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# Feeding ecology of autumn-spawned Atlantic herring (*Clupea harengus*) larvae in Trinity Bay, Newfoundland: Is recruitment linked to main prey availability?

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Atlantic herring (*Clupea harengus*) populations in Newfoundland, Canada, are characterized by spring- and autumn-spawning components, targeted as a mixed fishery. The spring-spawning component accounted for ~90% of the total catch until the early 2000s, but autumn-spawning herring now dominate the catch in most areas. We explored the links between recruitment of autumn-spawning herring and variability in larval prey and temperature during first winter. The main prey during the early larval stage was nauplii of the copepods *Tenora longicornis* and *Oithona similis*. In the mid-larval stage, *Pseudocalanus* sp. strongly dominated the diet. In the late-larval stage, larvae shifted to the larger calanoid copepods *Calanus* sp. The phenology of *Pseudocalanus* sp. shifted from a spring to autumn bloom during the mid-2000s, concurrent with the change of the spring- and autumn-spawning components. This change in zooplankton phenology suggests that conditions for herring larval survival have improved during autumn, although no significant relationships were found between recruitment and prey abundance or temperature. Our results suggest that multiple factors, rather than a single driver, interact in the regulation of herring year-class strength. Survival is the outcome of growth and mortality, making it important considering predation pressure along with prey availability in future studies.

**KEYWORDS:** fish larvae; trophodynamics; diet composition; main prey; year-class strength

## INTRODUCTION

Recruitment of fishes is variable and survival during the larval stage is generally considered the main driver of this variability (Hjort, 1914; Anderson, 1988; Cushing, 1990; Houde, 2008). The early life stage is characterized by extremely high mortality rates, with the majority of larvae lost to starvation and predation in the first few weeks of life (Bailey and Houde, 1989; Leggett and Deblois, 1994). Variability in preferred prey availability, through regulation of feeding success and growth, is often considered an important driver of survival during the larval stage (Hjort, 1914; Anderson, 1988; Cushing, 1990; Robert *et al.*, 2009; Murphy *et al.*, 2012). Therefore, any change in plankton production dynamics has the potential to impact the early life stages of fish (e.g. Beaugrand *et al.*, 2003; Castonguay *et al.*, 2008). Suboptimal prey availability and/or quality can directly result in increased mortality rates through starvation or indirectly through predation directed towards slow-growing larvae (Houde, 2009). Slow-growing larvae are generally considered more vulnerable to predation as a result of an extended larval duration where predation pressure is at its maximum (Leggett and Deblois, 1994; Takasuka *et al.*, 2003; Robert *et al.*, 2014). In order to provide a sound assessment of the links between variability in the feeding environment and larval vital rates, such as growth and survival, it is necessary to identify the main or preferred prey during the critical larval stage (Beaugrand *et al.*, 2003; Castonguay *et al.*, 2008; Murphy *et al.*, 2012; Robert *et al.*, 2014).

Atlantic herring (*Clupea harengus*) is a small pelagic forage fish in which populations are characterized by seasonal spawning components that experience high recruitment variability (Houde, 1987; Munk *et al.*, 1989; Folkvord *et al.*, 1997). Though spawning can potentially occur throughout the year (Sinclair and Tremblay, 1984), peak spawning in the Northwest Atlantic largely takes place during spring and autumn, with autumn spawners historically dominating to the south and fall spawners to the north (Melvin *et al.*, 2009). Spring-spawned larvae typically reach the size of metamorphosis (40–50 mm) before their first winter, while autumn-spawned individuals overwinter as larvae and metamorphose during the following spring (Cohen and Lough, 1983; Sinclair and Tremblay, 1984). Hence, the larvae of autumn-spawning herring emerge and grow during a period of limited prey production and are exposed to low winter temperatures for an extensive period (Graham *et al.*, 1990). In the Northeast Atlantic, variability in herring recruitment has been linked to survival rate during the larval stage (Ottersen and Loeng, 2000; Alvarez-Fernandez *et al.*, 2015). For example, the autumn-spawning component of North Sea herring has recently been reduced following a temperature

increase, which was related to a decrease and temporal shift in the peak abundance of preferred larval prey *Temora* sp. and *Pseudocalanus* sp. (Payne *et al.*, 2009; Alvarez-Fernandez *et al.*, 2015), that resulted in low larval growth and high mortality (Alvarez-Fernandez *et al.*, 2015).

In Newfoundland, Canada, herring populations have historically been dominated by spring spawners that comprised ~90% of the commercial catch until the mid-2000s (Wheeler and Winters, 1982; Bourne *et al.*, 2013). Over the last 10–15 years, spring-spawning herring has been characterized by poor recruitment and rapidly decreasing relative abundance, resulting in a dominance of autumn-spawning herring in the commercial catch for five out of six management units (White Bay–Notre Dame Bay, Bonavista Bay–Trinity Bay, Conception Bay–Southern Shore, St. Mary's Bay–Placentia Bay, Fortune Bay and NAFO Division 4R) around Newfoundland (Bourne *et al.*, 2013; DFO, 2016). This suggests a shift in the optimal early life survival window from spring to autumn. Moreover, there are indications of recent changes in the distribution and phenology of some of the main copepod species in the Northwest Atlantic, which could benefit feeding success of the early life stages of autumn-spawned herring (Head and Sameoto, 2007). However, linking changes in plankton phenology to stock dynamics in Northwest Atlantic herring stocks is currently impossible because diet composition during the larval stage remains largely unknown.

Among all management units located around Newfoundland, the Bonavista Bay–Trinity Bay herring stock has experienced the most pronounced shift from a dominance of spring spawners to one of the autumn spawners (Bourne *et al.*, 2013). Trinity Bay, therefore, represents an ideal area to study the drivers of changing population dynamics in Northwest Atlantic herring stocks. Here, we aim to describe the larval diet of herring in Trinity Bay at a high taxonomic resolution to further explore the relationships linking preferred prey supply and recruitment variability. We hypothesize that herring larvae from the Bonavista Bay–Trinity Bay population feed selectively and that interannual variability in main prey availability is a driver of year-class strength. To test these hypotheses, we first identified the primary copepod prey of Atlantic herring larvae from three annual autumn-spawned cohorts (2002, 2006 and 2013). To evaluate how changes in zooplankton phenology and first winter conditions may have affected larval survival, we assessed the potential changes in the timing of peak production of preferred copepod prey over the past decade using long-term abundance and temperature data collected by Fisheries and Oceans Canada (DFO) through the Atlantic Zone Monitoring Program (AZMP). Finally, we assessed the relationships

between the abundance of the main prey taxa during the larval stage, temperature during the first winter and recruitment of autumn-spawning herring from the Bonavista Bay–Trinity Bay stock.

## METHOD

### Study area

Trinity Bay (48°N; 53.5°W) is a large (3000 km<sup>2</sup>) embayment located on the east coast of Newfoundland, Canada (Fig. 1A). The bay is characterized by a 240 m deep sill at its mouth and a trench reaching a maximum depth of 630 m at its centre (Davidson and de Young, 1995). Atlantic herring that spawn in Trinity Bay belong to the Bonavista–Trinity Bay stock complex (Wheeler and Winters, 1984). Spawning occurs in late spring, summer and autumn throughout both Bonavista and Trinity Bays (Bourne *et al.*, 2015); the contribution of each bay to overall recruitment of the stock complex is unknown, but assumed to be relatively stable in time.

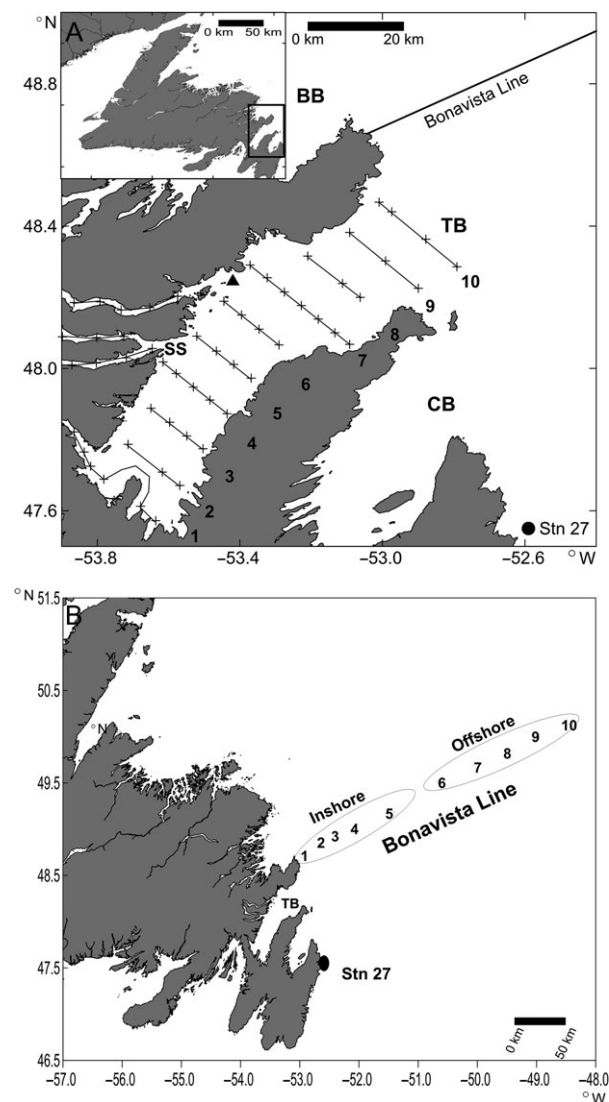
### Temperature

Sea surface temperature (SST) was retrieved directly from the ichthyoplankton sampling surveys (see below). At each station, an Applied Micro-systems STD-12 probe was attached to the bongo net and profiled the entire water column for salinity, temperature and depth to a maximum of 200 m or 10 m above the sea floor at shallower stations (Dalley *et al.*, 2002).

Winter SSTs (first 50 m) were obtained from Station 27 (52.59°W 47.55°N) of the AZMP. Winter sea temperatures have been monitored annually from 1999. Briefly at each station, a Seabird 911 CTD (conductivity–temperature–depth) was lowered to the maximum depth of the water column. Detailed methods for temperature sampling in DFO’s AZMP can be found in Mitchell *et al.* (2002).

### Zooplankton abundance

Zooplankton abundance data were obtained from the high-frequency sampling location (Station 27) and the Bonavista section of the AZMP (Fig. 1). Zooplankton abundance and distribution have been monitored since 1999, and data from 1999 to 2013 were used as an index of potential prey availability in the absence of zooplankton collections concurrent with ichthyoplankton sampling in Trinity Bay. Detailed zooplankton collection methods can be found in Mitchell *et al.* (2002). Briefly, zooplankton samples were collected using dual



**Fig. 1.** (A) Map of the study area with 10 transects comprising 56 sampling stations. All stations were sampled in 2002, while only Transects 4–7 were sampled in 2006 and 2013. SS, Smiths Sound; BB, Bonavista Bay; TB, Trinity Bay; CB, Conception Bay. (B) Map of Bonavista section with inshore and offshore zooplankton sampling stations.

0.75 m diameter bongo with 202  $\mu$ m mesh nets towed vertically from 10 m above the bottom or from a maximum depth of 1000 m, at a retrieving speed of 1 m s<sup>-1</sup>. Samples were then preserved in 2% formalin for later taxonomic identification and enumeration. A minimum of 200 organisms per net were counted and identified in the laboratory to the lowest taxonomic level possible (Pepin *et al.*, 2011). Station 27, which is located south of Trinity Bay near the entrance to St. John’s harbour, is sampled from one to six times per month during the ice-free season to characterize variability in the seasonal production cycle (Fig. 1B). The Bonavista section is

located off the mouth of Trinity Bay and offers the nearest zooplankton monitoring site relative to the sampling area in Trinity Bay (Fig. 1). This oceanographic section is generally surveyed three times per year in spring (April–May), summer (July–August) and autumn (November–December), which provides partial temporal overlap with the Trinity Bay ichthyoplankton surveys. The Bonavista section is comprised of 10 zooplankton sampling stations, distributed along an inshore–offshore axis (Fig. 1B). Zooplankton data from both of these sampling areas from July–November, which corresponded with the early larval period of the autumn-spawning herring, were used to develop indices of zooplankton prey abundance in Trinity Bay. Given that the 202  $\mu\text{m}$  mesh of the AZMP sampling gear cannot provide quantitative estimates for copepods nauplii, which are commonly ingested by early larvae, abundance of the adult stage (copepodite 6) was used as a proxy for nauplii and early copepodite production in the system (Ringuette *et al.* 2002).

### Ichthyoplankton sampling

Atlantic herring larvae were sampled during daylight hours by the DFO annual 2-week ichthyoplankton surveys in Trinity Bay in October 2002 (56 stations), September 2006 (19 stations, transects 4–7) and September 2013 (19 stations, transects 4–7) (Fig. 1A). While these surveys primarily target capelin (*Mallotus villosus*), herring larvae constitute the main by-catch. Herring that spawn after 1 July in Newfoundland populations are typically designated as autumn-spawned (Bourne *et al.*, 2013) and these larvae were considered to be part of the autumn-spawning component. Detailed methodology for these surveys was described by Dalley *et al.* (2002). Briefly, bongo nets measuring 61 cm in diameter with 333  $\mu\text{m}$  mesh nets were towed in a double oblique pattern to a depth of 200 m (or 10 m above the sea floor at shallower stations) at a winch speed of 10  $\text{m min}^{-1}$ , and a vessel speed of 2–2.5 kt. At each station, filtered water volume was measured using General Oceanic® flowmeters fastened at the mouth of each net. Plankton samples were immediately preserved in 95% ethanol. Ethanol was changed within 1 week after collection to ensure that the concentration remained at 95% in order to avoid sample degradation.

### Gut content analysis

Atlantic herring larvae were identified according to Fahay (2007). Standard length (SL) and gape width of all herring larvae were measured to the nearest 0.1 mm using a stereomicroscope (Olympus SZX16) at 40–60 $\times$  magnification. No adjustments to SL measurements were made to account for preservation because of the

minimal shrinkage of herring larvae preserved in ethanol (Fox, 1996). For the diet analysis, each larva was placed on a glass slide with a drop of glycerol to prevent desiccation of the gut contents during dissection. The tubular alimentary canal was dissected using tungsten needles under a stereoscopic microscope (Olympus SZX16) at 70 $\times$  magnification. Each prey item found in the gut was measured (prosome length and width for copepods) and identified to the lowest taxonomic level possible. Empty stomachs were also recorded. For the diet analysis, larvae were binned into 3 mm size classes in order to assess ontogenetic shifts in diet.

### Data Analyses

**Temperature** At each ichthyoplankton station, SST was derived from the STD based on the mean temperature in the first 3 m, which corresponds to the minimum depth of the surface mixed layer where the majority of fish larvae occur (Munk *et al.*, 1989; Lough *et al.*, 1996; Olivar and Sabatés, 1997). Contour maps of SST were created for each year. Temperature was interpolated using inverse distance weighting in SURFER 11 software. Data were weighted such that the influence of one data point relative to another declines with distance from each other, allowing for smoothing among data points. Larval density at each station was overlaid on the temperature contour maps to detect potential temperature associations.

**Zooplankton** To develop a zooplankton abundance index characterized by optimal temporal overlap with larval fish sampling, we used complete linkage cluster analysis and SIMPROF (PRIMER 6 software) to determine whether zooplankton abundances sampled at Station 27 were correlated with specific stations of the Bonavista section. Zooplankton abundance data were fourth root transformed to reduce the potential effect of the large differences in abundance of the four copepod species considered. The number of Bonavista section stations sampled on the same day as Station 27 ranged from three to five during each season considered [spring (April–May); summer (July–August); autumn (November–December)]. Regression analyses were then used to quantify the relationship between prey abundance at Station 27 and same-day mean prey abundance at relevant stations of the Bonavista section. Prey availability indices were then developed for prey taxa characterized by strong correlations. This allowed us to investigate the temporal patterns in main prey availability and how they may be related to larval survival.

Image mapping with inverse distance to power grids (SURFER 11 software), a method allowing interpolation of prey abundance between sampling days, was used to

produce contour figures of prey abundance during all seasons for the years 1999–2013.

**Larval diet** For the analysis of diet composition, we binned larvae into 3 mm size classes, which provided a minimum of four larvae per size class. We calculated percent prey contribution of each prey type as a percentage of the total number of prey items in the stomachs by size class for 2002, 2006 and 2013. Given the overall low number of larval herring captured in each year and the modest spatial scale of Trinity Bay, we did not investigate spatial differences in feeding processes but rather limited our analysis to temporal variability.

**Trophic niche breadth** Feeding dynamics of Atlantic herring larvae were also characterized by sized-based trophic niche breadth, which was used as an index to explore prey selectivity. Trophic niche breadth can be used to make inferences on changes in larval feeding strategy during ontogeny (Pearre, 1986; Pepin and Penney, 1997; Murphy *et al.*, 2012). An increase in niche breadth with larval length indicates that larvae feed on an increasing range of prey sizes throughout ontogeny, while a constant trophic niche breadth over a given larval size range indicates selective feeding where larvae gradually switch to larger prey taxa as they grow (Pearre, 1986; Pepin and Penney, 1997). Trophic niche breadth ( $\mathcal{N}$ ) of each 3 mm larval herring length class ( $L$ ) was calculated using the following equation:

$$\mathcal{N}_L = SD_L(\log W_L)$$

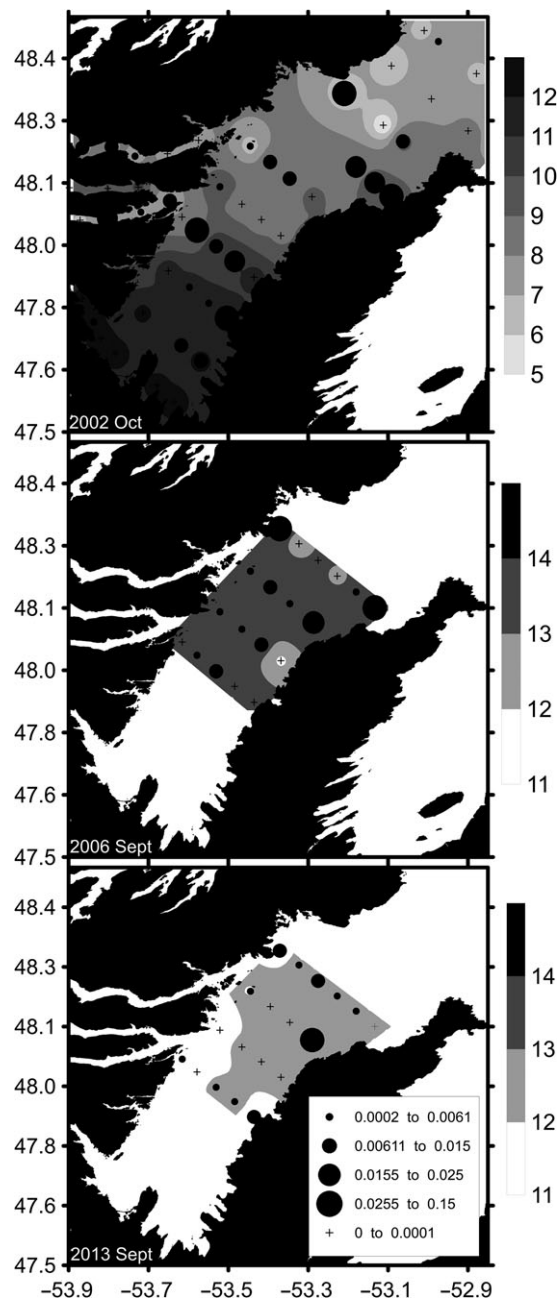
where SD is the standard deviation of log-transformed mean prey widths ( $W$ ) of all individuals in length class  $L$  (Pearre, 1986). We pooled larvae across the three sampling years to include three or more larvae with one or more prey items in each 3 mm length class (Pearre, 1986).

**Relationship between prey availability and herring recruitment** An Atlantic herring recruitment index was calculated by DFO using catch rates of age-4 herring from the spring research gill net survey for the Bonavista Bay–Trinity Bay stock (DFO, 2012). Autumn spawners are discriminated from spring spawners through otolith characteristics and maturation stages at the time of capture (DFO, 2012; Bourne *et al.*, 2013). A general linear model including the autumn recruitment index for the Bonavista Bay–Trinity Bay herring stock, abundances of the four main larval prey during autumn only as well as the full year, and mean temperature during the first winter was used to investigate potential links between year-class strength and interannual variability in first winter conditions and abundance of the key zooplankton prey taxa during the larval stage.

## RESULTS

### Temperature

In the three sampling years, there was no clear trend between larval herring abundance and SST at capture in Trinity Bay ( $r = -0.097$  for 2002,  $r = 0.38$  for 2006 and  $r = 0.33$  for 2013; Fig. 2). Mean temperature at



**Fig. 2.** Spatial variability in SST in Trinity Bay in September (2013 and 2006) and October (2002). Sampling stations are overlaid with four larval herring density intervals per  $m^3$  depicted by increasing circle size.

capture was 9.5°C in October 2002, 13.5°C in September 2006 and 12.4°C in September 2013. From 1999 to 2010, mean winter temperatures at Station 27 ranged from a minimum of 0.05°C in 2001 to a maximum of 1.6°C in 2006.

### Larval herring characteristics

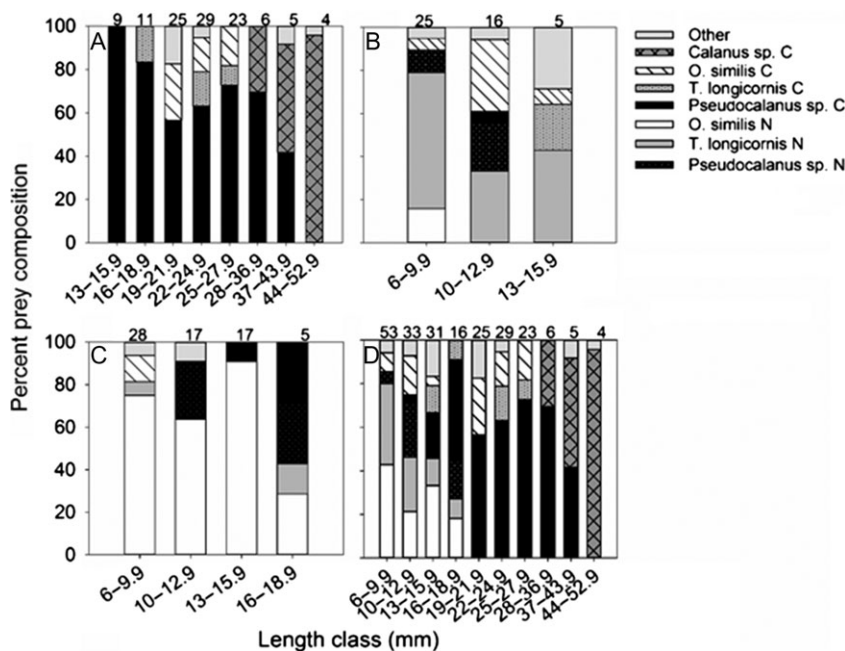
Overall, 112, 46 and 67 herring larvae were sampled in 2002, 2006 and 2013, respectively. SL of Atlantic herring larvae sampled in October 2002 ranged from 13 to 52 mm with the majority of individuals in the 19–27 mm SL size range (Fig. 3A). Larvae sampled in 2006 (size range 6–15 mm SL) and 2013 (size range 6–19 mm SL) had a more restricted size range and were smaller on average than in 2002 (Fig. 3B and C). Based on larval size and average growth rates from the literature (Lough *et al.*, 1982), herring larvae from our sampling years likely came from the autumn-spawning component (1 July–1 January) of the stock. For all three sampling years, highest larval densities were observed close to shore, with relatively few individuals caught in the central portion of the bay (Fig. 2).

### Larval herring diet composition

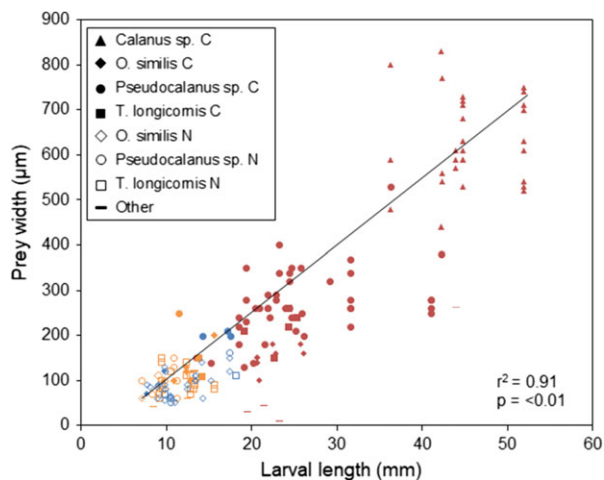
Copepodite stages of the mid-size calanoid copepod *Pseudocalanus* sp. were an important prey taxon,

representing 40–100% of all prey for larvae in the 13–37 mm size range in 2002 (Fig. 3A). For larval lengths >37 mm SL, which we considered the late-larval stage due to metamorphosis occurring within the 40–50 mm SL range, copepodite stages of the large calanoid copepod *Calanus* sp. (mainly *Calanus finmarchicus*) dominated diet composition, representing 30–96% of all prey in 2002 (Fig. 3A). Even though size ranges of larvae sampled in 2006 and 2013 were similar, their diet composition differed. In 2006, the early larval stage (5–15 mm SL) foraged mainly on nauplii of *T. longicornis* (33–63% of all prey) and *Pseudocalanus* sp. (10–22%), and to a lesser extent on *O. similis* nauplii and copepodites (0–16%) (Fig. 3B). In 2013, the early larval stage diet was dominated by *O. similis* nauplii and copepodites (28–91%), while the contribution of nauplii of *T. longicornis* (6–14%) and *Pseudocalanus* sp. (0–29%) was smaller (Fig. 3C). Copepodites of *Pseudocalanus* sp. appeared in the larval diet at 13 mm SL in all three years (Fig. 3A–C). Other prey items, primarily composed of copepod eggs, nauplius stages of the small calanoid copepod *Microcalanus* sp., the harpacticoid copepod *Microsetella norvegica* and bivalve larvae, represented a small overall contribution (2.9–16.7%) to larval diet (Fig. 3D; Table SI, supplementary data online).

Pooling larvae captured in all 3 years facilitated the identification of two ontogenetic shifts in diet based on



**Fig. 3.** Percent prey contribution by numbers as a function of size in Atlantic herring larvae from 3 sampling years, and all years combined: A: 2002, B: 2006, C: 2013 and D: all data (2002, 2006 and 2013) pooled. Larvae were grouped in 3 mm size classes, and larvae larger than 28 mm were grouped in 7–9 mm classes. Values above histogram bars indicate the number of larvae dissected for each size class. *N* and *C* indicate nauplii and copepodite stages, respectively.

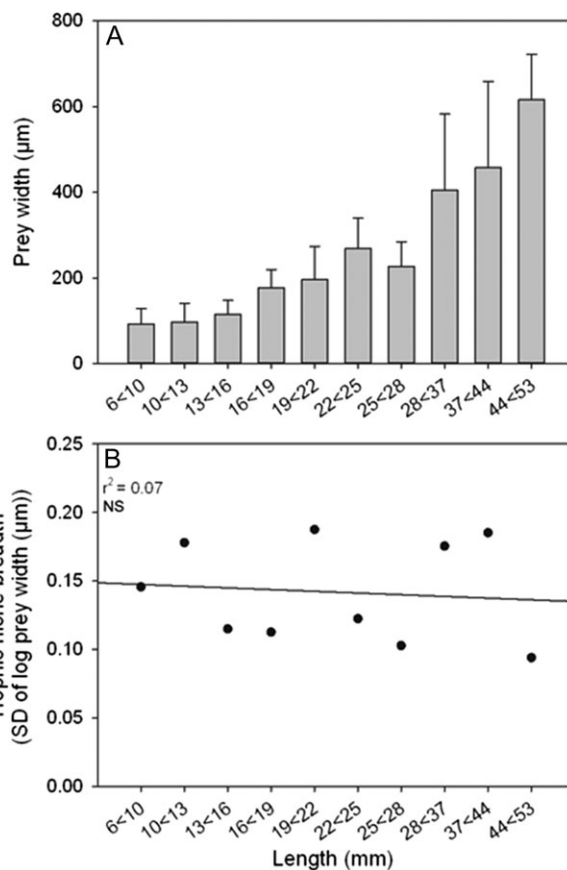


**Fig. 4.** Atlantic herring prey width in relation to larval length in 2002 (red), 2006 (orange) and 2013 (blue). Prey taxa are represented by different symbols. *N* and *C* indicate nauplii and copepodite stages, respectively.

prey taxa and size (Fig. 3D). At 13–19 mm SL, there was a shift from small copepod nauplii (*O. similis*, *T. longicornis* and *Pseudocalanus* sp. [in 2006 and 2013]) to mid-sized copepodites (*Pseudocalanus* sp. [in 2002 and 2013]). The second diet shift occurred from around 30 mm SL, when the large *Calanus* sp. copepodites were first observed in the diet of larvae captured in 2002 (Fig. 3D). At ~44 mm, *Calanus* sp. copepodites represented more than 95% of ingested prey. The proportion of empty guts in this study was on average 50%, which is consistent with previous studies on larval herring (Munk, 1992; Fox et al., 1999). The percentage of empty guts generally decreased as larval size increased (Fig. 3A–D; Table I supplementary data). In all years, prey width increased with larval length (Fig. 4). Even though larvae captured in 2006 and 2013 ingested different prey taxa, nauplii of *T. longicornis* (2006) and *O. similis* (2013) had a similar range of body widths (Fig. 4). Variability in prey width did not increase with larval size (Fig. 5A), and herring larvae had a constant and narrow trophic niche breadth (linear regression:  $r^2 = 0.068$ ,  $P = 0.466$ ) (Fig. 5B).

### Zooplankton abundance

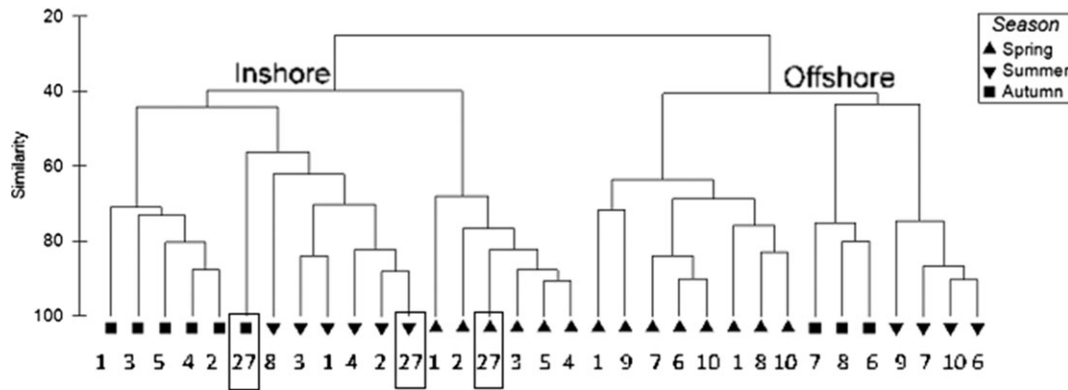
Only the four main prey taxa that contributed >80% to the larval diet were considered in zooplankton analyses. These four prey taxa were *O. similis*, *Pseudocalanus* sp., *T. longicornis* and *Calanus* sp. (dominated by *C. finmarchicus*). A cluster analysis based on these four zooplankton taxa from Station 27 and Bonavista section stations yielded two distinct clusters representing inshore and offshore stations, respectively, for all years (1999–2013; Fig. 6). Station 27



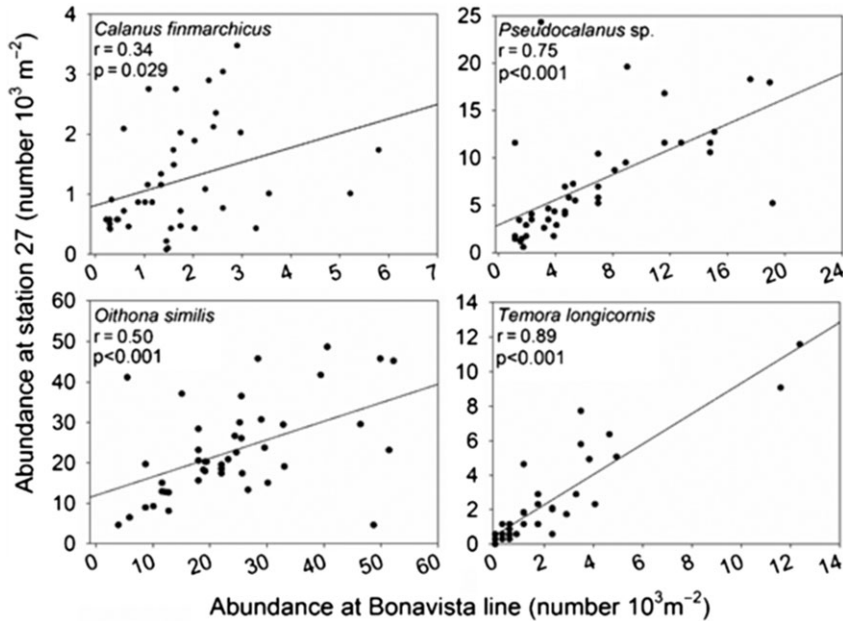
**Fig. 5.** (A) Mean (and standard error) width of prey ingested within each larval length class for all 3 sampling years. (B) Relationship between trophic niche breadth (standard deviation of log prey width) and larval length.

only clustered with the inshore stations of the Bonavista section. Based on the cluster analysis, inshore stations were classified as westward from 51°W and offshore stations were located eastward from the same point, at a distance of ~185 km from land. Abundances of the four zooplankton taxa from the Bonavista section inshore cluster were significantly correlated to zooplankton abundances sampled at Station 27 on the same day for the years 1999–2013 (Fig. 7); *T. longicornis* ( $r = 0.89$ ) and *Pseudocalanus* sp. ( $r = 0.75$ ) showed particularly strong correlation coefficients. On the basis of the overall consistency between the inshore Bonavista section and Station 27 copepod abundances, we used high-frequency data collected at Station 27 as an index of zooplankton abundance for Trinity Bay.

Peak adult stage (copepodite 6) abundance for three of the four main copepod prey species was characterized by an increase in abundance from spring to autumn (DFO 2016; Fig. 8). For *Pseudocalanus* sp., there was evidence of a shift in phenology, which occurred around 2005 (Fig. 8). For *O. similis*, there was an overall increase in abundance from 2005 to 2013, while *C. finmarchicus* had



**Fig. 6.** Example of Bray Curtis similarity cluster analysis for year 2002 comparing zooplankton assemblages of Atlantic Zone Monitoring Program’s Bonavista section stations and high-frequency sampling Station 27. Analysis was performed for each year (1999–2013) using abundances of the main larval herring prey taxa *Calanus finmarchicus*, *Pseudocalanus* sp., *Oithona similis* and *Temora longicornis*. Spring = April–May, Summer = July–August and Autumn = November–December. X-axis labels depict station number and season.



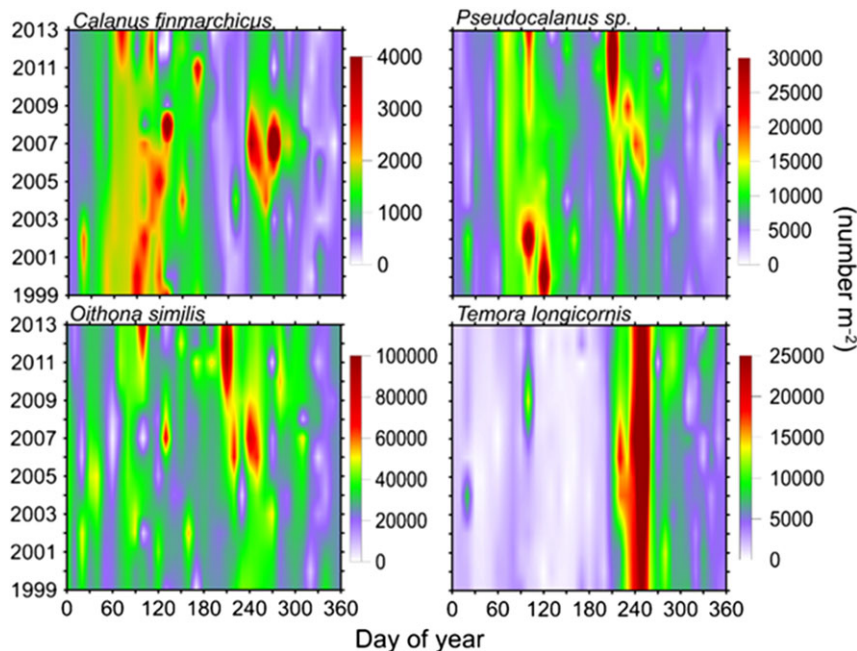
**Fig. 7.** Abundance of larval herring main prey taxa (*Calanus* sp., *Pseudocalanus* sp., *Oithona similis* and *Temora longicornis*) measured at Station 27 as a function of abundance measured on the same day at inshore stations of the Bonavista section during the period 1999–2013.

a relatively strong autumn component in 2004–2008 (Fig. 8). Peak abundance of the smaller calanoid copepod *T. longicornis* was characterized by relatively low abundance throughout the autumn of all years, with the exception of an abundance peak in September 2006, corresponding to an order of magnitude difference in the number of individuals relative to other years (Fig. 8). This large autumn value of *T. longicornis* recorded in 2006 was removed from the analysis to reveal temporal patterns of abundance (Fig. 8).

**Atlantic herring recruitment and larval prey abundance**

Autumn-spawning Atlantic herring in the Trinity Bay–Bonavista Bay stock showed increasing recruitment strength from 1999 to 2002 based on catch rates of age-4 Atlantic herring in the annual spring research gill net survey (Fig. 9; Bourne *et al.* 2015). After a period characterized by decreasing and low recruitment between 2003 and 2008, the two most recent years of the time series (2009 and 2010) were characterized by relatively



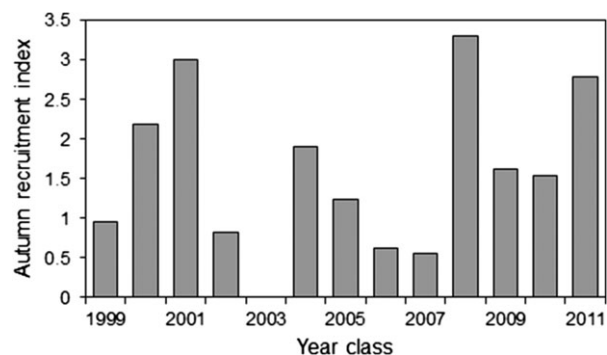


**Fig. 8.** Abundance time series (1999–2013) for the adult stage (C6) of the four prey taxa primarily contributing to larval herring diet, as a function of day of year. For *Temora longicornis*, a large value recorded in 2006 was removed from the analysis to reveal temporal patterns of abundance.

strong recruitment (Fig. 9). Recruitment in 2002 was twice as strong as that in 2006, while recruitment for the 2013 year-class is not yet known (Fig. 9; Bourne *et al.* 2015). The autumn herring recruitment index was not significantly related to variability in autumn or annual abundances of any of the four main copepod prey taxa, first winter temperatures, or an interaction between winter temperature and prey availability (Figs 10 and 11).

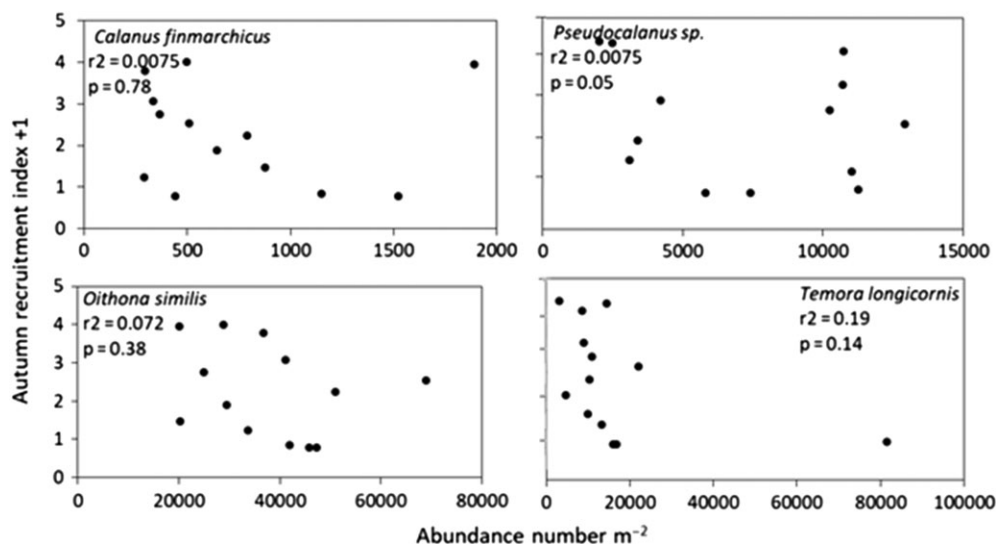
## DISCUSSION

There is a growing body of evidence that fish larvae do not prey on zooplankton taxa in proportion to their abundance in the environment, but rather strongly select for specific prey (reviewed by Llopiz, 2013), even at low prey availability (e.g. Young *et al.*, 2010; Murphy *et al.*, 2012). Despite past and recent evidence that Atlantic herring demonstrate strong prey preferences from the early larval stage (Hardy, 1924; Denis *et al.*, 2016), the taxonomic resolution used in recent research has varied widely, with a majority of studies only reporting prey to the subclass (e.g. copepod) and order (e.g. calanoida) levels (Munk, 1992; Arrhenius, 1996; Pepin and Penney, 1997). Relatively few studies have resolved prey to the genus and species levels (but see: Cohen and Lough, 1983; Last, 1989; Denis *et al.*, 2016). In the

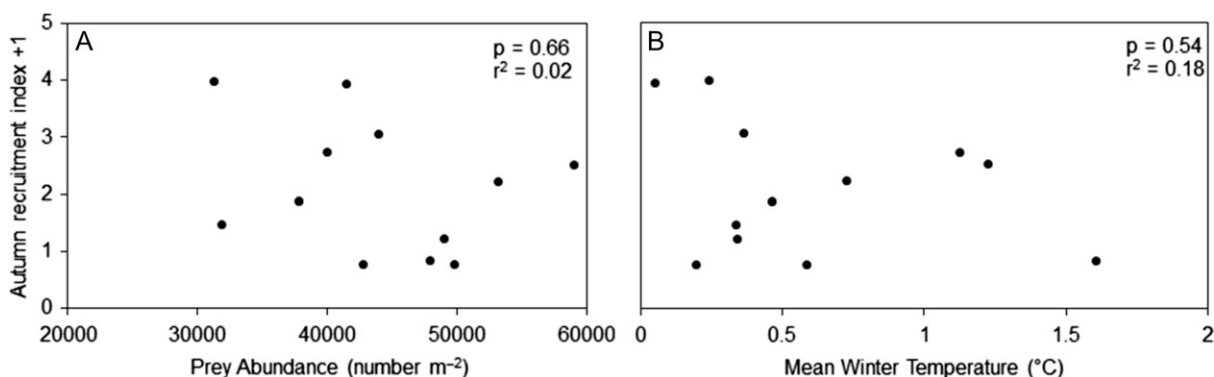


**Fig. 9.** Autumn recruitment index for the Bonavista Bay–Trinity Bay herring stock from 1999 to 2010 (Bourne *et al.*, 2013). Recruitment index is the natural log plus 1 of the number of age-4 autumn-spawning fish caught in DFO's annual research gill net survey for the Bonavista Bay–Trinity Bay stock management unit. Recruitment index was zero for 2003.

Northeast Atlantic, larval herring are known to prey primarily on calanoid copepods, including *Pseudocalanus* sp., *Paracalanus* sp., *C. finmarchicus*, *Acartia* sp. and *Eurytemora* sp. (Hardy, 1924; Blaxter, 1965; Arrhenius, 1996; Fox *et al.*, 1999; Arula *et al.*, 2012; Denis *et al.*, 2016). Knowledge of diet composition remains particularly limited in the Northwest Atlantic, including only one previous study of larval herring trophodynamics in Newfoundland waters, which reported that early stage herring larvae primarily foraged on nauplii of calanoid



**Fig. 10.** Autumn recruitment index for the Bonavista Bay–Trinity Bay herring stock in relation to the abundance of the four main prey taxa identified during the larval stage. Autumn herring recruitment index was lagged by 4 years in order to link survival to prey abundance during the larval stage in same cohorts.



**Fig. 11.** Recruitment of Bonavista Bay–Trinity Bay autumn-spawning herring as a function of (A) the average yearly abundance of the four main prey taxa abundance combined and (B) mean temperature during first winter.

and cyclopoid copepods (Pepin and Penney, 1997). Given that this broad definition includes the bulk of dominant copepod species occurring within this ecosystem, knowledge remained insufficient to date for the assessment of potential links between variability in secondary production, feeding success and survival.

For Atlantic herring larvae in Trinity Bay, only four copepod taxa constituted the majority of the diet: *O. similis*, *T. longicornis*, *Pseudocalanus* sp. and *Calanus* sp. Early herring larvae fed on the nauplii of *O. similis* and *T. longicornis*, mid-sized larvae (13–29 mm SL) preyed upon the copepodite stages of *Pseudocalanus* sp, and the largest larvae (>30 mm SL) primarily ingested copepodite stages of *Calanus* sp. Atlantic herring larval diet in Newfoundland was characterized by a narrow trophic niche breadth throughout early ontogeny, which is indicative of selective

feeding. Larvae go through a series of well-defined ontogenetic shifts to larger prey taxa (e.g. nauplii to copepodites) based on the size of these prey as larvae grow (Munk, 1992; Busch, 1996). Even though zooplankton were not sampled concurrently with ichthyoplankton in the present study, which precluded calculation of selectivity indices (e.g. Chesson, 1978; Pearre, 1986), we conclude from the combination of clear ontogenetic shifts in diet and narrow niche breadth throughout the larval stage that Atlantic herring larvae from Trinity Bay exhibited strong taxon- and size-dependent selectivity.

During the early larval stage, survival is primarily determined by the ability to detect and successfully capture potential prey (Hunter, 1980; Buskey *et al.*, 1993). As larvae grow, a succession of potential prey taxa of increasing size enters the optimal larval feeding window

where the ratio of capture success to detection rate and that of net energy gain per predation event are at their maximum (Buskey *et al.*, 1993). In the present study, early stage herring larvae from the 2006 cohort mainly foraged on the nauplii of the calanoid copepod *T. longicornis*, while the 2013 cohort mostly relied on the nauplii of the cyclopoid copepod *O. similis*. This interannual difference in dominant prey during the early-feeding stage was paralleled by a notable between-year difference in the relative abundances of these prey taxa in the environment. Over the 3 years considered in this study, *O. similis* generally dominated the copepod prey assemblage, with the exception of September 2006 when the abundance of *T. longicornis* peaked to more than an order of magnitude higher than maximum abundances in other years. While the diet of early stage herring larvae was only assessed in 2006 and 2013, we speculate that an exceptional *T. longicornis* production event in 2006 resulted in a preference shift towards that particularly abundant prey over the otherwise main prey *Oithona similis*.

After reaching a SL of 13 mm, larval herring diet shifted from small copepod nauplii to the larger copepodite stages of *Pseudocalanus* sp., a mid-size calanoid copepod. *Pseudocalanus* sp. is a species complex that often dominates the calanoid copepod assemblage from temperate to boreal ecosystems of the North Atlantic, where it plays a key role in the trophic linkage between primary producers and planktivorous fish due to its high production rate relative to larger zooplankton taxa (Corkett and McLaren, 1978; Johnson and Allen, 2012). In particular, *Pseudocalanus* sp. has often been reported as a main prey item for various larval fish species in the North Atlantic (Table I), including Atlantic mackerel (*Scomber scombrus*),

multiple gadoid species, and several Atlantic herring stocks (Table I). In this study, *Pseudocalanus* sp. contributed ~70% to the diet of herring larvae in the 13–30 mm size range in all 3 years. At 13 mm SL, herring larvae switched from a generalist diet based on small prey taxa to a specialist diet composed of a few larger copepod prey including *Paracalanus* sp., a group of species morphologically similar to *Pseudocalanus* sp (Denis *et al.*, 2016). This result, in line with our research, suggests that the dietary transition at ~13 mm could constitute an important life event regulating recruitment and that *Pseudocalanus* sp. could play a key role in explaining herring larval feeding success and survival in the Northwest Atlantic.

The marine ecosystem off the northeast coast of Newfoundland was characterized by a temporal change in the production of *Pseudocalanus* sp., with peak abundance of the adult stage shifting from spring to autumn in the mid-2000s. This change in phenology of an important larval prey species corresponded with significant environmental changes in the Northwest Atlantic including strong positive anomalies in air temperature, SST and bottom temperature, coupled with lower than average sea ice cover (Colbourne *et al.*, 2014). Zooplankton are particularly sensitive to environmental variability due to their poikilothermic physiology, and changes in their dynamics often reflect parallel changes in environmental variables such as temperature (reviewed in Richardson, 2008). Temperature-driven changes in the distribution and phenology of copepods, and resulting impacts on higher trophic levels, have been described in various ecosystems. For example, changes in abundance and phenology of North Sea copepods in the 1980s led to a temporal mismatch between the emergence of larval Atlantic cod and the production of their preferred prey, which in turn impacted

Table I: Summary of published literature on North Atlantic larval diet studies where *Pseudocalanus* sp. was identified as a main prey

Family	Species	Region	Larval stage	Prey stage	Reference
Clupeidae	<i>Clupea harengus</i>	Nantucket Shoals, Georges Bank	First feeding Late	N/A	Cohen and Lough (1983)
		Aberdeen Bay	First feeding	Nauplii	Checkley (1982)
		North Sea	First feeding Late	Copepodites	Last (1989)
		North Sea	Late	Copepodites	Denis <i>et al.</i> (2016)
Gadidae	<i>Arctogadus glacialis</i>	Canadian Beaufort Sea	First feeding Late	Nauplii Copepodites	Bouchard <i>et al.</i> (2016)
		Canadian Beaufort Sea	First feeding Late	Nauplii Copepodites	Bouchard <i>et al.</i> (2016)
	<i>Boreogadus saida</i>	Canadian Beaufort Sea	First feeding Late	Nauplii Copepodites	Heath and Lough (2007)
		Southern populations	First feeding Late	Nauplii Copepodites	and references therein
	<i>Melanogrammus aelefinus</i>	Greenlandic fjord	First feeding Late	Nauplii Copepodites	Swailethorp <i>et al.</i> (2014)
		North Sea	Late	Copepodites	Economou (1991)
<i>Merlangius merlangus</i>	Georges Bank	Late	Copepodites	Kane (1984)	
	North Sea	Late	Copepodites	Economou (1991)	
	English Channel	Late	Copepodites	Fortier and Harris (1989)	
Merlucciidae	<i>Merluccius bilinearis</i>	North Sea	First feeding Late	Copepodites	Last (1980)
		Western Bank, Scotian Shelf	First feeding Late	Nauplii Copepodites	Reiss <i>et al.</i> (2005)
Scombridae	<i>Scomber scombrus</i>	Magdalen Shallows	First feeding	Nauplii	Robert <i>et al.</i> (2008)
		Long Island Sound	First feeding	Nauplii	Peterson and Ausubel (1984)

recruitment strength (Beaugrand *et al.*, 2003). In the case of *Pseudocalanus* sp., generation time has been shown to be negatively linked to temperature (Huntley and Lopez, 1992; Lee *et al.*, 2003; Persson *et al.*, 2012). A temperature increase in a given system can thus potentially change the timing of production. While the factors driving changes in the phenology of *Pseudocalanus* sp. off the northeast coast of Newfoundland remain unknown, we hypothesize that the observed increase in temperature since the mid-2000s has resulted in an increase in the production rate of breeding generations, which may be an important driver in the increased survival of autumn-spawned herring larvae, even though the expected positive link between *Pseudocalanus* sp. abundance and herring recruitment could not be detected in the present study.

## CONCLUSION

The lack of relationship between the abundance of main prey and the autumn-spawning herring recruitment reported in our study could partly stem from a difference in the scales of larval fish and zooplankton sampling. Fish larvae primarily occur in the surface layer, while zooplankton was quantified over the entire water column. Differences in the timing and locations between zooplankton and ichthyoplankton sampling may also have reduced our ability to detect the expected relationship between prey availability during the larval stage of herring and recruitment. Beyond a potential effect of sampling scales, it is important to consider that recruitment strength is the result of the balance between growth and mortality drivers. In addition to the expected effects of variability in the amount and quality of prey supply, variations in predation pressure are a key potential factor that remains unknown in the present system. Takasuka *et al.* (2007) demonstrated that certain predators, such as raptorial fish, represent a mortality source that operates independent of larval growth. One important next step to the present study is to identify and quantify larval fish predators in Newfoundland coastal systems, the importance of which has been shown to vary in space and time (Paradis and Pepin, 2001; Baumann *et al.*, 2003; Pepin *et al.*, 2003). Even though some important herring recruitment drivers have yet to be identified, findings of the present study suggest that variability in the timing of *Pseudocalanus* sp. production represents a key element to consider moving forward with the study of larval herring recruitment in the region. Future research contrasting the dynamics of spring-spawned larvae to our findings on autumn-spawned individuals may provide a stronger basis to appreciate the effects of recent changes in prey phenology on larval survival and detect the primary drivers of recruitment variability in Newfoundland herring stocks.

## SUPPLEMENTARY DATA

Supplementary data can be found online at *Journal of Plankton Research* online.

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