

Forage fish as a predator: summer and autumn diet of Atlantic herring in Trinity Bay, Newfoundland

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ABSTRACT

Atlantic herring (*Clupea harengus*; hereafter herring) is a forage fish that transfers energy from lower to higher trophic levels and sustains high-volume fisheries in the North Atlantic. This study aims to improve our understanding of the ecology of Newfoundland herring and its vulnerability to climate change by identifying key prey items and describing adult herring feeding strategies. We compared plankton assemblages to stomach content and stable isotope analyses from herring collected in Trinity Bay, Newfoundland, in late summer and autumn 2017–2019. Six distinct zooplankton communities were identified across all years, with a shift in community structure in September 2018. This shift coincided with a change from fresher, warmer waters (12–17 °C) to more saline, cooler waters (10.5 °C). The most frequently consumed prey items were amphipods (*Themisto* spp.) and calanoid copepods (primarily *Calanus* and *Temora* spp.). Fish eggs, larvae, and juveniles, primarily identified as capelin, were observed in stomach contents in all years. Fish contributed most to diets in 2017, which corresponded with the peak year for larval densities in Trinity Bay, suggesting that piscivory may increase at higher larval densities. Herring were opportunistic feeders, although some individuals exhibited selective feeding on copepods, amphipods, euphausiids, and the early life stages of fishes. Stable isotope analyses supported the finding that herring piscivory is prevalent in eastern Newfoundland. Given its adaptive feeding strategy and wide range of consumed prey, we conclude that adult Newfoundland herring is resilient to bottom-up changes observed in the environment.

1. Introduction

Atlantic herring (*Clupea harengus*; hereafter herring) is an important fisheries resource in the North Atlantic (Alder et al., 2008; Pikitch et al., 2014) as well as a key forage species funneling energy from lower trophic levels (i.e., zooplankton) to larger predators, such as piscivorous fishes, seabirds, and marine mammals (Cury, 2000; Overholtz and Link, 2007). Herring also transport energy from the open ocean to the coast during spawning migrations (Varpe et al., 2005). Similar to other forage fish, boom and bust cycles resulting in an oscillation between periods of extremely high and low abundance characterize herring populations (Toresen and Østvedt, 2000; Montero-Serra et al., 2015; Jacobsen and Essington, 2018; Trochta et al., 2020). Boom-bust population dynamics have been attributed to changes in environmental drivers that modify

prey availability and result in bottom-up control of herring populations (Ottersen and Loeng, 2000; Toresen and Østvedt, 2000; Payne et al., 2009; Alheit and Peck, 2019), although top-down control by commercial fisheries and predation also influence forage fish population dynamics (Essington et al., 2015; Jacobsen and Essington, 2018).

Traditionally, stomach content analysis has been used to study the diet of herring and document changes in the utilization of food resources (Hyslop, 1980). However, this method only provides an instantaneous measure of diet, and easily digested, soft-bodied prey may be underestimated due to rapid gastric evacuation (e.g., 50% gastric evacuation in 1.75 h for herring in the Gulf of St. Lawrence; Darbyson et al., 2003). In contrast, stable isotope analyses integrate diet over several months, minimizing the bias of rare or infrequently consumed taxa (Sherwood et al., 2007). Combining both traditional diet and stable isotope methods

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produces a robust analysis that accounts for the weaknesses of each method (Drazen et al., 2008; Polito et al., 2011; Kadye and Booth, 2012; Knickle and Rose, 2014).

The diet of herring has been investigated using stomach content analyses on both sides of the North Atlantic. Calanoid copepods,

specifically *Calanus finmarchicus* and *C. hyperboreus* and, to a lesser extent, euphausiids, represent the primary prey items in herring diets (Koster and Mollman, 2000; Prokopchuk and Sentyabov, 2006; Segers et al., 2007). Secondary prey items vary regionally. Amphipods are commonly detected in diets of Baltic, Norwegian, and North Sea herring

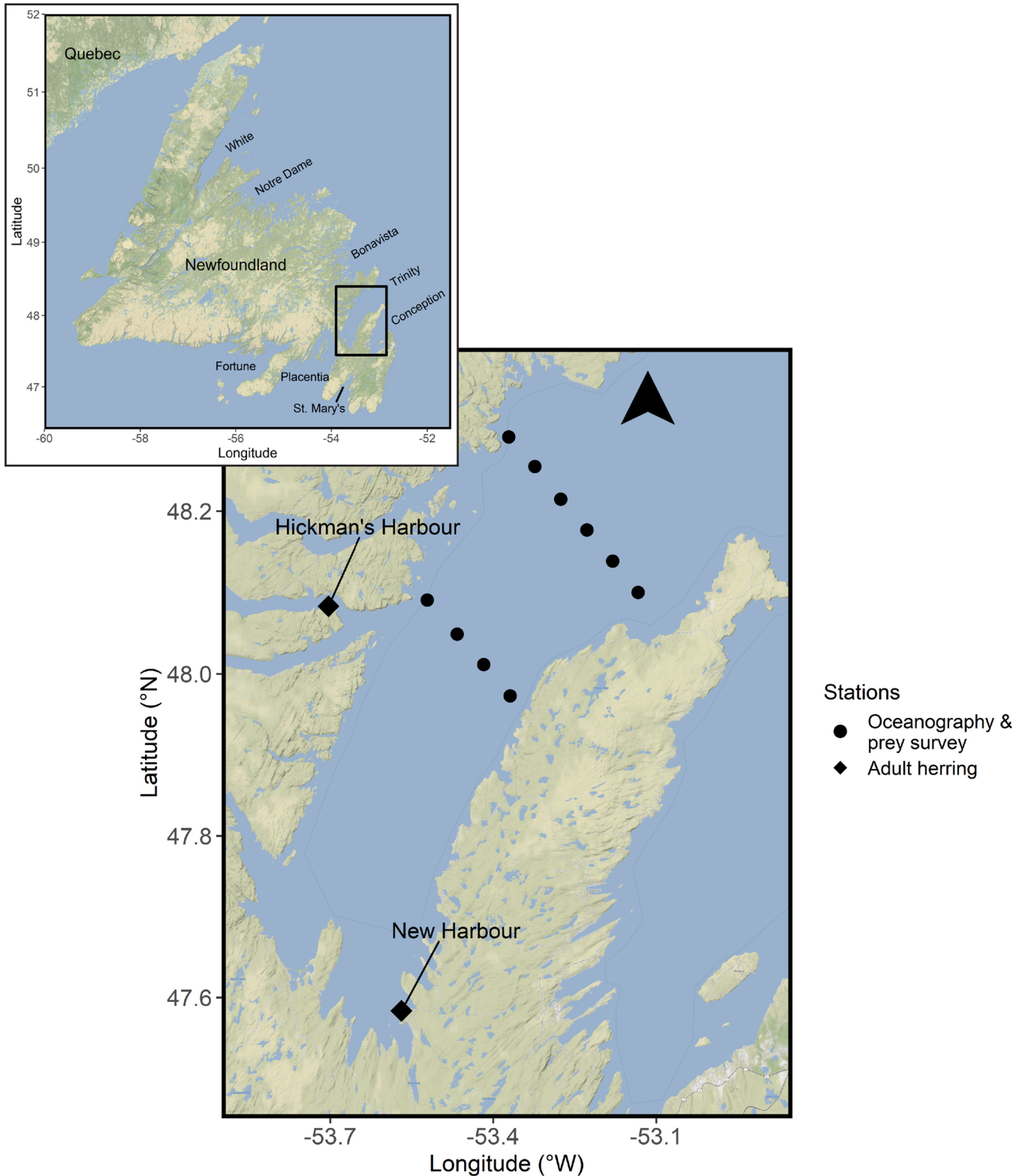


Fig. 1. Map of the study site in Trinity Bay, Newfoundland, with circles denoting stations along two transects (A and B) that were sampled for temperature and salinity, and where bongo nets were deployed to collect zooplankton. Diamonds indicate the locations where adult herring were sampled with gillnets.

(Koster and Mollman, 2000; Prokopchuk and Sentyabov, 2006; Segers et al., 2007), while chaetognaths and mysids are common in the diet of Gulf of St. Lawrence and New England herring (Bowman et al., 2000; Savenkoff et al., 2006). Herring also consume large numbers of fish larvae when they are present (Huse and Toresen, 2000; Hallfredsson et al., 2007; Hallfredsson and Pedersen, 2009). In the Barents Sea, juvenile herring feed heavily on larval capelin, and herring abundance has been related to recruitment variability of capelin in the region (Gjøsæter and Bogstad, 1998; Hjermann et al., 2010).

In contrast to the rest of the North Atlantic, information on the diet of herring in eastern Newfoundland is exceptionally scarce. A study from the 1940s revealed predation on capelin larvae in Fortune Bay, located on the southeast coast of Newfoundland (Templeman, 1948). However, the diet of herring from the northeast coast of Newfoundland remains unknown. Herring populations in this region have recently exhibited a change in spawning phenology, shifting from a spring-spawning population (estimated > 90%) to predominantly fall-spawning since the early 2000s (Bourne et al., 2018). Of the five stocks located in eastern Newfoundland, the most pronounced shift occurred in the Bonavista Bay-Trinity Bay stock complex, where fall-spawners now represent 80% of the population based on catch data (Bourne et al., 2018). Herring begin feeding immediately after spawning inshore, which potentially increases the predation pressure on the early life stages of capelin and Atlantic cod (*Gadus morhua*) that are present in the northeastern bays in late summer and fall (Baumann et al., 2003; Stanley et al., 2012, 2013). However, the lack of herring diet data from Newfoundland coastal ecosystems limits our understanding of the trophodynamics in the region.

This study aimed to improve our understanding of the ecology of Newfoundland herring and its vulnerability to climate change by relating the physical oceanography and prey field to herring feeding strategies in Trinity Bay. We hypothesized that adult herring in Trinity Bay exhibit a similar diet as other herring stocks in the Northwest Atlantic (i.e., dominated by copepods with a generalist feeding strategy) as well as prey on larval fishes (Templeman, 1948; Darbyson et al., 2003). To test our hypothesis, we compared physical oceanography and prey field data with the diet of adult herring sampled in late summer and early autumn of 2017–2019. Stable isotope analyses for two years (2018–2019) complemented our stomach analyses to allow for the evaluation of both short-term (instantaneous) and mid-term (integrated over two to three months) diets. Diet composition and selectivity analyses provided new insights into the resilience of Newfoundland herring to ongoing changes in the prey field due to bottom-up processes.

2. Methodology

2.1. Study area

Trinity Bay (48.0°N; 53.5°W), located on the northeast coast of Newfoundland, is approximately 100 km long by 30 km wide (Yao, 1986; Dalley, 2002) (Fig. 1). The mouth of the bay is oriented to the northeast and features a large sill at 240 m. The inshore branch of the Labrador Current transports water of Arctic origins (Lazier and Wright, 1993) into the bay from the northern side of its mouth, circulates counter-clockwise within the bay, and exits along the southern side of its mouth (Yao, 1986, Tittensor et al. Dalley, 2002, Baumann et al., 2003).

2.2. Oceanography and zooplankton

Two transects, parallel to the mouth of the bay with stations three nautical miles apart, were sampled for physical properties and plankton composition by Fisheries and Oceans Canada (DFO) in mid-August and September from 2017 to 2019, for a total of 6–10 stations sampled per survey (Fig. 1). In 2017, a Seabird 12 salinity-temperature-depth (STD) profiler was attached to bongo nets to collect temperature and salinity profiles, and in 2018–2019, a Seabird 19 Plus conductivity-temperature-

depth (CTD) was used to profile the water column. Variations in temperature and salinity remained minimal within each survey due to the proximity of stations and the bathymetry of the bay. Therefore, we pooled all CTD casts along Transect A (the transect with the highest sampling frequency; Fig. 1) to characterize the water column characteristics for a given survey. Casts were averaged by 1-m depth bins to create representative temperature and salinity curves for each month. Due to equipment malfunctions, two stations from August 2017 and one station from August 2019 were omitted from the analysis.

Methods for plankton sampling are detailed in Dalley et al. (2002). Briefly, plankton was collected by bongo nets of 61 cm diameter with 333 µm mesh nets and deployed in an oblique pattern to 10 m off the seafloor at each station or to a maximum of 200 m depth. General Oceanic flowmeters were attached to the mouth of each net to determine the volume of water filtered. The contents of one side of the bongo nets were preserved in 5% formalin for larval fish identification while the second side was either immediately frozen in seawater for stable isotope analysis or preserved in 95% ethanol.

Plankton samples from the second side of the bongo net were identified at the Université du Québec à Rimouski, Canada. Samples were diluted to known volumes, approximately 1000–2000 mL, with 10–30 mL subsampled (corresponding to a minimum number of 700 organisms), and zooplankton were enumerated and identified to the lowest taxonomic level possible. Larval fishes from samples preserved in formalin were sorted, enumerated, and identified at the Northwest Atlantic Fisheries Centre (NAFC), St. John's, Canada. Plankton samples designated for stable isotope analysis were thawed and identified to the lowest taxonomic level possible. Zooplankton taxa were either processed individually or grouped based on organism size and ability to produce approximately 1.0 mg dried weight (e.g., calanoid copepods were grouped while euphausiids were processed individually).

2.3. Herring sample processing

We sampled adult herring over ~12 weeks in late summer and autumn 2017–2019 at two sites in Trinity Bay: Hickman's Harbour and New Harbour (Fig. 1). Herring were collected biweekly from August to October in 2017 and from August to November in 2018, and weekly from August to November in 2019 following the survey design described in Bourne et al. (2018). Gillnets consisted of five multifilament nylon panels, measuring 34.3 m by 200 meshes deep with mesh sizes ranging from 50.8 to 76.2 mm in increments of 6.35 mm. The selected mesh sizes targeted the complete size range of adult herring, including the minimum size allowed in the commercial fishery (24.76 cm). Harvesters set the gillnets at sunset and pulled the nets approximately one hour after sunrise, which corresponded with peak herring stomach fullness (Darbyson et al., 2003) and minimal digestion. We collected the first ten fish encountered alive and in good physical condition (i.e., free of major abrasions or entanglements) in each gillnet for a maximum of 50 fish per sampling event. Herring were euthanized using a mixture of clove oil and ethanol (~50 mL, 1-part clove oil to 9 parts 99% ethanol added to a seawater bath) and immediately flash frozen on dry ice to halt digestion and preserve stomach contents. In 2018–2019, the first five fish from each 5 cm length bin over the 20–40 cm size range were subsampled for stable isotopes by removing a 1.25 cm² muscle plug from below the dorsal fin (Perga and Gerdeaux, 2005), and the tissue samples were flash frozen. Clove oil-ethanol euthanasia does not impact the stable isotope signatures of muscle tissue collected from fish (Hanisch et al., 2010, 2017).

Once the herring samples were back in the laboratory, herring were thawed and measured (Total Length, TL), weighed (total, gutted, and gonad), and sexed. Herring were assessed for maturity stage (Parrish and Saville, 1965; Appendix A). A single reader with 20+ years of experience aged a subset of herring otoliths. The reader assigned a spawning component for each aged fish as either spring (January 1st – June 30th) or fall (July 1st – December 31st) based on fish age, maturity, individual

otolith characteristics, and season of capture (see Wheeler et al., 2009 for details). Stomachs were removed with excisions anterior to the cardiac sphincter and posterior to the pyloric sphincter (Cunha et al., 2005) and re-frozen for later processing.

Because the morphometric and age data had non-normal distributions, we used non-parametric tests (Kruskal-Wallis tests) to test if there were significant differences in the age of herring between spawning components.

2.4. Herring diet analyses

Individual stomachs were thawed, weighed, and the stomach contents were removed to obtain the wet bolus weight. All prey items were enumerated and identified to the lowest taxonomic level possible using a Wild M3Z microscope (6.5–40.0×). Prey items were collectively weighed by taxa. While some prey were identified to species or genus, prey item categories (hereafter, prey items) were limited by the coarsest level of taxonomic resolution and pooled as such (e.g., some amphipods identified to species, but others only as Amphipoda so all were grouped as Amphipoda). All fish larvae in the stomachs were identified to the lowest taxonomic level possible. Any stomachs that were not fully intact or contained only unidentifiable material ($n = 19$, 1.50% of all processed herring) were omitted from the analysis.

Frozen herring tissue and zooplankton samples for stable isotopes analysis were freeze-dried for approximately 24–72 h, dependent on sample batch size, and pulverized to a fine powder using a sterilized mortar and pestle. Zooplankton samples were processed as whole organisms (Logan et al., 2008; Pomerleau et al., 2014) and were analyzed at the Cornell Stable Isotope Laboratory. Stable isotope ratios of C^{13} and N^{15} , as well as elemental C:N, were measured using a Thermo Delta V Advantage mass spectrometer, plumbed to a Carlo Erba NC2500 Elemental Analyzer via a ConFlo III interface. Samples were matched against in-house standards calibrated against international standards. Error, as assessed by sample replicate analysis, was 0.18‰ for $\delta^{15}N$ and 0.17‰ for $\delta^{13}C$. Delta values for C^{13}/C^{12} and N^{15}/N^{14} were calculated using Eq. (1):

$$\delta_{\text{sample-standard}}(\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] * 10^3 \quad (1)$$

where R_{sample} represents the ratio of heavy isotope to lighter isotope in the sample, R_{standard} is the ratio of heavy to light isotope in the reference sample calibrated against international standards, and $S_{\text{sample-standard}}$, either $\delta^{13}C$ or $\delta^{15}N$, is expressed as parts per-mille (‰).

It is essential to correct for lipid variability as many organisms accrue large lipid stores in summer months, particularly in high latitude regions (Hagen and Auel, 1999). Species' tissue-specific corrections were not available for all taxa so the following standard lipid correction for aquatic animals (Post et al., 2007) was applied *a posteriori*:

$$\delta^{13}C = 0.99 * C : N_{\text{ratio}} - 3.32 \quad (2)$$

A carbonate correction was applied to the shelled pteropods, *Limacina* spp., to account for potential $\delta^{13}C$ bias from inorganic carbon (Pomerleau et al., 2014):

$$\delta^{13}C_{\text{acid}} = 0.994 * \delta^{13}C_{\text{bulk}} - 1.096 \quad (3)$$

with C_{bulk} representing the lipid-corrected carbon value and C_{acid} representing the acidified (carbonate and lipid corrected) carbon value.

2.5. Plankton analyses

Mean densities and standard error (SE) of zooplankton and larval fish taxa (individuals·m⁻³) were calculated for all stations in August and September. To differentiate between plankton communities at all stations, we conducted a cluster analysis using e-PRIMER 6.0 software (Clarke, 1993). Plankton densities were fourth-root transformed to

equalize variance among species, and a Bray-Curtis similarity index was calculated. We determined which plankton taxa contributed to differences among cluster groupings using a similarity percentage analysis (SIMPER).

To determine the drivers of variability in plankton density between surveys, temperature, salinity, month, and year were used as independent variables in a distance-based linear model (DistLM) with forward selection and adjusted R^2 to determine the order of importance of the independent variables. Mean salinity and temperature were calculated at the surface (0–10 m) and at depth (180–190 m, which is the deepest interval possible across stations) at each station. Temperature and salinity were normalized and Euclidean distances calculated. A permutational multivariate analysis of variance (PERMANOVA) test, informed by the order determined by the DistLM, was used to assess the effect of temperature, salinity, and time on plankton density. Because these plankton data had a non-normal distribution, we used non-parametric tests (Kruskal-Wallis) to test the differences in zooplankton densities among months and years.

2.6. Diet metrics

Based on prey accumulation curves, the sampling effort of herring stomachs was sufficient in a majority of months and years to compare diet trends throughout the time series (Appendix B). However, due to insufficient samples sizes in November 2018–2019 and August 2019, these months were omitted from diet analyses (Table 1; Randall, 2020). Even though herring captured on a given day were likely feeding on the same prey assemblage, we followed Drazen et al. (2008) and Raab et al. (2012) and treated individual herring as independent observations in our diet analysis, as we were interested in evaluating individual diet selectivity. Herring diets were assessed using four metrics: gravimetric weight; mean partial and total fullness index (PFI and TFI, respectively); frequency of occurrence; and prey-specific abundance. The gravimetric weight provided an estimate of prey contribution to diet by weight and was calculated using Eq. (4):

$$\% G_i = \sum_{k=1}^n S_{ik} / S_k \quad (4)$$

where S_{ik} is the weight (g) of prey item i in the stomach of herring k ; S_k is the total weight (g) of all prey items in the stomach of herring k ; and n is the number of stomachs (Hyslop, 1980). Prey items that contributed < 5% to gravimetric weight in a given month were pooled as 'Other'.

Mean PFI provided a measure of stomach fullness for each prey item within a sample, accounting for length differences of herring and was calculated using Eq. (5):

$$PFI_i = \frac{1}{n} \sum_{k=1}^n S_{ik} / (L_k)^3 * 10^4 \quad (5)$$

where S_{ik} is the weight (g) of prey item i in the stomach of herring k , n is the number of stomachs, and L_k is the total length (cm) of herring k (Lilly and Fleming, 1981; Dalpadado and Bogstad, 2004).

The mean TFI provided a measure of total stomach fullness across all prey items, relative to fish length and was calculated using Eq. (6):

$$TFI = \frac{1}{n} \sum_{k=1}^n S_k / (L_k)^3 * 10^4 \quad (6)$$

where S_k is the total weight (g) of all prey items in the stomach of herring k ; and L_k is the total length (cm) of herring k (Lilly and Fleming, 1981; Dalpadado and Bogstad, 2004). We tested if there was a difference in TFI values between spawning components (fall and spring) using a non-parametric Kruskal-Wallis test.

Frequency of occurrence provided an estimate of the presence of prey items across all herring diets and was calculated using Eq. (7):

Table 1

Summary of Atlantic herring characteristics for each sampling month. Of the 1172 total fish suitable for stomach content analysis, 18 contained completely digested or unidentifiable material and 120 were empty. A total of 1052 stomachs contained prey items and were included in the diet analyses. Of the 260 herring muscle samples collected for stable isotope, 226 had complete data available for this study. Spawning component and age data were available for a subset of 747 herring. SCA: stomach content analysis, SIA: stable isotope analysis, SR: spawner ratio (fall:spring), FI: feeding incidence (number of stomach containing prey:total number of stomachs), TFI: total fullness index, TL: total length.

	Total	SCA	SIA	SR	FI	TFI	TL (cm)	Age (years)	Maturity Stage
Aug-17	288	263	–	0.99	0.90	0.12	32.75 ± 0.21	7.94 ± 0.17	3.91 ± 0.05
Sep-17	205	187	–	1.27	0.91	0.16	31.26 ± 0.24	6.56 ± 0.18	3.99 ± 0.08
Oct-17	47	35	–	1.35	0.65	0.49	31.48 ± 0.53	6.93 ± 0.42	3.59 ± 0.18
Aug-18	91	67	15	1.19	0.70	0.06	32.58 ± 0.33	7.33 ± 0.71	4.01 ± 0.09
Sep-18	119	112	50	0.75	0.93	0.13	31.30 ± 0.25	6.46 ± 0.33	4.24 ± 0.08
Oct-18	193	173	70	0.80	0.86	0.56	31.15 ± 0.17	6.51 ± 0.34	3.57 ± 0.07
Sep-19	115	110	45	1.17	0.95	0.04	31.85 ± 0.22	7.13 ± 0.38	4.64 ± 0.13
Oct-19	114	105	46	1.46	0.92	0.12	31.81 ± 0.20	6.93 ± 0.33	4.18 ± 0.12
Total	1172	1052	226						

$$\% F_i = n_i/n \quad (7)$$

where n_i is the number of stomachs containing prey item i and n is the total number of stomachs. Only prey categories with > 5% frequency for a given month were included.

Because estimates of prey availability in the environment were not available at the time of capture, we could not calculate traditional selectivity indices (Lechowicz, 1982a, 1982b) and instead used a graphical analysis to examine herring feeding preferences. Prey-specific abundance was calculated using a graphical analysis (Costello 1990, Amundsen et al., 1996) to examine feeding strategy, prey selectivity, and resource use at the individual and population level. The graphical analysis of feeding strategy plots the frequency of occurrence by a prey specific abundance:

$$P_i = \left(\frac{\sum S_i}{\sum S_{ij}} \right) \times 100 \quad (8)$$

where S_i is the weight (g) of prey item i in herring stomachs; and S_{ij} is the total weight (g) of all prey items in the stomach of herring which fed on prey i . The position of prey items on the plot from the lower-left to the upper-right corners reflects the relative importance of the prey item in herring diet (increasing from left to right) while the position of prey items along the y-axis indicates either a generalized (low values) or a specialized feeding strategy (high values; Amundsen et al., 1996). The position of prey items on the plot from the upper-left to the lower-right corners indicates niche width contribution, differentiating between high between-phenotypes (individuals focusing on different resources) and high within-phenotypes (population-level predation upon a range of common prey items).

To evaluate piscivory in the diet, we first pooled all fish data (i.e., eggs, larvae, juvenile/age-1 fishes as well as fish remnants such as skeletons, otoliths, tissue) into a collective 'ichthyoplankton' category for each diet metric. The 'eggs and gravel' category, which consisted of eggs adhered to gravel, was not included in the 'ichthyoplankton' category. As we were particularly interested in the consumption of fish eggs and larvae, we also evaluated these life stages separately using both frequency of occurrence and gravimetric weight analyses and included all values (no 5% cutoff, 'eggs and gravel' category included) to examine potential patterns of piscivory further.

2.7. Isotopic signatures

The mean, SE, and range of herring isotopic signatures were calculated for each month, and Spearman rank correlations were used to determine if changes in lipid-corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significant among months and years. Isotopic signatures were also evaluated with consideration to trophic discrimination factors, or fractionation (e.g., $\Delta\delta^{13}\text{C}$ or $\Delta\delta^{15}\text{N}$ from prey to predator in which isotopes in predators become slightly enriched through assimilation; Post, 2002; Olive et al.,

2003). Carbon is thought to vary minimally between trophic levels in the marine environment (DeNiro and Epstein, 1978; Barnes et al., 2007), while 3.4(‰) is the estimated fractionation value for nitrogen (Minagawa and Wada, 1984; Post, 2002). Some prey items found in herring stomach contents were not represented in the stable isotope samples, so we did not attempt to apply mixing models or calculate niche breadth (Matthews and Mazumder, 2005; Phillips et al., 2014), both of which require the full array of prey items. We used Kruskal-Wallis tests to assess potential differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ by spawning component. Analyses of herring diet metrics and stable isotopes were performed using base R v. 4.0.3 (R Core Teams 2020).

3. Results

3.1. Oceanography

The oceanography of Trinity Bay in August was similar across all years with warm, fresher water at the surface (10.5–16.6 °C and salinity 29.8–31.9) with a thermocline between 10 and 20 m (Fig. 2). The surface waters in August of 2017 were warmer (16.6 °C vs. 10.5–11.4 °C) and fresher (29.8 vs. 31.6–31.9) than either 2018 or 2019. The oceanography of Trinity Bay in September varied interannually, particularly in the depth of the mixed layer and thermocline. Surface temperatures in September were warm (10.6–12.5 °C) and less saline (30.3–30.8) but with a deeper, more variable thermocline between 25 and 70 m (Fig. 2). The shallowest thermocline in September was observed in 2017 at only ~30 m depth. In September 2019, cooler surface temperatures (10.5 vs. 11–12 °C) and a deep thermocline (70 m depth) suggest increased mixing in the upper levels of the water column relative to other months and years (Fig. 2).

3.2. Prey field

Zooplankton abundance was highest in 2018, followed by 2019 and 2017, with September generally more productive than August although these trends were not statistically significant (Kruskal Wallis tests: month effect: $p = 0.513$ and year effect: $p = 0.651$; Fig. 3a-b). A total of 57 different zooplankton and larval fish taxa were identified (ranging from species to phylum) in the plankton samples (Table 2). Only 12 zooplankton and ichthyoplankton taxa were present throughout all six surveys: seven genera of copepods (*C. finmarchicus*, *C. hyperboreus*, *Centropages hamatus*, *Paracalanus* spp., *Metridia longa*, *Temora longicornis*, *Oithona similis*), ostracods, chaetognaths, euphausiid larvae, gastropods, and capelin.

Copepods were the most abundant taxa by nearly an order of magnitude throughout all surveys with temporal differences detected in 2018 and 2019 (Fig. 3a). *Pseudocalanus* spp. comprised 58–62% of the copepod composition in August 2018 and 2019, while *Temora longicornis* comprised 44.3–61.6% of the copepod composition in September 2018

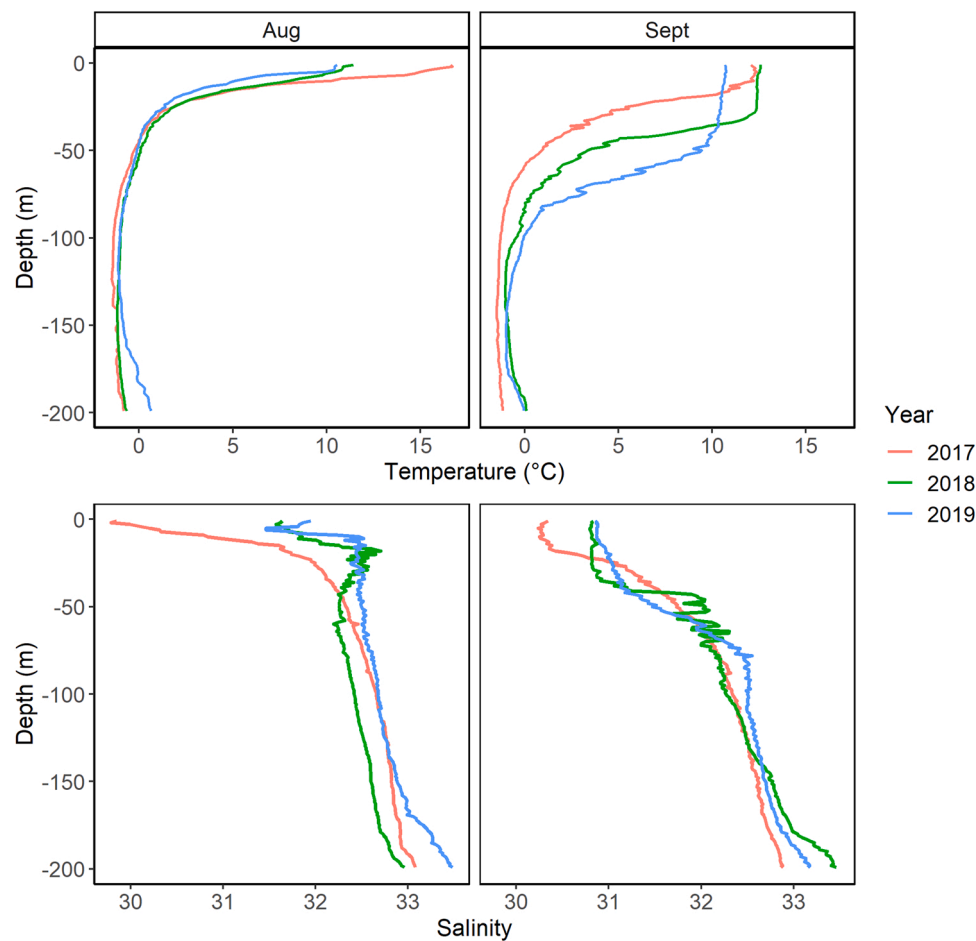


Fig. 2. Temperature and salinity profiles of the water column in Trinity Bay, Newfoundland in mid-August and mid-September of 2017 – 2019 with values averaged by 1-m depth intervals.

and 2019 (Fig. 3a). There was no trend in *Calanus* spp. densities, with *Calanus* spp. comprising between 15% and 37% of the copepod composition in all months (Fig. 3a).

There was temporal variability in the density of other key plankton taxa, including cladocerans, gastropods, chaetognaths, and fish larvae (Fig. 3b). Cladocerans were dominant in August 2017 and 2018, while gastropods were dominant in September 2018 and 2019 (Fig. 3b). Chaetognaths were present at higher densities in September than August with the highest densities observed in 2019 (Fig. 3b). Fish larvae were observed throughout the study, but at lower densities than other plankton taxa (<1 fish m^{-3}) (Table 2 and Fig. 3b). The dominant species of ichthyoplankton was capelin and they were sampled throughout all months and years (Table 1). The highest abundance and species richness of fishes occurred in August 2017 and September 2019.

The cluster analysis revealed six statistically distinct communities of zooplankton across all years with communities more similar from August 2017 to August 2018 and more dissimilar from September 2018 to September 2019 (Fig. 4, Appendix C). Copepods (namely *Calanus*, *Pseudocalanus*, and *Temora*) dominated the zooplankton communities, so the similarity among groups was set at a high cutoff (72%; Appendix D) and small differences in the contribution of other taxa drove the dissimilarity (Appendix C). Two groups, A and B, occurred exclusively in 2017 and August 2018 and were characterized by the high contributions of *Evadne* spp., *Acartia* spp., and euphausiids (Appendix C). Group C included only three stations between September 2017 and August 2018 and was distinguished by high contributions of *Metridia* spp. and ostracods (Appendix C). Intra- and inter-annual variability increased after August 2018, with all stations from September 2018, August 2019, and

September 2019 forming distinct groups (Fig. 4). High contributions of copepods (namely *Calanus*, *Pseudocalanus*, and *Temora* as well as *Metridia* and *Oithona*) helped distinguish communities in 2019 (groups E and F) relative to other years which had increased contributions of other non-copepod taxa (Appendix C).

Environmental factors were a strong driver of plankton variability. The distance-based linear model found all environmental variables to be significant ($p = 0.001$) in defining plankton communities. A PERMANOVA revealed that the ordered environmental variables with a joint year-month factor explained over 85% of the observed variability. Collectively, environmental variables explained more than 73% of the variability, with average bottom salinity being the primary driver of plankton communities (44.7%). An interaction was found between Year and Month, explaining 12.8% of the variation. There were significant differences between all month and year comparisons (Appendix E).

3.3. Herring size and age

A total of 1172 herring stomachs were analyzed in this study (540 in 2017, 403 in 2018, and 229 in 2019) (Table 1). Herring ranged in size from 24.1 to 40.0 cm TL, and the mean length in each month and year was similar at 31–32 cm TL (Table 1).

A total of 747 herring were aged. Ages ranged from 3 to 11 + years (maximum age counted) and there was a significant difference in the age of herring between spawning components (Kruskal-Wallis, p -value = 2.2×10^{-16}) with fall-spawners generally two to three years older than spring-spawners in a given month (Appendix F). The average maturity stage across all months was 4, indicating that most individuals were mature

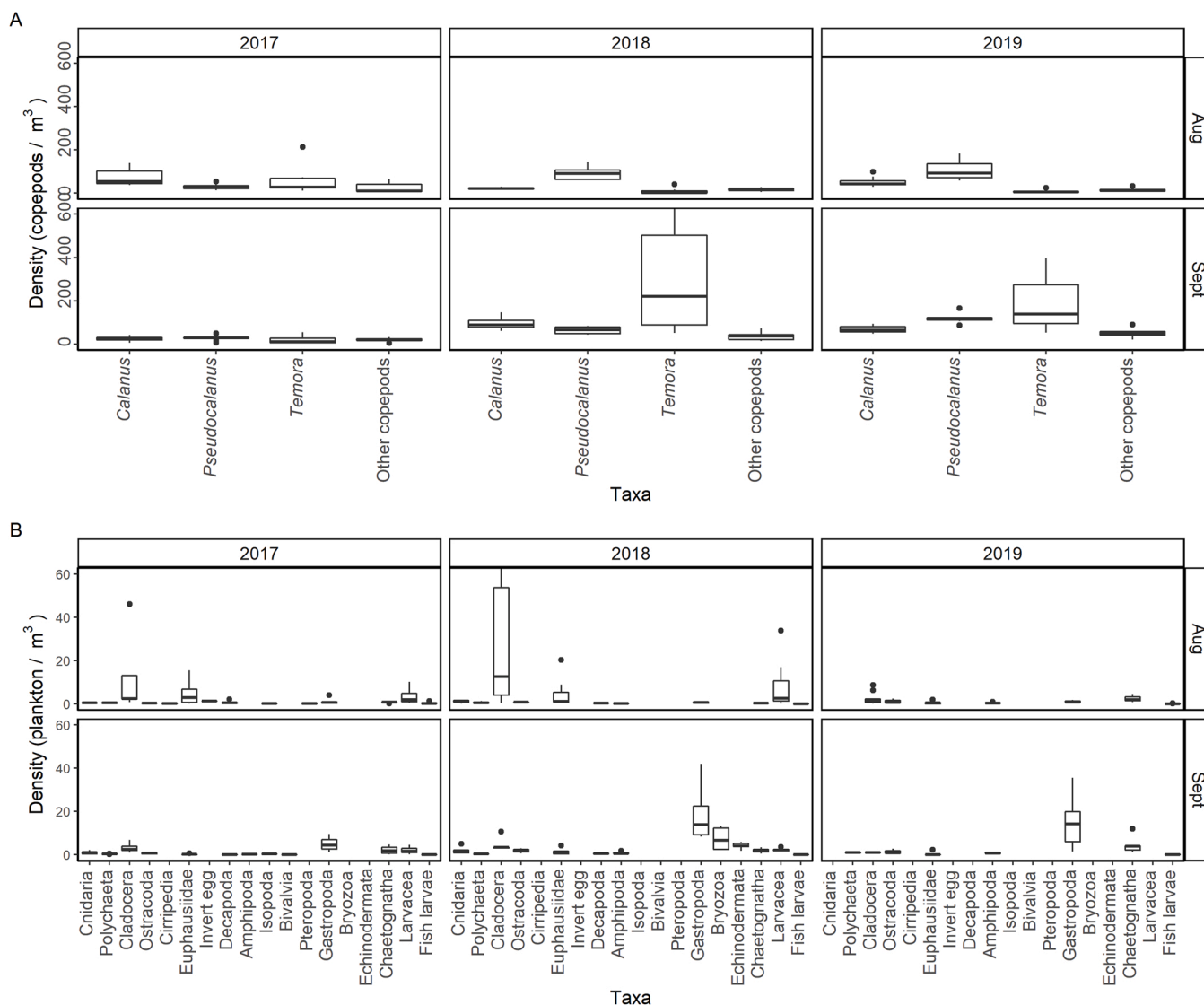


Fig. 3. Density of zooplankton taxa sampled in Trinity Bay, Newfoundland (August and September 2017–2019) with estimated total zooplankton density and SE reported in the upper right corner of each plot. Boxplots display the median with lower and upper box hinges representing the 25 th and 75 th quantiles, respectively. Whiskers represent either the minimum/maximum value or 1.5 * interquartile range. A) Density of three dominant copepod and the pooled value of all ‘Other’ copepod genera, B) Density of all non-copepod groups. Data not depicted (3b) to preserve scale: one outlier in Aug 2017 (77.6 Cladocera m⁻³) and upper whisker in Aug 2018 (115.7 Cladocera m⁻³).

(Table 2).

3.4. Herring diet

A total of 120 stomachs were empty or contained only parasitic nematodes (10.2% of all processed herring). Feeding incidence ranged from 0.65 to 0.95 and peaked in September of all years (Table 2). The TFI values ranged from 0.04 to 0.56 across all months, with fullness generally increasing from August to October (Table 2). The TFI tripled from September to October in all years although stomachs in September and October 2019 had the lowest TFI of the time series. There were no significant differences in TFI values between spawning components (Kruskal-Wallis, p-value=0.34).

The two prey items that contributed most to herring diets by weight were amphipods and copepods (Fig. 5a-b). Amphipods consistently comprised a large proportion of the diet by weight from August 2017 to September 2018 and thereafter copepods comprised a larger proportion of the diet (Fig. 5a). Both amphipods and copepods had high frequencies of occurrence in herring diets, but the proportion of the population

feeding on these prey items differed (Fig. 6). Amphipods were consumed by between 8% and 64% of the sampled herring each month, while copepods were consistently consumed by > 60% of the sampled herring, except for an anomalously low frequency of occurrence in October 2017, which coincided with peak amphipod consumption (Fig. 6). The PFI analysis revealed similar trends, showing that amphipods and copepods were important prey items by weight but, overall, copepods contributed less to diets once herring weight (and therefore consumption capacity) was accounted for (Fig. 5b).

In addition to amphipods and copepods, two additional zooplankton taxa were identified as key contributors to herring diet in the PFI, gravimetric weight, and frequency of occurrence analyses: euphausiids and decapods (primarily crab zoea and megalopa). Euphausiids contributed to the diet by weight primarily in August 2017, September 2017, and August 2018 (Fig. 5a-b) and were consumed by 19.1–27.6% of herring (Fig. 6). Decapods only contributed substantially by weight in September and October 2017 (Fig. 5a-b) and were consumed most frequently in 2017 (frequency of occurrence: 22.9–45.1%; Fig. 6). The remaining 16 prey items identified in the diet (e.g., polychaetes,

Table 2

Mean (\pm SE) density (individuals m^{-3}) of all larval fishes sampled with the bongo nets in Trinity Bay, Newfoundland, identified to the lowest possible taxonomic level. All fish taxa were pooled under the “ichthyoplankton” category for analysis.

Species	2017		2018		2019	
	Aug	Sept	Aug	Sept	Aug	Sept
<i>Clupea harengus</i>		0.01		0.01		0.01
<i>Gadus morhua</i>			0.01			0.01
<i>Liparis</i> spp.	0.01					0.01
<i>Sebastes</i> spp.			0.01			
<i>Sebastes fasciatus</i>	0.01					
Stichaeidae	0.01					0.01
<i>Ulvaria subbifurcata</i>	0.02					
<i>Tautoglabrus adspersus</i>	0.09 \pm 0.05	0.01				
<i>Mallotus villosus</i>	0.31 \pm 0.11	0.06 \pm 0.01	0.05 \pm 0.02	0.03 \pm 0.01	0.08 \pm 0.03	0.08 \pm 0.02
<i>Glyptocephalus cynoglossus</i>	0.02					0.01
<i>Limanda ferruginea</i>	0.01					0.01

larvaceans, pteropods, and organic material) occurred infrequently and only sporadically contributed to the diet by weight (Figs. 5a-b and 6). Although spring-spawners had a more diverse diet, these additional prey items contributed minimally to the diet by weight (Appendix G). The main prey items listed above were consumed by both spawning components in nearly all months (Appendix G).

Herring fed on ichthyoplankton (pooled fish eggs and larvae) in all months of the study (Fig. 6), though ichthyoplankton only substantially contributed to diet by weight in 2017 (Fig. 5a-b). Evidence of fish in the stomachs included single, hard structures (bones, fin rays, and otoliths), intact spines and digestive tracts, and reasonably well-preserved whole specimens. Varying degrees of digestion made it difficult to identify

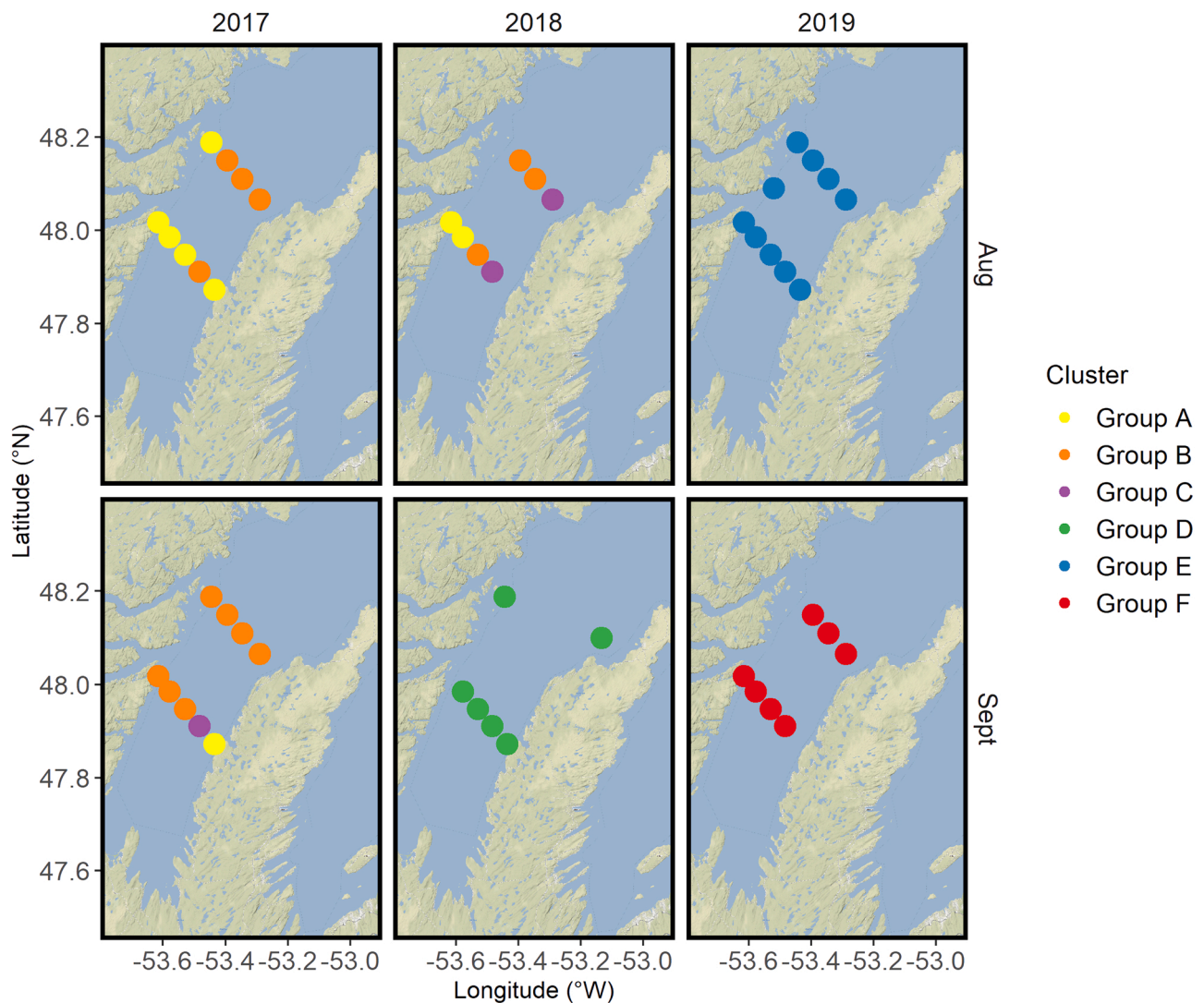


Fig. 4. Cluster groups identified across zooplankton communities sampled from 2017 to 2019 in Trinity Bay, Newfoundland, defined by Bray-Curtis similarity index and cluster analysis with a 72% cutoff.

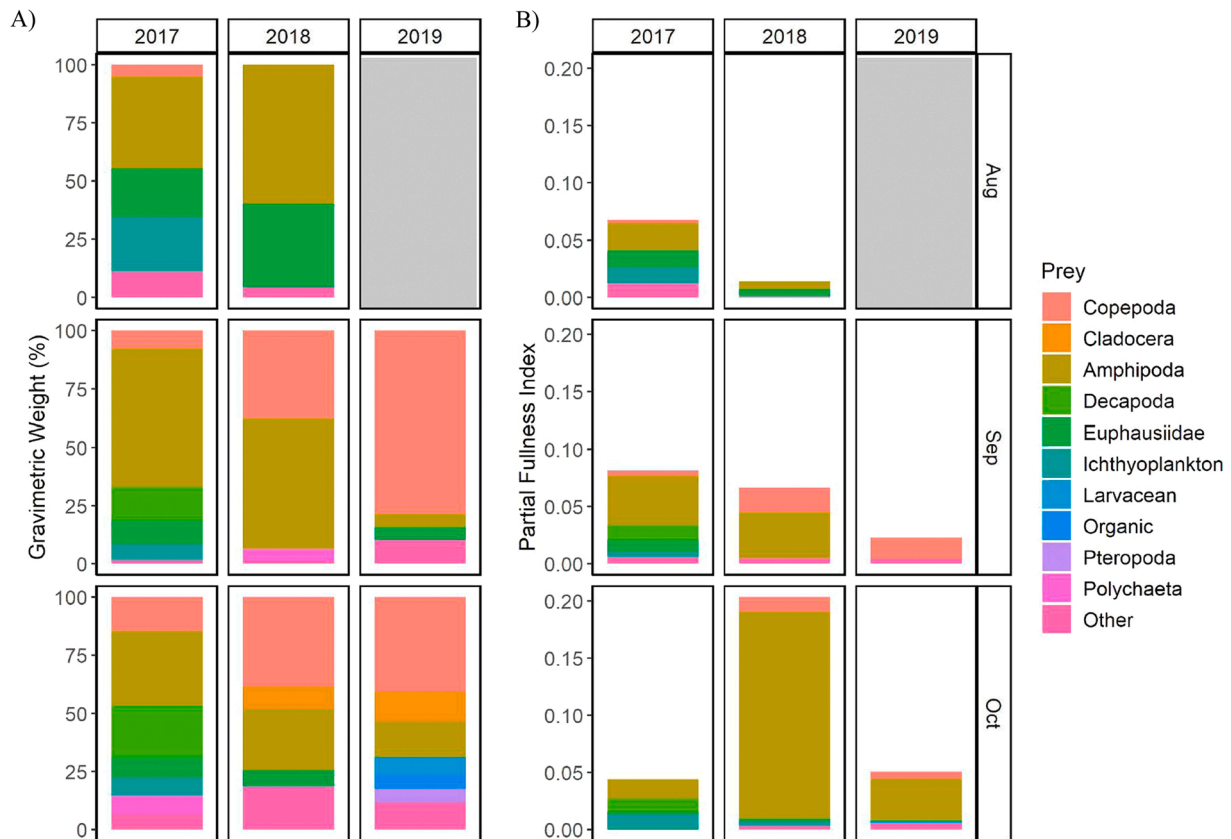


Fig. 5. Weight-based diet analyses of prey item contribution to Atlantic herring diets by A) gravimetric weight, B) partial fullness index. Prey items that contributed < 5% to gravimetric weight were pooled as ‘Other’.

most fish larvae in the diets. Capelin represented 57.9% of the fish that were identified. The forage species Arctic cod (*Boreogadus saida*, 21.1%), sand lance (*Ammodytes* spp., 15.8%), and daubed shanny (*Leptoclinius maculatus*, 5.2%) represented most other fish species in the herring diets. Although loose otoliths primarily appeared to be either from capelin or gadids, they could not be reliably paired for counts or assigned to specific taxa with certainty due to indeterminate exposure to gastric acid, which can rapidly erode fine structural details in a matter of hours (Jobling and Breiby, 1986).

Individual herring often consumed several different life stages of fishes and, when present in the stomach contents, early life stages of fishes were often highly abundant. Maximum numbers in a single stomach included > 300 fish eggs in one stomach and 32 fish larvae in another. The largest measurable fish prey was a 7.5 cm juvenile capelin. Across all years, fish eggs (present in 119 herring stomachs, 11.3%) were consumed more frequently than larvae (present in 60 herring stomachs, 5.7%) (Fig. 7a). Fish eggs were more often consumed in August and September, and fish larvae were more often consumed in October (Fig. 7a). The frequency of occurrence of fish eggs in herring diets in August 2018 was low (4.6%), relative to August 2017 (23.7%; Fig. 7b). In September 2019, frequency of occurrence of fish larvae in the diet was comparable or greater to 2017 but fish contributed little to the diet by weight (Fig. 7a-b). A single occurrence of ‘eggs and gravel’ in August 2017 in the diet analyses (Fig. 7a-b) was an indication that herring may forage on demersal, adhesive capelin eggs that were spawned on gravel. Although this prey category was detected in only a few herring, the proportion of eggs and gravel in the diet by weight was 7.89% in August 2017 (Fig. 7a-b) reflecting heavy predation by some individuals.

3.5. Stable isotope analysis

Of the 260 herring muscle samples collected for stable isotope

analysis, 226 had complete data available for this study (samples from August and September 2018 and September 2019). Stable isotopes from 99 potential zooplankton prey items were also analyzed. Herring isotope signatures were relatively stable among the months and years of the analysis (Fig. 8). The mean $\delta^{15}\text{N}$ ranged from 12.41 to 12.63‰ while the range of the mean $\delta^{13}\text{C}$ was slightly broader, from -20.22 to -20.87 ‰ (Fig. 8). No significant differences were detected between months for either $\delta^{13}\text{C}$ (Spearman rank correlation, $\rho = -0.05$, p-value = 0.43) or $\delta^{15}\text{N}$ (Spearman rank correlation, $\rho = 0.65$, p-value = 0.31). However, there was a statistically significant, albeit weak, negative correlation between $\delta^{13}\text{C}$ and year (Spearman rank correlation, $\rho = -0.387$, p-value = 6.50×10^{-9}) and a positive correlation between N^{15} ratios and year (Spearman rank correlation, $\rho = 0.15$, p-value = 0.2), indicating a shift towards a more pelagic source of carbon (more negative $\delta^{13}\text{C}$) and feeding at a slightly higher trophic level in 2019 relative to 2018. There was no effect of spawning component on either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ (Kruskal-Wallis, p-value = 0.94 and 0.45; respectively).

The carbon and nitrogen signatures of prey items varied more than that of the adult herring, both among individuals, as reflected in larger standard error values, and temporally, shown by fluctuations of the mean over time (Fig. 8). The mean $\delta^{13}\text{C}$ ranged between -18.21 to -23.82 ‰ for most prey items, except for shelled pteropods, which ranged from -11.98 to -13.93 ‰ (Fig. 8). As benthic sources of carbon are more enriched in C^{13} than pelagic sources, this suggests that *Limacina* may occupy a more benthic niche than other prey items. Although there was more variability in C^{13} depleted prey items among surveys, euphausiids, chaetognaths, and capelin were characterized by low C^{13} ratios (Fig. 8), which indicates pelagic feeding.

The mean $\delta^{15}\text{N}$ was broader than that of carbon ratios (6.8 – 13.32 ‰) and generally had a more extensive range within prey items (Appendix H). Both genera of pteropods, *Limacina* and *Clione*, had

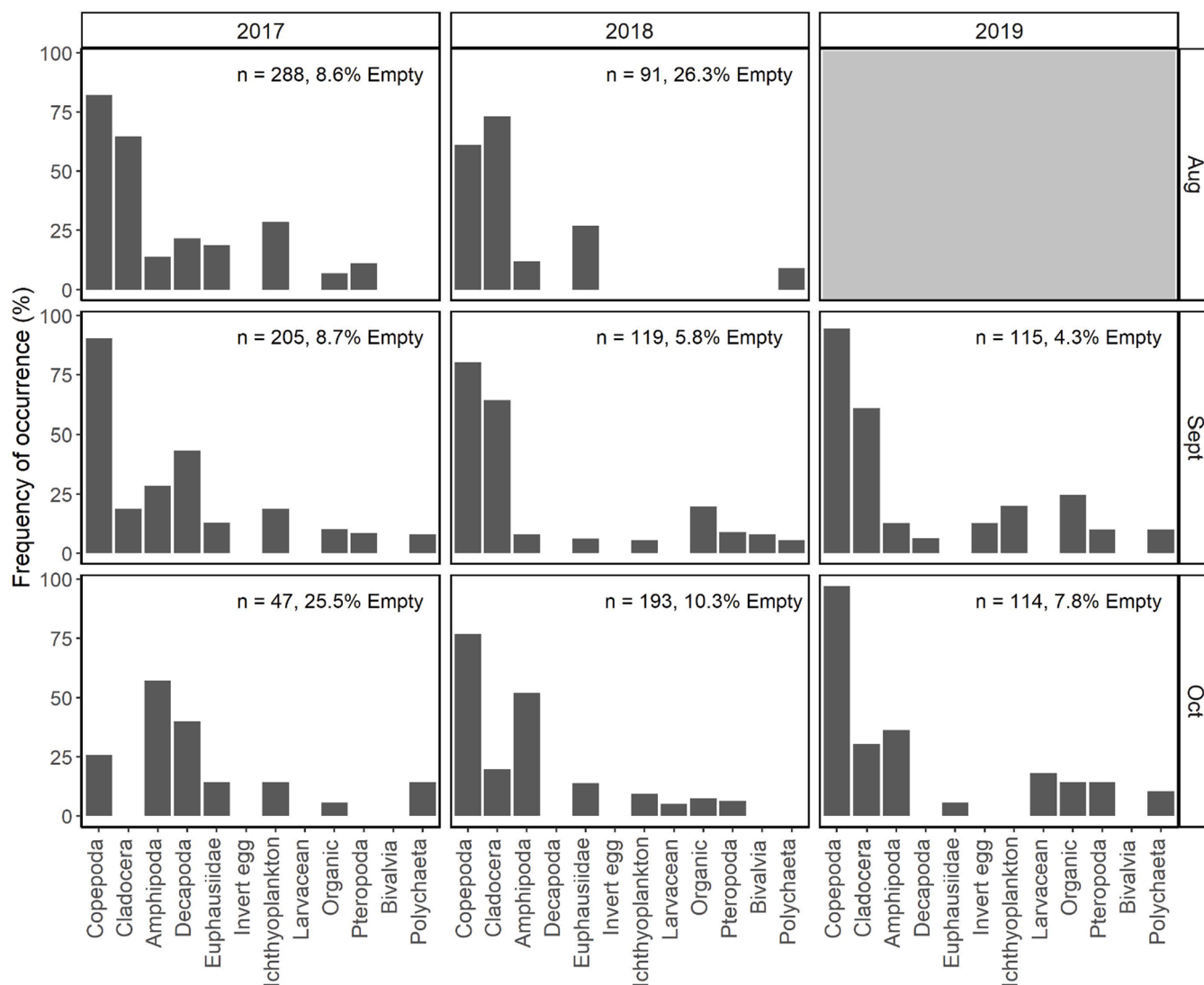


Fig. 6. Frequency of occurrence of each prey category in Atlantic herring diets by month and year. Only prey categories with > 5% frequency for a given month are shown.

the most depleted N^{15} ratios, suggesting a lower trophic position relative to other prey items. Fish eggs had the most enriched N^{15} ratios in August of both years at $13.32 \pm 1.84\text{‰}$ and $12.94 \pm 1.62\text{‰}$ (2018 and 2019, respectively), reflecting the maternal isotopic signatures. Ostracods had the most enriched N^{15} ratios in September 2018 (10.74‰) and chaetognaths in September 2019 ($11.36 \pm 0.62\text{‰}$). Other prey items with high $\delta^{15}N$ values included predators such as capelin larvae as well as omnivorous euphausiids, particularly in August of 2019 (Fig. 8; Appendix H). In both years of sampling, there was high variability in N^{15} ratios among individual herring for fish eggs, euphausiids, and decapods in August. Although sample sizes of prey items were small in both years ($n < 5$), there was much less variability in the N^{15} ratios in September for the same prey species (when present), which may suggest either a change in diet or change in the nitrogen source of primary producers between the two months.

3.6. Prey selectivity

Across all sampling periods, individual herring opportunistically fed on a variety of prey items that contributed little to the overall diet by weight (Fig. 9). Most herring also opportunistically consumed copepods in 2017–18, although the prey item contributed little to herring diets by

weight, except in September 2018 and 2019 when herring selectively consumed copepods (Fig. 9). Selective feeding occurred in all months by at least some individuals of the population, with consumption concentrated on one to four prey items. Although the preferred prey type varied among months, amphipods were the most commonly selected prey item (Fig. 9). Other selected prey items included ichthyoplankton in 2017, euphausiids in 2017 and August 2018, and decapods in August and September 2017.

4. Discussion

4.1. Importance of the prey field to herring diet

Herring diet reflected changes in zooplankton community composition in Trinity Bay. The main prey of herring in late summer and autumn in Trinity Bay were amphipods (primarily *Themisto* spp.) and calanoid copepods (primarily *Calanus* and *Temora* spp.), consistent with previous studies throughout the North Atlantic (Darbyson et al., 2003; Casini et al., 2004; Dommasnes et al., 2004). While herring mainly consumed crustaceans, 18 different prey items were observed in herring stomachs. Although it is possible that some soft-bodied prey may have been digested by the time we sampled and flash-froze the herring, the

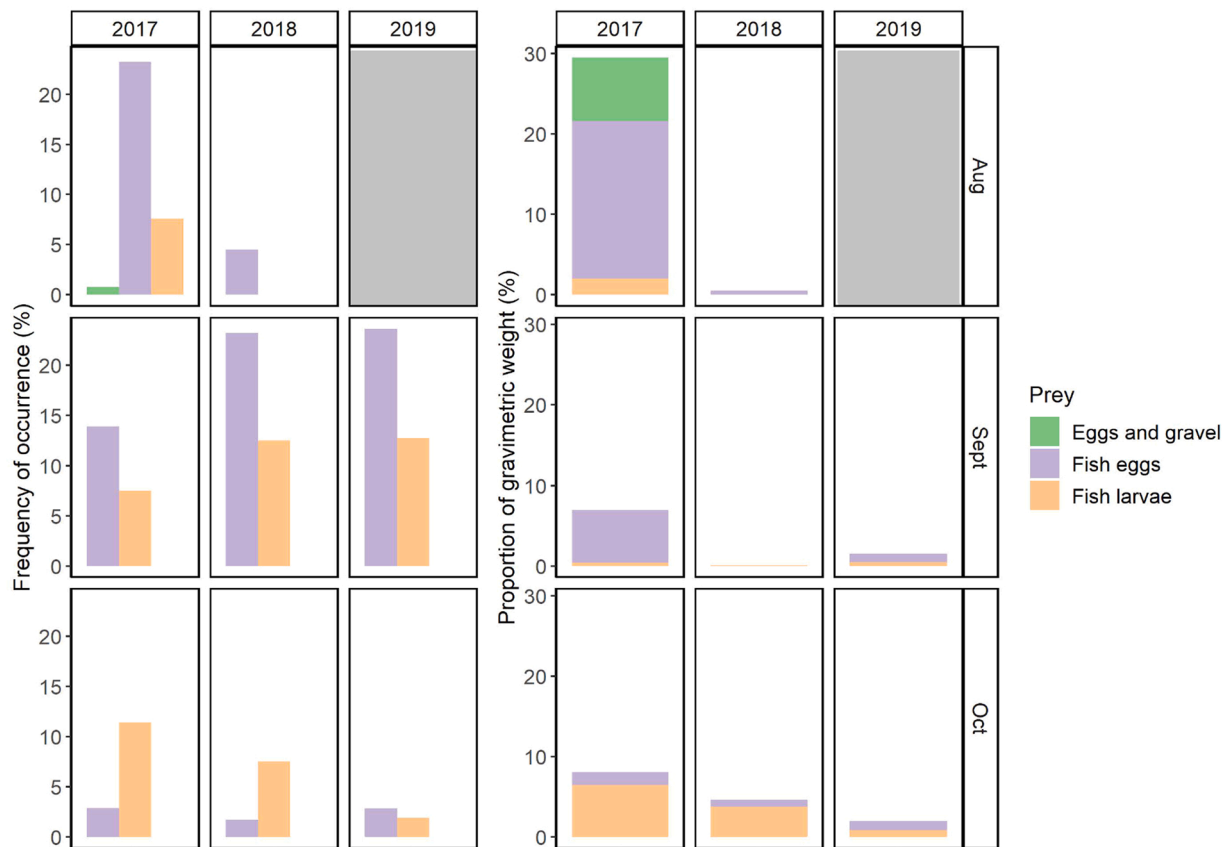


Fig. 7. Presence of early life stages of fishes in the diets of Atlantic herring represented by A) frequency of occurrence and B) gravimetric weight. 'Eggs and gravel' indicate benthic, adhesive eggs (likely capelin) that could not be separated from sediments. The category 'Fish larvae' includes all remnants of fish identified in the stomach contents.

occurrence of prey such as larvaceans and the tissues of fish suggests that digestion of these soft-bodied organisms was minimal. The selectivity analysis showed that herring fed both opportunistically on a variety of prey items that contributed little to diet by weight, and selectively on specific prey during periods of high prey densities in the environment (e.g., larval fish, decapods, and euphausiids before September 2018 and copepods during/after September 2018). There was less variability in herring diet in 2017 and August 2018 when zooplankton communities were more similar between months, relative to the latter half of the study. The observed concurrence between plankton prey fields and herring diets reinforces previous findings that herring have the capacity to adapt their diet and feeding strategies to changes in the abundance and composition of zooplankton (Flinkman et al., 1998; Casini et al., 2004; Prokopchuk and Sentyabov, 2006; Segers et al., 2007).

Differences in environmental conditions, primarily bottom salinity and temperature, explained the majority of intra- and inter-annual variability in zooplankton community composition. The increased strength of the Labrador Current (LC) and a more positive North Atlantic Oscillation Index (NAOI) in 2018 relative to 2017 (DFO, 2018, 2019) likely drove the variability in salinity and temperature. The stronger advection of the LC beginning in September 2018 resulted in more Atlantic water below the thermocline, which carried coastal zooplankton species from the North Atlantic into Trinity Bay. These Atlantic and surface waters mixed by upwelling along the western shore of Trinity Bay (Yao, 1986; Stanley et al., 2012, 2013) which, because of stronger winds associated with a positive NAOI (DFO, 2018, 2019), resulted in cooler and more saline waters in the upper portion of the water column in September 2018 and 2019. Additionally, post-tropical cyclone Dorian passed near Newfoundland in early September 2019, which brought hurricane-force gusts to much of Atlantic Canada (Avila

et al., 2020) and likely caused the deeper mixed layer (>50 m) observed later that month. Shifts in the distribution, phenology, and community composition of zooplankton are often attributed to changes in climate (Sanvicente-Añorve et al., 2000; Richardson, 2008; Mbaye et al., 2020). We show that these bottom-up effects ultimately impact herring trophodynamics in eastern Newfoundland, supporting previous findings from other regions of the North Atlantic (Arrhenius, 1996; Koster and Mollman, 2000; Mollmann et al., 2004; Frederiksen et al., 2006).

Since the mid-2010s, zooplankton populations along the Newfoundland shelf have exhibited a decrease in biomass but an increase in abundance (DFO, 2018, 2019). The loss of zooplankton biomass is primarily attributed to diminished numbers of the large-bodied calanoid copepods (DFO, 2018, 2019). In contrast, total zooplankton abundance has increased due to greater numbers of smaller-bodied copepods, such as *Temora* (Pepin et al., 2017), and copepod species associated with warmer waters in the region, including *Pseudocalanus*, *Acartia*, and *Oithona* spp. (Plourde et al., 2002; Brosset et al., 2019; DFO, 2019). This may partially explain the selective foraging of herring on copepods in late 2018 and 2019, when we observed increased densities of small-bodied copepods in Trinity Bay. Distribution shifts and decline of large-bodied copepods in high latitude systems have been reported throughout the North Atlantic and Pacific (Beaugrand et al., 2009) and are attributed to higher temperatures and reduced sea ice (Pitois and Fox, 2006; Coyle and Gibson, 2017). Given the importance of large copepods to forage fish diets, including herring, throughout the North Atlantic (Darbyson et al., 2003; Dommasnes et al., 2004; Prokopchuk and Sentyabov, 2006; Raab et al., 2012; this study), a shift in dominance from *Calanus* spp. to smaller, less-nutritious copepods could trigger bottom-up effects and alter forage fish energy budgets. Consequently, forage fish would need to allocate additional resources to

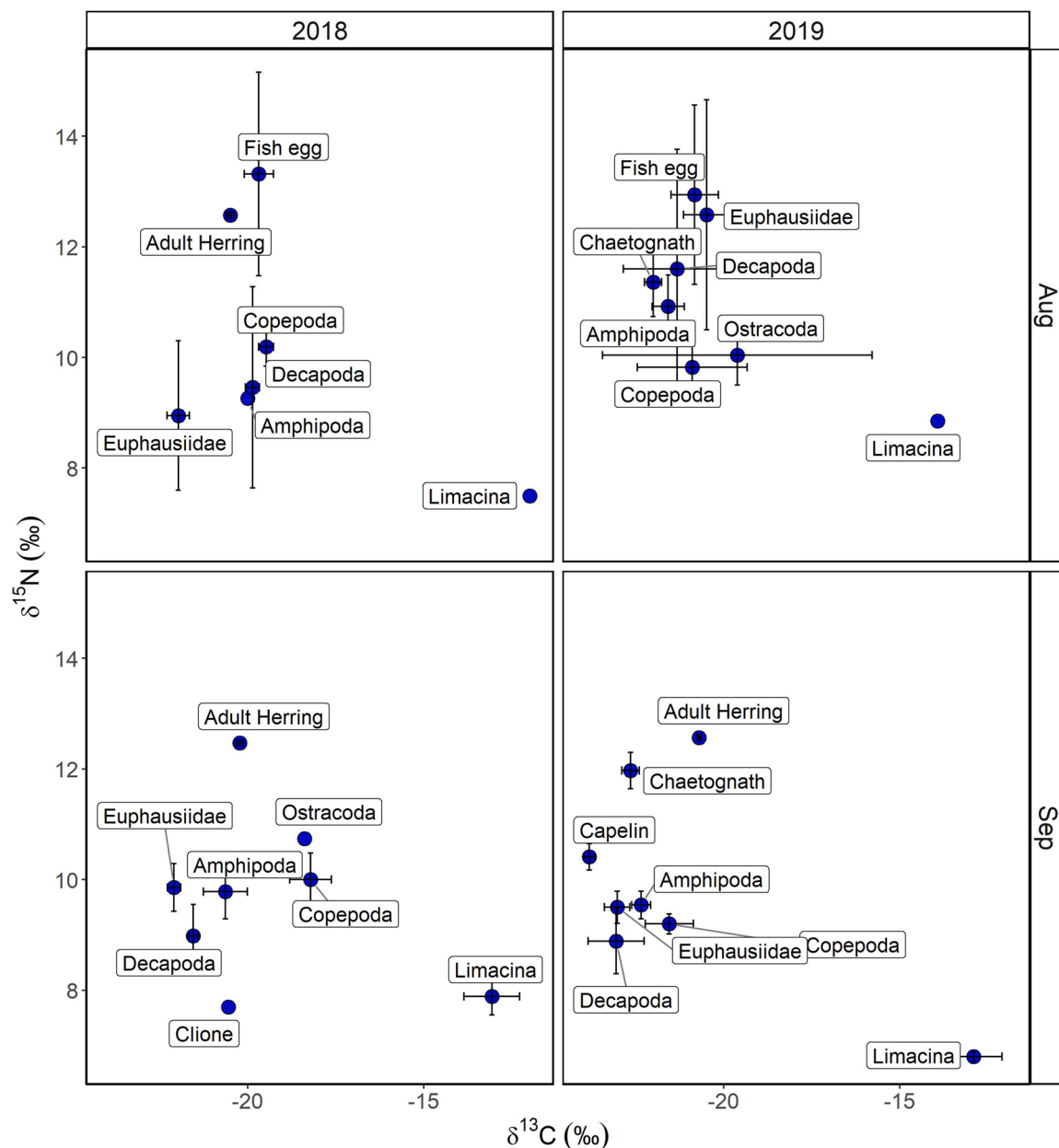


Fig. 8. Biplot of nitrogen and lipid-normalized carbon signatures (mean ± SE) of Atlantic herring and potential prey items collected in Trinity Bay, Newfoundland, in August and September of 2018 and September 2019. Values without error bars reflect a single occurrence of prey items, with the exception of adult herring which have low SE values. Herring in August 2019 were omitted due to low sample size.

foraging (Flinkman et al., 1998; Cury, 2000; van Deurs et al., 2015). Herring populations have shown resilience to altered composition and abundance of prey fields (Flinkman et al., 1998; Koster and Mollman, 2000; Casini et al., 2004), but a change in zooplankton community structure may be a mechanism by which such planktivorous forage fish species are negatively impacted by climate warming.

4.2. Piscivory in herring and its potential effect on the recruitment of other fish species

We found evidence of a piscivorous feeding strategy by herring in both the short-term (stomach content analysis) and mid-term (stable isotope analysis) diets, supporting the hypothesis that ichthyoplankton, and in particular capelin, constitutes an important prey item for adult herring in late summer and autumn (Shikon et al., 2019). This is best exemplified by the range of $\delta^{15}\text{N}$ ratios of prey items, which was larger

than the broadly-applied $\delta^{15}\text{N}$ fractionation value of 3.4‰ (Post, 2002). This suggests that herring were not at isotopic equilibrium with the prey items analyzed, even after accounting for fractionation (Olive et al., 2003). Therefore, herring were likely feeding on prey items at a higher $\delta^{15}\text{N}$ that eluded capture by the plankton net (e.g., larger fishes, such as age-1 capelin observed in one stomach). This was further supported by the presence of larger fish bones and fin rays in herring stomachs. These bones and fin rays could not be identified to species but indicated feeding on juvenile stage fishes.

Fish eggs and larvae were consistently present in adult herring stomachs throughout all months of the study and, at peak consumption, represented nearly a third of herring diet by weight. Herring selected for early life stages of other fishes during a period of peak abundance (in 2017), similar to previous reports on juvenile herring in the North Sea (Segers et al., 2007), Baltic Sea (Koster and Mollman, 2000), and Barents Sea (Gjøsaeter and Bogstad, 1998). The consumption of fish eggs and

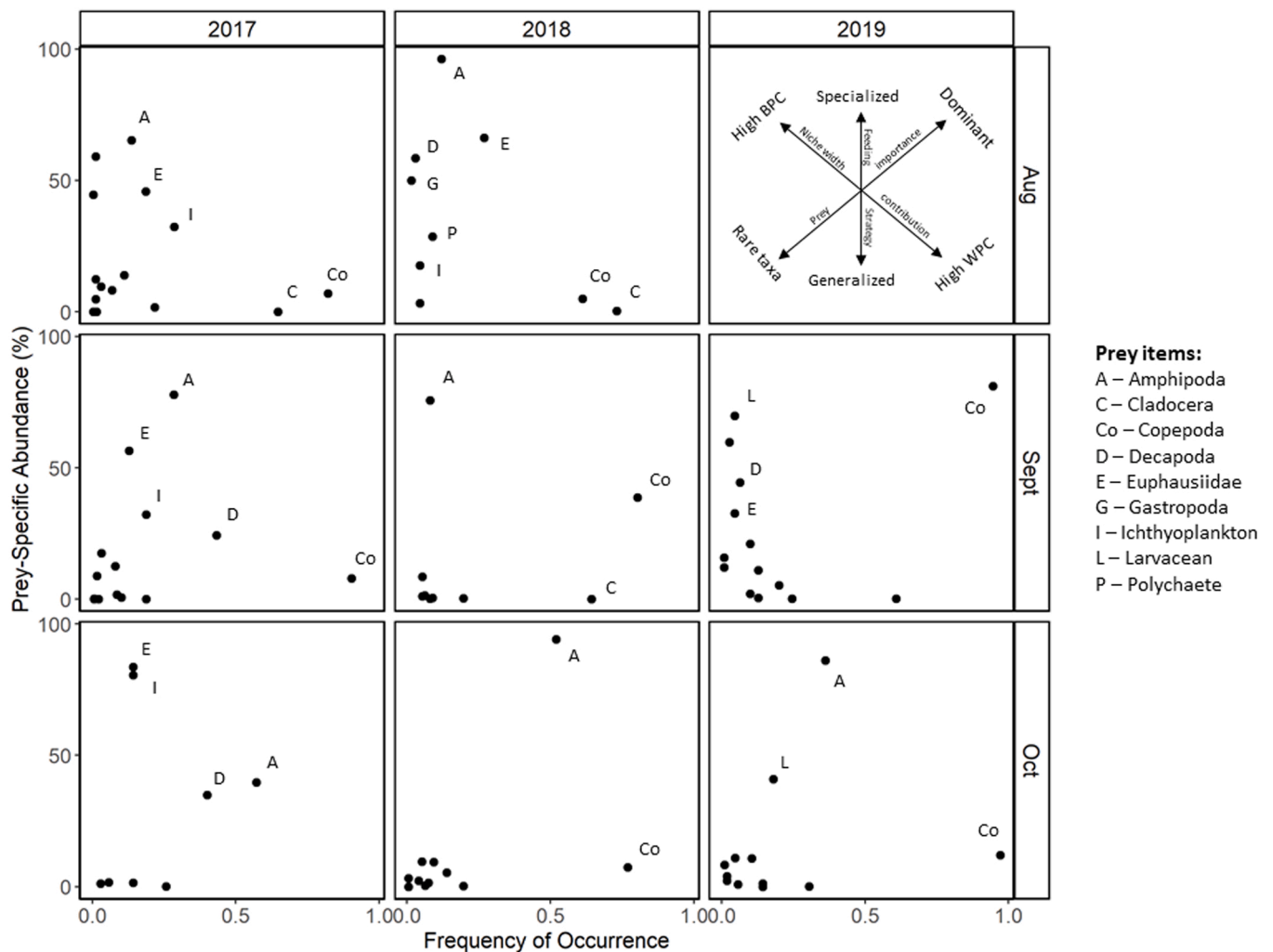


Fig. 9. Prey-specific abundance (%) relative to the frequency of occurrence for all prey items in Atlantic herring stomach contents, with key taxa identified. The explanatory axes in the bottom-left inset depict the foraging patterns described by Costello (1990) with modifications by Amundsen et al. (1996). The vertical axis reflects feeding strategy (prey preferentially consumed vs. generalized feeding), prey importance, and niche width contribution, differentiated as between-phenotype contribution (BPC; individuals specialized on different prey items) and high within-phenotype contribution (WPC; individuals exhibiting generalized feeding on common prey items).

larvae by adult herring suggests that both life stages (juvenile and adult) can exert predation pressure on the early life history of fishes, which has a currently unknown impact on recruitment dynamics of commercial species in the Northwest Atlantic. In coastal Newfoundland waters, capelin larvae were the most prevalent fish species in herring diet, although other forage fish, such as sand lance and Arctic cod, were also preyed upon. Despite the uncertainty in otolith identification in the present study, we consider it likely that herring also preyed on early life stages of Atlantic cod, as reported in other regions (Koster and Mollman, 2000). Herring could also account for a considerable portion of the size-selective mortality occurring during the larval and early juvenile stages of Atlantic mackerel in the Gulf of St. Lawrence, which is known to impact year-class strength (Robert et al., 2007; Khamassi et al., 2020).

While fish eggs were not identified to species in this study, the occurrence of eggs attached to gravel in the diet strongly suggests that herring are preying upon capelin eggs at demersal spawning sites. Capelin preferentially spawn on beaches but move to demersal sites when beach temperatures exceed 12 °C (Nakashima and Wheeler, 2002). Since 1991, capelin have been spawning approximately three weeks later compared to the 1980 s (Buren et al., 2019; Murphy et al., 2018, 2021). Later spawning in the summer increases the likelihood that capelin experience warmer temperatures at beaches, which may result

in a greater proportion of capelin eggs being deposited at demersal sites where they develop more slowly (Nakashima and Wheeler, 2002) and are vulnerable to predation (Templeman, 1948). Our observations of eggs attached to gravel in herring diets suggest that herring exert predation pressure on capelin from the egg stage. In combination with other known capelin egg predators such as winter flounder (*Pseudopleuronectes americanus*), our results point to the possibility of top-down control of capelin recruitment through egg predation (Frank and Leggett, 1984).

In Trinity Bay, herring displays both generalist and specialist feeding strategies. As visual predators, herring are limited to filter-feeding at night but can particle feed during the day, which allows them to select for larger, more mobile prey (Batty et al., 1990; Gibson and Ezzi, 1992; Darbyson et al., 2003). Selective feeding is known to be influenced by a suite of factors, including the behavioral and physical characteristics of both predator and prey, as well as the physical environment (Kitchell and Kitchell, 1980; Dill, 1983; Ranåker et al., 2014; Ljungström et al., 2020). Filter-feeding by herring may have increased in 2019 due to the increase in copepod availability, as filter-feeding is more efficient than particulate feeding at high prey densities, allowing herring to alternate between feeding modes to maximize energy intake while minimizing energy expenditure (Pepin et al., 1988; Gibson and Ezzi, 1992). This is consistent with a previous theory stating that plasticity in planktivorous

diets is an adaptive response to seasonal, highly variable prey fields (Eggers, 1978). Additionally, shifts in the composition of the prey field are known to affect predation pressure on the early life stages of fishes (Segers et al., 2007). Specifically, capelin larvae may experience a release from herring predation pressure when there are high densities of copepods (Hallfredsson and Pedersen, 2009). Our results support previous findings suggesting that herring have a broad niche width and are capable of adapting their feeding strategy to best exploit the prey fields they encounter (Gibson and Ezzi, 1992).

4.3. Herring and climate change

Sea surface temperatures (0–100 m) are forecasted to increase by 0.6–2.0 °C (relative to 1850–1900; Collins et al., 2013) in Arctic and sub-Arctic seas by the end of the century (IPCC 2014). In addition, freshening of the surface waters increases stratification and reduces convection, which may alter the inflow of Atlantic water in the Newfoundland shelf ecosystem (Alexander et al., 2020). Across the Northwest Atlantic, planktivorous fishes will lose a significant amount of their thermal habitat by 2030, with capelin and sand lance among the most impacted of the 46 species evaluated (Shackell et al., 2014). The biocomplexity of herring stocks, driven by its adaptive foraging strategy (Gibson and Ezzi, 1992) and plasticity in spawning phenology (Winters and Wheeler, 1996; Melvin and Stephenson, 2007) potentially increases herring resilience to climate change in the Northwest Atlantic.

Forage fishes exhibiting piscivory, such as herring, might be less susceptible to environmental change than the strictly-planktivorous capelin and sand lance because they can utilize a larger variety of prey (Shackell et al., 2014) and could colonize new areas in response to changing temperatures (Nye et al., 2009; Wisz et al., 2015). The dominant spawning phenology of herring is largely driven by environmental conditions, and as temperatures warmed in the late 1990's and early 2000's, fall-spawners became increasingly dominant in the northern stocks (i.e. eastern Newfoundland; Melvin et al., 2009). Our findings support this trend, with nearly 75% of all herring collected belonging to the fall-spawning component. The adaptive capacity of herring potentially explains why herring stocks in Newfoundland did not collapse with capelin and groundfish stocks in the early 1990 s (Hutchings and Myers, 1994; Link et al., 2009). However, climate warming may lead to an overall reduction or loss of herring phenotypic plasticity as spring-spawning sub-populations decline in abundance (Melvin et al., 2009).

5. Conclusion

This study provides rare baseline data on late summer and autumn adult herring diets in eastern Newfoundland, laying the foundation for future comparative studies across different spatiotemporal scales. Influenced by Arctic currents, the waters surrounding Newfoundland represent a low-latitude boreal ecosystem that will likely experience significant changes due to climate warming in the decades to come. Forage fish such as herring represent a critical trophic link in marine food webs and are particularly vulnerable to climate change through bottom-up processes related to the phenology, abundance, and composition of their zooplankton prey (Raab et al., 2012; Hill et al., 2015). Yet,

as herring are opportunistic feeders with a broad niche and plasticity in their diet and phenology, they may be more resilient than other forage fish species to environmental changes. We further demonstrate that, in eastern Newfoundland, herring also has the potential to impact the recruitment of other ecologically and commercially valuable fishes, such as capelin, through predation on their early life stages.

CRediT authorship contribution statement

Jessica R. Randall: Data collection and curation, Methodology, Formal analysis, Writing – original draft, Funding acquisition. **Hannah M. Murphy:** Supervision, Conceptualization, Data collection, Writing – review & editing, Resources, Funding acquisition. **Dominique Robert:** Supervision, Writing – review & editing, Resources. **Maxime Geoffroy:** Supervision, Writing – review & editing, Resources. All authors were responsible for funding acquisition, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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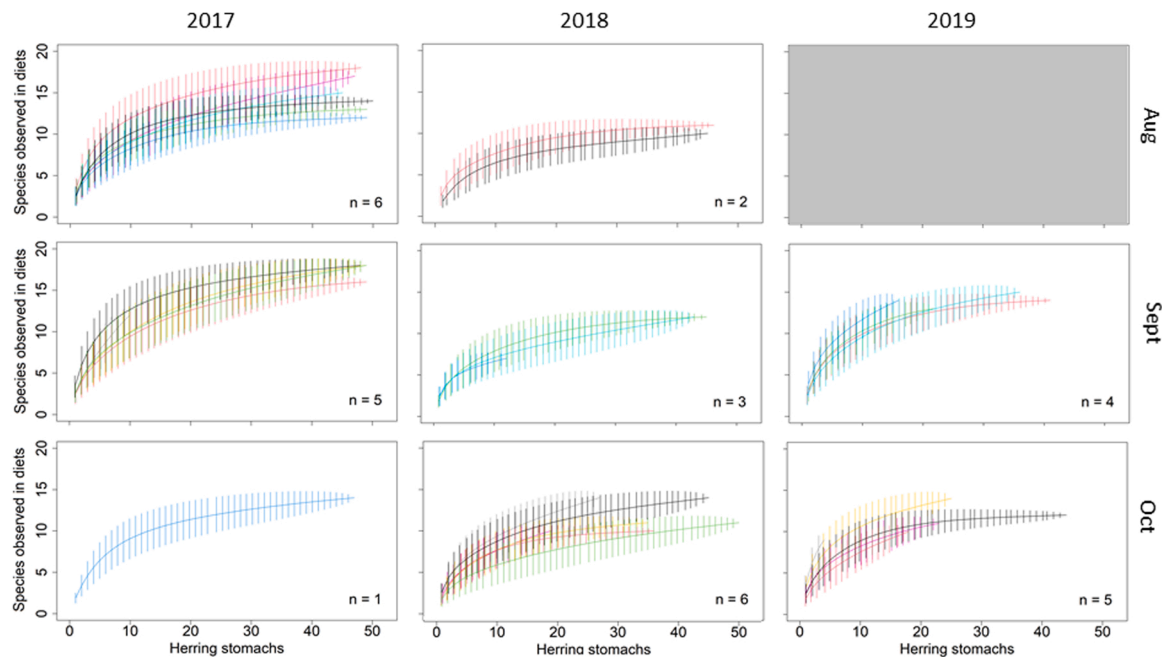
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Appendix A. Guide for maturity stages of herring used by Fisheries and Oceans Canada, St. John’s, adapted from Parrish and Saville (1965) with input from B. Squires (pers. comm.). After completing spawning, herring are classified as Stage VIII (Spent) then revert to Stage III as they prepare to spawn the next year

Maturity stage	Classification	Male description	Female description
I	Immature	Testes small, threadlike, whitish or grey-brown	Gonads small 2–3 mm width, ovaries dark red
II	Early maturation	Testes width 3–8 mm width, reddish grey in color	Ovaries width 3–8 mm, eggs only visible under a microscope
III	Maturing/pre-spawning	Testes occupy half of ventral cavity, 1–2 cm width. Reddish grey in color	Ovaries occupy half of ventral cavity, width 1–2 cm. Eggs distinguishable with naked eye, orange in color
IV	Ready to spawn	Testes nearly length of body cavity. Testes white	Ovaries fill body cavity, yellow in color. Eggs are large, some transparent but not actively flowing
VI	Actively spawning	Testes ripe, milt flows freely	Ovaries ripe, eggs transparent and flow freely
VIII	Spent	Testes firm and larger than Stage II. Walls of testes are striated, blood vessels prominent. Dark red in color	Ovaries firm and larger than Stage II. Eggs not visible to naked eye. Ovary walls striated, dark red in color

Appendix B. Species accumulation curves produced using the “specaccum” function in the package vegan in R (Okansen et al., 2020). Curves represent the average number of prey species detected and the 95% confidence interval, relative to the number of individual herring stomachs sampled. The number of individuals corresponding to the start of the curve asymptote (10–20 herring) suggests an adequate number of samples were collected to detect all prey species present



Appendix C. Plankton genera (or next lowest taxonomic level available) that contributed greater than 5% to observed similarities (SIMPER) within cluster groups. The three most abundant genera of copepods (*Calanus*, *Pseudocalanus*, and *Temora*) were pooled

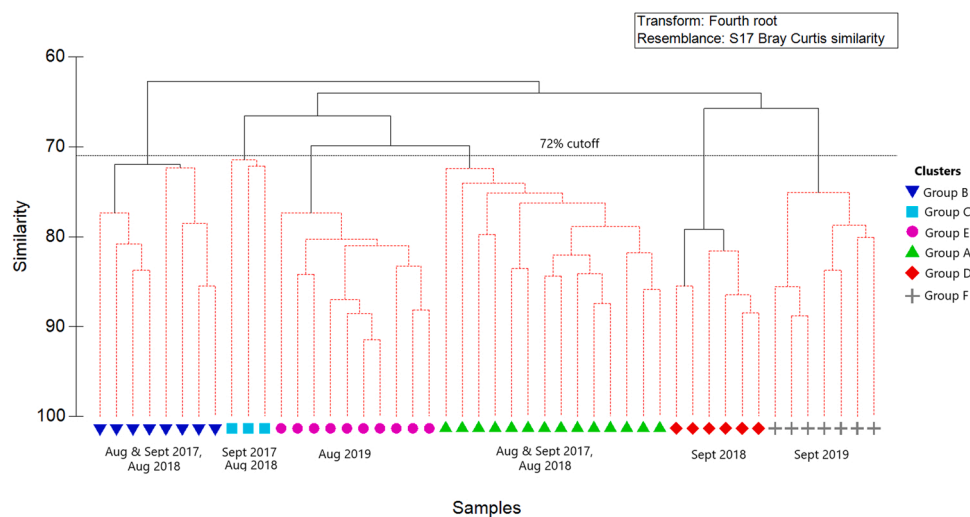
Group	Species	Contribution (%)
A	<i>Calanus/Pseudocalanus/Temora</i>	45.43
	<i>Evadne</i>	11.07
	<i>Acartia</i>	9.07
	Larvacean	7.57
	Euphausiidae	7.56
	<i>Oithona</i>	5.81
B	<i>Calanus/Pseudocalanus/Temora</i>	43.4
	<i>Metridia</i>	9.70
	<i>Evadne</i>	8.14
	Gastropoda	6.92
	<i>Oithona</i>	6.30
	<i>Acartia</i>	6.27
	Larvacean	5.06

(continued on next page)

(continued)

Group	Species	Contribution (%)
C	<i>Calanus/Pseudocalanus/Temora</i>	41.87
	<i>Metridia</i>	15.01
	Ostracoda	7.25
	Larvacean	6.80
	<i>Oithona</i>	6.79
	<i>Paraeuchaeta</i>	6.34
D	<i>Calanus/Pseudocalanus/Temora</i>	39.98
	Gastropoda	8.15
	<i>Metridia</i>	6.52
	<i>Evadne</i>	5.72
	<i>Oithona</i>	5.59
	Acartia	5.47
E	Larvacean	5.30
	<i>Calanus/Pseudocalanus/Temora</i>	56.42
	<i>Metridia</i>	14.06
	<i>Evadne</i>	7.56
	Chaetognatha	5.62
F	<i>Oithona</i>	5.40
	<i>Calanus/ Pseudocalanus / Temora</i>	65.34
	Gastropoda	10.72
	<i>Metridia</i>	7.92

Appendix D. Cluster analysis of stations across all months and years of sampling. The horizontal dashed line shows the 72% cutoff used to distinguish between cluster groups



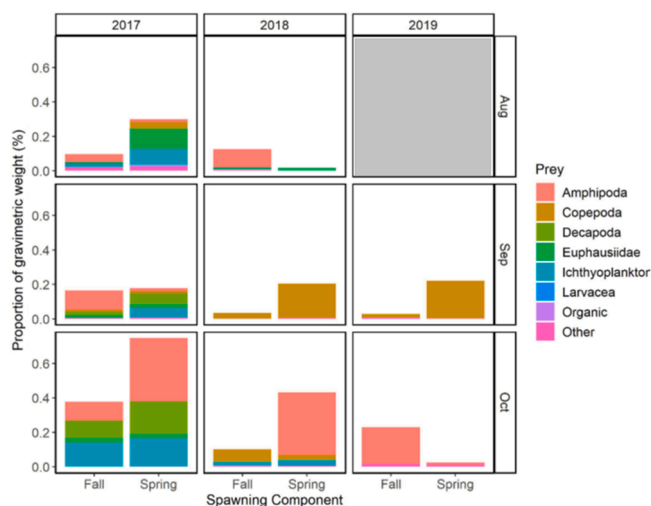
Appendix E. Pairwise PERMANOVA analysis exploring interaction between month and year defining zooplankton communities. Differences between month and year pairs were statistically significant (* indicates significance at $p = 0.5$, ** indicates significance at $p = 0.001$)

	August			September		
	2017	2018	2019	2017	2018	2019
2017	–			2017	–	
2018	0.012 *	–		2018	0.001 **	–
2019	0.001 **	0.001 **	–	2019	0.001 **	0.001 **

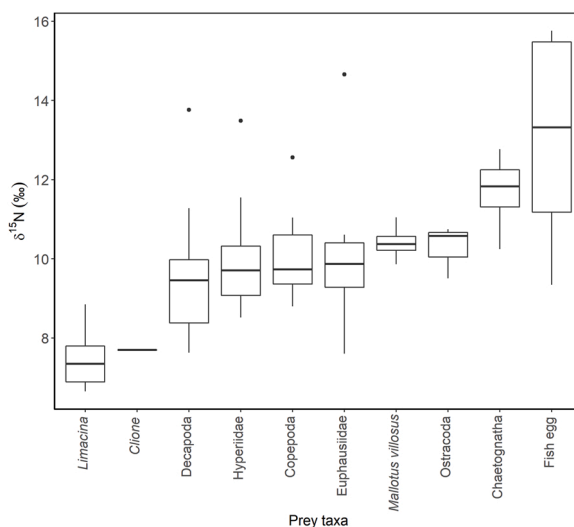
Appendix F. Summary of herring samples by month separated by spawning component (n = 780). SpR: fall to spring spawner ratio, FI: feeding incidence (stomach containing prey:total stomachs), TFI: total fullness index, TL: total length

	SpR	Fish collected		Feeding Incidence		Total Fullness Index		Total Length		Age		Maturity	
		Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring
Aug-17	6.57	250	38	0.89	0.91	0.10	0.30	33.39 ± 0.21	28.54 ± 0.45	8.45 ± 0.16	4.52 ± 0.32	4.08 ± 0.04	2.78 ± 0.15
Sep-17	4.39	167	38	0.88	0.96	0.16	0.18	31.93 ± 0.25	28.30 ± 0.41	7.07 ± 0.20	4.36 ± 0.30	4.22 ± 0.08	2.94 ± 0.23
Oct-17	2.36	33	14	0.59	0.75	0.38	0.75	31.87 ± 0.63	30.56 ± 1.01	7.39 ± 0.49	5.85 ± 0.72	3.90 ± 0.23	2.85 ± 0.17
Aug-18	6.50	13	2	0.68	0.74	0.13	0.02	32.54 ± 0.94	29.35 ± 0.15	7.76 ± 0.75	4.50 ± 0.50	4.38 ± 0.34	3.00 ± 1.00
Sep-18	4.00	40	10	0.96	0.91	0.03	0.21	31.30 ± 0.54	30.40 ± 0.85	6.70 ± 0.37	5.50 ± 0.70	4.20 ± 0.09	4.00 ± 0.49
Oct-18	0.73	22	30	0.87	0.86	0.10	0.43	30.56 ± 0.55	31.48 ± 0.55	6.22 ± 0.52	6.73 ± 0.46	4.31 ± 0.38	3.23 ± 0.09
Sep-19	14.00	42	3	0.97	0.94	0.03	0.22	32.07 ± 0.47	30.93 ± 1.30	7.28 ± 0.39	5.00 ± 1.00	4.80 ± 0.21	4.00 ± 0.00
Oct-19	1.37	26	19	0.91	0.94	0.23	0.02	32.31 ± 0.62	31.53 ± 0.57	7.09 ± 0.48	6.57 ± 0.42	4.61 ± 0.31	3.68 ± 0.27

Appendix G. Gravimetric weight of prey items that contributed more than 5% to diet by weight for both spring and fall spawning components of herring in the samples. Prey items that contributed < 5% were collectively pooled as ‘Other’



Appendix H. Mean nitrogen ratio of all prey taxa pooled across surveys, reflecting a spread of N¹⁵ ratios, likely encompassing multiple trophic levels. Boxplots display the median with lower and upper box hinges representing the 25 th and 75 th quantiles, respectively. Whiskers represent either the minimum/maximum value or 1.5* IQR (interquartile range)



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