Ontogenetic and temporal variability in the fat content and fatty acid composition of Atlantic herring (*Clupea harengus*) from the Bay of Fundy, Canada

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Abstract—Atlantic herring (*Clupea harengus*) is an ecologically and economically valuable species in many food webs, yet surprisingly little is known about the variation in the nutritional quality of these fish. Atlantic herring collected from 2005 through 2008 from the Bay of Fundy, Canada, were examined for variability in their nutritional quality by using total lipid content (n=889) and fatty acid composition (n=551) as proxies for nutritional value. A significant positive relationship was found between fish length and total lipid content. Atlantic herring also had significantly different fatty acid signatures by age. Fish from 2005 had significantly lower total lipid content than fish from 2006 through 2008, and all years had significantly different fatty acid signatures. Summer fish were significantly fatter than winter fish and had significantly different fatty acid signatures. For all comparisons (ontogenetic, annual, and seasonal) percent concentrations of omega-3, -6, and long-chain monounsaturated fatty acids were the most important for distinguishing between the fatty acid signatures of fish. This study underscores the importance of quantifying variation in prey quality synoptically with prey quantity in food webs over ontogenetic and temporal scales when evaluating the effect of prey nutritional quality on predators and on modeling trophic dynamics.

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Variation in prey abundance has been documented in a wide range of food webs (e.g., Colwell and Landrum, 1993; Forsman and Lindell, 1997; Greenstreet et al., 1998; Melvin and Stephenson, 2007); however, variation in the nutritional quality of those prey has not been well investigated. In most studies to date, the nutritional quality of prey is assumed to be constant over space and time (e.g., Chase, 2002; Krebs et al., 2003, Womble and Sigler, 2006; Woo et al., 2008), despite the fact that species can exhibit considerable variation in their value as prey items (e.g., Iverson et al., 2002; Diamond and Devlin, 2003; Jensen et al., 2007; Huynh and Kitts, 2009). Despite the ecological and economic importance of Atlantic herring (*Clupea harengus*), robust temporal and ontogenetic data quantifying the variation in the nutritional value of these fish do not exist. Here we show, using Atlantic herring as a model prey species, that considerable temporal and ontogenetic variation does exist in the nutritional value of a given prey item, underscoring the importance of collecting data on both the quantity and quality of prey when evaluating its impact on an ecosystem level.

Atlantic herring are a major portion of the diet of many upper trophic level predators in the western North Atlantic (wNA), such as seals, porpoises, dolphins, whales, predatory fish, sharks, and seabirds (Katona et al., 1993, and are also the target of several major fisheries (purse seine, weir) for human consumption. Herring feed mainly on zooplankton (De Silva, 1973) and thus serve as an important connection between lower and upper trophic levels in food webs and can be considered a keystone prey species in this ecosystem (Overholtz and Link, 2007). Herring in the wNA generally spawn in the fall (Boyar et al., 1973; Colton et al., 1979), eggs incubate for about 15 days (Messieh et al., 1985) and then enter a six-month pelagic larval phase (Sinclair and Tremblay, 1984). Rapid juvenile growth is observed for 1–2 years (Anthony, 1972), and maturity occurs at around age 3 (O'Brien et al., 1993). Historically the biomass of these stocks has undergone fluctuations in the wNA (Anthony and Waring, 1980; Overholtz and Friedland, 2002), but little is known about changes in Atlantic herring nutritional quality.

The substantial effort required to collect robust spatial and temporal data has created prey quality data sets that do not adequately capture the variability present in the prey

field that was sampled. For example, the few studies that exist to date on the nutritional value of Atlantic herring have been conducted with limited types of analyses or comprise small temporal and spatial ranges (e.g., Torcher et al., 1985; Bradford, 1993; Budge et al., 2002). Jensen et al. (2007) demonstrated that Baltic herring do exhibit significant variation in their fatty acid composition; however, comparable data are not available through most of the range of these fish. In fact, the most recent comprehensive examination of the lipid profiles of herring from the Bay of Fundy was conducted by Stoddard[1] over 40 years ago. Considering the ecological importance of herring in the Bay of Fundy, it is surprising that so little is currently known about the nutritional value of this species.

The high abundance of herring in the Bay of Fundy system combined with the role of this species as a main prey item creates a perfect model in which to evaluate variation in prey quality. We used total lipid content and lipid composition (specifically, fatty acid profiles) as indices of prey quality for two reasons: 1) the lipids of a fish can be used as indicators of its nutritional value and overall body condition (Sargent et al., 1988); and 2) lipids provide twice the energy per unit of mass when metabolized than do proteins and carbohydrates (Hadley, 1985) and therefore are the main determinants of the caloric value of lipid-rich fish such as Atlantic herring. Documenting the individual fatty acid components that comprise Atlantic herring lipids also has the potential to provide information about the nutritional value of a given fish because certain fatty acids have important and specific physiological (e.g., the familiar omega-3 and omega-6 molecules; Pond, 1998, Szlinder-Richert et al., 2010.) and energetic (long-chain saturates; Hadley, 1985) roles. Fatty acid (chemical profile) data can also be used as trophic markers to indicate shifts in diet (Bishop et al., 1983; Budge et al., 2002; Dalsgaard et al., 2003; Budge et al., 2006), however these types of trophic studies require an extensive library of data on the fatty acid composition of all members of an ecosystem, which is not currently available for the Bay of Fundy. This study is a first step in creating such a prey library because the main objective is to determine the total lipid content and fatty acid composition of different sizes of Atlantic herring collected between 2005 and 2008 across ontogenetic, annual, and seasonal scales.

Materials and methods

Sample collection

Atlantic herring samples were provided by local fishermen from stationary weirs or purse-seine nets in the Bay of Fundy, New Brunswick, Canada, from 2005 through 2008. During summer (June–September), fish were collected weekly, whereas during winter (October–May) fish were collected more opportunistically. Owing to sampling constraints, fish from only a single winter season were sampled (2006–07). Spring and fall fish were not collected because the largest differences in nutritional value were expected to occur between the seasons that were the most different in regards to climate and ocean productivity (summer and winter). All fish from each sampling period (typically 10–30 fish) were weighed to the nearest milligram, and their fork length was recorded to the nearest millimeter. After the initial measurements, 10 fish from each sample were selected to encompass the entire size range of the individuals collected in each sampling period, and each fish was individually homogenized in a food processor (KitchenAid®, St. Joseph, MI). Generally, the fish that were collected were sexually immature although sexually mature individuals were processed when available. Subsamples of the homogenate from each fish were sealed in cryovials under nitrogen gas and frozen at –20°C. Vials were kept extremely full to limit risk of oxidation, and all samples were processed within six months of collection (Budge et al., 2002; 2006).

Analysis of total lipid content and fatty acid composition

Total lipids were extracted from Atlantic herring samples using a modified Folch et al. (1957) chloroform/methanol extraction as described in Budge et al. (2002) and Koopman (2007) and are reported as a percentage of wet tissue weight. For gas chromatography (GC) analysis, fatty acid butyl esters (FABE) were prepared from total lipid extracts. Fatty acids were separated and analyzed by GC by using a Varian capillary (3800) gas choromatograph (Varian Inc, Division of Agilent, Santa Clara, CA) with a flame ionization detector (FID) in a fused silica column (30 mm length×0.25 mm inner diameter) (Zebron FFAP; Phenomenex, Inc., Torrance, CA). Helium was used as the carrier gas and the gas line was equipped with an oxygen and water scrubber. The following temperature program was used: start at 65°C for 2 min, hold at 165°C for 0.40 min after ramping at 20°C/min, hold at 215°C for 6.6 min after ramping at 2°C/min, and hold at 250°C for 5 min after ramping at 5°C/min. Up to 80 different fatty acids were identified by following the methods of Iverson et al. (1997; 2002) of which the molecular identities were confirmed by gas chromatography and mass spectrometry (S. Budge, personal commun.[2]) by using standard chemicals run on both machines. Each fatty acid was described by using the nomenclature of *A:Bn-X*, where *A* is the number of carbon atoms, *B* is the number of double bonds, and *X* is the position of the double bond closest to the terminal methyl group. Peak identification was confirmed in each run, and results were integrated with Galaxie GC software (vers. 1.8.501.1, Varian, Inc., Palo Alto, CA).

[1] Stoddard, J. H. 1967. Studies of the condition (fatness) of herring. Fish. Res. Board Can. Manuscript No. 1042, 15 p.

[2] Budge, Suzanne. 2009. Canadian Institute of Fisheries Technology, Dalhousie University, Halifax, Nova Scotia, Canada B3J 2X4.

Statistical analysis of total lipid content

Statistical analysis was conducted by using SPSS, vers. 16.0 (SPSS, Inc., Chicago, IL) and Plymouth Routines in Multivariate Ecological Research (PRIMER 6, Primer-E, Ltd., Ivybridge, UK) statistical software and a significance level of 0.05 for each test performed. Error was reported as standard deviation. Analysis of covariance (ANCOVA) tests were evaluated for equality of variance by using Levene's test. Kolmogorov-Smirnov and Shapiro-Wilk normality tests were conducted on raw total percent lipid data. For comparisons of age classes, the age of each fish was estimated from length-at-age curves published in the literature (Penttila et al., 1989). Corrected Akaike information criteria (AIC_c) scores were calculated for linear, quadratic, and cubic distributions to determine the best fit for the relationship between total lipid content and fish size (Burnham and Anderson, 2002), and the remaining analyses were conducted by using the model of best fit. The normalized relative likelihood of any model to best represent the data is its Akaike weight, w_i, and lower w_i values indicate better model fits. The AIC model w_i statistics heavily favored the linear model (linear: w_i=0; quadratic: w_i=0.46; cubic: w_i=0.54), and therefore the linear model was used in subsequent regression analyses.

The relationship between total percent lipid (wet weight) and fish fork length over the entire size range of fish collected was examined with linear regression. Because size had a significant effect on total percent lipid (see *Results* section), the remaining analyses were conducted by using ANCOVA to account for this covariation. The annual, seasonal, and monthly variation in total percent lipid content of Atlantic herring was examined by ANCOVA. Only samples from 2006–07 were included in seasonal analyses because the winter of 2006–07 was the only winter in which samples were collected.

Statistical analysis of fatty acid composition

Fatty acid signatures of individual fish were compared by using PRIMER, vers. 6 software (Clarke, 1993; Clarke and Warwick, 2001; Clarke and Gorley, 2006). Of the suite of 67 fatty acids present in herring, a subset of 23 were selected and analyzed to determine whether patterns existed in fatty acid signatures in herring of different sizes, years, and seasons. These fatty acids were 14:0, 16:0, 16:1*n*-11, 16:1*n*-9, 16:1*n*-7, 16:1*n*-5, 18:1*n*-11, 18:1*n*-9, 18:2*n*-6, 18:3*n*-3, 18:4*n*-3, 20:1*n*-11, 20:1*n*-9, 20:1*n*-7, 20:4*n*-6, 20:4*n*-3, 20:5*n*-3, 22:1*n*-11, 22:1*n*-9, 22:1*n*-7, 22:5*n*-3, 22:6*n*-3, and 24:1*n*-9. These fatty acids were chosen if they were present in at least 95% of the individual fish analyzed. If a particular fatty acid was not detected in an individual, the concentration of that fatty acid was changed from zero to 0.005% because it was below the minimum detectable level (0.01%), but it was not so small that it would result in extreme outliers (Iverson et al., 2002). Individual fatty acids were standardized before analysis by dividing the value of each fatty acid in each sample by the standard deviation of that fatty acid in all samples and resemblance matrices were created on the basis of Bray-Curtis similarity.

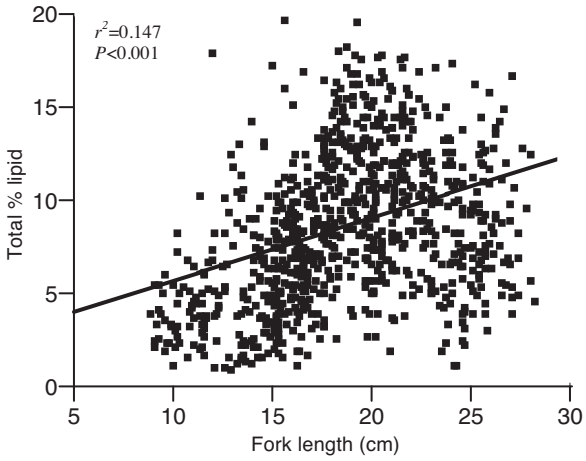

Figure 1

Bivariate scatterplot of total percent lipid by fork length for Atlantic herring (*Clupea harengus*, n=889). Although the linear r^2 value is low, the relationship is highly significant. The low r^2 value may be representative of the highly variable nature of the nutritional quality of herring in the Bay of Fundy ecosystem.

Nonmetric multidimensional scaling (MDS, 25 restarts, Kruskal scheme 1) analyses were conducted on the fatty acid profiles of all samples. MDS stress values range from 0 to 1. Low stress values indicate high confidence in the model, and stress values less than 0.2 were assumed to adequately represent the relationships of the samples in the model (Clark and Warwick, 2001). Analyses of similarities (ANOSIM, one-way, max. permutations=999) were conducted on all samples to evaluate the effect of fish age, year, and season on fatty acid signatures. Because similar patterns were observed when fish were separated first by age and then by year or season, all fish were pooled to examine annual and seasonal variability in fatty acid signatures to allow for higher power in the analyses. ANOSIM global r values range from 0 to 1, and higher global r values are more significant. One-way similarity percentages analysis (SIMPER, one-way, based on Bray-Curtis similarity, cut-off percentage=90) was conducted on all samples if the analysis of similarities was significant, to determine the fatty acids that contributed the most to the differences observed between groups.

Results

Total lipid content

A total of 889 individual fish collected between 2005 and 2008 were analyzed for trends in total lipid content (percentage of wet weight; Table 1). The linear regression of

Table 1

Number of fish sampled (total fish), and size range of Atlantic herring (*Clupea harengus*) analyzed for differences in total lipid content by year, season, and age class.

Year	Total fish	Size (cm)	Summer	Winter	Age 1	Age 2	Age 3	Age 4+
2005–2008	889	8.8–28.2	731	158	87	469	188	145
2005	113	9.0–25.0	113	0	2	66	37	8
2006	330	8.8–27.3	292	38	56	134	84	56
2007	334	10.7–28.2	214	120	26	206	37	65
2008	112	10.8–28.0	112	0	3	63	30	16

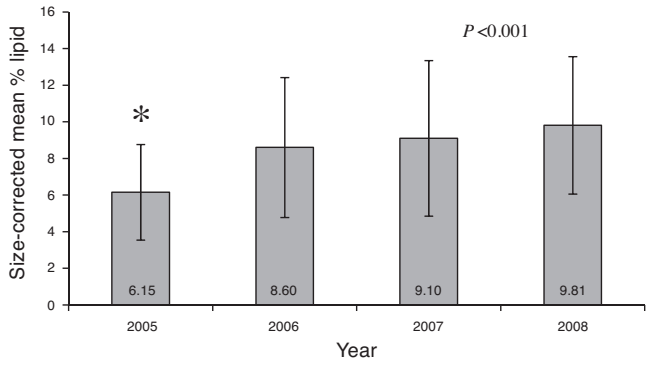

Figure 2

Size-corrected total lipid content in Atlantic herring (*Clupea harengus*) by sampling year (sample sizes: n_{2005}: 113, n_{2006}: 330, n_{2007}: 334, and n_{2008}:112). Error bars represent standard deviation; values inside bars graph are the yearly mean percent lipid.

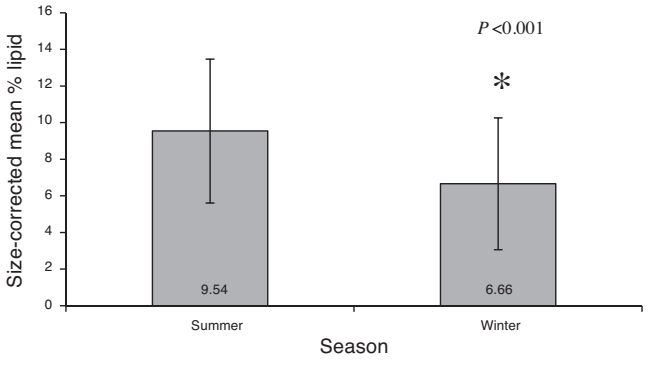

Figure 3

Size-corrected total lipid content by season for Atlantic herring (*Clupea harengus*) collected from 2006 through 2007 (n=158). Error bars represent standard deviation; values inside bars graph are the seasonal mean percent lipid.

total lipid content on fork length revealed a significant positive relationship (r^2=0.147, P<0.001, Fig. 1). The ANCOVA of total lipid content revealed significant differences (P<0.001) in the length-corrected lipid content of fish between years (Fig. 2). Multiple comparison tests (Bonferroni, α=0.05) showed that the total lipid content of fish from 2005 (6.15% ±2.61%, n=113) was significantly lower than the total lipid content of fish from 2006, 2007, and 2008 (P<0.001 for all comparisons), but fish from the latter three years were not different from each other (8.60% ±2.61%, n=330; 9.10% ±3.82%, n=334; and 9.81% ±3.75%), n=112, respectively; P>0.05). The ANCOVA of total lipid content by season was significant with summer fish having significantly more total lipid (9.54% ±3.93%, n=506) than winter fish (6.66% ±3.60%, n=158; P<0.001, Fig. 3).

Fatty acid composition

A total of 551 individual fish collected between 2005 and 2008 were analyzed for trends in fatty acid composition (Table 2). The ANOSIM of all fish showed a significant difference in fatty acid signatures of fish by age (global r=0.131, P<0.01, Fig. 4A). Figure 4A shows that age-1 and age-4+ fish group separately from age-2 and age-3 fish, but the clearest differences are seen between age-1 fish and all other age classes. The differences in the percent composition of these fatty acids by age can be seen in Table 3. For example, omega-3 and omega-6 fatty acids were significantly higher in concentration in age-1 fish than in age 2–4 fish (P<0.001, 25.88% ±6.42% and 20.73% ±3.57%, respectively), whereas long chain monounsaturated fatty acids (20:1n-11, 20:1n-9, 20:1n-7, 22:1n-11, 22:1n-9 and 22:1n-7) were higher in concentration in age 2–4 fish than in age-1 fish (P<0.001, 30.96% ±9.83% and 37.82% ±10.72%, respectively). However, the SIMPER analysis also showed that no fatty acid contributed more than 6.56% to the dissimilarity between the fatty acid signatures of fish by age, indicating that the variation observed

Table 2

Number of fish sampled (total fish) and size range of Atlantic herring (*Clupea harengus*) analyzed for differences in fatty acid signature by year, season, and age class.

Year	Total fish	Size (cm)	Summer	Winter	Age 1	Age 2	Age 3	Age 4+
2005–2008	551	8.8–28.2	480	71	70	272	131	78
2005	56	15.5–24.6	56	0	0	25	29	2
2006	260	8.8–27.3	225	35	52	108	60	40
2007	140	10.7–27.8	104	36	15	86	20	19
2008	95	10.8–28.0	95	0	3	53	23	16

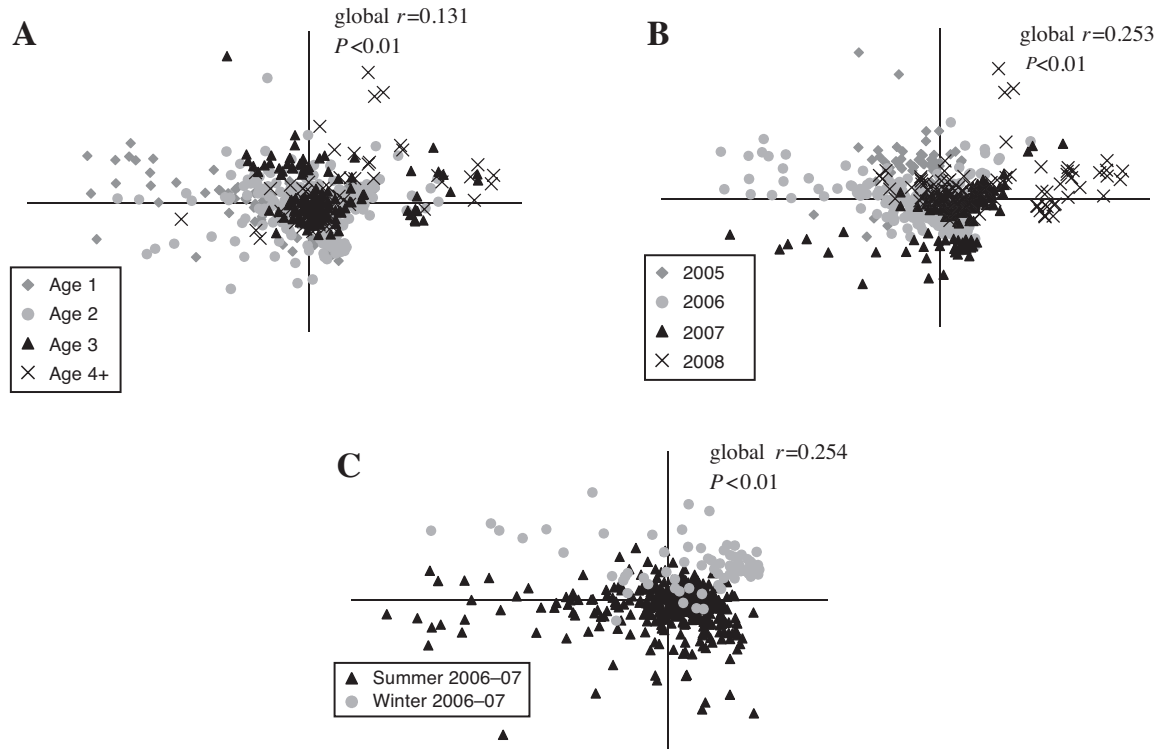

Figure 4

Multidimensional scaling plot of the fatty acid signatures of Atlantic herring (*Clupea harengus*) by (**A**) fish age, (**B**) sampling year, and (**C**) sampling season (2006–07 fish only). Symbols grouped together indicate similarity in fatty acid signatures between those symbols. Although all comparisons (age, year, and season) were significant, groupings were stronger by year (B) and season (C) than by age (A). Omega-3 and -6 and long chain monounsaturated fatty acids were important in distinguishing between the fatty acid signatures of fish ontogenetically, annually, and seasonally.

was in entire fatty acid signatures, not in just one or two individual fatty acids.

Significant differences were also found in the fatty acid signatures of fish by year (global r=0.253, P<0.01, Fig. 4B). Pairwise comparisons with ANOSIM indicated that fish from each year had significantly different fatty acid signatures (P<0.01), but the high r values for all pairwise tests that included fish from 2005 indicated that fish from 2005 were the most different in their fatty acid signatures (2005 vs. 2008: r=0.298; 2005 vs. 2007: 0.491; 2005 vs. 2006: 0.410; 2006 vs. 2007: 0.134; 2006 vs. 2008: 0.247; 2007 vs. 2008: 0.244). The separation of 2005 fish on the basis of fatty acid signatures was also evident from the results of the SIMPER analysis of fish by year. The average dissimilarities of comparisons including fish from 2005 were higher

Table 3

Age, sample size, mean percent composition, and standard error (SE) of all fatty acids that were included in non-parametric models to analyze Atlantic herring (*Clupea harengus*) for patterns in fatty acid signatures. Since significant differences were found in the fatty acid composition of fish by age, means for each age separately are shown as well as for all omega-3 (*n*-3) and omega-6 (*n*-6) fatty acids in the model.

		Mean % composition of fatty acid ±SE											
Age	*n*	14:0	16:0	16:1*n*-11	16:1*n*-9	16:1*n*-7	16:1*n*-5	18:1*n*-11	18:1*n*-9	18:2*n*-6	18:3*n*-3	18:4*n*-3	20:1*n*-11
1	70	7.61±1.67	14.38±2.56	0.06±0.02	0.11±0.03	4.26±0.84	0.27±0.05	0.53±0.40	6.70±1.54	1.06±0.21	0.56±0.34	1.66±0.79	1.05±0.57
2	272	8.32±1.09	12.45±1.58	0.06±0.04	0.10±0.02	4.85±1.08	0.28±0.05	0.63±0.72	5.61±1.39	1.07±0.28	0.62±0.48	1.96±1.04	1.10±0.51
3	131	8.07±0.73	12.27±1.05	0.08±0.07	0.11±0.02	5.48±1.16	0.26±0.07	0.99±1.43	5.46±1.64	1.05±0.45	0.82±0.57	2.22±1.03	1.13±0.61
4+	78	7.68±0.99	12.39±1.57	0.05±0.03	0.12±0.04	5.39±1.57	0.27±0.05	2.00±4.09	5.81±1.88	0.95±0.43	0.73±0.43	1.89±1.15	1.20±0.34

	Mean % composition of fatty acid ±SE											
Age	20:1*n*-9	20:11*n*-7	20:41*n*-6	20:41*n*-3	20:51*n*-3	22:11*n*-11	22:11*n*-9	22:11*n*-7	22:51*n*-3	22:61*n*-3	24:11*n*-9	Sum of all *n*-3	Sum of all *n*-6
1	10.87±3.62	0.21±0.06	0.46±0.19	0.39±0.07	7.33±2.40	17.97±6.03	0.69±0.19	0.17±0.06	1.07±2.62	12.44±4.51	0.78±0.24	24.09±7.01	1.79±0.31
2	13.78±2.46	0.23±0.06	0.27±0.15	0.45±0.13	6.82±1.79	21.46±3.78	0.96±0.32	0.15±0.07	0.78±0.53	8.32±3.13	0.66±0.24	19.51±4.06	1.59±0.36
3	13.54±1.61	0.27±0.11	0.25±0.08	0.49±0.57	6.73±1.20	21.75±2.39	1.03±0.23	0.18±0.05	0.86±0.53	7.30±1.10	0.57±0.36	19.07±2.29	1.59±0.43
4+	13.48±1.74	0.32±0.15	0.28±0.10	0.40±0.10	6.20±1.00	22.09±3.10	1.13±0.29	0.19±0.07	0.70±0.13	7.60±1.55	0.72±0.20	18.06±2.38	1.51±0.36

than comparisons including fish from the other three years (2005 vs. 2008: dissimilarity=18.15%; 2005 vs. 2007: 17.59%; 2005 vs. 2006: 16.36%; 2006 vs. 2007: 14.06%; 2006 vs. 2008: 16.10%; 2007 vs. 2008: 16.04%). As with the data on fatty acid signatures by fish age, the SIMPER analysis revealed that the separation of fish by year was also based on omega-3, -6, and long-chain polyunsaturated fatty acids (Table 4). However, in contrast to the age data, 16:1n-11 contributed to over 10% of the differences found in the fatty acid signatures of fish from 2005 in contrast to fish collected during the other years of the study. The reason for this strong difference in percent composition is unclear because this fatty acid has not been previously identified as biologically important.

Herring from 2006 and 2007 were analyzed for differences in fatty acid composition by season. The ANOSIM indicated significant differences in the fatty acid composition of fish by season (global r=0.254, P<0.01, Fig. 4C). The SIMPER analysis showed that omega-3 and -6 (specifically 20:5*n*-3) and long-chain monounsaturated fatty acids (specifically 20:1*n*-11 and 22:1*n*-11) were the most important fatty acids contributing to the differences in fatty acid signatures of fish by season (Table 4).

Discussion

Age was the strongest determinant of the total lipid content and fatty acid composition of Atlantic herring. Younger fish had less total lipid content, but this was paired with higher concentrations of certain classes of fatty acids, such as omega-3 and -6 fatty acids which are important for vertebrate growth and development early in life (Sargent et al., 1999; Szlinder-Richert et al., 2010.). This was in contrast to older fish, which had higher total lipid content paired with higher concentrations of long-chain monounsaturated fatty acids which are important for energy storage (Hadley, 1985). Although the r^2 value of the regression of fork length on total lipid content is relatively low, we believe this is indicative of the natural variability in the nutritional quality of Atlantic herring in this ecosystem. Although we do not know the direct cause of the ontogenetic variation in our sample, it is likely that small and large fish have different diets, especially considering the change in filtering ability as fish grow (Gibson, 1988). These differences in fatty acid composition could be manifested in one of two ways; either fish of different sizes are feeding on different prey items, or on different proportions of the same prey items (e.g., Iverson et al., 1997; 2002).

This study revealed significant annual variation in the lipid content and composition of herring. For example, 2005 fish had 37% less lipid than fish from 2006 through 2008, and their fatty acid signatures were also significantly different from fish collected in the other three years. Also, although not statistically

significant, fish from 2008 had the highest lipid content of any year in the study (Fig. 2) and also exhibited significant variation from the other years in their fatty acid signatures. Although significant differences were observed in the fatty acid composition of herring by year, these differences were not concentrated in any individual fatty acids (such as the biologically important polyunsaturated fatty acids) but were spread consistently throughout the entire suite of fatty acids sampled. These differences underscore the importance of measuring prey quality on annual scales to account for this variation. The source of the annual variation in total lipid content and fatty acid composition is not known and could be related to many factors including variation in prey availability or climatic shifts (Litz et al., 2010), but data for these factors are not currently available for the Bay of Fundy.

The seasonal variation in Atlantic herring lipid content and composition was not unexpected, considering the fall spawning habits of herring in the Bay of Fundy (Boyar et al., 1973). We found summer fish had significantly more lipid than winter fish (Fig. 3) and this high lipid content may reflect lipid storage in the summer before spawning occurs, and it may also reflect low prey availability in the winter for herring (Murison and Gaskin, 1989; Michaud and Taggart, 2007). However, almost all the fish in this study were sexually immature; therefore, even preparation for spawning may cause a shift in fatty acid composition. The differences in fatty acid composition may also be indicative of variation in the foraging habits of Atlantic herring throughout the year. The SIMPER analysis identified 20:5*n*-3 and 22:1*n*-11 as the most important fatty acids contributing to the seasonal differences in fatty acid signatures (Table 4). The data showed concentrations of omega-3 fatty acids necessary for growth and development (Sargent et al., 1988; Pond, 1998) are higher in summer fish than in winter fish. Specifically, the concentration of 20:5*n*-3 in winter fish was 4.24% ±1.41%, compared to 6.89% ±1.38% in summer fish. In contrast, winter fish had higher concentrations of long-chain monounsaturated fatty acids, typically used for energy storage over winter (Hadley, 1985), than did summer fish. Specifically, the concentration of 22:1*n*-11 in winter fish was 25.91% ±4.64, compared to 20.89% ±2.98% in summer fish, representing an increase of almost 25%. Overall,

Table 4

Year and season, sample size, mean percent composition, and standard error (SE) of all fatty acids that were included in non-parametric models to analyze Atlantic herring (*Clupea harengus*) for patterns in fatty acid signatures. Since significant differences were found in the fatty acid composition of fish by year and season, means for each year and season separately are shown as well as for all omega-3 (*n*-3) and omega-6 (*n*-6) fatty acids in the model. S=summer, W=winter.

		Mean % composition of fatty acid ±SE											
Year/Season	*n*	14:0	16:0	16:1*n*-11	16:1*n*-9	16:1*n*-7	16:1*n*-5	18:1*n*-11	18:1*n*-9	18:2*n*-6	18:3*n*3	18:4*n*-3	20:1*n*-11
2005/S	56	7.81±0.69	13.49±1.85	0.17±0.07	0.12±0.03	5.54±0.71	0.18±0.07	0.52±0.10	5.96±1.15	1.07±0.28	0.64±0.22	2.16±0.53	1.01±0.85
2006/S	225	7.93±1.09	13.10±1.91	0.05±0.02	0.10±0.03	4.79±1.09	0.27±0.04	0.51±0.24	6.45±1.32	1.17±0.22	0.69±0.37	2.25±0.92	0.98±0.44
2006–07/W	71	8.71±1.90	11.61±1.47	0.06±0.01	0.12±0.01	3.67±0.99	0.28±0.04	0.75±0.24	6.38±1.06	1.12±0.15	0.44±0.40	1.16±0.70	1.78±0.58
2007/S	104	8.31±0.58	11.87±0.94	0.04±0.01	0.11±0.02	5.14±0.94	0.33±0.04	0.53±0.40	5.08±1.11	1.08±0.25	0.49±0.49	1.97±1.26	1.03±0.18
2008/S	95	7.87±0.87	12.70±1.58	0.04±0.01	0.09±0.03	6.02±1.06	0.26±0.03	2.54±3.98	4.18±1.78	0.66±0.51	1.04±0.66	1.82±1.12	1.12±0.25

	Mean % composition of fatty acid ± SE										
Year/Season	20:1*n*-9	20:11*n*-7	20:41*n*-6	20:41*n*-3	20:5*n*-3	22:11*n*-11	22:11*n*-9	22:11*n*-7	22:51*n*-3	22:61*n*-3	24:11*n*9	Sum of all 1*n*-3	Sum of all 1*n*-6
2005/S	13.27±1.91	0.27±0.04	0.29±0.04	0.57±0.89	7.65±1.50	18.95±2.44	1.04±0.63	0.19±0.11	1.35±1.13	7.14±1.35	0.15±0.28	20.01±2.26	1.61±0.33
2006/S	12.02±2.45	0.24±0.08	0.33±0.18	0.44±0.09	7.02±1.43	20.36±4.00	0.88±0.22	0.17±0.04	0.85±1.49	9.61±3.55	0.75±0.25	21.55±4.66	1.79±0.27
2006–07/W	13.67±2.22	0.17±0.05	0.36±0.20	0.38±0.08	4.24±1.41	25.91±4.64	0.82±0.16	0.13±0.04	0.58±0.09	9.25±5.25	0.78±0.18	16.49±6.04	1.67±0.17
2007/S	15.70±1.73	0.26±0.09	0.20±0.04	0.45±0.08	6.75±0.99	21.42±1.68	1.12±0.16	0.17±0.04	0.71±0.11	7.06±1.10	0.67±0.13	18.03±2.09	1.59±0.30
2008/S	13.50±2.10	0.30±0.13	0.25±0.07	0.43±0.08	7.64±1.36	20.61±3.16	1.08±0.28	0.16±0.09	0.78±0.09	7.71±1.60	0.66±0.14	19.84±2.63	1.11±0.40

long-chain monounsaturated fatty acids were higher in concentration in the winter, and the omega-3 fatty acids were lower in winter. However, only concentrations of 20:5*n*-3, not the biologically important 22:6*n*-3, were observed to be lower in winter, indicating mobilization of 20:5*n*-3 or a shift in diet during winter.

The differences observed in total lipid content and fatty acid composition could also be a result of the differential allocation of resources to specific tissues within the body; however, this aspect of variability was not a goal of our research because Atlantic herring predators consume their prey whole. A small subset of large individuals (n=31, at least 21 cm in fork length) was examined for differences in total lipid content by tissue type, and muscle tissue was found to have significantly more total lipid content than gonad tissue (P<0.0001). However, because few of these individuals were sexually mature, these data indicate only that muscle tissue may be an important lipid store for fish as they begin to mature sexually.

Iverson et al. (2002) also identified ontogeny as the main factor responsible for the variation in the lipid content and fatty acid composition of Pacific herring (*Clupea pallasi*), and similar fatty acids (omega-3, -6, and long-chain monounsaturates) were identified as important in distinguishing between the fatty acid signatures of fish by age. Huynh et al. (2007) also found ontogenetic variation in the fatty acid signatures of Pacific herring fillets. As we found with the data from this study, Jensen et al. (2007) identified ontogeny, year, and season as important factors contributing to differences in the fatty acid composition of Baltic herring collected from 2001 through 2003. Budge et al. (2002) determined that the fatty acid signatures of Atlantic herring were significantly different from all other species found on the Scotian Shelf, Georges Bank, and the southern Gulf of St. Lawrence, with the exception of capelin (*Mallotus villosus*) and northern sand lance (*Ammodytes dubius*). The separation of Atlantic herring from other fish species in the Budge et al. study may be due to the high concentration of 22:1*n*-11 found in herring (17.27% ±5.68%) compared to other fish (haddock: 1.65% ±1.58%, mackerel: 6.0t% ±3.44%, pollock: 2.68% ±1.45%). We also found high concentrations of 22:1*n*-11 in the Atlantic herring examined; in fact, 22:1*n*-11 was the fatty acid in highest concentration in all fish (Tables 3 and 4). Combining previous work (Iverson et al., 2002; Jensen et al., 2007) on other ecosystems with the data presented here, it seems clear that there is significant variability in the nutritional quality of herring on ontogenetic, annual, and seasonal scales worldwide. In order to obtain a complete picture of prey quality, the total lipid content and fatty acid composition of the whole body, as well as body tissues (muscle, gonads), should be compared to identify possible differences due to sexual maturity stage. Further, these studies serve to emphasize that the characterization of prey from a physiological and biochemical perspective (quality) should be conducted synoptically with measures of biomass (quantity) to best determine the prey field of interest.

The variation in Atlantic herring nutritional quality observed in this study could have large impacts on the health of herring predators. During years or seasons of low lipid content, predators relying on herring would either have to spend more time foraging to meet energy demands or cope with less energy intake from the same amount of prey. The latter could result in a decline in body condition, health, or reproductive success if minimum caloric requirements are not met (e.g., Atkinson and Ramsay, 1995; Alonso-Alvarez and Tella, 2001). For example, Diamond and Devlin (2003) demonstrated a decline in breeding success of Arctic and common terns (*Sterna paradisaea, S. hirundo*) in the Bay of Fundy from 1995 through 2000 and directly linked it to a decline in lipid content of their main prey item, Atlantic herring. Although we do not know at which point, or whether, the lipid content of Atlantic herring falls below a level that would make them unprofitable for predators, the lowest mean percent lipid value observed in this study (6%) is still considered high for fish in general (compared to that for Atlantic cod [*Gadus morhua*]: 2.1%; haddock [*Melanogrammus aeglefinus*]: 1.4%; Atlantic mackerel [*Scomber scombrus*]: 3.4%; Atlantic pollock [*Pollachius pollachius*]: 3.0%; all values from Budge et al., 2002), many of which are important prey species despite their relatively low lipid content (Gannon et al., 1998; Pauly et al. 1998). Although it is likely that the lowest percentages observed in this study are still above this minimum level, the variation present in the nutritional quality of Atlantic herring has implications for the quality of food that predators are receiving. Predictability in the quantity and quality of available resources is an important element of food web dynamics, and some predators may depend heavily on the availability of a consistent type and level of energy intake. Such reliance can have serious implications for predators accustomed to high-energy prey; these predators may not be able to adjust to a high volume of low-quality food in place of a lower but more consistent amount of high-quality food, as has been shown in Steller sea lions (*Eumetopias jubatus*) by Rosen and Trites (2004).

The results of this study indicate significant ontogenetic, annual, and seasonal variation in the lipid content and composition of Atlantic herring from the Bay of Fundy. Herring are a critical prey species in the Bay of Fundy and the variation in lipid content and composition of these fish affects the nutritional quality of the prey that many upper predators in the Bay of Fundy are receiving. Because herring are a vital link between the upper and lower levels of the food chain, they are central to understanding the effects of variability in one species on the entire food web. Such variability has been shown to affect trophic dynamics in complex food webs across the globe (e.g., Duffy and Paul, 1992; Langvatn and Hanley, 1993; Toft and Wise, 1999; Rosen and Trites, 2004) and provides insight into the ecology and distribution of species in these environments. In the Bay of Fundy, predators of Atlantic herring are receiving nutritionally different “packages” depending

on which size of fish is eaten, and which season and year it is consumed in. The current study demonstrates the variability in the nutritional quality of species that may be assumed to offer consistent value in food webs and underscores the importance of characterizing species over broad temporal and developmental scales to capture this variability.

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