogadus</i>	0.201	<0.001	0.004	0.007

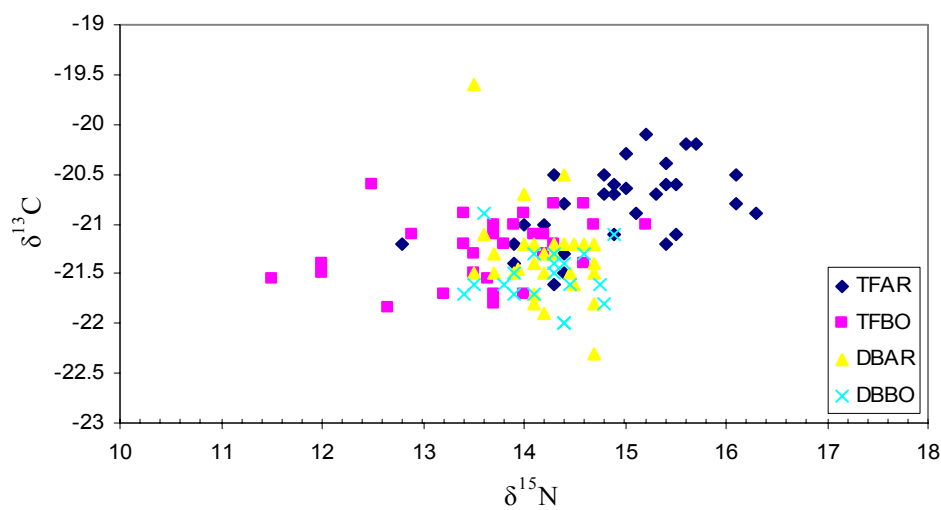


Fig. 6 Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the four groups of gadoid fish. *Arctogadus* from Tyrolerfjord had the highest $\delta^{15}\text{N}$ signal, whereas *Boreogadus* from Tyrolerfjord had the lowest $\delta^{15}\text{N}$ signal. The two species from Dove Bugt were in the middle. TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.

Trophic level

The derived trophic levels for the four size-classes examined for dietary composition are shown in Table 10. Large *Arctogadus* of Tyrolerfjord had the highest trophic level (3.75), if we ignore the high value of DBBO 4, which contained an outlier ($\delta^{15}\text{N} = 19.6\text{‰}$), whereas the lowest trophic level was displayed by *Boreogadus* (3.05) within the same habitat. The regression analysis of trophic level against body length was significant (Fig. 7), when two outliers were removed from the analysis ($p = 0.024$). The equation for the trend line ($\text{TL} = 1.236 \cdot 10^{-3} \cdot L + 3.2623$) revealed an increase in trophic level of $0.0124 \text{ TL cm}^{-1}$.

Table 10 Isotopic values and trophic levels of four groups of fish divided into four relative size-classes (1-4). TFAR = *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt. $\delta^{13}\text{C}$ = δ carbon content. $\delta^{15}\text{N}$ = δ nitrogen content. n = number of individuals in the size-class. Min = Minimum. Max = Maximum. SD = Standard Deviation. TL = Trophic Level.

Group	Class	n	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)				TL
			Mean	Min	Max	SD	Mean	Min	Max	SD	
TFAR	1	7	-21.2	-21.6	-20.7	0.34	14.2	12.8	14.8	0.64	3.44
	2	7	-20.9	-21.4	-20.5	0.31	14.7	13.9	16.1	0.84	3.59
	3	7	-20.5	-21.2	-20.1	0.36	15.1	14.3	15.6	0.43	3.69
	4	7	-20.7	-21.1	-20.3	0.33	15.3	14.8	16.3	0.51	3.75
TFBO	1	7	-21.5	-21.85	-21.1	0.27	12.7	11.5	14.2	0.98	3.05
	2	8	-21.3	-21.7	-20.9	0.33	14.0	13.2	14.7	0.54	3.39
	3	8	-21.1	-21.5	-20.8	0.24	13.9	13.4	14.6	0.43	3.36
	4	7	-21.1	-21.7	-20.6	0.34	13.9	12.5	15.2	0.81	3.38
DBAR	1	7	-21.5	-21.8	-21.2	0.26	14.3	13.9	14.7	0.33	3.46
	2	8	-21.3	-21.9	-20.7	0.35	13.9	13.5	14.2	0.26	3.36
	3	7	-21.2	-21.7	-19.6	0.72	14.2	13.5	14.7	0.38	3.45
	4	7	-21.3	-22.3	-20.5	0.54	14.5	14.4	14.7	0.14	3.53
DBBO	1	5	-21.6	-21.7	-21.4	0.13	13.8	13.4	14.3	0.36	3.34
	2	5	-21.6	-22.0	-21.3	0.27	14.3	13.8	14.8	0.36	3.47
	3	5	-21.3	-21.8	-20.9	0.35	14.4	13.6	14.9	0.52	3.49
	4	5	-21.6	-22.0	-21.3	0.32	15.7	14.1	19.5	2.57	3.83

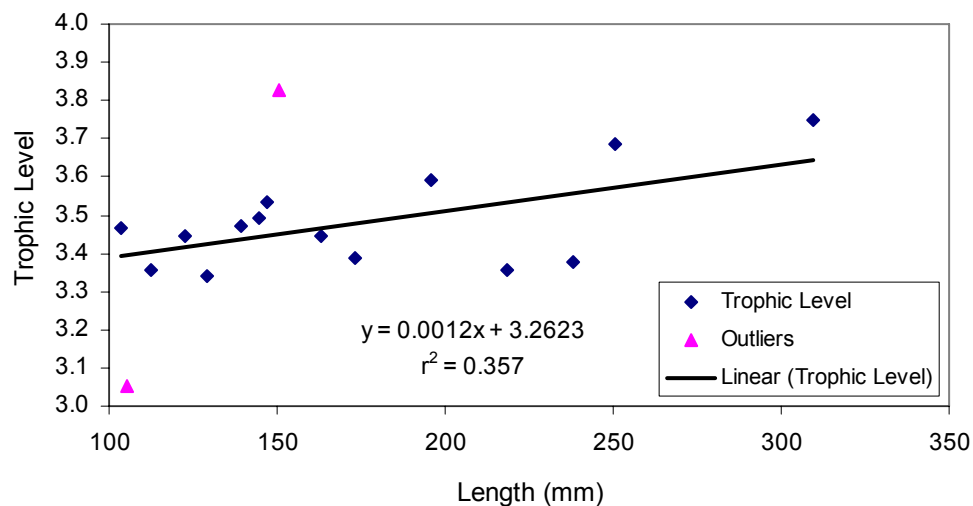


Fig. 7 *Arctogadus* and *Boreogadus*. The four groups (species at locations) divided into four size-groups and their mean trophic level (TL) plotted against body length (L). The equation for the trend line: $\text{TL} = 1.236 \cdot 10^{-3} \cdot \text{L} + 3.2623$, $r^2 = 0.357$.

Discussion

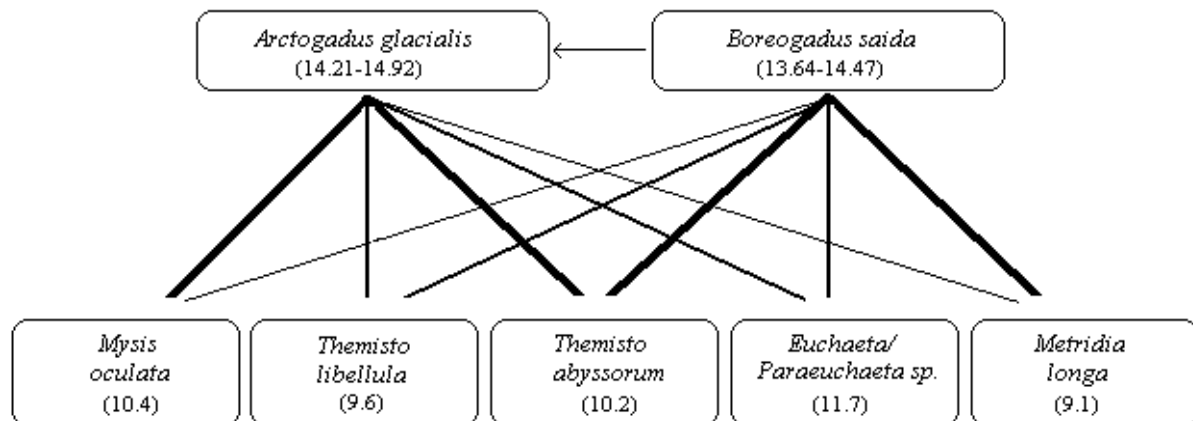


Fig. 8 A simplified model of the food web in NE Greenland fjords showing the relative proportion of a prey species in the predator's diet. A thick line is large proportion and a thin line is small proportion of the predator's diet (Table 4). The numbers in the in bracket are $\delta^{15}\text{N}$ values (‰); those of prey species are from West Greenland found in the literature (Table 11). The $\delta^{15}\text{N}$ values of the predators are from this study (Table 8).

The two gadoid species were sampled in two fjords with different physical characteristics: a sill fjord with a bottom temperature of $-1.7\text{ }^{\circ}\text{C}$, and an open fjord system with bottom temperature $0.8\text{-}1.1\text{ }^{\circ}\text{C}$ (Table 1, Appendix 3). Sill fjords have less exchange of water masses with the surrounding areas than open fjords (Aksnes et al. 1989; Cottier et al. 2005). The effect of freshwater discharge potentially has greater impact on $\delta^{13}\text{C}$ in sill fjords making the associated food web more depleted in $\delta^{13}\text{C}$ than open fjords since terrigenous material is less enriched in $\delta^{13}\text{C}$ (Hobson and Sealy 1991).

Both areas are covered by sea ice except for the period of August-October. The samples were caught at or near the bottom and not in the pelagic. Both *Arctogadus* and *Boreogadus* are known to be cryopelagic (Andriashev et al. 1980; Lønne and Gulliksen 1989). At the time of capture in October, the fjords were ice free and *Arctogadus* and *Boreogadus* had to utilize food sources, other than the ice fauna. They had been feeding at or near the bottom, the time before capture, since most of the prey items found in the Stomach Content Analysis (SCA) were deepwater pelagic or benthic species.

The other fish taxa (e.g. from families Cyclopteridae, Cottidae and Zoarcidae) caught at the two trawl stations all belonged to the benthic fish community (Christiansen 2003). Most of

them are reported as living on soft or muddy bottom (Fishbase 2008). This is an indication that the bottom substratum at the two stations was muddy. It is interesting, that *Arctogadus* and *Boreogadus* were the only species that are reported not to be bottom-associated.

Crustaceans were frequently found in the stomachs of the two gadoids, although some fish prey or remains were found in low numbers. A few annelids were found in *Arctogadus* from Tyrolerfjord. There were significant differences between the diet of the two gadoid predators, mainly in the proportions of the copepod *Metridia longa* and the mysid *Mysis oculata*. The former had a larger frequency of occurrence in *Boreogadus*, whereas *Mysis oculata* occurred more often in *Arctogadus*. The low occurrence of *Mysis oculata* in the stomachs of *Boreogadus* and high occurrence in the stomachs of *Arctogadus* was a clear indication that *Mysis oculata* was not a key component in the diet of *Boreogadus*, while it was a major component in the diet of *Arctogadus*. *Mysis oculata* is hyperbenthic and surface benthic, with a predatory and omnivorous feeding mode (Hobson et al. 2002a). Since most of the bottom-dwellers were found in *Arctogadus* and almost only pelagic prey were found in *Boreogadus*, it is likely that *Arctogadus* forages closer to the bottom than *Boreogadus*. Some differences were evident in the prey composition of small and larger fish. The small *Arctogadus* had a larger proportion of *Themisto abyssorum* in the stomachs than larger *Arctogadus*, while larger *Arctogadus* had more *Themisto libellula* and *Mysis oculata* in their stomachs. *Boreogadus* stomachs showed a different pattern: the small fish had more *Themisto libellula* in the stomachs while larger *Boreogadus* had more *Themisto abyssorum* and *Metridia longa*.

Metridia longa had a higher frequency of occurrence in fish stomachs from Dove Bugt than in those from Tyrolerfjord. The most plausible explanation is that this species was more abundant in Dove Bugt, although fish size dependent depth segregation or feeding preferences may also be part of the explanation. The proportion of *Metridia longa* in *Boreogadus* had a tendency to increase in the larger fish, while there was no increase in *Arctogadus*. Since the fish were smaller in Dove Bugt, the proportion of *Metridia longa* should be lower in Dove Bugt, but the opposite was the case, supporting that this prey was more abundant in the Dove Bugt ecosystem compared to Tyrolerfjord. The reason might be that Dove Bugt is 100 m deeper and *Metridia longa* tend to be more abundant in the deepest basins (Blachowiak-Samolyk et al. 2006). Dove Bugt has no sill and advection of coastal species might therefore be greater than in Tyrolerfjord. The other prey species did not differ much between Tyrolerfjord and Dove Bugt.

Most fish and remains of fish were found in *Arctogadus* from Tyrolerfjord. Ichthyoplankton were found in the stomachs of large *Arctogadus* from Tyrolerfjord and in small and large *Boreogadus* from Dove Bugt. Piscivory is known to be size dependent, since most fish switch to more energetically valuable fish prey when they are above a certain size (Hop et al. 1992). That pattern seems to be present in Tyrolerfjord with the few occurrences of fish and fish remains found in the stomach of the largest *Arctogadus*. Due to its small size, fish larvae are to be considered as zooplankton with limited capability of escaping when attacked by a predator. The occurrence of a few fish larvae in the stomachs of small and large fish indicated that they can be eaten by both juveniles and adults.

The Schoener index and the chi-square test are two different tests, which use two different measures, total number of prey species within the group and frequency of occurrence in a group. The Schoener indices of 0.64 in Tyrolerfjord and 0.70 in Dove Bugt showed a high dietary overlap and indicate possible competition between the two species. It is unknown whether resources are limited, since there are no investigations from the two areas of the prey availability. However, few of the fishes had empty stomach which indicated that the fish were not food limited. The chi-square test showed a difference between species in Tyrolerfjord ($p = 0.019$) and no significant difference in Dove Bugt ($p = 0.063$). Possibly the difference would have been significant if the number of fish sampled had been higher. There was a relative good agreement between the Schoener index and the chi-square test. The Schoener index in Tyrolerfjord was lower than in Dove Bugt, and the chi-square test showed a significant difference in Tyrolerfjord and almost significant difference in Dove Bugt (Table 5). In the between fjords comparisons, the Schoener index showed a low overlap for *Arctogadus* (0.34) and a relatively high overlap for *Boreogadus* (0.60), whereas the chi-square test showed no difference for *Arctogadus* ($p = 0.093$) and *Boreogadus* ($p = 0.310$).

The low similarities for *Arctogadus* in the Schoener index were partly because two fishes in Dove Bugt had a very high number of *Metridia longa* (52 and 59) in their stomachs (Appendix 5). This made a large impact on the total number of *Metridia longa* in the group making it artificially high and dissimilar from *Arctogadus* in Tyrolerfjord. The small prey species had a larger impact on the result in the Schoener index than in the chi-square tests. Small prey often occurred in large number, (e.g. *Themisto abyssorum*), whereas larger prey such as *Themisto libellula* was less abundant. The chi-square test was most likely the better approach in this study, due to relatively low numbers of fish, since frequency of occurrence

was used and did not take into account the number of prey in the stomach and is therefore considered more robust than the Schoener index. The total number of a prey species in the stomachs might not have been estimated well enough, due to relatively low number of fish and large variation in prey species number in individual fish stomachs. Also if the stomach contents are partially digested, this can make it difficult to estimate the total number of a certain species, but it is often possible to determine if a prey species is present or absent. This affects the Schoener index more than the chi square test making the former less accurate. Both methods were useful, however, in obtaining knowledge on the diet of the two gadoids. Furthermore, it must be emphasized that only the comparisons within fjord provided valid results.

The stable isotope method has been applied to ecological studies in recent years to determine trophic level of a species and food web structure (e.g. Minagawa and Wada 1984). Analysis of stomach contents has been used for many years, but has been found to be inadequate because it only gives a short-term picture of the diet (Hyslop 1980). The combination of SCA and SIA is a useful approach to determine the trophic level of a species. While SCA revealed the identity of the prey the fish had eaten recently, SIA can reveal what the species had eaten in the past as an integrated value. There are different turn-over rates of stable isotopes in different tissues. The muscle tissue used in this study has a turn-over rate of few months (Hobson and Clark 1992).

The extremes found in the Stable Isotope Analysis (SIA) included the highest mean $\delta^{13}\text{C}$ of *Arctogadus* from Tyrolerfjord and the lowest mean $\delta^{15}\text{N}$ of *Boreogadus* from Tyrolerfjord. The differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were tested statistically with regard to the difference in body size and it was significant, indicating that *Arctogadus* and *Boreogadus* feed at different trophic level.

Carbon isotope values are enriched in inshore or benthic food webs when compared to pelagic food webs (Hobson and Welch 1992; Hobson et al. 1994; France 1995). Benthic scavengers, such as necrophagous amphipods, usually are more enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, since they eat animal tissue from higher trophic levels. Fisk et al. (2003) reported a $\delta^{13}\text{C}$ of -19.5‰ and $\delta^{15}\text{N}$ of 13.5‰ for *Anonyx nugax*. Tamelander et al. (2006) reported $\delta^{13}\text{C}$ of -19.8‰ and $\delta^{15}\text{N}$ of 6.6‰ for *Ampelisca* sp. and $\delta^{13}\text{C}$ of -20.1‰ and $\delta^{15}\text{N}$ of 15.0‰ for *Anonyx* sp. Hobson

and Welch (1992) reported $\delta^{13}\text{C}$ of -15.0‰ and $\delta^{15}\text{N}$ of 15.1‰ for *Stegocephalus inflatus*. Ingestion of these benthic species regularly would result in a higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than only eating pelagic species. The differences in SIA between *Arctogadus* and *Boreogadus* in Tyrolerfjord might be due to the larger occurrence of benthic scavengers in the stomach of *Arctogadus*, such as amphipods *Ampelisca* spp., *Anonyx mugax*, and *Stegocephalus inflatus*. That might be the explanation for the difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Tyrolerfjord and why the $\delta^{15}\text{N}$ value of *Boreogadus* from Tyrolerfjord was much lower than the $\delta^{15}\text{N}$ value of this species from Dove Bugt (Figs. 4, 5). The chi-square test did not detect any difference in prey composition between the fjords. However, the difference can be a result of different Particulate Organic Matter (POM) values in the two fjords.

Because the POM values of the two fjords have not been estimated, a value from the North East Water (NEW) polynya (Hobson et al. 1995) was used as the closest alternative. However, it is not likely that a POM value from polynya waters is the same as POM values from fjords that are ice covered for most of the year. Tyrolerfjord has a larger input of terrigenous material from the rivers than Dove Bugt, which can be seen by the lower salinity (Appendix 3), and, in addition, the POM value varies seasonally (Søreide et al. 2006). In this study, the POM-value was assumed to be the same in the two fjords; comparisons of the trophic level of the species between the fjords will become biased if they are very different.

The trophic level (TL) calculations were based on the Enrichment Value (EV) and POM value from Hobson et al. (1995), with a POM value of 4.9‰ and an EV of 3.8‰. The EV of the two fjords can be assumed to be the same as the EV value of the NEW from Hobson et al. (1995), although this value originated from Hobson and Welch (1992) based on predator-prey relationship of polar bears-ringed seals in Arctic Canada. Enrichment values of 3-4‰ for ^{15}N are reported from many studies (e.g. De Niro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Hobson and Welch 1992), and an EV of 3.4 was determined recently for the lower marine food web in the Barents Sea (Søreide et al. 2006). However, there was good agreement with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the prey species and of the fish from our study. The EV of 3.8‰ from one trophic level to the next agreed well with isotopic differences between the prey species and the fish predators (Tables 8, 11).

The difference of the $\delta^{15}\text{N}$ values of *Boreogadus* and the values of the five most often occurring prey species are in good agreement, the fish having a mean $\delta^{15}\text{N}$ of 13.63‰ and 14.92‰ and the prey having values ranging from 8.3 to 11.7‰ with *Metridia longa* at 9.1 to 9.5‰ and *Mysis oculata* at 10.4 to 10.5‰. The difference of 1.2‰ in these two prey species is similar to the difference in *Arctogadus* and *Boreogadus* from Tyrolerfjord of 1.3‰. Since *Arctogadus* had more *Mysis oculata* in the stomach and *Boreogadus* had more *Metridia longa*, the difference could be caused by the different proportions of these two prey species. There were no large differences in the proportions of the other prey species. The difference in $\delta^{13}\text{C}$ in Tyrolerfjord might also be explained by differences in the $\delta^{13}\text{C}$ of *Mysis oculata* and *Metridia longa*, being 0.7‰ in Arctic Canada (-22.7 and -23.4‰, respectively) and 2.3‰ in West Greenland (-20.3 and -22.6‰, respectively) (Table 11).

Our $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Boreogadus* are in agreement with respective isotope values found in the literature (Table 11). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are size-dependent (Appendix 4), so the $\delta^{15}\text{N}$ values of the generally larger fish (Table 2) in this study are somewhat higher than those from the literature. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not differ in Dove Bugt. *Arctogadus* was smaller than *Boreogadus* in Dove Bugt, and this presumably affected the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values making them more equal (Table 8, Appendix 4). To our knowledge this is the first SIA on *Arctogadus*.

When the predator groups were divided into four size-classes, not all size-classes showed an increase in TL with fish length. The 16 size-classes had from 4-8 fish in them and this is not sufficient to get a good estimate of the TL, but when all size-classes were plotted together against length this showed an increase in TL of 0.012 cm⁻¹ fish length. Hobson and Welch (1995) found a stepwise increase in $\delta^{15}\text{N}$ as the diet of Arctic char (*Salvelinus alpinus*) switched from invertebrates to being cannibalistic eating smaller Arctic char. We found fish and fish remains in the stomach of the largest size-class of *Arctogadus* from Tyrolerfjord, but there was only a gradual increase in the $\delta^{15}\text{N}$ throughout the group (Appendix 4), probably reflecting size selective predation rather than fish prey in particular. The smallest *Arctogadus* with fish remains in the stomach was 304 mm (Appendix 5). If the fishes do not start feeding on fish, until they reach a length of about 300 mm, then the fish in the other three groups have not reached the minimum length for starting eating fish (Table 2). *Arctogadus* is a larger

Table 11 Isotope values of prey species from the literature.

	Arctic Canada						West Greenland						East Greenland						Barents Sea and Svalbard					
	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
<i>Calanus hyperboreus</i>	-22.0	-23.6	-20.4	8.5	7.7	9.2	-21.7	-23.2	-19.4	7.6	6.9	8.4	-22.7	-22.7	-22.7	7.6	7.6	7.6	-21.6	-24.0	-19.2	8.5	4.6	9.4
<i>Calanus finmarchicus</i>							-20.3	-20.3	-20.3	7.9	7.9	7.9							-21.9	-23.8	-20.1	7.5	6.4	9.7
<i>Calanus</i> spp.*													-22.3	-22.3	-22.3	8.2	8.2	8.2				7.3	7.3	7.3
<i>Calanus glacialis</i>							-19.9	-20.6	-19.2	9.2	9.1	9.2							-21.5	-23.6	-20.3	8.8	7.1	10.2
<i>Metridia longa</i>	-23.4	-23.4	-23.4	9.5	9.5	9.5	-22.6	-23.3	-21.2	9.1	8.7	9.6												
<i>Euchaeta glacialis</i>	-24.4	-24.4	-24.4	11.7	11.7	11.7	-23.4	-24.3	-21.8	11.7	11.6	11.8							-22.9	-23.7	-22.2	10.6	10.2	11.1
<i>Paraeuchaeta norvegica</i>																			-21.2	-22.0	-20.6	10.4	9.8	10.7
<i>Paraeuchaeta</i> spp.																			-22.5	-22.5	-22.5	10.1	10.1	10.1
<i>Mysis oculata</i>	-22.7	-22.7	-22.7	10.5	10.3	10.6	-20.3	-20.3	-20.3	10.4	10.4	10.4												
<i>Ampeliscidae</i>																			-19.8	-19.8	-19.8	6.6	6.6	6.6
<i>Anonyx nugax</i>	-19.3	-19.3	-19.3	13.5	13.5	13.5	-18.5	-18.5	-18.5	13.2	13.2	13.2												
<i>Anonyx</i> sp.													-26.3	-26.3	-26.3	8.3	8.3	8.3	-20.1	-20.1	-20.1	15.0	15.0	15.0
<i>Stegocephalus inflatus</i>	-15.0	-15.0	-15.0	15.1	15.1	15.1																		
<i>Stegocephalus</i> sp.																			-18.2	-18.2	-18.2	15.2	15.2	15.2
<i>Themisto abyssorum</i>							-21.8	-21.8	-21.8	10.2	10.2	10.2							-22.5	-23.5	-19.7	8.3	6.6	11.0
<i>Themisto libellula</i>	-21.8	-23.2	-20.3	10.9	10.0	11.7	-21.8	-22.9	-20.4	9.6	9.5	9.7							-22.1	-23.0	-21.2	9.2	7.9	10.7
<i>Themisto</i> sp.													-24.2	-24.2	-24.2	10.4	10.4	10.4						
<i>Boreogadus saida</i>	-19.4	-19.8	-18.9	13.2	11.1	15.2	-19.3	-20.0	-18.8	12.7	10.7	14.0	-21.9	-22.4	-21.6	13.4	12.9	13.7	-21.1	-22.0	-20.3	12.5	11.3	14.2
References	Hobson and Welch (1992) Fisk et al. (2003)						Hobson et al. (2002a) Hobson et al. (2002b) Møller (2006)						Hobson et al. (1995)						Hop et al. (2006) Søreide et al. (2006) Tamelander et al. (2006) Jæger (2007)					

**Calanus* spp. from East Greenland is *Calanus gracilis* (Hobson et al. 1995)

species than *Boreogadus* and it is therefore more likely that it preys more on fish than does *Boreogadus*.

Conclusion

Arctogadus and *Boreogadus* were living sympatrically in the two fjords sampled. The diets of the two species comprised mainly crustaceans. Significant differences were found in the composition of the diets of *Arctogadus* and *Boreogadus*. The main difference was that *Arctogadus* had a larger frequency of occurrence of *Mysis oculata* and more benthic prey in stomachs, whereas *Boreogadus* had a higher frequency of *Metridia longa* and almost exclusively pelagic prey in the stomach. The fish prey found in the stomachs occurred in large *Arctogadus* from Tyrolerfjord, although ichthyoplankton was found in both species. Our findings indicate that the largest *Arctogadus* were piscivorous, while all *Boreogadus* at the time of sampling were planktivorous. The SIA revealed that *Arctogadus* had a higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in Tyrolerfjord than in Dove Bugt. However, in Dove Bugt, *Arctogadus* were smaller than *Boreogadus* and the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were not significantly different indicating feeding at approximately the same trophic level. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from our study corresponded well with the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of prey species found in the literature.

Acknowledgements

I would like to thank Andrey V. Sikorski (Akvaplan-niva) for help with the classification of invertebrates, my supervisors Jørgen S. Christiansen (Norwegian College of Fishery Science, University of Tromsø) and Haakon Hop (Norwegian Polar Institute) for being very helpful and patient, my fellow students at the office for good company and help when needed, Fredrikka Martinussen, Jenny Jensen and Rúni Weihe for useful comments, Ingar Johansen (Institute for Energy Technology) for showing me how stable isotope analysis is performed, and Raul Primicerio (NCFS, Univ. Tromsø) for guidance with the statistical tests. This work forms part of the TUNU-MAFIG Programme, University of Tromsø.

References

- Aksnes DL, Aure J, Kaarstvedt S, Magnusen T, Richard J (1989) Significance of advection for the carrying capacities of fjord populations. *Marine Ecology Progress Series* 50: 263-274
- Andriashev AP (1964) Fishes of the northern seas of the USSR. In: Pavlovskii EN (Ed) Keys to the fauna of the USSR, Vol 53. Israel Programme Scientific Translation, Jerusalem, 566 pp
- Andriashev AP (1970) Cryopelagic fishes of the Arctic and Antarctic and their significance in polar ecosystems. In: Holdgate MW (Ed) *Antarctic ecology*, Vol 1, London, New York, pp 297-304
- Andriashev AP, Mukhomediyarov BF, Pavstiks EA (1980) O massovykh skopleniyakh kriopelagicheskikh treskovykh ryb *Boreogadus saida* i *Arctogadus glacialis* okolopalyusnykh rajonakh arktiki. (On mass congregations of the cryopelagic cod fishes (*Boreogadus saida* and *Arctogadus glacialis*) in circumpolar regions of the Arctic.) In: M.E. Vinogradov and I.A. Mel'nikov (Eds) *Biologiya Tsentral'nogo arkticheskogo bassejna*. (Biology of the central Arctic basin.) Shirsov Inst. Oceanology, Academy of sciences, U.S.S.R, pp 196-211 (Transl. by Northwest and Alaska Fisheries Center, Seattle, 1981, 14 pp)
- Bain H, Sekerak AD (1978) Aspects of biology of Arctic cod, *Boreogadus saida*, in the Central Canadian Arctic. LGL, Ltd, Toronto, Ontario, 104 pp
- Blachowiak-Samolyk K, Kwasniewski S, Richardson K, Dmoch K, Hansen E, Hop H, Falk-Petersen S, Mouritsen LT (2006) Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Marine Ecology Progress Series* 308: 101-116
- Borkin IV, Mel'yantsev RV (1984) New data on the distribution of polar cod, *Arctogadus glacialis* (Gadidae), in the Arctic region. *Journal of Ichthyology* 24:101-103
- Boulva J (1972) Morphometrics of three sympatric Arctic codfishes of the genera *Arctogadus* and *Gadus*. *Journal Fisheries Research Board of Canada* 29:243-249
- Bradstreet MSW, Cross WE (1982) Trophic relationships at high arctic ice edges. *Arctic* 35:1-12
- Bradstreet MSW, Finley KJ, Sekerak AD, Griffiths WB, Evans CR, Fabjan MF, and Stallard HE (1986) Aspects of the biology of Arctic cod (*Boreogadus saida*) and its

- importance in Arctic marine food chains. Canadian Technical Report of Fisheries and Aquatic Sciences 1491, 193 pp.
- Christiansen JS, Fevolden S-E (2000) The polar cod of Porsangerfjord, Norway; revisited. *Sarsia* 85:189-193
- Christiansen JS (ed) (2003) TUNU-I EXPEDITION. The Fish Fauna of the NE Greenland Fjord Systems. Technical Report. Norwegian College of Fishery Science. University of Tromsø, Norway
- Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. *Journal of Geophysical Research*, vol. 110, C12005, doi:10.1029/2004JC002757
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen in animals. *Geochimica et Cosmochimica Acta* 45:341-351
- Falk-Petersen I-B, Frivoll V, Gulliksen B, Haug T (1986) Occurrence and age/size relations of polar cod, *Boreogadus saida* (Lepechin), in Spitsbergen coastal waters. *Sarsia* 71:235-245
- Fishbase (2008) <http://www.fishbase.org/search.php>
- Fisk AT, Hoekstra PF, Gagnon J, Duffe J, Norstrom RJ, Hobson KA, Kwan M, Muir DCG (2003) Influence of habitat, trophic ecology and lipids on, and spatial trends of, organochlorine contaminants in Arctic marine invertebrates. *Marine Ecology Progress Series* 262:201-214
- France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: food web implications. *Marine Ecology Progress Series* 124:307-312
- Frost KJ (1981) Descriptive key to the otoliths of gadid fishes of the Bering, Chukchi and Beaufort seas. *Arctic* 34:55-59
- Gaevskoia NS (1948) Key to the fauna and flora of the northern seas of the USSR. Academy of Sciences of the USSR, Leningrad
- Gradinger RR, Bluhm BA (2004) In-situ observations on the distribution and behaviour of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the High Arctic Canada Basin. *Polar Biology* 27:595-603
- Hobson KA, Sealy SG (1991) Marine protein contributions to the diet of northern Saw-whet owls on the Queen Charlotte Islands: A stable-isotope approach. *The Auk* 108(2): 437-440

- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes turnover of ^{13}C in tissue. *The Condor* 94:181-198
- Hobson KA, Welsh HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 84:9-18
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63:786-798
- Hobson KA, Ambrose Jr. WG, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Marine Ecology Progress Series* 128:1-10
- Hobson KA, Welch HE (1995) Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 52(6):1195-1201
- Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002a) A stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep-Sea Research II* 49:5131-5150
- Hobson KA, Gilchrist G, Falk K (2002b) Isotopic investigation of seabirds of the North Water Polynya: Contrasting trophic relationship between the eastern and western sectors. *The Condor* 104(1):1-11
- Hop H, Gjørseter J, Danielssen DS (1992) Seasonal feeding ecology of cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. *ICES Journal of Marine Science* 49:453-461
- Hop H, Welch HE, Crawford RE. (1997) Population structure and feeding ecology of Arctic cod schools in the Canadian High Arctic. In: Reynolds J (Ed) *Fish ecology in Arctic North America*. American Fisheries Society Symposium 19, Bethesda, Maryland, pp 68-80
- Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Progress in Oceanography* 71:182-231
- Hyslop EJ (1980) Stomach content analysis—a review of methods and their application. *Journal of Fish Biology* 17:411-429
- Jæger I (2007) Total mercury and methyl mercury in selected species from an European Arctic food web. MS. thesis. University of Tromsø, 71 pp

- Krause G (ed) (1991) Die Expedition ARKTIS VII mit FS "Polarstern" 1990. Bericht vom Fahrtabschnitt ARK VII/2. Berichte zur Polarforschung/Reports on Polar Research 93:1-50
- Lønne OJ, Gulliksen B (1989) Size, age and diet of Polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biology 9:187-191
- Lønne OJ, Gabrielsen GW (1992) Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard. Polar Biology 12:685-692
- Minagawa M, Wada E (1984) Stepwise enrichment of $\delta^{15}\text{N}$ along food chains. Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. Geochimica et Cosmochimica Acta 48:1135-1140
- Martin FD (1984) Diets of four sympatric species of Etheostoma (Pisces: Percidae) from southern Indiana: interspecific and intraspecific multiple comparisons. Environmental Biology of Fishes 11:113-120
- Moskalenko BF (1964) On the biology of Arctic cod, *Boreogadus saida* (Lepechin). Voprosy Ikhtiologii 4(32):433-443
- Møller P (2006) Lipids and stable isotopes in marine food webs in West Greenland. Trophic relations and health implications. PhD thesis. Technical University of Denmark, 211 pp
- Nielsen JG, Jensen JM (1967) Revision of the Arctic cod genus, *Arctogadus* (Pisces, Gadidae). Meddelelser om Grønland 184:1-26
- Peterson BJ, Fry B (1987) Stable isotopes in ecological studies. Annual Review of Ecology and Systematics 18:293-320
- Ponomarenko VP (1968) Some data on the distribution and migrations of polar cod in the seas of the soviet Arctic. Rapports et Procès-Verbeaux des Réunions du Conseil International pour l'Exploration de la Mer 158:131-135
- Süfke L, Piepenburg D, Dorrien CF von (1998) Body size, sex ratio and diet composition of *Arctogadus glacialis* (Peters, 1874) (Pisces: Gadidae) in the Northeast Water Polynya (Greenland). Polar Biology 20:357-263
- Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Progress in Oceanography 71:59-87
- Svetovidov AN (1948) Fishes 4: Gadiformes. In: Pavlovskii EN (Ed) Keys to the fauna of the USSR, Vol 9. Israel Programme Scientific Translation, Jerusalem, 304 pp

- Tamelander T, Renaud PE, Hop H, Carroll ML, Ambrose Jr. WG, Hobson KA (2006)
Trophic relationships and pelagic-benthic coupling during summer in the Barents
Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope
measurements. *Marine Ecology Progress Series* 310:33-46
- von Dorrien CF, Piepenburg D, Schmid MK (1991) On the abundance of Arctic cod
Arctogadus glacialis in Northeast Water. *Polar Research* 27:362-364
- Welch HE, Bergmann MA, Siferd TD, Martin KA, Curtis MF, Crawford RE, Conover RJ,
Hop H (1992) Energy flow through the marine ecosystem of the Lancaster Sound
region, arctic Canada. *Arctic* 45:343-357
- Welch HE, Crawford RE, Hop H (1993) Occurrence of Arctic cod (*Boreogadus Saida*)
schools and their vulnerability to predation in the Canadian High Arctic. *Arctic*
46(4):331-339

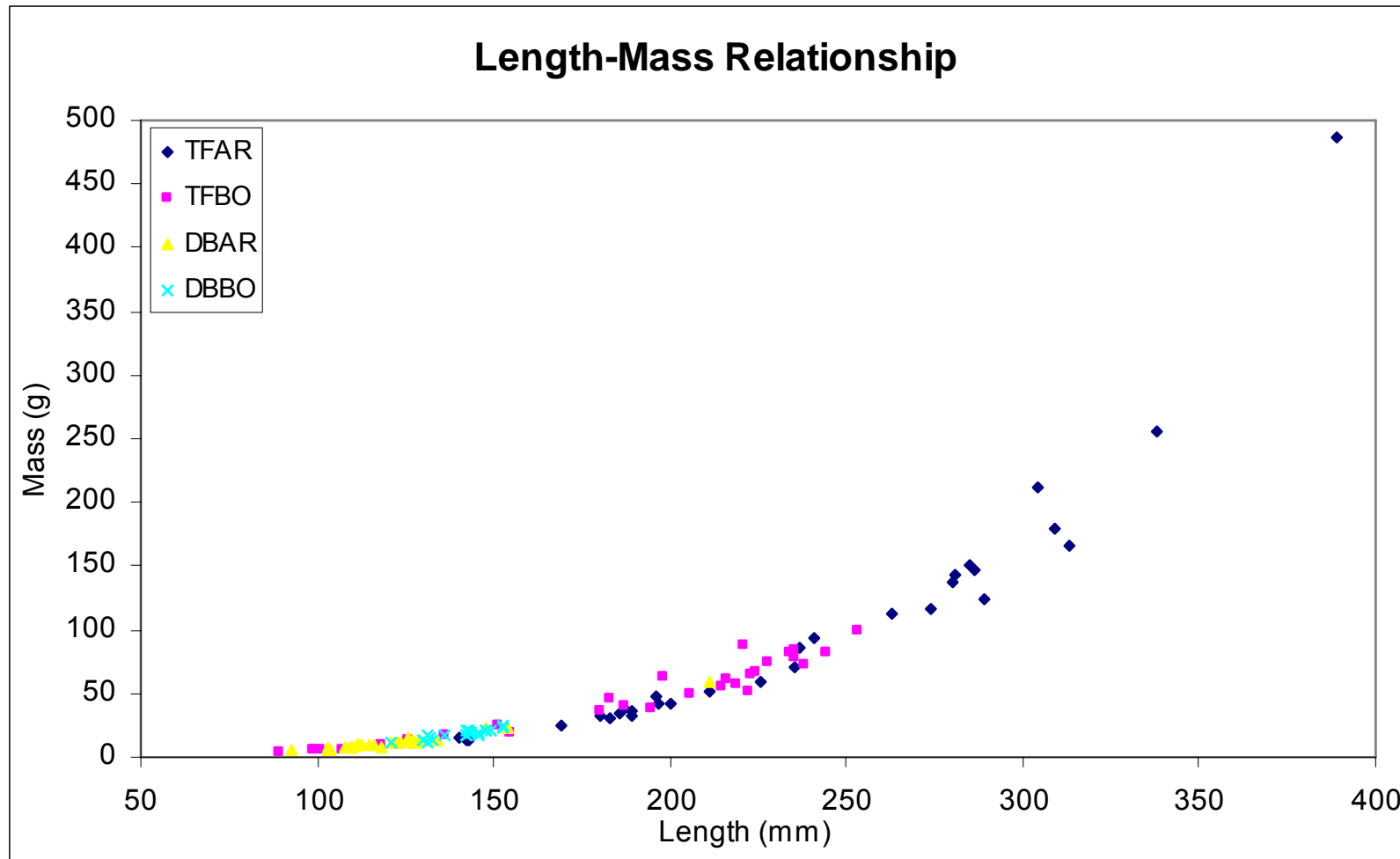
Appendices

Appendix 1

Digestion Stage

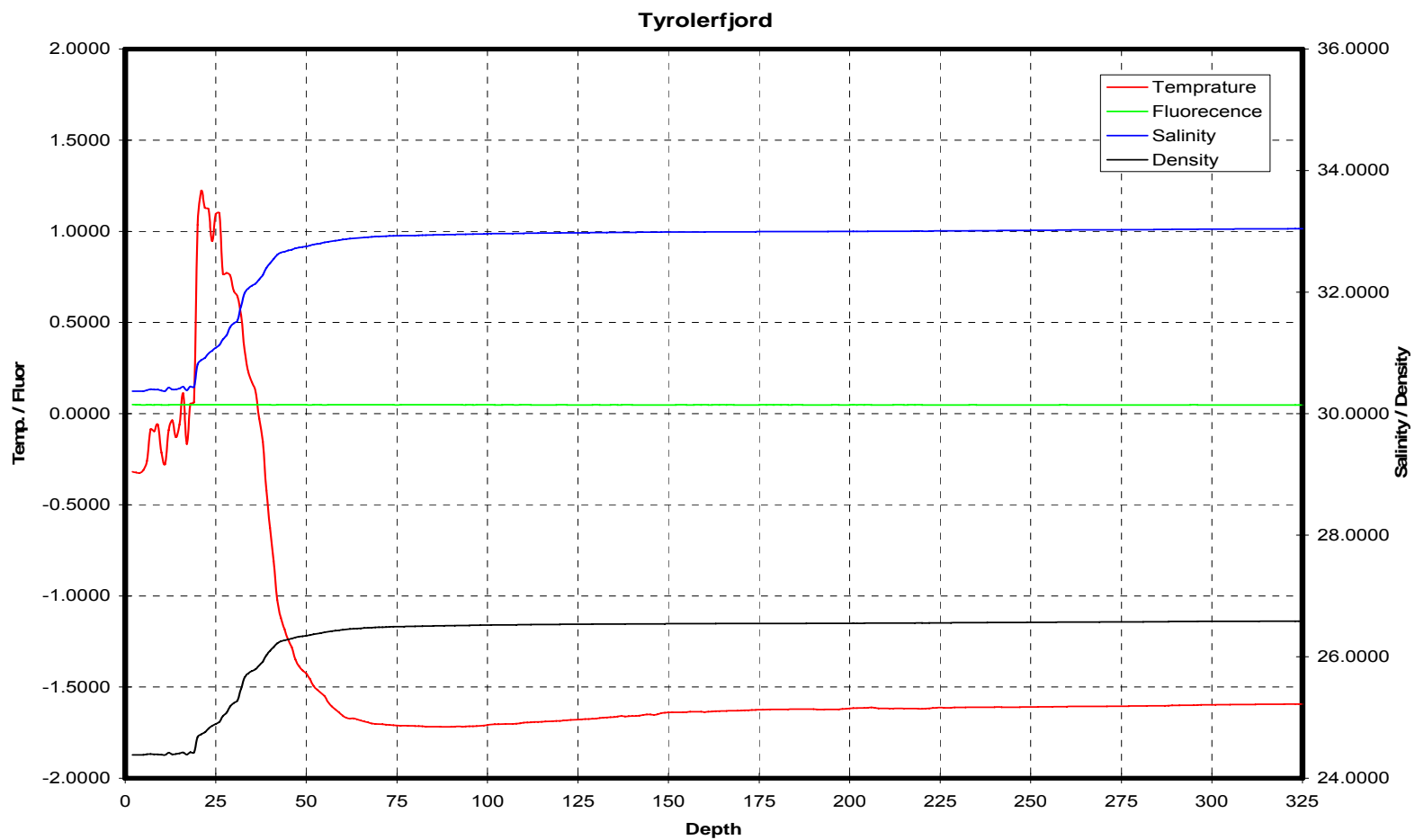
The stomach content was divided into 4 different stages, 1 to 4. Stage 1 is when the digestion of the prey has not begun. Stage 2 is when digestion has started. Stage 3 is when the prey is partly digested, and stage 4 is when the prey is digested and one cannot tell what it is without close examination of the remains.

Appendix 2

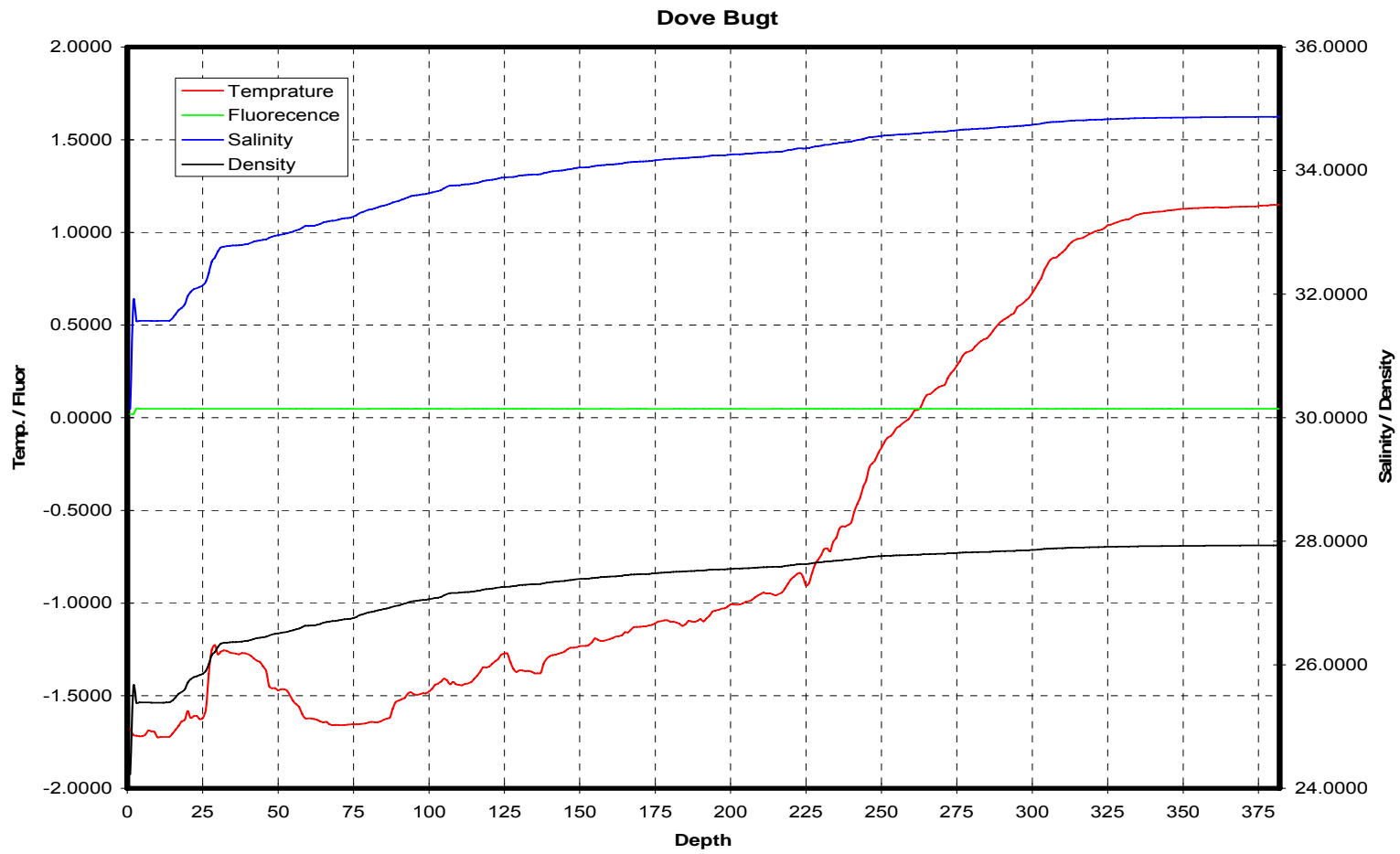


The length and mass of the fish from Tyrolerfjord and Dove Bugt. TFAR= *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.

Appendix 3

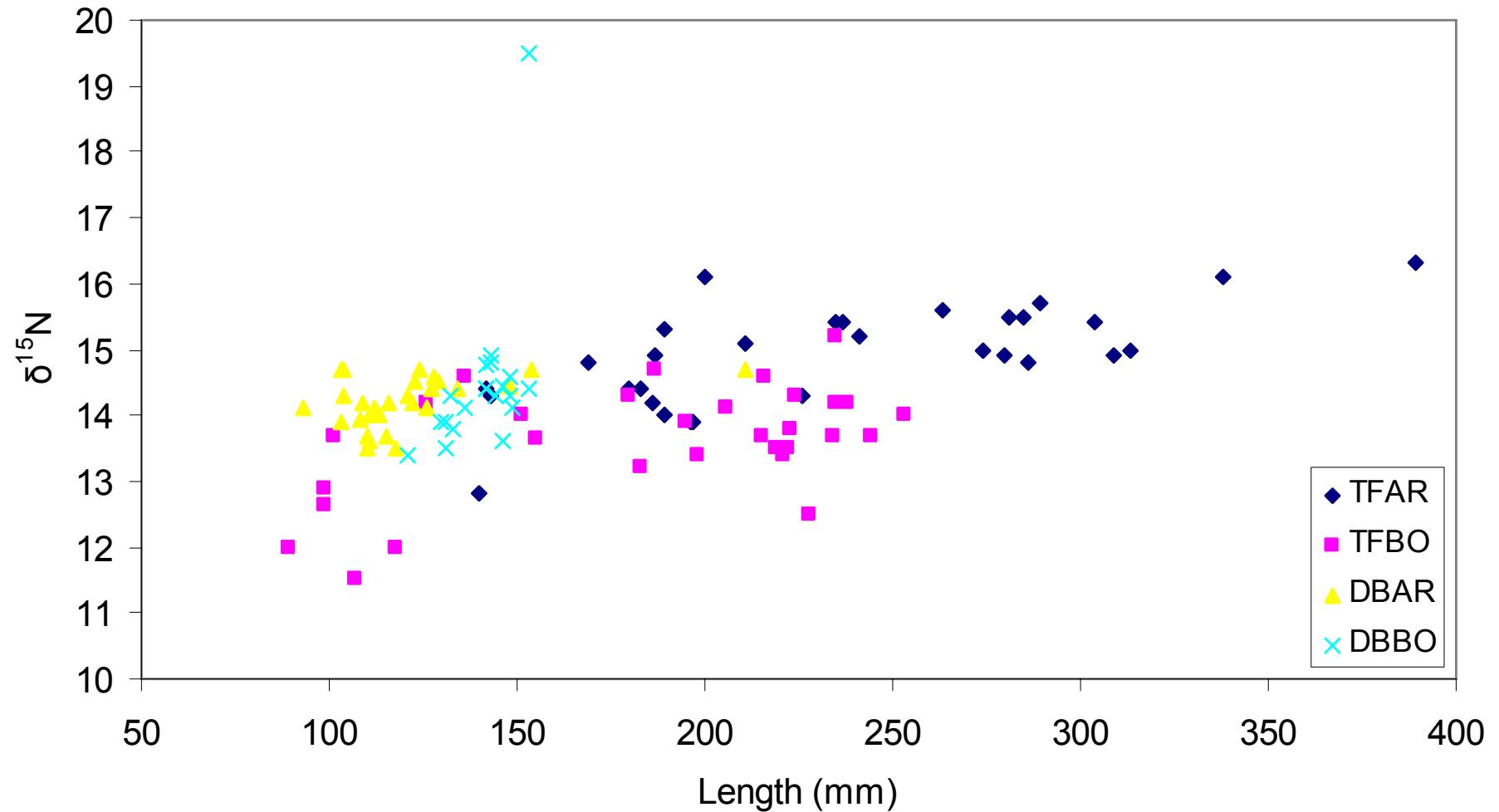


Temperature, fluorescence, salinity and density profile for Tyrolerfjord.

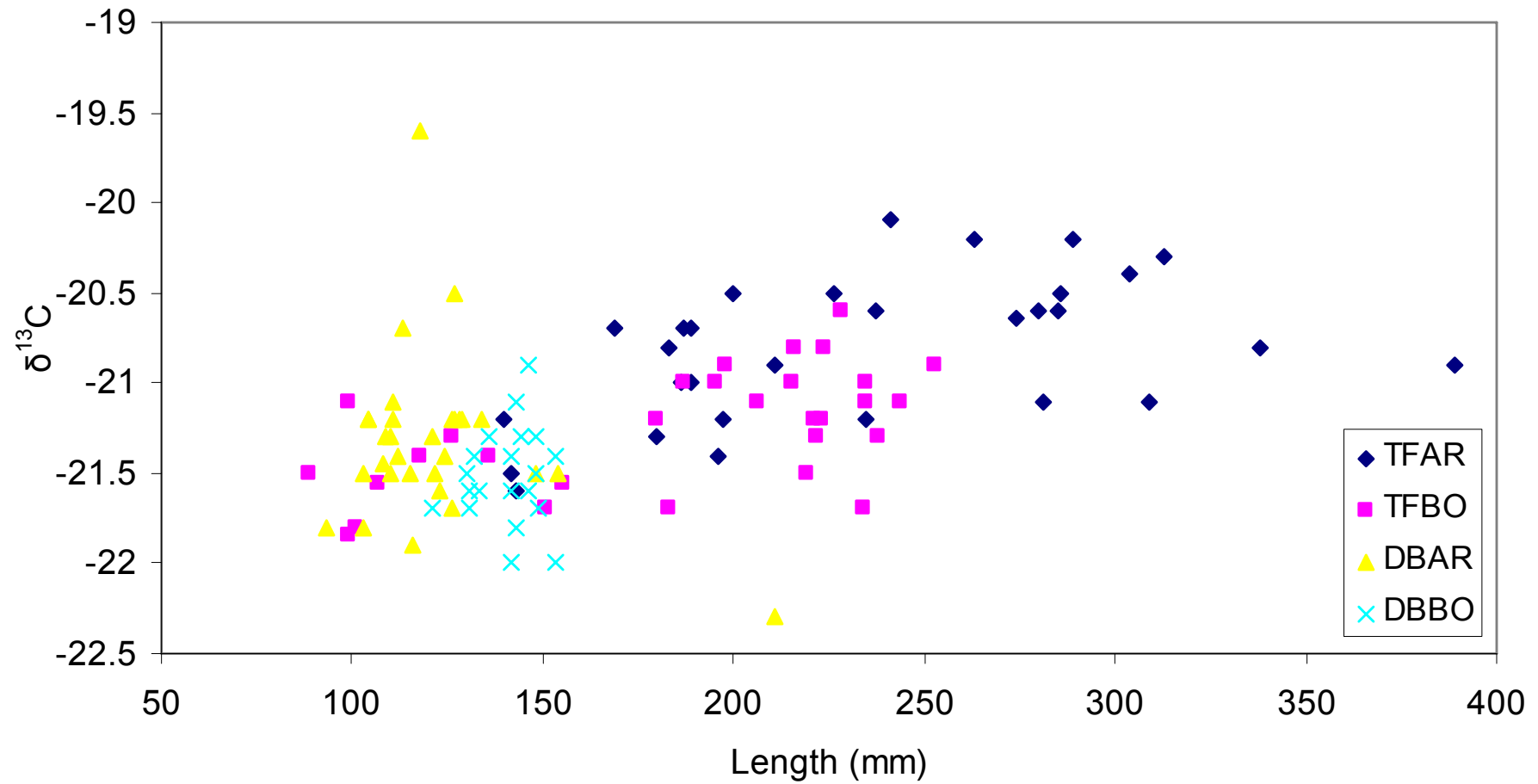


Temperature, fluorescence, salinity and density profile for Dove Bugt.

Appendix 4



Relationship between $\delta^{15}\text{N}$ and total length in the four groups of fish. TFAR= *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.



Relationship between $\delta^{13}\text{C}$ and total length in the four groups of fish. TFAR= *Arctogadus* from Tyrolerfjord. TFBO = *Boreogadus* from Tyrolerfjord. DBAR = *Arctogadus* from Dove Bugt. DBBO = *Boreogadus* from Dove Bugt.

Appendix 5

Fish #	TL	PL	Mass	Full stomach	Emptied stomach	Digestion stage	Liver mass	Gender	Gonad mass	Dressed-out mass	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
TFAR01	169	150	25.0	0.58	0.40	4	0.43	F	0.24	21.2	-20.7	14.8	3.19
TFAR02	189	171	32.3	0.87	0.52	2--4	1.02	M	—	27.3	-21	14	3.26
TFAR03	263	237	111.9	1.84	1.36	3	2.47	M	14.18	85.0	-20.2	15.6	3.24
TFAR04	280	251	137.0	6.10	2.49	3--4	7.88	F	16.57	97.5	-20.6	14.9	3.28
TFAR05	186	167	34.3	1.99	0.53	2--4	0.80	F	0.21	27.5	-21	14.2	3.25
TFAR06	289	261	124.9	2.04	2.01	?	5.65	F	2.28	105.7	-20.2	15.7	2.99
TFAR07	189	169	36.4	1.02	0.71	3--4	1.00	M	—	31.3	-20.7	15.3	3.03
TFAR08	200	186	42.9	1.12	0.87	3--4	1.27	F	0.50	36.7	-20.5	16.1	3.29
TFAR09	180	162	31.8	1.05	0.61	2--4	0.88	M	0.05	23.1	-21.3	14.4	3.15
TFAR10	274	247	117.2	4.27	1.77	3--4	2.71	M	7.69	93.1	-20.64	15	3.06
TFAR11	285	254	151.0	2.68	2.08	2--4	10.86	F	20.14	107.8	-20.6	15.5	3.05
TFAR12	338	303	254.8	5.75	5.75	?	11.69	F	23.89	196.9	-20.8	16.1	2.99
TFAR13	196	176	47.3	1.40	0.56	4	4.24	F	2.41	36.3	-21.4	13.9	2.66
TFAR14	313	283	166.4	6.25	3.52	1--4	9.01	F	13.50	116.5	-20.3	15	3.13
TFAR15	309	280	179.4	3.64	3.17	2--4	7.99	F	19.97	136.6	-21.1	14.9	2.95
TFAR16	140	127	15.7	0.67	0.29	2--4	0.82	F	0.13	12.6	-21.2	12.8	3.24
TFAR17	235	210	71.3	2.58	1.57	2--4	2.08	F	0.67	60.0	-21.2	15.4	2.94
TFAR18	389	347	487.1	45.55	12.47	2	39.82	F	59.98	302.9	-20.9	16.3	2.94
TFAR19	187	171	37.3	1.38	0.54	2--4	1.52	F	0.42	31.3	-20.7	14.9	3.07
TFAR20	237	211	85.8	2.11	1.08	1--4	6.14	F	7.16	65.2	-20.6	15.4	2.87
TFAR21	281	250	142.7	7.30	2.90	1--4	6.85	F	13.68	100.4	-21.1	15.5	3.05
TFAR22	143	130	14.0	0.42	0.28	1--4	0.35	F	0.09	11.7	-21.6	14.3	2.93
TFAR23	142	127	14.0	0.78	0.22	2--4	0.35	M	—	11.4	-21.5	14.4	3.03
TFAR24	183	165	30.7	0.93	0.37	2--4	0.86	F	0.27	25.9	-20.8	14.4	3.16
TFAR25	241	217	93.8	2.50	1.27	2--4	3.08	M	3.03	80.0	-20.1	15.2	3.13
TFAR26	286	265	147.1	4.43	2.88	1--4	8.32	F	13.39	110.9	-20.5	14.8	3.17
TFAR27	304	274	212.1	12.05	2.89	2--4	10.45	F	20.74	147.7	-20.4	15.4	3.14
TFAR28	197	176	41.8	1.17	0.64	2--4	1.16	M	0.07	36.2	-21.2	13.9	3.15
TFAR29	226	204	58.3	1.53	0.81	2--4	1.89	F	0.63	50.5	-20.5	14.3	3.31
TFAR30	211	191	51.2	1.11	0.87	3--4	1.49	F	0.74	43.8	-20.9	15.1	3.18

Fish #	<i>Aglaophamus malmgreni</i>	<i>Ophryotrocha</i> sp.	Polychaeta indet.	<i>Calanus finmarchicus</i>	<i>Calanus hyperboreus</i>	<i>Calanus</i> sp.	<i>Euchaeta/ Pareuchaeta</i> sp.	<i>Metridia longa</i>	Calanoida indet.	<i>Mysis oculata</i>	<i>Thysanoessa inermis</i>	<i>Thysanoessa</i> sp.
TFAR01												
TFAR02												
TFAR03							1					
TFAR04	1							4		13		
TFAR05								1				
TFAR06												
TFAR07							1					
TFAR08										3		
TFAR09							1			3		
TFAR10												
TFAR11												
TFAR12												
TFAR13												
TFAR14												
TFAR15							1			3		
TFAR16												
TFAR17										5		
TFAR18												
TFAR19										7		
TFAR20							2			10		
TFAR21				4			2	2		19		
TFAR22				3								
TFAR23												
TFAR24										4		
TFAR25										6		
TFAR26				2			1			5		
TFAR27										7		
TFAR28				2				1		3		
TFAR29										4		
TFAR30							1					

Fish #	<i>Ampelisca</i> sp.	<i>Anonyx nugax/</i> <i>liljeborgi</i>	<i>Stegocephalus</i> <i>inflatus</i>	<i>Gammarus</i> sp.	Gammaridea indet.	<i>Themisto</i> <i>libellula</i>	<i>Themisto</i> <i>abyssorum</i>	Crustacea indet.	Ophiuroidea indet.	Fish bone	Otoliths	Ichthyo plankton	Fish
TFAR01							7						
TFAR02			1			1	13						
TFAR03							3						
TFAR04	1					2	1					1	
TFAR05						5	5						
TFAR06													
TFAR07							14						
TFAR08													
TFAR09			1										
TFAR10						2	25						
TFAR11							22						
TFAR12													
TFAR13							5						
TFAR14						9							
TFAR15			1										
TFAR16							4						
TFAR17													
TFAR18													1
TFAR19													
TFAR20													
TFAR21						2						5	
TFAR22							9						
TFAR23							28						
TFAR24													
TFAR25		1	1										
TFAR26							16						
TFAR27						3				1	1		
TFAR28													
TFAR29													
TFAR30							11						

Fisk #	TL	PL	Mass	Full stomach	Emptied stomach	Digestion stage	Liver mass	Gender	Gonad mass	Dressed-out mass	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
TFBO01	224	202	66.0	1.32	1.02	3--4	6.27	M	6.27	47.0	-20.8	14.3	3.18
TFBO02	228	206	74.8	1.34	1.09	4	7.16	F	3.13	58.4	-20.6	12.5	3.11
TFBO03	183	164	45.3	2.99	0.92	3--4	3.32	M	7.68	28.0	-21.7	13.2	3.125
TFBO04	222	199	51.2	1.27	0.89	2--3	3.19	F	1.87	41.7	-21.3	13.5	3.13
TFBO05	244	216	81.9	1.84	1.28	3--4	10.77	F	3.44	61.2	-21.1	13.7	3.22
TFBO06	234	207	82.9	1.98	1.23	3--4	6.65	F	4.35	62.9	-21.7	13.7	3.13
TFBO07	216	196	61.5	1.20	0.95	3--4	6.70	F	2.41	46.7	-20.8	14.6	3.09
TFBO08	215	191	55.2	0.86	0.75	3--4	4.57	F	1.91	44.3	-21	13.7	3.14
TFBO09	180	163	35.9	1.17	0.47	3--4	1.97	F	1.05	27.9	-21.2	14.3	3.15
TFBO10	238	211	72.9	1.39	0.92	4	5.48	F	3.04	56.0	-21.3	14.2	3.16
TFBO11	235	212	79.1	1.79	1.39	4	6.86	F	2.53	59.1	-21	15.2	3.23
TFBO12	206	184	50.5	1.05	0.84	3--4	3.46	F	2.10	40.6	-21.1	14.1	3.16
TFBO13	187	168	40.5	0.78	0.64	3--4	5.34	F	1.38	30.4	-21	14.7	3.09
TFBO14	235	209	83.3	2.17	1.56	1--4	8.52	F	3.01	64.1	-21.1	14.2	3.14
TFBO15	219	197	56.5	1.14	1.00	4	6.43	F	2.18	43.3	-21.5	13.5	3.2
TFBO16	221	198	87.0	1.52	1.18	3--4	8.84	M	11.75	59.9	-21.2	13.4	3.06
TFBO17	198	176	62.7	2.04	0.91	4	4.15	M	8.43	43.9	-20.9	13.4	3.11
TFBO18	195	177	38.0	0.90	0.76	4	4.17	F	1.56	28.8	-21	13.9	3.13
TFBO19	223	199	64.0	1.71	0.96	3--4	6.60	F	2.12	49.3	-21.2	13.8	3.1
TFBO20	253	226	99.3	2.18	1.69	3--4	7.49	F	3.15	79.8	-20.9	14	3.07
TFBO21	89	81	4.0	0.25	0.12	3--4	0.30	M	—	2.9	-21.5	12	3.11
TFBO22	99	91	5.2	0.16	0.13	3--4	0.47	M	—	3.9	-21.1	12.9	3.09
TFBO23	118	108	10.2	0.29	0.20	4	0.87	M	—	7.9	-21.4	12	3.1
TFBO24	107	97	5.9	0.45	0.13	3--4	0.32	M	—	4.4	-21.55	11.5	3.105
TFBO25	99	91	5.2	0.24	0.15	3	0.33	F	0.06	3.8	-21.85	12.65	3.07
TFBO26	101	93	6.5	0.50	0.16	2--4	0.29	M	0.02	4.5	-21.8	13.7	3.08
TFBO27	126	114	13.1	0.35	0.22	3--4	0.85	M	2.80	8.0	-21.3	14.2	3.07
TFBO28	155	142	19.6	0.48	0.28	2--4	1.71	F	0.83	14.9	-21.55	13.65	3.075
TFBO29	151	138	24.2	1.48	0.41	1+4	1.72	M	2.87	16.3	-21.7	14	3.09
TFBO30	136	125	17.2	1.23	0.26	1--4	1.31	F	0.61	12.2	-21.4	14.6	3.07

Fisk #	<i>Aglaophamus malmgreni</i>	<i>Ophryotrocha</i> sp.	Polychaeta indet.	<i>Calanus finmarchicus</i>	<i>Calanus hyperboreus</i>	<i>Calanus</i> sp.	<i>Euchaeta/Pareuchaeta</i> sp.	<i>Metridia longa</i>	Calanoida indet.	<i>Mysis oculata</i>	<i>Thysanoessa inermis</i>	<i>Thysanoessa</i> sp.
TFBO01												
TFBO02							2					
TFBO03					1							
TFBO04												
TFBO05					2	1		3	2			
TFBO06												
TFBO07							2					
TFBO08							2					
TFBO09												
TFBO10								1				
TFBO11												
TFBO12								1				
TFBO13				1			1					
TFBO14						1	2	1				
TFBO15								1	1			
TFBO16							1			1		
TFBO17								1				
TFBO18						1						
TFBO19				5	1			2				
TFBO20						1		3		1		
TFBO21								1				
TFBO22												
TFBO23								1				
TFBO24												
TFBO25												
TFBO26												
TFBO27												
TFBO28							2					
TFBO29						1			1			
TFBO30												

Fisk #	<i>Ampelisca</i> sp.	<i>Anonyx nugax/</i> <i>liljeborgi</i>	<i>Stegocephalus</i> <i>inflatus</i>	<i>Gammarus</i> sp.	Gammaridea indet.	<i>Themisto</i> <i>libellula</i>	<i>Themisto</i> <i>abyssorum</i>	Crustacea indet.	Ophiuroidea indet.	Fish bone	Otoliths	Ichthyo plankton	Fish
TFBO01							6						
TFBO02							1						
TFBO03						6							
TFBO04						1							
TFBO05							1						
TFBO06							5						
TFBO07							1						
TFBO08							2						
TFBO09						1							
TFBO10													
TFBO11							1						
TFBO12							8						
TFBO13													
TFBO14							2		1				
TFBO15							1						
TFBO16							5						
TFBO17							2						
TFBO18							4						
TFBO19							4						
TFBO20													
TFBO21							2						
TFBO22													
TFBO23													
TFBO24						1							
TFBO25							2						
TFBO26						2	7						
TFBO27						1							
TFBO28													
TFBO29						1							
TFBO30						1							

Fisk #	TL	PL	Mass	Full stomach	Emptied stomach	Digestion stage	Liver mass	Gender	Gonad mass	Dressed-out mass	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
DBAR01	134	122	13.7	0.35	0.21	4	0.76	M	—	11.2	-21.2	14.4	3.04
DBAR02	123	112	11.6	0.31	0.22	4	0.84	M	—	9.2	-21.6	14.5	3.04
DBAR03	148	137	22.0	1.40	0.33	2--4	1.08	F	0.16	17.2	-21.5	14.45	3.075
DBAR04	154	141	23.6	1.73	0.34	3--4	1.39	F	0.14	18.3	-21.5	14.7	3.05
DBAR05	211	192	59.7	3.20	0.74	2--4	3.81	M	1.51	46.9	-22.3	14.7	3.02
DBAR06	110	101	7.0	0.12	0.09	2--3	0.27	F	0.04	5.6	-21.5	13.5	3.07
DBAR07	111	101	8.7	0.24	0.12	4	0.31	F	0.05	7.2	-21.1	13.6	3.11
DBAR08	103	94	6.8	0.13	0.08	4	0.32	M	—	5.4	-21.5	13.9	3.05
DBAR09	103	95	6.5	0.16	0.09	4	0.25	F	0.04	5.1	-21.8	14.7	3.05
DBAR10	124	112	11.4	0.88	0.18	1+4	0.61	F	0.07	8.6	-21.4	14.7	3.09
DBAR11	109	99	7.8	0.27	0.13	3--4	0.30	F	0.05	6.2	-21.3	14.2	3.1
DBAR12	126	113	13.5	1.18	0.18	2--4	0.82	F	0.08	10.4	-21.2	14.1	3.07
DBAR13	122	112	10.7	0.28	0.19	3--4	0.63	M	—	8.6	-21.5	14.2	3.08
DBAR14	129	119	13.1	0.25	0.21	0	0.65	F	0.08	10.9	-21.2	14.5	3.09
DBAR15	127	114	13.9	0.74	0.23	3--4	0.69	M	—	11.2	-20.5	14.4	3.11
DBAR16	112	106	10.4	0.56	0.17	3--4	0.48	F	0.05	8.1	-21.4	14.1	3.09
DBAR17	108	98	6.7	0.29	0.07	1+4	0.29	F	0.03	5.3	-21.45	13.95	3.095
DBAR18	111	104	9.5	0.70	0.12	3--4	0.45	F	0.06	7.1	-21.2	14	3.08
DBAR19	113	104	9.0	0.49	0.11	2--4	0.50	M	—	7.0	-20.7	14	3.07
DBAR20	121	110	12.0	0.79	0.15	3--4	0.74	M	—	9.1	-21.3	14.3	3.08
DBAR21	104	95	6.0	0.13	0.07	2--4	0.27	F	0.04	4.8	-21.2	14.7	3.07
DBAR22	128	116	12.0	0.43	0.20	4	0.77	M	0	9.7	-21.2	14.6	3.09
DBAR23	126	113	14.8	0.95	0.22	1--4	1.06	M	0.99	10.5	-21.7	14.1	3.07
DBAR24	127	115	11.1	0.30	0.15	3--4	0.53	M	—	9.1	-21.2	14.4	3.05
DBAR25	104	95	6.2	0.18	0.07	4	0.29	F	0.03	4.9	-21.2	14.3	3.11
DBAR26	116	105	9.7	0.43	0.15	3--4	0.60	M	—	7.5	-21.9	14.2	3.09
DBAR27	93	86	5.4	0.55	0.10	2--4	0.28	M	—	3.8	-21.8	14.1	3.14
DBAR28	115	104	8.8	0.37	0.12	3--4	0.68	F	0.32	6.4	-21.5	13.7	3.06
DBAR29	110	99	8.1	0.48	0.13	2--4	0.29	F	0.07	6.3	-21.3	13.7	3.11
DBAR30	118	107	8.3	0.23	0.11	2--4	0.25	M	—	7.0	-19.6	13.5	3.17

Fisk #	<i>Aglaophamus malmgreni</i>	<i>Ophryotrocha</i> sp.	Polychaeta indet.	<i>Calanus finmarchicus</i>	<i>Calanus hyperboreus</i>	<i>Calanus</i> sp.	<i>Euchaeta/Pareuchaeta</i> sp.	<i>Metridia longa</i>	<i>Calanoida</i> indet.	<i>Mysis oculata</i>	<i>Thysanoessa inermis</i>	<i>Thysanoessa</i> sp.
DBAR01		1							1			
DBAR02			1					4				
DBAR03								4		2		
DBAR04					1					3		
DBAR05				2						6		
DBAR06								1				
DBAR07							1	1				
DBAR08							2					
DBAR09												
DBAR10												
DBAR11										1		
DBAR12										1		
DBAR13										1		
DBAR14												
DBAR15							1			1		
DBAR16										1		
DBAR17												
DBAR18										2		
DBAR19												
DBAR20				1			2	52		1		
DBAR21							1					
DBAR22								59				1
DBAR23												
DBAR24								13		1		
DBAR25								1				
DBAR26												
DBAR27				1				1				
DBAR28									1			
DBAR29												
DBAR30									1			

Fisk #	<i>Ampelisca</i> sp.	<i>Anonyx nugax/</i> <i>lijeborgi</i>	<i>Stegocephalus</i> <i>inflatus</i>	<i>Gammarus</i> sp.	Gammaridea indet.	<i>Themisto</i> <i>libellula</i>	<i>Themisto</i> <i>abyssorum</i>	Crustacea indet.	Ophiuroidea indet.	Fish bone	Otoliths	Ichthyo plankton	Fish
DBAR01													
DBAR02													
DBAR03							1						
DBAR04													
DBAR05													
DBAR06													
DBAR07							1						
DBAR08													
DBAR09								1					
DBAR10						1							
DBAR11							4						
DBAR12													
DBAR13							2						
DBAR14													
DBAR15							3						
DBAR16													
DBAR17							1						
DBAR18													
DBAR19							3						
DBAR20													
DBAR21							1						
DBAR22													
DBAR23							2						
DBAR24							1						
DBAR25							1						
DBAR26							1						
DBAR27							5						
DBAR28					1								
DBAR29							3						
DBAR30							5						

Fisk #	TL	PL	Mass	Full stomach	Emptied stomach	Digestion stage	Liver mass	Gender	Gonad mass	Dressed-out mass	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
DBBO01	143	131	18.4	0.84	0.30	1--4	1.47	M	1.629	12.7	-21.1	14.9	3.21
DBBO02	143	131	20.5	0.91	0.36	2--4	1.35	M	1.904	14.6	-21.8	14.8	3.13
DBBO03	142	129	16.9	0.36	0.21	4	1.60	F	0.58	12.9	-21.6	14.75	3.14
DBBO04	142	129	20.7	1.48	0.29	3--4	1.50	M	3.156	13.0	-21.4	14.4	3.15
DBBO05	131	120	16.2	0.47	0.23	4	1.57	M	2.031	10.5	-21.6	13.5	3.17
DBBO06	146	132	19.1	0.76	0.24	2--4	1.90	F	0.821	13.8	-20.9	13.6	3.12
DBBO07	136	125	16.7	1.45	0.28	1--4	1.09	M	1.559	11.2	-21.3	14.1	3.12
DBBO08	149	137	21.9	0.85	0.29	3--4	2.10	F	0.846	16.4	-21.7	14.1	3.15
DBBO09	130	118	14.2	1.58	0.23	2--4	0.87	F	0.533	9.8	-21.5	13.9	3.16
DBBO10	121	112	10.8	0.59	0.23	3--4	0.89	F	0.168	7.9	-21.7	13.4	3.11
DBBO11	132	122	14.8	1.25	0.33	2--4	0.90	F	0.549	10.7	-21.4	14.3	3.11
DBBO12	133	121	14.0	0.37	0.18	3--4	0.89	F	0.179	11.2	-21.6	13.8	3.13
DBBO13	146	132	17.8	0.57	0.22	3--4	1.00	M	1.966	12.7	-21.6	14.45	3.155
DBBO14	148	133	20.3	1.71	0.29	1--4	1.25	F	0.85	15.0	-21.5	14.3	3.11
DBBO15	131	119	12.2	0.43	0.18	4	0.61	F	0.347	9.7	-21.7	13.9	3.12
DBBO16	142	130	17.0	1.24	0.26	2--4	1.52	F	0.715	12.1	-22.0	14.4	3.26
DBBO17	153	139	23.6	0.50	0.34	4	2.53	F	1.053	17.7	-22.0	14.4	3.1
DBBO18	153	140	24.5	1.09	0.32	2--3	2.26	M	4.093	15.3	-21.4	19.5	3.26
DBBO19	148	134	20.6	1.12	0.25	3--4	1.79	F	0.759	15.1	-21.3	14.6	3.14
DBBO20	144	131	18.7	1.17	0.25	2--4	1.61	F	0.85	13.5	-21.3	14.3	3.13

Fisk #	<i>Aglaophamus malmgreni</i>	<i>Ophryotrocha</i> sp.	Polychaeta indet.	<i>Calanus finmarchicus</i>	<i>Calanus hyperboreus</i>	<i>Calanus</i> sp.	<i>Euchaeta/Pareuchaeta</i> sp.	<i>Metridia longa</i>	Calanoida indet.	<i>Mysis oculata</i>	<i>Thysanoessa inermis</i>	<i>Thysanoessa</i> sp.
DBBO01				1				4				
DBBO02						1		2				
DBBO03								1				
DBBO04										1	1	
DBBO05												
DBBO06					1			5				
DBBO07				1				2				
DBBO08								1				
DBBO09						1	1	2			1	
DBBO10												
DBBO11				1				3				
DBBO12							1	1				
DBBO13												
DBBO14								1				
DBBO15								10				
DBBO16							1	2		1		
DBBO17								2				
DBBO18												
DBBO19												
DBBO20				2			2	16		1	1	

Fisk #	<i>Ampelisca</i> sp.	<i>Anonyx nugax/</i> <i>lijeborgi</i>	<i>Stegocephalus</i> <i>inflatus</i>	<i>Gammarus</i> sp.	Gammaridea indet.	<i>Themisto</i> <i>libellula</i>	<i>Themisto</i> <i>abyssorum</i>	Crustacea indet.	Ophiuroidea indet.	Fish bone	Otoliths	Ichthyo plankton	Fish
DBBO01							1						
DBBO02							1					1	
DBBO03							1						
DBBO04						1							
DBBO05								1					
DBBO06			1										
DBBO07						5							
DBBO08													
DBBO09				1									
DBBO10						2							
DBBO11							7					1	
DBBO12													
DBBO13													
DBBO14						1	13						
DBBO15							1						
DBBO16													
DBBO17													
DBBO18							5						
DBBO19							2						
DBBO20													