

Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*?

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Abstract During a recent period of increased influx of warm Atlantic water to the western coast of Svalbard, we have observed a northward expansion of boreal Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) into areas dominated by the native polar cod (*Boreogadus saida*). To determine the potential impact of new ecological interactions, we studied the diet of co-occurring juvenile gadoids in fjords, open water, and sea ice around Svalbard. We also reviewed the available literature on polar cod feeding in different habitats across the Arctic to determine whether region, habitat, or fish size may influence diet. Feeding by polar cod in the pelagic zone was size dependent, with small fish primarily consuming *Calanus* spp. and smaller copepods, with an increasing ration of *Themisto* spp. at larger sizes. In benthic habitats, diets were more varied and included considerably more unidentified material and sediment. Less than 40% dietary overlap was detected among the three species when they were found together. Stable isotope analyses indicated these patterns were representative of longer-term

assimilation. The low interspecific dietary overlap suggests little direct competition. Future increases in abundance and the high predation potential of the boreal taxa, however, may impact the persistence of polar cod on some Arctic shelves.

Keywords Arctic · Diet overlap · *Gadus morhua* · Habitat selection · Interspecific competition · *Melanogrammus aeglefinus* · Niche segregation · Sea ice · Svalbard

Introduction

Observation and modeling efforts indicate significant climatic changes over the past decades and well into the future. In the marine environment, these are manifested as increased sea temperatures, altered circulation patterns, and severe reductions in ice cover in high-latitude regions. Climate change is predicted to have particularly strong and possibly nonlinear effects in the Arctic. Atmosphere–ocean–ice feedback systems suggest that we will soon reach an ice-free Arctic Ocean in the summertime. This will have strong implications for biogeochemical cycles and ecological functioning. Specific consequences are unknown, but they are expected to include impacts from the very base of the food web, e.g., nutrient cycling and changes in productivity patterns, to the highest predators, including seabirds, marine mammals, and humans (ACIA 2005; Wassmann et al. 2010).

One important prediction that has recently been documented in some oceanic areas is a change in species distributions (e.g., Murawski 1993; Berge et al. 2005; Perry et al. 2005; Beaugrand 2009; Beaugrand et al. 2009; Narayanaswamy et al. 2010). A previous warming period

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in the European Arctic in the 1920s–1940s led to shifts in community structure within the Barents Sea and on the west coast of Greenland (reviewed by Drinkwater 2006; Renaud et al. 2008). Communities dominated by Atlantic species extended to northern Svalbard (Tåning 1949; Nesis 1960; Blacker 1965; Galkin 1998) and a stock of Atlantic cod (*Gadus morhua*) was sufficient to support a new fishery as far north as Thule in west Greenland (Hansen 1949). Temperate/boreal species are predicted to become established in Arctic regions and potentially displace resident taxa (ACIA 2005; Parmesan 2006), with potentially significant impacts on biodiversity, ecosystem structure, and ecological functioning (Renaud et al. 2008). This is especially critical when potentially displaced species play key roles in the current ecosystem (e.g., Harley et al. 2006) or in regional fisheries.

Polar cod (*Boreogadus saida*, referred to as “Arctic cod” in North America) is a gadoid fish with a circumpolar distribution, and a dominant fish species on Arctic shelves. It forms a central part of the diets of seabirds, marine mammals, and commercial fish species (e.g., Welch et al. 1992; Gjøsæter 2009; Loseto et al. 2009), and itself has been the target of directed fisheries in the Barents Sea. Its abundance and role in the ecosystem make it a key species across the Arctic shelf seas. Despite its widespread occurrence, there are surprisingly few studies of such basic biological characteristics as diet and habitat dependence (see Bradstreet et al. 1986; Lønne and Gulliksen 1989 as examples). Polar cod is found in both pelagic and benthic habitats during juvenile and adult phases of its life, and young polar cod are often observed within cracks and brine channels of sea ice (Gradinger and Bluhm 2004 and references therein). Vertical migration and mass schooling have been observed and presumed to be predator avoidance mechanisms (Welch et al. 1993; Hop et al. 1997a, b; Benoit et al. 2010). They are primarily planktivorous through their life cycle, and compete with other planktivorous fishes, such as capelin (*Mallotus villosus*), where they co-occur (Gjøsæter 2009; Orlova et al. 2009). These studies imply flexibility in habitat demands, but also suggest potential, but unknown, vulnerability to changes in both food supply and abundances of predators and competitors on Arctic continental shelves.

The family Gadidae includes some of the most economically valuable fish species in cold-temperate/boreal habitats of the northern hemisphere (Atlantic cod, Atlantic and Pacific pollack, haddock, hake). In the past decade, adult Atlantic cod and haddock (*Melanogrammus aeglefinus*) have expanded their ranges well into the Barents Sea (Drinkwater 2009), partially due to a shift in the location of cod spawning areas several hundred km to the north along the Norwegian coast (Sundby and Nakken 2008; Opdal 2010). Only since 2006, however, have concentrations of

juvenile Atlantic cod and haddock been observed in Svalbard coastal and fjord waters, where they are now frequently caught along with polar cod of similar sizes (Olsen et al. 2010). This sets the stage for potential niche overlaps and competition for food between the southern invaders and an Arctic resident, the polar cod.

Studies have shown closely related coexisting species to consume similar food (Horstkotte and Strecker 2005; Olsen et al. 2010), and where juvenile (0+ age class) Atlantic cod and haddock co-occur in the Barents Sea, there is considerable dietary overlap (Dalpadado et al. 2009). There is no record of these boreal species co-existing with polar cod juveniles, but all are planktivores as juveniles. Competition could result in complete displacement of one or more of these species, or habitat segregation (Matthews et al. 2010), where one species is restricted to a potentially less favorable habitat.

The recent findings that polar cod juveniles now coexist with similar-sized juveniles of closely related temperate/boreal species provide an opportunity for a first test of an important prediction related to ecosystem impacts of climate warming: ecosystem change due to range expansion of boreal species into the Arctic. Here, we investigate overlap in diet and discuss how it may lead to longer-term impacts in polar cod. Specifically we ask: What is the diet of polar cod in different habitats around Svalbard? How similar are diets of co-occurring juvenile gadoids in these waters? And finally, what are the potential consequences of increasing abundance of related boreal species to a resident and abundant pan-Arctic fish species?

Materials and methods

Gadoids were collected from the R/V *Jan Mayen* during cruises in 2006, 2008, and 2009 from fjords around Svalbard, and from open water and beneath sea ice north of the archipelago (Table 1; Fig. 1). All areas were predominantly influenced by water of the West Spitsbergen Current (of Atlantic origin), except Rijpfjorden, which is largely an Arctic-Water dominated fjord. All fjords are glacially influenced but only in Billefjorden were samples collected from near a glacier foot. Fish were collected using a Harstad pelagic trawl, which has a cod end with an inner liner of mesh size <0.20 mm. The benthic fish samples were collected using Campel 1800 shrimp trawl with rockhopper gear. The cod end of this shrimp trawl has an inner net with a mesh size of 20 mm. The trawling speed was about 3 knot for both the pelagic and the benthic trawl. In 2008, an EK-60 multifrequency hydro-acoustic profiler was used to identify concentrations of pelagic organisms, and these depth strata were targeted for collections. Depths and durations of pelagic and benthic trawls are presented in

Table 1 Sampling information for juvenile gadoids collected around Svalbard from 2006 to 2009 by pelagic trawl, benthic trawl, and collected by divers under sea ice

Trawl	Date	Region	Latitude (N)	Longitude (E)	Total depth (m)	Net depth (m)	Trawl time (min)
Pelagic	26.08.2006	Isfjorden 1	78°08.9'	13°53.2'	270	50	60
	28.08.2006	Kongsfjorden	78°59.0'	11°33.3'	315	50	60
	31.08.2006	Rijpfjorden	80°23.5'	22°01.9'	264	50	90
	07.09.2006	Isfjorden 2	78°12.3'	13°56.9'	270	50	90
	30.08.2006	Hinlopen	79°38.8'	18°48.8'	322	50	65
	26.08.2008	Billefjorden	78°38.1'	16°39.2'	194	50	30
	28.08.2008	Kongsfjorden	78°59.2'	11°29.8'	318	150	30
	02.09.2008	Ice edge	80°46.0'	14°56.0'	1,251	60	10
	Benthic	26.08.2006	Isfjorden	78°09.1'	13°16.0'	270	270
28.08.2006		Kongsfjorden	78°58.9'	11°35.1'	284	284	30
31.08.2006		Rijpfjorden	80°23.5'	22°01.9'	264	264	30
28.08.2008		Kongsfjorden	78°58.5'	11°36.7'	300	300	30
Diver	03.09.2009	Under ice	81°15.0'	13°14.0'	2,500	1–4	–

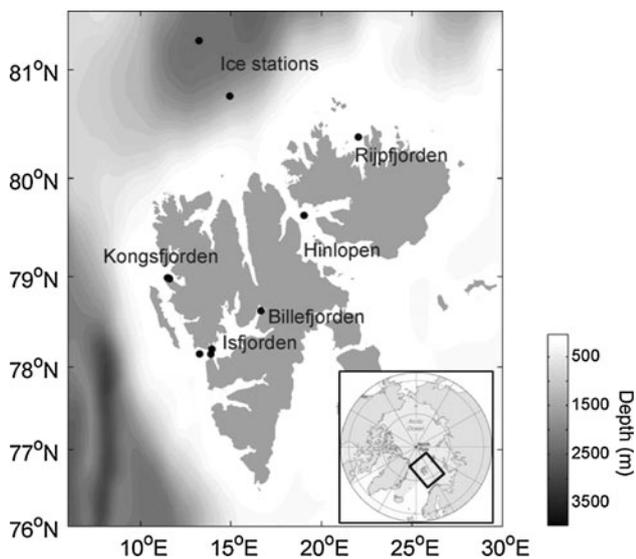
**Fig. 1** Map of Svalbard indicating sampling locations. See Table 1 for dates and exact locations of sampling. *Inset* shows Svalbard's location in the Arctic Ocean

Table 1. In 2009, polar cod were collected by divers from within close drift ice north of Svalbard by spearing fish in cavities within the sea ice with a long “harpoon”.

Juvenile gadoids were measured (caudal length) to the nearest mm, and stomachs were extracted immediately and placed in 70% ethanol until analysis. Stomach fullness was assessed on a quartile scale based on appearance of all collected stomachs. Since the aim of this study was to compare stomach contents and not feeding intensity, empty stomachs (0–14% of total per collection) were excluded from analyses. Contents were identified to lowest practical taxonomic level under a stereomicroscope. In 2006, dietary

contribution for each prey category was expressed as a numerical percentage of the total number of prey items in the stomach. In 2008 and 2009, a volume percentage was used. All measures of diet from stomach contents have biases. For example, numerical percentages may over-represent the importance of small taxa/individuals, whereas volumetric measures, perhaps the most widely used method, may still not be representative of nutrition *per se* (Hyslop 1980). These issues may be minimal in our samples as few taxa were recorded and most were of similar size and proportion of exoskeleton (most were crustaceans).

Another issue with stomach content analysis is that it represents a snapshot and may not depict longer-term diet. To address this question, samples of the dorso-lateral muscle were taken from 6 to 10 individuals of three species of gadoids collected from a pelagic trawl in open water (>0.5 km south of the ice edge) north of Svalbard (2008), and polar cod collected from under the sea ice (2009). This muscle tissue was frozen (−20°C) and brought back to the laboratory where it was freeze-dried and analyzed for stable nitrogen isotope composition to indicate relative trophic position, which is usually integrated in this biomarker over weeks to months. Lipid and carbonate removal was not conducted prior to stable nitrogen isotope analysis. Samples were run using standard methods (e.g., Hobson et al. 1995) in the Environmental Geochemistry Laboratory, Bates College, Lewiston, Maine USA, and data in per mil notation ($\delta^{15}\text{N}$) are expressed relative to an air standard. Acetanilide, caffeine, millet flour, and bulk Atlantic cod tissue were used as internal standards. A Kruskal–Wallis test was used to compare $\delta^{15}\text{N}$ values among fish taxa/habitats. A non-parametric multiple comparisons test was used to discern any significant ($\alpha = 0.05$) differences among the groups.

Dietary overlap between species or sampling locations was calculated using Schoener's index:

$$\text{Schoener's index of overlap} = 1 - 0.5 * \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right)$$

where p_{xi} and p_{yi} are the proportions of food item i in species (or locations) x and y , respectively, and n is the total number of prey items identified (Schoener 1970). This index has been recommended when dietary items are of approximately similar size in a review of the three most common overlap indices (Wallace 1981). The index is expressed as a proportion between 0 (no overlap) and 1 (complete overlap). Since methodology was different between 2006 (numerical percentage) and 2008 and 2009 (volume percent), interannual differences in diet were not analyzed by this technique.

Results

Stomach contents from a total of 530 polar cod, 62 haddock, and 121 Atlantic cod were analyzed, and average length of the fish ranged from 4.5–12.8 cm, 6.7–8.2 cm, and 7.2–7.4 cm for the three species, respectively (Table 2). All 3 species were collected together from single pelagic trawls on 4 occasions (twice in Isfjorden and once in Kongsfjorden in 2006, and once near the ice edge in 2008). Juvenile haddock and Atlantic cod were never found in benthic trawls in our sampling.

Intraspecific comparisons: polar cod

Polar cod collected from pelagic trawls mainly fed on small copepods (*Pseudocalanus* spp., small copepodites of *Calanus* spp.), larger *Calanus* spp., and the hyperiid amphipod

Themisto spp. (Fig. 2). Throughout the study, *Calanus* was represented by *C. finmarchicus* and *C. glacialis*, but we were not always able to reliably differentiate between the two species due to state of digestion. Similarly, the large majority of *Themisto* were *T. libellula*, although some *T. abyssorum* were found. At the ice edge, “other amphipods” comprised more than 50% of the polar cod stomach contents (Fig. 3). These ice-edge fish showed low dietary overlap with fish from either Billefjorden or Kongsfjorden in 2008, whereas fish from the latter two fjords had high overlap (Table 3A). Ice-edge fish had moderately high overlap with diver-collected fish within drift ice (59%; Table 3A). In the latter habitat, the sympagic amphipod *Apherusa glacialis* made up most of the “other amphipods” group. Polar cod collected in 2006 pelagic trawls had considerable dietary overlap (all > 70%), except for fish collected during the first sampling in Isfjorden, where the high proportion of *Themisto* spp. here contrasted sharply with the 4 other samples where copepods dominated (Table 3A; Fig. 2).

Polar cod caught in benthic trawls were generally larger than pelagic juveniles (Table 2). Their diets were more varied than fish sampled in pelagic trawls, and were dominated by *Themisto* spp., *Calanus* spp., “other” taxa, unidentified material, and euphausiids (Fig. 4). Dietary overlap from sampling locations in 2006 ranged from 43 to 80% (Table 3). With the exception of fish collected from Rijpfjorden in 2006 (<21%), there was considerable overlap in diets of fish collected in benthic and pelagic trawls in the same fjord (44–82%; Table 3A).

Intraspecific comparisons: Atlantic cod and haddock

Both Atlantic cod and haddock exhibited considerable intraspecific dietary fidelity among west Svalbard fjords in 2006, with overlap index values ranging from 68 to 86%

Table 2 Number of stomachs analyzed and caudal length of different gadoid species for each sampling location and year

Trawl	Year	Region	Boreo	N	Melan	N	Gadus	N
Pelagic	2006	Isfjorden 1	10.0 (2.2)	48	8.2 (–)	1	7.3 (0.8)	46
		Kongsfjorden	4.7 (0.9)	47	6.9 (0.8)	22	7.4 (1.1)	27
		Rijpfjorden	4.5 (2.2)	37				
		Isfjorden 2	6.1 (1.7)	49	7.0 (1.0)	11	7.2 (1.4)	18
		Hinlopen	4.8 (0.9)	44				
	2008	Billefjorden	13.3 (1.4)	80				
Kongsfjorden		8.0 (1.4)	34					
Ice edge		9.4 (1.7)	26	6.7 (0.8)	28	7.2 (0.6)	30	
Benthic	2006	Isfjorden	10.1 (1.3)	47				
		Kongsfjorden	12.8 (2.8)	44				
		Rijpfjorden	10.3 (1.5)	48				
	2008	Kongsfjorden	11.4 (1.8)	5				
Diver	2009	Under ice	9.9 (1.1)	21				
Total				530		62		121

Mean length (1 SD) in cm and N presented. Boreo: *Boreogadus saida*, Melan: *Melanogrammus aeglefinus*, Gadus: *Gadus morhua*. Fish with empty stomachs omitted

Fig. 2 Percent composition of stomach contents (2006: numerical, 2008: volume) of polar cod collected from pelagic trawls in fjords around Svalbard. See Tables 2 and 3 for number of replicates and fish sizes for each figure. *Color/shading* represents diet classification. Table 4 shows Schoener's Index of dietary overlap for relevant comparisons

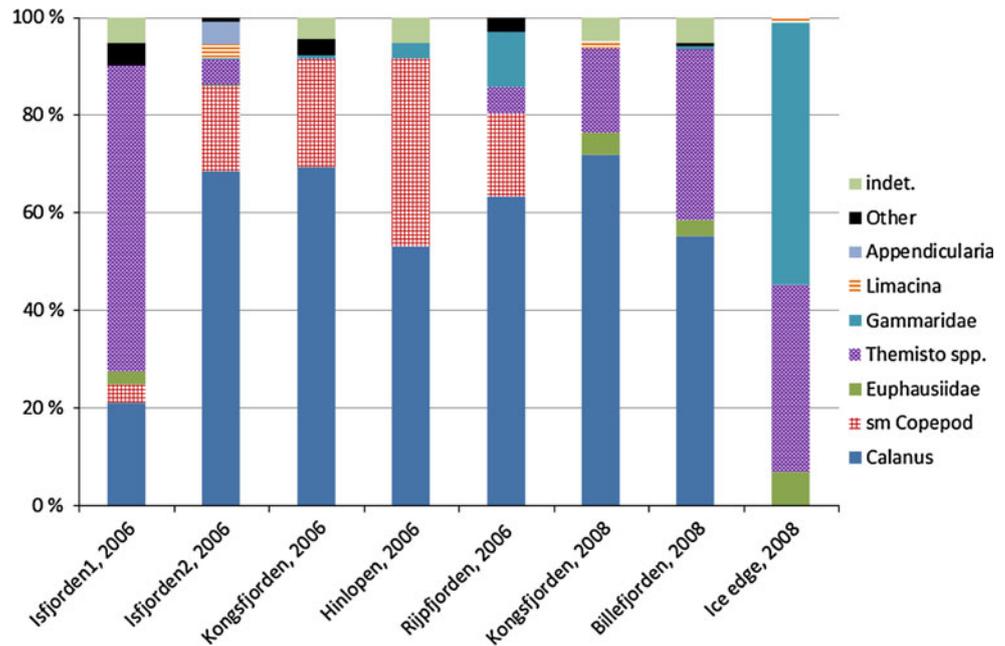
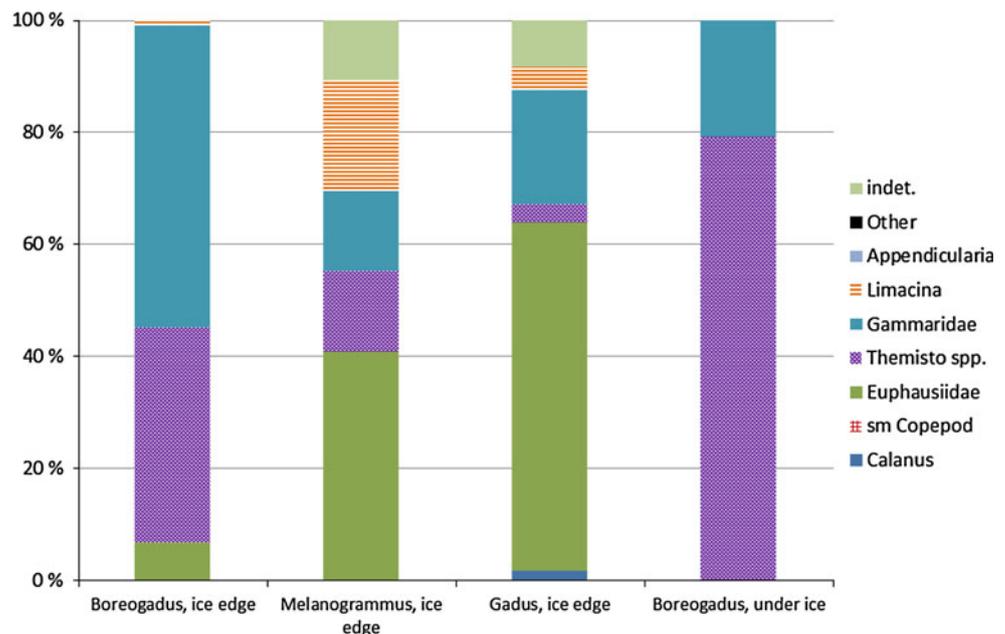


Fig. 3 Percent composition of stomach contents of polar cod, haddock, and Atlantic cod collected from pelagic trawls at the ice edge and polar cod collected from under the ice. See Tables 2 and 3 for number of replicates and fish sizes for each figure. *Color/shading* represents diet classification. Table 4 shows Schoener's Index of dietary overlap for relevant comparisons



(Table 3B). Haddock consumed primarily appendicularians, with some contribution of euphausiids and *Themisto* spp. in Kongsfjorden and Isfjorden2 (Fig. 5). The stomach contents of the one haddock collected in the Isfjorden1 trawl was also dominated by appendicularians and *Themisto* spp. Atlantic cod diets were largely composed of euphausiids, copepods, and *Themisto* spp. (Fig. 4). Atlantic cod and haddock diets at the ice-edge station in 2008 were dominated by euphausiids and “other amphipods,” with haddock also having large contributions of *Themisto* spp. and the pteropod *Limacina helicina* (Fig. 3).

Interspecific comparisons

There was very little dietary overlap (mostly under 40%) when the three species co-occurred. Only in 2008 at the ice-edge station did Atlantic cod and haddock have a strong overlap, but neither was more than 37% similar to polar cod (Table 3C; Figs. 3, 5). The $\delta^{15}\text{N}$ ratios of Atlantic cod and haddock sampled at the ice edge were 9.6 and 10.3‰, respectively, which contrasted with that of polar cod of 12.0‰. Polar cod collected under the ice by divers in 2009 had a $\delta^{15}\text{N}$ ratio of 10.7‰. Statistical analysis indicated

Table 3 Schoener's Index of dietary overlap for pairs of fish samples

A. <i>Boreogadus</i> intraspecific comparisons							
2006	IF2	IF1	KF	RF	if	kf	rf
IF1	0.309				0.817		
KF	0.873	0.327				0.696	
RF	0.866	0.331	0.840				0.207
HIN	0.709	0.299	0.802	0.734			
kf					0.431		
rf					0.798	0.490	
B. <i>Melanogrammus</i> and <i>Gadus</i> intraspecific comparisons							
2008		BF		KF		kf	Under ice
KF		0.806				0.441	
Ice edge		0.389		0.230			0.592
C. Interspecific comparisons							
2006	IF1		IF2		KF		
	Boreo	Melan	Boreo	Melan	Boreo	Melan	
Melan			0.151		0.146		
Gadus	0.380		0.363	0.448	0.349		0.366
2008							
			Ice edge				
			Boreo				Melan
Melan			0.363				
Gadus			0.314				0.710

Due to different techniques in calculating diets (numerical vs. volume percent), no interannual comparisons are made. Index values are between 0 and 1 with higher values indicating a higher proportional overlap. More than 50% overlap is highlighted in bold. Lower case abbreviations indicate benthic trawl samples whereas capital letters indicate pelagic trawls. HIN Hinlopen, RF Rijpfjorden, KF Kongsfjorden, IF Isfjorden (1 and 2), BF Billefjorden, Boreo *Boreogadus saida*, Melan *Melanogrammus aeglefinus*, Gadus *Gadus morhua*

that polar cod collected by pelagic trawl at the ice edge had a significantly higher $\delta^{15}\text{N}$ ratio than Atlantic cod or haddock, but was not different than polar cod collected under the ice. In addition, isotope ratios for Atlantic cod and haddock from the ice edge, and polar cod collected under the ice, were not significantly different from each other (Kruskal–Wallis test with nonparametric multiple comparisons test: $P < 0.001$, $n = 28$).

Discussion

Review: dietary comparisons of polar cod from different habitats

We reviewed the literature and identified 15 studies, including two masters' theses, reporting diets of post-larval polar cod (Table 4) from most major Arctic shelf regions. Many of these are from fish collected with benthic trawls,

and only three studies are from the sympagic habitat. Polar cod is a generalist planktivore, with diet presumably reflecting local prey availability, constrained by mechanical and behavioral capabilities of the fish. For example, a strong size-dependence was obvious in pelagic fish: smaller (≤ 8 cm) fish fed primarily on small copepods and *Calanus* spp., with a higher proportion of *Themisto* spp. evident with increasing length of polar cod (Fig. 2; and e.g., Ajiad and Gjørseter 1990). Gape size in gadoids is one mechanical constraint that has been suggested to lead to variations in dietary composition (Dalpadado et al. 2009). *Calanus* spp. and hyperiid amphipods were frequently found in stomachs in all three habitats and throughout the investigated geographical range. There was a more frequent inclusion of non-copepod food items, including decapods and gammarids, in benthic fish. Local importance of other food items (chaetognaths, the pteropod *Limacina helicina*) was also observed (Table 4), and may reflect patchiness of prey and/or low abundances of preferred food. This pattern

Fig. 4 Percent composition of stomach contents (2006: numerical, 2008: volume) of polar cod collected from benthic trawls in fjords around Svalbard. See Tables 2 and 3 for number of replicates and fish sizes for each figure. *Color/shading* represents diet classification. Table 4 shows Schoener’s Index of dietary overlap for relevant comparisons

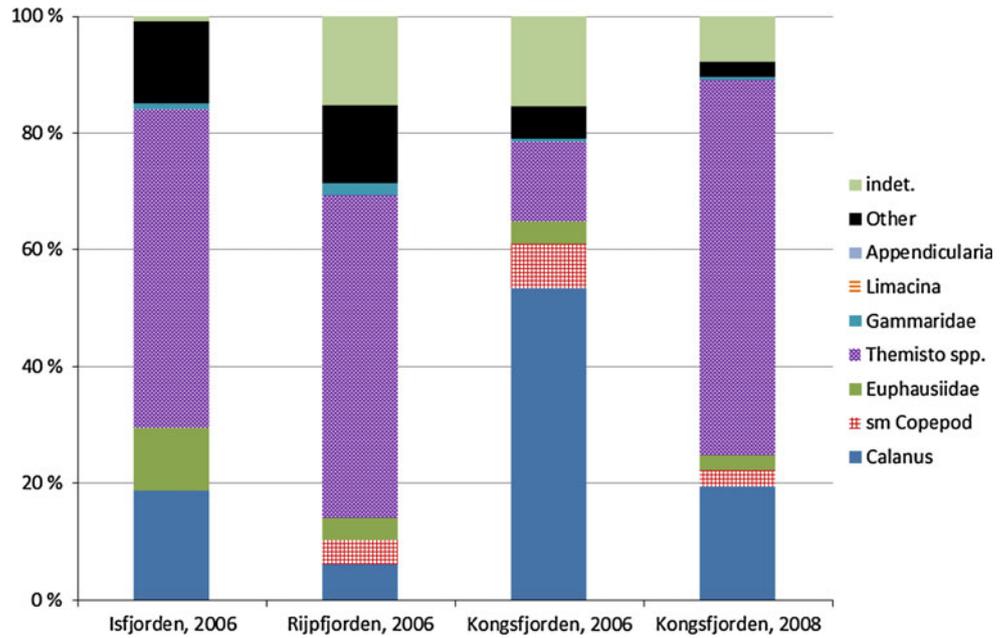
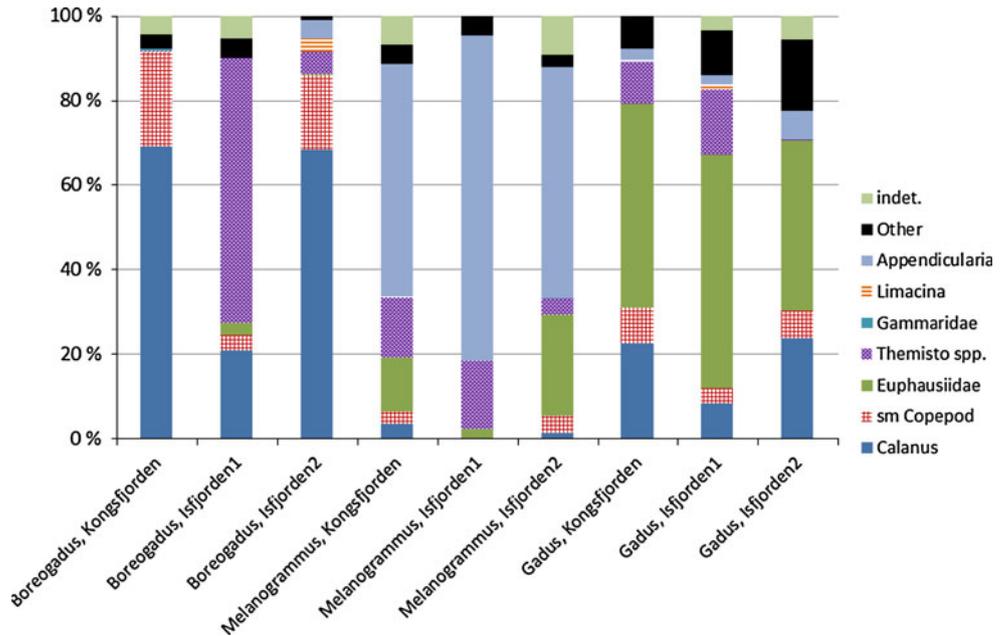


Fig. 5 Numerical percent composition of stomach contents of the three gadoid species collected in pelagic trawls from Svalbard fjords in 2006. See Tables 2 and 3 for number of replicates and fish sizes for each figure. Table 4 shows Schoener’s Index of dietary overlap for relevant comparisons. Polar cod figures are the same as in Fig. 2, but presented here as well for comparative purposes. The figure for *Melanogrammus* for Isfjord1 comes from only one fish examined in this habitat, but is presented to suggest consistency in haddock diets



has been observed for another Barents Sea planktivore, the capelin (Orlova et al. 2010). When collected from within sea ice, polar cod have been found to supplement typical food items from the pelagic habitat with sympagic amphipods, but ice fauna have never been found to comprise large proportions of the diet (Table 4; Fig. 3).

The seasonal resolution of polar cod diets in the literature is largely restricted to summer and autumn, but knowledge of diet during other seasons is potentially significant for both this species and the food web in such a seasonally variable system. Understanding how polar cod, and the species dependent upon it, will respond to

continued climate change requires substantial baseline information (Wassmann et al. 2010), especially that related to energetics and ecological interactions.

Habitat-related diet in polar cod

Pelagic habitat

The diet of polar cod collected from different habitats in Svalbard waters in this study showed many of the patterns seen in the fragmented studies from around the Arctic (Table 4). Polar cod collected from pelagic trawls outside

Table 4 Summary of habitat and size effects on the major elements of polar cod diets across the Arctic

Habitat	Location	Size (cm)	Copepods	Hyperiid	Gammarids	Euphausiids	Mysids	Other	Reference	
Pelagic	Svalbard	3–18	+++	++		+	+	++ (1) (2)	Hovinen (2007)	
	N Svalbard	4.8–5.5	+++	+				+	Falk-Petersen et al. (2008)	
	Beaufort Sea		+++ (also 4)					(5)	Benoit et al. (2010)	
	Russian shelf		+++ (6)		+++ (7)	+		Fish	Moskalenko (1964)	
Benthic	Barents Sea	7.1–9	+++	++		+			Orlova et al. (2009)	
		9.1–11	++	+++		+				
		13.1–17	++							
	N. Bering Sea	<12	++	+	+				++ (2)	Lowry and Frost (1981)
		>12	++	+	++					
	NE Chukchi/Beaufort	<10				+				
		>10				++				
	off Labrador	4.2–5.6	+++	+			++		+	Lilly (1980)
		7.7–11.5	+++	++						
		16–26	+	+++						
	S Beaufort shelf	1.5–10.9	+++ (6,8)	++				+		Lacho (1986)
	Canadian archipelago	6–10	+++	+++	+++			+		Hop et al. (1997a, b)
		10–28	+++	+++						
	NE Chukchi	11.7	+++	+++				+	+++	Coyle et al. (1997)
(mean)		+++						(9)		
12.5								+++		
(mean)								(9)		
	14.4									
	(mean)									
	16 (mean)									
Barents Sea	8–16.9	+++	+++			+++			Ajiad and Gjøsæter (1990)	
E Greenland		+++ (4)	+++				+	unid. fish	Joensen (2008)	
Sympagic	Barents Sea	5.9–11.9	+++	++				(2,9)	Lønne and Gulliksen (1989)	
		N Svalbard	8.5–16.8	++	+++			+		
	Coastal Alaska	1–6	+++ ++		++ (11)			+++ +++	Craig et al. (1982)	
		Canadian archipelago	5–10 (1y) 9–15 (2y) 12–20 (3y)	+++ +++ +++	++ ++ +++					Bradstreet and Cross (1982)

The + (approximately 1–10%), ++ (10–40%), +++ (>40%) symbols indicate relative importance (numerical, volume, etc.) in gut contents. Copepods are primarily *Calanus* spp. unless otherwise specified. Numbers in brackets refer to dietary items indicated below

(1) Cumacea; (2) Chaetognatha; (3) *Limacina helicina*; (4) *Euchaeta* sp., *Metridia longa*; (5) Invertebrate eggs; (6) *Limnocalanus macrurus*; (7) *Pontoporeia* sp.; (8) *Pseudocalanus elongatus*; (9) Decapoda; (10) Larvacea; (11) *Onisimus glacialis*

fjords (ice edge) had low overlap with fjord fish (Table 3A). Surprisingly, few studies exist on post-larval polar cod diets from pelagic trawls, despite the

observations of large schools in some locations (Welch et al. 1993; Hop et al. 1997a, b), so this study provides an important perspective into diets in this important habitat.

Benthic habitat

Benthic diets were generally more varied than pelagic diets, perhaps also reflecting in part the larger size class of fish (10–13 cm), and included greater abundances of euphausiids, benthic fauna, and “other” food items, and unidentified material (Fig. 4). Pelagic and benthic diet overlap was >50% similar in 2 of the 4 fjords where both habitats were sampled (Table 3A), but this comparison is only tentative since fish size often varied between habitats within a fjord. Benthic prey are not uncommon in polar cod collected from other studies sampling fish from this habitat (Craig et al. 1982), but sediment was also frequently found in stomachs of benthic-collected fish. This likely leads to lower total nutritional value of feeding bouts at the seafloor compared with feeding in the water column. The frequent similarity in diets of polar cod collected from benthic and pelagic trawls suggests that there may be some movement between habitats by these fish.

Sea ice habitat

Polar cod is frequently described as being associated with sea ice (e.g., Lønne and Gulliksen 1989). This is likely due to frequent observations by divers and from ships passing through the ice and turning over ice floes. Additionally, antifreeze proteins in polar cod (Osuga and Feeney 1978) have been found to be very active, suggesting an adaptation to this habitat (Enevoldsen et al. 2003). Still, there is little evidence that large numbers of juvenile fish either use the ice as an important habitat or derive considerable nutrition from ice fauna. In the best-documented study of polar cod densities under the ice, concentrations were quite low (never seen during seven 30 m video transects), and usually found singly or in small groups in cracks between ice layers (Gradinger and Bluhm 2004). This is in comparison with the thousands frequently caught in benthic or pelagic trawls (pers. obs.), and the millions found in large pelagic aggregations (e.g., Hop et al. 1997a, b). Further, whereas some ice fauna are observed in polar cod stomachs (pers. obs.; Lønne and Gulliksen 1989), it generally comprises less than 25% on a numerical basis, and potentially less in terms of energy if the data are on a volume basis since *Themisto* are always larger than the gammarids (mostly *Apherusa glacialis*) found in these stomachs. Regardless, adaptations to this habitat may be important for survival and longer distance dispersal of polar cod. In addition, low to moderate densities under the ice may serve as a valuable food source for ice-associated predators (seals, seabirds; Lønne and Gabrielsen 1992), and polar cod under the ice may influence the behavior and anti-predator adaptations of the sea ice fauna.

Dietary overlap in co-occurring gadoids

Where juvenile gadoids of similar size co-occurred there was little dietary overlap, and in all cases, haddock and Atlantic cod consumed different prey than polar cod (Table 4; Figs. 3, 5). Remarkably, Atlantic cod and haddock each had very consistent diets (krill and appendicularians, respectively), which were distinct from each other in different fjords in 2006 (Fig. 5). Despite more similar diets between these two species at the ice-edge station in 2008, there was still some differentiation in the relative amounts of krill versus *Limacina* sp. The large contributions of appendicularians and *Limacina* sp. in haddock diets, and krill in Atlantic cod diets, are consistent with similar findings from the open Barents Sea (e.g., Dalpadado et al. 2009). Contrary to our study’s findings, 9–10 cm juvenile Atlantic cod and haddock have been found to consume considerable amounts of *Calanus* spp. in the Barents Sea (Dalpadado et al. 2009). In the same Barents Sea study, dietary overlap between the two boreal gadoids varied from weak at 2 sites, moderate at one, and extremely strong at 2 others (Dalpadado et al. 2009).

Until now, there have been no reports of similar-sized juveniles of these three species being collected together. This presented a unique possibility to examine dietary overlap. Stomach contents offer only a snapshot (hours to a few days) of information on prey ingestion, so may not be representative of long-term diets and assimilation. The limited stable isotope data we present here (see “Results”), however, suggest that these dietary differences are indicative of longer-term feeding differences among fish species. Similar species composition between stomach contents in Atlantic cod and haddock is reflected in the isotopic signatures, whereas polar cod appears to feed at a higher trophic level, suggesting that the unidentified non-*Themisto* amphipods in their stomachs are predator/scavengers and different than the *Apherusa glacialis* in fish collected by divers from the ice.

Closely related species may have considerable dietary overlap, especially if food is not limiting (Horstkotte and Strecker 2005; Vinagre et al. 2005). In our study, Atlantic cod and haddock rarely had similar diets, and they were always different than polar cod. It is unclear whether this is specifically due to the presence of other gadoids, or if there are physiological or behavioral explanations for this. Just because fish are caught together, it may not mean that they are exposed to the same potential prey fields, due to potentially different swimming speeds, gape size, prey detection abilities, and other behaviors. Atlantic cod and haddock have not been found in Rjippfjorden, but 4–5 cm polar cod had similar diets here as in Kongsfjorden and Isfjorden where other gadoids are found. Polar cod, however, had distinct diets from Atlantic cod or haddock

everywhere they occurred together, regardless of whether they were 2 cm longer, 2 cm shorter, or approximately the same length as the other gadoids.

Co-occurring gadoids have been suggested to compete elsewhere in the Barents Sea (Dalpadado and Bogstad 2004; Dalpadado et al. 2009; Orlova et al. 2009). Whereas our data do not suggest these gadoids are competing at present, we cannot discount the possibility that periodic historical range overlaps resulted in evolutionary adaptations to avoid such competition (e.g., the “ghost of competition past” *sensu* Connell 1980). Invasion of the Arctic by boreal gadoids may be an example of this, and further investigations are required to determine if alternate prey are sufficient here for the lack of strong dietary overlap to continue. The potential for interspecific competition may also increase during different seasons when such alternate prey is less available, and when competition through food depletion could result in negative density-dependent effects. For example, capelin competing with polar cod in the northern Barents Sea exhibited an up to 40% reduction in body condition (fat content) compared to years where they did not co-occur in large numbers (Orlova et al. 2009).

Consequences of further warming and interspecific interaction

Both spawning areas (Sundby and Nakken 2008) and migration (Drinkwater 2006, 2009) of the North Arctic stock of Atlantic cod have shifted northward during the recent warming period of the last 10 years. This mirrors northward distribution shifts in other fish stocks (Murawski 1993; Perry et al. 2005; Grebmeier et al. 2006), and even in fouling community species (Sorte et al. 2010), documented elsewhere in the world’s oceans. There may be other explanations for these events (e.g., Opdal 2010), but temperature-driven shifts in species distributions have been forecasted as potential consequences of climate warming (e.g., ACIA 2005). It is likely that persistent warming trends will further enhance northern spawning and transport of Atlantic cod and haddock into the Barents Sea and around Svalbard. Long-term establishment in these new areas, however, depends on consistent supply of juveniles, suitable environmental conditions such as the ability of boreal species to be efficient predators in the extreme light environment of the Arctic (Kaartvedt 2008; Varpe and Fiksen 2010), and a sufficient food supply (Berge et al. 2005). Further, the pan-Arctic distribution of polar cod, and the recent descriptions of northward expansion of other predatory gadoids (e.g., Pacific pollock; Grebmeier et al. 2006), suggests that interactions among boreal gadoids and polar cod may occur throughout the Arctic as warming proceeds. Identification of the specific conditions that promote persistence of boreal gadoids on Svalbard and

elsewhere requires further study, e.g., it may not be an increase in average temperature, but instead changes in extremes (e.g., winter minimum) that are responsible for determining invasion success (Stachowicz et al. 2002). Furthermore, whereas some areas may be particularly susceptible to invasions due to relative differences in exposure to warmer waters and arriving larvae, other areas, such as silled fjords, may be more insulated from impacts of climatic change (Renaud et al. 2006; Berge et al. 2009).

Atlantic cod and haddock are now co-occurring with resident polar cod. We did not find evidence for strong interspecific competition among these gadoids, although it is unclear if this is consistent across all seasons. In addition, predation on polar cod is likely to increase if haddock and Atlantic cod become more abundant in the Arctic. The problem for polar species confronted with such a scenario, is that there may be few refuges for Arctic shelf species under threats of enhanced competition or predation (Renaud et al. 2008). Novel assemblages that may arise from climate-driven range expansions and the resulting community reorganization presents a challenge for managers, especially when economically important species are involved (Williams and Jackson 2007; Hoegh-Guldberg and Bruno 2010).

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