Feeding ecology of larval Atlantic herring (*Clupea harengus*): linking main prey availability and recruitment in Trinity Bay, Newfoundland

by

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A thesis submitted to the School of Graduate Studies

in partial fulfillment of the requirements

for the degree of Master of Science

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Centre for Fisheries Ecosystem Research

September 2016

St. John's, Newfoundland and Labrador

Abstract

Newfoundland Atlantic herring (*Clupea harengus*) populations are composed of spring- and autumn- spawning components, targeted as a mixed fishery. Until the early 2000s, the spring-spawning component accounted for ~90% of the total catch. Within the last decade, the relative abundance of spring-spawning herring has decreased and autumn-spawning herring now dominate the catch in most areas. Year-class strength is largely determined by survival rate during the larval stage. The objective of this study is to identify the main prey of larval herring and explore the link between main prey availability and subsequent recruitment strength. Herring larvae were collected using bongo tows in Trinity Bay, Newfoundland, in the autumns of 2002 (15-52 mm Standard Length), 2006 (5-15 mm SL) and 2013 (5-15 mm SL). Diet composition was identified and otoliths were extracted to estimate age. Nauplius stages of the calanoid copepod *Temora longicornis* and the cyclopoid copepod *Oithona similis* dominated the diet during the early larval stage (5-15 mm SL) in 2006 and 2013, respectively. In 2002, the mid-size calanoid copepod *Pseudocalanus* sp. strongly dominated the diet in the mid-larval stage (15-30 mm SL). In the late larval stage (>30 mm SL) in 2002, larval diet showed a shift to the larger calanoid copepod *Calanus* sp. The seasonal abundance peak of the main prey during the mid-larval stage, *Pseudocalanus* sp., shifted from spring to autumn during the mid-2000s, concurrent with the period of changing relative abundance of spawning components. A positive relationship was found between the abundance of *Pseudocalanus* sp. in October and recruitment of autumn-spawning herring, thereby supporting the idea that survival may be driven by preferred prey availability during the larval stage. We could not reject the hypothesis that the observed shift in herring population dynamics in the mid-2000s resulted from higher survival rates in autumn-hatched larvae through increased availability of their main prey.

Acknowledgements

First I would like to thank my supervisor, Dr. Dominique Robert, for providing me with this research opportunity and mentoring throughout my graduate program. It has been a privilege to work with someone so enthusiastic and knowledgeable in the field of larval fish science. I thank him for his insights, patience and guidance in writing and could not have completed without him. I would also like to thank my supervisory committee, Christina Bourne, Dr. Jonathan Fisher, and Dr. Patrick Gagnon for their comments and advice. I would like to thank the Department of Fisheries and Oceans Canada, particularly, Dr. Pierre Pepin for his collaboration, statistical advice, and continued input, the crew and DFO staff aboard the C.C.G.S. *Vladykov* for data collection, and Fran Mowbray for sharing historical samples and providing me with the opportunity to go on the vessel and collect new samples. I would also like to thank Dr. Hannah Murphy for her time and effort put into thesis edits. I also thank my fellow grad students and staff at the Centre for Fisheries Ecosystems Research for support. Finally, I thank my friends and family, including my life partner Daryl, who have fully supported me through the process.

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CHAPTER 1: GENERAL INTRODUCTION

Prey availability in relation to early life survival and recruitment

In fisheries ecology, recruitment is defined as the survival of offspring to the reproductive adult stage, when individuals start contributing to the fitness of a population (Fuiman and Werner, 2002). Recruitment of fishes is variable and survival during the larval stage is hypothesized to be the main driver of interannual variability in recruitment (Hjort, 1914; Anderson, 1988; Cushing, 1990). Fish have a complex life cycle composed of the egg, larval, juvenile and adult stages. The egg and larval stages experience extremely high mortality rates, with the majority (>99%) of individuals lost to mortality during the first few weeks post hatch (Fuiman and Werner, 2002). Even small changes in mortality rates during this critical life stage can have a large impact on recruitment strength (Houde, 1987; Anderson, 1988; Cushing, 1990). It is generally considered that early life survival is primarily regulated through starvation and predation (e.g. Leggett and Deblois, 1994). Larvae can only survive for a short time at low prey availability after the shift from endogenous to exogenous feeding following yolk sac depletion (Beaugrand et al., 2003; Castonguay et al., 2008). This concept, termed the 'critical period' hypothesis (*sensus* Hjort, 1914), predicts that massive mortality through starvation will occur at the onset of endogenous feeding if appropriate prey (usually copepods) are not available in sufficient densities (Hjort, 1914; Cushing, 1990; Robert et al., 2014). High early life mortality within a given cohort in turn results in a weak year class (Leggett and Deblois, 1994; Robert et al., 2007; Houde et al., 2016). For these reasons, understanding the drivers of recruitment variability has been the focus of fisheries science since the early 20th century (Hjort, 1914).

Several contemporary trophic hypotheses linking early larval mortality to recruitment strength originate from the critical period hypothesis. The 'match/mismatch' hypothesis expands the temporal framework of the critical period hypothesis, predicting that strong year classes will emerge when the spatial-temporal match between larvae and their prey persists throughout the entire larval stage (Cushing 1975; 1990). Furthermore, prey availability does not only dictate starvation rates but can also regulate larval growth. The 'growth-mortality' hypothesis assumes a positive relationship between larval growth and survival (Anderson, 1988). It incorporates three complementary mechanisms: bigger-is-better, stage-duration and growth-selective predation (e.g. Takasuka et al., 2007; Robert et al., 2014). The bigger-is-better hypothesis states that at a given time, larger larvae are less likely to be preyed upon relative to smaller conspecifics due to increasing ability to avoid predation and resilience to starvation with size (Leggett and Deblois, 1994). The stage-duration hypothesis predicts a positive correlation between growth and survival rates as fast-growing larvae reach the juvenile stage at a younger age and thus benefit from a reduced period in the vulnerable larval stage during which predation mortality is maximum (Houde, 1987). The growth-selective predation hypothesis suggests that at a given size, larvae with faster growth rates are less vulnerable to predation (Takasuka et al., 2003). Another main driver of larval growth is temperature, which can act directly on larval metabolism and indirectly on regulating prey production (Fuiman and Werner, 2002). Differences in adequate prey supply resulting in varying survival rates in the early life stages, may represent the main source of variability in recruitment strength (Castonguay, et al., 2008; Robert et al., 2014).

Atlantic Herring biology

Atlantic herring (*Clupea harengus*) is a schooling, small pelagic species found in coastal waters on both sides of the North Atlantic Ocean (Hardy, 1924; DFO, 2009). Larvae metamorphose into juveniles at a length of 40-50 mm and maturity is reached at a size of about 25 cm and age of 3-4 years. Adults reach a maximum size of 39 cm and weight of 680 g, and can reach 18 years of age (Reid et al., 1999). In the Northwest Atlantic, herring range from Cape Hatteras to Northern Labrador (DFO, 2009). Waters surrounding the island of Newfoundland are home to 6 distinct stock complexes that were defined based on tagging (Wheeler and Winters, 1983): 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 (West coast of Newfoundland). These stocks are known to exhibit an offshore-inshore migratory pattern, moving offshore to access feeding grounds in summer and returning to coastal embayments to overwinter and spawn (Wheeler and Winters, 1983). In the Northwest Atlantic, herring spawn from May to November with distinct peaks in spring (May-June) and autumn (September-October), and display homing behavior by returning to the same spawning locations each year (Wheeler and Winters, 1984). For management purposes, stocks are separated into two spawning components and are categorized as spring and autumn spawners. In general, fish that spawn before and after July 1st are respectively considered as spring and autumn spawners. Spawning takes place at specific locations either inshore or on offshore banks. Eggs are demersal and adhere to the bottom substrate which is usually gravel or rock (Messieh et al., 1985). The eggs are approximately 1 mm in diameter and hatch into 4-6 mm larvae within 10-30 days (Bigelow and Schroeder, 1953; Lough et al., 1982). Newly hatched herring larvae are pelagic. Some larvae are retained near spawning sites, while others are dispersed out of the spawning areas (Smith and Morse, 1993;

Huse, 2016). Depending on hatch date, spring-spawned larvae typically reach the size of metamorphosis (40-50 mm) before winter, while autumn-spawned individuals overwinter as larvae and metamorphose during the following spring (Cohen and Lough, 1983). Hence, the progeny of autumn-spawning herring is exposed to low temperatures and limited prey availability during an extensive period (Graham et al., 1990).

Atlantic herring is an important component of marine pelagic ecosystems of Atlantic Canada, as it plays a key role as a forage species transferring energy from secondary producers (zooplankton) to higher trophic levels such as piscivorous fishes (e.g., Atlantic cod *Gadus morhua*), birds (e.g., Northern gannet *Morus bassanus*) and marine mammals (e.g., humpback whale *Megatera novaeangliae*) (DFO, 2009). Atlantic herring also support the largest small pelagic fishery in Eastern Canada (FRCC, 2009). Fish are either sold for food or bait (FRCC, 2009). Herring populations are characterized by boom-bust dynamics, where a single year class typically dominates spawning stock biomass and supports the fishery for approximately a decade. In the Newfoundland region, there has not been a strong year class for over a decade, and adult growth rates have declined since the 1990s, remaining low throughout the region (DFO, 2012). Early records indicate that NL herring stocks have historically been dominated by spring spawners, and until the mid-2000s, the spring-spawning component comprised more than 90% of the total catch (Wheeler and Winters, 1982; Bourne et al., 2013). Within the last decade, the abundance of the spring-spawning component in the catch has progressively decreased, while that of the autumn-spawning component has increased over the years and is currently dominating the catch. For example, spring spawners in the Bonavista-Trinity Bay herring stock accounted for ~90% of the stock in 2000, before continuously decreasing to reach a proportion below 50% in recent years (DFO, 2012; Bourne et al., 2013). Even though the absolute abundance of NL

herring stocks is not monitored by DFO, the observed shift in dominance from spring-spawners to autumn-spawners in the catch is considered proportional to abundance of spawning components, as it has been shown to be the case for the acoustically-surveyed herring stock located off the West coast of Newfoundland (DFO, 2012). Identification of the factors driving this shift is required for a better understanding of herring stock dynamics.

The objective of the present study was to investigate the role of interannual variability in prey available to larval herring in the shifting relative abundance of Atlantic herring spawning components. To achieve this objective, diet composition of herring larvae captured in Trinity Bay in 2002, 2006 and 2013 was described at a fine taxonomical resolution. The Bonavista Bay-Trinity Bay herring stock has experienced a pronounced shift in the dominance of spring to autumn spawners, making it an ideal stock area to investigate the drivers of the observed shift in spawning stock composition. I then assessed how variability in the timing of peak production of the main copepod prey taxa over the 1999-2013 time series could have affected larval diet. Otolith microstructure was examined to estimate hatch dates of the three larval cohorts and evaluate whether differences in hatch dates could be related to larval survival. Finally, I examined the potential link between abundance of the main prey in autumn and recruitment of autumn-spawning herring from Bonavista Bay-Trinity Bay.

CO-AUTHORSHIP STATEMENT

The manuscript resulting from this thesis was co-authored with Dr. Dominique Robert, Christina Bourne, Dr. Pierre Pepin and Dr. Hannah Murphy. I was principal contributor for the field work (2013), laboratory analysis, and manuscript preparation. The Pelagic Section of the Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans Canada, provided access to samples from their 2002 and 2006 collections.

Publication and submission status: in preparation for the Journal of Plankton Research

Wilson, Murphy, Bourne, Pepin, Robert. Feeding ecology of larval Atlantic herring (*Clupea harengus*): linking main prey availability and recruitment in Trinity Bay, Newfoundland.

CHAPTER 2:

Feeding ecology of larval Atlantic herring (*Clupea harengus*): linking main prey availability and recruitment in Trinity Bay, Newfoundland

2.1 Introduction

Recruitment of fishes is variable and survival during the larval stage is generally considered the main driver of interannual variability in recruitment (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 survival during the larval stage has been largely attributed to variability in preferred prey availability by regulating feeding success and growth (Hjort, 1914; Cushing 1990; Anderson, 1988; Robert et al., 2008; Murphy et al., 2012). Therefore, any change in plankton production dynamics has the potential to impact larval survival and recruitment (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 predation directed towards slow-growing larvae (Houde 2009). Slow-growing larvae are generally considered more vulnerable to predation than their fast-growing conspecifics due to protracted development resulting in extended duration of the larval stage 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 (Robert et al., 2014). Studies presenting detailed information on larval diet composition and prey availability are critically needed to

reveal relationships between recruitment strength and variability in prey availability during the larval stage (Beaugrand et al., 2003; Castonguay et al., 2008, Murphy et al., 2012).

Atlantic herring populations are generally characterized by boom and bust dynamics, where a single large year class may dominate spawning stock biomass for a decade. In the Barents Sea, strong year classes of Atlantic herring have been positively linked to fast larval growth (Ottersen and Loeng, 2000). In the Newfoundland (NL) region, recruitment has been continuously low since the early 2000s and Atlantic herring stocks are currently at relatively low levels (Bourne et al., 2013). Newfoundland herring stocks are composed of spring- and autumn- spawning components. Early records indicate that herring in NL have historically been predominated by spring spawners, and until the mid-2000s, spring-spawning fish strongly dominated the population and represented more than 90% of the total catch (Wheeler and Winters, 1982; Bourne et al., 2013). Within the last decade, the relative abundance in the catch of spring spawners has decreased, and autumn spawners now dominate the commercial catch in most herring management units around Newfoundland (Bourne et al., 2013; DF0, 2016). This suggests a shift in the primary larval survival window from the spring to autumn. Parallel to this change, there are indications of recent changes in the distribution and phenology of some of the main copepod species in the Northwest Atlantic (Head and Sameoto, 2007). However, linking changes in plankton phenology to herring stock dynamics in the Northwest Atlantic is currently impossible because diet composition during the larval stage remains largely unknown. In the Northeast Atlantic, larval herring are known to prey primarily on calanoid copepods, including *Pseudocalanus* sp., *Calanus finmarchicus*, *Acartia* sp. and *Eurytemora* sp. (Hardy, 1924; Blaxter, 1965; Arrhenius 1996; Fox et al., 1999; Arula et al., 2012). Knowledge of diet composition remains particularly limited in the Northwest Atlantic with only one report of larval

herring diet in Newfoundland waters that concluded first-feeding larvae primarily foraged on nauplius stages of calanoid and cyclopoid copepods (Pepin and Penney 1997). Such low taxonomical resolution precludes linking vital rates to prey availability (Robert et al., 2014).

In the present study, we investigated the role of interannual variability in prey availability during the larval stage in driving the observed shift from spring to autumn spawners in the Bonavista Bay-Trinity Bay herring population. We first identified the primary copepod prey of Atlantic herring larvae based on the gut content analysis of individuals captured during ichthyoplankton surveys carried out in October 2002 (56 stations), September 2006 (19 stations) and September 2013 (19 stations) in Trinity Bay, Newfoundland, which is a key spawning area for the Bonavista Bay-Trinity Bay herring stock. We then assessed the potential changes in the timing of peak production of main copepod prey over a 1999-2013 time series obtained separately from the Atlantic Zone Monitoring Program (AZMP) of the Department of Fisheries and Oceans (DFO), and how these changes may have affected larval survival. Finally, we examined the potential links between abundance of the main prey taxa in autumn and survival of the autumn-spawning herring from the Bonavista Bay-Trinity Bay stock.

2.2 Materials and Methods

Study Area

Trinity Bay (48°N, 53.5°W) is a large (3000 km^2) embayment located on the east coast of Newfoundland. Trinity Bay is the location of spawning and nursery grounds for numerous fish species including Atlantic cod and American plaice (*Hippoglossoides platessoides*), as well as capelin (*Mallotus villosus*) and Atlantic herring (Davidson and de Young, 1995) (Fig. 1). 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 center (Davidson and de Young, 1995). Cold waters originating from the Labrador Current flow into the bay, especially in spring (Davidson and de Young, 1995). Among the six herring stock complexes located around Newfoundland, the Bonavista Bay-Trinity Bay herring stock has experienced one of the most pronounced shifts from a dominance of spring spawners to autumn spawners (Bourne et al., 2013). Trinity Bay, therefore, is considered to be an ideal area to study the drivers of changing population dynamics in Northwest Atlantic herring stocks.

Environmental data

Temperature

Sea surface temperature was retrieved directly from the ichthyoplankton sampling surveys (see below). At each station (Fig. 1), an Applied Micro-systems STD-12 probe was deployed to profile salinity, temperature and depth (Dalley et al., 2002). These temperature profiles were used to determine depth of the surface mixed layer in which larval fish generally occur, and to assess associations of herring larvae with certain temperatures. Temperature time series from 2002, 2006 and 2013 were retrieved from a Ryan thermograph operated by DFO at a depth of 10

m in Trinity Bay (48.25°N, 53.42°W; Fig. 1). These temperature time series were then smoothed using a 96 hour running mean to reveal patterns of variability at the monthly and yearly scales, for the period ranging from July to October in each year, which corresponds to the potential larval period of autumn spawners.

Zooplankton abundance

Zooplankton abundance data were obtained from DFO's AZMP. Zooplankton abundance and distribution have been monitored in nearshore areas of the Canadian Atlantic since 1999, and the 1999-2013 time series was used as an index of inshore prey availability in the absence of zooplankton collections concurrent with ichthyoplankton sampling in Trinity Bay. Detailed methods of the AZMP can be found in Pepin et al. (2005, 2011). Briefly, zooplankton were sampled at recurrent oceanographic sections along the northeast coast of Newfoundland three times a year (April-May July-August, and November-December). Zooplankton samples were collected using dual 0.75 m diameter bongo with 202 μm 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^{-1}. 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 taxonomical level possible (Pepin et al., 2011). The Bonavista line from the AZMP is located off the mouth of Trinity Bay and comprises 10 zooplankton sampling stations, sampled 3 times a year (spring, summer and autumn) distributed along an inshore-offshore axis (Fig. 2). Another high frequency sampling site, station 27 (47.55°N, 52.59°W), is located south of Trinity Bay near the entrance to St. John's harbour, and is sampled up to 6 times per month at approximately the same time periods every year (Fig. 2). Data from the Bonavista line and station 27 corresponding to the early larval period of autumn-spawning herring (July-October) found in

ichthyoplankton collections were used to develop indices of zooplankton prey abundance in Trinity Bay. Given that the 202µm mesh of the AZMP sampling gear cannot provide quantitative estimates of nauplius stages of copepods which are commonly ingested by early larvae, abundance of the adult stage (copepodite 6) was used as a proxy for nauplius and early copepodite production in the system (Ringuette et al. 2002).

Ichthyoplankton Sampling

Atlantic herring larvae were sampled during daylight hours during the DFO annual ichthyoplankton surveys in Trinity Bay in October and November 2002, September 2006 and September 2013 (Dalley et al., 2002). While these surveys are primarily targeting capelin (*Mallotus villosus*) larvae, autumn-spawned herring larvae represented the main by-catch. Bongo nets measuring 61 cm in diameter with 333 µm 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 m min^{-1}, and a vessel speed of 2-2.5 kt. A total of 56 stations was sampled in 2002, while 19 stations were sampled in both 2006 and 2013 (Fig. 1). 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 to preserve larval otoliths and gut content for further laboratory analysis. Ethanol was changed within one week after collection.

Gut content analyses

All fish larvae were sorted out from other plankton organisms and identified to species for each station. All Atlantic herring larvae found in the samples were stored individually in 95% ethanol and subsequently used in further analysses. Standard length (SL) and gape width of all herring larvae were measured to the nearest 0.1 mm using a stereomicroscope at a magnification of 40-

60×. No adjustments to SL measurements were made to account for preservation due to minimal shrinkage of herring larvae preserved in ethanol (Fox, 1996). In order to characterize larval herring diet composition, 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 at 70× 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 diet description, larvae were binned into 3 mm size classes in order to assess ontogenetic shifts in diet.

Otolith microstructure analyses

The otolith microstructure was analyzed to determine daily age and investigate the potential to estimate recent growth. Sagittal otoliths from each larva were removed under a stereomicroscope at 40× magnification using a polarizing filter and tungsten needles. The otoliths were mounted on a glass slide with clear glue for subsequent examination. Only otoliths of larvae >25 mm were polished using 3 µm lapping film, which allowed for increased readability of early increments. All other otoliths were not polished as polishing larvae smaller than 25 mm did not make a difference in the detection of daily increments for Atlantic herring. Otolith microstructure images were taken at 1000× magnification using an oil immersion lens on a Zeiss compound microscope connected to a digital camera. An image analysis system (Image Pro version 6.1©) was used to count the increments from the nucleus along the longest axis of the otolith. Each age reading was conducted twice and otoliths were only considered in the analysis if the readings were within 10% of each other. Only four otoliths were eliminated from the analysis. Daily formation of increments in Atlantic herring larvae has previously been validated, with the first increment deposited at a mean age of 15 days post hatch (dph) (Campana and Moksness 1991; Moksness,

1992; Folkvord et al., 1997; Fox et al., 2003). Hatch date was estimated by subtracting the number of increments from the date of capture and adding 14 days to account for delayed increment formation.

2.2.1 Data analyses

Temperature

At each station, sea surface temperature was derived from the STD based on the mean temperature in the first 3m, corresponding to the minimum depth of the surface mixed layer where the majority of larvae occur (Munk et al., 1989; Lough et al., 1996; Oliver and Sabatès 1997). Contour maps of sea surface temperature were created for each year and correlation of larval density and temperature was calculated. 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

Zooplankton abundance data from the AZMP time series were used as an index of potential prey abundance available to herring larvae. Even though the nearshore Bonavista line corresponds to the AZMP zooplankton transect located nearest to the inshore sampling area for larval herring, it was not possible to develop an index of prey availability given its low sampling frequency and poor temporal overlap with ichthyoplankton sampling in Trinity Bay. In order to develop a prey abundance index based on the high sampling frequency station 27, we first verified whether abundance of the 4 main prey taxa of larval herring identified from stomach content analysis

were correlated between Bonavista line stations and Station 27. We compared abundance of the 4 copepod species during days when both Bonavista line stations and Station 27 were sampled over the 1999-2013 time series using complete linkage cluster analysis and SIMPROF (PRIMER 6 software) to determine if Station 27 was associated with specific stations of Bonavista line. Zooplankton abundance data were fourth root transformed to reduce the potential effect of the large differences in abundance of the 4 copepods considered. Only the Bonavista line station that clustered with Station 27 were considered in further analyses. Because there were often temporal gaps in sampling between the Bonavista line and Station 27, we calculated mean zooplankton abundance from Bonavista line stations sampled on the same day as Station 27. The number of Bonavista line stations sampled on a same day as Station 27 ranged from 3-5 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 Bonavista line. Prey availability indices were then developed for prey taxa characterized by strong correlations. This allowed the investigation of 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 and years over the 1999-2013 time series.

Larval diet

For description of the diet of herring larvae, we binned larvae into 3 mm size classes, which provided a minimum of 4 larvae per size class. We calculated percent prey contribution by size class by representing the number of individuals of each prey type as a percentage of the total number of prey items in the stomachs in 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 and limited the analysis to temporal variability.

Trophic niche breadth

Feeding dynamics of Atlantic herring larvae were also characterized by sized-based trophic niche breadth. Trophic niche breadth was used as an index to explore selectivity. Trophic niche breadth can be used to make inferences on feeding strategy of the larvae (Murphy et al., 2012). An increase in niche breadth with larval length indicates that larvae tend to 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 items as they grow. Trophic niche breadth (N) of each 3 mm larval herring length class (L) was calculated using the following equation:

$$N_L = SD_L(\log W_L)$$

where SD is the standard deviation of log-transformed mean prey widths (W) of all individuals in length class L. 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).

Linking environmental prey availability to autumn recruitment

The recruitment index is calculated by DFO using abundance of age-4 herring caught in the spring research gill net survey throughout Bonavista Bay and Trinity Bay (DFO, 2012). To assess the potential role of variability in abundance of the key zooplankton prey taxa in driving recruitment, the autumn recruitment index for the Bonavista Bay-Trinity Bay herring stock was regressed against abundance of the main prey during the period when larvae from the same cohort were expected to feed on these prey.

2.3 Results

2.3.1 Zooplankton abundance

Only the four main prey taxa that contributed >80% to the larval diet were considered in zooplankton analyses. These four prey taxa consisted of *Oithona similis*, *Pseudocalanus* sp., *Temora longicornis*, and *Calanus* sp. (dominated by *C. finmarchicus*). Cluster analysis based on these four zooplankton taxa from station 27 and Bonavista line stations yielded two clusters representing inshore and offshore stations (Fig. 3). 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 approximately 100 nmi from land. Station 27 associated with inshore stations of the Bonavista line in all years of the 1999-2013 time series. Abundances of the four zooplankton taxa from the Bonavista line inshore cluster were significantly correlated to zooplankton abundances sampled at station 27 on the same day for the 1999-2013 time series (Table I; Fig 4). Among the four species, *Temora longicornis* (r=0.89) and *Pseudocalanus* sp. (r=0.75) showed particularly strong correlation coefficients (Fig. 4). A similar analysis using a subset of the data time series corresponding to the three years where larvae were captured (2002, 2006, and 2013) also resulted in strong correlations for three of the four species, although the relationship with *Calanus finmarchicus* was not statistically significant (Fig. 5). On the basis of the overall consistency between inshore Bonavista line 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 (C6) abundance for three of the main copepod prey species was characterized by a shift from spring to autumn for the time series 1999-2013 (Fig. 6). This shift in phenology, which occurred around 2005, was evident in *Oithona similis* and *Pseudocalanus* sp. populations, and was apparent to some extent in *Calanus finmarchicus* populations (Fig. 6). Peak abundance of the smaller calanoid copepod *Temora longicornis* occurred in autumn throughout the time series, and absolute abundance in the period 2005-2007 was an order of magnitude higher than in other years (Fig. 6-7).

Autumn abundance of larval herring main prey varied among 2002, 2006, and 2013 (Fig. 7). For all four copepod species, highest adult stage abundances during late summer – early autumn were recorded in 2006 (Fig. 7). *Calanus finmarchicus* abundance was relatively low in 2002 and 2013, with the exception of modest peaks in October and November in 2013 and 2006, respectively (Fig. 7). Abundance of *Pseudocalanus* sp. showed high interannual variability (Fig. 7). In 2002, *Pseudocalanus* sp. abundance increased through the autumn to reach a peak in late October-early November, while earlier October and September peaks were observed in 2013 and 2006, respectively. *Oithona similis* was generally the most abundant species in the autumn of all years, and no clear abundance peak could be observed with the exception of August-September in 2006. *Temora longicornis* was generally characterized by low abundances throughout the autumn of all years, with the exception of a massive abundance peak in September 2006, corresponding to an order of magnitude increase in the number of individuals relative to other years (Fig. 7).

2.3.2 Temperature

Daily mean temperatures recorded by the DFO thermograph in Trinity Bay ranged between 1 and 16 ^{o}C in July-September for the 3 years of this study, with a decreasing temperature trend from September to October (Fig. 8). The warmest of the three years was 2013 with a mean of 13.4 °C during August-September, while mean temperatures were 12.1 °C and 11.1 °C during the same period in 2006 and 2002, respectively.

In the three sampling years, there was no clear trend between larval herring density and sea surface temperature at capture in Trinity Bay (r=-0.097 for 2002, r=0.38 for 2006 and r=0.33 for 2013; Fig. 9). Mean temperature at capture was 9.5 °C in October 2002, 13.5 °C in September 2006 and 12.4 °C in September 2013.

2.3.3 Larval herring characteristics

In total, 112, 46 and 67 herring larvae were sampled in 2002, 2006 and 2013, respectively. Standard length 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 (Table II; Fig. 10a). Larvae sampled in 2006 (size range 6-15 mm SL) and 2013 (size range 6-19 mm SL) were similar in size and smaller on average than in 2002. For all sampling years, highest larval densities were observed inshore, with relatively few individuals caught in the central portion of the bay (Fig. 9).

2.3.4 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 (Table II; Fig. 10a). For larval lengths > 37 mm SL, copepodite stages of the large calanoid copepod *Calanus*

sp. (mainly *C. finmarchicus*) dominated diet composition, representing 30-96% of all prey (Table II; Fig. 10a). Even though size ranges of larvae sampled in 2006 (6-15 mm) and 2013 (6-19 mm) were similar, their diet composition differed. In 2006, herring larvae foraged mainly on nauplius stages of *Temora longicornis* (33-63% of all prey) and *Pseudocalanus* sp. nauplii (10-22%), and to a lesser extent on *Oithona similis* nauplii and copepodites (0-16%), (Table II; Fig. 10b). In 2013, larval diet was dominated by *Oithona similis* nauplii and copepodites (28-91%), while nauplius stages of *Temora longicornis* (6-14%) and *Pseudocalanus* sp. (0-29%) were secondary prey. Copepodite stages of *Pseudocalanus* sp. appeared in the larval diet at a size of 13 mm SL (Fig. 10c).

When pooling larvae from all years, two ontogenetic shifts in diet composition were identified (Fig. 10d). At 13-19 mm SL, there was an observed shift in main prey from copepod nauplius stages to *Pseudocalanus* sp. copepodites. The second diet shift was initiated at 30 mm, when the large *Calanus* sp. copepodites were first observed in the diet. At ~44 mm, *Calanus* sp. copepodites represented more than 95% of ingested prey. Other prey items (e.g., *Microsetella norvegica)* represented a small overall contribution (2.9-16.7%) to larval diet (Table III).

Percentage of empty guts generally decreased as larval size increased, with the exception of the 16-19 mm length class that showed particularly high feeding incidence (Tables II and III).

When all larval herring were pooled, a strong linear relationship (r^2= 0.79, $p<0.001$) was found between gape width and larval length (Fig. 11). Therefore, larval length was used in subsequent prey width analyses. In all years, prey width increased with larval length (Fig. 12). Variability in prey width did not show a major increase with larval size (Fig. 12). Even though larvae captured in 2006 and 2013 ingested different prey taxa, nauplius stages of *Temora logicornis* (2006) and

Oithona similis (2013) were characterized by a similar range of body widths. Mean prey width increased with larval length, with individual prey width showing little deviation from the mean in all size classes (Fig. 13a). This was reflected by a constant and relatively narrow trophic niche breadth over the full larval length interval (linear regression: r^2= 0.068, p= 0.466) (Fig. 13b).

2.3.5 Otolith microstructure analysis

The otolith microstructure was analyzed for larvae captured in 2002 (n=39), 2006 (n=33), and 2013 (n=43). A linear relationship was found between larval length and the number of daily increments recorded on the otolith (Fig. 14). A stronger linear relationship between otolith radius and standard length was found in 2002 in larvae larger than 14 mm SL (Fig. 15). In 2006 (r^2=0.106, p= 0.203) and 2013 (r^2= 0.134, p= 0.086), non-significant regressions were observed between otolith radius and standard length below the size of 10 mm SL. Given the absence of relationship between otolith radius and somatic size in the early larval stage, otolith and daily somatic growth trajectories could not be calculated. Although otolith growth and somatic growth were not linked, daily otolith increment formation has previously been confirmed in Atlantic herring (Campana and Moksness 1991), which allowed us to estimate age and hatch dates. In 2002, the estimated hatching period ranged from late July to late September. In 2006 and 2013, herring larvae were characterized by a contracted hatching period that ranged between mid-August and early September, with a strong relative peak in hatch dates in early September (Fig. 16).

2.3.6 Atlantic herring recruitment and larval prey abundance

Time series of autumn Atlantic herring recruitment for Trinity Bay-Bonavista Bay stock showed increasing recruitment from 1999 to 2002. After a period characterized by decreasing and relatively low levels between 2003 and 2008, the two most recent years of the time series (2009 and 2010) were relatively strong (Fig. 17). Recruitment for the cohort of 2002 was twice as strong as that in 2006, while recruitment for the 2013 year-class will only be known in 2017 (Fig. 17).

A significant linear relationship (r^2=0.41, p=0.025) was found between the limited time series of autumn recruitment index and abundance of the main prey *Pseudocalanus* sp. in October, when larvae reach the size category where they primarily feed on that prey (Fig. 16). No relationship was found between the abundance of other main prey taxa during the period when they are consumed (*Temora longicornis* in September, *Oithona similis* in September, *Calanus* sp. in November) and recruitment. The relationship of spring recruitment and *Pseudocalanus* sp. abundance in spring (April-June) was also explored but no relationship was found (Fig. 18).

2.4 Discussion

Larval herring trophodynamics

A growing body of evidence indicates that fish larvae do not prey on the different zooplankton taxa in proportion to their abundance in the environment as previously assumed, but strongly select for specific prey (Robert et al. 2008; reviewed in Llopiz 2013). Selective feeding in larval fish has been reported in multiple ecosystems and in various feeding conditions, including during low prey availability (Murphy et al, 2012, Young et al. 2010). Given the selective nature of larval fish feeding, relying on high taxonomical resolution of diet composition is essential to assess links between prey availability and larval vital rates (Llopiz et al. 2013; Robert et al. 2014). Despite early evidence that larval herring feeding was highly selective and stage dependent (Hardy, 1924), the taxonomic resolution considered by previous studies that have characterized herring diet through stomach content analysis has varied widely, with a majority of studies reporting prey to the subclass and order levels (e.g. copepod, calanoida) (Pepin and Penney 1997, Munk 1992, Arrhenius 1996), and relatively few studies resolving prey to the genus and species levels (Last 1989, Cohen and Lough 1983). Overall, these studies have described successive shifts in diet composition during early ontogeny (e.g., Hardy, 1924; Checkley 1982, Munk 1992, Arula et al. 2012) with prey preferences varying widely among ecosystems (Table IV), making it impossible to infer diet composition or prey preference in populations where data on diet composition do not exist. In Newfoundland waters, diet of first-feeding larvae was described as nauplius stages of calanoid and cyclopoid copepods (Pepin and Penney 1997). Given that this definition includes the bulk of dominant copepod species occurring within this ecosystem, it is necessary to resolve diet composition at a higher definition to assess potential links between preferred prey density, feeding success and survival.

As predicted by recent studies on larval fish prey selectivity, we found that herring larvae from Trinity Bay only preyed on a limited selection of potential prey taxa present in the environment. The overall proportion of empty guts was on average 50%, which is consistent with previous studies on larval herring (Munk, 1992; Fox et al., 1999). When considering all larvae captured in 2002, 2006 and 2013, two ontogeneti shifts in diet composition could be described over the first few weeks of life. During the mid-larval stage (13 mm SL), larval herring switched from nauplius stages of the small copepods *Oithona similis* and *Temora longicornis* to copepodite stages of the mid-size calanoid copepod *Pseudocalanus* sp. Larval herring then started transitioning to copepodite stages of the large calanoid copepod *Calanus* sp. from a size of ~30 mm SL. While our understanding of ontogenetic dietary shifts could partly be biased by a level of interannual variability in trophodynamic processes that could not be explored in our analysis due to between-year differences in the timing of sampling, herring larvae were also characterized by a narrow trophic niche breadth throughout early ontogeny. A relatively constant trophic niche breadth indicates a foraging strategy whereby predators show well-defined ontogenetic switches to larger prey (e.g. nauplii to copepodites) as they grow, which implies that variation in the size of prey remains constant throughout development (Pearre, 1986; Murphy et al., 2012). In contrast, a generalist diet would have been reflected by increasing trophic niche breadth with larval length, where larger prey taxa are gradually incorporated into the original larval prey assemblage (Munk, 1995; Young et al., 2010; Murphy et al., 2012). Even though environmental zooplankton abundance was not available to calculate classic selectivity indices in the present study (e.g. Chesson, 1978; Pearre, 1986), we conclude from the combination of clear shifts in main prey and the constant narrow niche breadth with larval size, that Atlantic herring larvae from Trinity Bay likely exhibited strong prey selectivity.

Prey selectivity during the larval stage is primarily determined by the ability to detect and successfully capture the different potential prey (Hunter, 1980; Buskey et al., 1993). As larvae grow, a succession of potential prey taxa of increasing size enter 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). For prey smaller than the optimal size, net energy gain is low relative to the energy expenditure related to capture; while for prey larger than the optimal size, high average capture cost reduces the potentially high net energy reward per capture event (Ivlev, 1961; Buskey et al., 1993). The optimization of net energy gain by a selective predator can explain the observed shifts in prey size from copepod nauplii to copepodites of increasing size during the early ontogeny. Within a given prey size range, species-specific prey selectivity can be driven by the abundance of the different potential prey taxa in the environment (Holling 1959, Ivlev 1961). When the relative abundance of the preferred prey taxon falls below a certain threshold, predators may switch to an alternative prey of higher relative abundance to increase the ratio of energy gained to energy expended in foraging (Holling 1959, Ivlev 1961). In the present study, early herring larvae from the 2006 cohort primarily foraged on the nauplius stages of the calanoid copepod *Temora longicornis*, while the 2013 cohort mostly relied on the nauplius stages of the cyclopoid copepod *Oithona similis*. This interannual difference in dominant prey during the first-feeding stage was paralleled by a notable between-year difference in the relative abundance of these prey taxa in the environment. Over the three years considered in this study, *Oithona similis* generally dominated the copepod prey assemblage, with the exception of September 2006 when abundance of *Temora longicornis* was more than an order of magnitude higher than its peak abundance in other years. While diet of first-feeding larvae was only assessed in 2006 and 2013, we speculate that due to

an exceptional production event in 2006, *Temora longicornis* became the main prey over *Oithona similis* during the first-feeding stage of the 2006 larval herring cohort.

After reaching a standard length of ca. 13 mm, herring larvae shifted their diet from small nauplius prey to the larger copepodite stages of *Pseudocalanus* sp., a mid-size calanoid copepod. *Pseudocalanus* sp. is a species complex that often dominate the calanoid copepod assemblage from temperate to boreal ecosystems of the North Atlantic, where they play a key role in the trophic linkage between primary producers and planktivorous fish due to their 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 V), including in Atlantic herring off the coast of England (Hardy, 1924) and on Georges Bank (Cohen and Lough, 1983). In the present study, *Pseudocalanus* sp. contributed on average ≥50% of the diet of all larvae in 2002, and ca. 70% in the 13-30 mm size range (Table II), suggesting that this species plays a key role for feeding success and survival of larval herring. The large calanoid copepod *Calanus* sp. started to dominate the diet by numbers only during the late larval stage, from a size of 37 mm. In the North Atlantic, *Calanus* spp. have often been reported as important prey during the late larval and juvenile stages of fish (Sameoto et al., 1994; Batchelder et al., 1995). Although variability in survival during the late larval and juvenile stages can potentially modulate recruitment, surviving individuals have already developed strong foraging capabilities and are less vulnerable to variability in prey supply than they were earlier in life.

Relationship between variability in Pseudocalanus sp. abundance and herring recruitment

In addition to its important contribution to the diet of multiple fish species, *Pseudocalanus* sp. has been identified as an important driver of larval growth and survival in the Northwest Atlantic (Corkett and McLaren, 1978; Johnson and Allen, 2012). Variability in the abundance of *Pseudocalanus* sp. was identified as a key driver for the early growth of Atlantic cod and haddock (*Melanogrammus aeglefinus*) on Georges Bank (Buckley and Durbin, 2006). In Atlantic mackerel from the Gulf of St. Lawrence, variability in preferred *Pseudocalanus* sp. prey abundance was linked to feeding success, growth performance and year-class strength (Castonguay et al., 2008; Robert et al., 2009). The critical importance of *Pseudocalanus* sp. as a regulator of survival during the larval stage of North Atlantic fish could be caused by a combination of generally high abundance in temperate to subarctic ecosystems, a body size that makes it an effective prey during the early to mid-larval stage when feeding success is critical, and a high lipid content to size ratio relative to other potential prey in the same size range (Lough et al., 1996).

In the present study, we found a significant positive relationship between the recruitment index of autumn-spawning herring and the abundance of *Pseudocalanus* sp. in October, corresponding to the period when autumn herring larvae reach the size range in which this copepod is the preferred prey. The link between *Pseudocalanus* sp. abundance and herring recruitment suggest that feeding success and larval survival are optimal under high preferred prey abundance. The relatively strong year class of 2002 corresponded to the second highest *Pseudocalanus* sp. abundance of the 1999-2010 time series (Fig. 16). To the contrary, the 2006 average/weak year class developed during a period when peak *Pseudocalanus* sp. abundance in the ecosystem

shifted from spring to autumn. This shift in peak production was characterized by particularly low *Pseudocalanus* spp. abundance throughout that year, including in October where it was less than half the abundance of 2002. Abundance of *Pseudocalanus* sp. in October 2013 was intermediate relative to 2002 and 2006. Even though year-class strength has not yet been determined for the 2013 cohort, we predict that, based on higher than average *Pseudocalanus* sp. availability, recruitment will be stronger than the time-series mean but will likely remain lower than that of 2002.

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. The dramatic change in phenology of this important larval herring prey occurred during the mid-2000s and corresponded with significant environmental changes in the Northwest Atlantic including strong positive anomalies for air temperature, sea surface temperature and bottom temperature, coupled with lower than average sea ice cover (Colbourne et al., 2014). Zooplankton organisms are particularly sensitive to environmental variability due to their poikilothermic physiology, and changes in their dynamics are often considered to 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, profound changes in abundance and phenology of North Sea copepods in the 1980s led to a temporal mismatch between larval Atlantic cod and their preferred prey, which in turn impacted recruitment strength (Beaugrand et al., 2003). In the sub-Arctic North Pacific Ocean, where a single species *Neocalanus plumchrus* dominates the copepod assemblage, warming conditions

resulted in a shift in peak production to 60 days earlier within the last 50 years (Mackas et al., 1998). This change in zooplankton phenology has impacted Cassin's auklet (*Ptychoramphus aleuticus*) breeding colonies by the reduced growth of their chicks (Bertram et al., 2001). 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 general 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 uncertain, we hypothesize that the observed increase in temperature since the mid-2000s has resulted in the parallel increase in the production rate of breeding generations, which would explain in part the overall increase in autumn herring abundance.

While *Pseudocalanus* sp. abundance during the larval stage was positively linked to autumn herring recruitment, 59% of the variance in year-class strength remained unexplained by the relationship. In conjunction with prey availability, predation and environmental factors influencing larval condition and growth could be important drivers of Atlantic herring larval survival. Predation is generally considered the most important source of egg and larval mortality in marine fishes (Leggett and Deblois, 1994, Houde 2008). Predation mortality can be linked to prey supply as poorly-fed larvae show increased vulnerability to predator attacks and slower growth implies a longer larval stage and extended period when predation mortality rate is maximum (Houde, 1987; Leggett and Deblois, 1994). Predation mortality can also act independently of prey supply with spatiotemporal variability in the overlap between fish larvae and their main predators potentially leading to differences of several orders of magnitude in mortality rates (Bailey and Houde, 1989). In the present study, the observed hatching frequency

distributions in 2006 and 2013 were much narrower than that of 2002. This suggests that herring larvae from the 2006 and 2013 cohorts have experienced high mortality outside of these time frames (e.g. Wright and Bailey 1996; Yoklavich and Bailey 1990). Alternatively, spawning may have occurred over a shorter period during these 2 years, increasing the risk of poor recruitment through the mismatch between larvae and their prey (Cushing, 1990). While the role of predation could not be quantified in the present study, our results nevertheless indicate that interannual variability in prey supply is an important determinant of larval survival.

CHAPTER 3: Conclusion

We could not reject the hypothesis that availability of the main prey *Pseudocalanus* sp. constitutes an important driver of recruitment strength in Newfoundland autumn-spawning herring. This link between zooplankton prey availability and survival could be revealed by first resolving larval diet at the prey species level. Further testing of the hypothesis that a change in the phenology of the main prey explains the shift in dominance from spring-spawning to autumn-spawning herring will require the assessment of diet composition and timing of feeding on the main prey in spring herring larvae as well as exploration of the effects of environmental factors (i.e. temperature). Assuming similar diet composition between larvae from the two spawning components of the Trinity Bay-Bonavista Bay herring stock, the shift in peak *Pseudocalanus* sp. production from spring to autumn could be responsible for an increase in abundance of autumn-spawning herring, concurrent with a decrease in that of the spring-spawning component through changes in feeding opportunities and survival rates during the larval stage.

CHAPTER 4: General Discussion

The shift from a dominance of spring spawners to a dominance of autumn spawners in Atlantic herring stocks from the Newfoundland region has led to questions on the nature and role of links between the environment, larval survival and recruitment dynamics in this ecosystem. We concluded that variability in the abundance of *Pseudocalanus* sp., the main prey taxon contributing to the diet of autumn-spawned herring larvae, was a driver of larval survival and recruitment for that component of the stock.

The vast majority of herring stocks in the Northwest Atlantic are composed of both autumn- and spring-spawning components. In the Georges Bank-Bay of Fundy region, herring is characterized by fast growth and 95% of the stock is made up of autumn spawners. In the Gulf of St. Lawrence, herring stocks are traditionally characterized by intermediate growth and an equal mixture of spring and autumn spawners. Finally, slow growth and a strong dominance of spring spawners (ca. 90%) were characteristic of herring stocks off the South and Northeast coasts of Newfoundland (Melvin et al., 2009). By modelling the effect of increasing sea surface temperatures on herring population dynamics, Melvin et al. (2009) predicted that warmer temperatures in the Newfoundland region would favor autumn-spawning components of the stocks. In that model, temperature was considered as an indicator of the changing environment, so that its effects of shifting spawning components could either be direct or indirect through an alteration of plankton production and phenology. Sea surface temperatures have remained higher than the long-term mean since the mid-2000s, leading to the current dominance of autumn-spawning contingent in most populations. It has also been recently proposed that milder winter conditions in recent years could be linked with the higher recruitment of autumn-spawning herring through higher larval survival (Bourne et al., 2015).

The opposite scenario occurred in the North Sea, where the autumn-spawning component of the stock has been reduced following a temperature increase (Payne et al., 2009; Alvarez-Fernandez et al., 2015). This decrease has been explained by a decrease and temporal shift in peak abundance of larval herring food supply (Payne et al., 2009; Alvarez-Fernandez et al., 2015). A reduction by half in the availability of preferred prey *Temora* sp. and *Pseudocalanus* sp. resulted in low larval growth and high mortality (Alvarez-Fernandez et al., 2015). The importance of preferred prey availability in the North Sea support our findings suggesting that herring population dynamics may be subject to bottom-up control during the larval stage. Our study revealed that a large portion of herring larvae captured in Trinity Bay in 2002, 2006 and 2013 from August to October were produced by adults spawning in August. Spawning components are classified based on the month in which adults spawn: autumn spawning ranges from July-December and spring spawning from January-June. In the Northwest Atlantic, peak autumn spawning times can range from August-October, depending on regions and stocks (Boyar 1968; Das, 1972; Pankratov and Sigaev, 1973; Kelly and Stevenson, 1985). In recent years, there has been evidence that spring spawners in Newfoundland stocks have shifted peak spawning time to later in the season (Bourne et al., 2013). There is a possibility that peak autumn spawning has also shifted earlier due to increasing temperature throughout the year in the system. Further research is needed to determine more precisely the timing of peak spawning for both spring- and autumn-spawning components, which will allow to confirm if peak spawning detected in August originates from autumn spawners as assumed, or could instead reflect late spawning from the spring-spawning component or an increased presence of a summer-spawning component that has increased over the past decade. Expanding the current research gillnet program primarily targeting spring-spawners throughout the potential spawning season would facilitate a better

characterization of spawning components and quantification of their recruitment. Refining our knowledge of current stock structure and timing of spawning of the different components is needed for a better understanding of current and future population dynamics of Newfoundland herring stocks.

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Tables

Table I: Parameters of the regression analyses between abundance of larval herring main copepod prey measured at Sation 27 and mean abundance measured at inshore Bonavista line stations on the same day, over the 1999-2013 time series.

Prey species	R	R^2	p-value	Obs. (n)	y-int.	m
Calanus finmarchicus	0.3354	0.1125	0.02989	42	756	0.2688
Pseudocalanus sp.	0.7532	0.5674	1.30E-08	41	2035	0.7291
Oithona similis	0.4985	0.2485	0.00057	44	11949	0.4586
Temora longicornis	0.8941	0.7993	4.70E-13	35	526	0.882

Table II: Diet composition of larval Atlantic herring by length classes and years, expressed as the percent contribution by numbers of the different prey taxa

	Length class (mm)														
	6 to <10		10 to <13		13 to <16			16 to <19		19 to <22	22 to <25	25 to <28	28 to <37	37 to <44	44 to <53
	2006	2013	2006	2013	2002	2006	2013	2002	2013	2002	2002	2002	2002	2002	2002
Prey taxon															
Copepods															
Eggs	-	-	-	-	-	-	-	-	-	8.7	5.3	-	-	8.3	-
Nauplii															
O. similis	15.8	75.0	-	63.6	-	-	90.9	-	28.6	-	-	-	-	-	-
T. longicornis	63.2	6.3	33.3	-	-	42.9	-	-	14.3	-	-	-	-	-	-
Pseudocalanus spp.	10.5	-	22.2	27.3	-	-	-	-	28.6	-	-	-	-	-	-
Microcalanus spp.	-	-	-	9.1	-	-	-	-	-	8.7	-	-	-	-	-
Copepodites															
O. similis	5.3	12.5	33.3	-	-	7.1	-	-	-	26.1	15.8	18.2	-	-	-
T. longicornis	-	-	-	-	-	21.4	-	16.7	-	-	15.8	9.1	-	-	-
Pseudocalanus spp.	-	-	5.6	-	100.0	-	9.1	83.3	28.6	56.5	63.1	72.7	69.5	41.7	-
Calanus spp.	-	-	-	-	-	-	-	-	-	-	-	-	30.5	50	95.7
Microsetella novegica	-	6.3	-	-	-	28.6	-	-	-	-	-	-	-	-	-
Cladocerans	-														
Bivalve larvae	5.3	-	5.6	-	-	-	-	-	-	-	-	-	-	-	-
Podon spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.3
Number of larvae analysed	25	28	16	17	9	5	17	11	5	25	29	23	6	5	4
Feeding incidence (%)	36	32	56	36	44	100	30	27	60	43	42	41	50	80	75
Mean number of prey	2.2	1.7	2.1	2.2	1.0	3	2.2	2	2.3	2.2	2.2	1.6	5	3.8	10.3

Table III: Diet composition of larval Atlantic herring by length classes with all years combined, expressed as the percent contribution by numbers of the different prey taxa

	Length class (mm)									
Prey taxon	6 to <10	10 to <13	13 to <16	16 to <19	19 to <22	22 to <25	25 to <28	28 to <37	37 to <44	44 to <53
Copepods										
Eggs	-	-	-	-	8.7	5.3	-	-	8.3	-
Nauplii										
O. similis	42.9	21.3	33.3	18.2	-	-	-	-	-	-
T. longicornis	37.1	25.0	12.5	9.1	-	-	-	-	-	-
Pseudocalanus spp.	5.6	25.0	-	18.2	-	-	-	-	-	-
Microcalanus spp.	-	3.6	-	-	8.7	-	-	-	-	-
Copepodites										
O. similis	8.6	17.9	4.2	-	26.1	15.8	18.2	-	-	-
T. longicornis	-	-	12.5	9.1	-	15.8	9.1	-	-	-
Pseudocalanus spp.	-	3.6	20.8	45.4	56.5	63.1	72.7	69.5	41.7	-
Calanus spp.	-	-	-	-	-	-	-	30.5	50	95.7
Microsetella novegica	2.9	-	16.7	-	-	-	-	-	-	-
Cladocerans										
Bivalve larvae	2.9	3.6	-	-	-	-	-	-	-	-
Podon spp.	-	-	-	-	-	-	-	-	-	4.3
Number of larvae analysed	53	33	31	16	25	29	23	6	5	4
Feeding incidence (%)	30	42	46	67	43	42	41	50	80	75
Mean number of prey	1.7	1.8	2.2	2.2	2.2	2.2	1.6	5	3.8	10.3

Table IV: Summary of published literature on Atlantic herring larval diet composition.

Location	First-feeding stage	Late larval stage	Reference
Aberdeen Bay	Day 4-24: Copepod and *Pseudocalanus* sp. N	Day 25-74: *Oithona* sp. C	Checkley, 1982
Baltic Sea	N/A	Calanoid copepods (*Acartia*, *Eurytemora*) , cladocerans C	Arrhenius, 1996
Blackwater Estuary England	*Acartia* C	*Acartia C*	Fox et al., 1999
England, Plymouth	Peridinium, larval mollusca, and harpacticio	*Pseudocalanus sp.*	Hardy, 1924
Gulf of Riga; off Baltic Sea	*Eurytemora affinis* and *Acartia* sp. N	*Eurytemora affinis C*	Arula et al., 2012
Maine coast	N/A	*Calanus finmarchicus* C	Blaxter, 1965
Nantucket shoals, Georges Bank	*Centropages* sp., *Pseudocalanus* sp. and *Paracalanus parvus*	*Centropages* sp., *Pseudocalanus* sp. and *Paracalanus parvus*	Cohen and Lough, 1983
North Sea	Copepod N	Copepod C	Munk, 1992
North Sea	*Calanus finmarchicus C, Temora longicornus C, Pseudocalanus elongates C, Paracalanus parvus C*	*Calanus finmarchicus C, Temora longicornus C, Paracalanus parvus C*	Last, 1989
Newfoundland	Calanoid N, cyclopoid N, bivalve larvae		Pepin and Penney 1997

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

Family	Species	Region	Larval stage	Prey stage	Reference
Clupeidae	*Clupea harengus*	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
Gadidae	*Arctogadus glacialis*	Canadian Beaufort Sea	First feeding Late	Nauplii Copepodites	Bouchard et al., 2016
	Boreogadus saida	Canadian Beaufort Sea	First feeding Late	Nauplii Copepodites	Bouchard et al., 2016
	Gadus morhua	Southern populations	First feeding Late	Nauplii Copepodites	Heath and Lough, 2007 and references therein
	Melanogrammus aelefinus	North Sea	Late	Copepodites	Economou, 1991
		Georges Bank	Late	Copepodites	Kane, 1984
	Merlangius merlangus	North Sea	Late	Copepodites	Economou, 1991
		English Channel	Late	Copepodites	Fortier and Harris, 1989
		North Sea	First feeding Late	Copepodites	Last, 1980
Merlucciidae	*Merluccius bilinearis*	Western Bank, Scotian Shelf	First feeding Late	Nauplii Copepodites	Reiss et al., 2005
Scombridae	*Scomber scrombrus*	Magdalen Shallows	First feeding	Nauplii	Robert et al., 2008
		Long Island Sound	First feeding	Nauplii	Peterson and Ausubel, 1984

Figures

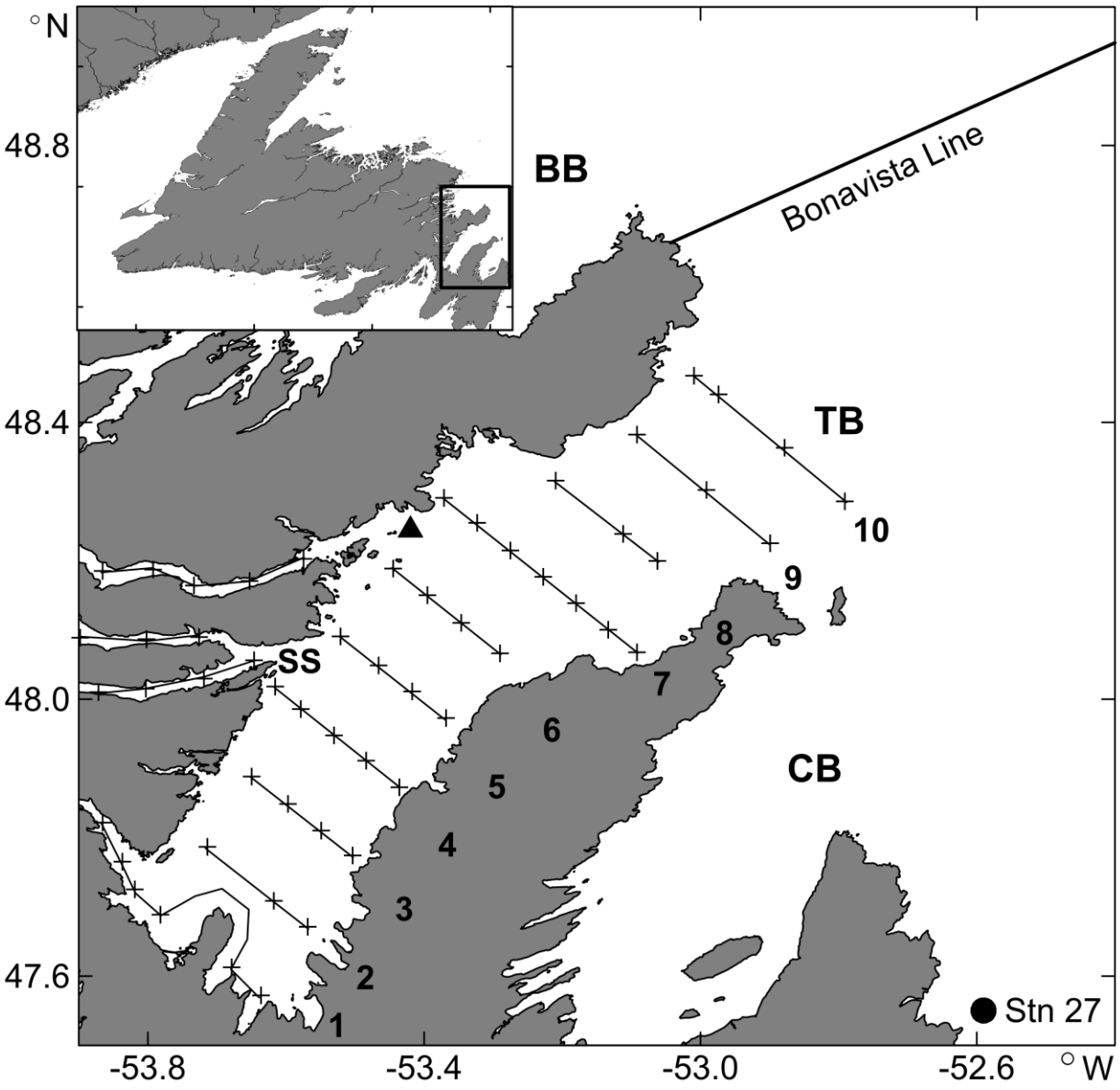

Fig. 1. Map of the study area with 10 transects comprising 56 sampling stations. All stations were sampled in 2002, while only transects 4-7 were sampled in 2006 and 2013. (SS, Smith Sound; BB, Bonavista Bay; TB, Trinity Bay; CB, Conception Bay; ●, Station 27; ▲, thermograph station).

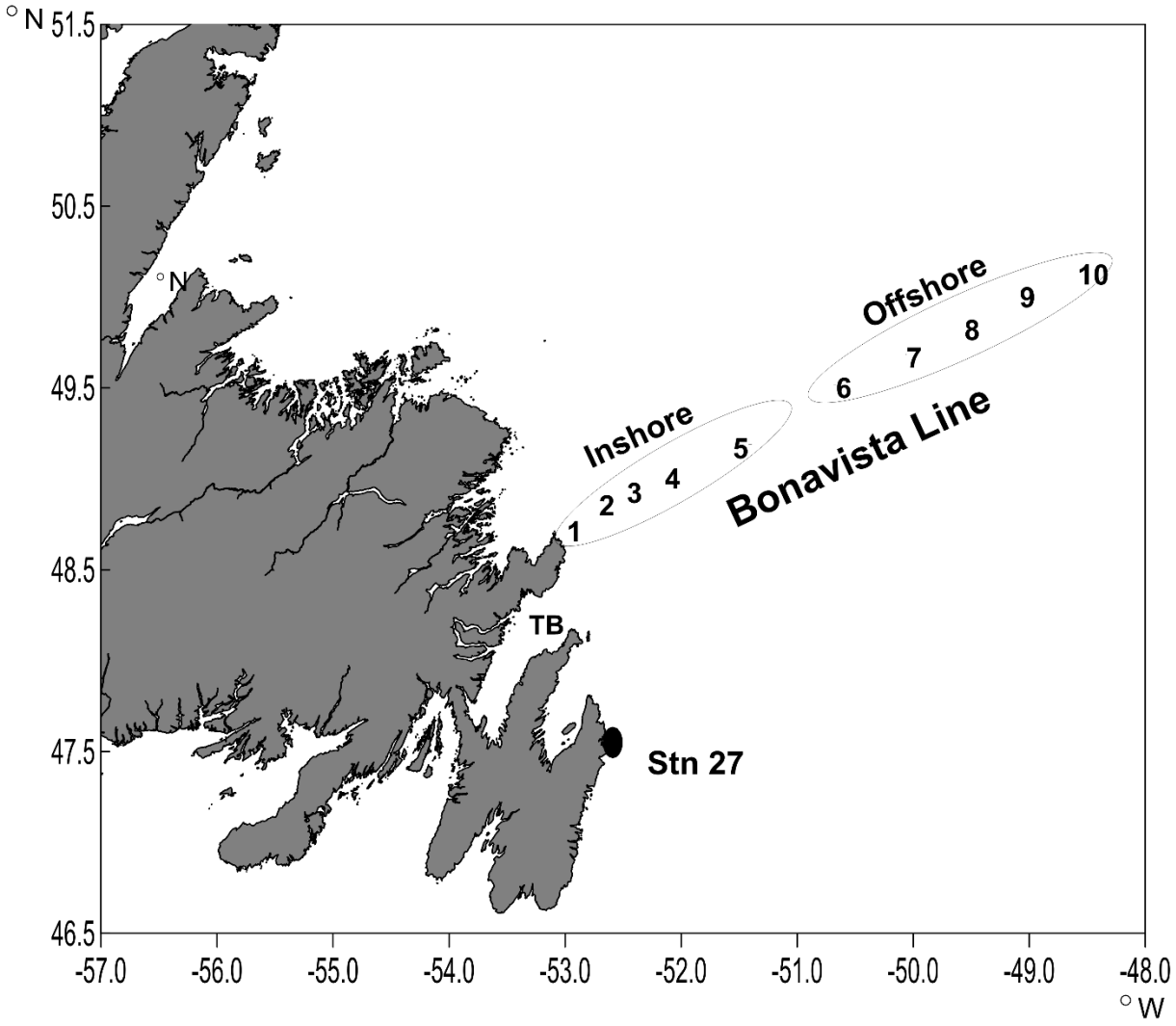

Fig. 2. Map of zooplankton sampling stations Bonavista line with 10 sampling stations and Station 27 indicated by a circle. TB represents Trinity Bay.

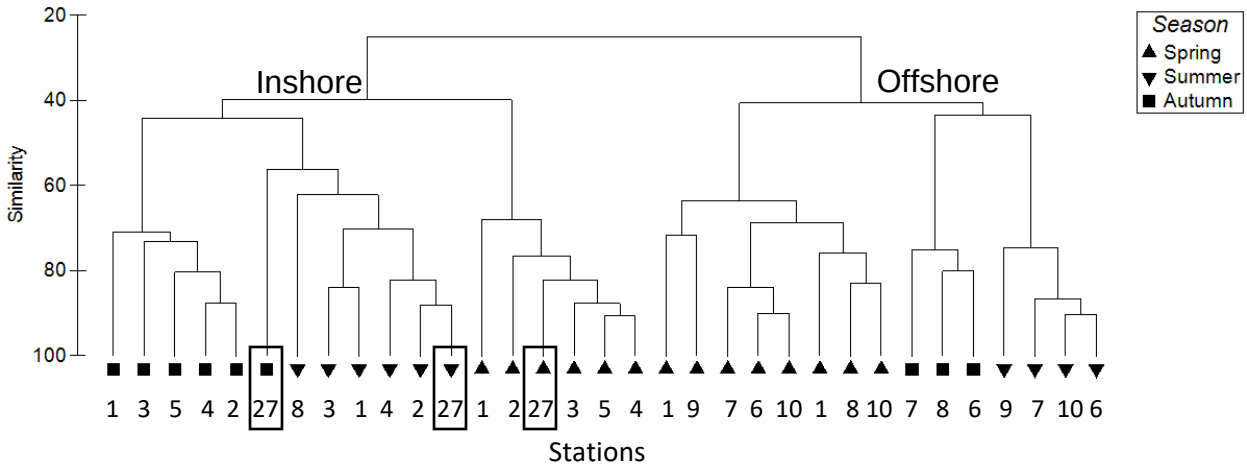

Fig. 3. Example of Bray Curtis similarity cluster analysis for year 2002 comparing abundance of *Calanus finmarchicus*, *Pseudocalanus* sp., *Oithona similis* and *Temora longicornis* among stations of the Bonavista line (Atlantic Zone Monitoring Program) as well as the high frequency sampling Station 27 (overlaid with a black box). Analysis was performed for each year and yielded similar results over the 1999-2013 time series. Sampling may have occurred more than once at each station during a given sampling season. Spring = April-May, summer = July-August, and autumn = November-December.

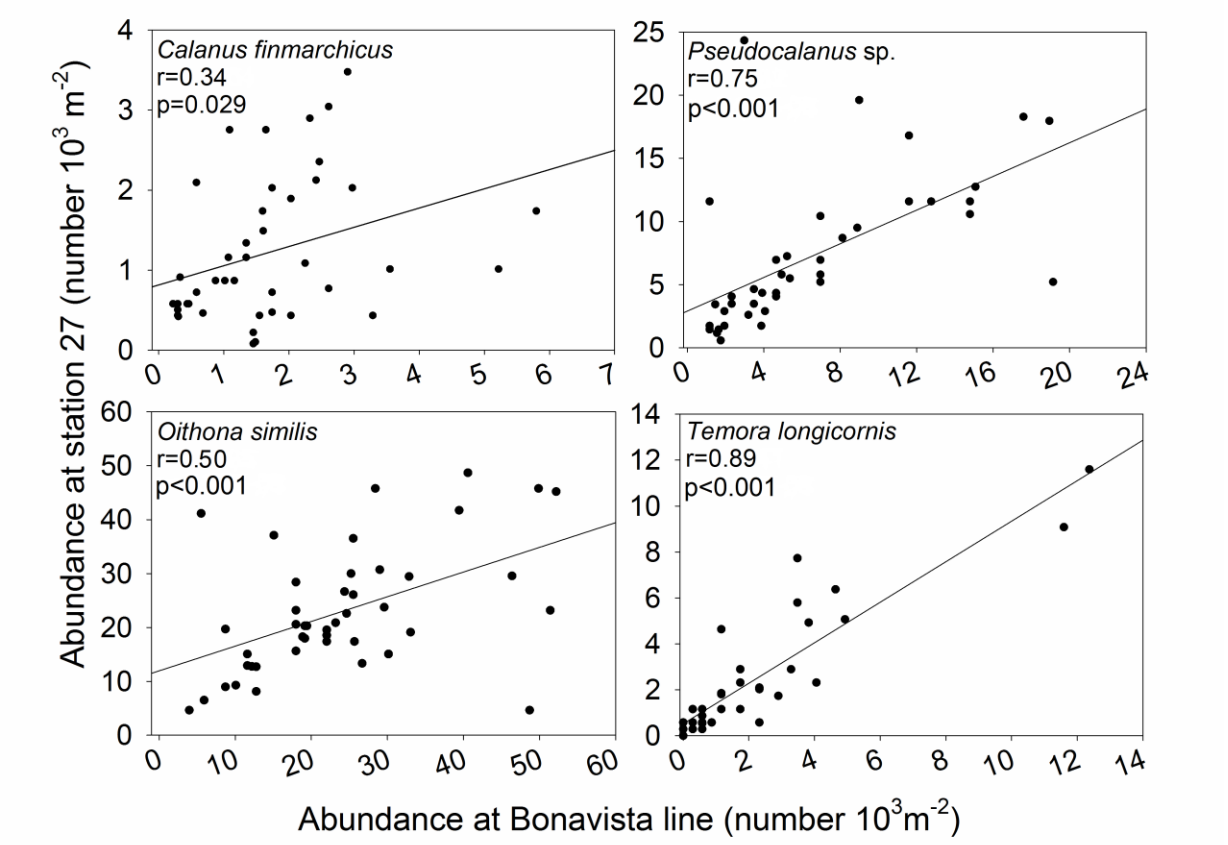

Fig. 4. Abundance of larval herring main prey taxa (*Calanus* sp., *Pseudocalanus* sp., *Oithona similis*, and *Temora longicornis*) measured at Station 27 as a function of mean abundance measured at inshore stations of the Bonavista line on a same day from spring to autumn over the time series 1999-2013.

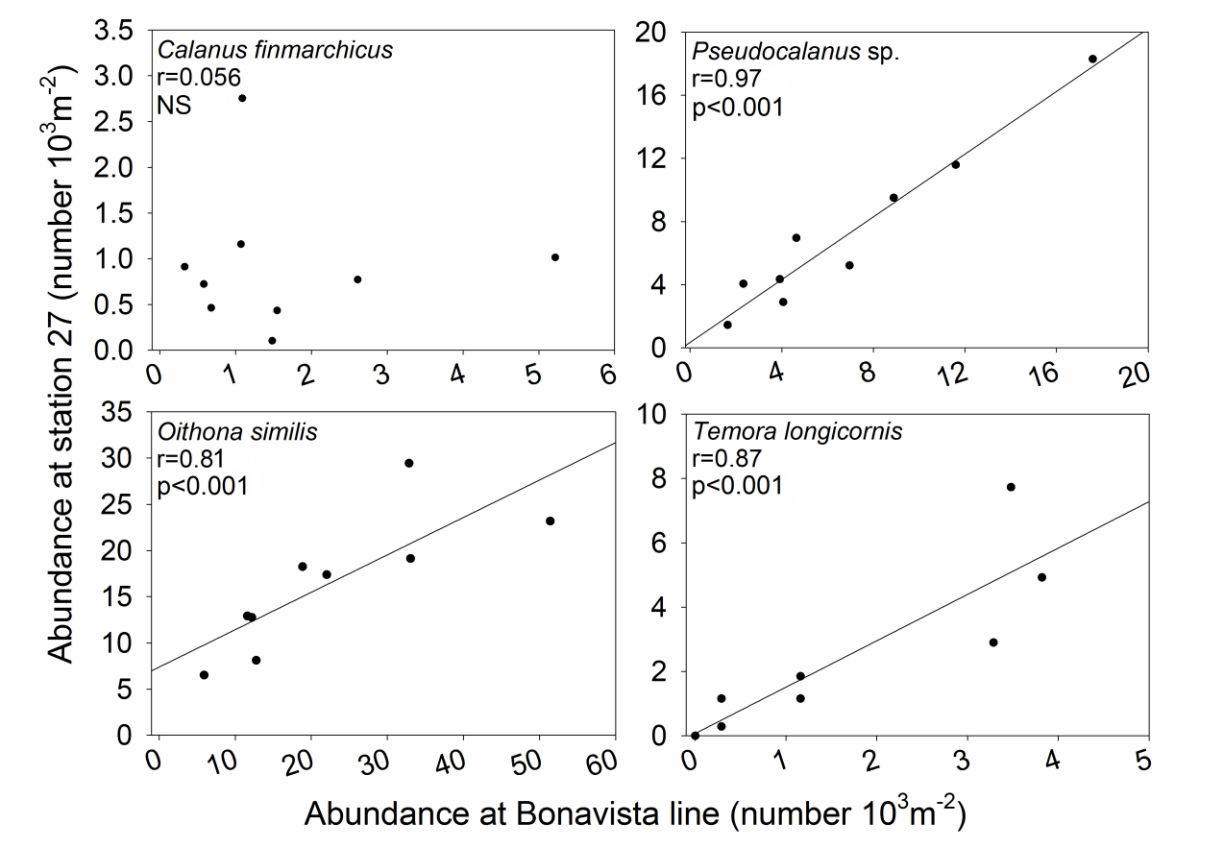

Fig. 5. Abundance of larval herring main prey taxa (*Calanus* sp., *Pseudocalanus* sp., *Oithona similis*, and *Temora longicornis*) measured at Station 27 as a function of mean abundance measured at inshore stations of the Bonavista line on a same day from spring to autumn for 2002, 2006 and 2013.

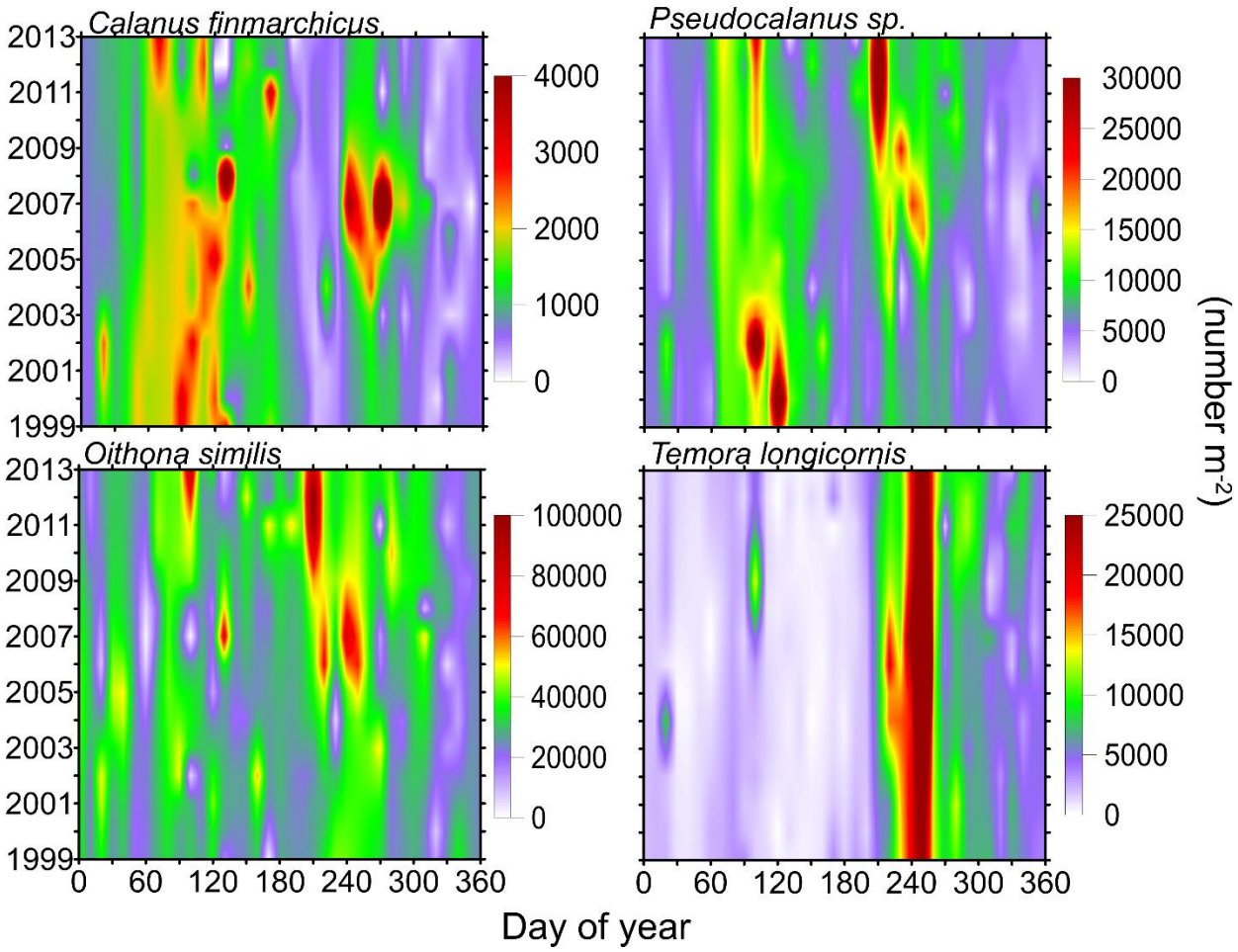

Fig. 6. Abundance time series (1999-2013) for the adult stage (C6) of the 4 copepod species, primarily contributing to larval herring diet, as a function of day of year. For *Temora longicornis*, a large value recorded in 2006 was removed from the analysis to reveal temporal patterns of abundance.

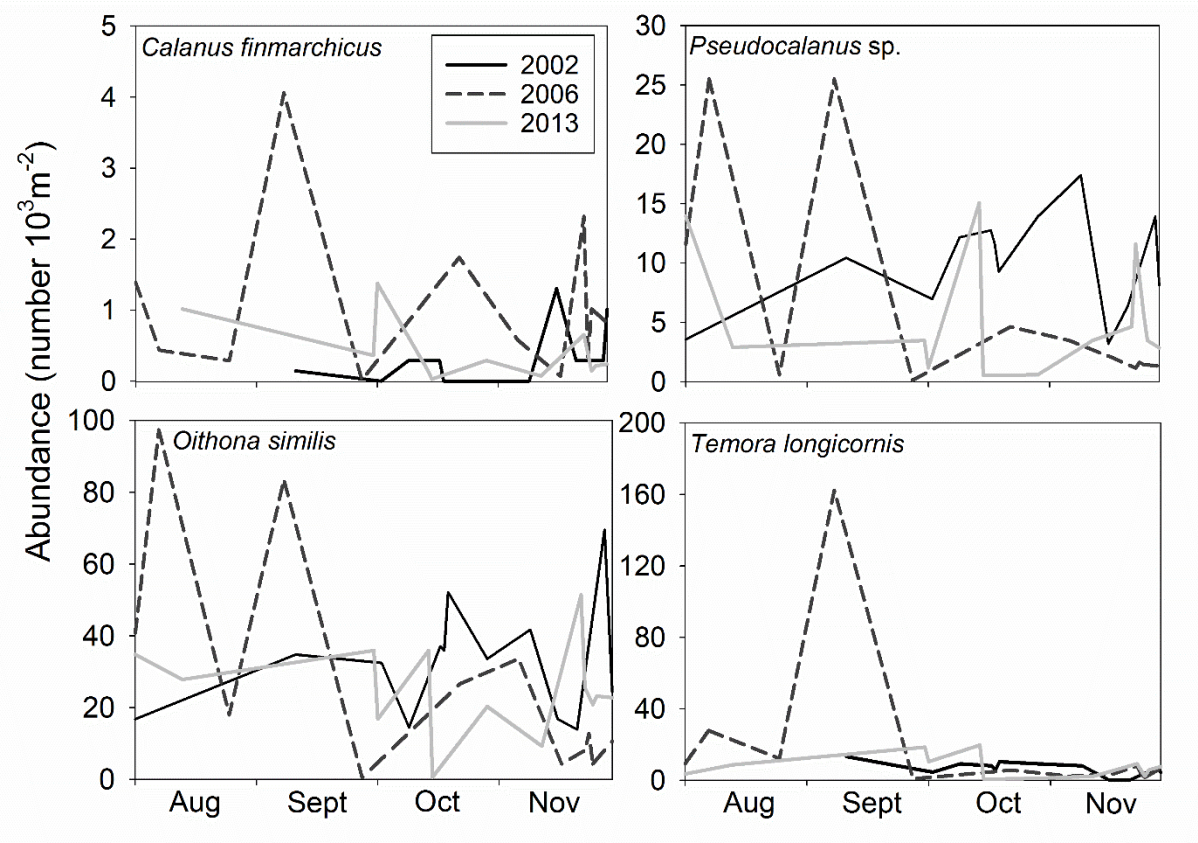

Fig. 7. Temporal pattern of abundance for the adult stage of larval herring main copepod prey in 2002, 2006 and 2013, as recorded at the high frequency sampling Station 27.

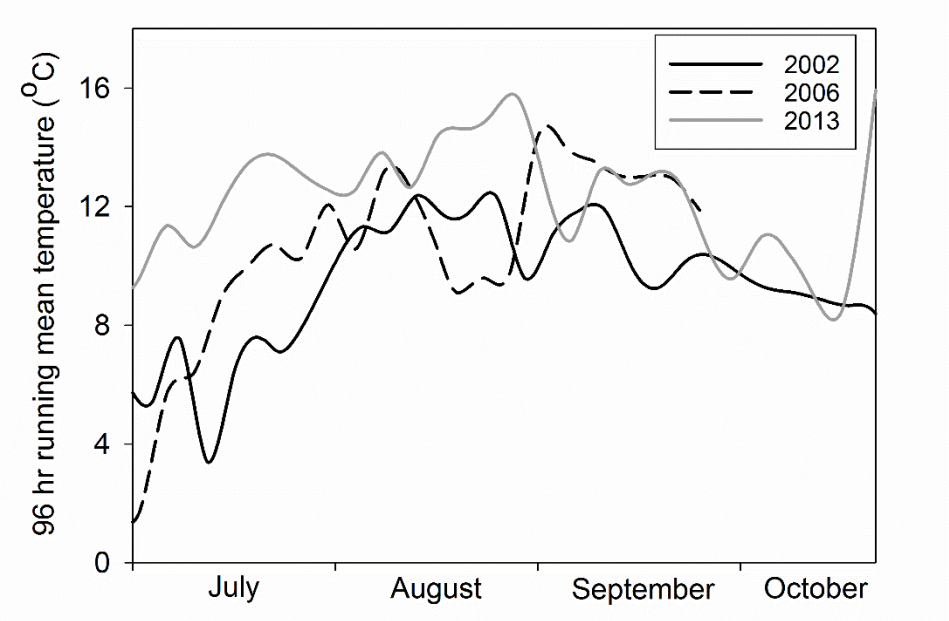

Fig. 8. July-October temperature time series (96 hour running mean) recorded by a thermograph set at a depth of 10 m in Trinity Bay in 2002, 2006 and 2013. Note that a portion of the data (late September and October) could not be recovered in 2006.

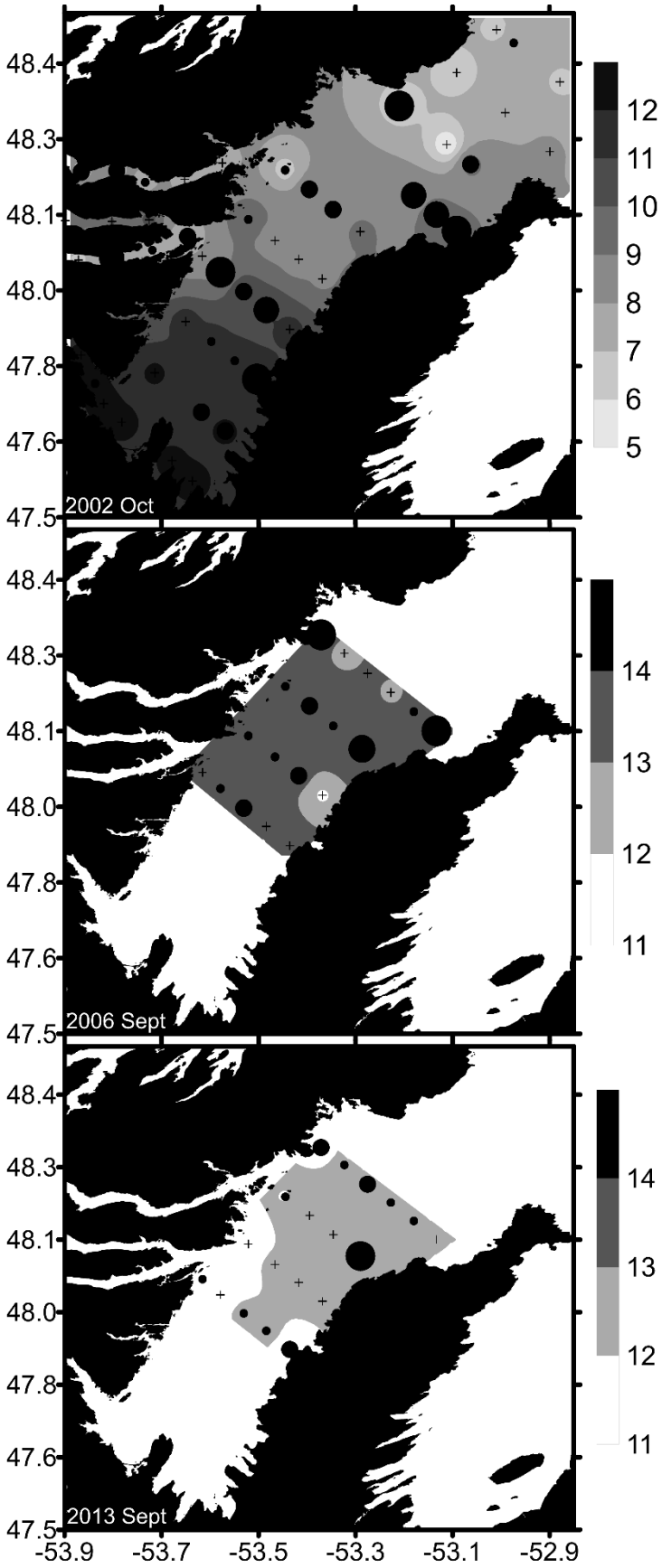

Fig. 9. Spatial variability in sea surface temperature in Trinity Bay in September (2013 and 2006) and October (2002). Sampling stations are overlaid with four Atlantic herring larvae density ranges (0-0.0061, 0.0062-0.015, 0.016-0.025, 0.026-0.105 larvae m^{-3}) depicted by increasing circle size. The symbol + represents the absence of larvae at a given station.

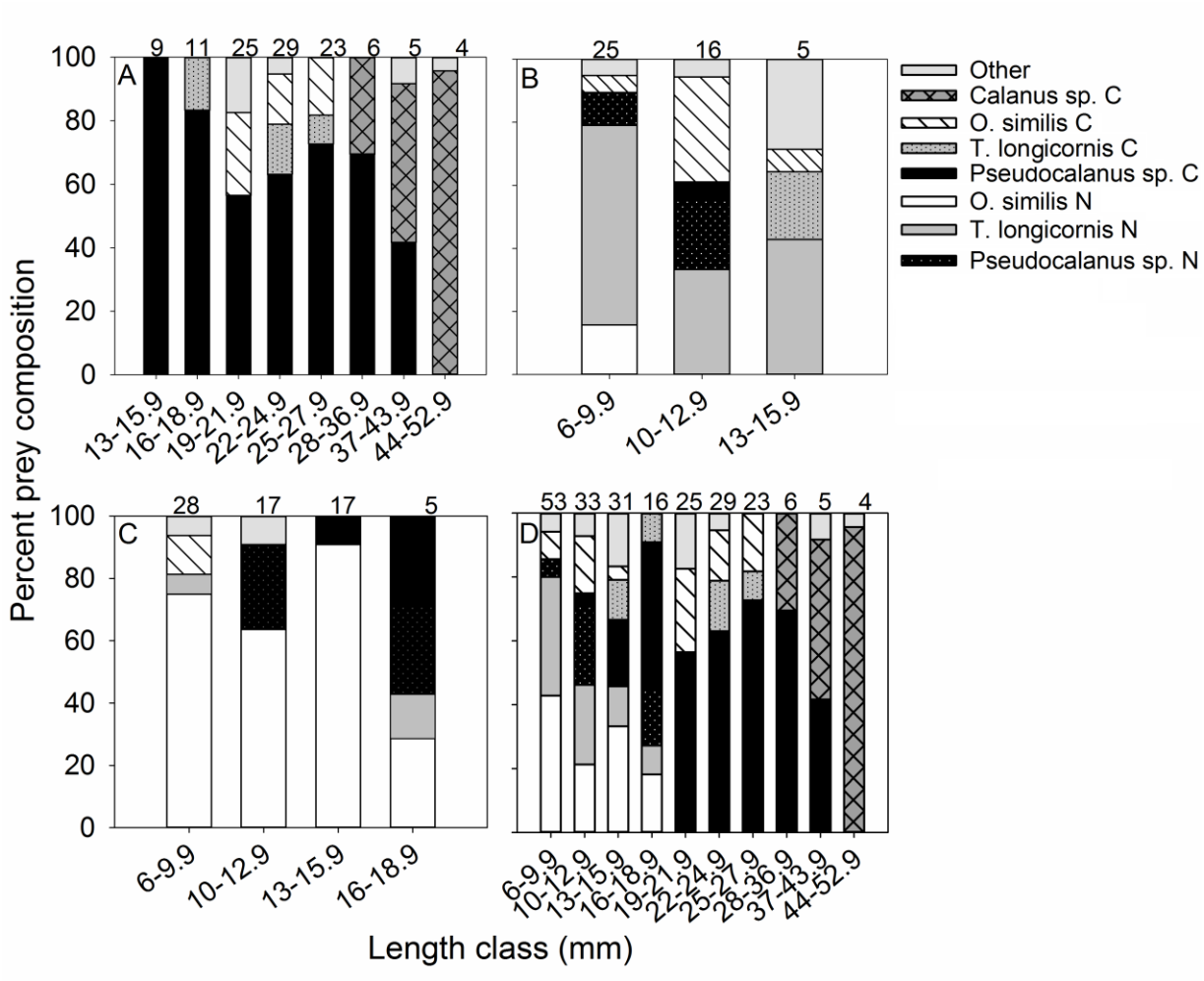

Fig. 10. Percent prey contribution by numbers as a function of size in Atlantic herring larvae from three sampling years and all years combined: A: 2002, B: 2006, C: 2013 and D: all years combined. Values above histogram bars indicate the number of larvae dissected for each size class. N and C indicate nauplius and copepodite stages, respectively.

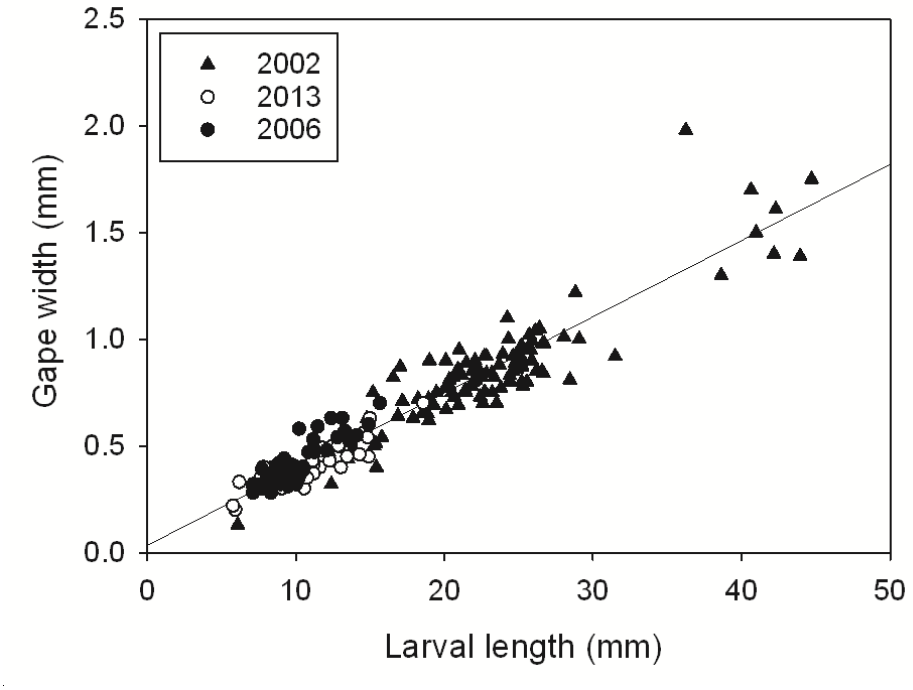

Fig. 11. Relationship between gape width and body length in Atlantic herring larvae sampled in 2002, 2006 and 2013 in Trinity Bay. Equation of linear regression y= 0.03x + 0.06 (r^2=0. 91, p<0.001, n=104).

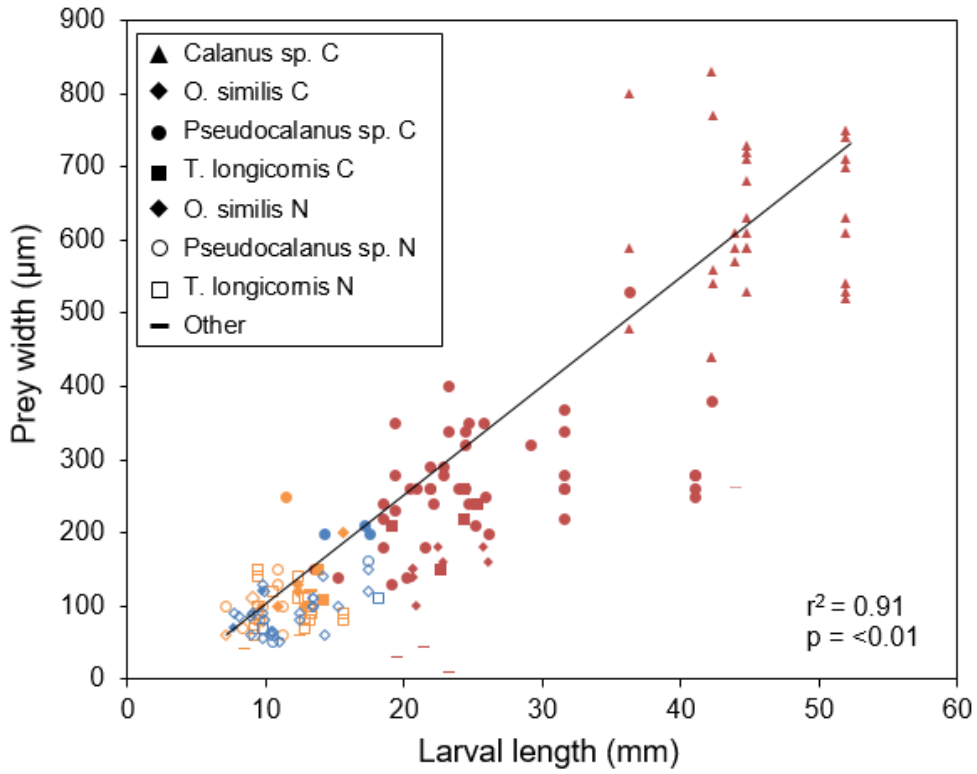

Fig. 12. Atlantic herring prey width in relation to larval length in 2002 (red), 2006 (orange) and 2013 (blue). Prey taxa are represented by different symbols. N and C indicate nauplius and copepodite stages, respectively.

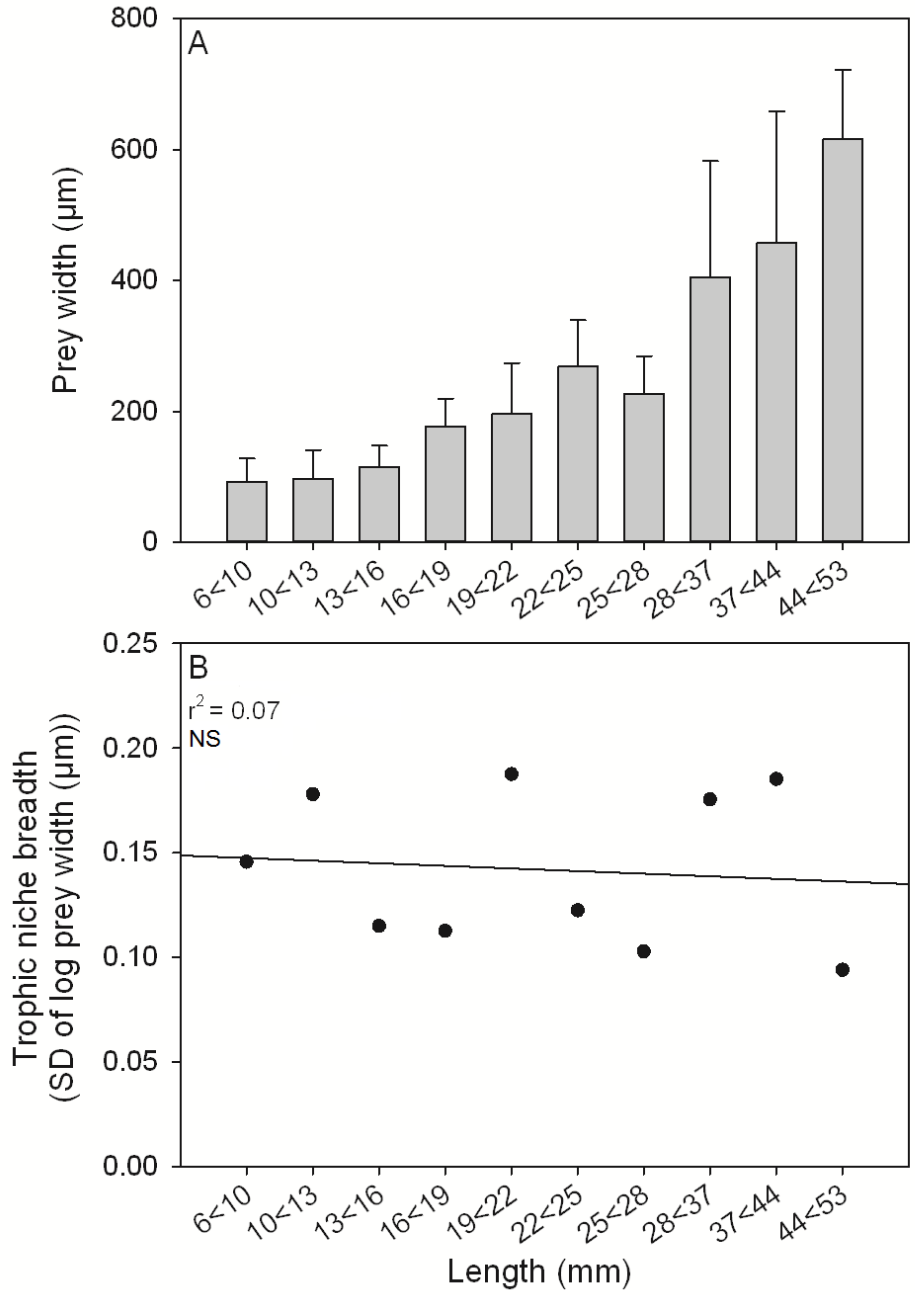

Fig. 13. A: Mean (and standard error) width of prey ingested within each larval length class for all three sampling years. B: Relationship between trophic niche breadth (standard deviation of log prey width) and larval length.

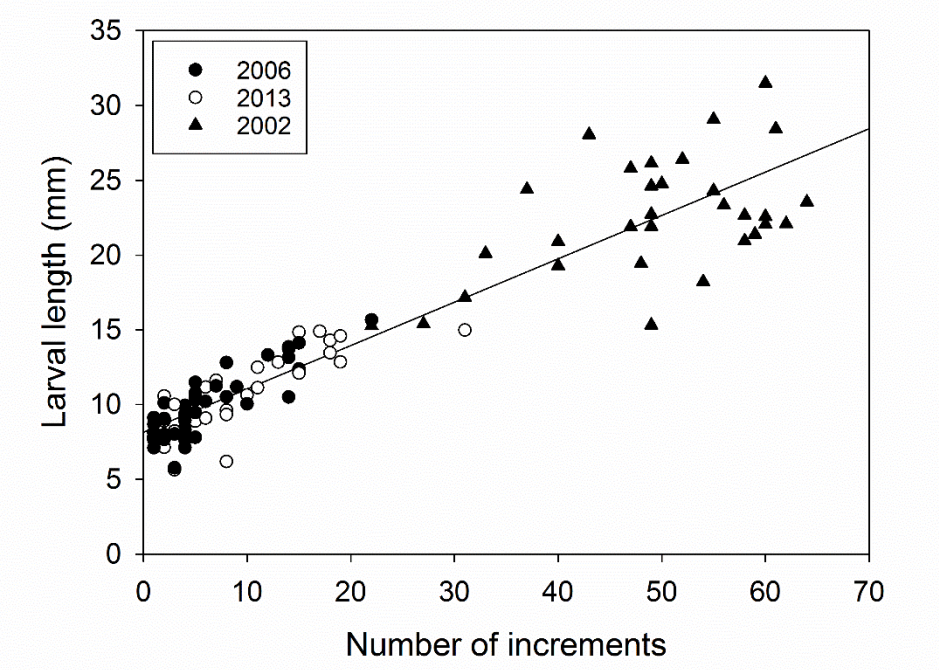

Fig. 14. Relationship between Atlantic herring larval length and the number of otolith increments observed on sagittal otoliths sampled in 2002, 2006 and 2013. Equation of linear regression y= 0.29x + 8.145 (r^2=0.88, p<0.001, n=104).

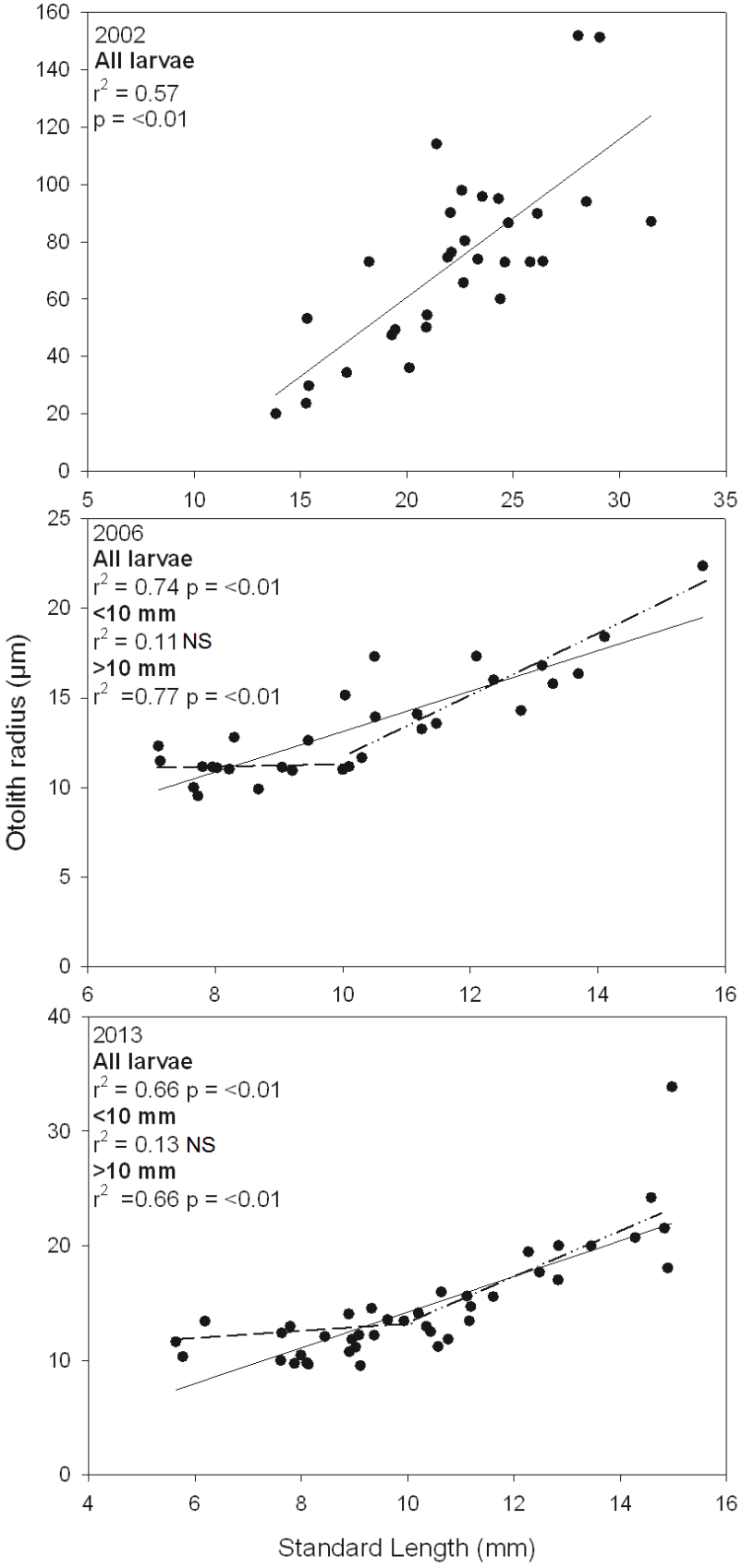

Fig. 15. Relationship between Atlantic herring larval length and the otolith radius observed on sagittal otoliths sampled in 2002, 2006 and 2013.

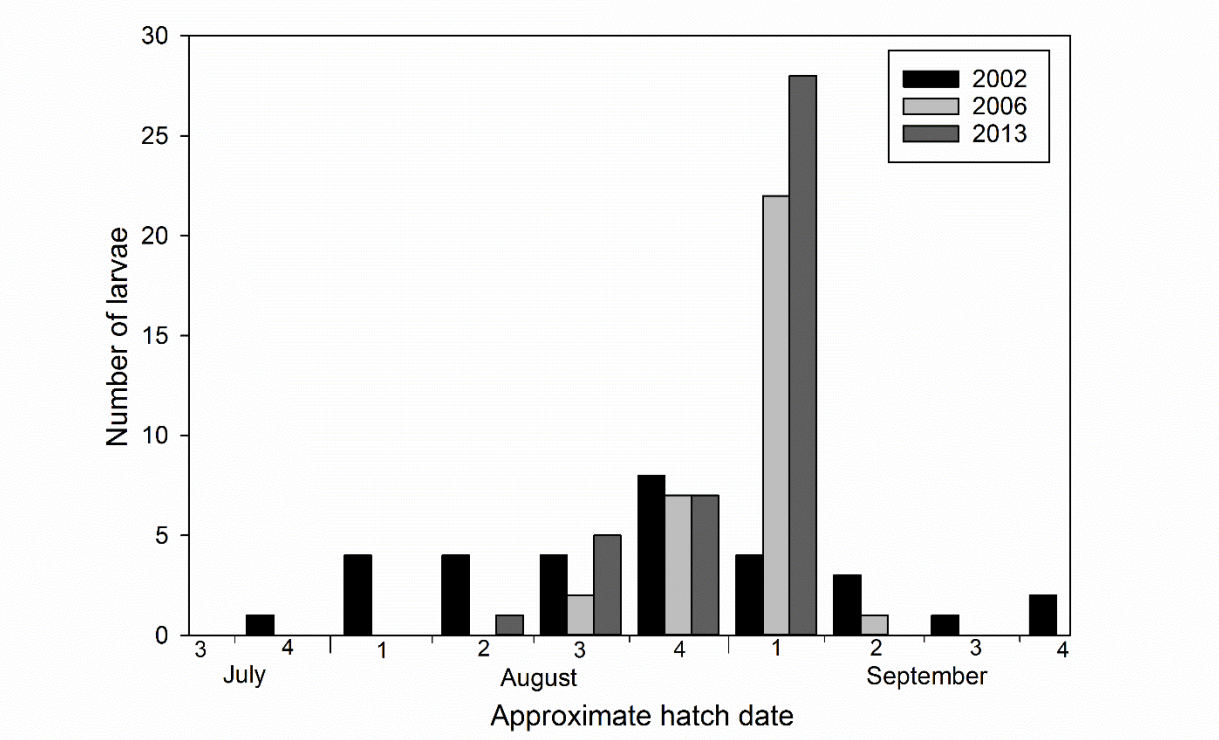

Fig. 16. Approximate hatch time for autumn-spawned Atlantic herring larvae in Trinity Bay in 2002, 2006, and 2013. Numbers 1-4 represent weeks in a given month.

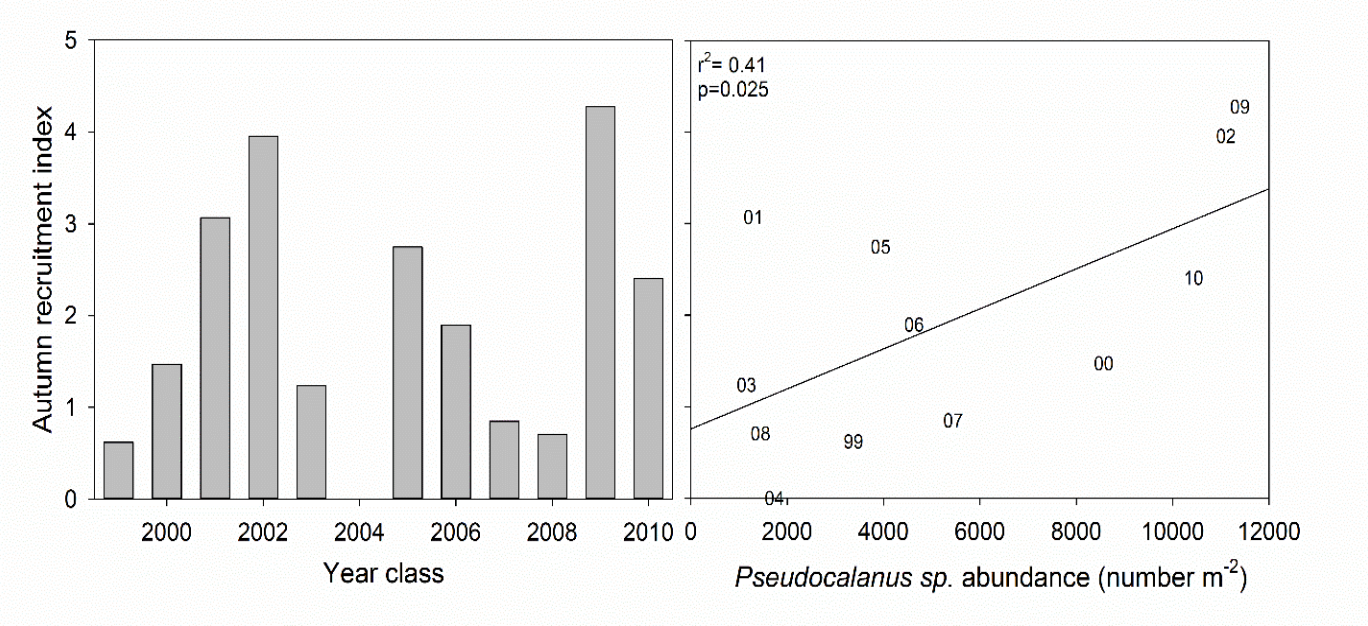

Fig. 17. Left: Autumn recruitment index for the Bonavista Bay-Trinity Bay herring stock during the 1999-2010 time series. Recruitment index is the natural log plus 1 of the number of age 4 autumn-spawning fish caught in DFO's annual research gillnet survey for the Bonavista Bay-Trinity Bay stock management unit. Right: Recruitment index regressed against mean abundance of the main prey *Pseudocalanus* sp. in October derived from DFO's station 27.

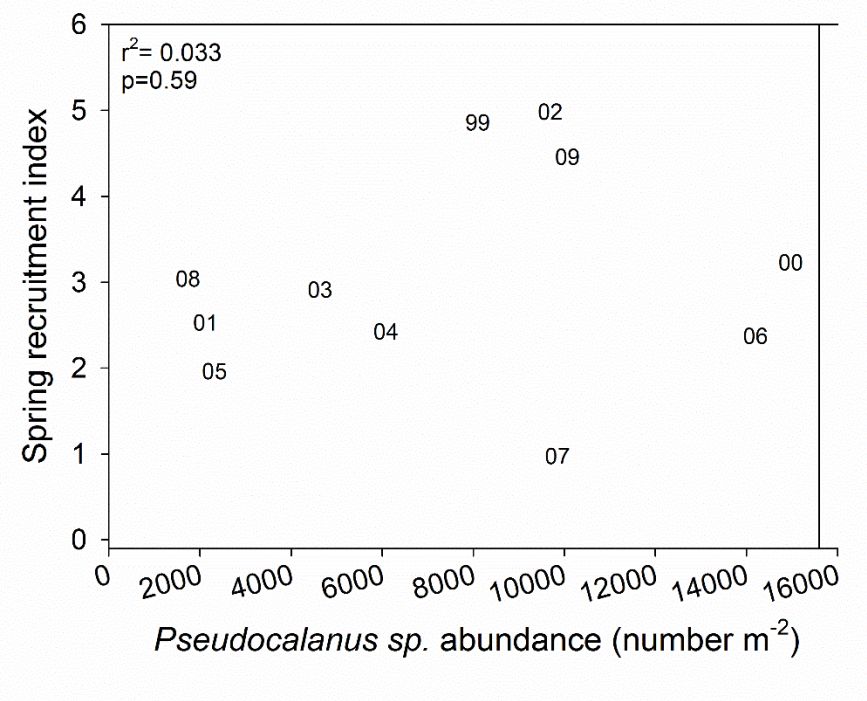

Fig. 18. Spring recruitment index for the Bonavista Bay-Trinity Bay herring stock during the 1999-2010 time series regressed against abundance of *Pseudocalanus* sp. from May-June derived from DFO's station 27.