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Understanding factors influencing Atlantic herring (*Clupea harengus*) recruitment: From egg deposition to juveniles

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Abstract

Recruitment is a critical component of population dynamics and variability in recruitment underpins large fluctuations in population abundances of commercially valuable marine fishes. Marine pelagic fishes such as Atlantic herring (*Clupea harengus*) experience relatively high variability in recruitment that is driven by a wide range of biotic and abiotic factors. The relative importance and interaction of each factor for determining recruitment is poorly understood, and consequently, recruitment estimates are one of the largest uncertainties in fisheries management and predictions of future population sizes. Poor recruitment of Atlantic herring has been identified as a major issue and bottleneck for the species; therefore, factors influencing successful recruitment are of great interest to fisheries managers. Here we review studies that have examined the factors influencing survival at the egg stage, early larval stage, late larval stage, and juvenile stage to develop a more comprehensive understanding of the recruitment of Atlantic herring and provide recommendations to guide future research. We identified nine biotic and eight abiotic factors that have been found to substantially impact the recruitment of Atlantic herring, with temperature, prey availability, and predation being the most commonly investigated factors. We conclude it is not one factor that primarily determines recruitment, but rather a collection of many factors that vary temporally and spatially that drive the large variation observed in Atlantic herring recruitment year over year. A holistic approach is required to better understand recruitment and improve fisheries management decisions regarding Atlantic herring.

KEYWORDS

environmental factors, fisheries, marine fishes, population dynamics, spawning, stock-recruitment

1 | INTRODUCTION

Recruitment is a critical component of population dynamics, yet variability in recruitment is poorly understood and consequently is one of the largest uncertainties in fisheries management and predictions of

future population sizes (Brosset et al., 2020; Dickey-Collas et al., 2010; Munch et al., 2018; Needle, 2002). Variability in recruitment underpins large fluctuations in population abundances of commercially valuable marine fishes with important consequence for fisheries (Leggett & Deblois, 1994; Szuwalski et al., 2015). Although

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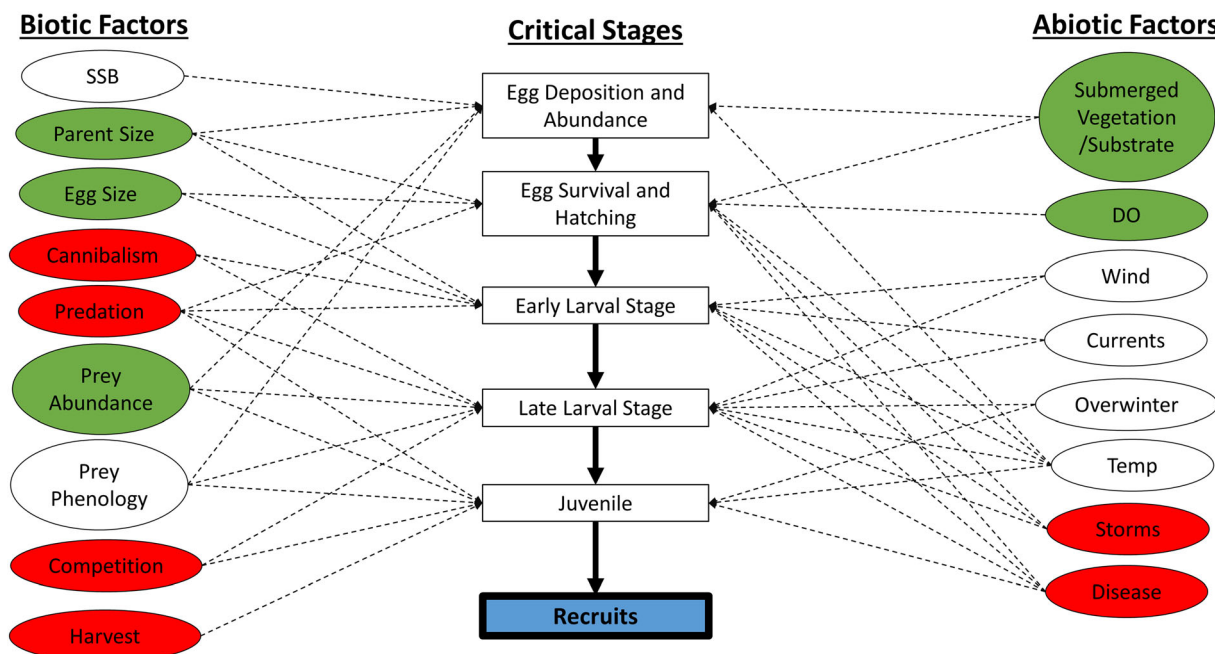


FIGURE 1 A conceptual diagram showing the various biotic and abiotic factors known to impact the recruitment of Atlantic herring at each specific critical early life-history stage. Factors are color coded to indicate if increases in each factor (i.e., increases in temperature, increases in predation, etc.) would have a positive affect (green), negative affect (red), or have the direction of affect be dependent on the population and environmental conditions (white). DO within the figure represents dissolved oxygen, and temp represents temperature. Note that many factors interact with one another, but interactions among factors are not shown to avoid excessive clutter.

stock-recruitment models (e.g., Beverton & Holt, 1957; Ricker, 1954) have been commonly used in fisheries management, they are controversial, and there is mounting evidence that additional environmental and biological factors have significant influences on recruitment (Cury et al., 2014; Subbey et al., 2014). In particular, marine pelagic fishes experience relatively high variability in recruitment that is driven by a wide range of biotic and abiotic factors (Figure 1) including but not limited to starvation (Leggett & DeBlois, 1994), prey availability and phenology (Martino & Houde, 2010; Wilson et al., 2018), predation (Richardson et al., 2011; Tsou & Collie, 2001), cannibalism (Corten, 2013; Hourston et al., 1981), age structure (Brunel, 2010; Melvin & Stephenson, 2007), water temperature (Brunel & Dickey-Collas, 2010; Fiksen & Slotte, 2002; Lazzari et al., 1997; Muhling et al., 2018), currents (Lee & Williams, 1999), spawning substrate quality and availability (Kanstinger et al., 2018), and storms (Moll et al., 2018). The relative importance and interaction of each factor for determining recruitment is poorly understood, and factors act at the local or population level, making recruitment difficult to predict. Despite a poor understating of the factors driving recruitment, it is well-documented that low recruitment can have substantial negative impacts on population abundance and can contribute to eventual population collapse with significant negative ecological and economic implications (Trochta et al., 2020). Alternatively, high recruitment can drive population recovery following collapse; therefore, factors influencing successful recruitment are of great interest to fisheries managers.

For instance poor recruitment of Atlantic herring (*Clupea harengus*) has been identified as a major issue and bottleneck for the

species and has contributed to the collapse of various stocks over the past seven decades (Dickey-Collas et al., 2010; Nash et al., 2009; Trochta et al., 2020). On the other hand, years with high recruitment have helped replenish stocks and can underpin the recovery of Atlantic herring stocks (Dickey-Collas et al., 2010). Atlantic herring is a small pelagic forage fish that serves as important prey for a wide range of marine species such as Atlantic cod (*Gadus morhua*), pollock (*Pollachius pollachius*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), white hake (*Urophycis tenuis*) (Langton & Bowman, 1981), grey seal (*Halichoerus grypus*) (Hammill & Stenson, 2000), and Atlantic bluefin tuna (*Thunnus thynnus*) (Turcotte et al., 2021). Furthermore Atlantic herring itself is an economically valuable commercial species that is marketed in a wide range of ways from bait for the lobster fishery (Grabowski et al., 2010) to bloater (smoked herring), filets, roe (DFO, 2022), fish oils, and pet food (Tacon & Metian, 2009). However, low recruitment of Atlantic herring has resulted in poor propagation of the species, which impacts the number of individuals available to the fishery and the long-term viability of the species.

Therefore, it is imperative to develop a comprehensive understanding of the factors impacting and limiting Atlantic herring recruitment to further elucidate the mechanism behind population declines and develop well-informed mitigation strategies to effectively manage and conserve populations of this critically important species (Dickey-Collas et al., 2010). Here, we examine research conducted on Atlantic herring recruitment from across its range to provide insight into the current state of knowledge on Atlantic herring recruitment while

identifying critical gaps in knowledge. We review studies that have examined the factors influencing survival at the egg stage, early (yolk sac) larval stage, late (post-yolk sac) larval stage, and juvenile stage. We develop a conceptual framework for further understanding and evaluating the factors that simultaneously impact recruitment of Atlantic herring at each early life-history stage and provide recommendations for future research.

2 | RECRUITMENT OVERVIEW

Recruitment of Atlantic herring is typically defined as the number of age two individuals in a given year (Axenrot & Hansson, 2003; Turcotte, 2022). Atlantic herring recruitment is impacted by a wide range of biotic and abiotic factors at each critical early life-history stage including egg deposition, egg survival and hatching, early larval, late larval, and juvenile stages (Figure 1). At any of these early life stages, mortality can occur reducing recruitment. Recruitment adds the most uncertainty to future population numbers, population projections, and potential sustainable yields estimated in stock assessments (Dickey-Collas et al., 2010). In essence poor recruitment regardless of high SSB can have cascading effects that rapidly diminish population sizes.

Without adequate knowledge of recruitment, projections of stock sizes can perform poorly and risk misleading management decisions. Atlantic herring has experienced both historic and recent fluctuations in recruitment for many stocks across its range such as spring-spawning Norwegian herring (Garcia et al., 2021), North Sea herring (Estrella-Martínez et al., 2019; Payne et al., 2013), Icelandic herring (Óskarsson & Taggart, 2010), Baltic Sea herring (Cardinale et al., 2009), and southern Gulf of St. Lawrence herring (Turcotte, 2022; Winters, 1976). For example, spring-spawning Atlantic herring in the southern Gulf of St. Lawrence has seen significant declines in recruitment (Turcotte, 2022). Statistical catch-at-age (SCA) models suggest recruitment was on average approximately 476 million fish per year from 1978 to 1991 and then underwent a regime shift where average recruitment dropped by about 42% to an average of approximately 275 million fish per year (Turcotte, 2022). The regime shift corresponded with a regime shift in sea surface temperatures from a cold state in 1982-early 1990s to a warm state in the early 1990s-present (Turcotte, 2022). Given the uncertainties surrounding recruitment and its importance for population dynamics, elucidating the factors influencing recruitment at each early life-history stage is critical to improving fisheries management decisions of this commercially and ecologically important species.

3 | FROM EGG DEPOSITION TO HATCHING

In order for an individual to be successfully recruited, they must first survive the egg stage, a volatile early life-history stage that

experiences high levels of mortality. In general, Atlantic herring reproduction is relatively well studied (dos Santos Schmidt et al., 2017; Melvin et al., 2009; Óskarsson et al., 2016; Winters & Wheeler, 1996). Individuals are known to spawn a large number of adhesive demersal eggs in an attempt to counteract high egg mortality rates. For example, estimates of fecundity for spring- and fall-spawning herring in the Gulf of St. Lawrence and along the Nova Scotia coast ranged from 23,000 to 261,000 eggs (Messieh, 1976). Atlantic herring are determinate and total spawners, such that individuals produce a finite number of eggs and spawn all eggs at once (Óskarsson, 2005). Additionally, the species exhibits a “bet-hedging” strategy, where spawning activity of a population is spread out over time in waves to increase chances of successful reproduction, larval survival, and recruitment (Lambert, 1990; Moll et al., 2018). Once fertilized, the egg incubation period depends on the ambient temperatures, and eggs have been observed to hatch after between 6 and 30 days in the Baltic Sea (Kanstinger et al., 2018; Peck et al., 2012), 14–19 days at temperatures between 3 and 10°C for spring-spawning herring in the southern Gulf of St. Lawrence, and after approximately 10 days at around 17°C for fall-spawning herring in the southern Gulf of St. Lawrence (Messieh, 1987).

For fish stocks in general, egg abundance is typically related to the number of recruits (Cardinale et al., 2009; Myers & Barrowman, 1996). Additionally, egg abundance is linked to, but, not directly proportional to the spawning stock biomass (Barrett et al., 2022) since individual fecundity exhibits plasticity and is impacted by maternal effects such as fish size, age, and condition (Óskarsson, 2005; Óskarsson & Taggart, 2010). For instance, larger and older individuals produce more eggs and contribute disproportionately to overall egg abundance (Barrett et al., 2022). However, recent examinations of fecundity-at-age and -size relationships for Atlantic herring suggest fecundity-at-age and -size is decreasing temporally. Barrett et al. (2022) illustrated individuals of a given age and size in the Bay of Fundy and Scotian Shelf exhibited lower fecundity in 2020 compared to 2000 and lower fecundity in 2000 compared to 1970. Such declines in fecundity at age and size could be related to zooplankton abundance. Dos Santos Schmidt et al. (2017) examined factors influencing the fecundity of Norwegian and North Sea herring and found that when zooplankton abundance was low in a given year, fecundity was substantially lower for subsequent years even if fish condition remained high. Therefore, a fish at a given size may exhibit lower than expected fecundity (i.e., based on established fecundity-at-size relationships) if zooplankton abundance has been low in previous years. This suggests that when food resources are limited, reproductive potential is negatively impacted, leading to lower amounts of egg reserves, lower fecundity, and an ultimate decline in overall egg abundance released by a population for several years following decreases in zooplankton abundance (dos Santos Schmidt et al., 2017), which would negatively impact recruitment.

Furthermore, a reduction in spawning stock biomass close to zero will restrict the abundance of eggs and thereby limit recruitment (Cardinale et al., 2009). Alternatively, a high spawning stock biomass may improve egg abundance but will not necessarily translate into

high recruitment due to density-dependent factors as illustrated by the Ricker curve relationship between spawning stock biomass and recruits generally exhibited by Atlantic herring. Research has shown at very high SSB, high egg production can lead to lower relative numbers of viable larvae, and an eventual reduction in recruitment as individuals will be pushed to suboptimal spawning grounds and be forced to spawn on less preferred, nonideal substrate (Taylor, 1971; Winters & Wheeler, 1987).

In general, Atlantic herring tend to show preference for specific substrate or vegetation when laying eggs and exhibit strong homing behavior, returning to similar spawning locations (Wheeler & Winters, 1984; Winters & Wheeler, 1987). Atlantic herring spawn adhesive eggs on coastal gravel beds or preferentially over underwater meadows of submerged macrophytes, depending on the spawning population (Messieh, 1987; Moll et al., 2018). For instance, in the southern Gulf of St. Lawrence, eggs deposited by spring spawners were found at depths of 0.8–5 m on rocky and sandy substrates covered in thick carpets of Irish moss (*Chondrus crispus*), rockweeds (*Fucus* sp.), and leafweeds (*Phyllophora* sp.), whereas eggs deposited by fall spawners were at depths between 15 and 20 m over relatively bare bedrock and rubble (Messieh, 1987). Spring-spawning eggs are thought to be found at depths less than 5 m due to a lack of adequate vegetation cover at greater depths. Similarly, Kanstinger et al. (2018) examined egg locations in lagoons of the Baltic Sea and observed Atlantic herring eggs adhered to submerged spermatophytes and algae but not stones and mussels. However, macrophyte coverage was predicted to be only about 5% of the study area compared to historical highs of approximately 90%, severely restricting the area available for egg deposition. It is evident that reductions in suitable submerged macrophytes or preferred spawning substrates can have profound impacts on Atlantic herring spawning activity and egg survival. Successful spawning and egg survival appear contingent on dense macrophyte forests (Kanstinger et al., 2018) for populations that preferentially spawn over submerged vegetation, which have undergone significant anthropogenic destruction worldwide. Therefore, reductions in suitable submerged macrophyte coverage or preferred spawning substrate in herring spawning locations are likely a major threat to successful spawning and thereby a limiting factor for recruitment.

Furthermore, the reduction in submerged macrophyte cover and suitable spawning substrate has resulted in Atlantic herring relying on shallower areas to deposit eggs (Moll et al., 2018). In these shallower areas, eggs may be even more susceptible to predation and destruction by natural events such as storms (Moll et al., 2018). Storm events have been observed to have significant negative impacts on egg survival (Heath & Richardson, 1989; Moll et al., 2018). For example, the complete destruction of egg beds by a major storm was reported in the Thames River Estuary in 1967 (Wood, 1981), which severely reduced the number of eggs that hatched to larval stages. Additionally, egg loss experiments conducted in the Baltic Sea showed a 29% loss of eggs on a single spawning bed following a major storm (Moll et al., 2018), indicating that storms can have substantial impacts on

egg survival and recruitment. However, relatively few studies have focused on understanding the impact of storms on egg survival and recruitment; thus, further research is needed to quantify this potentially significant threat factor.

Predation of eggs by resident predators can also have significant impacts on egg survival to hatch (Messieh, 1987; Richardson et al., 2011). Kotterba et al. (2017) conducted exclusion experiments and measured stomach contents of predators on Atlantic herring spawning grounds in the southwest Baltic Sea. The study estimated approximately 42% of eggs spawned were preyed upon between spawning and hatch, primarily by one species, three-spined stickleback (*Gasterosteus aculeatus*). Additionally, in Georges Bank, USA, significant declines in Atlantic herring egg survival and shifts to a lower stable population state have been attributed to egg predation by haddock (Richardson et al., 2011). Researchers observed that over four decades (1970s–2000s), years when haddock population had been high corresponded with very low survival rates of Atlantic herring eggs, shifting the herring population to a lower stable population level (Richardson et al., 2011). The study however has shortcomings as the authors did not directly observe and measure haddock predation on herring eggs; rather, indirect modelling approaches were implemented to estimate predation rates. Empirical observations of egg predation through stomach content analysis or other diet tracing methods such as stable isotope analysis are valuable and should be made when evaluating impacts of egg predation on hatching success. Atlantic mackerel (*Scomber scombrus*) and winter flounder (*Pseudopleuronectes americanus*) have also been observed to be major predators of spring- and fall-spawned herring eggs in the southern Gulf of St. Lawrence (Messieh, 1987). For instance, stomach content analysis of 30 winter flounder captured in the spring of 1980 found an average of 1527 herring eggs with a range of 0–14,450 eggs, suggesting frequent and sometimes intense consumption of herring eggs by winter flounder (Pottle et al., 1980). Such studies highlight that predation of eggs can have substantial impacts on the number of eggs that survive to hatch, which limits larval abundance and can lead to declines in recruitment. Future studies should continue to consider the importance of egg predation and implement methods such as stomach content or stable isotope analyses to quantify the impacts of egg predations on egg survival and recruitment.

Egg size, which is related to the size of parents and sea surface temperature, also has important implications for survival to hatch and early growth and survival of larval herring. Increases in egg size have been shown to correlate with larger length at hatch, longer duration of yolk sac, and increased growth rate of the early larval stage (Dickey-Collas et al., 2010). This increased egg size could improve egg hatching rates and result in increased early larval survival and stronger recruitment. There is however little knowledge on how egg health and lipid content varies among populations and how egg lipid content influences successful hatching. Future research can work to understand the implications of egg lipid content, egg deposition location, and egg density for successful hatching and eventual recruitment.

4 | EARLY (YOLK SAC) LARVAL STAGE SURVIVAL

The early larval stage is a crucial time in the life-history of Atlantic herring and is a time when high mortality can occur, restricting eventual successful recruitment. The “critical period” hypothesis posits that year-class strength is determined in the early larval stage during transition from feeding on the yolk sac to active feeding (Hjort, 1914). Early larval herring are particularly susceptible to predation, cannibalism, and starvation when relying on yolk sac reserves and prior to their first feeding. For instance, DNA analysis of Atlantic mackerel stomach contents from the Norwegian Sea has identified that Atlantic mackerel are important predators of early larval herring. Additionally, cannibalism on early larvae by juvenile and adult spring-spawning Norwegian herring has been observed in the stomach contents of individuals (Holst, 1992). Larvae typically begin their first feeding at time of yolk sac reabsorption (Kiorboe et al., 1985). To improve chances of survival, early larvae are required to undergo rapid growth and reach suitable nursery grounds prior to depletion of their yolk sac reserves and the point of no return (PNR) (Blaxter & Hempel, 1963). The PNR is defined as the point when starving early larvae are too weak to feed and die of starvation (Blaxter & Hempel, 1963). The time to PNR is influenced by egg size and yolk sac reserve size. Individual larvae with smaller yolk sac reserves have been shown to reach PNR within 8 days, and those with larger yolk sac reserves reach PNR in approximately 20 days (Blaxter & Hempel, 1963; Kiorboe et al., 1985). Thus, larger egg size, corresponding larger yolk sac reserves, and larger size at hatch provide more time to reach suitable nursery grounds, may reduce predation, and will improve survival through the early larval stage.

Furthermore, broader oceanic conditions such as prevailing winds, low-salinity anomalies, currents, and sea surface temperatures can have impacts on transport of larvae to high-quality nursery grounds (i.e., nursery grounds that consist of substantial amounts of prey, few predators, and suitable environmental conditions) during the larval drift period. Skagseth et al. (2015) studied oceanic conditions that impacted recruitment in spring-spawning Norwegian herring and found years where southwesterly winds prevailed and low-salinity anomalies occurred led to stronger northward currents that more effectively transported larvae to high-quality nursery grounds, resulting in years of notably high recruitment. Additionally, examinations of environmental factors impacting larval survival in the transition from yolk sac to the preflexion stage of spring-spawning Norwegian herring suggest years when rapid warming occurred during this transition coincided with weak recruitment (Tiedemann et al., 2021). Such research highlights that considerations of oceanic conditions, particularly those that alter transport to nursery grounds, in the early larval stage are critical when trying to predict larval survival and understand recruitment dynamics. Relatively few studies have focused on survival at the early larval stage, and more effort is required to gain a comprehensive understanding of the implications of various abiotic (i.e., wind, currents, temperature, and storms) and biotic factors (i.e., parent size, egg size, cannibalism, and predation) (Figure 1) on early larval survival

and recruitment. Specifically, further research is needed to understand transport of early-stage larval Atlantic herring to suitable nursery grounds, the ideal prey abundance and phenology at nursery grounds, and the interaction between spawn timing, hatch date, and arrival at nursery grounds.

5 | LATE (POST-YOLK SAC) LARVAL STAGE SURVIVAL

Research on Atlantic herring has indicated year-class strength is often determined during events that occur in the post-yolk sac (i.e., late) larval stage (Leggett & DeBlois, 1994; Nash & Dickey-Collas, 2005; Wilson et al., 2018); however, the mechanism by which recruitment and year-class strength are determined is unknown. The post-yolk sac larval stage is a period where individuals must forage for food and avoid predation and suboptimal environmental conditions to further improve chances of survival. Adequate feeding and energy acquisition are imperative for the growth and survival of larval Atlantic herring. Therefore, understanding the diet, prey preference, and prey availability of Atlantic herring larvae is imperative for understanding survival and developing effective management action.

Larval Atlantic herring have been observed to exhibit prey preference (Wilson et al., 2018), with spring-spawned larvae in the Gulf of St. Lawrence preferentially consuming cold-water high-energy copepod species and experiencing higher recruitment in years when cold-water copepod species such as *Metridia longa*, *Calanus glacialis*, *Acartia* sp., and *Pseudocalanus* spp. are abundant (Brosset et al., 2019). Autumn-spawned Atlantic herring larvae in Newfoundland, Canada, have been observed to preferentially consume nauplii of the copepods *Temora longicornis* and *Oithona similis* as young larval, *Pseudocalanus* sp. in the mid-larval stage and shifted to larger calanoid copepods *Calanus* sp. in the late larval stage (Wilson et al., 2018). Spring-spawned larvae in the Baltic Sea have been observed to preferentially consume copepodites of *Eurytemora affinis* and copepod nauplii of *E. affinis* and *Acartia* sp. (Arula et al., 2012). A lack of availability of preferred prey can lead to suboptimal feeding and slow growth that results in increased mortality from both starvation and higher vulnerability to predation. For example, Payne et al. (2013) observed a 12% gross reduction in growth rate for North Sea herring in years of poor recruitment (2003/2004) compared to previous years of high recruitment (1998/1999) and attributed this reduction in growth rate to a decrease in the quality and quantity of food available to larvae. The reduction in growth rate was linked to increased mortality of larval herring and subsequent low recruitment (Payne et al., 2013), indicating larval growth rate is fundamental to recruitment success. However, it is important to note that investigations of the effects of prey availability on recruitment can be complicated as prey preferences shift as individuals grow (Wilson et al., 2018).

Recently, predictive models to estimate recruitment based on zooplankton abundance and phenology were developed and are capable of predicting recruitment levels for southern Gulf of St. Lawrence spring-spawning herring (Turcotte, 2022). These zooplankton-based

models point to the importance of adequate zooplankton prey availability at the right time (i.e., prey phenology) during the larval stage in order to promote growth, survival, and recruitment (Brosset et al., 2019; Turcotte, 2022). Changes in zooplankton abundance and phenology directly contribute to changes in recruitment; thus, any environmental factors such as changes in temperature or dominant currents that alter prey availability and phenology will have direct impacts on Atlantic herring recruitment. Additional research in the Gulf of St. Lawrence herring pointed toward different abiotic and biotic factors influencing recruitment in spring compared to fall spawners (Brosset et al., 2019). Four decades of environmental, biological, and recruitment data were analyzed, and it was determined that the abundance of cold-water, high-energy copepod species was the most important driver of spring spawner recruitment, whereas the presence of warmer water and a high abundance of zooplankton were the main drivers of recruitment in fall spawners (Brosset et al., 2019). This information is useful; however, there are gaps in knowledge of the mechanism underlying how changes in prey abundance and phenology influence herring recruitment. Furthermore, Brosset et al. (2019) implemented multivariate approaches to estimate PCA axes and generate general additive models, which makes it difficult to draw direct links between the effect of each ecosystem factor on recruitment and limits transferability of the results to future studies. Further investigation is required to understand the mechanism by which a lack of suitable prey during the right time of year impacts growth and survival of larval herring. Insight into the energy content of prey and associated larval growth could help elucidate how high-energy prey fuels adequate growth to potentially boost survival. Nevertheless, it is apparent that prey availability and phenology as well as the environmental factors impacting prey abundance and phenology have profound impacts on larval Atlantic herring survival and recruitment. However, these factors do not act in isolation; rather, they act in conjunction with a wide suite of biotic and abiotic factors.

For instance, competition with other aquatic species such as jellyfish (*Scyphozoa*), which larval Atlantic herring share a similar diet, has been suggested to restrict larval feeding and reduce survival of larvae (Lynam et al., 2005). Researchers have noted years with high jellyfish medusa abundances correlated with years of poor Atlantic herring recruitment in the North Sea, implying jellyfish are outcompeting larval herring for important high-energy food resources (Lynam et al., 2005). The study however did not show clear evidence that jellyfish and larval herring were competing, they failed to show overlapping prey consumption, and limited prey availability, both of which are requisites for identifying interspecific competition (Burbank et al., 2019; Link & Auster, 2013). Potential competitive interactions between larval Atlantic herring and marine species with similar diets are important avenues for further research as they may impact feeding success. Future research must however incorporate examinations of the diets of both species, identify spatial overlap in feeding activity, and evaluate the availability of prey items consumed by both species to effectively evaluate potential competitive interactions.

Furthermore, research on larval Atlantic herring survival in Norway indicates that the frequency of high wind events in April

(i.e., when larval herring deplete yolk sac and begin feeding) correlates positively with herring larval survival and recruitment likely as a result of increased food availability associated with higher turbulence (Sætre, Toresen, Sjøland, & Fossum, 2002). A combination of average winter surface temperature, wind events in April, and Atlantic puffin (*Fratercula arctica*) fledging success was able to effectively predict the year-class strength of herring (Sætre, Toresen, & Anker-Nilssen, 2002). Interesting Atlantic puffin fledging success was positively correlated with larval herring abundance and survival, indicating that Atlantic puffins, which are important predator of larval herring, do better when larvae are abundant, potentially making Atlantic puffin fledging success a valuable biological indicator of larval herring abundance (Sætre, Toresen, & Anker-Nilssen, 2002). Similarly, research in the Gulf of Maine highlights seabird diet, particularly of common tern (*Sterna hirundo*), can be a valuable bioindicator of larval and juvenile Atlantic herring abundance and distribution, which can be applied in an ecosystem-based fisheries management framework to further the understanding of larval and juvenile herring survival and recruitment (Scopel et al., 2018). Further research should be conducted to assess the viability of seabird abundance and diet as indicators of larval herring abundance, distribution, and survival to improve our understanding of herring recruitment. It is worth noting that based on the research reviewed, predation of larval herring by Atlantic puffin and common tern does not appear to substantially effect larval herring abundance; rather, when larval herring are abundant, these seabirds are able to consume more and perform better and thus can act as a bioindicator for larval herring. However, these studies were not explicitly exploring negative predation effects, they were trying to identify bioindicators of recruitment; therefore, the results may be biased based on the scope of the examination. Alternatively, Atlantic mackerel have been found to prey on larval herring (Allan et al., 2021), and research in the southern Gulf of St. Lawrence and Norway suggests mackerel predation exhibits a negative effect on larval herring survival and recruitment (Garcia et al., 2021; Lett & Kohler, 1976; Winters, 1976).

Additionally, overwintering success is thought to be an important determinant of larval survival and recruitment (Winters & Wheeler, 1987), particularly as environmental (e.g., temperature) and biological conditions (e.g., prey availability) are suboptimal. The overwinter period may be particularly important for fall-spawned larval herring as they experience a limited growth window prior to the harsh winter period and thus, typically overwinter as larvae before metamorphosing in the following spring, whereas spring-spawned individuals are able to reach a suitable size for metamorphosis (approximately 55 mm) prior to overwintering (Melvin et al., 2009; Nash & Dickey-Collas, 2005). Nevertheless, spring-spawned larval herring must also undergo sufficient growth to optimize survival through the overwinter period. Despite the potential importance of the overwinter period for recruitment, few investigations have examined and addressed overwinter habitat use, feeding ecology, and survival of larval herring (Table 1). A study on Gulf of Maine herring used strontium/calcium ratios to investigate the overwintering habitat of fall-spawned larval herring and determined individuals who

TABLE 1 Selected publications that investigate or discuss factors related to Atlantic herring recruitment at each critical early life-history stage

Critical stage	Factor	Selected publications
Egg deposition and abundance	Submerged vegetation/substrate	(Kanstinger et al., 2018; Messieh, 1987; Moll et al., 2018)
	Temperature	(Cardinale et al., 2009; Messieh, 1987; Sætre, Toresen, & Anker-Nilssen, 2002; Winters & Wheeler, 1996)
	SSB	(Cardinale et al., 2009; Corten, 2013; Dickey-Collas et al., 2010; Nash & Dickey-Collas, 2005; Óskarsson & Taggart, 2010; Zheng, 1996)
	Parent size	(Barrett et al., 2022; Bradford, 1993; Brophy & Danilowicz, 2003; Cardinale et al., 2009; Kennedy et al., 2010; Lambert, 1990; Óskarsson & Taggart, 2010)
	Prey abundance	(dos Santos Schmidt et al., 2017)
	Prey phenology	(dos Santos Schmidt et al., 2017)
Egg survival and hatching	Submerged vegetation/substrate	(Kanstinger et al., 2018; Moll et al., 2018)
	Dissolved oxygen	(Kanstinger et al., 2018)
	Temperature	(Blaxter & Hempel, 1963; Messieh, 1987; Peck et al., 2012)
	Storms	(Moll et al., 2018)
	Disease	(Winters, 1976)
	Parent size	(Bradford, 1993; Heath & Richardson, 1989; Lambert, 1987, 1990; Óskarsson, 2005)
	Egg size	(Blaxter & Hempel, 1963; Hempel & Blaxter, 1967; Óskarsson, 2005)
	Predation	(Kotterba et al., 2017; Messieh, 1987; Richardson et al., 2011)
Early larval stage (yolk sac larval stage)	Wind	(Lazzari et al., 1997; Sætre, Toresen, & Anker-Nilssen, 2002; Sætre, Toresen, Søiland, & Fossum, 2002; Skagseth et al., 2015)
	Currents	(Corten, 2013; Heath & Richardson, 1989; Lazzari et al., 1993; Skagseth et al., 2015)
	Temperature	(Blaxter & Hempel, 1963; Peck et al., 2012; Tiedemann et al., 2021)
	Storms	(Lazzari et al., 1997)
	Disease	(Winters, 1976)
	Parent size	(Kiorboe et al., 1985)
	Egg size	(Blaxter & Hempel, 1963; Hempel & Blaxter, 1967)
	Cannibalism	(Corten, 2013)
	Predation	(Allan et al., 2021; T. Garcia et al., 2021; Lett & Kohler, 1976)
	Wind	(Arula et al., 2012; Lazzari et al., 1997; Sætre, Toresen, & Anker-Nilssen, 2002)
Late larval stage (post-yolk sac larval stage)	Currents	(Lazzari et al., 1993)
	Overwinter	(Lazzari et al., 1993; Townsend et al., 1989)
	Temperature	(Allan et al., 2022; Anthony & Fogarty, 1985; Arula et al., 2012; Brosset et al., 2019; Cardinale et al., 2009; T. Garcia et al., 2021; Nash & Dickey-Collas, 2005; Röckmann et al., 2011; M. Sinclair & Iles, 1985; Turcotte, 2022)
	Storms	(Lazzari et al., 1997)
	Disease	(Winters, 1976)
	Cannibalism	(Corten, 2013)
	Predation	(Allan et al., 2021; Gallego & Heath, 1994b; T. Garcia et al., 2021; Lett & Kohler, 1976; Sætre, Toresen, & Anker-Nilssen, 2002; Tsou & Collie, 2001)
	Prey abundance	(Allan et al., 2022; Arula et al., 2012; Blaxter & Hempel, 1963; Brosset et al., 2019; Cardinale et al., 2009; Payne et al., 2013; Polte et al., 2014; Sætre, Toresen, Søiland, & Fossum, 2002; Turcotte, 2022; Wilson et al., 2018)
	Prey phenology	(Brosset et al., 2019; Payne et al., 2013; Turcotte, 2022; Wilson et al., 2018)
	Competition	(Lett & Kohler, 1976; Lynam et al., 2005; Winters, 1976)
Juvenile	Temperature	(Bernreuther et al., 2013; Nash & Dickey-Collas, 2005; Röckmann et al., 2011; A. Sinclair et al., 1981)

(Continues)

TABLE 1 (Continued)

Critical stage	Factor	Selected publications
	Disease	(Winters, 1976)
	Predation	(Axelsen et al., 2001; Gallego & Heath, 1994b, 1994a; Hammill & Stenson, 2000; Scopel et al., 2018; Tsou & Collie, 2001)
	Prey abundance	(Brosset et al., 2019; Röckmann et al., 2011)
	Prey phenology	(Brosset et al., 2019)
	Competition	(Melvin & Stephenson, 2007; Winters, 1976)
	Harvest	(Huntsman, 1953)

overwintered offshore often survived and moved inshore in spring; however, those that attempted to overwinter inshore did not survive, highlighting the significance of overwinter habitat selection for survival and recruitment (Townsend et al., 1989). Uncertainty still exists regarding the optimal habitat for overwintering, whether individuals actively feed, and general behavior during the harsh winter period. Evidently, there are many factors (Figure 1) influencing survival at the late larval stage that directly impact recruitment, and further research is required to understand the relative importance of each environmental and biological factor for larval survival and recruitment.

6 | JUVENILES

Similar to the late larval stage, adequate feeding and growth are limiting factors influencing survival during the juvenile stage. Growth rate during the juvenile phase can have implications for age at first spawning, with faster growing individuals spawning at age 1 and slower growing individuals waiting until age 2 or 3 to spawn (Brophy & Danilowicz, 2003). Faster juvenile growth also corresponded with slightly increased growth rates until age 3 (Brophy & Danilowicz, 2003), which could have positive implications for survival and recruitment. Bernreuther et al. (2013) ran controlled laboratory experiments that quantified growth efficiency in relation to feeding ration and the relationship between metabolic rate and temperature for juvenile Atlantic herring. The experiments found higher growth efficiencies at higher food rations, determined metabolic rate increased with temperature from 9 to 14°C and identified a temperature optimum of between 15 and 16°C, above which metabolic rate decreases (Bernreuther et al., 2013). This implies that if juveniles acquire more food without significant increases in energy expenditure, they will grow more quickly. Therefore, the occupancy of juvenile nursery grounds with sufficient amounts of high-energy food resources will improve the growth, survival, and the eventual recruitment and successful reproduction of individuals. Alternatively, evidence from Georges Bank herring suggests when abundance of juveniles is high, density-dependent factors act leading to individuals maturing later and a decreased length-at-age of immature individuals (Melvin & Stephenson, 2007). Nevertheless, environmental factors impacting food availability and growth will likely have substantial impacts of juvenile survival rates.

Juvenile Atlantic herring have also been exploited by a targeted fishery in the Bay of Fundy and along the coast of Maine and marketed as canned “sardines” (Huntsman, 1953; Sinclair et al., 1981). The juvenile Atlantic herring fishery dates back to the mid-1870s and historically had heavily exploited juvenile herring with significant negative impacts on adult stock abundance (Huntsman, 1953). This indicates high fishing pressure on juveniles has negative impact on herring recruitment. In addition to human consumption, a range of species including northern gannet (*Morus bassanus*), cormorants (*Phalacrocoracidae* sp.), Atlantic white-sided dolphins (*Lagenorhynchus acutus*), gray seals, Atlantic bluefin tuna, Atlantic cod, and white hake prey upon juvenile herring (Benoît & Rail, 2016). Juvenile herring are known to be particularly susceptible to predation in the time before schooling behavior is fully developed (Gallego & Heath, 1994a). Schooling behavior generally becomes established by the end of metamorphosis but takes time to fully develop (Gallego & Heath, 1994a). Axelsen et al. (2001) observed schools of recently metamorphosed juvenile Atlantic herring exhibiting diverse and large predator responses when attacked by Atlantic puffins, and the predator response was found to last longer than predator responses observed for schools of adult Atlantic herring attacked by killer whales (*Orcinus orca*). The juvenile herring were thought to be acting selfishly, hiding behind conspecifics, which collectively elicits a diverse response based on the nature of the predator's attack and reduces mortality in the whole school as a result of the attack (Axelsen et al., 2001). As juveniles continue to grow, schooling behavior develops further (Gallego & Heath, 1994a), improving the species response to predators and reducing vulnerability to predation (Gallego & Heath, 1994b). The juvenile stage is the last early life-history stage that needs to be completed before recruitment and likely the least vulnerable. Nevertheless, substantial mortality can occur, impacting year-class strength, and further research is warranted to understand how the various abiotic and biotic factors influence juvenile survival and recruitment.

7 | KNOWLEDGE GAPS AND FUTURE DIRECTIONS

Despite the wide scope of research on herring recruitment across the geographic range of Atlantic herring over the past 60 years, a number

of important knowledge gaps relating to the survival of individuals at each early life-history stage remain. Knowledge gaps have been briefly eluded to within each of the early life-history sections, but the most pressing knowledge gaps are collected and expanded on here to provide guidance for future research. When considering egg deposition, abundance, survival, and hatching success, there is still uncertainty on how macrophyte cover and substrate type will influence egg deposition and hatching success. The potential consequences of a lack of preferred submerged macrophytes and substrate on spawning grounds are not well articulated in the literature. Reductions in preferred submerged macrophyte cover in the Baltic Sea have been identified (Kanstinger et al., 2018), yet the impacts of significant reductions in macrophyte cover such as decreases in egg deposition, reduced capacity to withstand storm impacts, and rates of successful hatching must still be quantified. Future research should employ a combination of laboratory and field observation studies including scuba or drone surveys to evaluate egg deposition locations, densities, and egg survival over several years to elucidate the impacts of habitat change associated with climate change and anthropogenic activity across the geographic range of Atlantic herring. Additionally, although it is evident larger egg size corresponds with larger size at hatch and longer yolk sac duration (Dickey-Collas et al., 2010), there is limited knowledge on the importance of egg size, lipid content, and health for egg survival and hatching success as well as the interaction between spawning habitat quality and egg viability. Field or laboratory experiments that quantify egg survival and hatching success in response to egg size, lipid content, and habitat quality would help resolve the functional role of habitat for egg health and survival.

Based on current knowledge, the influence of spawning phenology, which can be impacted by factors such as temperature and photoperiod (Burbank et al., 2022; dos Santos Schmidt et al., 2022), on egg abundance, hatching success, and transport of early larvae to suitable nursery grounds is not well studied. Therefore, experimental or modelling approaches that explore how spawning phenology impacts hatching success and larval transport by incorporating a range of ecosystem factors such as prey availability, temperature, wind, and currents would resolve uncertainty surrounding the importance of spawning phenology for egg and early larval survival. Furthermore, gaps in knowledge remain regarding the mechanism by which prey availability and competition impact the growth and survival of larval and juvenile herring, as well as eventual recruitment. Although larval herring diet has been described (e.g., Wilson et al., 2018), the energetic value of specific prey and relative importance of various prey items to the growth and survival of individuals is not well studied. Directed field or laboratory studies could evaluate the relationship between prey availability, prey consumption, growth, and lipid content of larval and juvenile herring to elucidate how various prey items fuel growth and contribute to recruitment. Additionally, examining the diet of potential competitors of larval and juvenile herring and comparing diets with prey availability could help identify competitive interactions that may be influencing survival and recruitment.

Research that works toward developing a holistic understanding of abiotic and biotic factors impacting recruitment from egg

deposition through the juvenile stage is essential to bridge the knowledge gaps currently present. For instance, Brosset et al. (2020) employed a fine-scale multistep approach that incorporated consideration of demographic and environmental factors on egg production and survival at the larval stage to improve understanding and predictions of recruitment for Atlantic mackerel. We suggest a similar multistep approach considering factors impacting each early life-history stage as individuals move from eggs, to larval, and to juveniles (i.e., using the conceptual framework presented in Figure 1) would advance the understanding and predictions of herring recruitment and contribute to better informed science advice and management decisions.

8 | SYNTHESIS

Overall a substantial number of biotic ($n = 9$) and abiotic ($n = 8$) factors have been found to impact survival at the egg, early larval, late larval, and juvenile stages, thereby directly influencing recruitment of Atlantic herring (Figure 1, Table 1). Based on our review of the literature, the most commonly investigated factors appear to be temperature, prey availability, and predation (Table 1). The vast majority of studies tend to focus on only one or a few factors in isolation, yielding claims that specific factors are “smoking guns” and the ultimate predictor of Atlantic herring recruitment. However, from reviewing approximately 60 years of research on Atlantic herring recruitment, it is evident the wide range of factors (see Figure 1) influencing recruitment act simultaneously and interact with one another to impact and determine year-class strength. It is not one standalone factor influencing recruitment, but rather a collection of many factors that vary temporally and spatially that drive the large variation observed in herring recruitment year over year. For instance, high predation pressure is not the sole cause of low recruitment, and the removal of predation pressure would certainly not result in high recruitment each year. Rather, other factors, including suitable spawning substrate, prey abundance, intra- and interspecific competition, temperature, storms, and dominant currents to name a few, will all collectively act on the various early life-history stages and drive fluctuations in recruitment. Therefore, despite the plethora of research conducted on factors influencing Atlantic herring recruitment, there remains substantial uncertainty when trying to predict recruitment.

It is difficult to assess the impact of so many interacting factors simultaneously, resulting in researchers focusing on one or a few factors at a time. Examining factors in isolation is logical and plays an important role in understanding recruitment dynamics of populations. However, the evolution of ecosystem-based approaches (Garcia & Cochrane, 2005; Yu et al., 2021) offers an effective framework for considering a wide range of interacting environmental and biological factors simultaneously and if utilized appropriately can provide a more comprehensive evaluation of recruitment. Before being able to effectively implement an ecosystem-based or holistic approach for examining recruitment of a given population, it is helpful to gain a mechanistic understanding of the influence of each factor on

recruitment of Atlantic herring. For instance, when considering prey abundance and phenology, it is essential to understand why and how changes in the abundance and phenology of prey items influence growth and survival of larval Atlantic herring. Examining the lipid content and energetic value of various prey and identifying specialization on certain prey can help determine how prey items contribute to growth and how a potential mismatch between the presence of preferred prey and larval herring could influence growth, survival, and ultimately recruitment.

Future research focused on understanding Atlantic herring recruitment should aim to provide a mechanistic understanding of the influence of factors on recruitment. Effort should be made to make a shift from simply identifying that a factor has an effect, to focusing on why a factor has the observed effect. Once a mechanistic understanding of how the wide range of factors influence survival at each early life-history stage, relative weights can be assigned to each factor and improve predictions of recruitment through a more holistic approach. Given the economic and ecological importance of Atlantic herring, significant effort has been invested over past decades to track the abundance and occupancy of larvae, juveniles, and adults. Researchers can make more frequent and effective use of the immense amount of data on herring and related environmental variables that have been collected during various monitoring programs (e.g., Ecosystem Monitoring Programme, Atlantic herring and sand lance surveys, and Marine Resources Monitoring, Assessment, and Predictions Programme) and are available in various databases (e.g., JGOFS-GLOBEC Database) to further the understanding of recruitment dynamics for the species (e.g., Richardson et al., 2010). Our review highlights that although substantial knowledge is available regarding herring recruitment, further, more holistic research must be conducted to better understand recruitment dynamics and reduce uncertainty in prediction of future recruitment, which could help refine and improve science advice and fisheries management decisions for Atlantic herring moving forward.

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CONFLICT OF INTEREST

There are no conflicts of interest for authors of this article.

AUTHOR CONTRIBUTION

JB conducted the literature search and wrote the manuscript. NR provided supervision and funding. NR, RJD, and FT provided revisions and valuable insight into the article.

DATA AVAILABILITY STATEMENT

There is no data directly associated with this paper.

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