Environ Biol Fish (2014) 97:343–355
DOI 10.1007/s10641-013-0156-0

Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and C-N isotopes

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Received: 9 January 2013 / Accepted: 15 July 2013 /

Abstract The feeding habits of co-occurring gadid species Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*) in coastal Newfoundland waters, examined using stable isotope (δ^{13}C and δ^{15}N) and stomach content analysis, indicated little dietary niche overlap and interspecific competition for food resources despite similar trophic levels. Both species consumed a variety of invertebrates and fish but showed a preference for different prey items. Polychaetes, fish and small crustaceans dominated *G. ogac* stomach contents while small crustaceans, in particular hyperiid amphipods and fish, dominated those of *G. morhua*. In general, *G. morhua* consumed more pelagic prey and had a significantly more pelagic (more negative) δ^{13}C signature while *G. ogac* consumed primarily benthic prey and had a more benthic (more positive) δ^{13}C signature. δ^{15}N levels were similar in these species suggesting similar trophic positions, with levels increasing with fish length in both species. Dietary overlap was not significant in both stomach and stable isotope analyses. We conclude that interspecific competition for food is low between *G. ogac* and *G. morhua* and is unlikely to be a factor in the slow rebuilding of Atlantic cod in this region.

Keywords *Gadus* · Cod · Niche partitioning · Diet overlap · Stable isotopes · Stomach contents

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Introduction

Despite the coexistence of similar species across many taxa, the basic principles of niche theory suggest that complete niche overlap is not evolutionarily possible (Gause 1934; Hutchinson 1957; Hardin 1960). Niche partitioning (Levins 1968; MacArthur 1972) (also termed *niche differentiation* or *niche segregation*), the process by which competing species evolve different forms of resource use is a fundamental process in community ecology and has been widely used to explain the coexistence of similar species (Schoener 1974; Giller 1984; Ross 1986). Coexistence may arise from the segregation of *specific resources* (classical resource partitioning) or from differences in *when* (temporal resource partitioning) and *where* (spatial resource partitioning) resources are utilized (Pianka 1969; Schoener 1974; Ross 1986). In fish assemblages, partitioning of food resources is often the principal mechanism of niche segregation (Gascon and Leggett 1977; Gerking 1994).

In coastal Newfoundland, the closely related gadids Greenland cod (*Gadus ogac*) and Atlantic cod (*Gadus morhua)* are opportunistic predators with overlapping geographic distributions (Scott and Scott 1988). Juveniles of both species are common nearshore inhabitants and found intermixed in most bays (Rose 2007) and there is a long-standing view that competition is likely between the two species (Cohen et al. 1990). Since the early 1990s, *G. morhua* stocks around Newfoundland have been in a depleted state (for much longer further north off Labrador) (Rose 2007). There is little data to assess changes in *G. ogac* stocks, but a priori inference would suggest less or no change, as unlike *G. morhua*, *G. ogac* is a cold water species (Kearley 2012) and would not have been negatively influenced by the cold conditions of the early 1990s. In addition, *G. ogac* were never commercially harvested. Local knowledge of fishermen along the Newfoundland coast tends to support this inference (pers. comms.). Feeding competition between these species in inshore waters, where most juvenile *G. morhua* (Lear et al. 1980; Dalley and Anderson 1997; Methven and Schneider 1998) and all *G. ogac* reside (Scott and Scott 1988; Mikhail and Welch 1989), could help explain the slow rebuilding of depleted *G. morhua* stocks over the past decades, but few data existed to test this hypothesis.

Despite its historic commercial importance, the feeding ecology of older *G. morhua* juveniles (ages-2-4) in coastal areas of Newfoundland is poorly known. Clark and Green (1990) examined their diel activity patterns in Conception Bay using sonic telemetry and inferred that the higher activity rates observed were related to feeding, but provided no information on prey selection. Studies on age 1–2 juveniles in Conception Bay yielded differing results: Keats et al. (1987) found small (<12.5 cm) juveniles fed on pelagic prey and larger (16–23.5 cm) juveniles fed on benthic organisms whereas Keats and Steele (1992) reported that all juveniles (<23.5 cm) consumed mainly pelagic crustaceans.

Previous studies of diet overlap between *G. morhua* and *G. ogac* further north have yielded conflicting results. Feeding patterns from two inshore locations in southern Labrador suggested that the two species had dissimilar diets (Chaput 1981). In contrast, substantial overlap in diets was reported from West Greenland by Nielsen and Andersen (2001). In coastal Newfoundland, no comparisons of diet overlap have been made.

Studies of dietary resource partitioning in co-occurring or closely related fish have typically used stomach content analysis to examine dietary overlap (e.g., Grossman 1986; Garrison 2000; Corrêa et al. 2009). This method offers several benefits: stomachs samples are relatively easy to collect and prey items can be identified often to species and life stage. However, stomach analyses provide only a “snapshot” of dietary habits, often with many empty stomachs, and may also show bias toward prey items with lower digestion rates (Hyslop 1980). In contrast, stable isotope (δ^{13}C and δ^{15}N) signatures reflect biologically integrated nutrients in the diet over a long time period—up to several months for muscle tissue (Peterson and Fry 1987; Lorrain et al. 2002). Hence, isotope analysis identifies the longer term feeding habits of an individual, no matter their last meal. Used in conjunction, these methods provide a more complete representation of an organism’s dietary habits.

In this study, our objective was to compare the feeding habits of *G. morhua* and *G. ogac* in coastal Newfoundland and quantify dietary overlap using both stomach content and stable isotope analyses. The degree of overlap in dietary resources was expected to reflect the amount of interspecific feeding competition between these co-occurring species. Working null hypotheses were that *G. morhua* and *G. ogac* would not differ in: 1) diet, 2) pelagic and benthic oriented feeding, and 3) trophic position within the coastal ecosystem.

Methods

Collection of samples

Forty-seven mostly juvenile *Gadus morhua* and 42 *Gadus ogac* of comparable sizes (17–63 cm) were caught by hook and line over several (2–7) days in July of 2009 and 2010 from a small research vessel (*RV Gecho II*) within an area of approximately 2.5 ha near Petley Beach in Smith Sound, Trinity Bay, Newfoundland (Figs. 1 and 2). Forty-one fish (20*G. ogac* and 21*G. morhua*) were collected in 2009 and 48 fish (22*G. ogac* and 26*G. morhua*) were collected in 2010. Water depths at the site varied from <1 m to >40 m; most fish were caught within 1–2 m of the bottom. All fish were put on ice onboard the vessel and later sampled for total length, weight, sex, and reproductive stage. Stomachs were removed, weighed and frozen for later analysis and a small sample (1–2 cm^2) of dorsal muscle tissue posterior to the head was removed and frozen for stable isotope analysis.

Stomach contents analysis

Stomachs contents were sorted and identified to species or nearest taxonomic level, with weights recorded to the nearest 0.01 g. Cumulative prey curves were used to judge if n was sufficient to effectively describe diet compositions (Hoffman 1979; Cailliet et al. 1986; Cortés 1997). The order in which stomachs were analyzed was randomized 10 times and the mean number of new prey items found consecutively in the stomachs plotted against the number of stomachs that contained prey. Linear

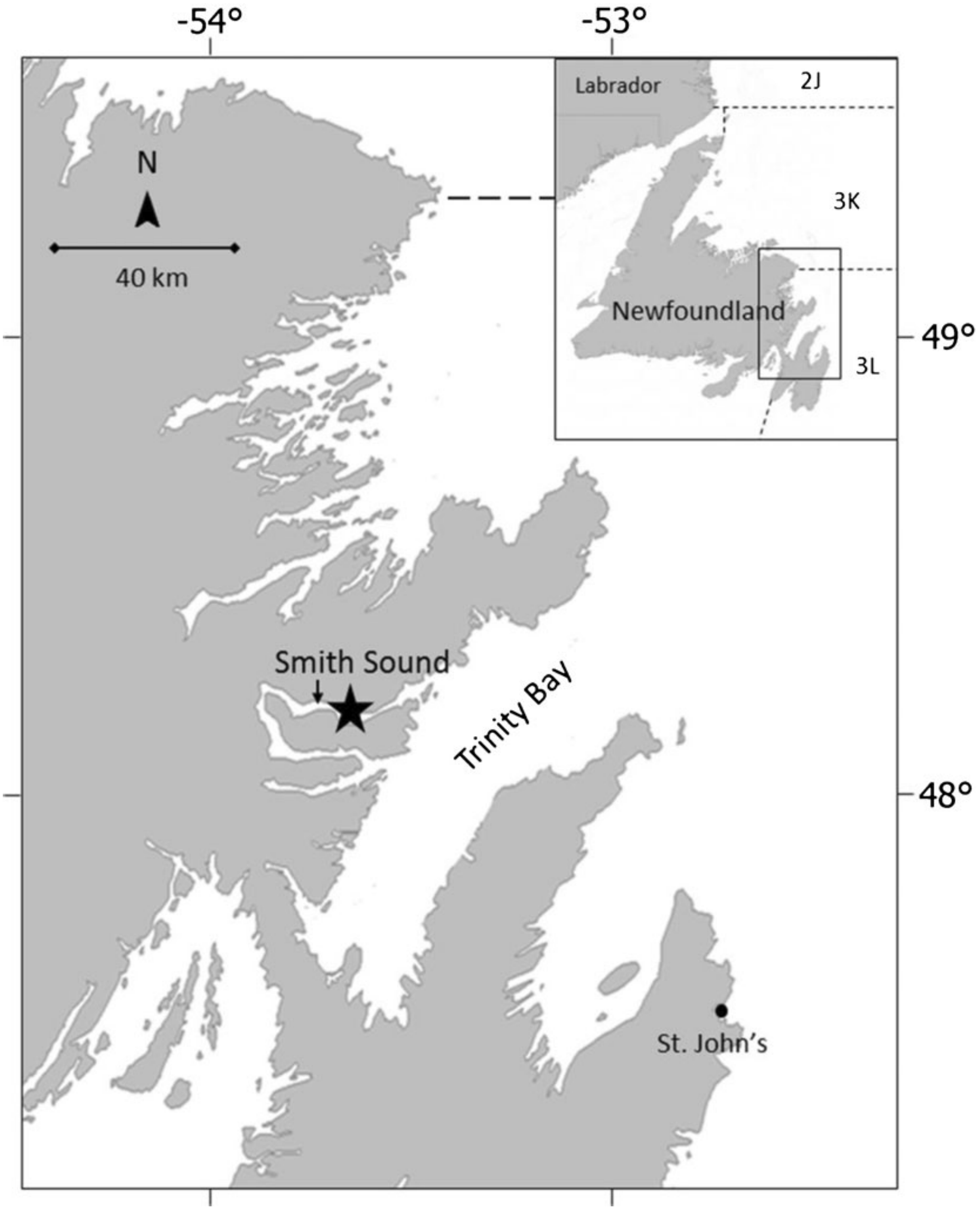


Fig. 1 Map of the Eastern portion Newfoundland showing location of sampling area (*black star*) within Smith Sound. Inset shows position of enlarged map relative to the Island of Newfoundland and NAFO Divisions 2 J, 3 K and 3 L

regressions were then performed on the last four points of the curve to assess if an asymptote had been reached (sensu Bizzarro et al. 2007). If the slope did not differ significantly from 0 (i.e., $p>0.05$), the curve was considered to have reached an asymptote with n adequate to describe diet.

The relative quantity of stomach contents and relative importance of individual prey types were assessed using the following indices: 1) relative frequency of occurrence (FO%) = number of stomachs with prey item, i, as a percentage of the total number of stomachs, 2) relative gravimetric abundance (W%) = total weight

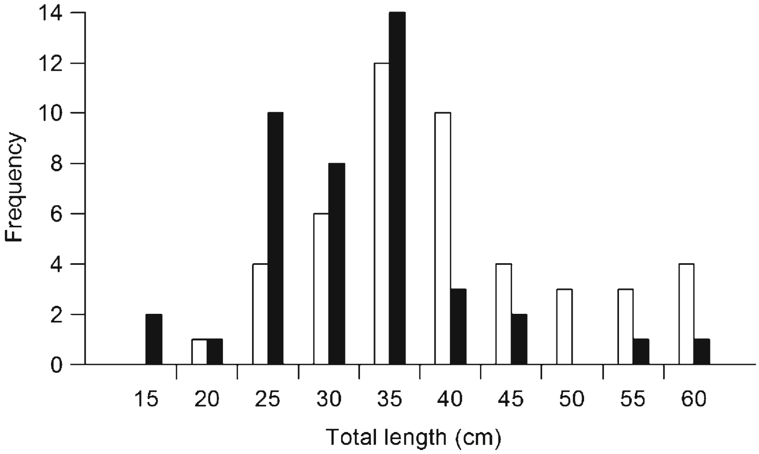


Fig. 2 Size frequency distribution of sampled fish. Black bars = *G. ogac*; open bars = *G. morhua*

of prey item *i*, as a percentage of the weight of total stomach contents summed for all fish, 3) mean total fullness index (TFI) $=\frac{1}{n}\sum_{f=1}^{n}(\text{weight of stomach contents of fish } f/(\text{length of fish } f)^3)\times 10^4$, and 4) mean partial fullness index (PFI) $=\frac{1}{n}\sum_{f=1}^{n}(\text{weight of prey item, } i\text{, in fish } f/(\text{length of fish } f)^3)\times 10^4$, where n is the number of stomachs examined, weight is in 0.1 g and fish length is in cm. Niche breadths for each species were estimated using Levins' standardized index (Levins 1968; Hurlbert 1978; Krebs 1989): $B=1/(n\sum p_{xi^2})$, where p_{xi} is the proportion of species x using prey item i, and n is the number of prey items available. Prey items available included all prey species identified in the study and availability was assumed to be the same for both species and size classes. B ranges from $1/n$ (use of a single resource) to 1 (equal usage of resources). Dietary niche overlap between species was assessed with Schoener's (1970) overlap index: $C=1–0{\cdot}5(\sum|p_{ix}–p_{iy}|)$, where p_{ix} and p_{iy} are the proportions by weight of prey item i in the diets of species x and species y, respectively. Index values range from 0 to 1, with 0 representing no overlap and 1 representing complete overlap and values ≥0.6 generally considered biologically significant (Wallace 1981).

Food items were also classified into pelagic, suprabenthic and benthic categories based on studies of the prey taxa and previous cod diet studies (e.g., Scott and Scott 1988; Parrish et al. 2009). To compare the relative importance of prey categories, the gravimetric abundance (W%) for each prey category was calculated for all individuals and tested statistically for differences between species using a Kruskal-Wallis test.

A one-way analysis of similarity (ANOSIM) (Clarke 1993) of gravimetric abundance (W%) and frequency of occurrence (FO%) of prey items for each individual was used to assess dietary differences between species. The proportion by mass of each prey item in the stomach contents of each individual was used to calculate gravimetric abundance (W%) while the presence or absence of each prey item was used to determine frequency of occurrence (FO%). Prior to analysis, data were square-root transformed and used to construct a Bray-Curtis similarity matrix. Similarity percentages (SIMPER) analysis was used to identify which prey categories contributed most to dissimilarities between species (Clarke 1993). Both ANOSIM and SIMPER were performed using PRIMER 6 software (Clarke and Gorley 2006).

Stable isotope analysis

Dorsal muscle tissue samples were thawed, dried to constant weight (48 h at ~80 ° C in a drying oven), crushed to a fine powder using a mortar and pestle and sent to the CREAIT Network Stable Isotope Lab Facility at Memorial University of Newfoundland. Stable carbon and nitrogen isotope ratios and elemental determinations for each sample were determined by analysis of CO^2 and N^2, respectively, produced by combustion using a Carlo Erba NA1500 Series II Elemental Analyser followed by gas chromatograph separation and online analysis by continuous-flow mass spectrometer. Stable carbon and nitrogen ratios were expressed in delta (δ) notation, defined as the parts per thousand (‰) differences from a standard material: $\delta X=[(R_{sample}/R_{standard})-1]\times10^3$, where δ = the measure of heavy to light isotope in the sample, $X={}^{13}C$ or ${}^{15}N$ and R = the corresponding ratio

Table 1 Importance of all prey items based on frequency of occurrence (FO%), relative weight (W%), and mean partial fullness (PFI) for *G. ogac* and *G. morhua*. Prey types: B = benthic; SB = suprabenthic; P = pelagic. Bold values indicate maximums for each index

		Gadus ogac			*Gadus morhua*		
		(*n*=42; size range=17–60 cm)			(*n*=47; size range=21–63 cm)		
Prey Item	Prey type	FO (%)	W (%)	Mean PFI	FO (%)	W (%)	Mean PFI
Invertebrates							
Ophiuroidea	B	0.0	0.0	0.000	2.1	0.3	0.005
Polychaeta	B	28.6	**36.5**	**0.797**	8.3	0.3	0.011
other annelids	B	0.0	0.0	0.000	4.2	19.1	0.136
All annelids	B	28.6	36.5	0.797	12.5	19.4	0.148
Bivalvia	B	2.4	0.0	0.000	0.0	0.0	0.000
Hyperiidae	P	2.4	0.1	0.002	62.5	**38.7**	**0.406**
other amphipods	P	4.8	0.9	0.021	6.3	0.0	0.000
All amphipods	P	7.1	1.0	0.023	68.8	38.7	0.406
Idotea balthica (Isopoda)	B	2.4	0.1	0.001	0.0	0.0	0.000
Mysidae	SB	2.4	2.9	0.071	8.3	0.1	0.002
Euphausidae	SB	11.9	8.6	0.165	37.5	5.4	0.114
Mysidae and/or Euphausiidae	SB	35.7	1.8	0.026	20.8	2.5	0.066
All mysids/euphausiids	SB	**50.0**	13.3	0.262	**66.7**	8.0	0.182
Pandalus montagui	B	0.0	0.0	0.000	2.1	0.1	0.002
Eualus fabricii	B	2.4	0.4	0.010	0.0	0.0	0.000
Spirontocaris sp	B	0.0	0.0	0.000	2.1	0.1	0.001
Sabinea sarsi	B	2.4	4.8	0.034	0.0	0.0	0.000
Hyas coarctatus	B	0.0	0.0	0.000	2.1	0.2	0.010
Hyas sp	B	0.0	0.0	0.000	0.0	0.0	0.000
Pagurus sp	B	0.0	0.0	0.000	6.3	0.4	0.016
All decapods	B	4.8	5.2	0.043	12.5	0.8	0.029
Fish							
Clupea harengus	P	0.0	0.0	0.000	2.1	0.0	0.000
Mallotus villosus	P	0.0	0.0	0.000	2.1	0.2	0.002
Gadus morhua	B	4.8	20.0	0.107	4.2	16.5	0.104
Gadus ogac	B	0.0	0.0	0.000	2.1	7.2	0.040
Gadus sp	B	0.0	0.0	0.000	2.1	2.1	0.012
Myoxocephalus sp	B	4.8	5.8	0.075	0.0	0.0	0.000
Myoxocephalus scorpius	B	2.4	0.1	0.001	0.0	0.0	0.000
Ulvaria subbifurcata	B	4.8	2.3	0.024	2.1	0.5	0.012
Stichaeus punctatus	B	2.4	0.1	0.001	2.1	1.2	0.033
Lumpenus maculatus	B	2.4	0.7	0.002	0.0	0.0	0.000
Unidentified fish	-	9.5	3.4	0.022	12.5	5.1	0.045
All fish	-	31.0	32.3	0.232	29.2	32.8	0.248
Other							
Stone	-	7.1	1.4	0.013	2.1	0.0	0.000
Unidentified organic material	-	2.4	9.1	0.064	2.1	0.0	0.001
Plant material/seaweed	-	9.5	1.0	0.010	4.2	0.0	0.000
N (%) of empty stomachs		10 (23.8 %)			2 (0.04 %)		

($^{13}C/^{12}C$ or $^{15}N/^{14}N$). International Standard references are Vienna Pee Dee Belemnite (VPDB) for carbon, and atmospheric N_2 for nitrogen.

To estimate trophic niche breadth and structure, quantitative metrics based on the position of individuals in trophic niche space developed by Layman et al. (2007) and described by Jackson et al. (2011) were applied at the population level using individuals as measurement units. Metrics were calculated using the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2008) for R statistical computing package (R Development Core Team 2007) and are briefly defined as follows: 1) $\delta^{15}N$ Range (NR): a measure of degree of trophic diversity calculated as the distance between the most enriched and most depleted $\delta^{15}N$ values for a given species or group; 2) $\delta^{13}C$ Range (CR): distance between the highest and lowest $\delta^{13}C$ which indicates the variability of food sources consumed; 3) Standard Ellipse Area (SEA): a measure of the total trophic niche breadth for a given species or group; 4) Mean distance to centroid (CD): average Euclidean distance of each individual to the mean $\delta^{13}C$ and $\delta^{15}N$ value which provides a measure of the average degree of trophic diversity within a species or group; 5) Mean nearest neighbour distance (MNND): mean of the Euclidean distances to each species' nearest neighbour in bi-plot space which provides a measure of the overall density of species packing (i.e., a group comprised of many individuals with similar trophic ecologies would show a smaller MNND than a group in which individuals are more varied in terms of their trophic niche); 6) Standard deviation of nearest neighbour distance (SDNND): a measure of the evenness of species packing in bi-plot space with lower SDNND values suggesting a more even distribution of trophic niches.

Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) and metric data (CD, MNND, and SDNND) were tested for normal (Gaussian) distribution using probability plots and frequency distributions and non-normal data were transformed using the Johnson transformation tool in Minitab 16. Between species differences in metrics and effect of body size on $\delta^{13}C$ and $\delta^{15}N$ values were evaluated using *t*-tests and regression analysis, respectively. Trophic niche overlap was estimated as the percent of overlapping SEA between species.

Results

Stomachs of *G. morhua* and *G. ogac* contained a substantial variety of prey items (Table 1). Cumulative prey curve regressions on the last four measures for both species had slopes that did not differ from 0 (regression, t=3.66, p=0.07 for *G. morhua* and t=2.54, p=0.13 for *G. ogac*) (Fig. 3).

Stomach contents

Indices of relative importance (FO%, W%, and PFI) for all prey items (Table 1) indicated that for *G. ogac*, polychaetes and mysids/euphausiids were the dominant prey items, occurring in 28.6 % and 50 % of stomachs

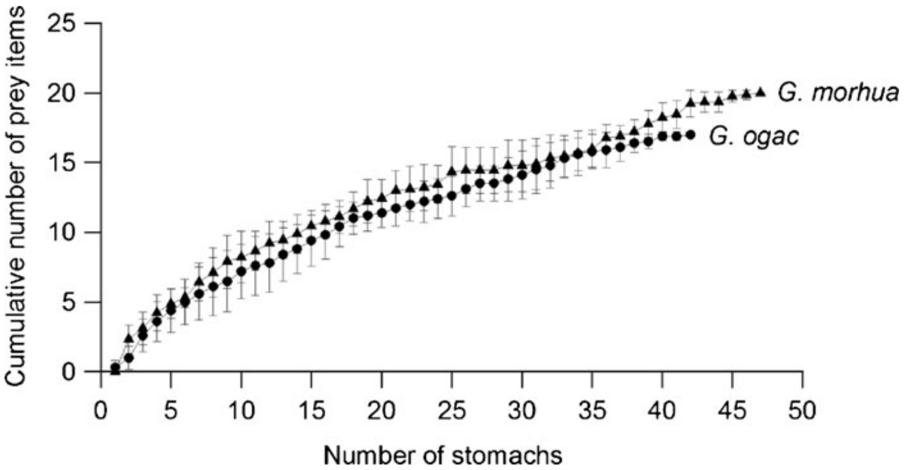


Fig. 3 Cumulative prey curves for *G. ogac* (*filled circle*) and *G. morhua* (*filled diamond*). Symbols show the mean cumulative number of prey items per stomach sampled and error bars indicate SD

and making up 36.5 % and 13.3 % of the total diet by weight. Polychaetes and mysids/euphausiids also had the highest PFI values at 0.797 and 0.262, respectively. Unidentified bony fish was the next most important prey item by frequency of occurrence (9.5 %) while *G. morhua* had the next highest relative weight (20 %) and PFI value (0.107).

In the stomachs of *G. morhua*, mysids/euphausiids and hyperiids had the highest frequency of occurrence (FO%) (mysids/euphausiids=66.7 %; hyperiids=62.5 %) and PFI

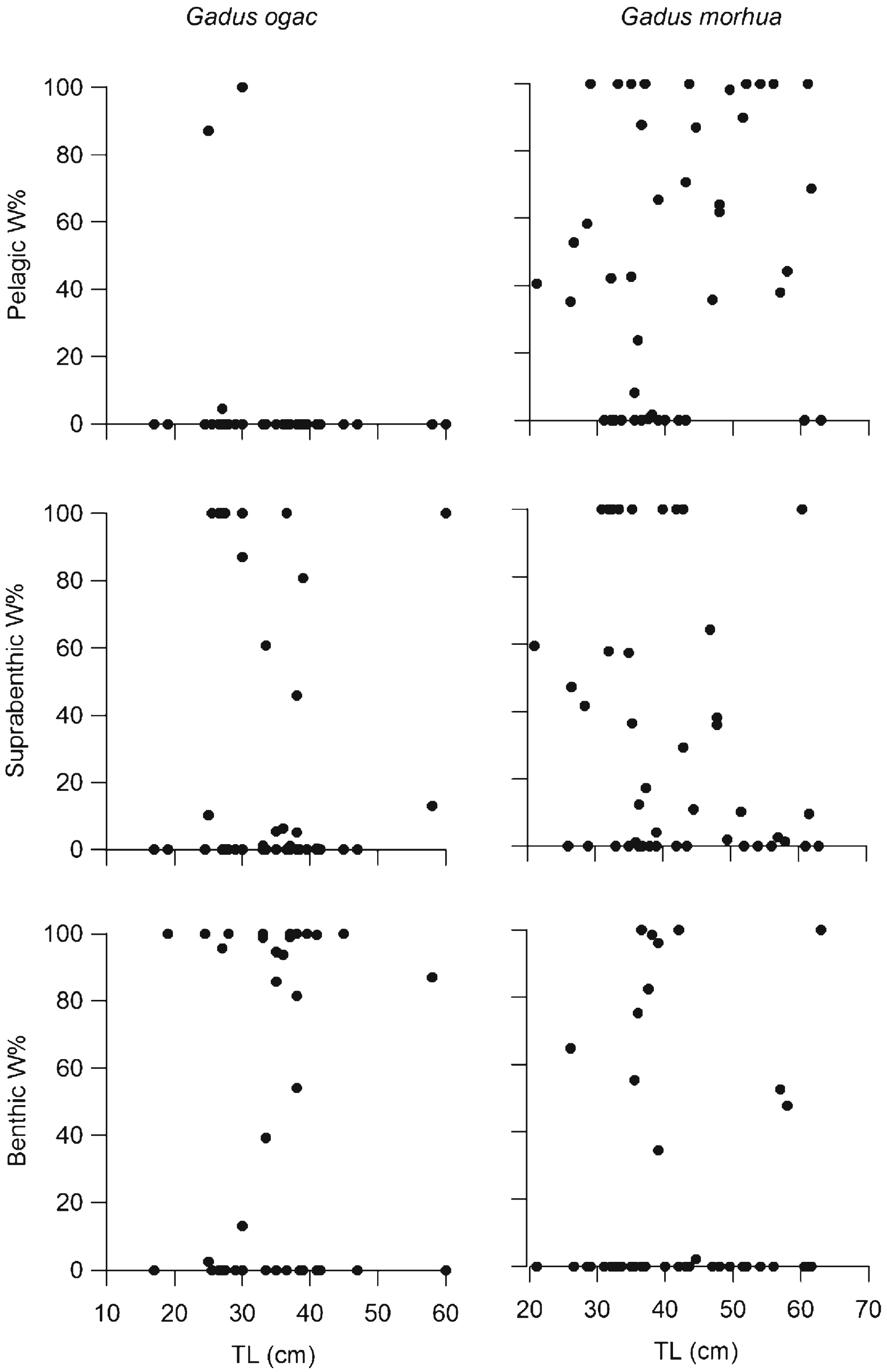


Fig. 4 Plots of relative gravimetric abundance (W%) of pelagic, suprabenthic and benthic prey categories by fish length (cm) for *G. ogac* and *G. morhua*

Table 2 Mean total fullness index (TFI), dietary niche breadth (*B*) (Levins 1968) and dietary overlap (Schoener 1970) for *G. ogac* and *G. morhua*

Species	n	Mean TFI (± SE)	Dietary breadth (*B*)	Niche overlap (*C*)
G. ogac	42	1.45±0.34	0.14	0.28
G. morhua	47	1.02±0.31	0.06	

values (mysids/euphausiids=0.182; hyperiids=0.406) while hyperiids and polychaetes had the highest relative weights at 38.7 % and 19.4 %, respectively. Annelids (12.5 %) and polychaetes (12.5 %) had the next highest frequency of occurrence while *G. morhua* had the next highest relative weight (16.5 %) and PFI (0.104) values.

G. morhua had significantly higher proportions by weight of pelagic prey items in their diet than *G. ogac* (Kruskal-Wallis, H=28.8, $p<0.01$) (Fig. 4). This was attributed almost entirely to the high relative weight of hyperiids in the stomachs of *G. morhua* (Table 1). In comparison, *G. ogac* had a higher relative abundance of benthic prey items (Kruskal-Wallis, H=5.25, $p=0.02$) (Fig. 4). No significant difference between species was found for the suprabenthic prey category (Kruskal Wallis, H=1.27, $p=0.26$) (Fig. 4).

Total fullness (TFI) values were somewhat higher for *G. ogac* than for *G. morhua* but did not differ significantly between species (Kruskal Wallis, H=0.13, $p=0.72$) (Table 2). *G. ogac* had a significantly lower niche breadth index than *G. morhua* (Kruskal Wallis, H=11.25, $p<0.01$) and low ($C=0.28$) overlap in diet was found between species (Table 2).

ANOSIMs showed significant differences in diet composition between *G. ogac* and *G. morhua* by both gravimetric abundance (W%) (R=0.243 $p<0.01$) and frequency of occurrence (FO%) (R=0.227, p |<0.01) (Table 3). Results from SIMPER analyses revealed high average dissimilarity between species (W%: 93.3 % dissimilarity; FO%: 90.3 %) with hyperiids, euphausiids, mysids/eupausiids and polychaetes contributing most to the dissimilarity for both dietary indices (Table 3).

Stable isotopes

Carbon isotope (δ^{13}C) levels in tissues of *G. ogac* were significantly more positive, or enriched in ^{13}C, as compared to those of *G. morhua,* which were relatively depleted in ^{13}C (*t*-test, $t=4.82$, $p<0.01$) (Table 4, Fig. 5). In contrast, no significant difference in mean δ^{15}N values was found between species (*t*-test, $t=1.59$, $p=0.12$) (Table 4). A significant positive relationship between body size (TL) and isotopic δ^{13}C values was evident in both species (regression, $t=3.52$, $p<0.01$ and $t=2.13$, $p=0.04$ for *G. morhua* and *G. ogac*, respectively) (Fig. 6). No significant relationship between body size and isotopic δ^{15}N values was observed for either species.

Neither mean distance to centroid (CD) or mean nearest neighbour distance (MNND) differed between

Table 3 Percent contribution to average dissimilarity by prey item and dietary index for *G. ogac* and *G. morhua*

FO%		W%	
Prey Item	% contribution	Prey Item	% contribution
Hyperiids	24.9	Hyperiids	27.2
Euphausiids	16.8	Euphausiids	16.5
Mysids/Euphausiids	16.0	Mysids/Euphausiids	14.7
Polychaetes	9.9	Polychaetes	12.0
Unidentified fish	5.9	Unidentified fish	4.9
Mysids	3.5	Gadus morhua	3.3
other amphipods	3.3	Other amphipods	2.4
Gadus morhua	2.4	*Ulvaria subifurcata*	2.3
Ulvaria subifurcata	2.3	*Myoxocephalus sp*	2.1
Pagurus sp	1.8	*Pagurus sp*	2.0
Myoxocephalus sp	1.8	Mysids	1.8
Stichaeuspunctatus	1.3	*Myoxocephalus scorpius*	1.2
other annelids	1.3		

Table 4 Summary of isotopic metrics by species. NR=δ^{15}N range; CR=δ^{13}C; SEA = standard ellipse area; CD = distance to centroid; MNND = mean nearest neighbour distance; SDNND = standard deviation of nearest neighbour distances

Species	n	Mean δ^{15}N±SE (‰)	Mean δ^{13}C±SE (‰)	NR	CR	SEA (units^2)	SEA overlap (units^2 (%))	CD	NND	SDNND
G. ogac	42	14.71±0.08	−17.91±0.15	2.06	4.15	1.50	0.65 (43.3)	0.96	0.22	0.16
G. morhua	47	14.50±0.11	−18.99±0.17	2.47	4.50	2.63	0.65 (24.7)	1.11	0.29	0.31

species (CD: *t*-test, *t*=−1.16, *p*=0.25; MNND: *t*=−1.30, *p*=0.20). SDNND was lower for *G. ogac* than for *G. morhua* (Table 4). The percentages of SEA overlap between *G. ogac* and *G. morhua* were moderate at 43.3 % and 24.7 %, respectively (Table 4; Fig. 5).

Discussion

Results from both stable isotope and stomach analyses provide support for dietary niche partitioning between *G. ogac* and *G. morhua* and suggest only minor competition for food resources between species during the summer. This conclusion is based on rejection of the working null hypotheses on diet similarity and benthic-pelagic prey similarity. Stomach analyses indicated differing prey and a higher proportion of benthic items for *G. ogac* and pelagic items for *G. morhua*. In support of these conclusions, isotopic signatures for *G. ogac* were significantly more enriched in ^{13}C, indicating more benthic feeding, whereas signatures for *G. morhua* were relatively depleted in ^{13}C, indicative of more pelagic feeding (Davenport and Bax 2002; Hobson et al. 2002; Sherwood and Rose 2005).

Consistent with the present study, Chaput (1981) concluded that diets of *G. morhua* and *G. ogac* were dissimilar based on low correlation coefficients for major prey items identified from stomachs from specimens caught in shallow (<25 m) water at two nearshore sites in Labrador (NAFO Div 2 J). The authors attributed these differences to the high frequency of occurrence and contribution to total fullness of pelagic invertebrates for *G. morhua* and shrimp, fish and polychaetes for *G. ogac*. In contrast, Nielsen and Andersen (2001) found no difference in the diet of *G. morhua* and *G. ogac* in West Greenland and concluded the two species compete for food where their ranges overlap.

The differing results between the present and Labrador study and the Greenland study may relate to timing and differing prey fields. The present results indicate that larger *G. ogac* feed primarily on fish (capelin, *Mallotus villosus*, when available), crustaceans and polychaetes,

Fig. 5 δ^{15}N - δ^{13}C bi-plots and group means (± 2 SE) of sampled *G. ogac* (*filled circle*) and *G. morhua* (*empty circle*). Enclosed areas represent the standard ellipse trophic niche area (SEA) occupied by each group (dashed line = *G. ogac*; solid line = *G. morhua*)

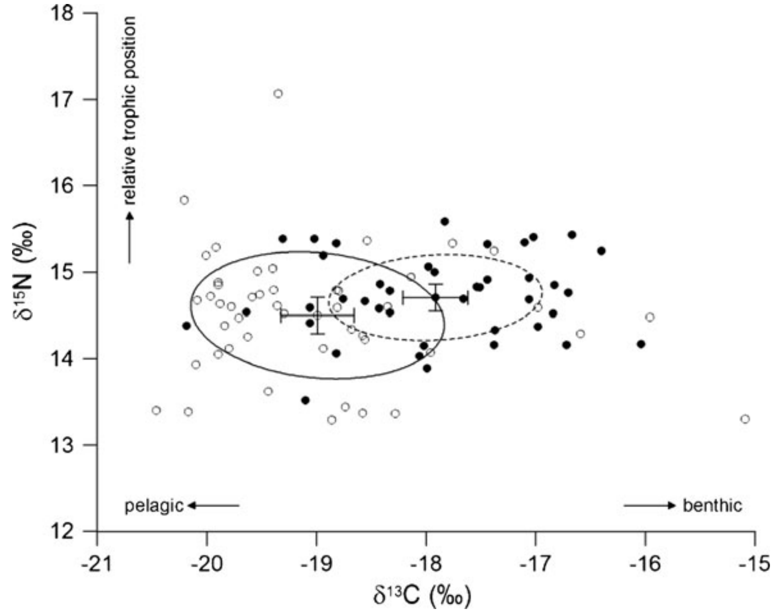
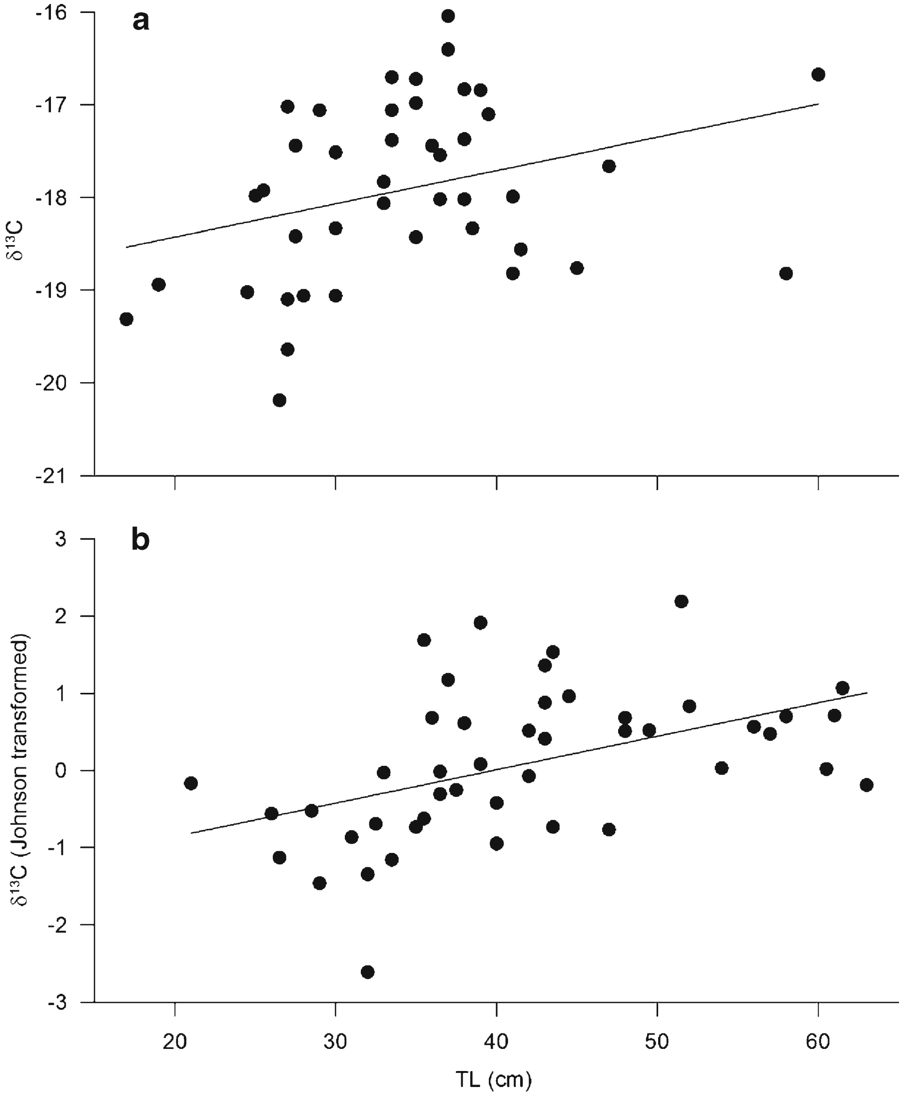


Fig. 6 Plots of δ^{13}C versus TL and regression slopes for **a** *G. ogac* and **b** *G. morhua*. Both regressions were significant at $p<0.05$



which is consistent with previous reports (Jensen 1948; Chaput 1981; Mikhail and Welch 1989; Morin et al. 1991; Nielsen and Andersen 2001). The main prey items for *G. morhua* found in the present study were in accordance with results from numerous feeding studies from Newfoundland waters (e.g., Templeman 1965; Lilly et al. 1984; Paz et al. 1991; Sherwood et al. 2007; Krumsick and Rose 2012) with the exception that capelin was found in only a single stomach. Capelin are only available seasonally in coastal Newfoundland, and have had depressed stock levels since 1990 (DFO 2010). In the present study, very few capelin were observed during daily echosounding of the study area, and none spawned on the beach prior to or during the course of the study. When capelin are available, they are likely to be preyed on heavily by both species, and this predation is likely to temporarily influence the degree of diet overlap. Nonetheless, competition may still be limited, as a consequence of the typical high density of spawning capelin. Similar increases in resource sharing at times of very high prey abundance has been demonstrated across several taxa (reviewed by Schoener 1982) including among co-occurring gadid species in south-western Norway (Høines and Bergstad 1999). Furthermore, in West Greenland, in contrast to Newfoundland, capelin have a quasi-continuous distribution along the coast and undergo more limited spawning migrations (Friis-Rødel and Kanneworff 2002). West Greenland *G. morhua* and *G. ogac* both had capelin as their dominant prey (Nielsen and Andersen 2001) but it remains unclear if feeding competition exists there.

Large *G. ogac* did show evidence of feeding on juvenile *G. morhua*, as did larger *G. morhua* to a lesser extent. Although the present study did not attempt to evaluate predation as a potential impact on either species, large *G. ogac* were relatively rare in our study area, hence despite their predatory habits they may be too few to impact the overall abundance of *G. morhua*.

The present stable isotope results were consistent with the wider ranging records for *G. morhua* from northeast Newfoundland (NAFO Division 3KL) (Sherwood and Rose 2005; Sherwood et al. 2007) and represent the first records of stable isotope signatures (δ^{15}N and δ^{13}C) for *G. ogac* in Newfoundland waters. For both gadids, isotope values shifted from pelagic (more negative δ^{13}C values) to more benthic (more positive δ^{13}C values) with increasing body size. This shift is consistent with diet transitions from invertebrates to fish as gape size increases and young gadids are able to exploit the higher energy content of piscivorous prey (e.g., Høines and Bergstad 1999; Nielsen and Andersen 2001; Link and Garrison 2002; Sherwood et al. 2007).

Although no significant differences were found, mean total fullness indices for *G. ogac* were higher than for *G. morhua,* a pattern previously reported by Chaput (1981), who suggested that in the absence of capelin, *G. ogac* are more efficient predators (in terms of prey weight consumed per predator body weight). It is possible that slight differences in relative stomach fullness between species may be due to differences in preferred prey availability or from differential habitat utilization. It may also be that *G. ogac* has a more generalist (less discriminate) feeding approach than *G. morhua*. This theory is supported by dietary breadth indices that were more than twice as high for *G. ogac* as for *G. morhua* of the same size. However, it should be noted that in the absence of prey availability data indices of niche breadth must be interpreted with caution (Hurlbert 1978; Feinsinger et al. 1981; López et al. 2009).

Differences in diet between *G. morhua* and *G. ogac* could also reflect differences in pelagic habitat use that lead to differences in prey availability (e.g., Baker and Ross 1981; Shpigel and Fishelson 1989; Helland et al. 2008). Specifically, *G. morhua* could occupy a broader vertical distribution that encompasses both benthic and pelagic environments while *G. ogac* maintain a closer association with the bottom (Scott and Scott 1988). This hypothesis will be tested in a further study. In addition, the more slender body and lighter colouration of *G. morhua,* is suggestive of more pelagic behaviour, whereas the stouter form and darker colouration of *G. ogac* is consistent with more demersal habits.

In contrast to the competition hypotheses, the trophic position null hypothesis was not rejected, as ^{15}N signatures were similar between species (Minagawa and Wada 1984; Post 2002). These results suggest that despite differing diets, *G. morhua* and *G. ogac* occupy similar trophic positions within the coastal Newfoundland ecosystem. However, it should be noted that in the absence of measured isotope values for specific prey items some degree of caution must be used in the interpretation of the results.

In conclusion, *G. morhua* and *G. ogac*, that co-occupy much of the coastal zone of Newfoundland and Labrador and other areas of the north Atlantic, appear to have similar trophic positions but limited diet competition. Our evidence provides little support for the notion that feeding competition could be limiting *G. morhua* recovery in these waters.

Acknowledgements We thank E. Stern, D. Pike, and T. Clenche for support in the field and K. Krumsick and S. Fudge for lab assistance. This work was approved by the Animal Care Committee at the Memorial University of Newfoundland and was funded by grants from the Newfoundland and Labrador Department of Fisheries and Aquaculture and the Natural Sciences and Engineering Research Council of Canada to GAR, and a scholarship from the Institute for Biodiversity, Ecosystem Science & Sustainability (IBES), Department of the Environment of Newfoundland and Labrador, to DCK

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