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Drivers of Atlantic herring decline and evidence basis for fisheries closures and rebuilding plans

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Abstract

Atlantic herring (*Clupea harengus*) are economically and ecologically significant but have been in decline in Atlantic Canada due to an uncertain combination of environmental recruitment controls, predation, and fishing (commercial fishery and poorly documented bait removals). Fisheries and Oceans Canada partially closed Atlantic mackerel (*Scomber scombrus*) and herring fisheries in March 2022 amid controversy and disagreement. Here, we develop a conceptual model for natural and anthropogenic controls on herring abundance centered on the southern Gulf of St. Lawrence (sGSL) and evaluate the likely importance of each. We provide the first estimates of the magnitude of bait fishery withdrawals in the sGSL. The decline in sGSL herring is likely driven by natural predation exacerbated by fishing. Bait fishery removals were 182 tonnes in 2021, suggesting that previous estimates for removals of spring-spawning herring were ~30% too low. Fisheries closure is consistent with a precautionary approach given uncertainties and irreversibility of stock collapse. Ecosystemic models are needed but will be difficult to develop given the incomplete understanding of prey substitutability and net effect of interacting environmental processes.

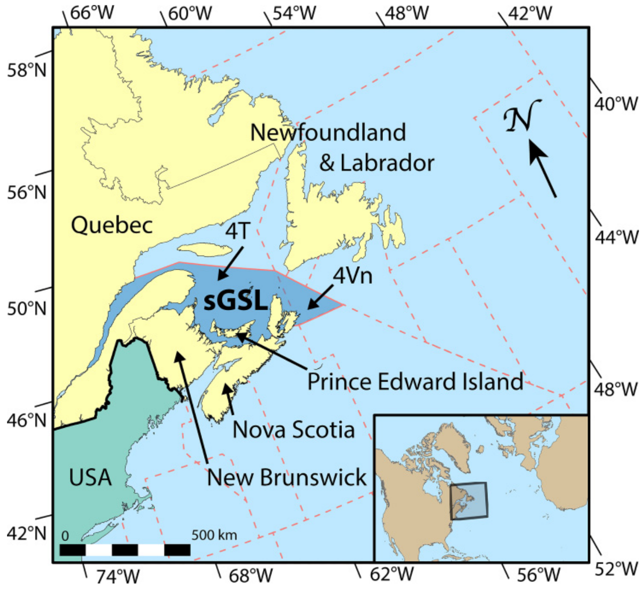
Key words: Atlantic herring, bait fishery, fishery rebuilding, fishery closure, environmental modelling, precautionary principle

1. Introduction

Forage fish fulfil large economic, environmental, and social roles worldwide; commercial landings of forage fish have been valued at $5.6 billion per year globally, with landings of species supported by forage fish valued at a further $11.3 billion per year (Pikitch et al. 2012). In Canada, Atlantic herring (*Clupea harengus*) are by far the most economically significant forage species, accounting for roughly 60% of the value of national forage fish landings in 2018 (DFO 2020*d*). Atlantic herring is targeted by a lucrative commercial fishery, as well as a bait fishery wherein a licence is issued to all commercial fish harvesters who hold a licence for species and fishing gear requiring bait. Beyond its significance in commercial fisheries, Atlantic herring is an important prey species for many predators in the Atlantic, including grey seals (*Halichoerus grypus*) (Hammill and Stenson 2000; Hammill et al. 2007, 2014), seabirds (Cairns et al. 1991), cetaceans (Fontaine et al. 1994; Benoît and Rail 2016), Atlantic bluefin tuna (*Thunnus thynnus*) (Pleizier et al. 2012; Varela et al. 2020; Turcotte et al. 2021*a*), and various benthic and benthopelagic fish. In particular, this includes Atlantic cod (*Gadus morhua*) (Hanson and Chouinard 2002) and white hake (*Urophycis tenuis*) (Benoît and Rail 2016), which themselves have imperilled commercial fisheries (McQuinn and Jech 2009). However, herring abundance has been in steep decline in Atlantic Canada for many years. For example, in the southern Gulf of St. Lawrence (sGSL; Fig. 1), estimated biomass declined by roughly half in the period 1995–2015. Available evidence suggests that biomass of spring-spawning herring peaked in the 1990s and declined by ~80%, while fall-spawning herring peaked in the early 2010s with biomass declining by ~60% by 2019 (DFO 2020*c*; Turcotte et al. 2021*b*).

Recent amendments to the Fisheries Act require Fisheries and Oceans Canada (DFO) to develop rebuilding plans with clear targets and timelines to improve the stability and sustainability of depleted stocks including sGSL spring-spawning Atlantic herring (DFO 2019*b*). This amendment legalizes the Sustainable Fisheries Framework and Precautionary Approach policies that introduced the requirement for a rebuilding plan for stocks identified as being in a critical state (DFO 2009). In March 2022, DFO closed the Atlantic mackerel (*Scomber scombrus*) and sGSL spring-spawning component of Atlantic herring bait and commercial fisheries because of their critical status despite controversy and disagreement between industry and government (Coalition of Atlantic and Quebec Fishing Organizations 2022; Dean-Simmons 2022; Palmeter 2022). The merits of fisheries closures and alternative rebuilding scenarios are debated because of an

Fig. 1. Map of northwest Atlantic Ocean, northeastern USA, and eastern Canada (provinces labeled). Hatched lines demarcate Northwest Atlantic Fisheries Organization (NAFO) zones. The southern Gulf of St. Lawrence (sGSL) corresponds to NAFO zones 4T and 4Vn (labeled). Projection: Lambert conformal conic. Base map (North America) from USGS (2022). NAFO zones from NAFO (2022). Inset map (world) from Natural Earth (2022).



incomplete understanding of the relative importance of the drivers of decline of these forage fish and the trade-offs implied by potential interventions. For example, herring stocks are likely impacted by interactions with many other species that support commercial fisheries, strongly suggesting the need for synergistic or complementary management strategies (Read and Brownstein 2003). At present, these strategies are hampered by a fragmented understanding of the factors controlling Atlantic herring stocks, notably the relative importance of environmental factors, human withdrawals, and predation.

Data-driven investigations into the declines of Atlantic herring biomass have by definition been limited by the types of data available and have produced paradoxical results that may warrant further conceptual evaluation. For example, in the Scotian Shelf and Bay of Fundy regions, Boyce et al. (2019) documented an overall reduction in herring spring-spawning biomass (and other indicators of fish stock "health") between the periods 1965–1989 and 1990–2016 notwithstanding an increase in recruitment. Meanwhile, Brosset et al. (2018) suggest that rising temperatures have favored proliferation of warm-water copepods in the Gulf of St. Lawrence (GSL), supporting recruitment of fall-spawning herring while negatively impacting cold-water copepods that support spring spawners. However, these results do not explain the >50% reduction in fall-spawning biomass in the sGSL since 2010, which coincided with an increase in recruitment number of at least four orders of magnitude (Brosset et al. 2018).

The limitations of bottom-up explanations for the decline in herring stocks point to the potential importance of predation and competition. For example, a recent assessment observed that the 81% decline in spawning stock biomass (SSB) among spring-spawning sGSL herring in the period 1995–2015 coincided with a 20-fold and threefold increase, respectively, in the abundance of predatory bluefin tuna and grey seal (DFO 2020*c*; Turcotte et al. 2021*a*, 2021*b*). Since 2015, the North Atlantic right whale (*Eubalaena glacialis*) has also undergone a distributional shift into the sGSL, likely introducing competition for copepods (Cronin et al. 2017; Simard et al. 2019). Other regions have also seen important ecosystem changes alongside decreasing forage fish populations. For example, the northern Gulf of St. Lawrence (nGSL) has seen a 26-fold increase in biomass of Atlantic redfish (*Sebastes* spp.) and a >60% reduction in biomass of herring since 2010 (Koen-Alonso et al. 2018). Redfish populations have also increased dramatically in the sGSL (Rolland et al. 2022). While both herring and redfish prey heavily on (increasingly environmentally limited) marine copepods (Pedersen and Riget 1993; Runge and Lafontaine 1996; Laurel 2001; Arula et al. 2012), we have identified only limited and inconclusive investigations into the potential for interaction or competition between these species. For example, Koslow (1984) characterized correlations between recruitment of herring and redfish in the Eastern Scotian Shelf and the New Jersey coast and found no significant relationship. Overall, such interspecies interactions are poorly captured by the concept of "natural mortality" used in stock assessments (Read and Brownstein 2003).

Commercial landings of herring totaled 81 445 tonnes across Atlantic Canada in 2020, corresponding to a reduction of about half since 1995 in line with the decline in estimated biomass (DFO 2016, 2022*a*). The total withdrawals are subject to considerable uncertainty because reported landings are only for the commercial fishery and do not include herring captured through bait licences. Bait licences are issued to all commercial fish harvesters who hold a licence for species and fishing gear requiring bait, including American lobster (*Homarus americanus*), snow crab (*Chionoecetes opilio*), bluefin tuna, and halibut (*Hippoglossus hippoglossus*) fisheries (DFO 2014). In the sGSL alone, there are roughly 4475 harvesters licensed to fish herring as bait for other fisheries, though only a portion of these licences are active in a given year. The bait fishery overwhelmingly targets spring-spawning herring, which accounted for 6% of commercial landings in the sGSL in 2019 (fall-spawning herring accounted for 94%) (Turcotte et al. 2021*b*). Commercial lobster landings, which depend on herring as bait, have increased by 2.4 times since 1995 to a total of 97 381 tonnes in 2018 across Atlantic Canada (DFO 2016, 2020*b*). Meanwhile, the snow crab fishery has been relatively constant with reported landings of 72 297 tonnes across Atlantic Canada in 2018, close to the 73 244 tonnes reported in 1995 (DFO 2016, 2020*b*). Atlantic mackerel has also traditionally served as lobster bait (Boudreau and Giard 2022) but has also collapsed with landings down by roughly half since 1995 to 10 787 tonnes in 2018 (DFO 2016, 2020*b*; Van Beveren et al. 2017). Until 2020, catches from the bait fishery were estimated using the small fraction of log books that were returned. Altogether, the bait fishery may have a significant and increasing impact on overall withdrawals, particularly on spring-spawning herring, but this is at present poorly understood.

Here, we present a critical review of the science of Canadian Atlantic herring populations with particular focus on the sGSL. We present a conceptual understanding of the factors driving population decline and, where possible, quantitative and qualitative descriptions of the likely importance of each factor. This includes aggregation of previously reported data and presentation of data for the Atlantic herring and mackerel bait fisheries between 2015 and 2021. Where quantitative evaluation is not possible, we identify near-term data collection priorities to allow evaluations in the future. Overall, we aimed to synthesize observations and insights from disparate empirical and modeling studies to provide a basis for better informed management of Atlantic herring and the species it supports.

2. Methods

We mined the peer-reviewed literature and publicly available government databases to develop a conceptual relationship of factors governing Atlantic herring (*Clupea harengus*) abundance as measured by biomass, noting evidence availability (Section 2.1). We queried FishBase (Froese and Pauly 2019) and SeaLifeBase (Palomares and Pauly 2019) to develop a conceptual food web in which Atlantic herring is embedded (Section 2.2). Finally, we present quantitative data on removals associated with the herring bait fishery and evaluate the likely role of the bait fishery in comparison to other drivers of herring abundance (Section 2.3). We synthesize this information to evaluate the likely impact of potential policy levers (e.g., reductions in fishing quotas) and to identify key science gaps (Section 3).

2.1. Literature review

We reviewed the peer-reviewed literature and Canadian government databases for information on factors governing population abundance of Atlantic herring. We recorded the types of evidence available for each mechanism evaluated or asserted.

2.1.1. Peer-reviewed literature

We searched Web of Science (WoS) for all literature on herring and forage fish more generally in Atlantic Canada. We included a comparatively broad geographic scope to better characterize the methods and mechanistic inferences made in the peer-reviewed literature more generally. We searched abstracts in WoS for strings referring to herring (Search 1) or forage fish (Search 2) and Canada or Atlantic Canada (both searches) in English or French. We searched all databases included in the WoS Core Collection as of 29 April 2022. The herring search returned a total of 363 references, and the forage fish search returned a total of 134 references. A total of 480 unique references were identified (17 references appeared in both searches, and one reference was returned twice in the herring search).

Search results were reviewed for relevance to our task of characterizing the mechanisms controlling Atlantic herring stocks in Canada. In total, we retained 89 articles (25%) from Search 1 and 31 articles (23%) from Search 2. Articles were excluded based on geographic area of study (we retained articles on the Atlantic fishery only); an emphasis on method development and validation rather than generation of insights into biophysical or ecological mechanisms; a focus on freshwater environments; and a focus on the ecology of other species, environmental bioaccumulation, or irrelevant areas of study (e.g., astronomy). Table 1 summarizes the search syntax and overall retention statistics for both WoS searches. Table 2 provides a breakdown of articles not retained for further analysis by exclusion reason. The 17 articles that appeared in both herring and forage fish searches were reviewed to ensure that they were excluded for the same reason in both searches (12 papers) or retained in both (5 papers).

Articles were reviewed for causal mechanisms evaluated or asserted with like concepts grouped with a common name following the method set out in Calder et al. (2020). The relationships asserted or evaluated in the peer-reviewed literature informed the development of a conceptual model as described in Section 2.3.

We include in the supplemental information (SI) a list of all WoS results. Results from Search 1 included for analysis are tabulated in SI Table S1. Papers returned by Search 1 but excluded from analysis are tabulated by exclusion reason in SI Table S2. Included and excluded papers from Search 2 are likewise tabulated in SI Tables S3 and S4.

2.1.2. Government databases

We supplemented our search of the peer-reviewed literature with a search of Canadian government databases for scientific studies and stock assessments pertaining to the GSL. We focused on the sGSL for more specific stock assessments given the similarity of methods employed by DFO analysis across regions. On 16 October 2020 and again on 4 May 2022, we searched databases maintained by the Canadian Science Advisory Secretariat (CSAS) (DFO 2022*b*) and the Federal Science Library (Government of Canada 2022). The CSAS coordinates and archives peer-reviewed stock assessments and scientific research conducted by DFO.

We searched the CSAS database for reports indexed for the DFO Gulf region (i.e., sGSL) matching “herring” across all years. This returned five Stock Status Reports (one each for years 2000–2004), 12 Science Advisory Reports (2005–2020), two Science Responses (2007 and 2015), and 79 Research Documents. The Science Advisory Report succeeded the Stock Status Report as a category. Therefore, we reviewed the last two Science Advisory Reports and both Science Responses.

We searched the DFO Collection of the Federal Science Library for documents matching “Gulf herring” published within the past 5 years. This search returned 42 results. Of these, we retained 15 for review. Publications were excluded for having the wrong geographic focus (14), being duplicates of the CSAS search above (4), or having been returned twice in this search (both English and French versions of the report returned) (9). We include in the SI a list of all government

Table 1. Web of Science search summary.

Search	Syntax	Returned	Retained
1	AB = ((herring OR hareng) AND (canad* OR maritime OR lawrence OR laurent OR brunswick OR scotia* OR ecoss* OR edward OR edouard* OR newfoundland OR terre-neuv*))	338	96
2	((“forage fish” OR “prey fish” OR “poisson* fourrage” OR “poisson* proie”) AND (canad* OR maritime OR lawrence OR laurent OR brunswick OR scotia* OR ecoss* OR edward OR edouard* OR newfoundland OR terre-neuv*))	121	27

Table 2. Count of articles returned by Web of Science excluded by reason.

Exclusion reason	1. Herring	2. Forage fish
Geography		
British Columbia	47	8
Arctic (Canada and Alaska)	4	9
Other	10	2
Method development		
SONAR/acoustic methods	7	0
Fish oil extraction	3	0
Other	9	6
Environment		
Lakes	17	21
Rivers	6	3
Reservoirs	0	2
Subject		
Contaminants and bioaccumulation	46	31
Ecology of seabirds	59	11
Ecology of other species	13	7
Aquaculture	8	1
Biological sciences	7	0
Other earth and environmental sciences	6	0
Other subject (e.g., astronomy)	24	1
Inability to confirm peer review (books and abstracts)	7	1
Duplicate in same search	1	0
Total	274	103

Note: Counts include a total of 12 articles returned in both searches and excluded for the same reason in each.

reports identified, noting which were excluded from our review and why.

2.1.3. Evidence review of journal articles and government reports

We reviewed retained journal articles and government reports for causal relationships claimed or evaluated. We structured these relationships into a conceptual diagram (Fig. 2) to represent the mechanisms governing herring abundance (as measured by biomass) as currently understood. We consolidated similar concepts using more general vocabulary to avoid exponential proliferation of causal relationships in the conceptual diagram following the method of Calder et al. (2020). We also recorded qualitative descriptions of the types of evidence available for each relationship and whether the relative importance of competing or interacting mechanisms had been evaluated quantitatively.

The conceptual graphical model represents herring abundance (the outcome of interest) as the product of interacting environmental and social processes. There has been an increasing interest in the use of graphical approaches such as “theories of change” or “results chains” to structure reviews of complex environmental systems in terms of underlying causal mechanisms (Qiu et al. 2018; Tallis et al. 2019). These approaches promote comprehensive analysis of the “overall” effect of interventions (e.g., fishing quotas) on outcomes of interest (e.g., fish stocks) in the context of confounding and mediating environmental phenomena. To our knowledge, these approaches are not widely used in fisheries science but are increasingly popular in social and other environmental sciences.

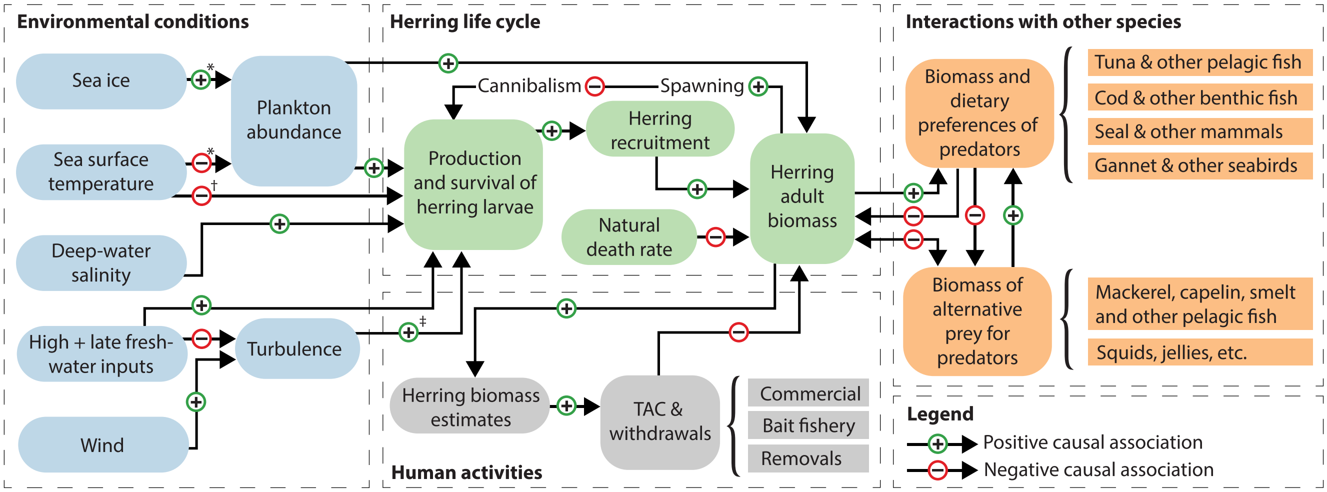
Recent work has shown that causally explicit, physically interpretable mechanisms are associated with a more consistent evidence base than the “overall” associations frequently of interest to practitioners and researchers (Calder et al. 2020). Explicit representation of relationships among environmental phenomena allows for clear identification sources of uncertainty in systems of interest (O’Leary et al. 2017; Tallis et al. 2017). These uncertainties may relate to the net effect of competing or confounded phenomena, or to conflicting evidence on the direction or strength of effect of individual mechanisms. In either case, graphical modeling approaches allow these determinations to be made in an explicit way so as to orient further data collection and quantitative modeling.

2.2. Conceptual aquatic food web

Articles we reviewed presented extensive discussion around the concepts of predation, energy sufficiency, and (to a lesser extent) competition. However, in many cases, authors were not explicit about the array of other species that interact with Atlantic herring, complicating the task of evaluating evidence availability and gaps.

Therefore, we developed a conceptual food web structure for the sGSL using AquaMaps (Kaschner et al. 2019), which provides a cartographic interface to FishBase (Froese and Pauly 2019) and SeaLifeBase (Palomares and Pauly 2019) online databases. We queried AquaMaps for all species having a probability of occurrence ≥50% in the sGSL, which AquaMaps aggregates together with the Scotian Shelf ecosystem. This returned 418 species across 34 taxonomic classes. These

Fig. 2. Conceptual figure showing causal relations with prevailing direction of effect revealed by literature review. Endpoints of interest (e.g., herring adult biomass) are the net effect of interacting environmental, ecological, and human processes. Relative importance of each mechanism is likely site specific. *Direction of effect is for spring-spawning herring; fall-spawning herring has opposite direction of effect (Melvin et al. 2009; Brosset et al. 2018). †Direct effect of temperature on production and survival of larvae is inconsistent and likely site specific (Couillard et al. 2016); findings may be confounded by countervailing effects on plankton abundance and/or reduced turbulence-driven feeding. ‡Turbulence promotes feeding (positive effect) when plankton are scarce and hinders feeding when plankton are abundant (Muelbert et al. 1994). TAC = total allowable catch.



included all species for which we had prior knowledge of occurrence within the sGSL with the exception of Atlantic halibut (*Hippoglossus hippoglossus*) and Atlantic bluefin tuna (*Thunnus thynnus*). AquaMaps listed these two species as having a probability of occurrence <50%. However, Atlantic halibut and bluefin tuna abundance has been increasing for the last decade in the GSL (DFO 2021; Turcotte et al. 2021*a*). We included them in our conceptual framework given their importance within the Atlantic fishery and known occurrence in the area, bringing the total number of species included in the conceptual framework to 420.

We grouped the 420 species into 19 categories defined by approximate trophic position and common predator/prey interactions. These categories range from primary producers (phytoplankton) to marine mammals. We identified predator/prey interactions based on information returned by FishBase through the rfishbase R package (Boettiger et al. 2019). For each group, we identified species corresponding to a commercial fishery based on DFO (2020*b*). The approach of discretizing complex food webs into trophic/species categories based on significant flows of energy or environmental contaminants is a widely used method to support quantitative modeling (Allesina and Pascual 2007; Schartup et al. 2019). Here, we adapt this approach to structure a review of evidence available to support quantitative inferences about interspecies interactions in the sGSL. This is similar to the "functional group" categorization strategy adopted by Savenkoff et al. (2007*b*). Here, we structure categories to minimize intracategory predation, explicitly identify relevant species in each category with a commercial fishery, and note relevant cross-category predator–prey interactions. This approach minimizes the number of individual categories retained (19 in our analysis vs. 30 in Savenkoff et al. (2007*b*)). This structure allows us to more readily identify evidence gaps and facilitate future ecosystemic modeling.

2.3. Assessment of importance of the bait fisheries

Herring removals reported by DFO are focused on the commercial fishery and do not include those captured by the bait fishery as reporting is generally unreliable or absent (McDermid et al. 2018). While removals from the bait fishery are expected to be lower than the commercial landings, the total reported removals are underestimated by an unknown amount (DFO 2014).

Here, we present data compiled from bait fishery logbooks for the period 2015–2020. Fishers have been required to record bait catches in logbooks since 1996, but historically, only a small fraction of logbooks have been turned in to DFO (Bourne et al. 2015). As of 2020, it has been mandatory to report catch estimates at every port landing in the sGSL (DFO 2020*a*). However, because the bait is for personal use in other commercial fisheries, there is no requirement for mandatory weighing of these removals. Therefore, reported bait landings may still be underestimated. Consequently, we have lower bound estimates for years prior to 2020 and more reliable (but still possibly low) estimates for 2020 and 2021. We use these to estimate total annual catch of the bait fishery.

3. Results and discussion

Recent investigations into sGSL herring (*Clupea harengus*) dynamics are oriented around the steep drop in herring (landings and stock abundance). For example, between 2010 and 2019, combined spring and fall spawner landings fell from

49 000 to 17 000 tonnes and estimated SSB fell from 579 000 to 210 000 tonnes (DFO 2020*c*). DFO compares SSB with the limit reference point (LRP) and upper stock reference (USR) benchmarks for stock health, where SSB < LRP is considered "critical", LRP < SSB < USR is considered "cautious", and SSB > USR is "healthy" (DFO 2012). Modeling by DFO suggests that LRP and USR are, respectively, 46 000 and 133 000 tonnes (spring spawners) and 54 000 and 335 000 tonnes (fall spawners); at any catch level, including zero, there is <25% probability of spring spawners being above the critical zone (i.e., SSB > LRP) and <40% probability of fall spawner increasing into the healthy zone (i.e., SSB > USB) by 2026 (DFO 2020*c*).

Figure 2 summarizes the causal relations among physical, ecological, and social variables attested in the literature with an ultimate incidence on adult herring biomass. We represent relationships for which there is apparent consensus on causality (i.e., empirical observations explained by a physical mechanism) and a prevailing direction of effect. In general, however, there is significant uncertainty about the net effect of combinations of causal relationships on common outcomes, as explained below.

3.1. Environmental controls

A large scientific literature characterizes environmental controls on Atlantic herring recruitment, notably via effects on plankton abundance. Warming conditions have been invoked to explain the decline of spring spawners and comparative stability and abundance of fall spawners through the early 2000s and 2010s (Melvin et al. 2009; Brosset et al. 2018). This reasoning holds that environmental conditions adverse to cold-water copepods and favorable to warm-water copepods had divergent impacts on recruitment and abundance of spring-spawning (adverse) and fall-spawning (favorable) herring populations. The GSL has been experiencing conditions consistent with climate warming such as low sea ice, warm water intrusions, and record high sea-surface temperatures (Galbraith et al. 2021). Zooplankton biomass indices in the GSL have been below normal in recent years, associated with a decrease in large-bodied copepods (Blais et al. 2021).

More recent data, however, reveal sustained declines in abundance and recruitment of fall-spawning as well as spring-spawning herring in spite of environmental conditions that would support recruitment under this causal framework. Fall-spawning average SSB declined by 34%–43% and recruitment declined by 0%–35% in 2015–2019 compared with 2010–2014 despite sustained warming and stable levels of warm-water copepods (DFO 2020*c*; Blais et al. 2021). This adds to literature from elsewhere in the North Atlantic that has found an inconsistent ("dome-shaped") relationship between recruitment and temperature; this suggests that positive effects on copepod abundance can be outweighed by increased metabolic demands in early life stages of herring and other forage fish caused by warmer temperatures (Stocker et al. 1985; Arula et al. 2015; Couillard et al. 2016; Boldt et al. 2019).

Figure 2 summarizes the physical–biological mechanisms that have been posited to explain ecosystem-scale herring observations across the North Atlantic. Causal relationships have been decomposed to the level at which there is consensus on the prevailing direction of effect, and inconsistencies in findings have been noted. Production and survival of herring larvae are heavily influenced by diverse environmental factors, but in general, the range of conditions under which each factor dominates is poorly understood. For example, turbulence-driven mixing can promote or hinder the feeding of herring larvae depending on the abundance of prey (Muelbert et al. 1994). Turbulence is in turn impaired by stratification caused by warm freshwater inflows (e.g., high and late spring freshet). However, these conditions have also been associated with improved larval abundance notwithstanding the potential countervailing effect on larval feeding (Couillard et al. 2016). Moreover, the importance of turbulence-driven mixing may be less important in environments with comparatively weaker tidal currents (e.g., GSL). Meanwhile, warming temperatures are likely adverse to cold-water copepods on which spring-spawning herring prey and may increase the metabolic demands of larvae (Melvin et al. 2009; Couillard et al. 2016; Brosset et al. 2018). We did not identify any studies that explain ecosystem-scale observations in the context of all relevant mechanisms identified here, and many mechanisms were not characterized in more than one fishery (e.g., we did not identify investigations into the importance of turbulence-driven mixing in the GSL).

In general, studies that use statistical approaches to relate outcomes such as larval abundance to environmental conditions are limited by (1) poor prior knowledge of temporal lags between modeled variables; (2) interactions among measured variables (Fig. 2) that are generally not reflected in model structures (for example, the complex role of water temperatures described above); (3) large uncertainties around the relationship between underlying physical phenomena of interest and the quantified variables used in models in the context of perpetually evolving ecosystems (notably "indices" of recruitment and abundance); (4) an array of potential mechanisms that can be invoked to explain counterintuitive findings that may otherwise challenge the model structure framing the statistical analysis, but which are rarely if ever the subject of follow-up investigation; and (5) the use of datasets where each point corresponds to quantities averaged over 1 year or season, limiting the possible statistical power of even multiyear investigations.

For example, in the setting of the sGSL, Couillard et al. (2016) observe a significant positive linear relationship between sea surface temperature (degree-days between spawning and sampling) and body length of Atlantic herring but an inconsistent relationship (no significant linear relationship, speculated to be a "dome-shaped relationship") for body length of rainbow smelt (*Osmerus mordax*). The authors posit potential explanations such as species-specific impacts of temperature on metabolic demands that countervail impacts of temperature on prey availability. While this study incorporates data collected over more than a decade, each point in the statistical analysis corresponds to a whole year. Consequently, these mechanistic inferences are made on the basis of only two points that do not conform to a trend. Other relationships (e.g., between larvae density and freshet strength) are driven by one point with high statistical leverage. Overall, there is a gap in the literature between ecosystem-scale observations on proxies for stock health and underlying physical–biological mechanisms; more experimental investigations are urgently needed, as it is very difficult to infer mechanistic explanations at the ecosystem scale given great variability inherent in environmental systems and long timescales required to generate data.

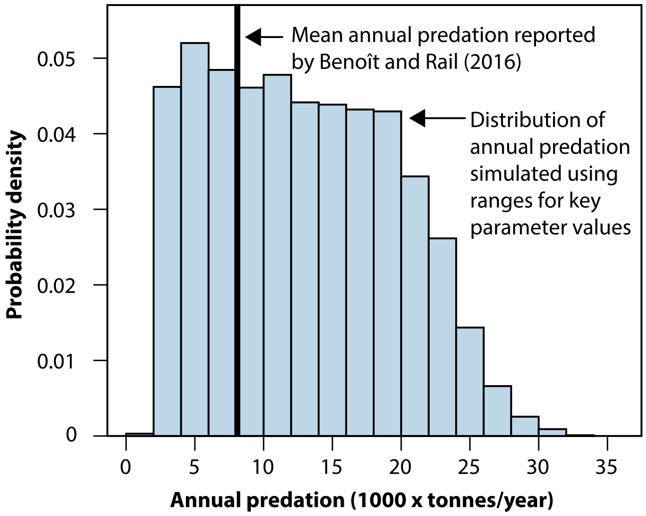
Comparison of findings across studies is likewise limited by great diversity in the definition of variables taken to symbolize quantities of common interest. For example, across studies in the North Atlantic, herring recruitment is represented variously as an index or normalized with respect to biomass; biomass can refer to age-0, age-2, or other age groups; and temperature is reported for varying depths and clines (or not further defined). This is problematic because (1) environmental variables can have net impacts that are age specific due to the dominance of different mechanisms at different ages (for example, the complex effect of temperature on fall-spawning herring described above); and (2) ecosystem nonstationarities have different effects on different proxies for quantities of common interest (for example, the collapse of benthic predator Atlantic cod (*Gadus morhua*) increased the vertical distribution of pelagic fishes and hence bottom trawl indices while real stocks remained constant or decreased) (Frank et al. 2005; McQuinn and Jech 2009; Jech and McQuinn 2016). While most analysis suggests that herring biomass is likely to remain low regardless of recruitment scenarios, investigations into the environmental controls on recruitment and abundance have not converged on a consistent mechanistic explanation. This reinforces the urgent need for experimental investigations to characterize the physical–biological mechanisms that govern recruitment and abundance as described above.

3.2. Predation pressures

More recently, research has focused on the role of nonfishing mortality and, specifically, increased abundance of herring predators in driving down biomass (Sinclair et al. 2015; Brosset et al. 2019). Modeling by Savenkoff et al. (2007*b*) suggested sGSL herring predation and fishing mortality of roughly 1.3 tonnes km^{-2} year^{-1} each in the mid-1990s, compared with a biomass of 7.42 tonnes km^{-2}. By comparison, predation and fishing mortality were estimated at 0.54 and 0.56 tonnes km^{-2}, respectively, in 2013 compared with an SSB of roughly 2.8 tonnes km^{-2} (assuming sGSL surface area of 64 075 km^2) (Savenkoff et al. 2007*b*; Surette et al. 2015; Benoît and Rail 2016). Total herring predation was estimated at 34 800 tonnes in 2013 (Benoît and Rail 2016).

Overall, these estimates suggest predation and fishing rates are declining more slowly than total biomass, but they conceal wide uncertainties that are rarely quantified. For example, probabilistic modeling of yearly sGSL herring acoustic biomass by Surette et al. (2015) revealed 95% confidence intervals spanning a factor of 2–5. Similarly, a recalculation of predation rates estimated by Benoît and Rail (2016) that considers the possible magnitude of uncertainties reveals a plausible distribution of total predation that includes values many times higher than reported means. Figure 3 illustrates this using the example of gannet (*Morus* spp.), a group of herring predators in the sGSL: we recalculated the mean annual predation reported by Benoît and Rail (2016) simulating uncertainty with uniformly distributed random values for the relevant parameters across 10 000 independent trials. We considered the reported range of 10%–92% for annual average fraction of herring in gannet diets and used nominal reported values ± 10% for other parameters (gannet population sizes, energy requirements, prey energy density, residential days per year and importance of sGSL in foraging). The result is a probability distribution where an annual predation greater than three times the reported nominal value of 8093 tonnes per year falls within the 95% confidence interval.

Fig. 3. Annual predation of sGSL herring by gannet calculated by Benoît and Rail (2016) with simulated uncertainties.



Investigations into the role of predation in suppressing biomass of herring and other species in the northwestern Atlantic have identified Atlantic white-sided dolphins (*Lagenorhynchus acutus*), bluefin tuna (*Thunnus thynnus*), grey seal (*Halichoerus grypus*), and seabirds as key drivers (Benoît and Rail 2016; Turcotte et al. 2021*a*). Of these, grey seal and bluefin tuna predation are receiving increasing attention in the literature due to recent population increases. For example, Benoît and Rail (2016) calculate that seal predation of all prey in the sGSL has increased more than 10-fold since the 1960s to more than 120 000 tonnes in 2014, with herring accounting for roughly 7500 tonnes. Seal populations in the sGSL have been increasing exponentially since the 1960s, doubling roughly every 10 years to reach nearly 500 000 in 2013 (Neuenhoff et al. 2019). Meanwhile, tuna detections increased 22-fold between 2002 and 2012, resulting in herring predation that has roughly doubled to between 4300 and 20 000 tonnes (Turcotte et al. 2021*a*). As demonstrated above, uncertainty in model parameter values results in mean estimates that may substantially underestimate true predation. This is consistent with modeling of other sGSL species such as Atlantic cod and winter skate (*Leucoraja ocellata*), finding that high and increasing predation has impaired rebuilding (Neuenhoff et al. 2019; Swain et al. 2019).

Models representing competition, predation, and simultaneous impacts of physical and chemical processes (e.g., temperature, circulation, nutrient concentrations) on interacting biota can be used to generate and evaluate hypotheses for ecosystem shifts (Johanson et al. 2017). Such models could be particularly useful for the sGSL where hypotheses based on environmental, social (i.e., withdrawals), and ecological (i.e., predation) processes have all been advanced to explain low herring stocks. In principle, hypotheses may be rejected when they cannot explain observed shifts in ecosystem structure for any plausible ranges of parameter values. We did not identify any such models addressing herring in the sGSL.

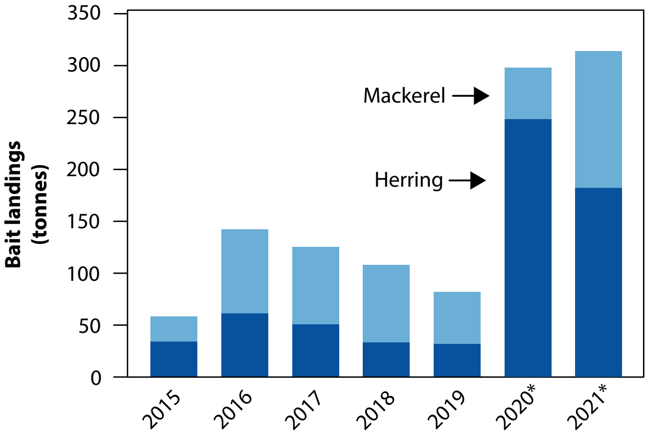
Such models, however, present challenges. In principle, the number of interaction terms increases exponentially with the number of species represented, requiring subjective judgments about which interactions to represent numerically. Models representing interactions between individual fish are not computationally possible at the spatial scales relevant to commercial fisheries, and modeling individuals as groups presents poorly understood trade-offs with respect to model accuracy (Johanson et al. 2017). Finally, assigning relationships between environmental variables and biotic endpoints requires interpretation of an evidence base featuring inconsistent operational definitions and incompletely represented causal structures (as described above in the context of the role of temperature); even simple mechanistic models feature dozens of parameters that must be selected on the basis of such evidence.

In SI Table S5, we include a conceptual food web for the sGSL using data from SeaLifeBase and FishBase (Section 2.2). Species with a commercial fishery are specifically enumerated to highlight these interactions, which may be important for multispecies management. Given the spatial resolution of these databases, this conceptual food web is likely applicable to the entire Scotian Shelf and GSL. The conceptual food web is organized as a predator/prey matrix, showing the complex trophic relationships between species. Most species prey on a wide variety of other species. However, there is a lack of data on diet substitutability or preferences, complicating forecasts for the impacts of the decline or recovery of one fish stock on other fish stocks.

3.3. Magnitude and relative importance of bait fishery

The majority of the domestic commercial herring fishery is landed and then sold as bait (DFO 2020*c*). Additionally, commercial lobster and other fishers withdraw herring in a parallel bait fishery for their personal use, which is not included in commercial landing numbers. In 2020 and 2021, herring landings from bait licences were 249 and 182 tonnes, respectively (Fig. 4). Reported estimates for 2020 and 2021 are higher than for previous years (Fig. 4) because in 2020 it became compulsory to report catch estimates at every port landing in the sGSL (DFO 2020*a*). In 2020 and 2021, total commercial herring landings were 10 668 and 11 237 tonnes, respectively, including 603 and 403 tonnes of spring spawners and 10 065 and 11 237 tonnes of fall spawners (Turcotte et al. 2021*b*). Because withdrawals from the bait fishery occur overwhelmingly in the spring, commercial landing numbers underestimate total removals of spring spawners by roughly 30%. As discussed above, populations of spring spawners have declined substantially and are now in DFO's "critical" zone due to an uncertain combination of predation, withdrawals, and environmental pressures.

Fig. 4. Bait fishery landings for the sGSL.*Starting in 2020, it has been mandatory to report catch estimates upon arrival in port; prior years are estimated from logbooks returned to DFO.



Bait withdrawals for personal use in other commercial fisheries likely represent a small fraction of overall herring mortality, on the same order as predation by white hake (*Urophycis tenuis*) (245–511 tonnes per year between 2010 and 2014); for comparison, total predation was estimated at 34 800 tonnes in 2013 (Benoît and Rail 2016). The sGSL ecosystem has undergone a shift over the past several decades from being dominated by groundfish species to crustaceans specifically, snow crab (*Chionoecetes opilio*), and lobster (*Homardus americanus*) (Savenkoff et al. 2007*a*; Boudreau et al. 2015). This is reflected in the changing landscape of the commercial fisheries; lobster landings in particular continue to increase with each season (DFO 2019*a*, 2019*c*). Because many lobster licence holders have a companion bait licence, the demand for bait will continue to be high. Total bait usage in the fisheries is not currently known, but Harnish and Willison (2009) estimated the mass ratio of bait to catch as 2:1 in the Nova Scotia lobster fishery. With the closure of the sGSL bait and commercial fisheries in 2022, demand for bait will be displaced to other species, either local or imported. Potential local substitutes include locally caught foragers, such as rainbow smelt and capelin (*Mallotus villosus*); common but poorly recorded bycatch, such as cunner (*Tautogolabrus adspersus*), male rock crabs (*Cancer irroratus*), and sculpin (*Scorpaeniformes* spp.); and foragers commercially purchased for bait, such as gaspereau (*Alosa pseudoharengus* and *A. aestivalis*) and Atlantic silversides (*Menidia menidia*) (Boudreau and Giard 2022).

4. Conclusion

Atlantic herring (*Clupea harengus*) are a schooling fish with established spawning grounds vulnerable to environmental changes. The decline of herring stocks in the northwest Atlantic and, specifically, the sGSL has caused quotas and landings to fall and has sparked research into the drivers of this decline and barriers to recovery. That research has probed the possible role of environmental factors in limiting herring recruitment and survival ("bottom-up" hypotheses) as well as pressures exerted by predation and fishing ("top-down" hypotheses). These investigations have produced a large literature on the roles of physical, ecological, and social processes. The strength and consistency of current evidence suggests that top-down predation pressures are currently controlling overall herring abundance in the sGSL and likely other Atlantic Canadian fisheries.

Purely bottom-up analyses have not converged on a consistent mechanistic explanation for herring stocks that remain low despite favorable environmental conditions at least for fall-spawning herring. This may be because these variables play a small role, or because of methodological challenges associated with developing statistical relationships between biological endpoints and environmental conditions. Conversely, top-down analyses have demonstrated that predation from marine mammals such as grey seal (*Halichoerus grypus*), seabirds, and other fishes such as Atlantic bluefin tuna (*Thunnus thynnus*) are likely at least as significant pressures as human withdrawals; this pressure appears to be growing, and cannot be easily controlled with current policy levers. Furthermore, we have demonstrated that predation mortality may be significantly underestimated given the compounding uncertainties in parameter values used to derive those estimates (Fig. 3).

Previous analysis has called for a balanced conception of a system mediated by both top-down and bottom-up processes (Greene 2013). To that end, we have synthesized the primary causal relations studied into the literature into a conceptual model presented in Fig. 2. This conceptual model reveals how environmental drivers (e.g., temperature, plankton availability) can result in inconsistent or site-specific net impacts on outcomes of interest (e.g., recruitment, biomass) in ways that are not frequently accounted for in retrospective statistical investigations. Mechanistic modeling resources exist and may be useful for the purposes of ruling out explanations for observed equilibria or for scoping the plausible range of outcomes under (1) likely future environmental conditions and (2) future policy actions.

The current weight of evidence points overwhelmingly to the role of top-down pressures in explaining the imperilled state of Atlantic (and, in particular, sGSL) herring. We did not find consistent evidence for a relationship between recent changes in recruitment and changes in SSB of either spring-spawning or fall-spawning herring. This conclusion is largely in line with recent simulations that have found that stocks are likely to remain in a critical state regardless of near-term recruitment patterns (DFO 2018, 2020*c*). There is clear evidence that recruitment has been declining, and there are plausible mechanistic/environmental hypotheses for this decline (Fig. 2). However, there are currently many uncertainties about the aggregate effects of interacting environmental phenomena on recruitment that preclude us from identifying a combination of factors responsible for recruitment declines in the sGSL and elsewhere. It is possible that these declines will start to play a more decisive role in overall herring abundance, and so developing a quantitative model of ecosystemic factors governing recruitment, and the influence of recruitment on SSB, is a near-term research priority.

Recently, the quality of data on herring removals by the bait fishery has improved given the requirement for bait fishers to report their catches upon hailing at port (Fig. 4). The magnitude of these withdrawals in the sGSL suggests that commercial landings have underestimated total withdrawals of spring-spawning herring, the most imperilled component of the herring fishery, by roughly 30%. We note that this may still be an underestimate, given the absence of a rigorous enforcement mechanism for bait landings reporting. With the closure of the commercial and bait fisheries, demand for bait is likely to be displaced to other species, either domestic or imported, to support lobster (*Homardus americanus*) and other commercial fisheries. It is not currently known how the demand for bait will be absorbed by other species. When the commercial and bait fisheries reopen, continued surveillance of bait withdrawals will be important for accurately characterizing top-down pressures on herring stocks.

Given the top-down pressures on herring stocks in Atlantic Canada and the sGSL in particular (e.g., exponentially increasing predation by grey seal and Atlantic bluefin tuna), policies to reduce withdrawals (e.g., the recent closure of commercial and bait fisheries) are justified. However, natural predation of Atlantic herring is a much greater source of overall mortality than all human withdrawals, even after considering the frequently overlooked bait fishery. Recent modeling by DFO suggests that closure of the fishery is not likely to result in recovery of herring populations already in "critical" (spring spawners) or "cautious" (fall spawners) management zones by 2026 (DFO 2020*c*). There is thus a need for ecosystem-wide approaches that consider the pressures imposed by the proliferation of predators, notably grey seal and bluefin tuna.

Such approaches are currently hindered by a lack of modeling capacity able to assess the plausibility of alternative evolutionary trajectories of marine ecosystems. For example, the cull of a predator may result in rebounding of its prey, or it may result in the proliferation of another species to occupy new space in the ecological niche. Data on species' dietary preferences and substitutability of prey are needed. To this end, we have developed a conceptual food web to structure efforts at ecosystem-wide modeling (SI Table S5). This organization of "functional groups" (Savenkoff et al. 2007*b*) seeks to identify the minimum number of categories to structure ecosystemic modeling by drawing categories around groups with the least intracategory interaction. Ultimately, however, this approach can only ever be a simplification given cannibalistic interactions within species and intracategory age-dependent predator/prey relationships. Ideally, such ecosystem models will incorporate insights from the large literature on environmental controls on copepod abundance and other bottom-up factors. Development of a quantitative ecosystem model incorporating mechanisms at a range of scales will further refine basic research needs outlined here.

A central challenge to these modeling efforts is estimating the independent effect of individual environmental processes on quantities of interest such as biomass and recruitment given the nonstationarity and site specificity of confounding variables. For example, recruitment may be promoted by higher and later spring freshet, but this may be offset by concomitant reductions in the availability of cold-water copepods and/or reductions in turbulent mixing (Fig. 2). Inconsistent effect sizes complicate the use of many frequentist statistical investigations that attempt to derive models from ecosystem-scale datasets. Laboratory investigations that report variables in quantities that can be scaled to ecosystem-scale models may help bridge this gap, and the conceptual model presented here may allow these investigations to be structured with reference to relevant confounding processes.

Atlantic herring are crucial prey for numerous other species in the aquatic ecosystem, including species that themselves have imperiled commercial fisheries, notably Atlantic cod (*Gadus morhua*) and white hake (*Urophycis tenuis*). Atlantic herring therefore has economic value significantly greater than the reported value of landings in addition to the inherent conservation value of the herring itself and many other species. Adaptive ecosystemic approaches to the stock assessment and science advice will need to be integrated into the fisheries management plans but are currently underdeveloped in the sGSL and elsewhere. This work has conceptualized the relationships that ecosystemic models may aim to evaluate quantitatively. Meanwhile, the sGSL spring-spawning herring and mackerel (*Scomber scombrus*) fisheries have been closed. Other policy levers immediately available include the closure of the bait fishery. Such policies alleviate the likely dominant top-down pressures on key forage fishes in a context where the relative role of each driver is still open to scientific reevaluation. This is consistent with a precautionary approach to ecosystem management in the context of potentially irreversible species collapse.

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Competing interests

The authors declare that there are no competing interests.

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Supplementary material

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