The foraging ecology of Arctic cod (Boreogadus saida) during open water (July–August) in Allen Bay, Arctic Canada

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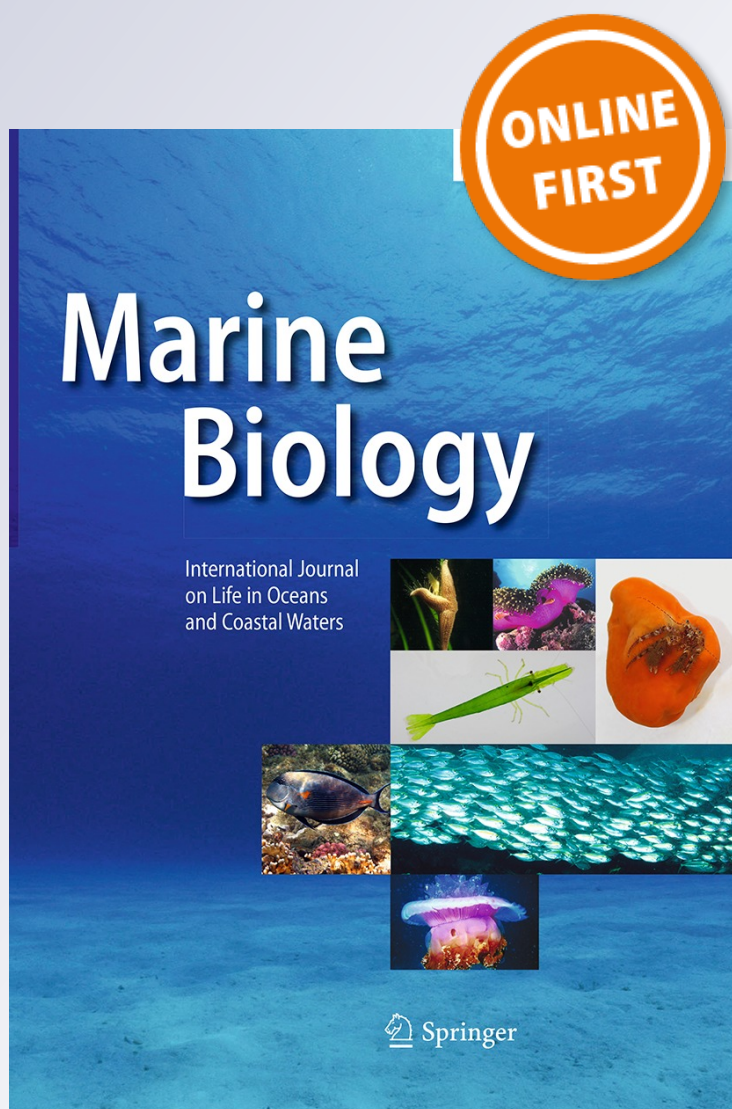
Jordan K. Matley · Aaron T. Fisk ·
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Abstract Arctic cod (*Boreogadus saida*) is a schooling fish providing a critical link between lower and upper trophic levels in the Arctic. This study examined foraging of Arctic cod collected from Allen Bay, Cornwallis Island, Canada (~ 75 N 95 W), during summer 2010 using temporal indicators of diet including stomach content, and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes of liver and muscle. Foraging at the time of capture reflected sympagic and epi-benthic habitats indicated by the prevalence of cyclopoid and harpacticoid copepods in stomachs, whereas stable isotope data, which provide an estimate of feeding over a longer period, indicated pelagic prey as important. Prey selection of juveniles differed from adults based on stable isotopes, while large adults showed the most separation based on stomach contents, suggesting size-related diet shifts. Compared to studies near Resolute in the 1970s, 1980s, and 1990s, growth and pre-spawning gonadal conditions of Arctic cod have not changed.

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Introduction

Arctic cod (*Boreogadus saida*) is a critical link structuring energetic pathways in marine ecosystems throughout the Arctic (Bain and Sekerak 1978; Welch et al. 1992). Understanding its role in an ecological context is essential because it is responsible for transferring the majority of energy from lower trophic levels, mainly invertebrates, to top predators such as seabirds, seals, and whales (Bradstreet et al. 1986; Welch et al. 1992). As prey, Arctic cod directly impact habitat use, predator migration patterns, and seasonal concentrations of multi-species predator complexes (Bluhm and Gradinger 2008; Matley et al. 2012).

Arctic cod has a Holarctic distribution, occupies demersal, pelagic, and sympagic habitats (Gradinger and Bluhm 2004; Crawford et al. 2012), and often aggregates in abundant and dense shoals (Benoit et al. 2008). The life history of Arctic cod is typified by early maturity, small body size, and short life span, which is conducive to living in an environment where high mortalities occur (Craig et al. 1982). Male gonad development for spawning begins in August while female spawning condition is reached by December (Graham and Hop 1995). Spawning occurs in winter between December and March (Bain and Sekerak 1978; Craig et al. 1982). Growth is slow and seasonal, basal metabolism is low, and growth and assimilation efficiencies are high (i.e., efficient energy converters) (Hop et al. 1997a). However, specific information on the general biology of Arctic cod remains limited and the interrelationship between growth, energy storage, and gonadal development is not well understood.

Stomach content analysis has been used to describe short-term diet and foraging behavior of Arctic cod. Prey selection is size-dependent with calanoid copepods and amphipods as the most common food items (Bradstreet and

Cross 1982; Walkusz et al. 2011). Diet also varies seasonally in relation to the distribution of prey. For example, ice-associated prey (e.g., gammarid amphipods) is consumed during ice algae proliferation (Bradstreet and Cross 1982), while pelagic crustaceans (e.g., calanoid copepods and hyperiid amphipods) are consumed during the ice-free period (Renaud et al. 2012) or in deep ice-covered waters (Benoit et al. 2010). Stable isotopes are increasingly used in ecology to study diet and food web interactions as they reflect tissue assimilation from prey and are not hindered by biases associated with stomach content analysis (Hobson et al. 1996). Carbon (δ^{13}C) is used because it indicates food sources or habitat (i.e., <1 ‰ enrichment between predator and prey; Michener and Schell 1994), while nitrogen (δ^{15}N) can identify the organism consumed (i.e., $\sim$3.4 ‰ enrichment between predator and prey; Minigawa and Wada 1984). Further, since the isotopic turnover (i.e., the time tissue of prey takes to be integrated into consumer tissue) is influenced by metabolic activity (Tieszen et al. 1983; Kurle and Worthy 2002), temporal trends can be elucidated. For example, the turnover of stable isotope signal is higher in the metabolically active liver and represents more recent food intake compared to muscle due to tissue-specific fractionation (Hobson and Clark 1992). Multiple temporal indicators of diet are important because seasonal availability of resources often leads to diet switching in the Arctic (Sakshaug 2004; Kaufman et al. 2008).

Ontogenetic niche shifts (i.e., changes in resource use with body size or age) are common in animals and affect how different resources are exploited by a population or from a habitat (Werner and Hall 1988; Hammerschlag-Peyer et al. 2011). Hobson et al. (2002) cautioned against pooling different body sizes within species due to ontogenetic changes and suggested that more detailed size-specific analyses could greatly improve the understanding of the Arctic marine food web. To our knowledge, no study has segregated prey selection of Arctic cod based on the size of individuals (and size of prey) to directly explore intraspecific dietary overlap. Similarly, no study has supplemented stomach content data with stable isotopes in Arctic cod to provide a time line of feeding, habitat, and intraspecific isotopic niche overlap.

As the Arctic continues to face significant environmental changes, it is important to compare the current ecological niche and biology of Arctic cod with the past to prepare for future trends. Considering the importance of this species, these types of investigations are essential to further knowledge of local Arctic food webs and the impacts of a changing environment. The purpose of this study was to examine the general biology and feeding habits of Arctic cod locally in a small Canadian high-arctic bay that has a history of research on this key forage fish species. Sampling

was limited to one period, and therefore, the goal was to provide baseline information and potential temporal patterns with which future studies could be compared. Specifically, the objectives were to (1) describe biological parameters such as growth and age distribution, (2) determine the dietary overlap between Arctic cod size-classes, and (3) investigate diet and habitat using temporal and spatial indicators (stomach content and stable isotopes).

Materials and methods

Study area

Arctic cod were collected from Allen Bay, Cornwallis Island (74°43′36.78″N 95°09′25.23″W; see Matley et al. 2012 for map) between July and August 2010. Allen Bay is a shallow area (generally <40 m deep) located near the community of Resolute Bay and is an important area for subsistence hunting.

Sample collection

Arctic cod were collected using gillnets and seine nets. Gillnets were mostly set near-bottom (28 sets total; July 29–August 25; $n = 207$ cod collected) in water <25 m deep and seine nets (29 sets total; July 25–29; $n = 175$ cod collected) were deployed along the shore in water <2 m deep. Arctic cod aged $\geq$2 + years were captured by gillnets and all 1 + cod were captured by seine nets. These fish were frozen after collection (~-20 °C) until further analysis. Additionally, 19 larval cod were collected along the shore by hand and preserved in 5 % buffered formalin (with seawater).

General biology

Individuals were thawed, weighed (wet weight, 0.01 g), and measured (fork length, 1 mm). Total length of larval cod is presented after correcting for shrinkage due to preservation in formalin (i.e., 4.1 % shrinkage; Fox 1996). The relationship between weight and length was fitted with a power regression and further explored using Fulton's condition factor: $CF = (TW \times 10^5)/FL^3$, where TW and FL are total weight and fork length, respectively. Liver and gonads were removed and weighed to obtain hepatosomatic (HSI) and gonadosomatic (GSI) indices, respectively, using the following: GSI (or HSI) = GW (or LW)/TW × 100, where GW and LW represent gonad weight and liver weight. Differences between female and male GSI, HSI, size, and CF were determined by a Student's *t* test. Sagittal otoliths were removed, cleaned, dried, weighed, and measured to allow size extrapolations for future studies. Otolith length (OL) was defined as the longest

dimension between the posterior and anterior edges of the otolith (Hunt 1992). Otoliths were broken to provide a cross-section at the nucleus, burned, and annual rings counted (Chilton and Beamish 1982). A von Bertalanffy model (Von Bertalanffy 1938) was used to describe the age–growth relationship:

$$FL_t = A \times 1 - e^{-K(t)}$$

where FL_t represents fork length at age t, A is asymptotic length, and K is the rate at which the theoretical asymptotic length is reached.

The presence of internal and external parasites was noted during necropsies as a part of Arctic cod biology.

Stomach content analysis

The wet weight (0.001 g) of stomach contents was taken and diet items examined immediately or stored in 70 % ethanol for later examination. Diet items were measured and divided into five groups based on total length (<1 mm, 1–3 mm, 3–5 mm, 5–10 mm, 10 + mm). Arctic cod were also divided into length size-classes such as class 1 (<100 mm, $n = 50$); class 2 (123–159 mm, $n = 13$); class 3 (160–184 mm, $n = 13$); and class 4 (185–256 mm, $n = 12$) to determine prey size selection. The minimum sample size for each size-class was selected based on $n \geq 10$ being adequate to differentiate diet overlap among salmonids (Vinson and Budy 2011). Frequency of occurrence (FO_i), percent composition (N_i), and weight contribution (P_i) of prey were used to examine diet among Arctic cod size-classes.

$$FO_i(\%) = (S_i/S_t) \times 100$$

where S_i represents the number of Arctic cod with prey type i, and S_t represents the total number of Arctic cod.

$$N_i(\%) = (n_i/n_t) \times 100$$

where n_i represents the total number of prey type i, and n_t represents the total number of prey. The mean weight of individual prey was determined by dividing the weight of stomach contents with only one size range by the number of individuals. The weight contribution (P_i) from each prey size-class was then determined by multiplying each mean weight by the percent composition of prey. Diet overlap between Arctic cod size-classes was calculated using Schoener's index (SI):

$$SI = 1 - 0.5 \times \left(\sum |N_{xi} - N_{yi}| \right)$$

where N_{xi} and N_{yi} are the proportions of prey size-class i in the stomach of Arctic cod size-class x and y, respectively (Schoener 1970). Index values range between 0 (no overlap) and 1 (complete overlap), and values ≥ 0.60 are generally considered to be biologically significant (Zaret and Rand 1971). Using the same approach as the prey size selection analyses described above, prey items were also examined based on major taxonomic groups.

Stable isotope analysis

Liver and muscle tissue from individual cod, along with the following prey items *Onisimus* sp. ($n = 11$), *Gammarus* sp. ($n = 7$), *Themisto* sp. ($n = 1$), and copepods ($n = 2$, pooled from >100 harpacticoids and cyclopoids), were dried at 70 °C for 48 h and ground into powder using a ball mill grinder (SPEX CertiPrep 8000-D ball milling unit, SPEX CertiPrep, Metuchen, NJ, USA). Lipids were removed using 5 ml 2:1 chloroform/methanol solvent, vortexed for 30 s, and left for 24 h. The process was repeated and remaining solvents were dried from the tissue by placing samples in an oven (60 °C) for 24 h. Tissue (400–600 µg) was weighed into tin capsules, and $\delta^{13}C$ and $\delta^{15}N$ were determined using a continuous flow isotope ration mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA). Stable isotope ratio values are expressed in parts per thousand (‰) using δ notation as calculated using the following equation:

$$\delta X = \left[\left(R_{Sample}/R_{standard} \right) - 1 \right] \times 1000$$

where X is ^{15}N or ^{13}C, R_{sample} is the ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) in the sample, and $R_{standard}$ is the ratio in the standard. The standard reference material was Pee Dee Belemnite carbonate and atmospheric N_2 for carbon and nitrogen samples, respectively. Every 12th sample was run in triplicate to assess precision, where the standard deviations of $\delta^{13}C$ and $\delta^{15}N$ were generally <0.1 and <0.2 ‰, respectively. Further, laboratory and National Institute of Standards and Technology (NIST) standards were analyzed every 12 samples for quantification of samples. The analytical precision (standard deviation) for NIST standard 8414 (bovine muscle, $n = 29$) and an internal laboratory standard (tilapia muscle, $n = 29$) for $\delta^{13}C$ was 0.03 and 0.06 ‰, respectively, and for $\delta^{15}N$ was 0.14 and 0.22 ‰, respectively. The NIST standards (sucrose and ammonium sulfate, $n = 3$) were within 0.01 and 0.07 ‰ of certified values for $\delta^{15}N$ and $\delta^{13}C$.

The relationships between size, sex, and $\delta^{15}N$ and $\delta^{13}C$ values (for liver and muscle) were investigated using a general linear model (GLM) as the isotope data followed normal distribution (i.e., Shapiro–Wilk test, $p > 0.05$). Mean liver and muscle $\delta^{15}N$ and $\delta^{13}C$ values were plotted for each Arctic cod size-class. Differences between groups were considered significant if their 95 % confidence intervals (CIs) did not overlap. This method is a conservative approach (Payton et al. 2003), but provided a simple visual way for detecting differences.

Isotopic niche overlap between size-classes of Arctic cod was assessed using the R package SIAR (Parnell et al. 2010), following Jackson et al. (2011). This Bayesian multivariate approach generates convex hulls encompassing isotope values for all individuals in a group (i.e., size-class), as well as standard ellipses that represent "typical" niche width of members in a population (Jackson et al. 2011; Layman and Allgeier 2012). The areas of standard ellipses (SEA_B) (bivariate equivalents to univariate standard deviations) were obtained to calculate niche overlap between size-classes. To minimize bias associated with sample sizes among classes, corrected SEA_B values were used (Jackson et al. 2011). Niche overlap is presented as the percentage of the SEA_B of a size-class that is encompassed by another size-class. All statistical analyses (except isotopic niche overlap) were run in SAS 9.2 and results were considered significant when $p < 0.05$.

Results

General biology

Arctic cod between the ages of $0 +$ and $5 +$ ranged in fork length and total weight from 10–273 mm and 0.1–102.1 g, respectively (Table 1). Total weight (TW $= 1.72E - 05(FL)^{2.8}$, $n = 322$, $R^2 = 0.96$) and age (FL$_t = 226.95 \times 1 - e^{-0.43t}$, $n = 327$, $R^2 = 0.92$) fit strongly with fork length (Fig. 1a, b). The age distribution from gillnet catches was mostly $3 +$ (32 %) and $4 +$ (51 %) with similar frequencies of male and females. A significant linear relationship existed between fork length and otolith length (FL $= 24.20(OL) - 4.29$, $n = 251$, $R^2 = 0.91$, $p < 0.01$), and fork length and otolith weight (FL $= 3250.20(OW) + 76.31$, $n = 202$, $R^2 = 0.93$, $p < 0.01$).
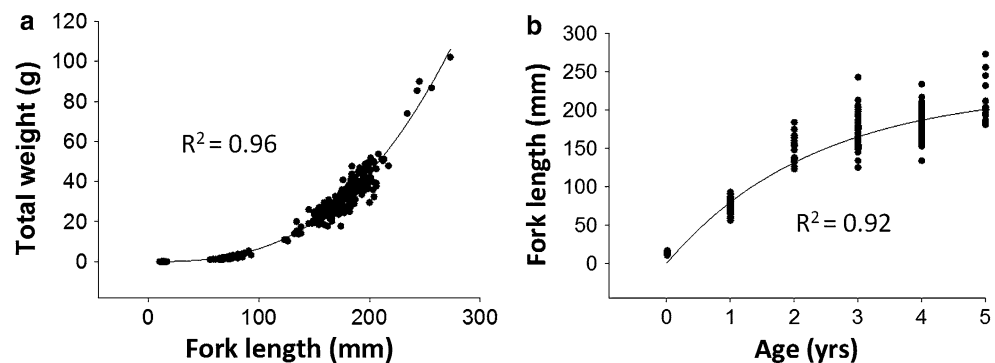
The GSI was significantly higher in males (one-tail t test, $t_{195} = -5.47$, $p < 0.01$), and HSI (one-tail t test, $t_{196} = 4.14$, $p < 0.01$) was higher in females (Table 2). Condition factor (two-tailed t test, $t_{197} = 1.25$, $p = 0.21$) and size (two-tailed t test, $t_{202} = 1.73$, $p = 0.09$) were not significantly different between males and females (Table 2).

Three groups of parasites were identified. Endohelminthes comprised encysted nematodes within the mesentery and on organs in the body cavity in $\sim$50 % of individuals $\geq 2+$. Trematodes were present in the stomach, ceca, or intestinal tract in $\sim$65 % of adults and $\sim$80 % of juveniles. Finally, parasitic copepods were collected from the gills on 2 occasions ($\sim$2 % of individuals).

Table 1 Mean ($\pm$ SD) values and ranges for length and weight of Arctic cod (*Boreogadus saida*) age groups collected in Allen Bay, Nunavut, during July–August 2010

Age	Fork length (mm)				Total weight (g)			
	n	Mean	SD	Range	n	Mean	SD	Range
0	19	13.8	1.8	10–17	19	0.018	0.006	<0.1
1	100	75.1	7.2	56–93	100	2.3	0.8	1.0–5.3
2	19	149.2	16.7	123–184	19	20.9	7.4	10.3–35.8
3	66	170.5	19.7	125–243	64	29.6	11.0	11.0–85.4
4	106	182.4	16.3	134–234	104	35.1	9.4	17.7–74.0
5	17	207.9	27.2	181–273	16	51.5	21.6	29.5–102.1
Total	327	136.8	58.8	10–273	322	21.7	18.4	0.1–102.1

Fig. 1 **a** Weight–length (TW $= 1.72E - 05(FL)^{2.8}$, $n = 322$, $R^2 = 0.96$) and **b** age–length (FL$_t = 226.95 \times 1 - e^{-0.43t}$, $n = 327$, $R^2 = 0.92$) relationship of Arctic cod (*Boreogadus saida*) collected in Allen Bay, Nunavut, during July–August 2010 using a power and von Bertalanffy regression, respectively, where TW is total weight, FL is fork length, and t is age in years

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Stomach contents

A total of 42.3 % (i.e., $n = 83$ of 196) of Arctic cod ($\geq 2+$) stomachs contained food. Diet items from 38 individuals were analyzed (i.e., 123–159 mm, 2–4 years, $n = 13$; 160–184 mm, 2–4 years, $n = 13$; and 185–256 mm, 3–5 years, $n = 12$). A total 47 of 50 stomachs from Arctic cod aged $1 +$ (56–93 mm) contained identifiable food. There was a strong size-dependent relationship where smaller Arctic cod consumed smaller prey such as copepods and larger individuals consumed larger prey such as amphipods (Tables 3, 4). Prey <3 mm was comprised (>95 %) of harpacticoid and cyclopoid copepods, and nauplii (barnacle and copepod), while prey >3 mm were predominantly (>95 %) hyperiid or gammarid amphipods. Schoener's index (based on percent composition of prey sizes) showed that the diet of size-classes 1, 2, and 3 overlapped, but these size-classes did not overlap with

Table 2 Mean (±SE) gonadosomatic (GSI) and hepatosomatic (HSI) indices, condition factor (CF), and fork length (FL; mm) of male and female Arctic cod (*Boreogadus saida*) collected in Allen Bay, Nunavut, during July–August 2010

	GSI	HSI	CF	FL
Male	3.72 ± 0.13	3.66 ± 0.13	0.57 ± 0.01	174.30 ± 2.19
Female	2.93 ± 0.07	4.47 ± 0.15	0.59 ± 0.01	179.66 ± 2.18
p value	<0.01	<0.01	0.21	0.09
n	197	198	199	204

Significant differences ($p < 0.05$) between sexes was determined using Student's *t* tests

Table 3 Frequency of occurrence (% occ.), percent composition (% diet), and percent weight (% weight) of Arctic cod (*Boreogadus saida*) food items based on size ranges of prey and cod

Prey size	Size-class 1 (56–93 mm; $n = 47$)			Size-class 2 (123–159 mm; $n = 13$)			Size-class 3 (160–183 mm; $n = 13$)			Size-class 4 (185–256 mm; $n = 12$)		
	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% weight
<1 mm	78.3	64.8	47.5	61.5	94.6	81.8	38.5	60.3	26.3	0	0	0
1–3 mm	97.8	34.5	50.3	46.2	3.9	6.7	23.1	21.4	18.6	16.7	3.4	0.8
3–5 mm	13	0.6	1.6	0	0	0	7.7	5.3	8.4	8.3	0.7	0.3
5–10 mm	8.7	<0.1	0.6	0	0	0	46.2	7.6	26.3	41.7	38.9	37.5
>10 mm	0	0	0	7.7	1.5	11.5	23.1	5.3	20.4	58.3	57.0	61.4

See "Materials and Methods" section for stomach content calculations

Table 4 Frequency of occurrence (% occ.), percent composition (% diet), and percent weight (% weight) of Arctic cod (*Boreogadus saida*) food items based on prey groupings

Group	Size-class 1 (56–93 mm; $n = 47$)			Size-class 2 (123–159 mm; $n = 13$)			Size-class 3 (160–184 mm; $n = 13$)			Size-class 4 (185–256 mm; $n = 12$)		
	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% weight
Harpacticoida	97.8	41	39.3	61.5	15.8	13.6	30.8	59.6	27.6	16.7	15.7	2.5
Cyclopoida	67.4	58.3	55.9	30.8	10.9	9.4	23.1	22.1	10.3	8.3	0.3	0.1
Calanoida	0	0	0	7.7	0.2	0.2	0	0	0	0	0	0
Nauplii	0	0	0	30.8	70.6	60.9	0	0	0	8.3	0.6	0.1
Ostracoda	0	0	0	7.7	1	6.1	0	0	0	0	0	0
Onisimus sp.	10.9	0.2	1	7.7	1.5	9.8	53.8	13.7	46.5	58.3	58.7	68.4
Gammarus sp.	6.5	0.5	3.6	0	0	0	15.4	2.3	7.8	41.7	24.1	28.1
Themisto sp.	4.3	<0.1	0.2	0	0	0	7.7	2.3	7.8	8.3	0.3	0.4
Mysidacea	0	0	0	0	0	0	0	0	0	8.3	0.3	0.4

Note One Arctic cod otolith was collected from the stomach of a cod (size-class 4) and is not included in the analysis above. Nauplii consisted of cirripedian and copepod nauplii. See "Materials and Methods" section for stomach content calculations

class 4 (Table 5). There was no significant overlap among the cod size-classes when prey items were compared (Table 5).

Stable isotopes

The GLM analyses showed that size (ANOVA, $F_{(1, 100)} = 9.84$, $p < 0.01$) and sex (ANOVA, $F_{(1, 100)} = 156.28$, $p < 0.01$) were significant predictors of $\delta^{15}N$ in liver, but only size was significant for muscle (ANOVA, $F_{(1, 103)} = 8.32$, $p < 0.01$). Values of $\delta^{13}C$ in muscle were significantly correlated with cod size (ANOVA, $F_{(1, 104)} = 6.00$, $p < 0.01$). There were no interaction effects in the above analyses. Arctic cod $\delta^{15}N$ showed a strong positive relationship with length, where muscle tissue ($\delta^{15}N = 1.5e^{-02}x + 12.6$, $n = 149$, $R^2 = 0.71$, $p < 0.01$) was higher (i.e., enriched) than liver tissue ($\delta^{15}N = 1.5e^{-02}x + 11.5$, $n = 121$, $R^2 = 0.43$, $p < 0.01$) (Fig. 2a). By contrast, $\delta^{13}C$ values decreased slightly (i.e., became depleted/more negative) as length increased, although not significantly, where muscle ($\delta^{13}C = -1.4e^{-03}x - 20.6$, $n = 149$, $R^2 < 0.01$, $p = 0.48$) was typically higher than liver ($\delta^{13}C = -1.0e^{-03}x - 20.1$, $n = 121$, $R^2 = 0.02$, $p = 0.14$). Variation in liver was high (Fig. 2b).

Liver and muscle $\delta^{15}N$ of juvenile cod (i.e., 1 + year) was significantly lower than in older cod based on non-overlapping CIs (Fig. 3). Liver $\delta^{13}C$ values for all size-classes were similar (i.e., overlapping CIs) and were typically lower than muscle values (Fig. 3). Arctic cod isotope values from other studies are plotted for comparison (Fig. 3). The isotopic niche overlap analyses revealed that size-class 1 shared no overlap with any other size-class (Fig. 4). For liver, size-class 2 shared 48 and 38 % overlap with size-classes 3 and 4, respectively, and size-class 3 had 86 % overlap with size-class 4 (Fig. 4a). For muscle, size-class 2 encompassed 80 and 35 % overlap of size-classes 3 and 4, respectively, and size-class 3 shared 51 % overlap with size-class 4 (Fig. 4b).

Larval cod $\delta^{15}N$ and $\delta^{13}C$ were lower than older Arctic cod (Fig. 3). Values of $\delta^{15}N$ in prey were similar to each other, while $\delta^{13}C$ of *Themisto* sp. was lower than the other amphipods and copepods (Fig. 3). A summary of $\delta^{15}N$ and $\delta^{13}C$ for liver and muscle from each size-class is presented in Table 6.

Discussion

General biology

This study examined several aspects of the biology of Arctic cod, including size at age, growth, sex ratio, parasites, and the relationship between gonad and liver weight with total weight in Allen Bay, a small bay in the high arctic of Canada. The oldest Arctic cod collected in Allen Bay in 2010 was 5 years of age, and the most abundant age classes from gillnetting were 3 + and 4 + , which is consistent with previous collections in Allen Bay (Table 7 and references therein). There was appreciable overlap in size among age classes likely because Arctic cod growth is influenced by several factors including feeding (Jensen et al. 1991), season (Craig et al. 1982), location (Bain and

Table 5 Schoener's index (SI) representing dietary overlap between Arctic cod (*Boreogadus saida*) size-classes (1: 56–93, 2: 123–159, 3: 160–184, 4: 185–256 mm) for stomach content analyses using prey sizes and prey items as variables

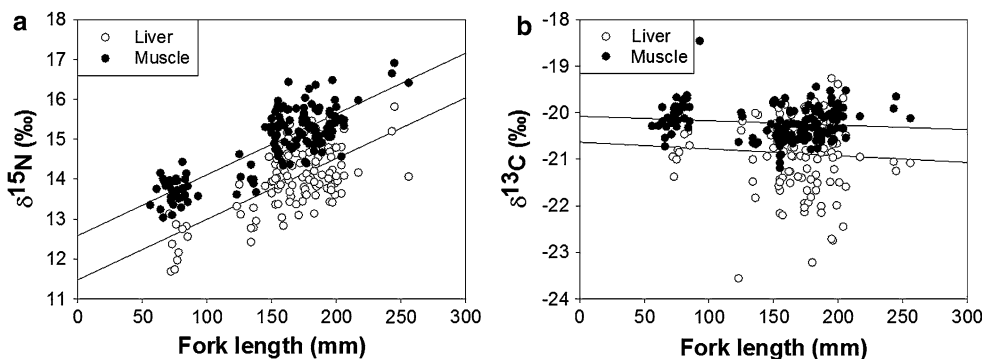| Size-class comparisons	SI (Prey size)	SI (Prey item)
1 versus 2	**0.69**	0.27
1 versus 3	**0.82**	0.34
1 versus 4	0.04	0.10
2 versus 3	**0.66**	0.34
2 versus 4	0.05	0.46
3 versus 4	0.17	0.19

SI values ≥ 0.60 (in bold) are considered biologically significant (Zaret and Rand 1971). The first three size-classes consumed similar-sized individuals, but prey items did not overlap between size-classes

Fig. 2 Linear regression comparing Arctic cod (*Boreogadus saida*) fork length (mm) with **a** $\delta^{15}N$ (‰) and **b** $\delta^{13}C$ (‰) for liver (*white symbols*) and muscle (*black symbols*). The increase in $\delta^{15}N$ with fork length for both liver and muscle indicates larger individuals feeding at a higher trophic level, whereas carbon sources are not changing based on constant $\delta^{13}C$ signatures

Sekerak 1978), temperature (Hop and Graham 1995), and hatching date (Bouchard and Fortier 2011). Since there is inherent subjectivity (and error) to aging fish using otoliths, it is not surprising to note some differences between our values and the literature values. Age was lower in our study compared to Hop et al. (1997b), who collected individuals up to 7 years of age, and Gillispie et al. (1997), who reported cod 8 years of age. By contrast, Bain and Sekerak (1978) only collected individuals that were 5 years or younger ($n > 900$ pairs of otoliths). Our aging estimate technique was verified by an independent Fisheries and Oceans Canada otolith aging specialist; therefore,

differences between this study and others may be explained by a lower sample size of older individuals or fewer females, which typically grow larger (e.g., Hop et al. 1997b).

The exponent of growth for weight–length relationships, in our case 2.78, supports Bain and Sekerak (1978) that cod follow negative allometric growth during the summer (i.e., weight < length³). The proportion of males and females was similar, which differs from other studies that sampled at the same time of year (Table 7). For example, Craig et al. (1982) reported that females accounted for 74 % of Arctic cod aged 3–6 years from the Beaufort Sea. The difference has been suggested to be due to higher mortality in males throughout the summer (Bain and Sekerak 1978) and faster growth rates in females (Hop et al. 1997b).

The GSI values in this study are similar to the data presented by Bain and Sekerak (1978) and Hop et al. (1997b) (Table 7), and suggest the onset of gonadal development has not changed significantly. Male gonads begin to develop in August and female gonads develop closer to December (Hop et al. 1995). Surprisingly, our HSI values (Table 7) were >2x lower than those of Bain and Sekerak (1978), despite a similar sampling period. The lower liver weight suggests energy was mobilized from lipid stores in the liver (Nahrgang et al. 2010). The stomachs of approximately 58 % of adult cod in our study were empty indicating they were primarily schooling individuals (cf. Hop et al. 1997b), whereas only 8 % were empty in Bain and Sekerak (1978). Although schooling probably has little influence on condition factor (Hop and Graham 1995), it may still elicit energetic mobilization from the liver due to low food availability, high competition, and/or high predation.

The parasites identified were similar to Bradstreet et al. (1986) who found that Arctic cod captured in Resolute and Allen Bay had high nematode (*Thynnascaris* sp.) and trematode (*Genolinea* sp. and *Derogenes varicus*) infection rates. These organisms infect many copepod and amphipod
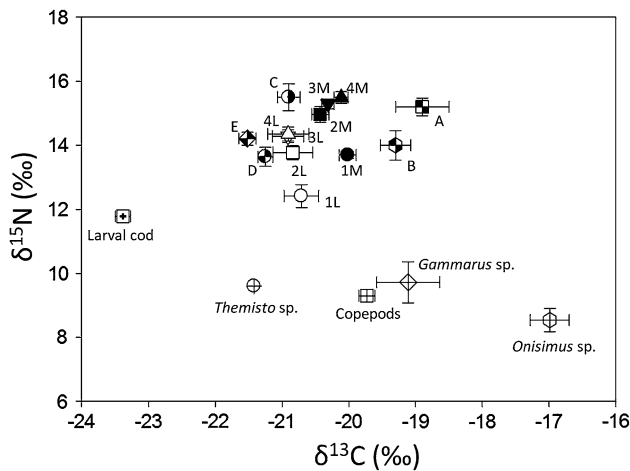

Fig. 3 Mean ± 95 % confidence intervals of liver (*white symbols*, L) and muscle (*black symbols*, M) δ^{15}N (‰) and δ^{13}C (‰) for Arctic cod (*Boreogadus saida*) separated by size-classes (Larval cod: 10–17 mm; 1L, 1 M: 56–93 mm; 2L, 2 M: 123–159 mm; 3L, 3 M: 160–184 mm; 4L, 4 M: 185–256 mm) collected from Allen Bay, Nunavut, 2010. Size-class 1 shows large separation from other size-classes in both liver and muscle tissue suggesting different prey selection. Common prey species sampled in this study are plotted. Assuming slight δ^{13}C enrichment from prey to predator, the pelagic *Themisto* sp. is an important prey item. Arctic cod values from other studies are also included: **a** Hobson and Welch 1992; **b** Hobson et al. 2002; **c** Dehn et al. 2007; **d**, **e** Christiansen et al. 2012)

Fig. 4 Isotopic niche overlap for (a) liver and (b) muscle between Arctic cod (*Boreogadus saida*) size-classes (*1*: 56–93 mm, *2*: 123–159 mm, *3*: 160–184 mm, *4*: 185–256 mm). Convex hulls of total niche width are depicted using gray dashed lines. Standard ellipse area (SEA_B) representing isotopic niches is depicted using *black lines* (size-class 1, size-class 2, size-class 3, and size-class 4). Size-class 1 shows little overlap with other size-classes in both tissues
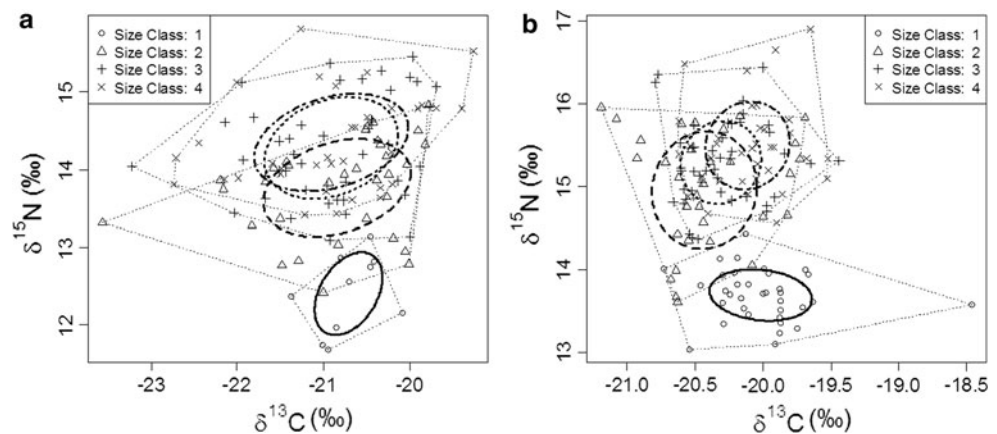
Table 6 Arctic cod (*Boreogadus saida*) $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) (mean ± 1 standard error (SE)) by size-class (1: 56–93, 2: 123–159, 3: 160–184, 4: 185–256 mm) from liver and muscle tissue

Size-class	Liver			Muscle		
	n	$\delta^{15}N$	$\delta^{13}C$	n	$\delta^{15}N$	$\delta^{13}C$
Larval (10–17 mm)	8	11.8 ± 0.2	−23.4 ± 0.1			
1 (56–93 mm)	10	12.4 ± 0.2	−20.7 ± 0.1	35	13.7 ± 0.1	−20.0 ± 0.1
2 (123–159 mm)	33	13.8 ± 0.1	−20.8 ± 0.2	33	15.0 ± 0.1	−20.4 ± 0.1
3 (160–184 mm)	44	14.3 ± 0.1	−20.9 ± 0.1	44	15.3 ± 0.1	−20.3 ± 0.0
4 (185–256 mm)	34	14.4 ± 0.1	−20.9 ± 0.2	36	15.5 ± 0.1	−20.1 ± 0.1
Total	121	14.0 ± 0.1	−20.9 ± 0.1	148	14.9 ± 0.1	−20.2 ± 0.0

Note Larval Arctic cod liver values represent isotopic analysis of whole body where 2 individuals were pooled into a sample. They are not included in the *Total* row

Table 7 Comparison of biology and diet of Arctic cod (*Boreogadus saida*) sampled from the same locations over the last 30 years

	Bain and Sekerak (1978)	Hop et al. (1997b)	Present study (2010)
Location	Allen Bay, Resolute Bay	Allen Bay, Resolute Bay, 3 other locations off Devon Island	Allen Bay
Sampling time	July–September 1976–1977	July–September 1985–1991	July–August 2010
Samples (*n*)	920	3757	327
Size range	5–298 mm	65–260 mm	10–273 mm
Age distribution	1–5	1–7	1–5
	3 + (68 %) and 4 + (22 %)	3 + and 4 + dominant (mean 3.7)	3 + (32 %) and 4 + (51 %)
Sex ratio (male/female)	Range 1:1.6–1:4.0	Mean 1:1.18 Range 1:0.81–1:1.81	1:1.13
Exponent of growth (length–weight)	1976: 2.92 1977: 2.70	[a]3.42	2.78
GSI	Males: July = 3.51 % August = 4.15 % September = 9.71 % Females: July = 2.66 % August = 2.73 % September = 3.84 %	Males: 3.8 % Females: 2.8 %	Males: 3.72 % Females: 2.93 %
HSI	Males: 8.19 % Females: 9.44 %	NA	Males: 3.66 % Females: 4.47 %
Diet	Copepods and amphipods accounted for >90 % of food items (mainly *Onisimus* sp., *Themisto libellula*, and calanoid and harpacticoid copepods) Cod <100 mm consumed mainly copepods while larger cod consumed mainly amphipods	Juveniles from schools (mean = 83 mm) fed on calanoid copepods while adults (mean = 165 mm) fed rarely (64 % empty) but consumed amphipods and copepods	Harpacticoids and cyclopoids present in >90 % of stomachs (with food) Amphipods became more important as size increased

Many aspects of Arctic cod biology are similar among studies including mean age, exponent of growth, and gonad weight/total weight (GSI). Major differences in the present study were lower liver weight/total weight (HSI) and greater consumption of harpacticoid and cyclopoid copepods

[a] Exponent of growth obtained from Hop (1994)

species as intermediate hosts (Køie 2009) and identify these prey items as long-term food items of Arctic cod. We also found larval ascarid nematodes encysted along the viscera and body cavity wall of Arctic cod, and this intermediate parasitic stage is infective to marine mammal predators.

Stomach contents

Copepods and amphipods have been documented as the major diet items of Arctic cod throughout its distribution (see Renaud et al. 2012). The primary copepods consumed are planktonic/pelagic calanoids (Hobson et al. 2002), but harpacticoid and cyclopoid copepods were the dominant stomach content of the Arctic cod sampled in our study. Many harpacticoids and cyclopoids possess suitable mouth parts and appendages for grasping and holding prey, and are especially equipped to remove food from surfaces (Grainger 1991). As a result, they are rarely found in the water column, and are mainly epi-benthic and ice-associated (Grainger 1991). Arctic cod aggregate near or within ice (Lønne and Gulliksen 1989) and inhabit demersal layers in both offshore (Geoffroy et al. 2011) and inshore (Matley et al. 2012) waters. Therefore, selection of harpacticoids and cyclopoids may be related to habitat preference by Arctic cod. Further, other main prey items such as *Onisimus* sp. and *Gammarus* sp. also form strong associations with benthic and ice habitats supporting habitat-specific prey selection. Alternatively, harpacticoid and cyclopoid copepods may have been important due to an absence of pelagic calanoids in the water column. For example, zooplankton tows (August 10, 11, and 19) using a Wisconsin plankton net with 153-um mesh and 5-inch opening were mostly empty (35/46) and only a few calanoids were collected per tow. Hop et al. (1997b) suggested that schools of Arctic cod deplete resources locally, particularly larger calanoid copepods, which may explain their low numbers.

Size-dependent prey selection was evident among Arctic cod size-classes. Size-classes 1 and 2 primarily consumed prey <3 mm (e.g., copepods and nauplii) and as cod reached size-class 3, they shifted toward larger prey such as amphipods. The diet of size-class 4 did not significantly overlap with any others as prey >5 mm made up the majority of the diet. These findings support other studies examining Arctic cod prey size selection. For example, the mean lengths of ingested copepods and amphipods were significantly correlated with the length of offshore and inshore Arctic cod, respectively, near Pond Inlet, Nunavut (Bradstreet and Cross 1982). Further, copepods made up 99.8 % of the dry weight of inshore one-year olds while amphipods made up 44.6 % in three-year olds (Bradstreet and Cross 1982). Interestingly, a large proportion

of >1 year cod had not fed recently, while the stomachs of younger Arctic cod contained food remains. Due to sampling difficulty and gear bias, the diet of 1 + individuals offshore could not be examined. Consequently, we can only speculate on the importance of habitat on feeding frequency. Lønne and Gulliksen (1989) found few empty stomachs in Arctic cod aged 1 and 2 years collected in or around drifting sea ice. Similarly, small ice floes were lodged along shore during our collection of 1 + individuals indicating sympagic prey was readily available nearshore. By contrast, older Arctic cod were collected in deeper water where the presence of ice was variable and the availability of prey may have been different. The role of schooling is also an important factor influencing feeding frequency. For example, Hop et al. (1997b) proposed that adult Arctic cod either school and reduce feeding or disperse to feed individually. Juveniles appear to feed frequently whether they are schooling or not (Hop et al. 1997b), which may indicate age-dependent (or size-dependent) energetic requirements that necessitate frequent feeding (Jobling 1988).

Stable isotopes

As Arctic cod size increased, δ^{15}N values increased in liver and muscle, supporting size-selective prey consumption. By contrast, δ^{13}C did not show significant change as length increased, except in muscle when separated by size-class (i.e., based on GLM and see Fig. 3). This suggests that prey sources are selected differently based on Arctic cod size as represented by tissue assimilation in muscle. The large variation in liver isotopic values indicates either considerable variation in diet sources or that liver is intrinsically more variable. Isotopic niche models revealed a greater overlap in liver δ^{15}N values of size-classes 3 and 4 than muscle suggesting greater partitioning of diet between the two classes in muscle tissue. The main difference between our findings in δ^{15}N values and the stomach content analysis was that size-class 1 separated strongly from the other classes based on isotopes, while size-class 4 showed the clearest separation from the other classes based on diet. Perhaps during the winter and spring, larger cod (i.e., ≥2+) consume larger pelagic prey such as *Mysis* sp. and *Themisto* sp., but during the summer as primary production increases, size-classes 2 and 3 switch to smaller, more abundant food sources. Hobson and Welch (1995) demonstrated ontogenetic isotopic niche shifts in Arctic char (*Salvelinus alpinus*) near Resolute and suggested that large adults were cannibalistic as a means to reduce intrapopulation niche competition. Similarly, Arctic cod may switch diet items or foraging habitat in response to local food availability and competition with conspecifics, albeit constrained by physiological, behavioral, and/or

mechanical limitations, such as gape size. Further support for this behavior has been shown where Arctic cod avoid competition with sympatric species by utilizing different habitats or prey (Christiansen et al. 2012; Renaud et al. 2012). The large separation between size-class 1 and larger Arctic cod provides further support that smaller prey are exploited to a greater extent by juvenile cod, which are able to exploit a unique niche.

Arctic cod liver and muscle $\delta^{15}N$ reflected trophic positions between 3.4 and 3.8, similar to those reported by Hobson and Welch (1992) and Christiansen et al. (2012), supporting the role of this species as an important intermediary between lower and upper trophic levels. Although stomach content analysis revealed mainly ice-adapted or epi-benthic prey, carbon stable isotopes from liver and muscle indicated a diet originating from pelagic sources. For example, the pelagic amphipod *Themisto* sp. appears to be of greater dietary importance based on carbon isotopes. Stable isotope data from other studies support a pelagic lifestyle (e.g., Søreide et al. 2006; Christiansen et al. 2012); however, sympagic organisms are commonly noted as diet items (Lønne and Gulliksen 1989; Hop et al. 2006). The temporal resolution between sampling techniques (i.e., stomach content and stable isotope analysis) may explain why sympagic organisms such as *Onisimus* sp. are not well represented as prey by stable isotope data. Although isotopic turnover is not known for Arctic cod, it should reflect the metabolic activity of the tissue examined (Tieszen et al. 1983), suggesting liver will reflect more recent diet assimilation than muscle. For example, Buchheister and Latour (2010) calculated turnover rates of summer flounder (*Paralichthys dentatus*) and found that half-lives of carbon and nitrogen ranged from 10–20 days in liver and 49–107 days in muscle. Therefore, the pelagic signatures likely originate from when water was ice-covered and Arctic cod still remained deep offshore consuming pelagic prey (Benoit et al. 2010). By contrast, sympagic organisms appear to be more important when Arctic cod move into shallower water in Allen Bay during ice breakup, based on stomach contents. Muscle $\delta^{15}N$ and $\delta^{13}C$ values were typically higher than liver also indicating that different prey items (or similar prey with different isotopic signatures) are consumed prior to open water. Alternatively, the difference in isotope values between liver and muscle may be due to a shift in nutrient cycling in the environment (e.g., pelagic–benthic coupling during ice melt, Wassmann et al. 2006; Link et al. 2011) or different diet–tissue discrimination factors of the two tissues (e.g., Buchheister and Latour 2010).

Larval Arctic cod are unable to actively swim and are restricted to the upper water column (Sameoto 1984). The highly negative $\delta^{13}C$ values of larval Arctic cod support a planktonic diet influenced by ocean currents (Sekerak 1982).

Conclusion

Environmental changes affecting the Arctic marine ecosystem are increasingly a topic of concern (e.g., Cheung et al. 2009). Arctic cod is a vital component of the Arctic marine food web yet still remains sparsely and infrequently studied. Following our first objective, we provided current data on several aspects of Arctic cod biology and compared to studies from the same area and season over the last three decades. This is one of the few studies to examine diet of Arctic cod using stomach content and stable isotope analysis (e.g., Christiansen et al. 2012), and to our knowledge is the first to include isotopic date for liver tissue. Our approach enabled dietary comparisons between size-classes (second objective) reflecting possible diet shifts in response to prey availability and competition with conspecifics. Multiple dietary indicators were also used to investigate prey and habitat selection (third objective). The findings indicated temporal differences in the contribution of pelagic, demersal, and sympagic prey to the diet. Since we were unable to sample Arctic cod seasonally or long-term, we can only speculate about broader temporal trends. Clearly, more structured zooplankton sampling is required to examine prey distribution using gear that is designed to sample from benthic and ice habitats. Changing ice patterns and the rapid loss of Arctic ice will affect Arctic cod feeding patterns but these shallow productive Arctic bays, with or without ice, will continue to a play key role in cod energetics. Further, laboratory-based discrimination studies specifically for Arctic cod are needed to accurately determine prey and seasonal diet shifts because discrimination factors vary between species and among individuals (see Zhao et al. 2006). Arctic food sources undergo significant seasonal changes, and using multiple indicators, we are better suited to obtain a comprehensive view of prey selection and availability.

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