Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): Insights from stable carbon isotopes ($\delta^{13}C$)

Graham D. Sherwood[*], Rick M. Rideout, Susan B. Fudge, George A. Rose

Fisheries Conservation Group, Marine Institute, Memorial University, P.O. Box 4920, St. John's NL, Canada A1N 5R3

Abstract

Cod populations in Newfoundland and Labrador waters have shown differing growth, condition and recruitment since near-universal declines in these properties during the cold period of the late 1980s and early 1990s. To assess the influence of variable prey communities on these parameters, we compared cod energetics and diet in populations off Labrador and the northeast and south coasts of Newfoundland. Many properties were highest in the southern group(s) and lowest in the northern group(s), including growth, somatic condition, liver index and age-at-maturity. Most differences could be explained by variations in diet, as measured by stomach contents and stable carbon isotopes ($\delta^{13}C$). The diet of Labrador cod consisted almost entirely of northern shrimp (*Pandalus borealis*), and these cod displayed the most benthic $\delta^{13}C$ signatures. Northeast cod had a more varied diet that included capelin and other fish, but still had mostly benthic $\delta^{13}C$ signatures, suggesting the importance of benthic prey like shrimp in this population. South coast cod exhibited the most varied diet, including capelin (*Mallotus villosus*), zooplankton, crabs and other fish, and had the most pelagic $\delta^{13}C$ signatures. Among and within populations, the benefits of a more pelagic diet in medium-sized (30–69 cm) cod included higher somatic condition, higher liver index (lipid stores) and greater spawning potential (decreased incidence of atresia). It is hypothesized that major rebuilding of Newfoundland and Labrador cod stocks will require a return to a system that supports mostly pelagic feeding (i.e. capelin) in cod.
© 2007 Elsevier Ltd. All rights reserved.

Keywords: Atlantic cod; Capelin; Condition factor; Diet; Newfoundland and Labrador; Reproduction

1. Introduction

The failure of most Newfoundland and Labrador (NL) cod stocks to rebuild following catastrophic stock declines in the late 1980s and early 1990s has rekindled some debate regarding the relative importance of ecosystem-wide versus fishing-only effects on current NL cod productivity and stock recovery. Early models of recovery, in the wake of a fishing ban introduced in 1992/1993, were optimistic in their predictions (Lear and Parsons, 1993; Roughgarden and Smith, 1996). More than a decade later however, the reality is that the formerly large northern and Grand Banks cod stocks off NL have undergone little, if any, rebuilding (DFO,

*Corresponding author. Present address: Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA. Tel.: +1 207 228 1644; fax: +1 207 772 6855.
E-mail address: gsherwood@gmri.org (G.D. Sherwood).

2004; Osborne, 2005). It is becoming increasingly evident that the moratorium approach alone has not been adequate for rebuilding what was once one of the largest fisheries in the world. Instead, it is being questioned whether the current low productivity of most NL cod stocks, which was no doubt precipitated by overfishing, may have become amplified and prolonged by fundamental ecosystem changes (e.g., Carscadden et al., 2001).

Feeding habits in NL cod in particular are posited to have changed in the past decade as a result of natural or fishing-related shifts in the structure of the NL continental shelf food web (Rose et al., 2000). Specifically, capelin (*Mallotus villosus*), once

the most abundant pelagic forage fish in the Northwest Atlantic from Labrador to the southern Grand Banks, and previously (1978–1990) very important in Newfoundland cod diets (Gerasimova and Kiseleva, 1998), are now greatly reduced in the diet of northern cod (Rose and O'Driscoll, 2002). This change has a latitudinal component such that the largest declines occurred over the northern banks regions, while capelin are still represented to varying degrees in the diet of cod from Newfoundland's southern coast and inshore bays (see Fig. 1). The exact cause(s) of this change in feeding regimes remain(s) unclear, but may be related to cooling ocean trends starting in the late 1980s (Carscadden
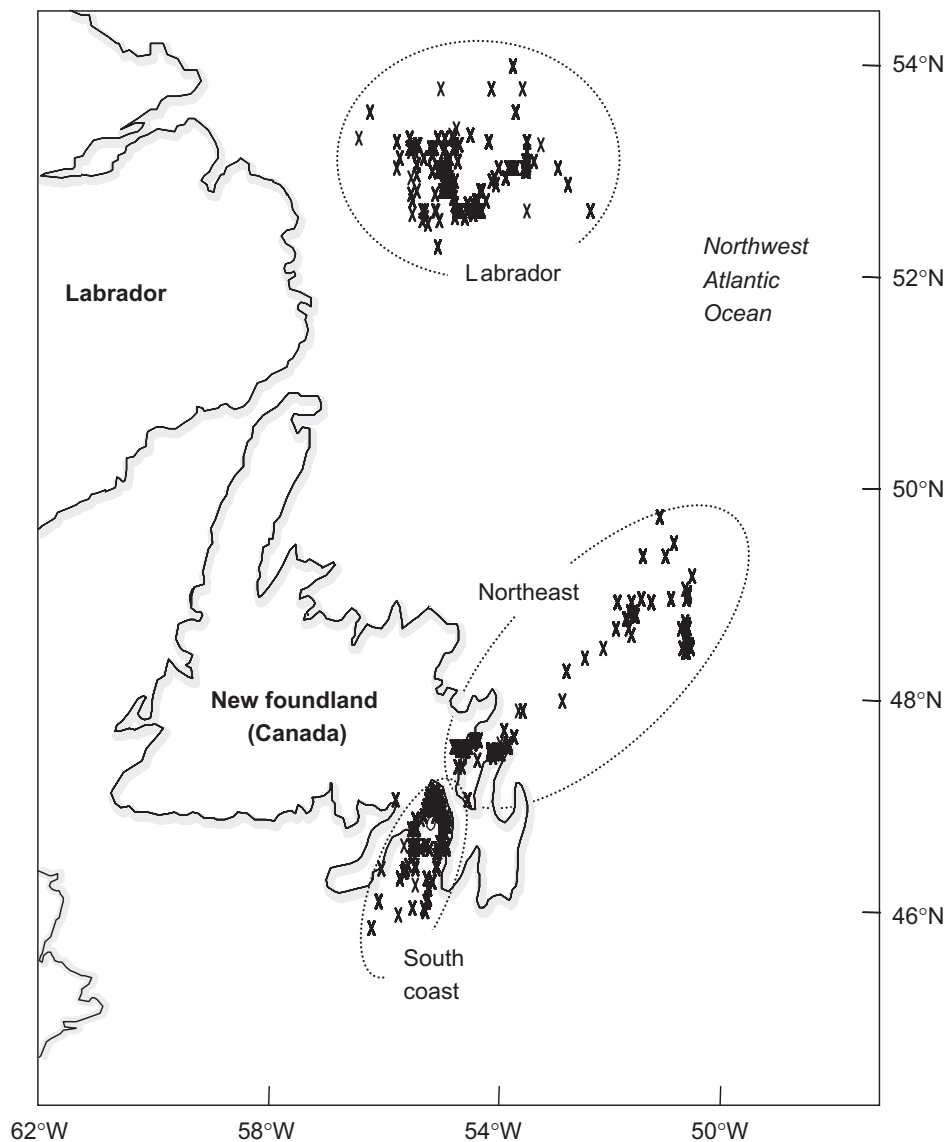

Fig. 1. Map showing the location of sampling sites (x) for cod around Newfoundland and Labrador from 1996 to 2003. Ellipses represent lumping of sites into putative cod populations (but not range of populations).

and Nakashima, 1997) or, as yet poorly understood trophic cascades triggered by heavy fishing pressure (Frank et al., 2005).

The purpose of the present paper is to synthesize and document current trends in NL cod feeding, growth, condition and reproductive capacity. Spatial (among-population) changes in these properties may provide a basis for understanding how temporal changes in food-web characteristics (and cod feeding), perhaps as a consequence of climate variability, may be contributing to temporal variability in the production and recovery potential of NL cod stocks. Specifically, we set out to document among-population/region variations in growth, condition (via indices of somatic and liver energy reserves) and reproductive endpoints (age-at-maturity and spawning potential) of cod from NL waters. We then test whether any differences in bioenergetic and reproductive status can be explained by variations in diet among populations/regions. Our characterization of NL cod diet is unique in that we employ both traditional stomach content and stable carbon isotope (δ^{13}C) analyses. Stomach contents (in this case, from over 12,000 individual cod, sampled over the course of 8 years) provide information on the presence/absence of various prey taxa at the time and place of sampling. Stable carbon isotopes, on the other hand, help to identify the time-averaged and energetically-weighted importance of broad prey categories (e.g., benthic vs. pelagic) to the overall diet of aquatic consumers (Sherwood and Rose, 2005). Given the generalist nature of cod feeding (Garrison, 2000), we expect that any variations in cod diet among populations/regions should be reflective of spatial variations in food-web structure and relative prey availability.

2. Methods

2.1. Study areas and sample collection

Cod were sampled from NL continental shelf waters at depths of 30–450 m and distances from shore of less than 1 km to over 200 km. Sampling sites (see Fig. 1) fell within three general areas which represent three putative NL cod populations: 'Labrador cod' within North Atlantic Fisheries Organization division 2J (samples were taken entirely from the offshore in and around Hawke Channel); 'northeast cod' from NAFO divisions 3KL (sampling occurred in the inshore mostly at Smith Sound and Trinity Bay, and offshore at or

near the Bonavista Corridor); and 'south coast cod' from NAFO division 3Ps (samples were mostly from Placentia Bay). Although Labrador cod and northeast cod are managed as one stock (2J+3KL, distinct from 3Ps cod), genetic analyses suggest that these comprise distinguishable populations (Ruzzante et al., 2001).

Between 1996 and 2003, a total of 21,235 NL cod were sampled during various months (mostly January or June) from one or more of the three sampling areas aboard the C.C.G.S. *Teleost*. Cod sampling was conducted with Campelen 1800 research shrimp bottom trawls fitted with a small mesh liner, and occasionally by handline at shallower depths. At sea, all cod were routinely measured (total length; nearest cm), and weighed (wet weight; nearest g), stomachs were removed and saved (frozen) for later diet analysis, livers and gonads were removed and weighed (nearest g), otoliths were removed for age determination and the remaining viscera was discarded before taking gutted (somatic) weight (nearest g).

2.2. Stable carbon isotope analysis

In 2002/2003, a subset of cod were sampled for stable carbon isotope analysis (δ^{13}C); a small sample ($\sim$1–2 g) of dorsal muscle tissue directly posterior to the head was excised immediately following capture, placed in a 1.5-ml centrifuge vial, and frozen at $-20\,^\circ$C for δ^{13}C analysis at a later date. Between six and ten samples for each available 10-cm cod length interval were collected from each area/trip for δ^{13}C analysis (total $n = 225$). Frozen cod muscle samples were dried to constant weight (for 48 h at 75 $^\circ$C in a drying oven) and crushed to a fine powder using a mortar and pestle. Dried, crushed samples were sent to G.G. Hatch Isotope Laboratories at the University of Ottawa, Canada, for stable carbon isotope analysis (http://www.isotope.uottawa.ca). Here, powdered samples were weighed into 4 × 6-mm tin capsules and stable carbon isotope ratios of these samples were determined by the analysis of CO_2 produced by combustion on a CE Elemental Analyser followed by gas chromatograph separation and on-line analysis by continuous flow with a Deltaplus isotope ratio mass spectrometer. Stable carbon isotope ratios were expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material (equivalent to Pee Dee belemnite limestone): δ^{13}C = ([R_{sample}/

$R_{standard}] - 1) \times 1000$; $R = {}^{13}C/{}^{12}C$); 5% of the samples were analysed in duplicate; the average standard error of the mean for replicates was 0.11‰. Cod muscle samples were not lipid extracted prior to analysis. Lipid content (inferred from C:N ratios) of cod muscle is low and relatively invariable among samples (Sherwood and Rose, 2005).

2.3. Stomach content analysis

Of the 21,235 cod sampled between 1996 and 2003, 16,501 were sampled for stomach contents, of which 12,693 contained food. In the laboratory, stomachs were thawed at room temperature, opened and analysed for contents. Prey items were identified to the lowest possible taxa and weighed to the nearest 0.1 g. Excess mucous and fluid were removed prior to weighing stomach contents, which were grouped into seven major prey species/categories: Atlantic cod, capelin, 'other fish' (includes sandlance, *Ammodytes* sp., Atlantic herring, *Clupea harengus*, other Gadidae and other unidentifiable fish), shrimp (mostly *Pandalus borealis*), crab (mostly *Chionoecetes opilio*), zooplankton (unidentifiable) and benthic invertebrates (various species/taxa). For the purposes of this study, fish other than cod and capelin were grouped into one major prey category ('other fish'); the individual fish species/groups comprising this category never made up more than 5% of the diet on their own, and more often less than 1%.

FO and mean partial fullness index (PFI) were used to assess the relative importance of each prey species/category to the diet of cod from each area by 10-cm cod length interval. FO (%) was calculated as

$$FO = \frac{N_i}{N_{tot}} \times 100,$$

where N_i is the total number of stomachs with prey i and N_{tot} the total number of stomachs examined for a specified group of fish (e.g., a length category/area). Mean PFI is a length-standardized way of expressing relative volumetric prey importance (Bowering and Lilly, 1992) and was calculated as

$$Mean\ PFI = \frac{1}{n} \times \sum \frac{w_{ij}}{L_j^3} \times 10^4,$$

where w_{ij} is the weight of prey i for fish j (g), L_j the length of fish j (cm) and n the total number of stomachs (fish) sampled for a specified group of fish. Mean total fullness index (mean TFI) also was calculated as the sum of all mean PFI values.

2.4. Condition indices

We considered two common indices of biological condition in cod. These were Fulton's condition factor K and the liver-somatic index (LSI); K was calculated as gutted weight (g) $\times$ total length^{-3} (cm^{-3}) $\times$ 100, and LSI as liver weight (g) $\times$ gutted weight^{-1} (g) $\times$ 100 (Lambert and Dutil, 1997). K is primarily an indicator of protein reserves (i.e. muscle mass), while LSI indicates excess lipid stores in cod (Yaragina and Marshall, 2000). To remove any seasonal variability in these indices, we calculated seasonally adjusted values. For example (for Fulton's K), $K_{adj} = K - K_{avg}$, where K_{avg} is the average condition factor (all sizes and areas combined) by month. We purposely made no attempt to remove the effect of size on either condition index. To the contrary, we were interested in examining how each index varies with size and related diet ontogeny. Mean (± 1 standard deviation) values (all areas and sizes combined) for K and LSI, respectively (i.e. K_{avg} and LSI$_{avg}$), by month were: 0.749 (0.059) and 0.057 (0.020) for January ($n = 1934$); 0.722 (0.049) and 0.044 (0.015) for April ($n = 955$); and 0.730 (0.054) and 0.036 (0.013) for June ($n = 1942$). Only condition data from 2002/2003 were compared in order to overlap with our stable isotope analysis; January, April and June were the only months sampled in these 2 years.

2.5. Spawning condition

In 2004, 30 females between 40 and 60 cm in length were sampled from Smith Sound (inshore northeast cod) for additional $\delta^{13}C$ analysis in conjunction with work on spawning condition (i.e. skipped spawning, Rideout et al., 2005). The reproductive status of these fish was determined via macroscopic inspection of the ovaries. Females were classified as immature ('nonspawners') if ovaries were small and pink, ripening ('potential spawners') if opaque eggs were visible, and 'Spent L' ('non-spawners') if ovaries were small and red with no opaque eggs (Templeman et al., 1978; Rideout et al., 2005). Ovaries classified as 'Spent L' in January were previously verified to be undergoing the mass atresia (egg resorption) of all ripening oocytes and therefore would not have been capable of spawning in the subsequent spawning season (Rideout et al., 2000).

2.6. Data analysis

Differences in growth among cod populations and sexes were assessed by comparing means and 95% confidence intervals of von Bertalanffy growth

function (VBGF) parameter estimates obtained from the nonlinear regression function in SPSS 10.0 and the following equation:

$$L_t = L_{inf}(1 - e^{(-k(t-t_o))}),$$

where L_t is the length (cm) at age t, L_{inf} the asymptotic length (cm), k the Brody growth coefficient (yr^{-1}), and t_o the x intercept (yr) (von Bertalanffy, 1938). Among-population differences in seasonally-adjusted condition indices (K_{adj} and LSI_{adj}) were explored within 10-cm size intervals using analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test. Our approach of comparing within size intervals acknowledges that condition factor may not always follow a predictable linear trend with size in fish and therefore might not lend itself to general linear model comparisons. Indeed, recent evidence in yellow perch (*Perca flavescens*), and other freshwater species, shows that bioenergetic budgets can be 'reset' at random diet shift points, which has the overall effect of creating discontinuous trends (with size) in parameters like activity rates, growth (Sherwood et al., 2002) and condition factor (G.D. Sherwood, unpublished data). Variations in maturity were assessed by comparing mean age at 50% maturity (X_m) for females:

$$M_x = \frac{1}{1 + e^{-r(X-X_m)}},$$

where M_x is the proportion of mature females as a function of age X and r is a constant describing the steepness of the maturity curve (Quinn and Deriso, 1999); estimates for r and X_m for each population were obtained using the nonlinear regression function in SPSS 10.0. Variations in cod diet were explored qualitatively by comparing PFI and FO values for various prey species/taxa by 10-cm size intervals for two different months (January and June, the most intensively sampled) representing two different seasons (winter and summer), and quantitatively by comparing $\delta^{13}C$ values among populations with length as a covariate in an analysis of covariance (ANCOVA). Among population differences in $\delta^{13}C$ were also explored within 10-cm size intervals by ANOVA and Tukey's HSD to coincide with our approach for comparing condition indices. Finally, we compared liver condition (LSI_{adj}) and spawning condition to diet ($\delta^{13}C$) directly, and on an individual basis, by linear regression (LSI_{adj} vs. $\delta^{13}C$) and student's t-test

($\delta^{13}C$ of potential spawners vs. non-spawners from the northeast).

3. Results

3.1. Growth and biological condition

Length–frequency distributions for NL cod from three different areas sampled between 1996 and 2003 are shown in Fig. 2. Captured cod rarely exceeded 60 cm in Labrador, whereas cod larger than 90 cm were encountered in the other two areas (see Table 1 for maximum sizes). Length-at-age (later ages), for both females and males, was generally highest in northeast cod, followed by south coast and Labrador cod (Fig. 3); Labrador cod did not exceed 8 years of age (and rarely 6 years), compared with cod from the other two areas that attained ages of 14 and 15 years (females and males, respectively). VBGF parameter estimates (L_{inf} and k) varied significantly among areas (by sex) with k (the Brody growth coefficient) being
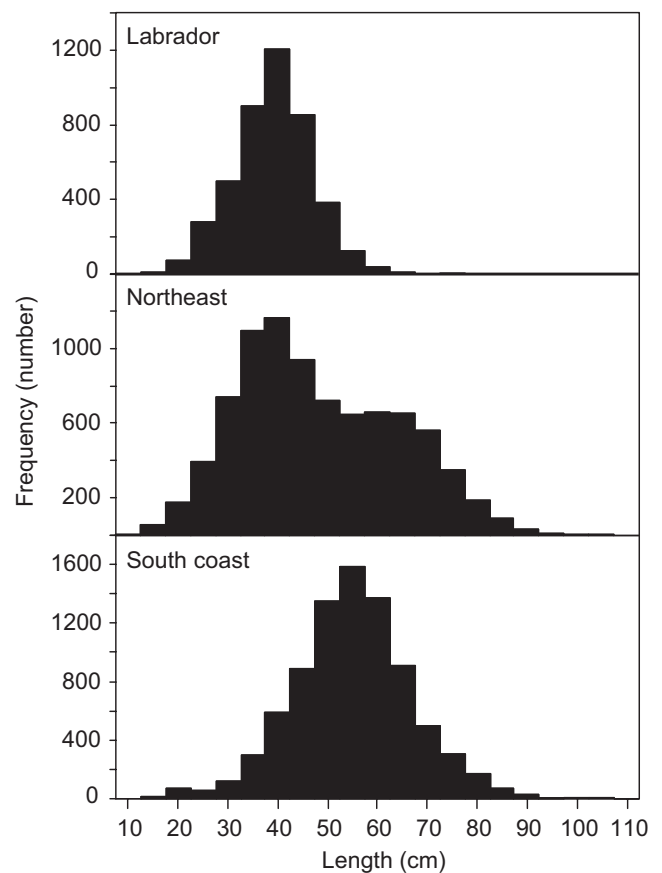

Fig. 2. Length–frequency distributions for Labrador, northeast, and south coast cod (1996–2003).

Table 1
von Bertalanffy growth function parameter estimates (by sex) for three populations of NL cod (1996–2003), and maximum observed size L_{max} and age A_{max} from each population by sex over the same time period

Sex/population	L_{inf} (cm)	k	t_o (yr)	R^2	N	L_{max} (cm)	A_{max} (yr)
Females							
Labrador	84.2	0.175	0.130	0.67	2238	73	8
	(73.1, 95.3)	(0.130, 0.219)	(−0.121, 0.382)				
Northeast	110.7	0.125	0.327	0.90	4553	110	14
	(107.2, 114.2)	(0.117, 0.133)	(0.242, 0.413)				
South coast	98.9	0.146	0.039	0.74	4019	112	14
	(94.5, 103.4)	(0.131, 0.161)	(−0.150, 0.228)				
Males							
Labrador	77.90	0.180	0.021	0.65	2101	64	8
	(67.2, 88.5)	(0.134, 0.231)	(−0.249, 0.291)				
Northeast	95.0	0.154	0.393	0.90	3931	99	15
	(92.6, 97.4)	(0.146, 0.164)	(0.307, 0.479)				
South coast	85.7	0.183	0.181	0.75	4333	104	15
	(83.3, 88.0)	(0.169, 0.197)	(0.234, 0.338)				

Values in brackets are upper and lower 95% confidence limits.
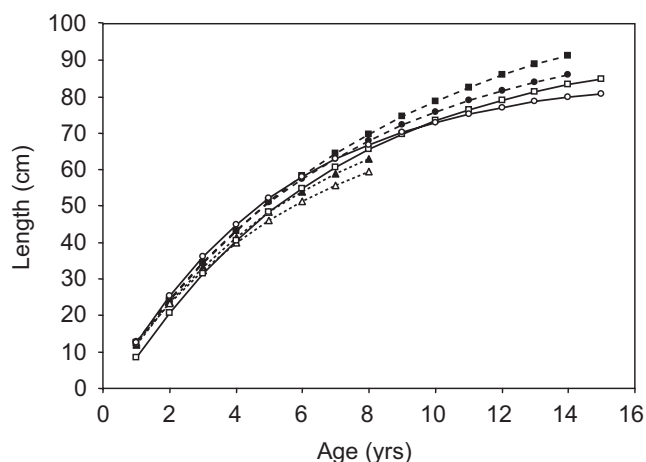

Fig. 3. Length-at-age curves for Labrador (dotted lines, triangles), northeast (dashed lines, squares), and south coast (solid lines, circles) cod by sex (1996–2003); closed symbols are females, open symbols are males. See Table 1 for von Bertalanffy growth function parameter estimates.

generally highest in the south and L_{inf} being highest in the north, when comparing only among south coast and northeast cod (Fig. 4, Table 1); Labrador cod tended to have high growth coefficients and small asymptotic lengths compared to northeast cod.

Mean (± 1SE) values (by 10-cm cod-size interval) for seasonally adjusted Fulton's condition factor K_{adj} of cod from the three sampling areas in 2002/2003 are shown in Fig. 5A. Overall, mean K_{adj} values followed a biphasic pattern with size; in most cases, mean K_{adj} tended to increase to a maximum at 30–39 cm, decrease to a minimum at about 50–69 cm and increase again to a second maximum at about 90–100 cm (where sizes allowed for comparison). There were also significant spatial differences in mean K_{adj}. Specifically, cod from all areas displayed the initial increasing and subsequent decreasing pattern in mean K_{adj} with size. However, Labrador cod had significantly lower maximum mean K_{adj} values than did cod from the other two areas and did not show any signs of recovering body condition in the 50–69 cm range; no cod larger than 60–69 cm were captured in Labrador. In addition, following the first K_{adj} maximum, south coast cod maintained significantly higher mean values than cod from the other two areas until 60–69 cm, after which there were no significant differences in mean K_{adj} (between the two areas where cod were larger than 60–69 cm). Overall, significant differences in K_{adj} among areas (within 10-cm cod-size intervals) existed only in the 30–69 cm range with south coast cod maintaining the highest body condition over these intermediate sizes.

Mean (± 1SE) values (by 10-cm cod-size interval) for seasonally adjusted LSI_{adj} of cod from the three sampling areas in 2002/2003 are presented in Fig. 5(B). Labrador cod displayed consistently low mean LSI_{adj} at all sizes. For the other two areas, LSI_{adj} followed the same general biphasic pattern as described for K_{adj}. That is, minima in mean LSI_{adj} occurred in the 50–69 cm range with maxima occurring first at about 20–39 cm and then again at about 90–100 cm. As was the case with K_{adj},
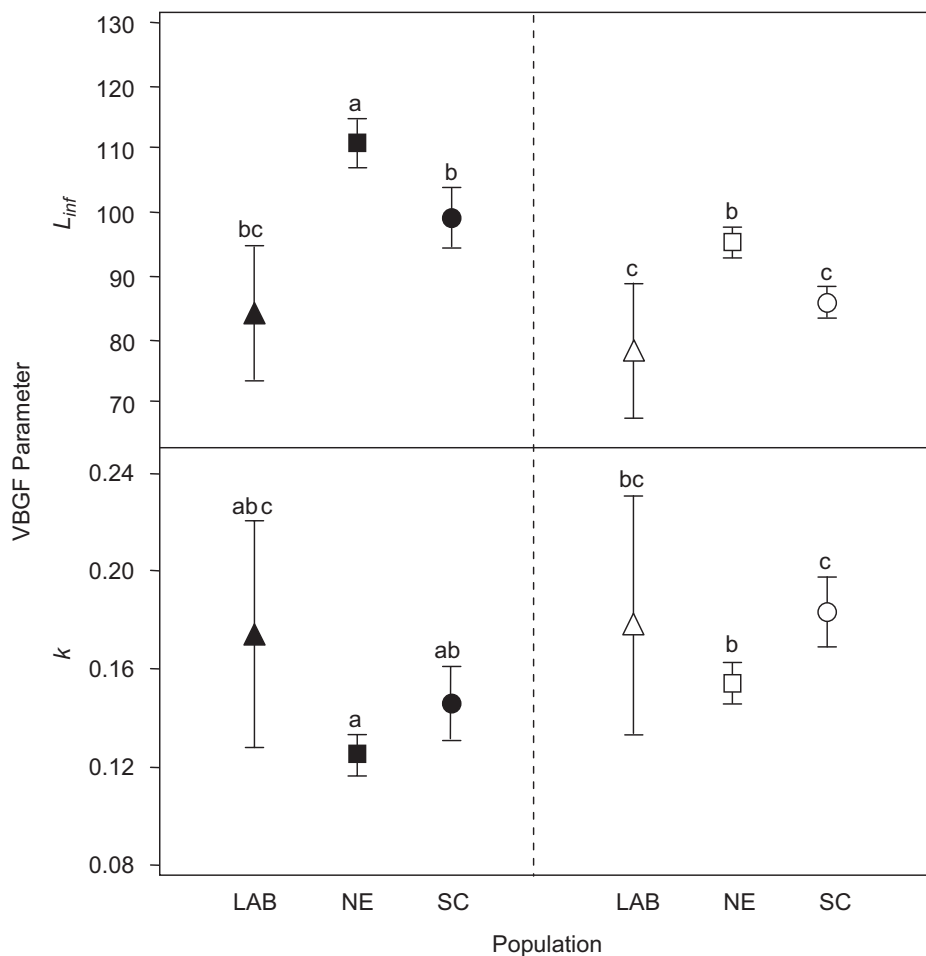
Fig. 4. von Bertalanffy growth function parameters (L_{inf} and k) by area and sex for NL cod (1996–2003). Error bars represent 95% confidence intervals. Estimates with same letter (among both areas and sexes) have overlapping confidence intervals and are not significantly different ($p > 0.05$).

significant differences in mean LSI_{adj} values occurred only in the 30-69 cm size range, over which south coast cod maintained the highest liver condition.

3.2. Age-at-maturity

The mean proportion of maturing female cod (1996–2003) as a function of age is shown for each population in Fig. 6. Mean age at 50% maturity (X_m; see Section 2.6 for equation) occurred a full year earlier in Labrador ($X_m = 4.29[0.11]$, $r = 1.58[0.24]$, $R^2 = 0.89$, $n = 34$) than in northeast ($X_m = 5.31[0.05]$, $r = 1.64[0.12]$, $R^2 = 0.96$, $n = 112$) and south coast cod ($X_m = 5.18[0.04]$, $r = 1.55[0.08]$, $R^2 = 0.98$, $n = 85$, values in square brackets are SE; sample sizes are the product of ages represented and number of years sampled) and about 2 years earlier than historical data for northern cod (age at 50% maturity in northern

cod was about 6 years prior to the cod collapse; Olsen et al., 2004).

3.3. Cod diet and stable carbon isotopes

Stomach content results expressed as PFI and FO of seven major prey items found in the diet of NL cod (1996–2003) are listed in Table 2 (by population, size interval and month) and shown graphically in Fig. 7. Cod diet varied substantially among populations, suggesting major differences in food-web structure from north to south. Labrador cod fed almost exclusively on shrimp (*P. borealis*) while pelagic prey (zooplankton and capelin, *M. villosus*) were much more important in the more southerly populations. Based on PFI values, northeast cod fed almost equally on pelagic (e.g., capelin) and benthic (e.g., shrimp) prey. Capelin feeding, which was highly prominent in south coast cod, was confined
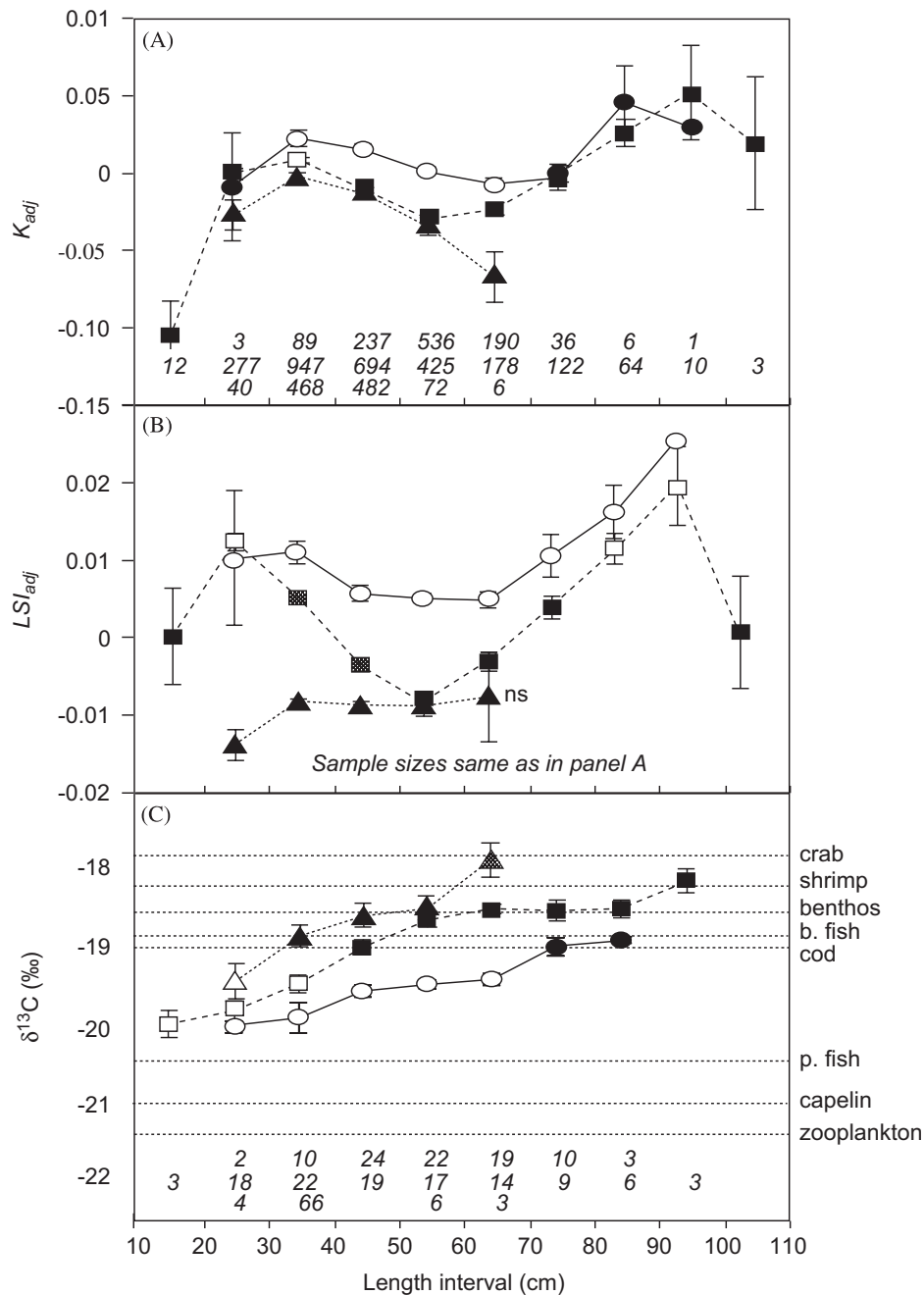
Fig. 5. Mean ($\pm$1SE) values (2002/2003) for: (A) seasonally adjusted Fulton's condition factor (K_{adj}); (B) seasonally adjusted liver index (LSI$_{adj}$); and (C) δ^{13}C signatures by 10-cm length interval for Labrador (triangles, dotted line), northeast (squares, dashed line), and south coast cod (circles, solid line). Within size intervals (and panels), symbols with different shading are significantly different among areas (ANVOVA; $p<0.05$, Tukey's HSD); 'ns' means not significantly different than other two areas within that size interval. Mean δ^{13}C signatures for the seven prey categories are indicated in panel A by horizontal dotted lines; 'other fish' were split into benthic fish (b. fish) and pelagic fish (p. fish, data from Sherwood and Rose, 2005). Numbers at bottom of panels are sample sizes for each 10 cm length interval; rows from top to bottom are for south coast, northeast and Labrador cod.

mostly to the summer (June) when capelin presumably moved into inshore areas.

The results of our stable carbon isotope analysis (2002/2003) for cod are presented in Fig. 5(C), which also shows average δ^{13}C values for all of the seven

major prey categories (prey δ^{13}C data are from Sherwood and Rose, 2005; see this reference also for an analysis of stable nitrogen isotope ratios, δ^{15}N, in NL fish and invertebrates). In general, δ^{13}C values of cod (combined areas) increased significantly
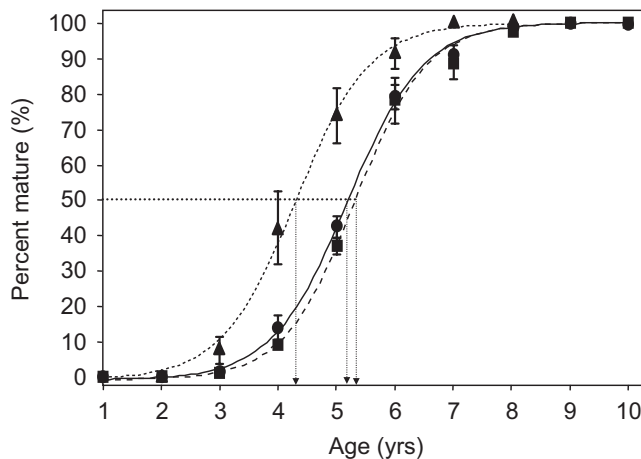
Fig. 6. Mean proportion of maturing females versus age for Atlantic cod from Labrador (dotted line, triangles) and the northeast (dashed line, squares) and south coasts (solid line, circles) of Newfoundland (1996–2003). Error bars represent standard error. Arrows show age at 50% maturity.

with increasing cod length (linear regression [not shown]: $\delta^{13}C = -20.13[0.11] + 0.02[0.00] \times \text{length}$; $R^2 = 0.29$, $F_{1,224} = 89.4$, $p < 0.0001$; values in square brackets are SE). In other words, as they grew, cod from all areas tended to progress from $\delta^{13}C$ signatures indicative of pelagic feeding (e.g., zooplankton, with more negative $\delta^{13}C$ values) to $\delta^{13}C$ signatures indicative of benthic prey (e.g., shrimp, with more positive $\delta^{13}C$ values). In most cases, cod had intermediate $\delta^{13}C$ values (between benthic and pelagic prey values) implying a high degree of diet mixing. In addition to a significant and strong effect of size on cod $\delta^{13}C$ values, there was a significant effect of sampling area (ANCOVA [not shown]: $\delta^{13}C = -19.71[0.11] + 0.02[0.00] \times \text{length} - 0.47[0.09] \times A - 1.04[0.09] \times B$; $R^2 = 0.58$, $F_{2,224} = 78.9$, $p < 0.0001$; values in square brackets are SE) such that cod from Labrador had the most benthic $\delta^{13}C$ values, while cod from the south coast displayed the most pelagic $\delta^{13}C$ signatures (coded variables A and B have the following values: 0 and 0 for Labrador cod; 1 and 0 for northeast cod; and 0 and 1 for south coast cod). Our $\delta^{13}C$ results are consistent with diet observations that indicate a high degree of shrimp (benthic) feeding in the north compared to a higher reliance on more available capelin (pelagic) in the south (Table 2, Rose and O'Driscoll, 2002). Despite an overall significant finding for the effect of area (i.e. previous ANCOVA results), significant spatial differences in cod $\delta^{13}C$ signatures existed only over the size range 30–69 cm where south coast cod had more pelagic

signatures than cod from the other two areas (by 10-cm length intervals; ANOVA, $p < 0.05$, Tukey's HSD; Fig. 5(C)). Otherwise, all cod smaller than 30 cm had diets that were highly pelagic in origin (i.e. zooplanktivorous; small shrimp may also have more pelagic $\delta^{13}C$ signatures, G.D Sherwood, unpublished data), and all cod 70 cm and larger (where sizes allowed for comparison) had mostly benthicly derived diets (either benthivorous or piscivorous).

3.4. Liver and spawning condition vs. $\delta^{13}C$ signatures among individuals

The relationship between liver condition (seasonally adjusted; 2002/2003) and stable carbon isotope signatures in medium-sized cod (30–69 cm; the only size range for which significant among-population differences in feeding and liver index exist) is shown in Fig. 8. Seasonally adjusted liver index LSI_{adj} was significantly related to $\delta^{13}C$ signatures for all cod combined (linear regression: $LSI_{adj} = -19.2[4.1] - 1.0[0.2] \times \delta^{13}C$; $R^2 = 0.16$, $F_{1,114} = 21.8$, $p < 0.0001$), and for south coast cod only (linear regression: $LSI_{adj} = -30.3[6.5] - 1.6[0.3] \times \delta^{13}C$; $R^2 = 0.23$, $F_{1,74} = 22.1$, $p < 0.0001$; values in square brackets are SE); no such significant relationships were found for Labrador and northeast cod, although cod from these areas followed the same downward trend in LSI_{adj} with increasing reliance on benthic prey as inferred by $\delta^{13}C$ signatures. No significant correlation between somatic condition (K_{adj}) and $\delta^{13}C$ signatures was found within any size range/area.

Fig. 9 shows the mean and 95% confidence intervals of $\delta^{13}C$ values for cod sampled in 2004 from Smith Sound that were designated either as potential spawners (ripening) or non-spawners (immature or Spent L). Cod that were deemed to be in spawning condition had significantly more negative (i.e. pelagic) $\delta^{13}C$ signatures (t-test; $t_{28} = -3.645$, $p < 0.001$) (indicating use of pelagic prey; e.g., capelin) than cod that were either undergoing atresia or that were immature. Again, only medium-sized cod (30–69 cm) were used in this comparison as smaller cod are mostly immature and larger cod tended to have more narrowly defined benthic $\delta^{13}C$ signatures (Fig. 5C).

4. Discussion

The objective of the present study was to explore current spatial (among-population/region) variations

Table 2
Mean partial fullness index PFI, and frequency of occurrence FO (underlined) of seven major prey species/taxa found in the diets of NL cod from three separate populations by 10-cm size class (1996–2003)

	Length class (cm)																			
	10–19		20–29		30–39		40–49		50–59		60–69		70–79		80–89		90–99		>100	
Labrador cod (Jan)																				
Mean PFI/FO:																				
Zooplankton	0.16	9.1	0.02	16.8	0.01	11.4	0.00	11.8	0.00	10.0	0.00	0.0								
Benthos	0.04	18.2	0.02	14.2	0.01	7.0	0.00	11.1	0.00	2.0	0.00	0.0								
Shrimp	0.16	27.3	0.40	39.6	0.31	43.8	0.34	48.5	0.39	50.0	0.00	0.0								
Crab	0.00	0.0	0.01	2.0	0.02	1.7	0.00	1.1	0.00	0.0	0.00	0.0								
Capelin	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0								
Other fish	0.05	9.1	0.00	2.0	0.01	7.0	0.00	7.6	0.06	18.0	0.01	100.0								
Cod	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0								
Mean TFI	0.50		0.49		0.45		0.49		0.65		1.27									
N_{tot}	11		197		299		262		50		1									
Labrador cod (June)																				
Mean PFI/FO:																				
Zooplankton	0.00	0.0	0.00	3.6	0.00	3.9	0.01	5.3	0.01	5.0	0.02	8.3								
Benthos	0.20	33.3	0.02	9.1	0.01	8.9	0.01	6.8	0.00	5.8	0.00	8.3								
Shrimp	0.77	11.1	0.71	61.4	0.64	63.9	0.53	66.0	0.50	60.6	0.66	83.3								
Crab	0.13	11.1	0.00	0.5	0.00	1.7	0.01	2.2	0.05	3.3	0.05	16.7								
Capelin	0.00	0.0	0.04	1.0	0.02	0.6	0.01	0.7	0.00	0.8	0.00	0.0								
Other fish	0.46	22.2	0.04	7.6	0.03	8.4	0.05	13.7	0.05	17.0	0.16	33.3								
Cod	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.1	0.00	0.0	0.00	0.0								
Mean TFI	1.44		0.89		0.77		0.69		0.71		0.83									
N_{tot}	9		197		1280		1352		241		12									
Northeast cod (Jan)																				
Mean PFI/FO:																				
Zooplankton	0.32	31.8	0.20	15.0	0.03	14.3	0.01	16.7	0.01	21.0	0.00	9.9	0.00	8.5	0.00	10.2	0.00	7.1	0.00	0.0
Benthos	0.05	13.6	0.02	12.1	0.01	12.9	0.01	20.7	0.01	24.9	0.01	14.8	0.01	14.3	0.05	14.4	0.04	7.1	0.00	0.0
Shrimp	0.14	13.6	0.37	36.0	0.44	34.6	0.12	14.1	0.08	12.2	0.04	9.4	0.02	9.1	0.00	6.8	0.00	14.3	0.00	25.0
Crab	0.00	0.0	0.00	0.0	0.01	1.0	0.00	0.7	0.01	2.0	0.01	1.6	0.01	1.0	0.06	4.2	0.00	0.0	0.00	0.0
Capelin	0.00	0.0	0.31	10.9	0.22	8.8	0.07	2.7	0.03	3.5	0.01	0.6	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Other fish	0.03	4.5	0.07	8.9	0.05	7.1	0.04	4.8	0.04	6.7	0.03	2.9	0.02	5.2	0.00	3.4	0.18	7.1	0.04	75.0
Cod	0.01	4.5	0.00	0.0	0.00	0.3	0.01	0.8	0.00	0.7	0.00	0.2	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Mean TFI	0.50		0.96		0.67		0.23		0.16		0.08		0.04		0.10		0.31		0.04	
N_{tot}	22		247		720		875		686		487		307		118		14		4	
Northeast cod (June)																				
Mean PFI/FO:																				
Zooplankton	0.09	17.4	0.05	11.2	0.00	6.5	0.01	15.8	0.02	23.4	0.04	39.6	0.02	34.0	0.01	28.9	0.00	14.3		

Table 2 (*continued*)

	10–19		20–29		30–39		40–49		50–59		60–69		70–79		80–89		90–99		>100	
	Length class (cm)																			
Benthos	0.13	22.1	0.04	13.9	0.02	13.3	0.02	11.6	0.01	13.2	0.02	10.0	0.01	15.5	0.00	15.6	0.00	28.6		
Shrimp	0.76	23.3	0.43	30.6	0.28	26.3	0.31	35.2	0.21	28.3	0.04	10.9	0.03	12.9	0.01	17.8	0.00	0.0		
Crab	0.00	0.0	0.00	0.9	0.00	0.4	0.00	0.9	0.00	0.4	0.00	0.6	0.01	1.0	0.06	6.7	0.35	28.6		
Capelin	0.05	2.3	0.32	7.0	0.29	10.6	0.35	12.5	0.48	12.1	0.18	8.4	0.35	5.2	0.17	4.4	0.00	0.0		
Other fish	0.00	2.3	0.10	8.2	0.07	12.4	0.05	13.2	0.05	16.6	0.03	19.6	0.03	13.9	0.15	15.6	0.00	0.0		
Cod	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.5	0.00	0.0	1.01	14.3		
Mean TFI	1.02		0.92		0.67		0.74		0.81		0.42		0.41		0.41		1.62			
N_{tot}	86		330		904		577		265		321		194		45		7			
South coast cod (Jan)																				
Mean PFI/FO:																				
Zooplankton			0.09	25.0	0.11	34.3	0.07	20.3	0.09	21.6	0.07	27.9	0.01	21.6	0.00	0.0				
Benthos			0.06	38.9	0.04	29.3	0.03	31.0	0.09	31.3	0.01	20.9	0.03	29.7	0.00	0.0				
Shrimp			0.06	5.6	0.00	1.0	0.01	4.4	0.00	3.9	0.01	4.7	0.00	2.7	0.00	14.3				
Crab			0.00	2.8	0.00	1.0	0.00	0.0	0.02	2.7	0.00	1.2	0.00	2.7	0.00	0.0				
Capelin			0.00	0.0	0.05	6.1	0.04	3.8	0.04	1.9	0.03	1.2	0.00	2.7	0.43	28.6				
Other fish			0.03	16.7	0.07	22.2	0.08	35.4	0.05	31.7	0.07	24.4	0.02	8.1	0.00	0.0				
Cod			0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0				
Mean TFI			0.71		0.58		0.69		0.80		0.59		0.52		0.46					
N_{tot}			36		97		156		252		74		29		3					
South coast cod (June)																				
Mean PFI/FO:																				
Zooplankton	0.58	82.4	0.31	49.2	0.35	40.8	0.49	33.2	0.22	25.5	0.15	24.9	0.11	17.0	0.08	12.0	0.00	14.3	0.00	0.0
Benthos	0.01	5.9	0.03	9.8	0.08	18.0	0.05	15.5	0.03	13.2	0.02	11.9	0.03	14.0	0.00	0.0	0.00	14.3	0.00	0.0
Shrimp	0.00	0.0	0.07	4.9	0.19	23.2	0.15	22.3	0.16	23.7	0.09	23.7	0.03	20.0	0.00	0.0	0.01	28.6	0.00	0.0
Crab	0.00	0.0	0.00	1.6	0.00	2.4	0.01	3.1	0.03	5.9	0.06	11.3	0.07	10.0	0.00	0.0	0.08	14.3	0.00	0.0
Capelin	0.00	0.0	0.21	11.5	0.76	24.6	0.58	33.9	0.50	36.4	0.43	42.1	0.38	42.0	0.63	64.0	0.03	28.6	0.16	50.0
Other fish	0.00	0.0	0.02	8.2	0.25	22.3	0.11	23.5	0.11	23.4	0.11	25.2	0.19	28.0	0.04	12.0	1.36	57.1	0.00	25.0
Cod	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.2	0.00	0.2	0.00	0.9	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Mean TFI	0.93		1.10		1.47		1.73		1.78		1.43		1.17		1.32		1.58		0.28	
N_{tot}	17		61		211		587		577		337		100		25		7		4	

Total fullness index *TFI* as well as total number of stomachs analysed (N_{tot}) by size class/population is also shown.
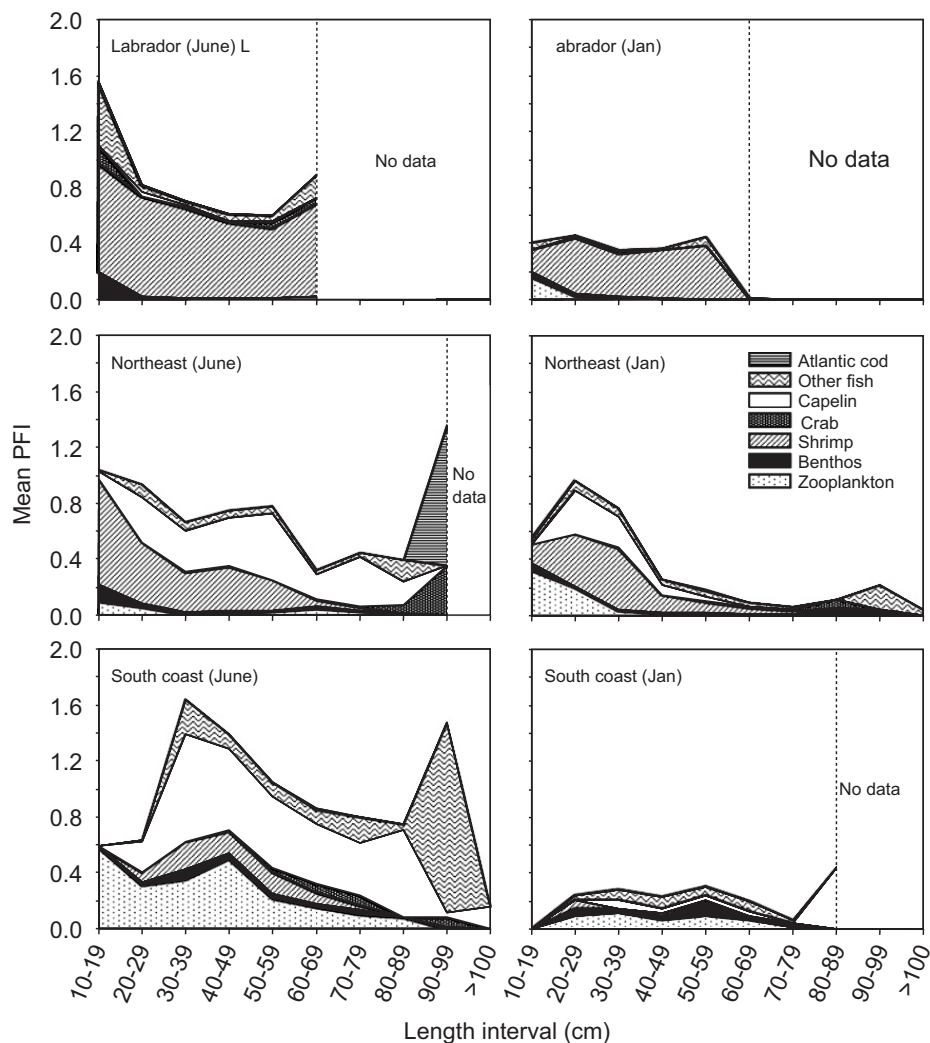
Fig. 7. Stacked area graph of mean partial fullness index (mean PFI) by 10 cm length class and season (January and June) for seven major prey species/taxa (see legend) of Labrador, northeast and south coast cod (1996–2003).
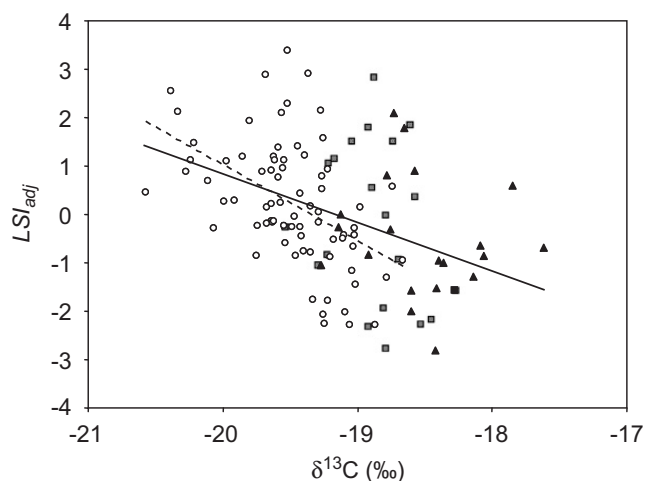
Fig. 8. Seasonally adjusted liver index (LSI$_{adj}$) as a function of δ^{13}C signatures in medium-sized (30–69 cm) Labrador (closed triangles), northeast (shaded squares) and south coast (open circles) cod (2002/2003). Lines represent significant linear regressions ($p < 0.0001$) for cod from all areas combined (solid line) and south coast cod (dashed line).

Fig. 9. Mean δ^{13}C signatures of medium-sized (30–69 cm) female cod from the northeast (2004) with ovaries classified either as 'ripening' (potential spawners) or 'immature' and 'Spent L' (non-spawners). Error bars represent 95% confidence intervals; values in brackets are sample sizes.

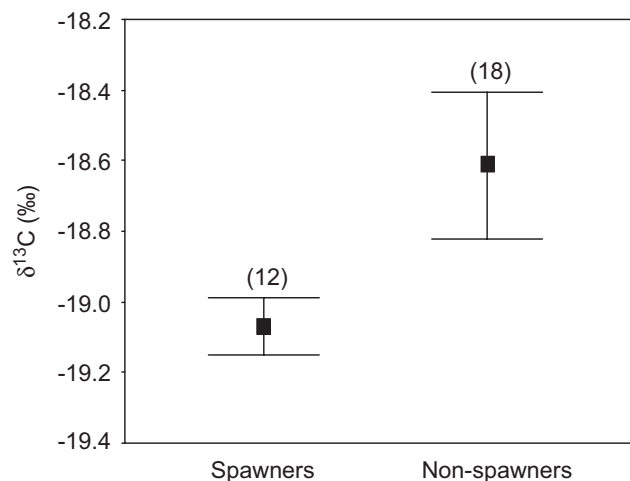in growth, condition and reproductive capacity of NL cod and relate these to potential differences in feeding (assumed to reflect prevailing food web conditions). The rationale for our approach was to provide a basis (in future studies) for understanding and predicting the effects of climate change/variability on NL cod production and recovery potential via intermediary changes in food-web structure (e.g., Rose, 2005) and function of the NL continental shelf ecosystem. Significant differences were observed among NL cod populations with respect to some or all of the following properties: biological condition (Figs. 5(B) and (C)); age-at-maturity (Fig. 6) and diet ontogeny as evidenced by differences in stomach contents and stable carbon isotope signatures (Figs. 7 and 5(A), respectively). What follows is a detailed discussion of how differences in energetics (specifically, condition indices and spawning potential) may be mechanistically linked to variations in food-web structure and feeding in NL cod and how this information may be used in future monitoring of food-web conditions of the Northwest Atlantic.

4.1. The importance of a pelagic diet for medium-sized NL cod

The most consistent finding of this study, with respect to a correspondence between biological condition and diet endpoints in cod, was our observation that among-population differences in these parameters manifest significantly only over medium size ranges ($\sim$30–69 cm), the size range that is represented in all populations and wherein gape size would allow for varied diet (Scharf et al., 2000). Our diet analysis (Table 1, Fig. 7) suggests that the most important prey species/taxa in this size range are capelin and zooplankton in south coast cod shrimp and capelin in northeast cod, and shrimp almost exclusively in Labrador cod. Thus, there are only three major prey groups that appear to be contributing to the productivity of this important size class of NL cod. From a broad comparative point of view, low production potential in NL cod (poor condition, small maximum size and age, and early age-at-maturity) appears to be associated with shrimp feeding (i.e. for Labrador cod); high production potential, on the other hand, appears to be most directly related to the presence of capelin in the diet (i.e. as in south coast cod).

Further evidence for an association between diet and condition came from two complementary approaches where spawning potential and liver condition were compared directly to past feeding histories of medium-sized NL cod (via δ^{13}C signatures). The strength of this stable isotope approach is that correlations could be made on an individual basis, thereby greatly enhancing effective sample size and statistical power. Our previous analyses of stable isotope signatures of NL fish and invertebrates revealed major differences in δ^{13}C among shrimp (mostly benthic consumers), on the one hand, and zooplankton and capelin (both pelagic consumers) on the other (Sherwood and Rose, 2005) (see Fig. 5(C) for a representation of some of this data). Thus, highly benthic δ^{13}C signatures in the diet of medium-sized NL cod can be interpreted as evidence of preying heavily on shrimp, while pelagic δ^{13}C values in NL cod can be construed as evidence for past feeding on zooplankton, capelin or both; although pelagic δ^{13}C signatures in larger cod are likely to be more indicative of capelin feeding than zooplankton feeding (Fig. 7). Based on this information, we conclude that feeding on capelin (a pelagic prey option) leads to a higher liver index (Fig. 8), which is a good indication of high excess energy reserves (Yaragina and Marshall, 2000) and, all other factors being equal, a greater likelihood of spawning (Fig. 9) than would be possible if feeding only on shrimp (the only major benthic prey option over medium sizes). These results suggest that skipped spawning in cod (Rideout et al., 2005) may have a food-web component related to long-term variations in ocean conditions.

4.2. The capelin–cod connection

Our analyses support the hypothesis that capelin is a key species in the overall productivity and recovery potential of NL cod (Rose and O'Driscoll, 2002). Capelin have long been thought to be a preferred prey of cod in the large boreal ecosystems of the North Atlantic from the Barents Sea to Icelandic and Newfoundland waters (e.g., Hjort, 1914; Templeman, 1948; Gerasimova and Kiseleva, 1998). Numerous studies on the large cod stocks in these regions have reported positive relationships between capelin availability and cod growth and/or condition (Krohn et al., 1997; Vilhjálmsson, 1997; Yaragina and Marshall, 2000; Rose and O'Driscoll, 2002). The results of the present study agree with the growing recognition in the literature that 'capelin are good for cod' (Rose and O'Driscoll,

2002). However, our study takes this notion one step further by identifying the developmental stage at which capelin are most important for cod (i.e. medium sizes) and, by corollary, the sizes of cod most likely to be affected by changes in capelin availability that may arise as a result of changes in ocean and/or food web conditions in the Northwest Atlantic.

It is important to point out that our findings for a cod–capelin link should only apply to cod populations where capelin feeding is of historical importance (i.e. boreal cold-water populations in NL and Icelandic-Greenland waters and the Barents Sea). In more southerly stocks, other pelagic prey species, such as sand lance or herring, may be of greater importance. In addition, Atlantic-wide variations in cod condition (and related productivity) are almost certainly related to differences in temperature regimes, with cod from warmer waters (where capelin are absent) displaying the highest condition factors (Rätz and Lloret, 2003). Nevertheless, in the cold-water stocks of NL, the range of bottom temperatures is comparatively small (Rätz and Lloret, 2003), and therefore unlikely to effect major changes in cod biology. In keeping with this notion, among-year variations in water temperature were shown to play only a minor role in determining NL cod growth, compared to the effect of variations in prey availability (as measured by capelin biomass), particularly for Labrador and offshore 3K (northeast) cod (Krohn et al., 1997).

It is interesting to speculate on why capelin are so good for NL cod. Most arguments rely on prey quality issues, particularly, the importance of lipids (e.g., Yaragina and Marshall, 2000; Rose and O'Driscoll, 2002). Not all prey provide the same amount of energy per unit mass consumed. Proximate composition (percent lipid, protein, ash and water) and related energy density ($kJ\,g^{-1}$) can vary dramatically among various types of prey (Lawson et al., 1998); in general, prey species with high lipid content (e.g., capelin) have the highest energy densities, whereas prey rich in proteins (e.g., shrimp) have the lowest. Further, diets rich in high-energy lipids may be important for fueling various energetic costs in fish, including gonadal maturation (Kjesbu et al., 1991), fasting (Lambert and Dutil, 1997) and long-distance migrations (Rose and O'Driscoll, 2002). All else being equal, lipid-rich prey like capelin should represent one of the highest quality diet choices for an actively foraging predator like cod, and whenever available, cod should benefit

from capelin feeding. Consistent with this expectation, results of the present study show that capelin feeding (inferred via δ^{13}C) is correlated with high body and liver condition and increased spawning potential. What this prey quality argument does not explain, however, is our finding that high-lipid prey, like capelin, cannot account for the difference between high and low biological condition in cod of *all* sizes. Specifically, both condition indices (K and LSI, seasonally adjusted) tended to decline with size over the size range where capelin feeding was most prominent in cod (i.e. 30–69 cm; Figs. 5(B), and (C)), and recover only when diet shifted to mostly benthic prey types, which are likely to represent a lower quality food source (Lawson et al., 1998). These patterns suggest that there is more to prey choice in cod than strict prey quality arguments. One possibility is that in the absence of high capelin availability (as may be the case even for south coast cod), high returns in terms of high lipid content diminish as the cost of foraging increases with increasing body size. In other words, it may be more expensive for large cod to continue searching for and attacking a rare and relatively small, albeit high energy density prey item (i.e. capelin), than it would be for them to switch to larger prey of lower quality (e.g., other demersal fish species, including cannibalism). The growth-limiting cost of feeding on too-small prey (in terms of high burst activity costs) has been demonstrated in other fish species (Sherwood et al., 2002).

5. Conclusions

There is a growing consensus that capelin in the Northwest Atlantic have undergone major changes in abundance and distribution since the late 1980s (Frank et al., 1996; reviewed by Rose, 2005). Given the importance of capelin to the diet of NL cod, demonstrated in this study, we propose that monitoring cod diet may be a powerful way to track future changes in the status of capelin in NL waters. Using far-ranging marine predators as a means to track changes in ocean food-web conditions is not a new idea. Seabirds have been used for this exact purpose (e.g., Davoren and Montevecchi, 2003). To simplify the task even further, we suggest that monitoring δ^{13}C signatures of medium-sized cod over a number of sentinel populations around NL would be a powerful means of tracking changes in capelin distribution and relative abundance. Beyond this, more work needs to be done on what

drives changes in capelin status in the Northwest Atlantic, an area of research that currently has very little input.

On a final note, we suggest that the results of the present study add an alternate explanation for recent (post-moratorium) changes in cod biology in northern populations (i.e. Labrador). In particular, age-at-maturity in these cod is about 2 years earlier than it was prior to stock collapse. This change has been argued to be an example of 'rapid evolution' induced by heavy fishing pressure (Olsen et al., 2004). Alternatively, it may be argued that changes in cod biology (i.e. age-at-maturity) coincided with changes in food-web structure (i.e. declines in capelin availability). Results from the present study show that early maturation also coincides with poor energetic status (i.e. low condition) and low quality diets (among populations). Thus, as opposed to being an evolved trait, early maturation in Labrador cod may be a plastic response to poor feeding opportunities and energetic stress (i.e. environmentally induced stunting; Heath and Roff, 1987). Further, stunted fish tend to mature earlier (Trudel et al., 2001), and our growth results (Figs. 3 and 4) suggest that Labrador cod may indeed be stunted. Additional support for a phenotypic plasticity argument comes from the fact that all populations around NL underwent major stock declines (from heavy fishing pressure) in the late 1980s/early 1990s, yet age-at-maturity still varies quite substantially among populations. We suggest that the potential for variations in food-web structure to induce changes in maturation schedules (via changes in energetic status) deserves more careful attention.

Overall, the results of the present study support the notion that variations in food-web structure (as evidenced by cod diet) can have major consequences on the energetic well-being and reproductive capacity of NL cod and, as such, should not be left out of models of stock recovery and future productivity. We argue that major rebuilding of cod stocks in NL will require a return to a system that supports high capelin availability to cod, which in turn should foster improved condition and spawning potential.

Acknowledgements

References

Bowering, W.R., Lilly, G.R., 1992. Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland (Northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). Netherlands Journal of Sea Research 29, 211–222.

Carscadden, J.E., Nakashima, B.S., 1997. Abundance and changes in distribution, biology, and behaviour of capelin in response to cooler waters of the 1990s. In: Forage Fishes in Marine Ecosystems, Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Alaska Sea Grant College Program Report, 97-01, University of Alaska, Fairbanks, pp. 457–468.

Carscadden, J.E., Frank, K.T., Leggett, W.C., 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences 58, 73–85.

Davoren, G.K., Montevecchi, W.A., 2003. Signals from seabirds indicate changing biology of capelin stocks. Marine Ecology Progress Series 258, 253–261.

DFO, 2004. Northern (2J+3KL) cod. Canadian Science Advisory Secretariat, Stock Status Report 2004/011.

Frank, K.T., Carscadden, J.E., Simon, J.E., 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Canadian Journal of Fisheries and Aquatic Sciences 53, 1473–1486.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308, 1621–1623.

Garrison, L.P., 2000. Spatial and dietary overlap in the Georges Bank groundfish community. Canadian Journal of Fisheries and Aquatic Sciences 57, 1679–1691.

Gerasimova, O.V., Kiseleva, V.M., 1998. Long-term variations in cod distribution and feeding on the Newfoundland shelf in spring and summer. NAFO Scientific Council Studies 31, 79–110.

Heath, D., Roff, D.A., 1987. Test of genetic differentiation in growth of stunted and nonstunted populations of yellow perch and pumpkinseed. Transactions of the American Fisheries Society 116, 98–102.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. ICES Rapports et Procés-Verbaux des Réunions 20, 1–228.

Kjesbu, O.S., Klungsøyr, J., Kryvi, H., Witthames, P.R., Walker, M.G., 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body

composition. Canadian Journal of Fisheries and Aquatic Sciences 48, 2333–2343.

Krohn, M., Reidy, S., Kerr, S., 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54 (Suppl. 1), 113–121.

Lambert, Y., Dutil, J.-D., 1997. Can simple condition indices be used to monitor and quantify seasonal changes in energy reserves of Atlantic cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Sciences 54 (Suppl. 1), 104–112.

Lawson, J.W., Magalhaes, A.M., Miller, E.H., 1998. Important prey species of marine vertebrate predators of the northwest Atlantic: proximate composition and energy density. Marine Ecology Progress Series 164, 13–20.

Lear, W.H., Parsons, L.S., 1993. History and management of the fishery for northern cod in NAFO divisions 2J, 3K and 3L. In: Parsons, L., Lear, W. (Eds.), Perspectives on Canadian Marine Fisheries Management, Canadian Bulletin of Fisheries and Aquatic Sciences, vol. 226, pp. 55–890.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Emande, B., Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428, 932–935.

Osborne, D.R., 2005. Canadian research report for 2004: part 1. Newfoundland and Labrador region. NAFO SCS Doc. 05/12.

Quinn II, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Rätz, H.-J., Lloret, J., 2003. Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. Fisheries Research 60, 369–380.

Rideout, R.M., Burton, M.P.M., Rose, G.A., 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod from Smith Sound, Newfoundland. Journal of Fish Biology 57, 1429–1440.

Rideout, R.M., Rose, G.A., Burton, M.P.M., 2005. Skipped spawning in female iteroparous fishes. Fish and Fisheries 6, 50–72.

Rose, G.A., 2005. On distributional responses of North Atlantic fish to climate change. ICES Journal of Marine Science 62, 1360–1374.

Rose, G.A., O'Driscoll, R.L., 2002. Capelin are good for cod: can the northern stock rebuild without them? ICES Journal of Marine Science 59, 1018–1026.

Rose, G.A., deYoung, B., Kulka, D.W., Goddard, S.V., Fletcher, G.L., 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences 57, 644–663.

Roughgarden, J., Smith, F., 1996. Why fisheries collapse and what to do about it. Proceedings of the National Academy of Sciences 93, 5078–5083.

Ruzzante, D.E., Taggart, C.T., Doyle, R.W., Cook, D., 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. Conservation Genetics 2, 257–269.

Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208, 229–248.

Sherwood, G.D., Rose, G.A., 2005. Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf ecosystem. Estuarine, Coastal and Shelf Science 63, 537–549.

Sherwood, G.D., Pazzia, I., Moeser, A., Hontela, A., Rasmussen, J.B., 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Canadian Journal of Fisheries and Aquatic Sciences 59, 229–241.

Templeman, W., 1948. The life history of the capelin (*Mallotus villosus*) in Newfoundland waters. Research Bulletin No. 17, Newfoundland Government Laboratory, St. John's.

Templeman, W., Hodder, V.M., Wells, R., 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. ICNAF Research Bulletin 13, 53–65.

Trudel, M., Tremblay, A., Schetagne, R., Rasmussen, J.B., 2001. Why are dwarf fish so small? An energetic analysis of polymorphism in lake whitefish (*Coregonus clupeaformis*). Canadian Journal of Fisheries and Aquatic Sciences 58, 394–405.

Vilhjálmsson, H., 1997. Interactions between capelin (*Mallotus villosus*) and other species and the significance of such interactions for the management and harvesting of marine ecosystems in the northern North Atlantic. Rit Fiskideildar 15, 32–63.

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Human Biology 10, 181–213.

Yaragina, N.A., Marshall, C.T., 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES Journal of Marine Science 57, 42–55.