Energy Density of Capelin (*Mallotus villosus*) and Sand lance (*Ammodytes americanus* and *Ammodytes dubius)* during the summer in Coastal Newfoundland

by

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A thesis submitted to the Department of Biological Sciences, University of Manitoba, in
partial fulfilment of the requirements for the course
BIOL 4100 (Honours Thesis)
For the degree of
Bachelor of Science (Honours)

Abstract

Spawning capelin (*Mallotus villosus*) and non-spawning Atlantic sand lance (*Ammodytes americanus, A. dubius*) adults and juveniles are important forage fish species in coastal Newfoundland during July and August when high abundances of top predators rely on them as critical energy sources. To determine whether these prey types differ in their energy content, and interannual changes in quality, samples of each prey type were collected during July-August 2020 and 2023. Bomb calorimetry was used to measure whole-body dry energy density (kJ/dry g) and calculate wet energy density (kJ/wet g) and water content. Although sand lance are at the peak of their annual lipid cycle and capelin are at their minimum during the summer, adult female sand lance had lower dry energy density (mean of both years ± SE, 20.7 ± 0.11 kJ/dry g) than all capelin sex and maturity categories, and wet energy densities (4.4 ± 0.09 kJ/g) did not differ from capelin. Within capelin, wet and dry energy densities did not differ among gravid females, spent females and males, which contrasts previous findings from before the capelin population in Newfoundland collapsed. Within sand lance, juvenile dry energy density (20.8 ± 0.14 kJ/g) did not differ from adult females. Juvenile sand lance wet energy density was the only prey type that varied interannually, where energy density in 2020 was higher (5.3 ± 0.15 kJ/g), but this is thought to be because the samples were more dried out before collection. Overall, our findings indicate that although sand lance adults and juveniles are similar in wet energy densities to capelin, their lower wet mass per fish would result in a higher number of sand lance needed to reach a fixed energy content per meal. Other factors, including abundance and distribution of each species, also impact foraging costs and must be paired with energy densities to estimate prey type quality.

Acknowledgements

I would like to thank my supervisor, Gail Davoren, for the opportunity to do my honours with her and for the abundant guidance and encouragement she offered throughout this project. I would also like to thank the members of my honours committee, Joy Stacey and Jason Treberg, for their constructive feedback. Thank you to Lauren Lescure for letting me use the samples she collected and prepared for bomb calorimetry in the summer of 2020, and thank you to the rest of the Davoren Lab members for all of their help in the field and support during the process of writing this thesis. Thank you to the captain and crew of the Lady Easton III and the Natural Sciences and Engineering Research Council of Canada for funding this project. Lastly, thank you to my family, partner, friends and pets for their support and moments of laughter over the past year.

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Introduction

Foraging is the process of searching, handling and consuming a food source. While foraging, the main trade-off is between the benefits of the energy consumed and the costs of the energy expended during searching and handling prey (Stephens and Krebs 1986). Given that individual fitness increases when animals have more energy to allocate towards reproduction, growth and survival, optimal foraging behaviours that maximize net energy gain will evolve through natural selection (Stephens and Krebs 1986). Predators are affected by the energy content and abundance of prey and, thus, an optimal foraging strategy would include consuming high-quality prey while spending minimal time and energy searching and handling (Stephens and Krebs 1986).

In marine ecosystems, there are typically only a few forage fish species that occupy the intermediate trophic positions. Forage fish feed on zooplankton and in turn are eaten by many top predators, thereby representing a key energy link between species at lower and higher trophic levels (Carscadden and Vilhjálmsson 2002). Forage fish species are characterized by schooling behaviour, small body size, short lifespan, high fecundity and highly variable population dynamics known as "boom-bust" population cycles (Pikitch et al. 2012). These "boom-bust" cycles are thought to be due to bottom up, or resource-driven, regulation (Pikitch et al. 2012). For example, ocean temperature and the timing of sea ice retreat influence the timing and magnitude of the spring phytoplankton bloom and thus the zooplankton bloom in temperate ecosystems, which affect forage fish larval survival and ultimately recruitment (Buren et al. 2019; Boldt et al. 2022). The "bust" phase of forage fish population cycles are often asynchronous among species, which increases the stability of the community (Tilman 1999; Pikitch et al. 2012) because top predators can shift their diet toward the more abundant forage fish species (Arimitsu et al. 2021). However, not all forage fish species are of equal quality for predators. The "junk food hypothesis" predicts that if predators shift to consume more low-quality prey they will experience a decrease in fitness (Romano et al. 2006). Romano et al. (2006) found support for this hypothesis when Tufted Puffins (*Fratercula cirrhata*) and Black-legged Kittiwakes (*Rissa tridactyla*) experienced decreased reproductive success when fed a diet of lipid-poor Walleye Pollock (*Theragra chalcograma*), with lower energy density (3.9–5.1 kJ/wet g), than when fed lipid-rich forage fish with higher energy densities (5.1–7.1 kJ/wet g).

Capelin (*Mallotus villosus*) is a key forage fish species in many northern marine ecosystems (Carscadden and Vilhjálmsson 2002). On the Newfoundland Shelf, capelin reside offshore for most of their lives and sexually mature adults undergo extensive (~250 km) inshore migrations at 2-3 years of age to spawn at coastal intertidal and subtidal sites during July-August (Carscadden and Vilhjálmsson 2002; Davoren et al. 2012). During the spawning period, capelin is the dominant prey type for many top predators in coastal regions, including migratory whales, breeding and non-breeding seabirds and piscivorous fish (Davoren 2013; Carvalho and Davoren 2019; Berard and Davoren 2020; Jenkins and Davoren 2021; Johnson and Davoren 2021). During the summer inshore period, spawning capelin are also commercially fished for their roe (Buren et al. 2019). The capelin population on the Newfoundland Shelf experienced a collapse in 1991 which was associated with an anomalous cold-water event (Buren et al. 2014; Buren et al. 2019). Changes to the capelin population occurred immediately after the collapse, including delayed spawning by three weeks (late-June to mid-July), maturation at a younger age and decreased body condition at older ages (i.e. mass to length ratio; Carscadden and Frank 2002; Buren et al. 2019). Since 1991, the capelin population has not recovered and, although their “boom-bust” cycles continue, the maximum and minimum population sizes are both lower than before the collapse (Buren et al. 2019).

Sand lance (*Ammodytes* spp.) is another group of forage fish species that are present in coastal Newfoundland and are found in the diet of whales, seabirds and piscivorous fish (Berard and Davoren 2020; Jenkins and Davoren 2020; Johnson and Davoren 2021). Two species, *A. americanus* and *A. dubius,* co-occur on the Newfoundland Shelf, where *A. dubius* is thought to reside primarily offshore and *A. americanus* primarily inshore (Staudinger et al. 2020). Although they are considered separate species, they are difficult to distinguish and there is little known about their biology and population dynamics because they are not commercially fished and there is little published literature (Staudinger et al. 2020). Both species appear to reach maturity at 2-3 years and spawn during the fall to winter (Staudinger et al. 2020). Both species are thought to be non-migratory as their distribution is linked to fine-scale areas of coarse sand in which they burrow and emerge from daily to feed and lay their eggs on during spawning (Staudinger et al. 2020). As they are a resident species, juveniles are also present in coastal Newfoundland and available to top predators during the summer (Jenkins and Davoren 2021).

Prey energy quality is determined primarily by the lipid content (lipid= 39.3 kJ/g) within the fish and is often expressed as energy density (kJ/g) based on wet or dry mass (Montevecchi and Piatt 1984; Van Pelt et al. 1997). The energy densities of adult forage fish species vary throughout the year due to a number of factors (e.g., food availability, temperature), the most important of which is reproductive status (Lawson et al. 1998). As forage fish are short-lived, they have fewer reproductive events during their lifetime relative to other fish groups, and have adapted a life history strategy that involves high fecundity (Pikitch et al. 2012). Due to the development of many eggs and sperm, as well as secondary sexual characteristics, adult capelin and sand lance reach their greatest whole-body lipid content in their non-breeding season, and lowest whole-body lipid content during the spawning season (Figure A1; Winters 1970; Robards et al. 1999). During spawning, the gonads of females contain a higher percentage of lipids than the non-reproductive body tissues (somatic tissues), due to the transfer of lipids from the somatic tissue to the many energy rich eggs (Henderson et al. 1984; Montevecchi and Piatt 1984; Robards et al. 1999). In addition, capelin cease feeding once they reach the spawning sites, and sand lance stop feeding while developing their gonads, which contributes to the decrease in somatic lipids during the spawning period (Winters 1970; Robards et al. 1999). In contrast to sexually mature adults, the energy densities of immature forage fish also vary over the annual cycle but to a lesser extent than adults (Winters 1970; Paul et al. 1998). For example, Pacific sand lance (*Ammodytes hexapterus*), a closely related species to the Atlantic sand lance species off the coast of Newfoundland, increase in lipid content prior to over-wintering as they rely on these lipid stores during this low productivity period (Robards et al. 1999). By contrast, adults rely largely on protein stores as energy for the winter (Robards et al. 1999). Therefore, although immature forage fish tend to have lower percent lipids than adults (Winters 1970; Paul et al. 1998), Pacific sand lance juveniles have similar lipid content as adults during July and August, resulting in similar energy density values (dry energy density, juvenile: 16.67 – 19.68 kJ/g; adult: 19.56 – 21.08 kJ/g; Robards et al. 1999).

While there have been studies on capelin and sand lance energy densities, the energy densities of co-occurring capelin and sand lance during July and August in coastal Newfoundland is unknown. During this time, spawning (gravid) and immediately postspawning (spent) female and male capelin, along with non-breeding adult and juvenile sand lance are available to predators inshore (Carscadden and Vilhjálmsson 2002; Staudinger et al. 2020). One study measured the energy density of both capelin and sand lance on the Newfoundland Shelf during the summer, however; each species was collected from different regions (inshore vs offshore), across six months (April to September) encompassing multiple parts of their annual cycle and fish of different sex and maturity status were combined (Table A1; Lawson et al., 1998). Another study reported energy density of male, gravid and spent female capelin caught inshore in June (spawning period), but importantly, this study was conducted during the pre-collapse period (i.e. pre-1991; Table A1; Montevecchi and Piatt 1984; Carscadden and Frank 2002). Although other studies report energy densities of sand lance and/or capelin in other regions (Table A1; Robards et al. 1999, Elliot and Gaston 2008), providing important insight into species-specific differences, it is important to simultaneously quantify energy densities of both species in coastal Newfoundland during July and August when high abundances of multiple top predator species rely on these species as prey to meet the energetic demands of breeding (seabirds), moulting (non-breeding seabirds) and restoring energy reserves prior to breeding (baleen whales, piscivorous fish).

The main objective of this research was to determine the energy content (dry and wet energy density, kJ/g) of co-occuring capelin and sand lance as prey for top predators in coastal Newfoundland during July and August. To compare prey quality, both forage fish species were simultaneously caught inshore across two years (2020 and 2023) for whole-body energy density determination. A subobjective was to explore interannual variation in species-specific quality. I tested the hypothesis that sex and maturity categories among capelin and sand lance affect energy density. First, I predicted that adult sand lance would have higher energy density than gravid and spent female capelin and male capelin, due to forage fish generally having higher percent lipids in their non-spawning period relative to the spawning period. Secondly, I predicted that gravid female capelin would have higher energy density than spent female capelin and male capelin, due to their lipid-rich eggs. Thirdly, based on previous research on the closely related Pacific sand lance (*A. hexapterus;* Robards et al. 1999), I predicted that the adult and juvenile sand lance collected in coastal Newfoundland would have similar energy density in the late summer, as juvenile and adult Pacific sand lance accumulate similar percent lipid content in the summer months. I examined these predictions for both wet and dry energy density values, due to the mixed reporting of wet and dry energy densities in the literature (Table A1). This study is important because it provides insight into whether sand lance are an adequate alternative prey type for top predators during years with less capelin (i.e. “bust” years; “Junk food hypothesis”).

Materials and Methods

Study Area and Sample Collection

The Notre Dame Bay study area is located on the Northeastern coast of Newfoundland (Figure A2). Within the study area, there are known intertidal and subtidal spawning sites of capelin, and one subtidal spawning site has had sand lance consistently present (i.e. buried in the sediment) since 2012 (Figure A2). During July and August 2020 and 2023, gravid female capelin, male capelin, adult sand lance and juvenile sand lance were opportunistically collected. Unfortunately, we were unable to collect male sand lance in 2020 and male or female sand lance in 2023. All sampling was approved by the

University of Manitoba, Fort Garry Animal Care Committee (Protocol numbers: F20-017/1/2/3).

Capelin were collected at intertidal spawning sites using dip nets (38 cm diameter, 0.32 cm mesh) from land. When possible, a representative sample of 220 capelin were collected. This sample was previously found to be representative of a school of capelin (Maxner et al. 2016). Sand lance were sampled at the one subtidal capelin spawning site using a 30 cm^2 Ponar Grab system. As low numbers of typically adult sand lance are caught in the bottom grab per year (n = 20–30), these samples were supplemented with collections on a nearby seabird colony (James Island; Figure A2). On the island, mist-nets were used to catch adult Atlantic puffins (*Fratercula arctica*) carrying whole fish (typically juvenile sand lance) in their bills back to feed their young (Lescure et al. 2023). To increase independence of the samples, fish were collected from multiple birds on different days. Although puffins likely do not randomly sample the sand lance available in their environment, and instead may select contingents of the population, combining these sampling techniques provided an opportunity to collect adult and juvenile sand lance.

Sample Processing

All fish were frozen within 4 hours of collection. In the lab, capelin were thawed and total length (tip to tail, mm), sex, and maturity (juvenile, maturing, gravid, partially spent, spent) of all individuals were recorded. Sex and maturity were determined by macroscopic visual inspection of the gonads and secondary sexual characteristics. Capelin were subsampled using a length stratified subsampling method in which up to two individuals per sex per 5 mm category were kept. For these fish, total wet body mass (g) and gonad mass (g) were recorded and these fish were used for energy density analysis. A further subsample of the gravid capelin in each year with the same length range were artificially spent by surgically removing the ripe gonads to separately quantify somatic energy density (i.e. artificially spent capelin) and energy density of the egg mass, similar to Montevecchi and Piatt (1984). Wet mass was not obtained from a few artificially spent body and egg masses (n=4) and wet mass was estimated using a regression of the dry and wet mass of measured individuals (n=17), for body mass and egg mass separately. Naturally spent female capelin were not included in the dataset because they are difficult to collect, as they do not remain at spawning sites after releasing their eggs (Maxner et al. 2016). For sand lance, the total length (mm), sex, maturity, wet mass (g) and gonad mass (g) of all fish were recorded and these fish were used for energy density analysis.

Prior to energy density determination, whole fish and egg masses were freeze-dried for 3-4 days to ensure water removal. Samples were then homogenized separately using a coffee grinder which was disinfected with ethanol between each sample and the dry mass (g) was recorded. To determine dry energy density (kJ/dry g), samples were combusted in a 6400 calorimeter or 6725 semi-micro calorimeter, following instructions in the equipment manuals (Parr Instrument Company, n.d.). The semi-micro calorimeter was used for samples with dry mass <0.8 g (n=28), and the 6400 calorimeter was used for the remaining samples (n=129). Every fifth sample was run in duplicate to determine the precision of the calorimeter and we included the first value in the final dataset. Precision was calculated by determining the standard deviation between samples run in duplicate and then by averaging the standard deviations across all duplicate samples. The standard (benzoic acid) was run every tenth sample to ensure each calorimeter remained calibrated. The accuracy of each calorimeter was calculated by averaging the energy density of the benzoic acid standardization runs and then determining the absolute difference from the known value of the benzoic acid (6318 cal/g). The precision of the 6400 calorimeter was ±0.013 cal/g (n=28) and the accuracy was 1.0 ± 7.2 cal/g. The precision of the 6725 semi-micro calorimter was ±0.102 cal/g (n=6) and the accuracy was 36.8±41.2 cal/g. A conversion factor of 0.004184 kJ/cal was used to convert energy density from cal/g to kJ/g. To obtain wet energy density (kJ/wet g), the dry energy density was multiplied by the dry mass and divided by total wet mass. To obtain the percent water of each sample, we subtracted dry mass from wet mass to obtain the amount of mass due to water, and divided by the wet mass.

Statistical Analysis

We ran two-way ANOVAs to compare differences in wet energy density, dry energy density and percent water (continuous response variables) among our species/sex/maturity categories (hereafter referred to as ‘prey types’; categorical predictor variable) and between years (categorical predictor variable). Although capelin eggs are not technically a ‘prey type’, as predators would not only consume egg masses, we included egg masses in our analysis of prey types to interpret differences between gravid and spent female capelin, as done in a previous publication (Montevecchi and Piatt 1984). As we were interested in whether the sampling year influenced differences in energy densities among prey types, we included an interaction term (prey type * year). Similar length ranges were sampled in both years (Table 1) and, thus, length was not included as a predictor variable in the models. We investigated outliers (i.e. datapoints outside the whiskers on boxplots) and determined that they could not be attributed to measurement error and, thus, removal could not be justified. Analyses were run without the outliers, and, although there were slight differences in the post-hoc p-values, the overall results were the same, therefore, we present the ANOVAs with all data included.

After running the two-way ANOVAs, the underlying assumptions (normality and homogeneity of variances) were checked by visually inspecting histograms of the residuals and q-q plots, along with conducting Shapiro-Wilk and Levene's tests. The percent water data were arcsin square root transformed prior to analysis, as suggested by Sokal and Rohlf (1995). Visual inspection of the q-q plots and histograms of the residuals for all three response variables indicated a fairly normal distribution, although Shapiro-Wilk tests indicated non-normal distributions (wet energy density: $W=0.925$, $p<0.0001$; dry energy density: $W=0.973$, $p=0.003$; percent water: $W=0.838$, $p<0.0001$). Levene's tests also revealed lack of homogeneity of variance for dry energy density ($F_{5,151}=13.6$, $p<0.0001$), but variance was homogeneous for wet energy density ($F_{5,151}= 2.24$, $p=0.053$) and percent water ($F_{5, 151}=2.03$, $p=0.077$). Box-cox transformations were attempted, but transformations did not improve normality. Given that ANOVAs are robust to violations of underlying assumptions (Quinn and Keough 2002), the results of these two-way ANOVAs are presented.

Results

The final dataset consisted of the following prey types: gravid female capelin, artificially spent female capelin (& egg masses), spawning male capelin, adult non-reproductive female sand lance (2020 only) and juvenile sand lance (Table 1).

Table 1. Sample size (n), length range (mm), mean (±standard error) of dry energy density (ED; kJ/dry g), water content (% wet body mass), wet energy density (ED; kJ/wet g), and total energy (kJ) per fish of spawning adult capelin (*Mallotus villosus*) and non-reproductive adult female and juvenile sand lance (*Ammodytes* spp.) collected during July and August 2020 and 2023 (and years combined) in Notre Dame Bay, Newfoundland, Canada. Spent female capelin were artificially spent (i.e. gravid capelin with egg mass removed). Total energy per fish (kJ) was calculated by multiplying the mean wet ED (kJ/g) and the mean wet mass (g) for each prey type.

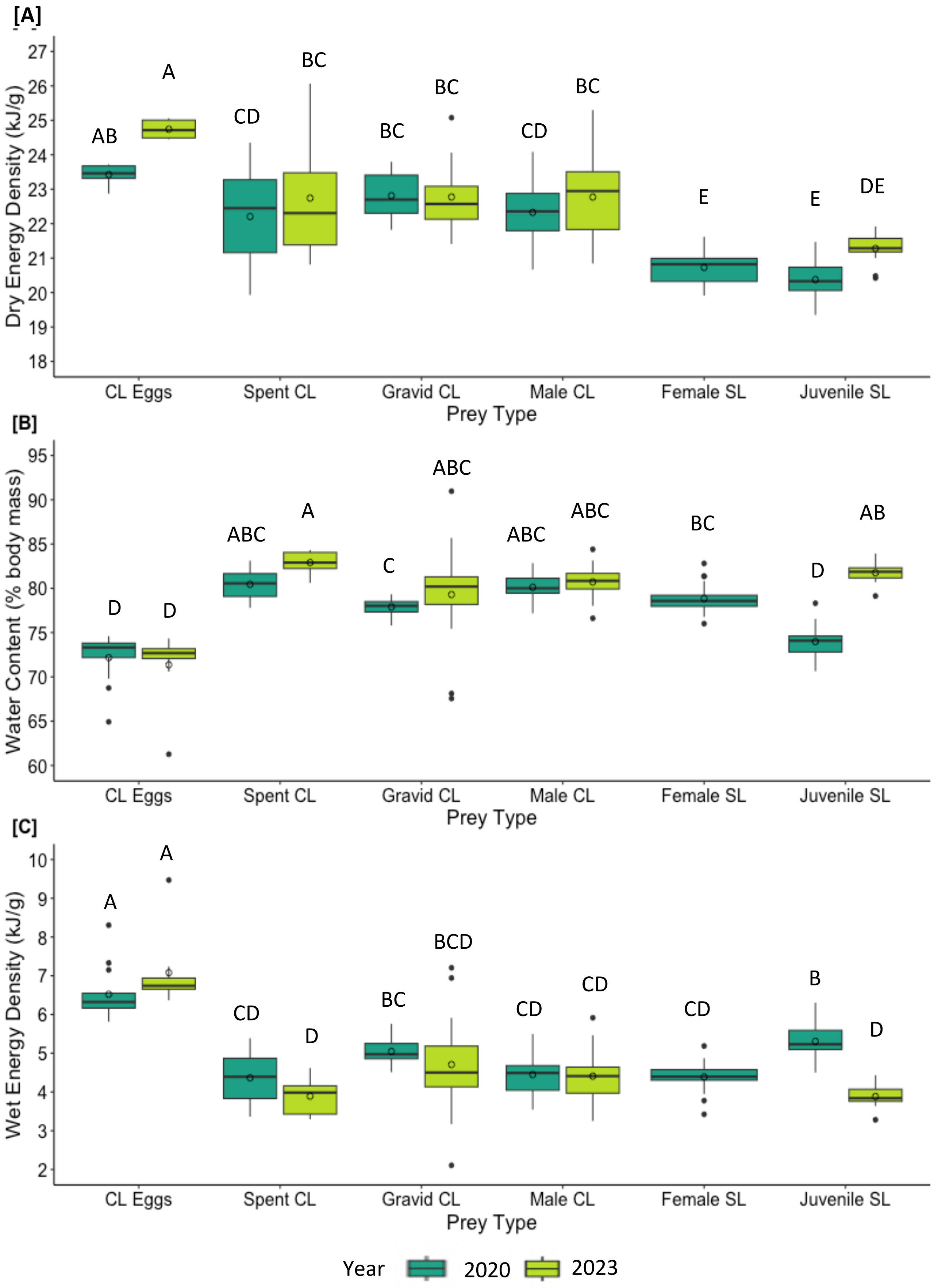
	Capelin Eggs	Spent Female Capelin	Gravid Capelin	Male Capelin	Female Sand lance	Juvenile Sand lance
2020						
N	13	13	13	21	19	12
Length (mm)		130-164	132-164	141-161	122-191	57-89
Dry ED (kJ/dry g)	23.4±0.07	22.2±0.40	22.8±0.17	22.3±0.19	20.7±0.11	20.4±0.16
% Water	72.2±0.77	80.4±0.49	77.9±0.26	80.1±0.31	78.9±0.11	74.0±0.61
Wet ED (kJ/wet g)	6.5±0.19	4.4±0.18	5.1±0.092	4. 5±0.10	4.4±0.09	5.3±0.15
Total Energy (kJ/fish)	33.2±2.55	54.5±2.38	92.5±4.30	97.4±3.17	29.7±3.64	2.5±0.276
2023						
N	8	8	15	23	0	12
Length (mm)		136-175	130-176	143-165	-	53-87
Dry ED (kJ/dry g)	24.7±0.10	22.7±0.67	22.8±0.25	22.8±0.25	-	21.3±0.14
% Water	71.4±1.49	82.9±0.45	79.3±1.51	80.7±0.36	-	81.8±0.35
Wet ED (kJ/wet g)	7.1±0.35	3.9±0.17	4.7±0.34	4.4±0.13	-	3.9±0.09
Total Energy (kJ/fish)	45.4±3.70	65.4±8.28	98.5±9.39	112.0± 4.78	-	3.8±0.388
Years combined						
Dry ED	23.9±0.15	22.4±0.35	22.8±0.15	22.6±0.16	20.7±0.11	20.8±0.14
% Water	71.9±0.73	81.4±0.43	78.6±0.82	80.4±0.24	78.9±0.39	77.9±0.88
Wet ED	6.7±0.18	4.2±0.14	4.9±0.19	4.4± 0.08	4.4±0.09	4.6±0.17
Total Energy (kJ/Fish)	37.9±2.45	58.7±3.56	95.7±5.35	105.0±3.10	29.7±3.64	3.2±0.27

Dry energy densities differed among prey types ($F_{5, 146}$= 37.8, p<0.0001) and between years ($F_{1,146}$=12.6, p=0.00053), but the interaction between prey type and year was not significant ($F_{4, 146}$=1.78, p=0.14; Figure 2A). Tukey-Kramer post-hoc tests revealed that in 2020, capelin eggs did not differ from gravid capelin (p>0.05) and had higher dry energy density than all other prey categories (p-values=0.049 to <0.0001). In

2020, female sand lance and juvenile sand lance did not differ from each other ($p=0.996$) and had lower dry energy density than all other prey types (p-values=0.0012 to <0.0001). In 2023, capelin eggs had higher dry energy density than all other prey categories (p-values=0.0018 to <0.0001), while juvenile sand lance had lower dry energy density than all other prey categories (p-values= 0.035 to 0.00083). Spent capelin, gravid capelin and male capelin did not differ in dry energy density during 2023 ($p>0.05$). Although dry energy densities in 2023 appeared higher than 2020, each prey type did not differ between years (p-values>0.05).

Percent water differed among prey types ($F_{5, 146}= 35.9$, $p<0.0001$) and between years ($F_{1,146}=24.5$, $p<0.0001$), and there was a significant interaction between prey type and year ($F_{4, 146}=9.53$, $p<0.0001$; Figure 2B). Tukey-Kramer post-hoc tests revealed that in 2020, capelin eggs and juvenile sand lance did not differ in water content ($p= 0.90$), and were lower than all other prey categories (p-values= 0.019 to <0.0001). In 2020, spent female capelin, gravid capelin, male capelin and female sand lance did not significantly differ in water content (p-values>0.05). In 2023, capelin eggs had significantly less water than all prey types ($p<0.0001$), including less than juvenile sand lance which differs from the 2020 data. Spent female capelin, gravid capelin, male capelin and juvenile sand lance did not differ in water content in 2023 (p-values>0.05). The only category that differed between years was juvenile sand lance, with higher water content in 2023 than 2020 ($p<0.0001$).

Wet energy densities differed among prey types ($F_{5, 146}= 43.8$, $p<0.0001$) and years ($F_{1,146}=7.67$, $p=0.0055$), and the interaction between prey type and year was significant ($F_{4, 146}=6.62$, $p<0.0001$; Figure 2C). Tukey-Kramer post-hoc tests revealed that in both years capelin eggs had higher wet energy density than all other prey types (p-values<0.0001). In 2020, juvenile sand lance had higher wet energy density than spent capelin (p=0.026), male capelin (p=0.024) and female sand lance (p=0.013), but did not differ from gravid capelin (p=0.997). Spent, gravid and male capelin and female sand lance did not differ from eachother (p-values>0.05). Juvenile sand lance had lower wet energy density in 2023 than 2020 (p<0.0001), which resulted in a lack of significant differences in wet energy densities among prey type categories in 2023 (p-values>0.05). Juvenile sand lance was the only prey type that had a difference in wet energy density between years.



[A]
Dry Energy Density (kJ/g)
27
26
25
24
23
22
21
20
19
18
AB
A
CD
BC
BC
BC
CD
BC
E
E
DE
CL Eggs
Spent CL
Gravid CL
Male CL
Female SL
Juvenile SL
Prey Type
[B]
Water Content (% body mass)
95
90
85
80
75
70
65
60
D
D
ABC
A
C
ABC
ABC
ABC
BC
D
AB
CL Eggs
Spent CL
Gravid CL
Male CL
Female SL
Juvenile SL
Prey Type
[C]
Wet Energy Density (kJ/g)
10
9
8
7
6
5
4
3
2
A
A
CD
D
BC
BCD
CD
CD
CD
B
D
CL Eggs
Spent CL
Gravid CL
Male CL
Female SL
Juvenile SL
Prey Type
Year
2020
2023

Figure 1. A) Dry energy density (kJ/dry g), B) water content (% wet body mass), and C) wet energy density (kJ/wet g) of spawning adult capelin (*Mallotus villosus*) and non-reproductive adult female and juvenile sand lance (*Ammodytes* spp.) collected in 2020 (light green) and 2023 (dark green). Prey types are: capelin eggs (CL Eggs), artificially spent female capelin (Spent CL), gravid capelin (Gravid CL), spawning male capelin (Male CL), non-reproductive adult female sand lance (Female SL) and juvenile sand lance (Juvenile SL). For sample sizes, see Table 1. Prey types labelled with the same letter are not significantly different ($p>0.05$). The box represents the interquartile range (25th and 75th percentiles), the horizontal line inside the box is the median, the unfilled circle is the mean value, and the whiskers extend up to 1.5 times the interquartile range.

Discussion

There was support for the hypothesis that sex and maturity categories among capelin and sand lance affect energy density. Variation among prey types in wet and dry energy densities generally followed the same trends within a year due to their similar water content (exception: juvenile sand lance). Wet energy density differed between prey types in 2020 but not 2023. In 2020, juvenile sand lance wet energy density did not differ from gravid capelin but was significantly higher than the other prey types. In both years, wet and dry energy densities did not significantly differ between the capelin sex/maturity categories. In both 2020 and 2023, juvenile sand lance had lower dry energy density than the other prey types, although dry energy density did not differ between juvenile and female sand lance in 2020. The only prey type that differed in energy density between years was juvenile sand lance. Indeed, juvenile sand lance wet energy density was higher in 2020 than 2023, most likely due to lower water content in 2020.

Our first prediction, that non-reproductive, adult sand lance would have higher energy density than spawning capelin, was not supported. In fact, during 2020, adult female sand lance did not differ in wet energy density and had lower dry energy density than all capelin categories. Our first prediction was based on findings that capelin and Pacific sand lance (*Ammodytes hexapterus)*, closely related to the Atlantic sand lance species in our study (*A. dubius* and *A. americanus*), generally have higher percent lipids during their non-breeding period compared to the gonad development and spawning periods (Winters 1970; Henderson et al. 1984; Robards et al. 1999). As previously reported energy densities of capelin and sand lance in the Atlantic were within a similar range (Table A1; Lawson et al. 1998), it seemed reasonable to predict that sand lance would have higher energy density if sampled during July and August, when capelin are actively spawning, and sand lance have not started gonad development (based on *A. hexapterus* cycle; Robards et al. 1999). As the exact spawning timing for sand lance in the Atlantic is unknown (fall-winter), it is possible that our prediction was not supported because female sand lance had begun gonadal development, resulting in lower whole-body lipid content (Robards et al. 1999; Staudinger et al. 2020). However, our sand lance dry energy density (20.7 kJ/g) was similar to peak values of Pacific sand lance in July (21.1 kJ/g) and August (20.6 kJ/g) who spawn in October (Robards et al. 1999), suggesting a similar spawning time. Therefore, adult sand lance are either a similar quality prey type (in terms of wet energy density) or a lower quality prey type (in terms of dry energy density) than capelin, even during the peak in their annual lipid cycle. Comparing our non-reproductive Atlantic sand lance wet energy densities (4.4 ± 0.09 kJ/g) to those of capelin in the winter non-reproductive months (10.7 ±0.66 kJ/g; Lawson et al. 1998) suggests that sand lance is a generally lower quality prey type. This lower energy content of sand lance may be explained by adult sand lance storing protein as their primary energy source, in comparison to other forage fish species, thus containing fewer lipids which are more energy rich (lipid = 39.3 kJ/g, protein = 17.8 kJ/g; Robards et al. 1999).

Contrary to our second prediction, gravid female capelin generally did not differ in wet or dry energy densities from other capelin sex and maturity categories. This prediction was based on the findings of Montevecchi and Piatt (1984), which showed higher wet energy densities for gravid capelin than spent male and female capelin. Despite the lack of differences between capelin categories, capelin egg masses had significantly higher wet and dry energy densities and lower water content than all prey types in both years, indicating that female gonads during spawning are energy-rich structures, as found previously (Montevecchi and Piatt 1984). Although spent male and female capelin tended to have lower minimum and maximum wet and dry energy densities than gravid capelin, the high variation in energy densities of these three capelin categories likely contributed to their lack of differences. High variation among male capelin may be related to their spawning behaviour. Males remain at spawning sites for up to several weeks to mate with multiple waves of spawning females, during which time they do not feed (Templeman 1948; Winters 1970). This behaviour results in a high percentage of males dying due to physical body damage and reduced body condition (Templeman 1948). If our sampled males had been at the spawning site for varying periods, then individuals that had been there longer would likely have lower lipid content than those that had arrived more recently. Although females remain at spawning sites just long enough to release their eggs (Templeman 1948), they form pre-spawning shoals and remain there for 2-3 weeks during which time they stop feeding (Davoren et al. 2006). Therefore, if our sampled females had stopped feeding for varying periods, this would contribute to the observed variation in energy densities. It is also possible that this higher observed variation in energy densities may be typical of capelin during the post-collapse period, in contrast to the pre-collapse energy densities reported in Montevecchi and Piatt (1984). Although body condition (mass/length) of adult capelin was shown to decrease in the ~10 years post-collapse (Carscadden and Frank 2002), our post-collapse wet energy densities of all capelin sex/maturity categories were higher than pre-collapse values (Tables 1, Table A1). Higher wet energy densities post-collapse support observations of faster growth and earlier age of sexual maturity of Newfoundland capelin since the population collapsed, interpreted as a density-dependent response to lower population sizes (Buren et al. 2019).

Our third prediction was supported, as juvenile and adult sand lance had similar dry energy densities in the year we sampled both categories (2020). This prediction was based on *A. hexapterus* juveniles which had similar dry energy density to adults going into the winter (Robards et al. 1999). Although dry energy density did not differ between adult female and juvenile sand lance in July and August, juveniles had lower water content in 2020 (relative to 2023) and, thus, wet energy density was higher in juveniles than adults. As methods of collection and freeze drying were similar in both years, it is unlikely that the lower water content of juveniles was due to methodological differences. Juvenile sand lance (in both years) were sampled from chick-rearing puffins that were carrying fish in their bills, caught during at-sea foraging trips, back to the colony to feed their offspring. Tracking of another similar seabird species (*Alca torda*) breeding on the same island revealed that birds had longer foraging trips during the chick-rearing period in 2020 than 2023 due to lower forage fish abundance (Lescure et al. 2023, Legard pers. comm.). As fish carried in bills dry out during the flight back to the colony (Montevecchi and Piatt 1987), longer foraging trips during 2020 could explain the lower water content of juvenile sand lance in 2020, resulting in a higher wet energy density. Overall, the 2023 juvenile sand lance wet energy density, which was lower than 2020, may be more representative across years.

Wet energy density of forage fish is important to consider in the context of prey quality for marine predators, as they consume fresh fish. In the case of seabirds, the amount of fresh mass that an adult seabird is able to carry back in their bill is limited by their body mass/wing area ratio (wing loading; Elliot et al. 2013), therefore breeding seabirds should maximize energy delivery to offspring by preferentially selecting prey with high wet energy densities. Based on our results, gravid female capelin might be the preferred prey type as they had generally higher average wet energy densities than the other prey types in both years. In support, chick-rearing common murres (*Uria aalge*) tend to deliver more gravid than spent female or male capelin to their chicks when capelin spawning matches the chick-rearing period (Davoren et al. 2012). Based on our results, if adult seabirds were able to carry a maximum fixed meal size of 100 g of fresh fish to their chicks, they would on average carry more total energy (wet total energy, kJ) with a meal of gravid capelin (total energy: 490 kJ), followed by female sand lance and/or male capelin (440–445 kJ), spent female capelin (415 kJ), and lasty juvenile sand lance (390 kJ; wet energy density in 2023). Although maximal chick growth may be achieved with the most energy-rich meal (total kJ), there is a trade-off between the energy delivered to the chick and the energy expended by the parent to capture the chick's meal (Stephen and Krebs 1986). To illustrate, if Atlantic Puffin (*Fratercula arctica*) chicks in coastal Newfoundland achieve maximal growth when fed at least 500 kJ per day, as was found for Tufted Puffin (*Fratercula cirrhata*; Romano et al. 2006), parents would need to capture 6 gravid capelin (500 kJ ÷ 95.7 kJ/gravid capelin), 5 male capelin, 9 spent female capelin, 17 adult female sand lance or 159 juvenile sand lance. Therefore, if the same amount of energy is expended to capture each fish of all prey types, then male and gravid capelin should be preferred, followed by spent capelin, then female sand lance, and juvenile sand lance. Of course, it is unrealistic to assume similar energy expenditure to capture each fish of all prey types because density and distribution patterns likely vary among prey types, thereby affecting prey type preferences (Stephens and Krebs 1986; Lescure et al. 2023).

Conclusion

In conclusion, this study has important implications for top predator foraging strategies during July and August in coastal Newfoundland, which is a critical period for a variety of top marine predators (Davoren 2013; Carvalho and Davoren 2019; Berard and Davoren 2020; Jenkins and Davoren 2021; Johnson and Davoren 2021). Knowing the differences in prey quality that are available to predators is also important in understanding how predators may be affected by dynamics in capelin spawning phenology (Davoren et al. 2012), the asynchronous "boom-bust" population cycles among forage fish species (Tilman 1999; Pikitch et al. 2012; Arimitsu et al. 2021), and large scale changes in community structure, which occurred in association with the capelin population collapse in the 1990s (Buren et al. 2019). To better understand the consequences of inter-annual variation in forage fish species abundance, density and distribution patterns of these prey types should be further studied. Capelin aggregate to spawn in high densities at annually persistent sites along the coast (Davoren et al. 2006), providing predators with abundant prey associated with low energetic costs to search and capture. Although sand lance can also be predictably located at one capelin spawning site in the study area, their densities appear to be much lower than capelin (Morrison and Davoren 2024). As little is known about the abundance of sand lance throughout coastal Newfoundland, it is difficult to determine whether this prey type supports the high energy demands of top predators during the summer. Further research on sand lance will be critical, as sand lance are one of the few forage fish species occupying the intermediate trophic level in the coastal Newfoundland ecosystem and, thus, are important for energy transfer through the food web, especially when other forage fish species are less abundant (Carscadden and Vilhjálmsson 2002). Energy density determinations in more years will also increase our understanding of interannual variation, and highlight trends in energy density between capelin and sand lance.

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Appendix

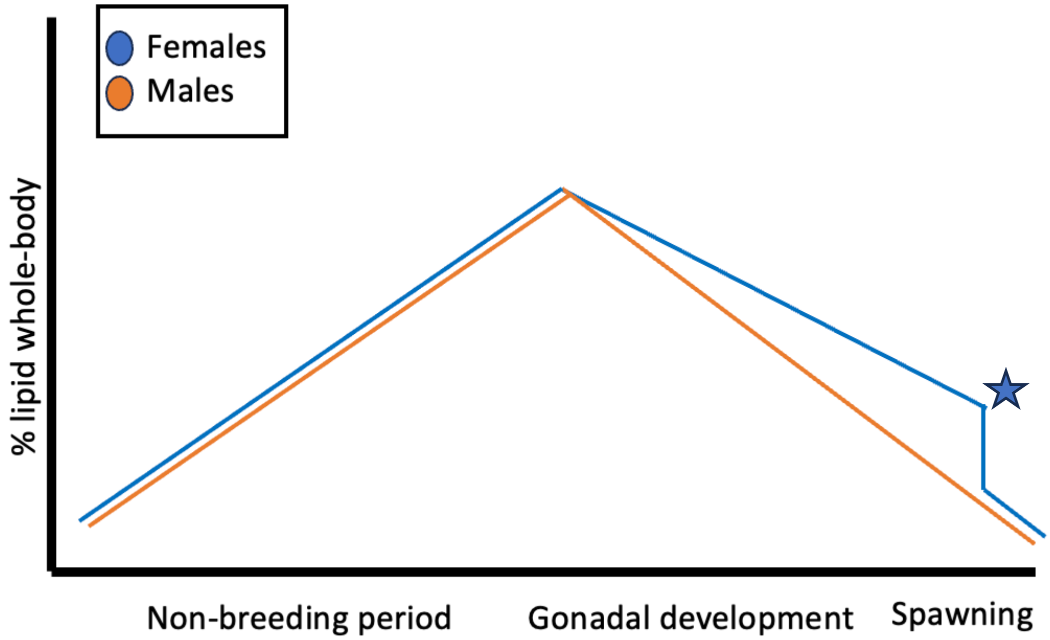

Figure A1. General trend of the lipid content of female (blue) and male (orange) sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*) throughout the year during the non-breeding, gonadal development and spawning periods. Blue star: during spawning, females carrying eggs have higher whole-body lipid content, which drops once they spawn. Adapted from Winters 1970 and Robards et al. 1999.

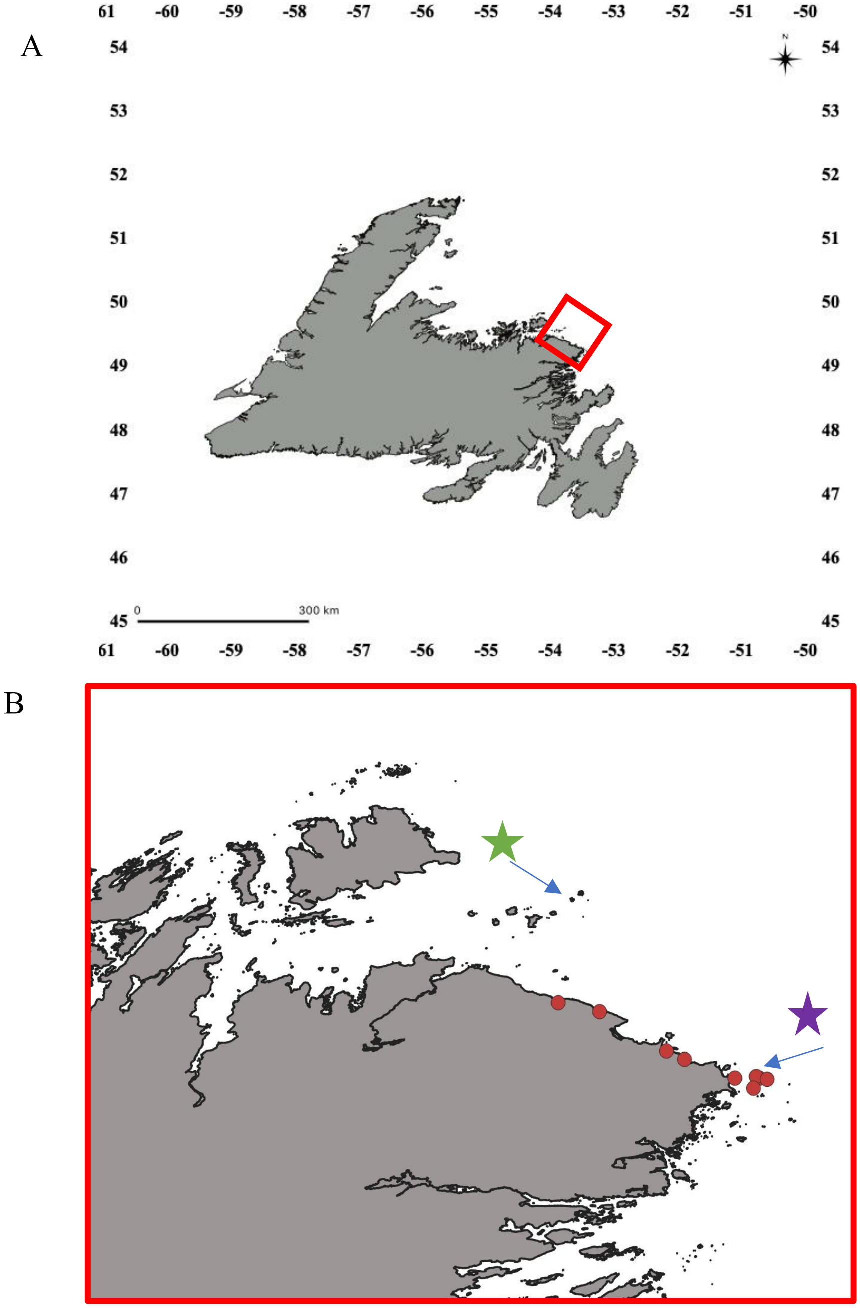

Figure A2. A) Newfoundland, Canada. Red square showing location of Notre Dame Bay. B) Study sites in Notre Dame Bay. Green star: James Island (seabird colony). Red dots: intertidal and subtidal capelin spawning sites. Purple star: capelin spawning site where sand lance are consistently present.

Table A1. Energy densities (ED) (dry and wet kJ/g), % lipid content, % water content, maturity, length, sampling time and sampling location of capelin (*Mallotus villosus*) and sand lance (*Ammodytes* spp.) published in the literature for periods that include July and August, when there are many top predators present in temperate ecosystems (Buren et al. 2014). NL=Newfoundland. Method of energy density determination: proximate composition (PC), bomb calorimetry (BC). Sources: 1=Lawson et al. 1998, 2= Elliot and Gaston 2008, 3= Montevecchi and Piatt 1984, 4= Robards et al. 1999.

Species	**Sex/ Maturity**	**Length (mm)**	**Sampling Time**	**Sampling Location**	**% lipids**	**% water**	**Wet ED (kJ/g)**	**Dry ED (kJ/g)**	**Method**	**Source**
M. villosus	Combined Sexes	140 ± 10.9	Apr-Sept 1995-1996	Inshore Labrador and offshore eastern NL, Canada	–	–	4.71±0.81	–	PC	1
M. villosus	Unknown	60-150	Jul-Aug 1984-2006	Hudson Strait, Nunavut, Canada	–	–	4.90 ± 0.16	23.47 ± 0.46	BC	2*
M. villosus	Male	183 ± 6.2	June 1984	Inshore, southeastern NL, Canada	2.4 ± 1.3	80.2 ± 1.4	3.8 ± 0.5	–	PC	3
M. villosus	Gravid female	158 ± 18.6	June 1984	Inshore, southeastern NL, Canada	4.1 ± 0.8	76.5 ± 1.0	4.6 ± 0.3	–	PC	3
M. villosus	Spent female	158 ± 12.7	June 1984	Inshore, southeastern NL, Canada	2.7 ± 2.0	80.0 ± 2.6	3.9 ± 0.8	–	PC	3
A. dubius	Combined sexes	179.1± 17.0	Apr-Sept 1995-1996	Offshore, eastern NL, Canada	–	–	4.56 ± 0.732	–	PC	1
A. sp	Unknown	50-200	Jul-Aug 1984-2006	Hudson Strait, Nunavut, Canada	–	–	5.06 ± 0.11	23.39 ± 0.54	BC	2*
A. hexapterus	Female	140 ± 6.9	July	Lower Cook Inlet, Alaska	27.2±1.8	72.7 ± 1.2	–	21.08 ± 0.34	PC	4
A. hexapterus	Male	140 ± 9.8	July	Lower Cook Inlet, Alaska	25.5 ± 2.8	73.4 ± 1.7	–	20.91 ± 0.44	PC	4
A. hexapterus	Juvenile	85-89	1996	Lower Cook Inlet, Alaska	17.5	75.3	–	19.68	PC	4

*samples from seabird bill load.